sommerfeltia supplement

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R.H. Økland

Vegetation ecology: theory, methods and applications with reference to Fennoscandia

1990

sommerfeltia

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Technical editor: Rune Halvorsen Økland.
Address: SOMMERFELTIA, Botanical Garden and Museum, University of
Oslo, Trondheimsveien 23B, N-0562 Oslo 5, Norway.
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ISBN 82-7420-006-3

ISSN 0802-8478

PREFACE

During the 1980s there has been a proliferation of textbooks in ecology, emphasizing theory and numerical methodology. Even though, there was an unfilled gap: no book so far has combined vegetation ecological theory and methods, spanning both the introductory and graduate levels, and using examples from the Northern systems (boreal forests, mires, and alpine heaths). My purpose with the present book is to fill this gap. The presentation heavily relies on research carried out by the author and colleagues in Oslo during the 1980s, and examples have, as far as possible, been selected from these studies.

I will thank students and colleagues at the Botanical Garden and Museum, University of Oslo, who have contributed to this book via discussions and a stimulating scientific milieu. I will thank Egil Bendiksen, Odd Eilertsen, Oddvar Pedersen, Knut Rydgren, and, in particular, my wife Tonje Økland, for stimulating discussions, for making unpublished material available, and for commenting on earlier versions of the manuscript. I also want to thank John Birks and Peter Minchin, who improved the book through clarifying discussions.

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INTRODUCTION

INTRODUCTION

Ecology is the study of relationships between organisms, and between organisms and their surroundings. Ecological research is carried out at three levels of integration: the organism level, the population level, and the community level. Vegetation ecology is plant ecology at the community level, that is, the study of relationships within the vegetation, and between vegetation and ecological factors. The history of vegetation ecology shows that descriptive approaches have been favoured; mostly within the phytosociological traditions. However, for the understanding of relationships, description must be followed by explanatory investigations. During the last two decades, international vegetation ecology has benefited from the development of efficient numerical methods for summarizing relationships in the vegetation, and for relating vegetational variation to ecological factors. These methods, coupled with observer-independent sampling, have brought the descriptive approach one step further, from being purely hypothesis-generating to the stage where hypotheses can also be tested. Furthermore, experimental vegetation ecology has increased its importance, and the limits between vegetation ecology and related disciplines of plant ecology are being weakened.

For most of this century, vegetation has been one of the major fields of interest of Fennoscandian plant ecologists. This interest was the basis for foundation of a distinctive Scandinavian approach to classification of vegetation, often called the Northern tradition (Whittaker 1962). The prevalent aim of researchers within the Northern tradition has always been description of vegetation. Understanding of the ecological conditions causing development of vegetational patterns has mostly come along with description, but has not been considered a goal in itself. This descriptive approach has been a part of the phytosociological tradition, by which vegetation is described by means of sample plots subjectively selected by the investigator. For periods, the interest in description of vegetation has been so strong in Fennoscandia that progress and developments in international ecology have failed to attect the attention of the vegetation scientists. Thus, in an international evaluation of ecology and systematics in Norway (NAVF 1988), it was concluded that several fields of considerable international importance have influenced the plant ecological milieu in Norway only to a very small extent or not at all). The same is more or less true for the other Nordic countries. At present, there is a strong tendency away from the descriptive approach, and as far as Norway is concerned, vegetation ecology is in touch to become a field of much lower priority than only a few years ago. In this situation it seems important to provide a link between the Northern tradition and international vegetation ecology, as a fundament for future plant ecological research.

The importance of vegetation ecology within the group of ecological sciences stems not only from the importance of knowledge of structure and function of vegetation in itself, but also from the importance of vegetation ecological knowledge as a framework for investigations at the population and organism levels, and the increasing importance of applied vegetation ecology. For instance, demography of plant populations should be related to the ecological amplitude of the species studied, and hence to the conditions at the sampling sites. Similarly, genetic variability of plant populations on different scales must be related to the variation in vegetation and ecological conditions at these scales. Understanding of morphological variation is also greatly enhanced by reference to ecological

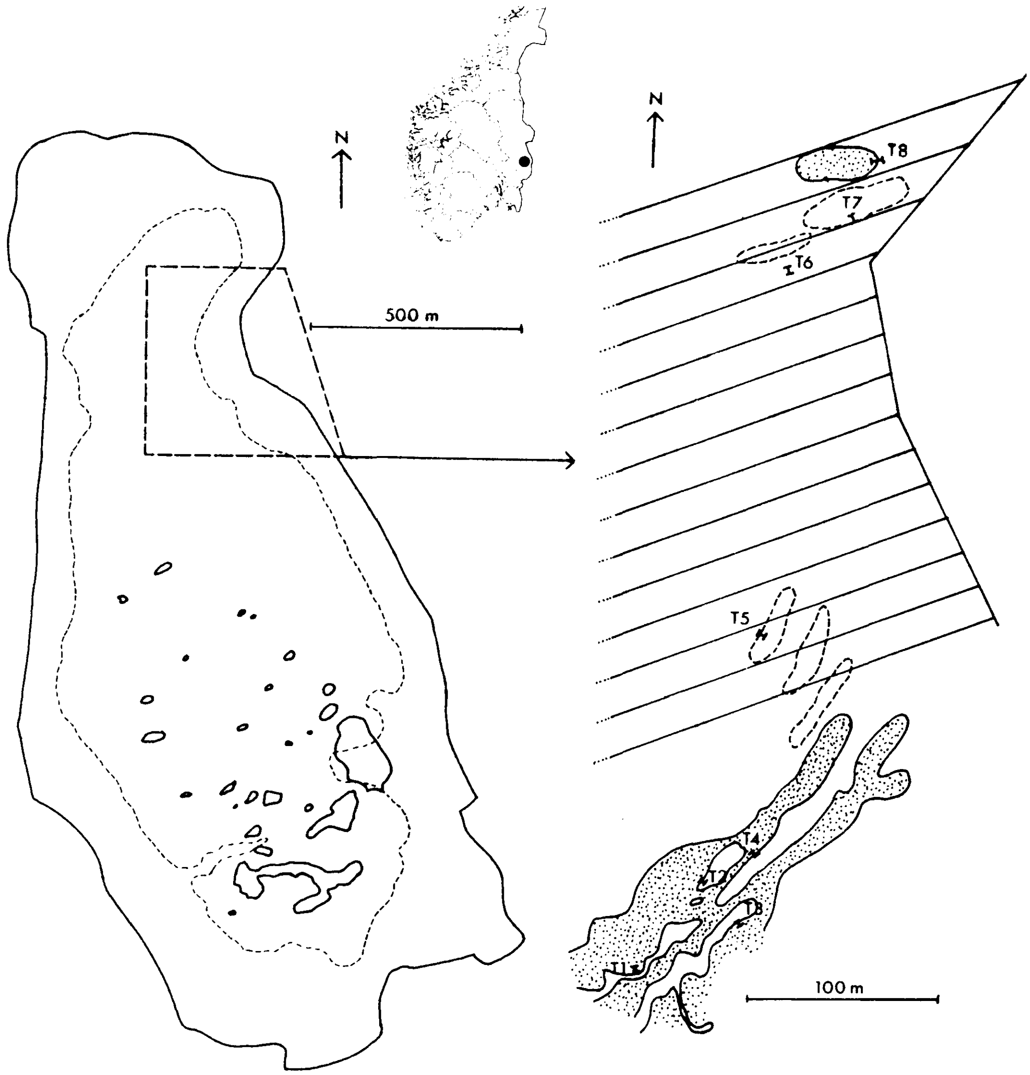


Fig. 1. The standard example; Rønnåsmyra, Grue, Hedmark: geographic position (above, indicated by dot), outline of the mire complex (left; broken line indicate border between mire expanse and mire margin), and position of transects T1-T7 relative to plugged ditches and to hollows (dotted).

data. Hopefully, these examples will show that good knowledge of the theory and methods of vegetation ecology will maintain its importance for botanists working in a wide range of fields, and that reduced interest in vegetation description should not lead to a reduction in effort spent on vegetation ecology as a whole.

The intention of this book is to provide an updated account of the methods of descriptive vegetation ecology, with particular emphasis on sampling methods and numerical

Tab. 1. Species composition of sample plots from virgin bog vegetation (transects T1-T4) at Rønnåsmyra, Grue, Hedmark. For each species and sample plot, frequency in subplots is shown on a 0-16 scale. F - frequency in the set of 51 sample plots. MFS - mean frequency in subplots. DEPT - depth to the water table (cm). P PR - assumed peat-producing ability (0 - strongly peat-producing, 2 - slightly or not peat-producing, 1 - intermediate).

Transect No.	T1											T2										T3																		T4												F	MSF
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51		
DEPT	4	3	3	4	5	8	11	30	34	41	35	2	0	1	-2	5	14	21	15	13	11	3	1	5	6	7	7	8	13	10	8	10	10	8	11	17	16	22	27	8	6	7	11	18	16	23	23	23	19	25	25		
P PR	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	2	2	2	2	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	1	2	2	1	2	2		
Andromeda polifolia	11	11	14	16	16	16	16	16	14	5	9	16	16	16	16	16	16	16	16	16	16	15	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	13	16	16	12	100	15.2
Betula nana	.	.	.	.	.	.	4	.	5	14	4	.	.	.	5	14	14	13	10	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	6	5	5	8	10	33	8.1
Calluna vulgaris	.	.	.	.	.	.	11	1	16	16	16	.	.	.	.	.	1	1	.	6	15	.	.	.	.	.	.	.	.	1	.	1	7	14	16	16	15	15	16	.	.	.	.	.	4	16	16	16	16	16	10	49	12.0
Empetrum nigrum	.	.	.	.	.	.	.	.	.	.	15	.	.	.	.	7	.	16	14	2	6	.	.	.	.	.	.	.	.	.	.	.	2	7	3	11	15	16	16	.	.	.	.	.	3	8	.	.	8	6	8	43	9.3
Pinus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	3	4	.	.	.	.	8	2.2
Vaccinium microcarpum	.	.	.	.	.	.	3	13	16	16	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	3	1	5	2	4	12	16	16	16	15	.	.	2	12	16	16	16	16	9	12	3	1	51	10.0
Vaccinium oxycoccos	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	13	.	1	.	.	16	16	16	16	16	16	16	16	16	16	16	16	14	.	12	5	4	8	16	16	16	16	16	16	12	9	3	6	3	2	92	13.5
Drosera rotundifolia	.	1	.	.	.	7	12	11	14	9	.	1	2	3	2	.	.	.	.	.	.	.	.	1	2	1	.	3	10	6	6	3	11	3	6	11	11	6	12	.	.	.	2	7	11	9	1	.	3	.	.	61	6.0
Rubus chamaemorus	.	.	.	.	1	4	13	16	16	16	16	.	.	.	.	.	2	6	1	4	7	.	.	.	.	2	2	1	2	.	1	10	6	10	14	13	12	11	13	.	.	3	3	9	12	15	16	15	12	13	12	69	8.8
Eriophorum vaginatum	14	16	14	16	16	16	16	3	5	8	14	14	43	10	12	13	12	6	5	14	9	14	14	16	16	15	16	16	16	16	16	16	15	16	16	15	16	16	15	16	16	16	16	16	16	16	16	14	6	1	1	100	13.3
Rhynchospora alba	5	6	6	3	.	.	.	.	.	.	.	16	16	16	14	6	.	.	.	.	.	16	16	7	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25	9.8
Scheuchzeria palustris	2	1	8	9	5	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	14	4.6
Scirpus cespitosus	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	1	1	11	6	13	10	12	16	9	5	4	5	.	.			.	.	.	.	.	.	.	.	.	.	.	.	25	7.3
Dicranum undulatum	.	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	1	1	6	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	5	.	4	9	20	4.6
Pleurozium schreberi	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	11	16	14	7	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	7	7	12	16	22	10.2
Sphagnum balticum	16	16	16	16	16	16	14	4	.	.	.	16	16	16	16	16	11	.	.	1	.	16	16	15	16	16	16	16	16	16	16	16	16	16	14	13	8	3	3	16	16	16	16	16	16	4	.	.	.	.	.	78	13.8
Sphagnum cuspidatum	16	16	15	16	11	8	.	.	.	.	.	16	13	12	13	16	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16	16	16	8	.	.	.	.	.	.	.	.	31	13.4
Sphagnum fuscum	.	.	.	.	.	.	11	16	16	16	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	15	16	16	16	15	.	.	.	3	3	10	9	16	8	10	2	.	37	12.4
Sphagnum majus	16	16	16	16	14	7	.	.	.	.	.	13	9	9	2	8	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	13	7	2	.	.	.	.	.	.	.	.	31	9.6
Sphagnum rubellum	2	10	.	.	8	14	12	16	16	12	7	.	.	.	.	.	.	.	.	.	.	.	2	5	12	14	15	15	16	16	16	16	16	16	16	16	16	12	14	.	1	4	15	16	16	16	10	1	3	.	.	69	11.8
Sphagnum tenellum	16	16	16	16	16	16	8	.	.	.	.	16	16	16	16	16	1	.	.	1	.	16	16	16	16	16	16	14	5	12	16	16	15	4	.	.	.	.	.	16	16	16	14	.	.	.	.	.	.	.	.	61	13.7
Calypogeia sphagnicola	.	.	.	1	2	4	2	4	1	4	.	.	3	6	1	3	.	.	.	.	.	.	.	.	.	1	.	2	2	11	1	1	4	.	.	1	.	1	.	.	1	5	1	.	5	2	.	.	.	.	.	49	2.8
Cephalozia loitlesbergeri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	.	.	5	1	.	3	4	1	2	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	20	2.2
Cephalozia lunulifolia	.	.	.	1	.	.	.	.	.	.	.	.	.	1	2	2	.	.	.	.	.	.	.	6	.	4	4	6	.	.	3	.	.	.	.	.	3	1	1	.	.	.	.	.	.	.	.	.	.	.	.	24	2.8
Cephaloziella spp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	10	2.5
Cladopodiella fluitans	12	16	16	15	16	8	7	.	.	.	.	16	16	16	16	15	2	.	.	.	.	16	16	16	16	16	15	15	14	12	16	8	13	.	.	.	.	.	.	.	4	5	8	7	5	1	.	.	.	.	.	63	12.1
Kurzia pauciflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	6	2	11	1	2	.	.	.	.	.	2	.	.	.	2	.	.	16	3.0
Mylia anomala	.	.	.	3	8	12	12	14	16	16	.	.	9	11	5	10	3	1	.	7	1	.	3	7	4	8	8	15	16	15	16	16	16	16	16	16	16	16	16	.	.	.	5	14	16	16	16	10	10	2	1	82	10.6
Cladonia arbuscula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	10	16	16	.	.	.	.	.	.	.	.	.	.	.	1	.	2	1	1	.	6	1	.	.	.	.	.	.	4	11	13	11	16	16	33	8.6
Cladonia cenotea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	5	8	1	12	3.2
Cladonia chlorophaea agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	9	3	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	5	5	.	.	.	.	.	.	5	7	11	7	13	5	31	4.9
Cladonia rangiferina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9	15	14	11	.	.	.	.	.	.	.	.	.	.	.	.	.	2	6	7	2	11	12	.	.	.	.	.	.	4	14	16	16	16	16	35	10.6
Cladonia squamosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	1	.	2	.	1	4	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16	1.8
Cladonia stellaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	14	12	13	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	3	5	.	.	.	.	.	.	.	.	.	.	.	1	18	7.9
Cladonia sulphurina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	2	.	10	1.6

Additional species: Vaccinium uliginosum 50:1, 51:3; Drosera anglica 12:1; Carex limosa 1:6, 2:2; Dicranum leioneuron 48:6; D. scoparium 19:1, 20:8; 21:10; Drepanocladus fluitans 16:1; Sphagnum magellanicum 6:16, 7:16, 13:1; Calypogeia neesiana 20:4, 21:3; Cephalozia connivens 17:1, 20:7, 21:3; Ptilidium ciliare 19:1, 21:2; Cladonia botrytes 19:4, C. carneola 19:1; C. cornuta 19:3, 21:2; C. cyanipes 19:1, 50:1, 51:1; C. deformis 50:8, 51:2; C. gracilis 21:1; C. uncialis 20:1.

Tab. 2. Species composition of sample plots from drained bog vegetation (transects T5-T7) at Rønnåsmyra, Grue, Hedmark. For each species and sample plot, frequency in subplots is shown on a 0-16 scale. F - frequency in the set of 44 sample plots. MFS - mean frequency in subplots. DEPT - depth to the water table (cm).

Transect No.	T5																T6									T7																			F	MFS
Plot No.	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95		
DEPT	4	6	5	3	15	6	6	4	6	12	22	19	32	29	35	35	5	5	6	13	13	18	28	36	38	6	8	8	6	10	7	7	10	7	13	11	7	7	21	19	35	33	38	45		
Andromeda polifolia	4	13	15	13	16	13	9	16	13	3	12	13	15	4	11	16	15	15	15	15	15	11	8	8	.	1	14	14	9	14	15	1	11	16	16	6	.	.	9	1	.	1	.	4	89	10.7
Betula nana	.	.	.	.	.	.	.	.	.	.	.	9	2	1	3	2	.	.	.	.	4	1	.	.	.	1	.	.	1	.	.	2	4	.	1	.	.	1	.	1	15	14	2	4	41	3.8
Calluna vulgaris	13	12	15	12	12	14	11	16	14	10	16	16	16	14	8	16	13	14	14	13	7	3	.	8	11	14	16	13	6	10	12	13	15	13	12	16	16	14	8	16	3	.	7	2	95	11.9
Empetrum nigrum	.	.	.	.	.	.	.	.	1	9	14	13	16	7	15	16	.	.	.	11	16	16	16	16	16	.	.	1	.	3	1	.	2	.	.	.	.	13	16	16	16	16	15	16	57	11.9
Pinus sylvestris	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	3	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	5	1	1	.	.	.	.	.	20	1.8
Vaccinium microcarpum	.	.	.	.	.	.	.	.	.	2	12	1	2	2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	1	.	.	7	20	3.9
Vaccinium oxycoccos	.	.	12	14	4	.	.	.	.	.	3	.	11	2	1	14	14	16	16	9	16	14	9	7	6	.	.	.	3	.	.	.	4	11	12	16	16	16	16	16	10	7	5	11	68	10.4
Vaccinium uliginosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	12	1	3	.	2	.	.	.	.	.	.	.	.	.	.	.	1	8	15	14	20	6.4
Rubus chamaemorus	14	13	2	.	.	.	1	4	11	11	9	11	9	9	10	9	6	8	14	16	16	16	15	16	16	7	1	.	.	.	.	.	.	.	7	5	2	13	.	16	16	16	16	16	75	10.6
Eriophorum vaginatum	7	14	11	10	14	14	15	16	11	13	7	5	7	5	4	8	14	3	15	13	14	11	.	.	.	10	16	14	16	15	14	16	16	16	16	15	15	8	12	3	.	.	.	.	84	11.7
Dicranum polysetum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	6	9	3	.	.	.	9	4.8
Dicranum scoparium	.	.	.	.	4	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	3	2	.	.	.	2	2	.	9	2	4	.	.	.	.	23	3.1
Dicranum undulatum	1	.	.	.	1	.	.	.	.	.	7	13	8	7	9	10	4	6	.	.	1	.	11	13	16	.	2	4	2	1	2	2	.	.	1	7	2	10	6	8	4	.	.	.	61	5.9
Drepanocladus fluitans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	4	13	.	.	1	.	.	.	5	.	.	1	.	15	7	.	9	.	3	7	5	.	.	.	.	.	.	27	6.7
Pleurozium schreberi	.	.	.	.	.	.	.	.	.	.	12	16	16	12	14	13	.	.	.	.	.	.	.	14	15	.	.	.	.	13	2	.	.	.	.	1	.	.	8	3	.	5	10	.	34	10.3
Pohlia nutans	4	1	.	.	.	1	.	.	.	.	1	.	.	.	.	.	8	12	8	16	14	12	.	1	4	.	8	7	11	9	7	14	12	13	15	16	15	13	15	15	1	2	1	2	68	8.6
Polystrichum strictum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	6	3	.	.	1	11	15	4	5	.	9	4	.	3	2	16	4	1	.	.	.	1	.	.	.	36	5.5
Sphagnum angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	14	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9	6.5
Sphagnum balticum	16	14	13	12	12	14	8	11	16	16	10	.	.	.	.	.	16	16	15	13	16	7	.	.	.	16	14	15	16	16	15	16	16	16	16	16	16	16	5	.	.	.	.	.	70	14.0
Sphagnum capillifolium	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	9	1.2
Sphagnum cuspidatum	.	4	8	10	2	.	.	1	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14	4.8
Sphagnum fuscum	.	.	.	.	.	.	.	.	.	2	8	.	1	.	2	15	.	.	.	.	.	7	.	7	9	.	.	.	.	.	.	1	.	.	.	.	.	.	4	8	1	.	.	.	27	5.4
Sphagnum magellanicum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5	6	16	13	1	.	5	.	.	.	.	.	.	.	1	1	5	.	.	5	6	.	.	.	.	.	27	5.4
Sphagnum rubellum	5	1	2	.	.	.	.	.	.	.	.	.	.	.	1	10	.	.	5	5	2	.	.	.	.	.	2	1	5	.	.	.	.	.	.	1	.	.	8	2	.	.	.	.	32	3.6
Sphagnum tenellum	16	16	15	16	11	16	16	16	16	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25	13.7
Calypogeia sphagnicola	.	3	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	2	.	.	.	.	.	1	.	.	.	.	.	.	11	2.6
Cephalozia connivens	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	9	1.2
Cephalozia loitlesbergeri	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	9	1.2
Cephalozia lunulifolia	.	.	4	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	12	3	7	12	9	.	.	.	1	.	3	.	.	.	.	.	.	.	.	25	5.0
Cephaloziella spp.	1	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	4	.	.	1	1	1	.	.	.	.	5	4	3	2	12	4	6	3	4	6	6	8	.	3	2	.	4	6	52	3.8
Cladopodiella fluitans	14	16	14	16	10	15	16	16	16	6	.	.	.	.	.	.	7	5	7	.	1	1	.	.	.	4	4	.	9	11	10	1	.	4	1	2	.	1	.	.	.	.	.	.	57	8.3
Kurzia pauciflora	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	9	15	6	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14	6.2
Mylia anomala	16	8	7	6	9	2	6	3	.	10	10	.	.	.	.	2	5	11	12	11	10	3	.	.	.	7	11	4	4	4	4	4	1	1	8	10	4	2	.	.	.	.	.	.	68	6.6
Cetraria pinastri	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	.	9	1.5
Cladonia arbuscula	.	.	.	.	3	.	1	1	.	1	12	16	8	14	14	5	2	4	2	4	.	1	.	.	.	.	3	2	.	1	2	1	2	1	5	3	1	1	.	.	.	.	.	2	61	4.2
Cladonia bacillaris	.	.	.	1	8	3	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	3	2	2	1	6	5	1	1	6	.	3	.	2	5	.	.	5	43	3.4
Cladonia bacilliformis	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	1	.	.	.	.	1	.	11	1.2
Cladonia botrytes	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	1	.	.	1	.	1	.	7	3	.	1	.	1	4	.	7	8	4	7	.	1	2	.	.	.	41	3.0

Tab. 2 (continued)

Transect No.	T5																T6									T7																			F	MFS
Plot No.	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95		
Cladonia carneola	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	1	2	.	.	.	2	1	.	.	.	.	.	.	1	8	3	1	.	4	.	.	2	.	27	2.4
Cladonia cenotea	.	.	.	.	6	1	.	.	.	2	5	6	1	5	8	.	3	2	2	4	.	2	6	.	.	.	8	4	2	2	1	4	6	1	8	11	5	6	4	10	3	.	4	3	71	4.4
Cladonia chlorophaea agg.	5	.	4	.	12	4	5	4	.	14	11	14	6	11	2	.	3	6	4	12	5	1	2	.	.	.	5	3	.	2	1	3	7	.	3	8	.	8	5	6	7	2	3	4	77	5.6
Cladonia coccifera agg.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	1	.	.	2	4	.	.	.	.	1	.	2	.	.	1	.	20	1.8
Cladonia cornuta	1	.	1	1	10	2	1	.	.	3	.	.	.	5	3	.	2	5	2	5	.	3	9	.	.	.	10	4	2	3	3	1	3	1	3	7	5	13	12	14	7	.	5	3	72	4.7
Cladonia crispata	4	.	.	.	1	.	.	.	.	.	1	.	.	1	.	.	.	.	3	2	.	1	.	.	.	.	.	1	.	2	.	.	.	.	.	1	.	.	.	2	.	.	.	.	25	1.7
Cladonia cyanipes	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	2	1	4	3	.	.	.	.	.	4	1	2	.	.	.	1	.	.	5	.	.	.	1	2	.	.	1	32	2.1
Cladonia deformis	5	1	2	3	11	3	6	5	.	2	2	.	.	3	7	.	3	8	3	3	.	.	.	.	.	.	1	4	2	.	.	1	3	.	3	1	3	4	.	3	2	.	2	2	66	3.4
Cladonia gracilis	.	.	.	.	2	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	3	2	3	.	.	1	1	1	1	1	.	.	.	1	1	2	.	.	1	.	.	.	.	36	1.4
Cladonia rangiferina	.	.	1	.	6	1	1	2	.	5	12	16	16	16	16	8	2	4	4	5	2	3	5	.	4	.	8	3	1	2	3	2	6	1	6	9	3	6	3	11	4	11	7	5	86	5.8
Cladonia squamosa	11	10	10	6	8	12	9	10	1	10	3	1	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	27	7.8
Cladonia sulphurina	1	.	.	1	11	2	2	1	.	5	.	2	.	3	.	.	2	1	2	3	2	3	8	.	.	.	10	9	2	6	5	7	8	3	9	12	9	11	2	6	1	.	3	2	75	4.7

Additional species: Picea abies 92:1; Drosera rotundifolia 79:1; Dicranum fuscescens 83:2; 88:2, 89:1; D. leioneuron 71:1, 75:1, 76:3; Polytrichum longisetum 52:11; Sphagnum majus 87:3, 88:6, 89:1; Calypogeia neesiana 86:1; Lophocolea heterophylla 76:1; Cetraria islandica 54:1, 65:4; Cladonia fimbriata 94:1, 95:9; C. floerkeana 56:1, 61:1; C. uncialis 52:1.

techniques and the way they extend the scope of a descriptive approach. I have aimed at giving this account with due attention to the Northern tradition, in order to combine the knowledge accumulated during a long series of intensive investigations with the prospects provided by modern methods. I have tried to find examples from Nordic vegetation throughout.

STANDARD EXAMPLE

One data set has been chosen as a standard example to be used throughout this book for illustration of several aspects of the theory and methods of vegetation ecology. This data set is derived from a study of the mire Rønnåsmyra, Grue, Hedmark, SE Norway (Fig. 1; Økland, unpubl.). This mire is a typical unilaterally (excentrically) sloping kermi raised bog complex, one of the more typical of its kind in SE Norway. The value of this mire from the point of view of nature conservation became apparent in the 1960s, and in 1973, shortly after the plans for protection became known to the land owners, the northern part of the mire was subjected to extensive ditching. Fig. 1 shows the mire with the ditches drawn in. In spite of the damage caused to its northern part, the mire was made a National Nature Reserve. In 1982 an attempt was made at reclamation of the drained part of the mire. Peat plugs were entered into the transverse ditches near their outlets into the lateral, main ditches and these main ditches were similarly plugged downslope. Within a short time, the ditch walls began to sink in, and in 1988 the ditches were inconspicuous and some places even hard to trace.

In 1979, the vegetation of both drained and virgin parts of the mire was described by Mette Korsmo, who observed drastic drainage effects in the drained parts of the mire

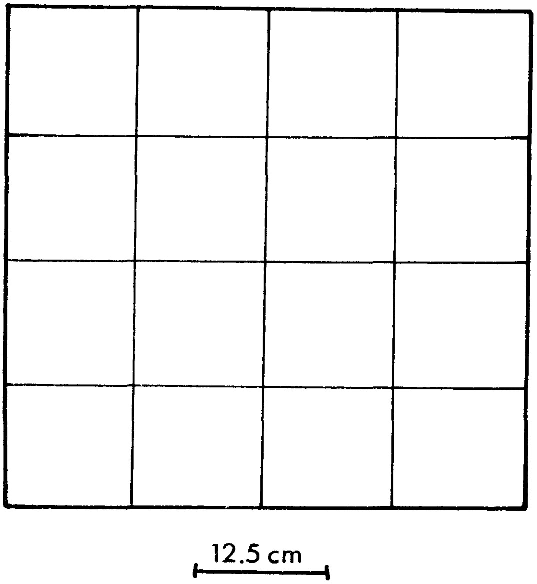
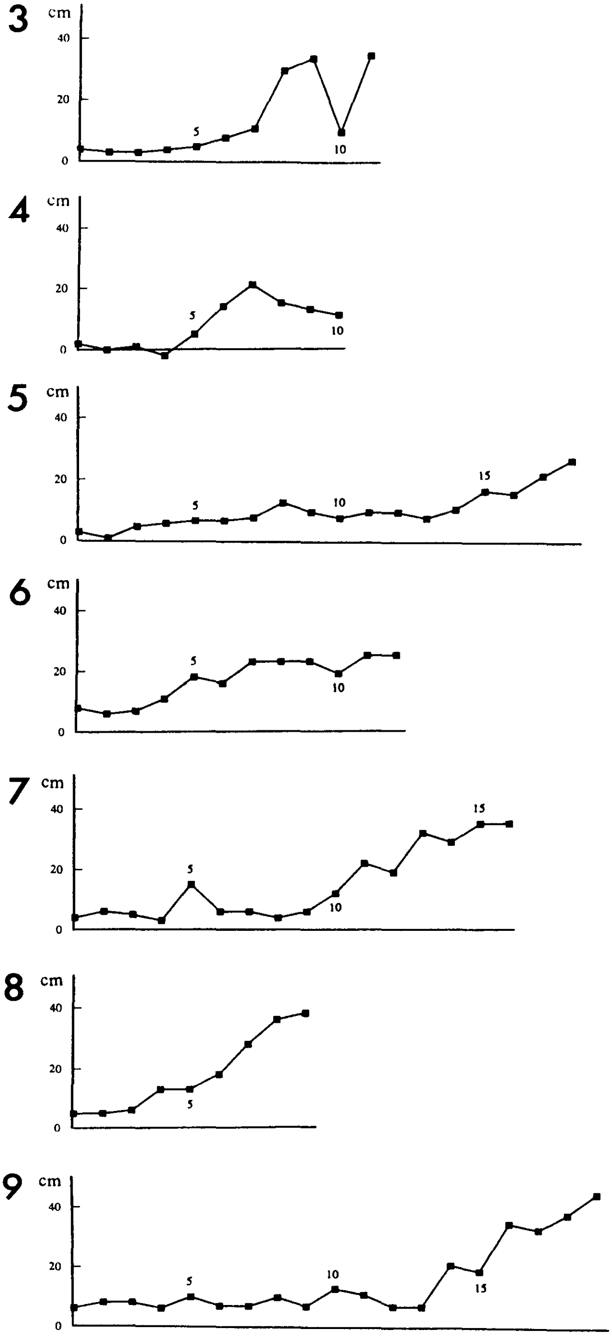


Fig. 2. Division of a sample plot into 16 subplots.



Figs 3-9. Microtopography of transects T1-T7; positions of sample plots relative to water table at one specific day. Fig. 3. T1. Fig. 4. T2. Fig. 5. T3. Fig. 6. T4. Fig. 7. T5. Fig. 8. T6. Fig. 9. T7.

(Korsmo 1980). The *Sphagnum* spp. of the bottom layer had almost disappeared completely, and the former hollows were in touch to be colonized by dwarf shrubs like *Calluna vulgaris* and *Betula nana*. In order to judge the success of the reclamation attempt, the study providing the standard example was initiated in 1987 by the environmental protection authorities of Hedmark County. In 1988 seven transects were selected, each running from the central parts of a hollow (or a former hollow) to the centre of an adjacent hummock (Figs 3-8). Each transect consisted of 9 to 19 sample plots, 0.50 x 0.50 m, placed edge by edge along the transect. Each sample plot was divided into 16 subplots, 12.5 x 12.5 cm (Fig. 2). Presence or absence of all species was recorded in each subplot, and **frequency in subplots** was calculated. A total of 69 species were recorded in 95 sample plots; 52 species in 51 plots from the undrained part of the mire (virgin bog vegetation; Tab. 1) and 61 species in 44 plots from the reclamation experiment area (vegetation of the drained bog; Tab. 2). Water pits, each with the side walls reinforced by a polyethylene pipe, were established at regular intervals along the transects, and the distance to the water table was measured in all pipes one day in October 1988. Water table measurements at one occasion give good estimates of the rank order of the sample plots with respect to distance to the water table (R. Økland 1989b), but at an arbitrary scale. Distance to the water table was estimated for all subplots. The arithmetic mean of subplot values was calculated and taken as the value representative for the sample plot. The virgin plots were classified as strongly peat-producing (with fresh, healthy *Sphagnum*), slightly or not peat-producing (with dominance of lichens, mosses except *Sphagnum* and hepatics), or intermediate in this respect. The material from Rønnåsmyra can be divided into several data subsets, differing with respect to vegetation, sample plot number and species number. Several subsets are used throughout this book to illustrate particular theoretical points and the application and interpretation of different methods.

THEORY: BASIC CONCEPTS OF VEGETATION ECOLOGY AND THE RELATIONSHIP BETWEEN VEGETATION AND ECOLOGICAL FACTORS

TERMINOLOGY OF GRADIENTS

Variation in vegetation and ecological factors along gradients is a major field of interest in modern vegetation ecology. The terminology of gradients proposed by Whittaker (1967, 1978b) is now commonly accepted: An **ecological gradient** is the gradual change in any ecological factor. Ecological factors are often correlated with each other, and act on the plants in combination, not as single factors. A complex of ecological factors varying more or less in parallel, make up a **complex-gradient** (Whittaker 1956). An example of a complex-gradient is the nutrient gradient in a boreal forest system, made up by several correlated parameters. Among the many factors contributig to the nutrient gradient, the gradients in cation concentrations (Ca^{2+}, Mg^{2+}, Mn), soil pH, base saturation, available nitrogen, rate of decomposition of organic matter (for instance measured as loss on ignition) can be mentioned. The gradual change in the composition of vegetation, for example from the hollows to the hummocks on Rønnåsmyra (T1-T4 in Tab. 1), is termed a **coenocline**. Frequently the variation in vegetation within an area varies in several directions more or less independently, as in a mire with a nutrient (poor-rich) gradient in addition to the hollow-hummock gradient. Thus the coenocline can be generalized to more dimensions. Two independent gradients in vegetation make up a **coenoplane** and three gradients make up a **coenocube** (Gauch et al. 1977). The variation in vegetation (the coenocline) is mostly correlated with, and partly caused by, the variation in an underlying complex-gradient. If we consider the coenocline as a function of a known complex-gradient and want to emphasize both the vegetational and ecological variation, we use the concept **ecocline**. An **ecotone** is a relatively sharp change in one, two or three of complex-gradient, coenocline and ecocline (Gauch 1982a).

Complex-gradients can be classified according to the scale on which they operate (R. Økland & Bendiksen 1985); **local** complex-gradients vary on a relatively fine scale, **regional** complex-gradients on a broad scale. Local complex-gradients are mostly due to geological and geomorphological variation, regional complex-gradients due to (macro)climatic variation. The terms local and regional may also be applied to single environmental gradients, coenoclines and ecoclines. The distinction between local and regional gradients is not a sharp one; snow cover in winter in alpine areas is considered to be a local gradient, but is influenced by annual mean temperature and oceanicity of climate (R. Økland & Bendiksen 1985).

The ecological factors differ greatly in the way they influence plants (cf. Wielgolaski 1978). Several purposes call for a classification of ecological factors according to mode of action, and, in fact, several different classifications of ecological factors have been proposed.

Scandinavian literature often distinguishes between **primary** and **secondary environmental factors**, the terminology first proposed by T. Fries (1925). Primary ecological factors depend upon the parent material (the bedrock underlying the soil), the weathering and leaching of the soil and the supply from precipitation (Dahl et al. 1967). Examples of primary ecological factors are cation concentrations. Secondary ecological factors are the results of processes in the ecosystem (Dahl et al. 1967). Examples are numerous; the content of nitrogen in the humus, the amount of light reaching the understory in a forest, the amount of organic matter in the humus, etc. The distinction between the two categories is not sharp (Dahl et al. 1967); for instance pH takes an intermediate position as it is dependent on the bedrock as well as precipitation and litterfall.

Austin (1980, also see Austin & Cunningham 1981) classified ecological gradients into three types, emphasizing their way of influencing the plants rather than their source. The three kinds are: (1) ***Indirect environmental gradients***: the environmental factor involved does not have a direct physiological influence on plant growth. Examples are altitude, organic content of the soil, soil depth, and local topography. (2) ***Direct environmental gradients***: the environmental factor has a physiological influence on plants without being a resource for plant growth. Examples are pH, influencing the availability of various nutrients; temperature, aspect and inclination. (3) ***Resource gradient***: the environmental gradient is an essential resource for plant growth, for which competition may occur. Examples are nutrient concentrations. Water availability and light may be resource gradients in some ecosystems.

Despite the usefulness of gradient classifications for many applications, it should be emphasized that the types of such classifications are deemed to be vaguely separated. There will always be environmental factors that cannot be classified to one type, or that may be of one kind in one system and another type in another system. Anyway, such classifications are important aids for understanding the responses of plant species to ecological gradients, and hence the structure and function of ecosystems.

DIVERSITY

Diversity indices are used to measure different aspects of variability within, and between communities. We can divide the diversity indices into three main categories: (1) **species richness**, or **α diversity**, (2) **species turnover**, or **ß diversity**, and (3) equitability or **evenness** indices. We will consider these in somewhat more detail.

Species richness

Species richness relates to the number of species within a specified area, at some scale. Most simply, the species richness of an area can be defined as the total number of species occurring within this area, or the average number of species within each sample plot (of a given constant size) within this area. Species richness can be calculated for the whole species composition or for one taxonomic fraction of the vegetation (**taxocene**, cf. Whittaker 1972).

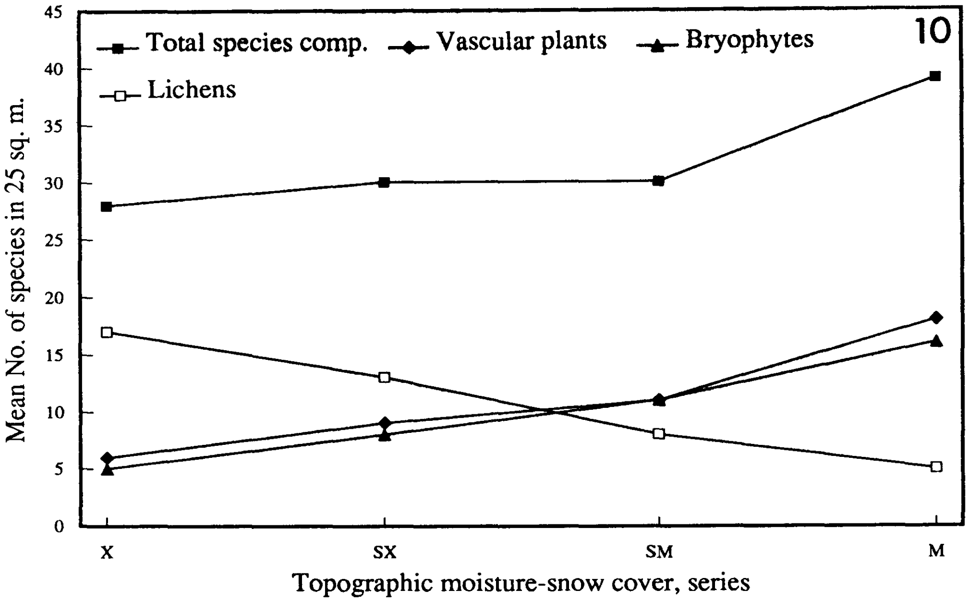
Whittaker (1972, 1977) defined 3 categories of species richness according to scale: His α, or within-community diversity, relates to the species richness within a particular vegetation type. His γ, or within-gradient diversity relates to the species richness along one gradient (variation along other gradients kept constant), and his δ diversity relates to a larger area, the variation along all gradients included.

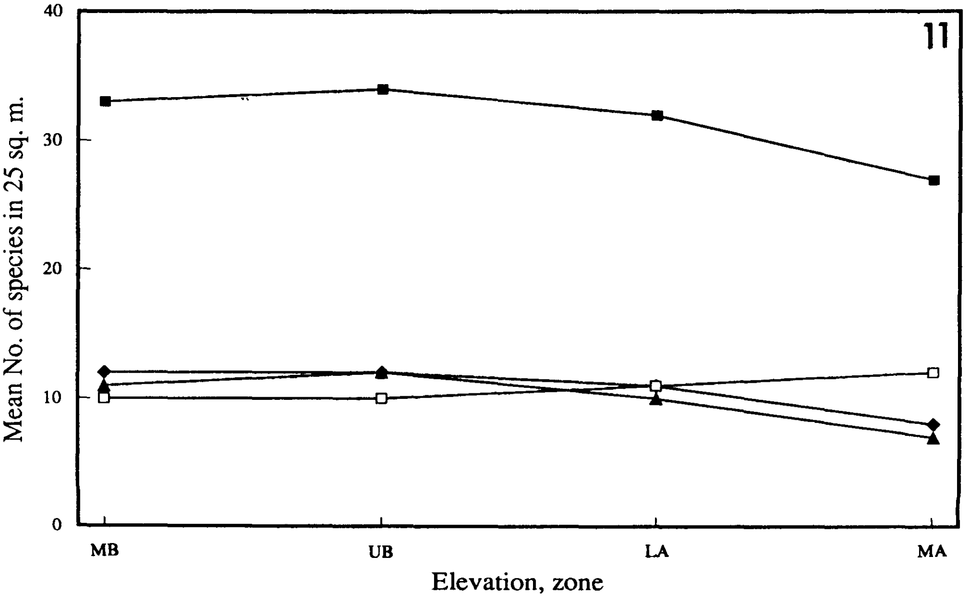
The mean number of species per sample plot in a set of sample plots is perhaps the most frequently used measure of species richness at the within-community (vegetation type) level. This measure is dependent on sample plot size (Peet 1974), as any increase in sample plot size invariable leads to an increase in the environmental heterogeneity and thus to increased number of species per sample plot. This does not cause problems with interpretation if only species richness estimates based on the same sample plot size are compared. Total species number in a sample set, a site or region are often used as measures of γ or δ diversity (that is, species richness on larger scales). These measures are dependent on the area of the site or region, and the total number of species in a sample set is dependent both on sample size and number of sample plots (Dahl 1960). Indices of species richness other than species counts have often been proposed, but failed to gain broad acceptance. The following statement on species richness measures, provided by Peet (1974) still remains valid: "Direct species counts, while lacking theoretical elegance, provide one of the simplest, most practical and most objective measures of species richness."

Several attempts have been made at generalizing patterns of species diversity, at different scales (e.g., Whittaker 1972, 1977, Shmida & Ellner 1985). This is partly a biogeographical subject, and will only briefly be considered here. Species richness is often believed to increase towards more productive environments. This is based on the assumption that better resource availability should increase the carrying-capacity of a system and thus the ecosystem should be able to accomodate more species. However, a review of evidence supporting this view (Begon et al. 1986) demonstrated trends strongly differing between studies; increase, decrease and irregular relationships between productivity and species performance were all found. Thus the common view that species richness increases from more to less "extreme" environments is hard to confirm by evidence (Begon et al. 1986). Partly this is related to difficulties with defining what is "extreme".

In addition to the productivity gradients, trends in species richness along other gradients have been frequently studied. Gradients in species richness along elevation and topographic moisture gradients have often been considered, as in the study of the forest-alpine transition in Grunningsdalen, Telemark, SE Norway by R. Økland & Bendiksen (1985). This transition contained four elevation zones (middle boreal, upper boreal, low alpine and middle alpine) and four steps (series) were considered along the topographic moisture-snow cover gradient (xeric, subxeric, submesic, and mesic). The mean number of species per sample plot in each of the four categories along each of the two gradients was calculated. This is a simple, but sound measure of species richness, as a constant sample plot size of 25 m^2 was used throughout the study. The mean number of species was also divided onto taxocenes (vascular plants, bryophytes, and lichens). Trends in species diversity shown in Figs 10-11 represent τ diversities in the terminology of Whittaker (see above). It is seen that vascular plants and bryophyte richness decrease with increasing elevation, while the opposite is true for lichens. Total species diversity is highest in the upper boreal (subalpine) zone, and decreases considerably in the alpine zones. Along the topographic moisture-snow cover gradient, vascular plant and bryophyte richness increase from xeric to mesic sites, while the opposite is true for lichens. Total species richness shows a strong increase from submesic to mesic sites. These trends are interpretable by taking into account the physiological and ecological restrictions set on the different taxocenes, the history of the area, etc. However, trends along similar gradients in other parts of the world show a bewildering diversity of trends. This amplifies the view that trends in species richness (and diversity as such) can hardly be generalized; results from one study area must be explained by virtue of the local conditions. However, species richness may be an informative summarizing statistic on the local or regional scale.

Species richness increases with increasing area. Shmida & Ellner (1984) partition species richness into four categories operating at different spatial scales: (1) *Niche relations*, interactions among species and between species and environment; most important at the within-community scale. (2) *Habitat diversity*, microsite heterogeneity at a small to very small scale (actually intergrading with niche relations), giving rise to among-community differences in environmental conditions (also contributing to increase ß diversity, see below),





Figs 10-11. Species richness along gradients in topographic moisture-snow cover (Fig. 10; X - xeric, SX - sunxeric, SM - submesic, M - mesic) and elevation (Fig. 11; MB - middle boreal zone, UB - upper boreal zone, LA - low alpine zone, MA - middle alpine zone) in

and on a broader scale giving rise to among-regions differences (increasing δ diversity). (3) *Mass effect*, the temporarily establishment of species that cannot maintain their populations; most important on a broader, regional scale. (4) *Ecological equivalence*, the occurrence of species with similar niches, increasing its importance towards broader scales. The relative importance of factors (1) and (2) for the structure and function of vegetation will be discussed in more detail later (pp. 49-56).

Species turnover

Species turnover, or ß diversity, is the degree of compositional turnover, or change in the species composition, occurring along a coenocline. The main source of species turnover is the environmental variation along the underlying complex-gradient. Several different measures of beta diversity have been proposed. As the estimation of beta diversity is conceptually strongly tied to the problem of scaling of coenoclines, we will return to beta diversity estimation later (pp. 35-36).

Evenness

Evenness or equitability indices measure the equality of abundances in a community (Alatalo 1981). A large number of measures have been proposed, the most popular is Shannon-Weaver's entropy index (Shannon & Weaver 1949), H:

$$H = - \mathrm{SUM}_{i=1..s}\ p_i{*}\ln(p_i) \qquad (1)$$

where p_i is the probability of occurrence of species i in the community (e.g., the fraction of the total number of individuals in the community belonging to species i), and s is the total number of species. In practice, the p_i values will not be known, but have to be estimated. Thus H' is mostly estimated from the formula

$$H' = - \mathrm{SUM}_{i=1..m}\ (a_i/a)\ln(a_i/a) \qquad (2)$$

where a_i is the estimated abundance of species i, a is the total estimated abundance for all species, $a = \mathrm{SUM}_{i=1..m}\ a_i$, and m is the number of species recorded.

The biological interpretation and significance of evenness is unclear, except for being related to dominance relationships. Evenness is high if all species have equal abundance, and decreases with increasing dominance of a few or one single species. However, the H' formula also has a component of species richness, as H' increases with increasing number of species (Peet 1974, Alatalo 1981). The ecological significance of evenness measures have been seroiusly questioned (Hurlbert 1971, Alatalo 1981). A comment by Alatalo (1981) illustrates this: "In spite of their popularity, the diversity and evenness concepts have not produced much useful information in ecological studies. One of the reasons for the failure is the uncritical use of various indices, with no knowledge of their response behaviour and the looseness in definitions of the concepts."

the Grunningsdalen area, Lifjell, Telemark, S Norway. Species richness is given as mean number of species in 25 m² plots at each point along each gradient. After R. Økland & Bendiksen (1985).

MODELS FOR SPECIES' RESPONSES TO ENVIRONMENTAL GRADIENTS

Introduction and basic concepts

Fundamental to understanding the structure and function of vegetation is knowledge of the way species respond to the underlying complex-gradients. There has been considerable (and increasing) interest in development of models for species-gradient relationships during the last twenty years. Such models may be of two kinds (Austin 1980); **descriptive models** and **functional models**. Descriptive models aim at describing the species response curves with respect to the gradients, while functional models also include the underlying physiological mechanisms.

It is important to distinguish between **physiological response curves**, the response of species to a gradient given no influence from other species, and **ecological response curves**, response curves under field conditions. Each of these curves have an **optimum** (often termed the **mode**), the **physiological optimum** and the **ecological optimum**.

Fundamental questions of vegetation models can be organized under four headings (Austin 1980): (1) The shape and position of ecological response curves along ecological gradients. (2) The shape and position of physiological response curves along ecological gradients. (3) Patterns of variation in carrying capacity along ecological gradients. (4) Patterns of variation in species richness along ecological gradients.

We will treat questions (1) and (2) later on as these questions are likely to have generally valid answers. Questions (3) and (4) have to be answered for different systems separately; as is evident from the variation in diversity trends demonstrated above (p. 19).

Some vegetation models

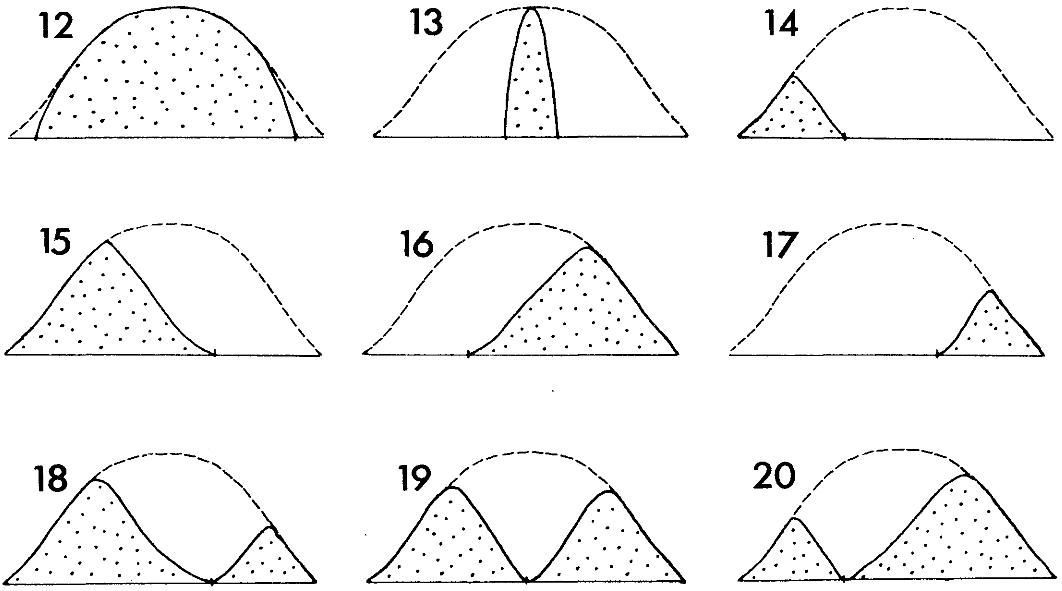
Ecological displacement model (Ellenberg in Mueller-Dombois & Ellenberg 1974, see also Austin 1976a, 1980). In its original version, put forward by Ellenberg, this model has aspects of both functional and descriptive models. Each species has a parabola-shaped physiological response curve relative to the gradient (Figs 12-20). Dependent on interactions with other species, the species' amounts are reduced along the whole or a portion of the gradient, thus giving rise to a variety of ecological response curve shapes, including skewed and bimodal (two-topped). The model also allows the ecological optimum to be displaced along the gradient relative to the physiological optimum.

Austin (1976a) develops the model further. By variation of the parameters of the beta function, physiological response curves with variable skewness etc. can be generated. Austin assumes that the carrying capacity (total abundance of all species) is fixed at each position along the gradient. Ecological response curves are made by partitioning the carrying capacity among the species according to their physiological response and coefficients of interaction (competition) with other species. The mathematical formulas based on the **beta function** are given by Minchin (1987b). In the one-dimensional case (one coenocline) it is as follows:

$$A = 0 \text{ if } x < m\text{-}cr \text{ or } x > m+dr,$$

$$A = A_0 b^{-1}\ [(x-m)r^{-1}+c]^{\alpha}[(m-x)r^{-1}+d]^{\tau} \ \text{ if } m\text{-}cr < x < m+dr \qquad (3)$$

where x represents a position along the gradient, A_0 is the modal abundance, that is the abundance at the optimal position (mode) along the gradient, m - is the optimum along the gradient (mode), r is the range of the species, that is the portion of the gradient in which the species occur, α and τ are constants controlling the skewness of the response curves, and c, d, and b are constants depending on α and τ the following way: $c = \alpha(\alpha+\tau)^{-1}$, $d = \tau(\alpha+\tau)^{-1}$, and $b = c^{\alpha}d^{\tau}$. Fig. 21 illustrates the meaning of the parameters A_0, m and r,



Figs 12-20. Ecological displacement model (after Mueller-Dombois & Ellenberg 1974 and Austin 1980). Continuous line - ecological response, broken line - physiological response. Range of occurrence of the species indicated by dots. Figs 12-13. Physiological and ecological optima coincident. Figs 14-17. Ecological optimum displaced relative to physiological optimum, 4 different ecological response curve shapes. Figs 18-20. Bimodal (two-topped) ecological response, 3 different ecological response curve shapes.

and Fig. 22 shows six examples of response curves, created by varying parameters of the beta function. When the parameters α and τ are equal, the function is symmetrical, when α is greater than τ, the curve is skewed to the right, when τ is greater than α, the curve is skewed to the left. If α and τ are equal and greater than 4, the curve approaches the Gaussian (normal) curve.

The Gaussian model (Whittaker 1956, Gauch & Whittaker 1972a, 1976, Gauch 1982a). Based on the pioneering studies of species-gradient relationships by Whittaker (1956 et seq.), showing species response curves tending to be bell-shaped along the major gradients, the Gaussian model was formulated. The fundamental property of this model is that the abundances of species along an environmental gradient are assumed to approximate bell-shaped, unimodal curves, resembling the Gaussian (normal) distribution curve. The equation for the Gaussian curve is

$$A = A_0 \exp\,[-(z-\mu)^2 2^{-1} \sigma^{-2}], \qquad (4)$$

where z represents the position along the gradient, A_0 is the modal abundance, that is the abundance at the optimal position (mode) along the gradient, μ - is the optimum along the gradient and σ is the dispersion of the species, the standard deviation of the curve (Fig. 23). The Gaussian model can be extended to more gradients by assuming Gaussian responses to all gradients. The multidimensional response surface will then be multivariate Gaussian. The Gaussian model was intended as a purely descriptive model, as an approximation, not a rigid model (Gauch 1982a).

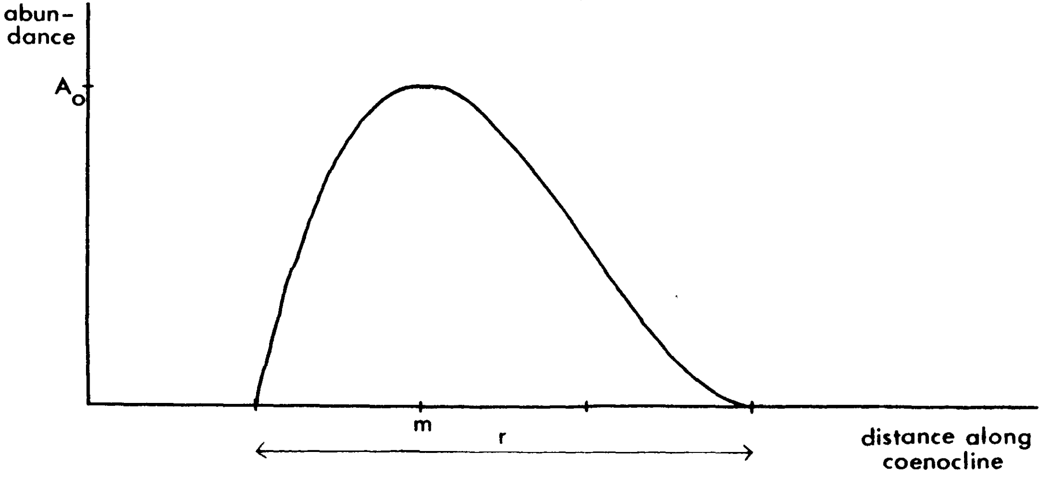


Fig. 21. Physiological response curve based on the beta function (after Minchin 1987a). A_0 - modal abundance, m - position of mode along the gradient, r - range of occurrence along gradient).

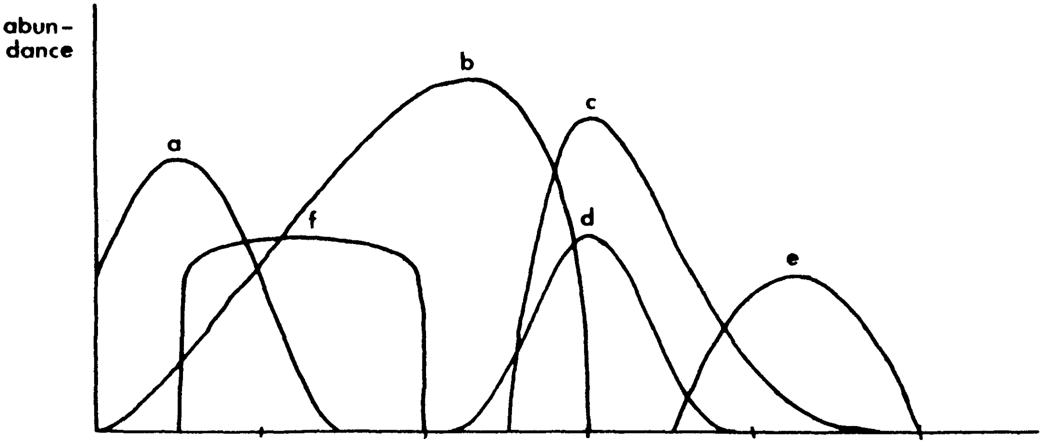


Fig. 22. Physiological response curves based on the beta function (after Minchin 1987a). Parameters of curves as follows: (a) $A_0 = 70$, $m = 10$, $r = 40$, $\alpha = \tau = 2$, (b) $A_0 = 90$, $m = 45$, $r = 60$, $\alpha = 1.5$, $\tau = 0.5$, (c) $A_0 = 80$, $m = 60$, $r = 50$, $\alpha = 1$, $\tau = 4$, (d) $A_0 = 50$, $m = 60$, $r = 40$, $\alpha = \tau = 4$, (e) $A_0 = 40$, $m = 85$, $r = 30$, $\alpha = \tau = 1$, (f) $A_0 = 50$, $m = 25$, $r = 30$, $\alpha = \tau = 0.1$.

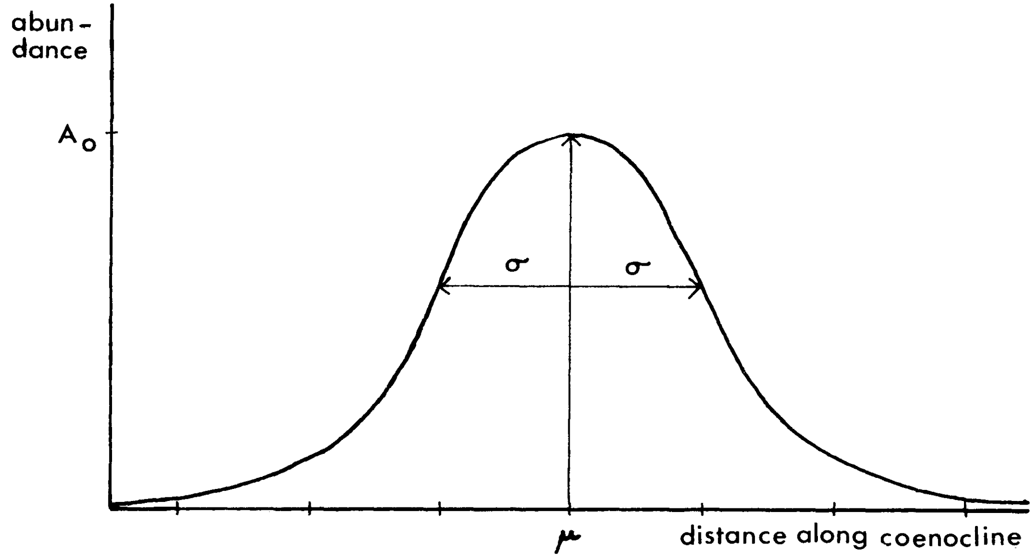


Fig. 23. Gaussian response curve. μ - position of the mode (optimum), σ - standard deviation of the curve, A_0 - modal abundance.

The Gaussian model includes generalizations of several properties of the ecosystem: (1) Response curve shape, see above. (2) The modes of species distributions are scattered individualistically along an environmental gradient. The modes of major species tend to show regular spacing while modes of minor species are scattered at random. (3) Modal abundances (maximum recorded abundance) show lograndom (or lognormal) distribution, that is, if the abundance scale is transformed into a logarithmic scale and divided into equal groups along this scale (e.g., 0.75-1.5, 1.5-3.1, 3.1-6.25, 6.25-12.5, 12.5-25, 25-50, 50-100), the number of species in each group is roughly equal (in the case of a lognormal distribution, the frequencies approximate the normal distribution). (4) The dispersion of the species response curves varies, and is normally distributed with a standard deviation about 0.3 times the mean. (5) Environmental gradients may be partly correlated, so that axes in multidimensional Gaussian models are not necessarily orthogonal. (6) Modal abundance and dispersion are not correlated. (7) The species richness (α diversity) may vary along the coenocline, and the total number of species occurring along the gradient (τ diversity) varies between areas. (8) Gaussian response surfaces may be modified by competition. (9) The Gaussian curve is characterized by flanks extending infinitely, while species have definite ranges along gradients. (10) Field data are noisy, that is, they contain statistical error (to be discussed later).

Points (1-10) are a summary of what is called the **individualistic continuum theory** of vegetation (Gleason 1926, Whittaker 1956, McIntosh 1967).

Other models are mentioned, inter alia, by Austin (1976a, 1980, 1987) and Austin and T.M. Smith (1989), but will not be considered further here. These models mostly deal with the physiological mechanisms underlying species responses and/or the effects of competition (e.g., Grime 1979, Tilman 1982).

Evidence on shape of response curves

Two sources provide evidence on the shape of species response curves (Austin 1980): (1) Field data on species responses to measurable ecological gradients. (2) Experimental studies of species' distributions along controlled environmental gradients. We will consider both:

Field data. The unimodal response curves for species' responses to ecological gradients presented by Whittaker (1956, 1960, 1967) formed the basis for the Gaussian model of vegetation. In his 1956 study he presented abundance nomograms for 44 tree species in a coenoplane with elevation and topographic moisture as axes. Of these, 38 species response curves were unimodal (essentially Gaussian), 5 were bimodal, and 1 was trimodal. However, the validity of the results relative to the topographic moisture gradient as evidence has been questioned, as positions along the gradient are determined by subjective inference and ordination rather than by environmental measurements (Austin 1980).

The extensive survey of the distribution of British grassland species along a pH gradient by Grime & Lloyd (1973), provide further evidence on the shape of ecological species response curves. As shown in Fig. 24, the curves for the six selected grassland species are largely one-topped (at least they would be after some smoothening), but often skewed. The curve for *Festuca ovina* is distinctly two-topped. Species richness increases from low pH up to a maximum between 6.5 and 7.0, then decreases again. This supports the view that the highest alpha diversity, and hence the highest niche capacity, is most often encountered in the middle parts of the gradients (Whittaker 1969, Grime 1973), while the species number decreases towards the gradient extremes.

Austin (1987) presents data on the distribution of Australian *Eucalyptus* species relative to a gradient in temperature, while restricting variation along other gradients. Thus he reduces the interference of partly correlated gradients. His results indicate that symmetric response curves are not universal, in fact many species show skewed curves. Species modes are distributed more or less randomly rather than systematically along the gradients. The distribution of species modes and lower and upper limits for species ranges along the gradient are confounded by species richness; the higher species richness, the higher number of modes and limits.

Minchin (1989a) presents data from Tasmania, Australia, on species distributions relative to complex-gradients in soil moisture and elevation (altitude). About one half of the species (45 %) showed symmetric, unimodal response surfaces relative to the two gradients, 33 % showed response surfaces that were skewed in at least one direction, and 22 % of the response surfaces were complex. The hypotheses of the Gaussian model that modes of minor species are scattered at random while modes of major species are more regularly spaced, are not supported by the data, except for the distribution of minor species' modes for each structural plant group (trees, shrubs, graminoids, pteridophytes, herbs). Modes of major species were randomly distributed. Modal abundances (proposition 3 of the Gaussian model) were lognormally or lograndomly distributed for each structural group, but not for all species taken together. Alpha diversity (species richness) for each structural group was unimodal along the gradient, but total alpha diversity showed a complex pattern.

R. Økland (1989a) provides evidence from mires in inner Østfold and adjacent part of Akershus for unimodal species response curves on a geographical scale, as he establishes a strong correlation between local abundance of species and the position of the investigated area relative to the range limits of the species. Extension of the Gaussian model to biogeographic scales is suggested and discussed by Brown (1984).

R. Økland (1986b, 1989b) studied the distribution of mire species relative to a gradient in three-year median distance from the surface of the bottom layer to the water

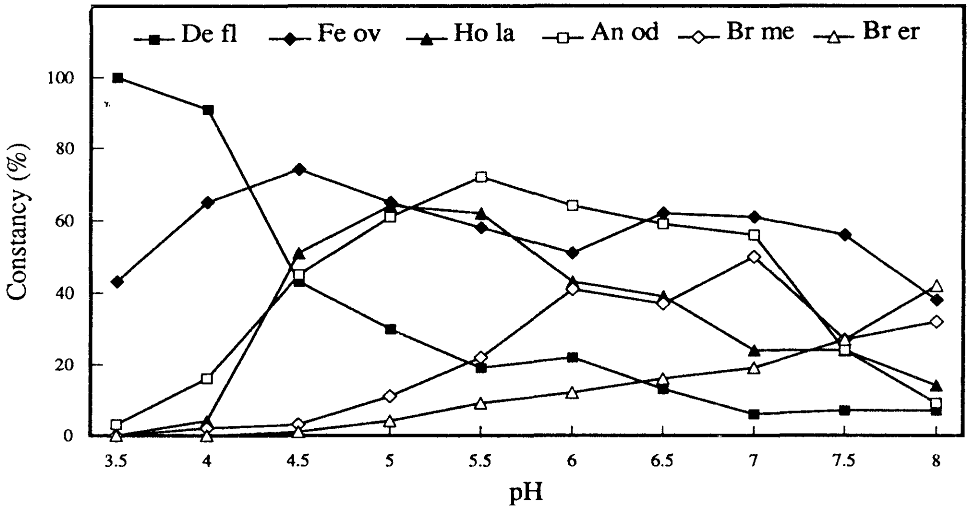


Fig. 24. Ecological response curves for six selected grassland species in C England relative to a gradient in pH. Data from Grime and Lloyd (1973), after Austin (1980). Each step along the gradient represents 0.5 pH units. The upper limit of each interval is shown on the abscissa. Percent constancy of each species in the set of samples in the pH interval is scored on the ordinate. De fl - *Deschampsia flexuosa*. Fe ov - *Festuca ovina*. Ho la - *Holcus lanatus*. An od - *Anthoxanthum odoratum*. Br me - *Briza media*. Br er - Bromus erectus.

table. A total of 699 sample plots, randomly distributed on the mire Northern Kisselbergmosen, Rødenes, Østfold, SE Norway, were included in the study. For each 2-cm-interval along the water table gradient, an importance value was calculated for each species, based on species cover and constancy in the sample plots. Fig. 25 shows the ecological response curves for six major *Sphagnum* species along this gradient. Symmetrical curves are exceptions, many curves are skewed to the right. Five of the curves are unimodal, the last (*Sphagnum magellanicum*) is weakly trimodal. The ecology of *Sphagnum magellanicum* has been discussed by several authors (e.g., Malmer 1962), and it cannot be excluded that the species consists of more ecotypes (or taxa), as demonstrated for *Sphagnum imbricatum*, a species with a similar, bimodal response, by Flatberg (1984, 1986). R. Økland (1986b) discussed the source of skewness in the response curves, and demonstrated that the skewness was strongly related to trends in ß diversity (species turnover) along the gradient. It is apparent from Fig. 25 that the species turnover is much greater in the left, than in the right part of the figures. The species turnover per cm along the gradient is constant, and large, for 0 cm < depth to the water table < 10 cm, then abruptly drops (cf. p. 34, Figs 48-49). If the gradient is rescaled in units of compositional turnover, the skewed curves largely turned into symmetric ones, but all skewness in the curves is not removed.

Further evidence is provided by the distribution of species along the distance to the water table gradient in virgin bog at Rønnåsmyra (the standard example). Figs 26-45 show response curves for ten species relative to this gradient, scaled in cm (Figs 26-35) and scaled in units of compositional turnover (Figs 36-45). Although the number of samples,

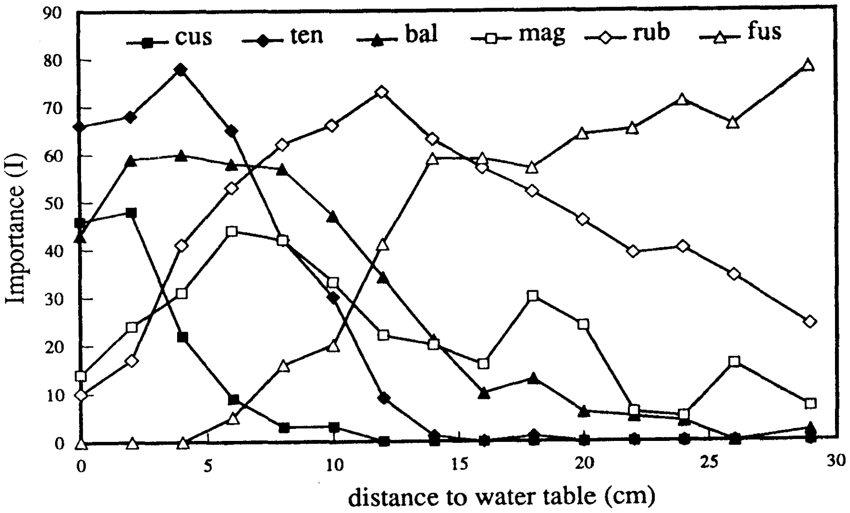
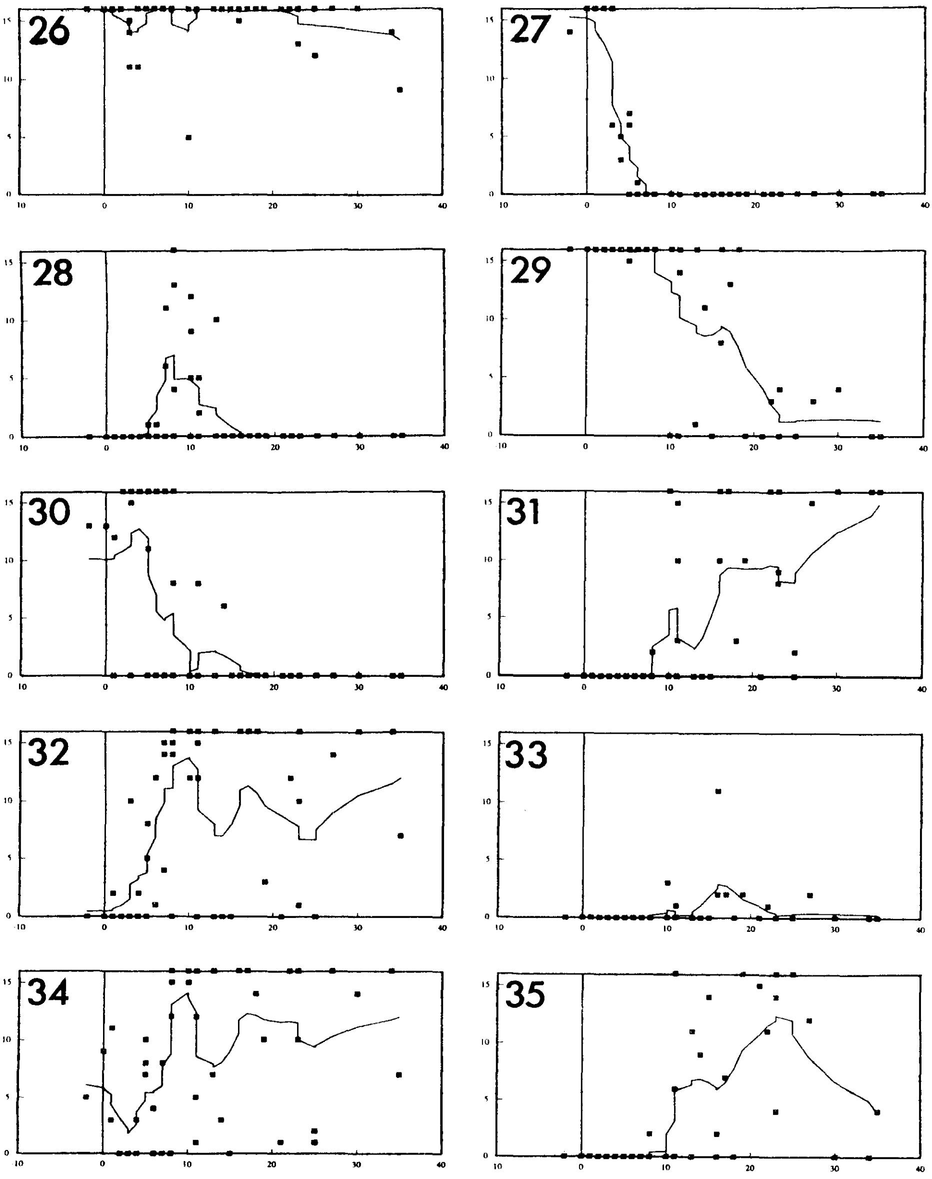


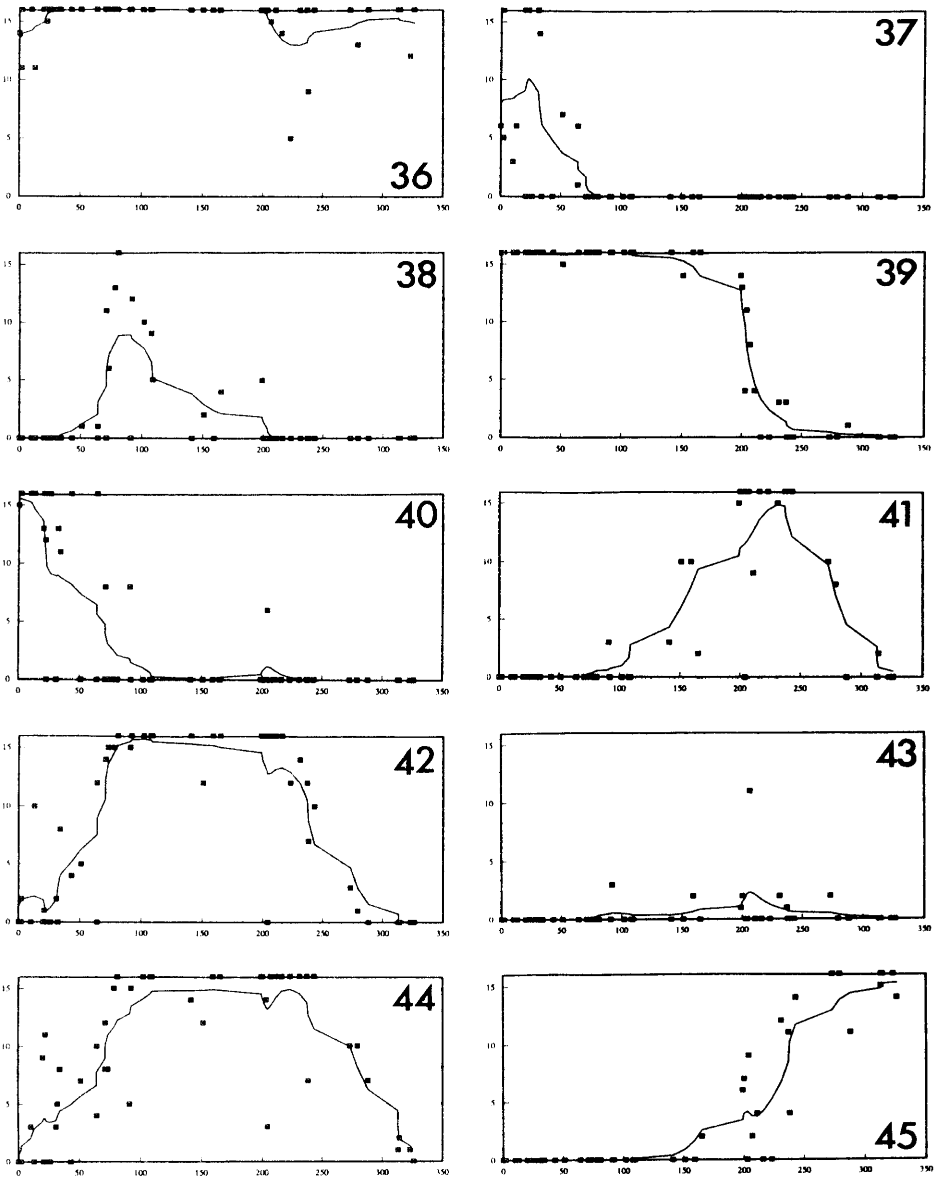
Fig. 25. Ecological response curves for six *Sphagnum* species on the mire N Kisselbergmosen, Rødenes, SE Norway, relative to a gradient in distance to the water table. Data from R. Økland (1989b: Tab. 7). Abscissa represents 2 cm-intervals for three year median distance from the surface of the bottom layer (moss carpet) to the water table. Importance of each species in each interval, scored on a 0-100 scale, is expressed on the ordinate. Importance values are calculated by combining constancy and mean cover in all sample plots in the interval in question. cus - *Sphagnum cuspidatum*. ten - *Sphagnum tenellum*. bal - *Sphagnum balticum*. mag - *Sphagnum magellanicum*. rub - *Sphagnum rubellum*. fus - *Sphagnum fuscum*.

51, is relatively low, the figures illustrate the points made above, in particular the occurrence of skewness that is partly removed by rescaling in units of species turnover. Irregularities may be due to sparse material. Several curve shapes may be distinguished: (1) Flat-topped (**platycurtic**) curves or curve parts are frequently appearing. The most pronounced example is *Andromeda polifolia* (Figs 26, 36), displaying a flat-topped curve (constant value along the gradient). (This is partly a result of the scale used for quantification of abundance, frequency in subplots, giving high frequency of the maximum possible abundance in the material, cf. pp. 86-87). Flat-topped curves are also observed for *Sphagnum balticum* (Figs 29, 39) and *Sphagnum rubellum* (Figs 32, 42). (2) Almost perfect **unimodal** curves are shown for *Scirpus cespitosus* (Figs 28, 38) and *Kurzia pauciflora* (Figs 33, 43). Truncated, possibly unimodal response curves, with modes near or just outside of the sampled portion of the gradient, are shown for *Rhynchospora alba* (Figs 27, 37) and *Sphagnum cuspidatum* (Figs 30, 40), both with modes near the wet end of the gradient, and *Sphagnum fuscum* (Fig. 31, 41) and *Cladonia rangiferina* (Fig. 35, 45), both with modes near the dry end of the gradient. (3) An irregular pattern is shown by *Mylia anomala* (Figs 34, 44).

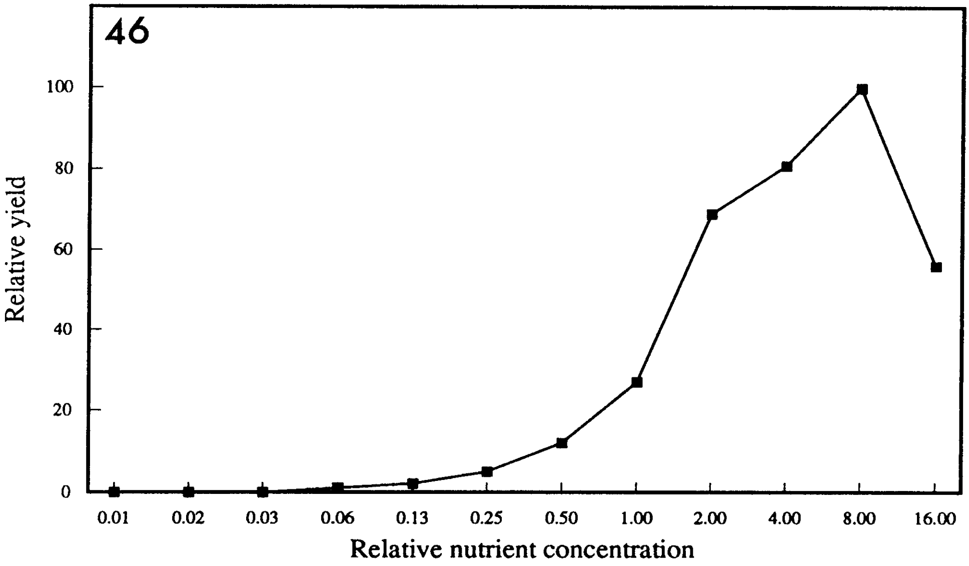
Experimental data. Several experimental studies provide data on physiological response curves relative to ecological gradients. We will consider the results provided by one of these studies in some detail. Austin & Austin (1980) grew six grass species, singly and in combinations, in a general nutrient solution of different concentrations, thus

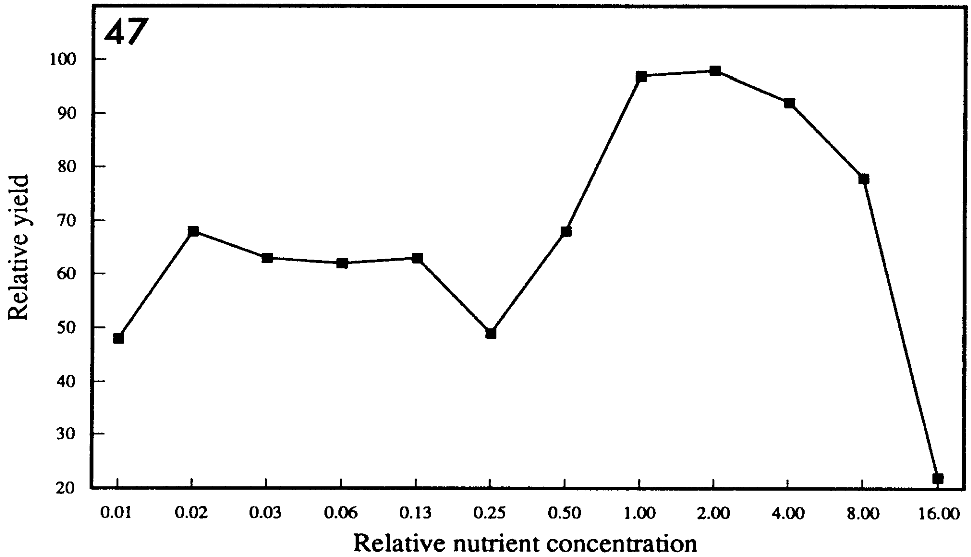


Figs. 26-35. Ecological response curves for ten species along the gradient in distance to the water table at Rønnåsmyra, Grue, SE Norway. Curve is fitted to observations by applying a moving averaging smoothening procedure twice. Frequency in subplots is expressed on the ordinate. Fig. 26. *Andromeda polifolia*. Fig. 27. *Rhynchospora alba*. Fig. 28. *Scirpus cespitosus*. Fig. 29. *Sphagnum balticum*. Fig. 30. *Sphagnum cuspidatum*. Fig. 31. *Sphagnum fuscus*. Fig. 32. *Sphagnum rubellum*. Fig. 33. *Kurzia pauciflora*. Fig. 34. *Mylia anomala*. Fig. 35. *Cladonia rangiferina*.



Figs. 36-45. Ecological response curves for ten species along the gradient in distance to the water table at Rønnåsmyra, Grue, SE Norway, rescaled by detrended correspondence analysis (DCA) in units of standard deviation of species turnover (S.D. units). Curve is fitted to observations by applying a moving averaging smoothening procedure twice. Frequency in subplots is expressed on the ordinate. Fig. 36. *Andromeda polifolia*. Fig. 37. *Rhynchospora alba*. Fig. 38. *Scirpus cespitosus*. Fig. 39. *Sphagnum balticum*. Fig. 40. *Sphagnum cuspidatum*. Fig. 41. *Sphagnum fuscum*. Fig. 42. *Sphagnum rubellum*. Fig. 43. *Kurzia pauciflora*. Fig. 44. *Mylia anomala*. Fig. 45. *Cladonia rangiferina*.





Figs 46-47. Physiological response curves for *Arrhenatherum elatius* along an experimental nutrient gradient (concentration of a general nutrient solution). Fig. 46. Response (ordinate) scored as yield (biomass) in percentage of maximal yield for this species in any of the nutrient solutions. Fig. 47. Response scaled as relative nutrient utilization values, that is, the yield as percentage of the maximal yield for any of the nine tested species in any of the nutrient solutions.

constructing a nutrient gradient. Physiological response was measured as dry weight of ten shoots grown in a pot without influence from other species. Fig. 46 shows a typical response curve; position along the gradient is expressed on a logarithmic scale. Response is low at low solute concentration, and increases until a maximum is reached at relatively high concentrations. When concentrations are increased even further, the response drops rapidly due to toxic effects. If, however, species response is scored as the yield as fraction of maximum yield in this solution by any of the investigated species (relative nutrient utilization values; Austin 1980), the shape of response curves change (Fig. 47). The difference between Figs 46 and 47 is due to the variation in carrying capacity (α diversity) along the gradient. This variation is not taken into account in Fig. 46, but is corrected for in Fig. 47. When response is expressed as relative nutrient utilization values, a more realistic estimate of the species' abitity to exploit an environment is obtained. Austin & Austin (1980) compared physiological response curves based on the two ways of scaling with experimental ecological response curves obtained by growing the species in multi-species mixtures. They demonstrated significant differences in curve shapes when ecological response (measured as proportion of mixture) was compared to physiological response measured as biomass. These differences included displacement of ecological and physiological optima along the gradient. If, however, the physiological response was measured as relative utilization values, ecological and physiological optima coincided to a much greater extent. This supports the hypothesis forwarded by Ernst (1978) that given comparable measurements of ecological and physiological response, ecological and physiological optima should coincide because ecological optima are not displaced relative to physiological optima by competition.

Assessment. Since Gauch & Whittaker (1972a) forwarded the Gaussian model, it has gained enormous popularity among ecologists. Austin (1976a) characterized the ecologists' attitude to the Gaussian model the following way: "Everyone believes in it. For the field ecologists fancy that it is a theoretical principle and the theoretical ecologists that it is a field observation." Recent research on species responses to ecological gradients has shown that the Gaussian model is at best an oversimplification. It is, however, no doubt that a large share of the species show unimodal response curves with respect to ecological gradients, provided that some conditions are satisfied (R. Økland 1986b, cf. also Austin et al. 1984): (1) The response is with respect to a dominant ecological factor, (2) the range of variation (ß diversity) studied is sufficient, (3) the distribution of sample plots is adequate, and (4) the gradient is scaled in units of compositional turnover (ß diversity units). R. Økland (1986b) illustrate these points by examples from the mire N. Kisselbergmosen (see pp. 33-35). The gradient in distance to the water table is a dominant gradient spanning a considerable range in vegetational variation. Several examples show that weak bimodality can be produced by insufficient sampling, that flat-topped curves may be observed for species for which the gradient studied is not important (at least in the flat segments of the curves), and that skewed curves are turned into symmetric ones by excluding variation along partly correlated gradients, and by scaling gradients in units of compositional turnover. R. Økland (1986b) gives the following explanation for the prevalence of symmetric, unimodal curves relative to gradients scaled in units of compositional turnover: "(1) the co-ordinated variation in species abundances along ecological gradients (Poore 1956), (2) the influence of the most important ecological gradients on nearly all species (cf. Whittaker 1956, 1967), mostly also in a similar way, resulting in synchronous steep or flat response curve segments, and (3), the existence of zones along a gradient differing with respect to beta diversity; probably the most important reason for skewness of response curves relative to a scaling in a physical or chemical parameter."

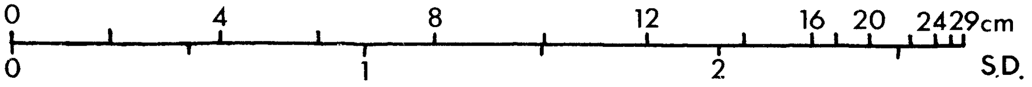
Thus we may conclude that the Gaussian model is not strictly applicable to vegetation, but that a unimodal response model is a realistic generalization, provided that the conditions given above are satisfied (also see ter Braak 1987e). Furthermore, there seems to be a general trend in the variation in carrying capacity along gradients; lower near extremes, higher in the middle portions. Further investigations are needed to know whether, and in case how, species modes are distributed along gradients, species maximum values are distributed, etc. (cf. Minchin 1987b, 1989a).

SCALING OF ECOLOGICAL GRADIENTS

Arguments in favour of scaling in units of compositional turnover

Two principally different approaches to scaling of ecological gradients are available (M. Wilson & Mohler 1983, R. Økland 1986a): (1) in terms of a physical or chemical parameter, e.g., nutrient content, water-level, or incoming radiation, and (2) in units of compositional turnover (ß diversity units). R. Økland (1986a: 653) gives the following arguments in favour of the second approach to scaling: "The use of physical paramaters for scaling of ecological gradients has serious disadvantages. Ecological gradients are rarely made up by one factor, but should be conceived as complex-gradients (Whittaker 1967, R. Økland & Bendiksen 1985). Then no single physical parameter (or combination or transformation of parameters) will account for all biological variation. If, however, variation along a gradient is paralleled by a single physical parameter, the biological responses are mostly too complex to be represented by simple transformations of this parameter. Thus I agree with the view of M. Wilson & Mohler (1983) that "compositional turnover is the essence of ecological gradients, and that environmental change is ecologically significant primarily to the extent that it influences the relative abundances of species." Consequently, gradients should be scaled in units of compositional turnover for the calculation of ecological distance."

Wartenberg et al. (1987) and Minchin (1989a) take the opposite view, stating that all scalings are arbitrary. The choice among different approaches for scaling in units of compositional turnover may be somewhat arbitrary, but in my opinion, compositional turnover as the essence of ecological gradients can hardly be challenged. An example from the mire N. Kisselbergmosen (R. Økland 1986b, 1990a) most clearly illustrates this point. The response of species to the gradient in three year median distance to the water table has been considered in an earlier section (pp. 26-28, Fig. 25). Species importance values were calculated for all species and 2 cm-intervals along the gradient (0-29 cm). The gradient was rescaled in S.D. units (units of compositional turnover, see below), and the mean compositional turnover at each point along the gradient was calculated (Figs 48-49). Fig. 48 shows that the upper half of the cm-scaled gradient only comprised one fifth of the total ß diversity. Fig. 49 shows that the rate of compositional turnover was constant from 0-12 cm, then dropped abruptly from 12 to 16 cm, remained nearly constant to 22 cm, and again dropped slightly towards the upper end of the gradient. The reason for the differences between the two scalings are evident from the way the water influences the mire species. Median depth to the water table, that is the most frequently occurring depth, is strongly correlated with maximum water tables (R. Økland 1989b). The difference between the median and maximum depths at N. Kisselbergmosen amounted to 8-10 cm (R. Økland 1989b). Thus the 10 cm median depth to the water table, where the drop in compositional



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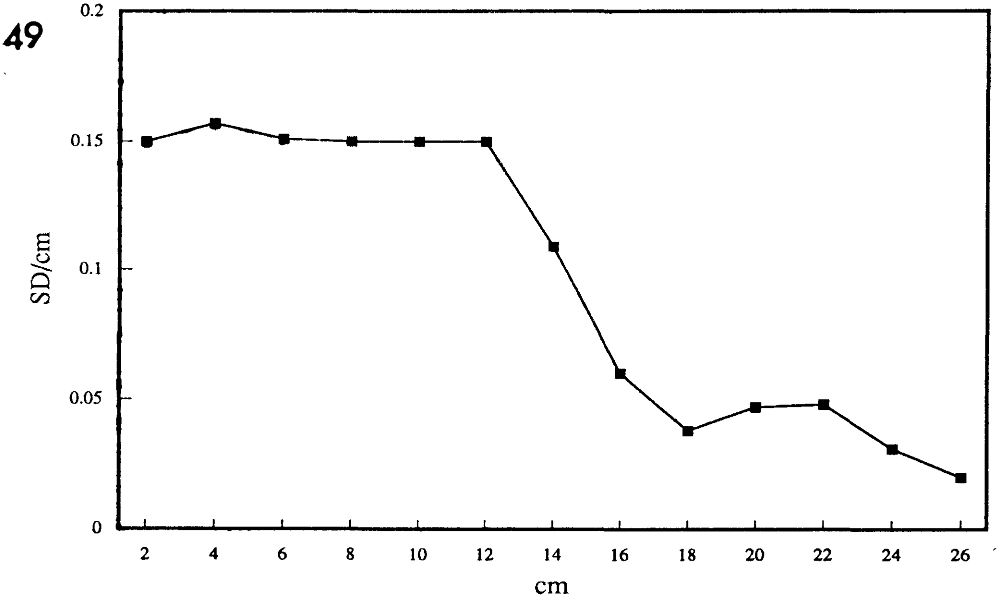


Figs 48-49. Comparison of two scalings of a gradient in median distance to the water table at the mire N Kisselbergmosen, Rødenes, SE Norway (after R. Økland 1986b). Fig. 48. Position of 2 cm-intervals along the gradient scaled in units of compositional turnover (S.D. units). Fig. 49. Mean compositional turnover (in S.D. units/cm) at each point along the gradient.

turnover begins, closely corresponds to the level of the maximum water table, that is the upper limit for inundation of the bottom layer. This is the limit between hollows and hummocks on the mire. Above this limit, there are always aerobic conditions in the peat, and the vascular plants mostly have mycorrhiza and lack root aerenchyma (Metsävainio 1931, Sjörs 1948). Below the level corresponding to a 10 cm median depth to the water table, small vertical differences result in considerable differences in duration of waterlogging and the periods of anaerobic conditions in the peat. Consequently, small vertical differences must be expected to have greater effects on plants in hollows than in hummocks. Water acts directly on the species below the 10 cm level, above this level differences in depth to the water table influences the plants indirectly by affecting water availability. The trends in ß diversity along the water table gradient is due to the existence of zones along the gradients, differing with respect to mechanism and intensity of influence of the ecological parameter on the plants. Clearly, scaling in units of compositional turnover is the more meaningful way of scaling in this particular case.

Measures of compositional turnover

Several measures of compositional turnover, or ß diversity, have been proposed. We will consider four such measures; of which the S.D. units in somewhat more detail.

(1) *S.D. units*. Gauch & Whittaker (1972a) proposed to use the average standard deviation of the species' response curves (Fig. 23) as a unit of ß diversity related to the Gaussian model of vegetation. This unit was termed the *S.D. (standard deviation) unit*. An example of a gradient scaled in S.D. units is the gradient in median distance to the water table on N. Kisselbergmosen referred to above (cf. Figs 48-49). The total compositional turnover along this gradient amounts to 2.67 S.D. units. Assuming validity of the Gaussian model, the S.D. units have a very simple relationship to species turnover along gradients (Hill 1979a, Hill & Gauch 1980, Gauch 1982a): an average species turns up, reaches its optimum (mode) and disappears within 4 S.D. along the gradient (6 S.D. according to Minchin 1987b). A rescaling of gradients in S.D. units is provided by the ordination method detrended correspondence analysis (DCA, see pp. 148-155), but the interpretation of the S.D. units in terms of the Gaussian model is only strictly valid when all species show Gaussian response curves. A thorough treatment of the properties of this nonlinear rescaling procedure of DCA and interpretation of the resulting S.D. units, is provided on pp. 149-150 and 153. So far, we can use the interpretation in terms of the Gaussian response curve as a very rough generalization. Advantages of the S.D. unit are the simple interpretation, and the relative robustness of DCA as a method for rescaling single gradients (R. Økland 1986a, p. 153). Disadvantages are the inaccuracy of DCA for gradient length estimation when ß diversity is low (Oksanen 1983), and the potential problems posed by deviations from the unimodal response model.

(2) *Half-changes*. Whittaker (1960) defined a measure of compositional turnover, the half-change, to be equal to an ecological distance corresponding to a floristic similarity between two samples half of the similarity between two replicate samples. We will consider measures of relationships between sample plots (including sample similarity) in a later section (pp. 105-112), but may define sample similarity as the similarity in floristic composition between samples. Whittaker used PS (percentage similarity, cf. p. 109) for half-change estimation. Floristic similarity measures range from 0 (the samples have no species in common) to 1 (the samples have identical species composition and identical amounts of all species). **Replicate samples** are taken from exactly the same position along the gradient(s) in question. Thus the ecological conditions in replicate samples are identical. However, such samples will only in exceptional cases (extremely species-poor vegetation) have identical species composition. The reason for this apparent discrepancy is variation in species amounts not co-ordinated with variation in the amounts of other species, often termed noise (the reason for such variation will be dealt with later, see pp. 96-97). The similarity of replicate samples, often termed the **internal association** (Bray & Curtis 1957), is often taken as the highest similarity value between any of the sample plots in a data set. There is, however, no generally acceptable way of estimating the internal association (cf. pp. 110, 112). Calculation of beta diversity in half-changes is based on the assumption that sample similarity (e.g., measured as percentage similarity) has a negative exponential relationship to ecological distance as measured in half-changes (Whittaker 1960, Gauch 1973a). This assumption can, however, be questioned (see M. Wilson & Mohler 1983). The formula for calculation of beta diversity in half-changes is as follows:

$$\mathrm{HC}\ (a,b) = \{\ln\ [\mathrm{IA}] - \ln\ [\mathrm{PS}\ (a,b)]\}\ /\ \ln 2 \qquad (5)$$

where IA is the internal association, PS (a,b) is percentage similarity between sample plots a and b (the end-points of the gradient). The appropriateness of the half-change as a measure of compositional turnover depends on the suitability of the measure of similarity as a measure of ecological distance. The serious conceptual weaknesses of the approach will be demonstrated later (pp. 110-112).

Minchin (1989b) presents another approach to calculation of HC units by a regression of ß diversity (in HC units) on percentage dissimilarity.

(3) *Gleasons*. In an attempt to correct the half-change measure for some of its weaknesses, M. Wilson and Mohler (1983) proposed a second unit of compositional turnover, the gleason. This unit is defined as "the amount of compositional turnover which would occur if all changes were concentrated into a single species whose abundance changed 100 %" (M. Wilson & Mohler 1983: 131). Computationally, this approach is not very different from the half-change approach, and it shares many of the conceptual weaknesses of the latter.

t is strongly vulnerable to noise in the data.

(4) *R units*. Minchin (1987b) proposed the use of the mean species range along a gradient, the R unit, as a measure of β diversity. This measure is conceptually very simple, but suffers from lack of robustness because of its monothetic nature. Being based on the occurrence of species at the ends of their ranges, the R unit will be strongly affected by the occasional presences in habitats outside the normal range of the species, for instance by single individuals which will not etablish permanently. Furthermore, the ranges of species will inevitably increase with increasing sample plot number along the gradient, as the probability of finding a species outside its proper range then increases. Hence, the length of a gradient in R units is expected to decrease with increasing number of sample plots.

Comparison of β diversity measures. Gauch (1973b) showed that if data had no noise (un-coordinated variation; see pp. 96-97), that is, when all species responded smoothly to the gradients, 1 HC unit is equivalent to 1.349 S.D. units. Under field conditions, this factor is considered to be close to 1 (Hill 1979a). Minchin (1987b) considered "the effective range of a Gaussian response curve" to be approximately 6 S.D. units, thus indicating that 1 R unit equals 6 S.D. units. No generally valid equations for interconversion of β diversity measures exists, as there is no common conceptual basis for the different measures.

The half-change and gleason units have serious disadvantages as they involve the dubious concept of internal association, and are based on a poorly documented relationship between sample similarity and β diversity. The half-change approach is burdened with the problem that sample similarity is close to zero when samples are separated by more than 4-6 S.D. along a gradient (have no or very few species in common). Beyond this β diversity level the number of half-changes cannot be measured by formula (5). This problem can be circumvented by segmentation of the gradient. The gleason unit has almost not been used. Being based on summation of compositional turnover between neighbouring samples along the gradient, it will accumulate the problems involved in estimation of the internal association. The R and S.D. units are likely to be more robust estimates of β diversity, each with weaknesses mentioned above. The S.D. unit has been chosen throughout this book at the measure of beta diversity because of its simplicity of interpretation. The choice is supported by the observations that the responses of species to the major gradients in boreal and alpine ecosystems (alpine heath, boreal forest, mire) is largely unimodal (R. Økland 1986b, 1989b, unpubl., cf. pp. 32-33).

THE CONTINUUM CONTROVERSY

The two extreme standpoints

Throughout this century much of the debate over the nature of vegetation has centered upon the question of continuity or discontinuity of vegetation stands. This question is, in fact, only one of the questions relevant to discussions of models for species-gradient relationships. The high importance attributed to this question, and its importance for the historical development of traditions in descriptive vegetation ecology, motivate a brief reconsideration of the continuum controversy.

The concept of the plant association as a superorganism analogous to the species was developed more or less independently several times during the 1910s and 1920s. Phytosociologists central to this development were the American F.E. Clements and the Swede G.E Du Rietz. They forwarded their views in several influential monographs (e.g., Clements 1916, Du Rietz et al. 1918, 1920, Du Rietz 1921). Their views were, however, strongly critizised by their contemporaries, and eventually given up. The associated theory of a discontinuous vegetation was, however, maintained. Du Rietz (1921: 189, translated) expressed this view as follows: "... the limits between the associations, even when the environmental change is fully continuous, never show ... continuous intergradation, to the contrary they are astonishingly sharp and clearly visible."

The two contrasting views developing during the 1920s (and debated vigourously up to the 1980s) can be formulated as follows (Whittaker 1962):

(1) Vegetation as a "*complex population pattern*" (Whittaker 1956, 1967) in which

species are distributed individualistically (Gleason 1926, Ramensky 1930), with population centres scattered along gradients ("*the individualistic association concept*"; Austin 1985). Vegetational variation along continuous environmental gradients is continuous ("*the continuum concept of vegetation*"; Curtis & McIntosh 1951, McIntosh 1967), although some relative discontinuities are allowed to occur. The mechanism responsible for this pattern is the evolution of species towards reduced competition (Whittaker 1956, Whittaker et al. 1973).

(2) The "*community-unit theory*" (Whittaker 1956, 1962). Natural groups of species with more or less coincident patterns of distribution occur (Du Rietz et al. 1920, Du Rietz 1921). More or less pronounced discontinuities occur between vegetation stands, also along continuous environmental gradients. The mechanisms responsible for the scattering of species distributions is the co-adaptation of plant species to environmental factors and to each other, eventually forming an integrated plant community (cf. Du Rietz et al. 1920).

These two concepts are extremes, allowing for the full range of intermediate standpoints. The positions of scientists representing different phytosociological traditions are reviewed by Whittaker (1962).

Evidence on the nature of borderlines

Each of the two theories on the nature of vegetation consists of a set of assumptions. These are not necessarily linked. For instance, the continuum concept of vegetation, that is the principle of continuous vegetational variation along continuous environmental gradients, does not per se imply individuality of species (Goodall 1963). To the contrary, a discontinuous vegetation is more or less dependent on co-ordinated species boundaries and hence not possible to connect with species individuality.

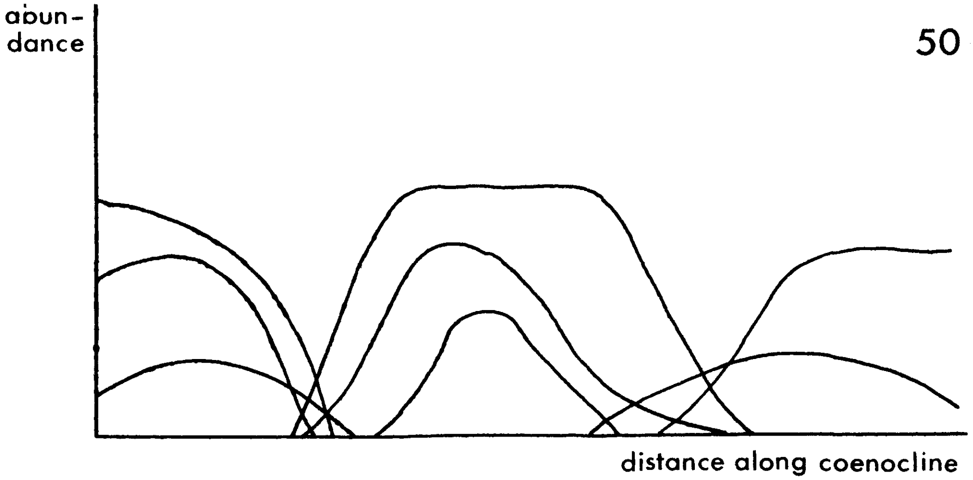
Austin (1985, 1987) states that the continuum concept still awaits verification by reliable statistical tests. With the exception of the formulation of the Gaussian model of vegetation as a number of propositions by Gauch & Whittaker (1972a)(see p. 25), the two theories have not been explicitely formulated. The Gaussian model is in fact an extension and a quantitative expression of the individualistic continuum, and a number of the propositions are possible to test by statistical methods.

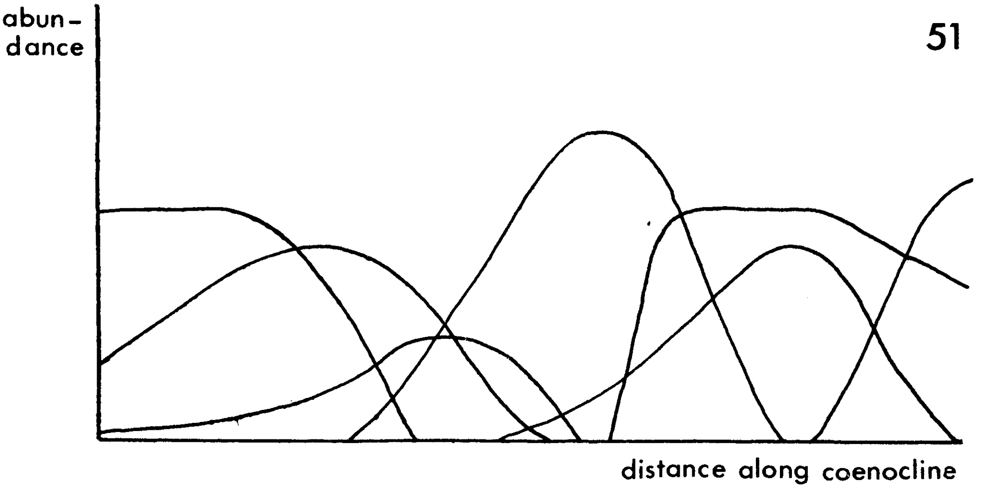
An attempt at such a test was performed by Shipley and Keddy (1987), who reformulated the two theories as hypotheses concerning the distribution of species boundaries along gradients (Shipley & Keddy 1987: 48):

"The individualistic hypothesis states that: (i) the average number of boundaries (both upper and lower) in each interval of the gradient should be equal except for random variation about the mean; (ii) the number of upper boundaries per interval of the gradient should be independent of the number of lower boundaries.

The community-unit hypothesis states that: (i) there should be significantly more boundaries (both upper and lower) in some intervals of the gradient than in others, i.e. boundaries are clustered; (ii) the number of upper and lower boundaries per interval should increase and decrease together along the gradient."

Figs 50-51 show species response curves with respect to a hypothetical environmental gradient under each hypothesis. In order to test the hypotheses, Shipley and Keddy used data on vascular plant distributions in transects from a lake to the adjacent lakeshore marsh in a Canadan study site. For each 5 cm-interval in height relative to "standard water level" in the lake, and each of thirteen belt transects, the number of species distributional limits (termed boundaries by Shipley and Keddy) were noted. The statistical test of proposition (i) showed significantly more boundaries in some intervals than others along the gradient,





Figs 50-51. Predicted species response curves relative to a hypothetical environmental gradient under the two community concepts. Fig. 50. The individualistic continuum concept. Fig. 51. The community-unit concept.

interpreted in favour of the community-unit hypothesis. The test of proposition (ii) showed independence of lower and upper boundaries, in favour of the individualistic continuum. Thus Shipley and Keddy concluded that none of the theories accounted fully for the patterns observed.

The "tests" performed by Shipley and Keddy (1987) are quoted to demonstrate the difficulties involved in formal statistical testing of the individualistic and community-unit hypotheses. In fact, the cited tests are completely invalidated by the lack of attention to variation in species richness and species turnover along the environmental gradient. I have previously demonstrated that the effect of water on the plants changes along with changes in depth to the water table in a mire, and that this leads to considerable variation in compositional turnover along the gradient (pp. 33-34; Fig. 49). Variation in beta diversity is also likely to occur along the gradient used by Shipley and Keddy for their tests. In fact, such a variation seems probable from the illustration of species distributions presented (Shipley & Keddy: Fig. 4). Segments with high species turnover are likely to contain many boundaries. Furthermore, the number of boundaries are likely to increase with increasing species richness. Thus such "tests" are inconclusive in the absence of data on α and ß diversity (cf. Austin 1987). The test of the second proposition is also likely to be confounded by differences in ß diversity along the gradient, and is likely to be inconclusive as well.

Having demonstrated that formal statistical testing of the two hypotheses is very difficult (and still not satisfactorily done, as pointed out by Austin 1985), we have to consider the huge pile of circumstantial evidence available. Circumstantial evidence is of two major kinds: (1) species distributions along gradients, and (2) observations of similarity and continuity of vegetation stands. We will consider these two points without going into details. Extensive evaluation of the circumstantial evidence has been carried out by Daubenmire (1966), McIntosh (1967), Austin (1985) and others. R. Økland & Bendiksen (1985) give a survey of relevant evidence from Fennoscandia.

(1) *Species distributions.* Belt transects provide material on species distributions along gradients. Examples are the transects from the standard example from Rønnåsmyra (Tabs 1-2). From the tables it can be seen that the changes in species composition along the transects are gradual, and that the sudden changes in species composition are mostly due to abrupt changes in depth to the water table. Results indicating scattering of species limits along transects and individuality of species are further provided by Gjærevoll (1956) and Dahl (1957) from Norwegian mountain vegetation.

(2) *Similarity and continuity of vegetation stands.* Evidence on similarity of stands is provided by studies using a randomized sampling procedure. One example, from mire vegetation at N. Kisselbergmosen, is provided by R. Økland (1990a). A fully continuous scattering of sample plots can be observed in ordination diagrams. Similar results are provided by ordination of sample plots from a beech forest (Fritzøehusparken, Brunlanes, SE Norway) by T. Økland (1988). Inference of continuity of vegetation stands must be based on material from transects along gradients. However, the interpretation of transect data is subjective, and the same transect may be interpreted as showing pronounced discontinuities and continuous intergradation, depending on which aspects of the variation are emphasized. For example, a few species may dominate one part of the gradient each, with none or some overlap between them, while the remaining species (the vast majority) appear randomly distributed.

Assessment

A considerable amount of circumstantial evidence has accumulated in favour of the continuum concept of vegetation, that is continuous variation in vegetation along continuous environmental gradients. During the last two decades, the continuum theory has been accepted by concensus among ecologists belonging to different schools (cf. Westhoff & van der Maarel 1978, Gauch 1982a). A close examination of discontinuities in the nature mostly reveals an environmental discontinuity or a very steep environmental gradient, as occurring on lake shores, along alpine snow cover gradients, etc. In some cases, apparent vegetational discontinuities occur in species-poor vegetation with strong competition between the dominant species (e.g. in shore zonations). In most cases, however, the apparent discontinuity between dominants is not followed by coincident borders of subordinate species. The individuality of species is, however, not unproblematic. There is little evidence supporting a more regular spacing of modes of major species along the gradients, claimed to indicate that these species to some extent influence each other (cf. Gauch & Whittaker 1972a, Gauch 1982a). Skewed or complex species responses to environmental gradients can also indicate species interactions (cf. Minchin 1989a). Furthermore, numerous examples or parasitism, allelopathy and mutualism contradict the concept of species individuality. However, in most cases it seems that species react to other species as a response to structure (shading etc.) rather than as a response to specific properties.

The present state of the art is summarized by Harper (1977: 748): "There is nothing in the theory of evolution in natural selection that supposes any way in which "the species" reacts to or responds to events other than as the collective behaviour of its individuals. Moreover, there is nothing in the process of evolution that should lead us to imagine some community goal, nothing to suggest that the collective evolution of the populations in a community is towards some ideal - community structure, diversity, productivity, efficiency, information content, entropic level."

Austin and T.M. Smith (1989) claim that the circumstantial evidence forwarded for the continuum concept of vegetation is "less than convincing". They point out that the continuum refers to continuity in an abstract ecological space, while the vegetation (often termed "community" in ecological literature) is a spatial concept dependent on landscape pattern. They suggest a reformulation of the continuum concept as eight testable hypotheses of the relationship of the response of vegetation to environmental gradients. Hopefully, future research will add considerably to our understanding of vegetation-environment relationships. It is more than likely, then, that the assumption of a largely continuous variation in vegetation along continuous environmental gradients, will be confirmed. Such tests will probably improve our understanding of the processes that determine niche relationships among species and that give rise to the observed continuum in vegetational variation.

THE NICHE CONCEPT

Definitions

The concept of the **niche** has played a fundamental role in ecology over the last 30 years. The concept is an abstract one, in its classical definition by Hutchinson (1957) being the set of variables in some way having impact on an organism, a population of organisms, or a set of populations, e.g. a species. Begon et al. (1986) give the following characterization of the niche: "It is an abstract concept that brings together, in a single descriptive term, all of an organism's requirements, i.e. all of the environmental conditions that are necessary for an organism to maintain a viable population, and the amounts of each of the resources that it requires to do so." The niche of a species can be considered in one, two, three or more dimensions by invoking one, two, three or more of the important variables for the species. If we consider each of these variables as a niche dimension, the niche may be conceived as n-dimensional **niche hyperspace** (Hutchinson 1957, Whittaker et al. 1973).

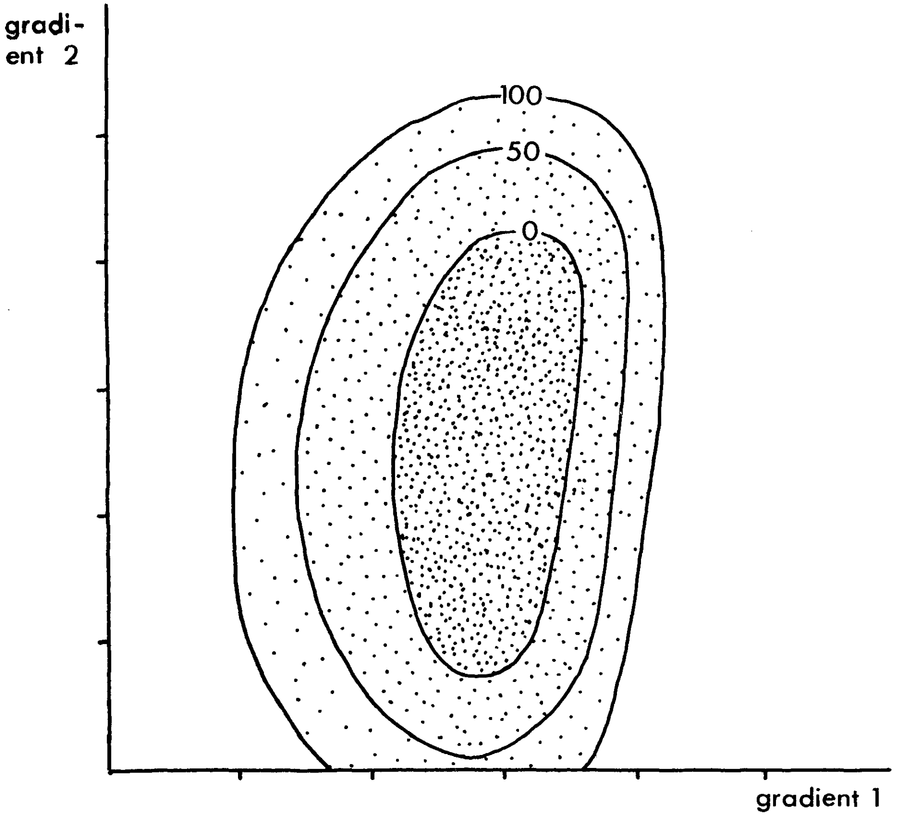


Fig. 52. The niche in two dimensions, indicating critical levels of species performance. Isolines for percentage mortality is shown.

In this space, the probability of occurrence of a species forms a population cloud, dense at centre, sparse at margins (Whittaker et al. 1973). The **fundamental niche** is the part of the niche hyperspace, the intervals along a set of niche dimensions, that the species can potentially occupy, that is, the physiological potentialities of the species. The **realized niche** is the niche of the species under field conditions, also allowing for interactions with other species. The realized niche may be conceived as a multidimensional response surface, enclosing the population cloud.

The concept of **habitat** is used for the site in which the organisms grow. One habitat may thus provide niches for a lot of species due to physical separation of organisms within the habitat (e.g. by layering of vegetation), or due to the occurrence of a set of environmental factors affecting different organisms in different ways, or affecting only some of the organisms.

The axes of the niche hyperspace, the niche dimensions, may be of several kinds, of which the most important for plants are: (1) **Habitat gradients**, that is the set of environmental gradients affecting the organisms. Examples are gradients in temperature, salinity, light, soil moisture, nutrient availability, etc. This is the habitat in the terminology

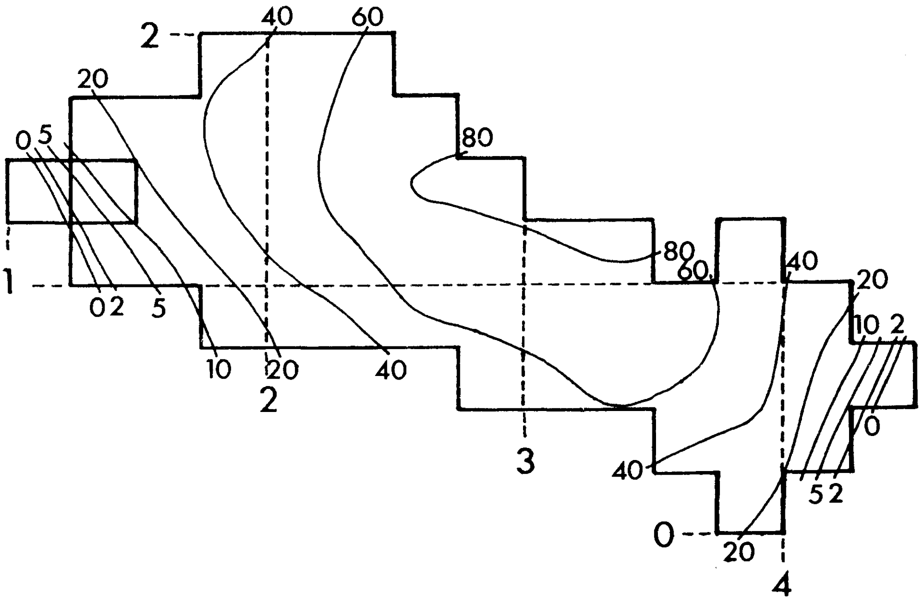


Fig. 53. The habitat niche of *Sphagnum rubellum* at the mire N Kisselbergmosen, Rødenes, SE Norway, relative to complex-gradients in distance to the water table (abscissa) and nutrient availability (ordinate), as summarized by an interpreted DCA ordination (after R. Økland 1990b). Isolines indicate species importance as calculated on a 0-100 scale by combining constancy and cover.

of Whittaker et al. (1973), the **habitat niche** in the terminology of R. Økland (1990b). (2) **Functional relationships**, that is the set of factors affecting the function of the organisms. Examples are the influence of other plants, predators, and competition for pollen vectors. Whittaker et al. (1973) proposed to restrict the use of the term niche to this kind of niche dimensions, but this has not become commonly accepted. Functional niche may be used as an alternative term. (3) **Regeneration niche** (Grubb 1977), that is the set of conditions necessary to allow establishment of an organism (including requirements for effective seed set, characteristics of dispersal in time and space, requirements for germination, establishment etc.) often significantly different from the conditions necessary to provide maintenance of already established individuals. Whittaker et al. (1973) proposed to use the term ecotope for what is here called niche, that is the total relationship of an organism, population or species to its surroundings. (4) **Life form niche** (Cody 1986, Grubb 1986), the life form of a species, reflecting its structural characteristics, the way it survives the most unfavourable season, etc. (5) **Phenological niche** (Grubb 1986), time of year for seedling emergence, photosynthetis, flowering, seed dispersal.

Within the niche hyperspace or some subspace (emphasizing only a few, selected niche dimensions), one may conceive the species' response as a multidimensional response surface. If attention is restricted to the habitat niche of a species, we consider the response curve of this species relative to the environmental gradients in question. This response surface has an optimal position, or mode, that is the combination of conditions making the species reach its maximal performance value. The **optimal niche** is some interval in more dimensions around the mode, in which the species satisfy some performance criteria, e.g., reach a certain importance value, or suffer no mortality. Other critical performance levels may also be defined (Fig. 52), e.g., by ability to regenerate (the regeneration niche will mostly be a part of the total niche, but may invoke new niche dimensions as well). The term realized niche usually refers to the conditions necessary to maintain an established population of the species. Fig. 53 shows the realized habitat niche of *Sphagnum rubellum* at the mire N. Kisselbergmosen, with respect to complex-gradients in depth to the water table and nutrient availability, as summarized by an interpreted DCA ordination. Critical levels of species importance in sample plots, are indicated.

The concept of a **guild**, that is a group of species that exploit the same class of environmental variables in a similar way (Root 1967), is central to niche analysis, as comparison of niche characteristics is particularly relevant within guilds.

Plant and animal ecology have usually focused on different kinds of niche dimensions, indicating differences between the organisms studied, the data sets normally collected, and the research traditions. The niche dimensions most strongly focused in zooecological studies are both of habitat and functional types, while environmental gradients (the habitat type) strongly prevails in plant ecological studies.

Estimation of niche dimensions

The study of niche relationships involves estimation of niche dimensions. The formal way of doing this is by calculating **niche metrics**, that is, indices of **niche breadth** and **niche overlap**. Niche breadth is an expression of how large a part of one or more niche dimensions is occupied by a group of organisms, for instance a species. Niche overlap is an expression of the extent of overlap between to species in niche space.

Niche breadth

Niche breadth is most simply estimated in the unidimensional case. On the basis of a set of sample plots providing presence/absence data for a species at different positions along a gradient (scaled in some way), we want to calculate the fraction of the gradient in which the species occur. One example is the occurrence of a mire species, for instance, *Kurzia pauciflora*, along the depth to the water table gradient on Rønnåsmyra (the standard example), see Fig. 33. This species occurs from 10 to 27 cm along the gradient, and is absent from -2 to 10, and from 27 to 41 cm. A possible measure of niche breadth for this species is the fraction of the total gradient length including the species, that is

$$b_i = 17/43 = 0.395.$$

However, from Fig. 33 we see that the species is not equally abundant in all parts of its realized niche, in fact it shows a more or less Gaussian response to this habitat niche dimension. Thus a more sound way of measuring niche breadth might involve a weighting of each of the intervals containing the species according to the species' importance in that interval. This leads us to the classical equation of Levins (1968) for measurement of niche breadth, later amended by Colwell & Futuyma (1971) and Vitt & Slack (1984). Given a niche dimension k, for instance an environmental gradient, that is divided into n_k categories, and data on the abundance of species i in each category j, I_{ij}, the niche breadth of this species is

$$B_i = [n_k * \mathrm{SUM}_{j=1..nk} (I_{ij}/I_{i.})]^{-2} = I_{i.}^2/(n_k * \mathrm{SUM}_{j=1..nk} I_{ij}^2) \qquad (6)$$

where $I_{i.}$ is the sum of I_{ij} over all n_k categories. The division by n_k, the number of categories, is a scaling operation by which niche breadths is expressed on a 0-1 scale. The use of the abundance of species i in each category instead of, for instance, merely counting the number of samples containing the species, is to avoid effects of variable number of samples in each category.

This approach can be applied to *Kurzia pauciflora* on Rønnåsmyra (cf. Tab. 1), by dividing the water table gradient into 8 intervals, each approximately spanning a 5 cm vertical interval, -2-5, 6-10, ..., 31-35, 36-41 cm. For each interval, the mean frequency in subplots of *Kurzia* is recorded: In interval 2 (6-10 cm), the species occurs in one out of 13 plots with a frequency in subplots of 3, its importance in this interval being

$$I_{i2} = (3+0+0+0+0+0+0+0+0+0+0+0+0)/13 = 0.231.$$

Similarly, we obtain:

$$I_{i3} = (0+0+0+0+0+0+6+0)/8 = 0.750$$
$$I_{i4} = (2+11+0+2+2)/5 = 3.400$$
$$I_{i5} = (0+1+0+0+0+0+0)/7 = 0.143$$
$$I_{i6} = (0+2)/2 = 1.000$$

I_{i1}, I_{i7}, and I_{i8} are all zero. The sum $I_{i.} = 0+0.231+0.750+3.400+0.143+1.000+0+0 = 5.524$. Thus we get the niche breadth according to (6):

$$B_i = 5.524^2/[8*\mathrm{SUM}\ (0.231^2+0.750^2+3.400^2+0.143^2+1.000^2)] = 30.514/[8*13.196] = 0.289.$$

It should be noticed that this value for the niche breadth is lower than the value based on distributional limits, 0.395, above. This is due to the inclusion of a component of evenness in occurrence between the categories in equation (6). If a gradient is divided into 8 categories, as in the example above, B_i equals 0.5 for a species that is equally abundant in four categories and absent from the remaining four. B_i is successively reduced as a larger fraction of the total abundance is concentrated into one of the categories, approaching a lower limit of 0.125 when one category contains all occurrences for the species. Thus equation (6) measures the tolerance of the species along the gradient, taking the abundance of the species into account.

Colwell and Futuyma (1971) address three problems with the niche breadth approach: (1) range; that indices of niche breadth do not provide information of absolute niche breadth, e.g., measured in some unit allowing for comparison of different niche dimensions, (2) spacing; that relative positions along a gradient and relative size of categories may influence niche metrics, and (3) non-linearity; the lack of conformity between scales provided by physical or chemical variables and an ecological scale in units of effect on the organisms in question. R. Økland (1986c) analyzed the effects of variable scaling and adjustments to equation (6) on B_i values, and discussed the points made by Colwell & Futuyma (1971) and some related problems. The following points were made:

(1) The fixed range, 0-1, of niche breadth as estimated by equation (6) is inappropriate. Niche breadth should be ranged (Gower 1971) to a 0-l_k scale by multiplication of B_i by l_k, the length of gradient k, on an appropriate scale (see point (3) below for choice of scale). By allowing a flexible range, the B_i index automatically provides a ranking of gradients according to beta diversity.

(2) Spacing. The problem of spacing is solved by a first rescaling of the gradient in units of compositional turnover, and a subsequent partitioning of the gradient into intervals of equal beta diversity.

(3) The non-linearity problem can be solved by rescaling in units of compositional turnover. R. Økland (1986c: 675) addresses the relevance of such rescaling to niche studies: "A scaling in units of compositional turnover has particular relevance to niche studies. Niche breadth is then a measure of the relative importance of a species, compared to the species with which it co-occur. ... However, if the gradient is scaled in units of a physical parameter, niche breadths of species occurring in different parts of the gradient cannot be given a direct biological interpretation, owing to possible variation in beta diversity along the gradient ... ."

(4) Choice of gradients. Calculation of niche metrics should be restricted to gradients demonstrated as important for the species in question, that is mainly the direct and resource gradients in the terminology previously adopted (p. 18), cf. Austin et al. (1983). If a set of independent niche dimensions are dealt with, one can calculate the n-dimensional niche breadth simply by multiplication of B_i values for the independent gradients (May 1975).

(5) Number of samples has to be so large that the response curves for the species with respect to the gradients are adequately recovered.

(6) Comparability. Comparison of niche metrics between gradients in the same study or between studies should be restricted to situations where data are strictly comparable.

R. Økland (1986c) recommends an amended version of Levins' (1968) formula for estimation of niche breadth:

$$B_{ik}' = l_k*[n_k*\mathrm{SUM}_{j=1..n_k}\ (I_{ijk}/I_{i.k})]^{-2} = l_k*I_{i.k}^2/(n_k*\mathrm{SUM}_{j=1..n_k}\ I_{ijk}^2) \qquad (7)$$

where B_{ik}' is niche breadth for species i along gradient k, l_k the beta diversity of gradient k, I_{ijk} the abundance of species i in category j along gradient k, and $I_{i.k}$ the sum of abundances of species i along gradient k.

R. Økland (1986c) and Peet et al. (1988) suggest the use of scaling in S.D. units by DCA ordination for niche studies. R. Økland (1990b) presents results of such an approach to the mire vegetation of N. Kisselbergmosen, SE Norway.

Niche overlap

Several indices exist for estimation of the degree of overlap between the realized niches of a pair of species. Actually, any index of similarity of distribution of two species over a sample set (appropriately modified) can be used. One frequently used measure is the index

$$O_{ilk} = [SUM_{j=1 \ldots n_k} I_{ijk}*I_{ljk}]/[(SUM_{j=1 \ldots n_k} I_{ijk}^2)(SUM_{j=1 \ldots n_k} I_{ljk2})]^{0.5} \tag{8}$$

where O_{ilk} is the overlap between species i and l along gradient k, n_k is the number of categories j along gradient k, and I_{ijk} and I_{ljk} are the abundance of species i and l in category j along gradient k (cf. Pianka 1973, Watson 1980a).

The points made above regarding scaling of gradients and division of gradients into categories are equally relevant to niche overlap. However, niche overlap is meaningfully expressed on a 0-1 scale so that the ranging procedure is not appropriate in this case. Multidimensional niche overlap with respect to independent niche dimensions can be calculated by multiplication.

Problems of the niche breadth and overlap approaches

Before we consider the inference of competition from niche metrics, we will consider the relationship of niche breadth and overlap to some other gradient and community descriptors.

The relationship of niche breadth and abundance. Several plant ecological studies have demonstrated a strong positive correlation between niche breadth and abundance (measured as frequency of a species in the data set; the fraction of sample plots containing the species)(e.g., McCune & Antos 1981, Vitt & Slack 1984, del Moral 1985, R. Økland 1990b). Thus one might ask whether niche breadth is just an expression of abundance. However, R. Økland (1990b) demonstrates that habitat niche breadth for mire species at N. Kisselbergmosen can be partitioned into a frequency-dependent and a frequency-independent component. The frequency-dependent component is the minimum niche breadth, a function of the species' overall frequency in the material. It can be found by a regression of niche breadth on frequency. The frequency-independent component is the difference between the realized niche breadth and the frequency-dependent component. The existence of such a frequency-independent component indicates that niche breadth provides information qualitatively different from abundance.

Species occurring outside the sampled portion of gradients constitute a major problem of the approach. This problem is somewhat reduced by correcting for abundance, as species with optima near gradient end-points or outside the sampled portions of gradients are generally less abundant than other species. For this reason, niche metrics exclusively refer to the data set and extreme care should be taken when results are generalized.

Sampling influences niche metrics by effects on frequency of species and scaling of gradients (R. Økland 1990b).

The relationship between niche breadth and niche overlap. Niche overlap is strongly correlated with niche breadth (e.g., Watson 1980b, 1981, del Moral 1985, Glime & Vitt 1987, R. Økland 1990b). R. Økland (1990b) demonstrates that niche overlap, just as niche breadth, is correlated with abundance, and can accordingly be decomposed into a frequency-independent and a frequency-dependent component. He also shows that the frequency-independent component of niche overlap expresses the position of a species' niche relative to the species with which it is compared. The lower niche overlap, the fewer species of its group is present in its niche (cf. Vitt & Slack 1984). The same information is apparent from a comparison of habitat niche breadth, occurrence along gradients, and gradients in species richness for the group. The calculation of niche overlap thus does not seem worthwhile.

Interpretation of niche relationships in plants

The "Lotka-Volterra" competition model and its predictions

Based on laboratory studies of two-species mixtures, a simple logistic model of interspecific competition between two species has been established. In honour of its originators, the model has commonly been referred to as the "Lotka-Volterra model". This model is described in most ecological textbooks (e.g., Begon et al. 1986), and will not be considered in detail here. Based on knowledge of initial population sizes of the two species, the carrying capacities and intrinsic rates of increase of the two species, and the competition coefficients for the species (indicating the competitive effect of one species on the other), the outcome of competition can be predicted. Possible outcomes are predictable exclusion of one species, exclusion dependent on initial population sizes, and stable coexistence.

The simple experiments that lead to formulation of this model almost invariably led to the same result: when closely related species (of the same guild) competed for the same resource, the inferior interspecific competitor eventually became extinct. Coexistence was associated with a differentiation of realized niches. This is the **competitive exclusion principle** or **Gause's principle**, namely that the coexistence of two competing species prerequisites a differentiation of realized niches. Without such differentiation, one species will exclude the other. Throughout this century, the competitive exclusion principle gradually gained general acceptance.

The Lotka-Volterra model has been used to quantify the competitive exclusion principle in terms of niche metrics (MacArthur & Levins 1967, May 1973). If we consider response curves (resource utilization curves) for the species of a guild along a niche axis, and denote the distance between modes of adjacent species d, and the standard deviation of each species response curve w (Fig. 54), then coexistence of adjacent species along the axis is conditioned by a d/w-ratio of 1 or higher (given equal carrying capacity of the two species). This criterion for coexistence is often referred to as the **limiting similarity**.

Inference of competition from niche relationships

Interpretation of niche relationships with reference to predictions from the Lotka-Volterra model was attempted by many zoo-ecologists in the 1970s, and led to vigourous discussions about the premises for the Lotka-Volterra model, and whether they are satisfied in natural communities. In the 1980s, plant ecologists entered this discussion (see Watson 1980b, Shmida & Ellner 1984, Austin 1985, 1986, Shmida & M. Wilson 1985, Noy-Meir & van der Maarel 1987), and vast amounts of evidence relevant to plant niches and vegetational organization are now available. The available literature treats many aspects of plant niche differentiation, but only major points will be taken up here. In particular, I will address the application of the competitive exclusion principle to plants, and the consequences for interpretation of niche metrics in terms of community processes.

Application of the competitive exclusion principle to plants. Plant ecological studies have repeatedly shown that the separation of modes of species (belonging to the same guild) along the critical (habitat) niche dimensions is below 1.0 S.D. units (R. Økland 1990b). This apparently violates the competitive exclusion principle, as quantified in the limiting similarity constraint: the species should not be able to coexist. Let us start by considering the conditions to be satisfied for the Lotka-Volterra model to be applicable:

(1) The system has to be at equilibrium; there is no density-independent mortality (Silvertown & Law 1987). Competitive exclusion is the predicted outcome of long-lasting competition in a stable environment that persists for sufficiently long time for exclusion to occur and given several initial constraints on the organisms. One important aspect of stability is that the system is saturated by species; the species have been present in the habitat for sufficient time to reach all sites within their fundamental niche by diaspores. We will return to a discussion of instability in the next chapter.

(2) All important niche dimensions have been detected and included in the analysis.

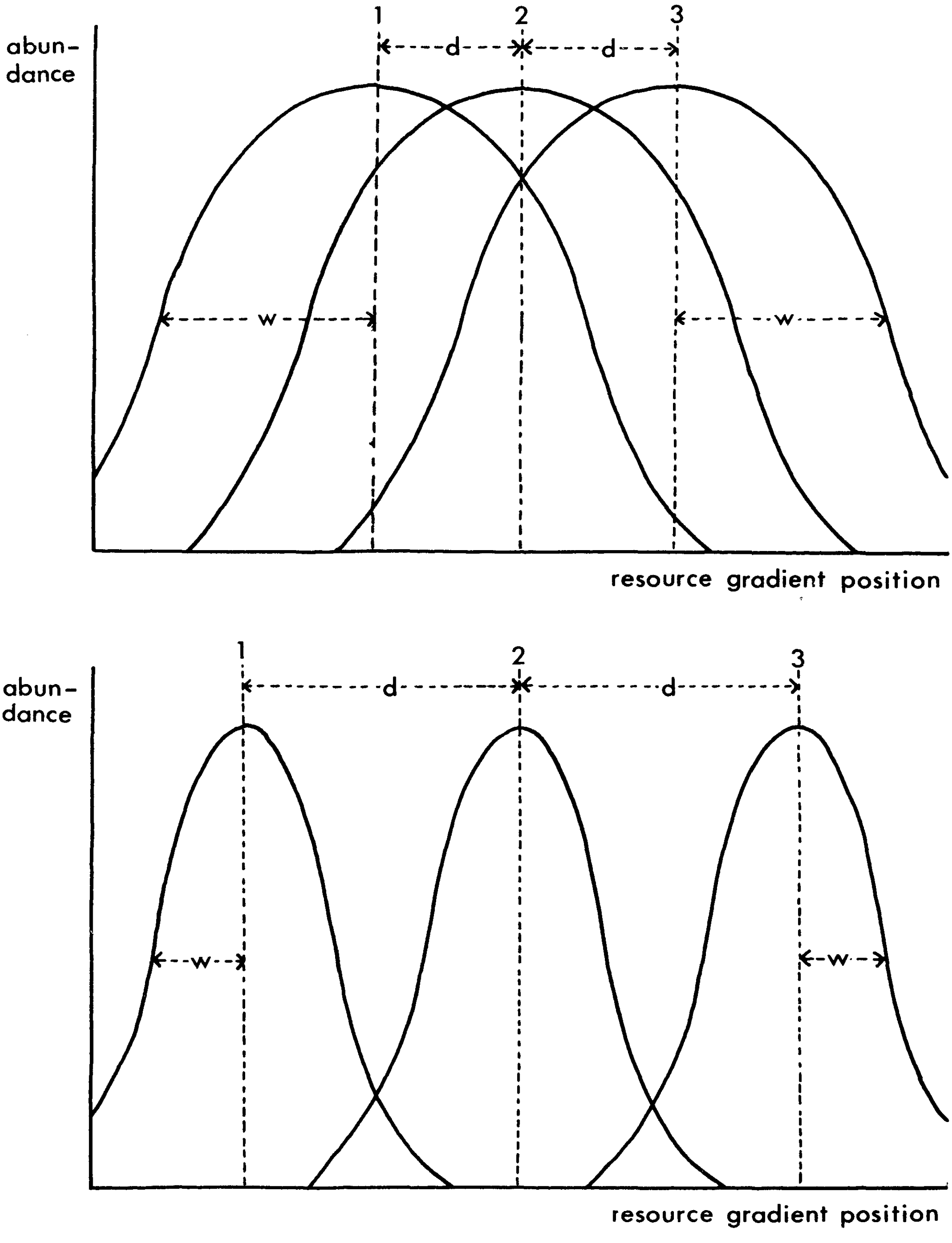

1
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Fig. 54. Illustration of the competitive exclusion principle and the concept of limiting similarity. Above, d < w, and exclusion should occur, below d > w, and coexistence is permitted. d - distance along gradient between adjacent species' modes, w - tolerance of responce curves (measured as the standard deviation of curves).

Of course the gradients cannot be considered one by one. Several authors have pointed out that the gradients must be considered en suite to give a realistic picture of niche relationships, e.g., Platt and Weis (1977), Watson (1981), and Austin (1987). This also applies to the dimensions of the regeneration, the life-form and phenological niches; thus the species are not to differ in dispersal capacity, life-form or any other trait that might reduce competition. There is strong evidence for the existence of several significant parameters of the regeneration niche, e.g. the availability of different kinds of microhabitats for germination and seedling recruitment (Grubb 1977). The importance of the regeneration niche has been repeatedly emphasized during the 1980s (e.g. Shmida & Ellner 1984). Classical niche theory (based on the Lotka-Volterra model) inherently assumes no age structure in populations, no size structure, and no spatial structure (Silvertown & Law 1987). Cody (1986) points to the strong variation in structural properties of plants (with respect to above ground as well as below ground parts), giving rise to "structural niches". He considers lifeform diversity a fundamental niche dimension. Two species apparently not conforming to the principle of limiting similarity may be separated along niche dimensions that have so far not been detected. Because the search for more niche dimensions can be continued endlessly, coexistence by niche separation is essentially an unfalsifiable hypothesis (Austin 1985, Silvertown & Law 1987).

(3) The equilibrium has to be characterized by resource limitation (Wiens 1977), and competition should primarily be competition for limited resources. Plants provide a special problem with respect to the assessment of competition: they are immobile or move very slowly (through runners etc.), and competition therefore to a large extent reduces to be a neighbour phonomenon (Watt 1947, Werner 1976, Turkington & Harper 1979a, 1979b). Separation of inter- and intraspecific competition in plants is therefore difficult (Huston & Smith 1987). In fact, this may imply that in natural situations competition between different age states within one species is more intense than between species, different in size, growth form etc. (Goldberg & Werner 1983). The assumption of resource limitation may apply to some plant groups, e.g. diatoms (cf. Tilman 1982), but is strongly questionable for terrestrial plants.

Shmida & Ellner (1984) conclude that the concept of limiting similarity does not apply to plants. There is growing evidence in favour of this conclusion for many systems, but this does not mean that competition (intra- and interspecific) among plants does not occur.

Possible explanations for niche differences. Several authors have pointed out the problems involved in interpretation of niche metrics. In the 1970s, the interpretation of niche differences as evidence for ongoing competition was fairly common in zoo-ecological applications. This is, however, an unjustified simplification of a most complicated problem. Three alternative explanations are, at least, possible (Begon et al. 1986):

(1) As current competition: the species studied coexist as a consequnce of the niche differentiation, but compete in the overlap zone. This is the classical situation that niche overlap is reduced by competitive displacement, and that interspecific competition occurs in the overlap zone.

(2) Evolutionary avoidance of competition; this is what Connell (1980) has termed "the ghost of competition past". In a situation where competion occurs, those individuals in a population that are most strongly influenced by competition are likely to suffer from higher mortality and lower reproduction than those, for some reasons avoiding competition. The process of natural selection is likely to act on this difference in fitness, eventually leading to a population that has escaped competition. Selection for empty niches and avoidance of competition is likely to have played (and still to play) an important part in the evolutionary process. Thus present niche differentiation may be the outcome of past

competition.

(3) Past divergence by response to natural selection in different and independent ways. The species presently do not compete, nor have thay done so in the past.

When habitat niche differences are found, we cannot decide whether they are the cause or effect of coexistence (Connell 1980, Shmida & Ellner 1984, Noy-Meir & van der Maarel 1987, Silvertown & Law 1987).

Assessment: interpretation of niche differences. There are considerable amounts of circumstantial evidence indicating that the intensity of interspecific interactions increases as habitat niche breadth decreases (Christensen & Peet 1984, del Moral 1985). One example is provided by the comparison of biological characteristics of the species, species richness, species turnover and frequency-independent niche breadth for guilds of mire species at N. Kisselbergmosen (R. Økland 1990b). However, it is not possible by calculation of niche metrics to differentiate between the three determinants of niche relationships of Yodzis (1986): competition for resources, competition for space, and environmental heterogeneity. The pertinent hypothesis is "that the co-occurrences and co-abundances are determined only by the overlap, or the segregation in the species distributions over habitats, and that the distributions are all independent of each other" (Noy-Meir & van der Maarel 1987: 11-12). Deviations from the hypothesis indicate interactions between species (positive or negative). Tests along these lines have been performed by Rogers (1983). In order to differentiate between the three determinants of niche relationships proposed by Yodzis (1986), supplementary information from many sources is potentially useful (cf. Abrams 1980, Alley 1982). Such information is α and ß diversity, patchiness of microhabitats, autecological data, physiological data, experimental evidence, careful vegetation ecological analysis, and data on niche shifts, that is the variation in realized niche dimensions between different, spatially close sites, for instance transects on a mire (Rydin 1986). The most important value of niche metrics, particularly data on niche breadths, is for an efficient summarization of relationships between species in the data set. This summarization may have an important hypothesis-generating function in an ecological analysis as patterns in niche relationships call for explanations in terms of process (competition, stability, evolutionary history).

STRUCTURING PROCESSES AND COMMUNITY THEORIES

The ongoing discussions of the relationship between structure and function in vegetation has its roots in the vigourous discussions of the importance of interspecific competition as a structuring process in nature. Recent literature, for instance the book "Community ecology" edited by J. Diamond and T.J. Case (1986), shows that there is at present a strong increase in number of theories put forward to explain pattern and process in vegetation. These theories have their basis in field and laboratory investigations with plant groups or assemblages of plant groups differing widely in fundamental properties. As the search for universal trends in patterns of species diversity of the 1970s have been replaced with acceptance of a wide diversity of patterns, each applicable to one local area, one kind of system, etc., the expected outcome of the discussion of vegetational theories should be a corresponding diversity of explanations. As this book has the scope of presenting basic principles rather than numerous applications, I will restrict the treatment of these topics to an overview of structuring processes and a survey of types of theories. When available, examples from boreal and alpine vegetation will be given.

Structuring processes

Four main types of structuring processes in vegetation may be considered: (1) Interspecific interactions. (2) Destabilizing factors; disturbance and fluctuations. (3) Stress. (4) Chance.

Interspecific interactions

Several kinds of interspecific interactions occur between plants. Plants with strong competitive ability have been termed **competitors** by Grime (1979), who lists several characteristics of competitors: small proportion of annual production devoted to reproduction, perennation by dormant buds and diaspores, photosynthetic activity correlated with vegetative growth, etc.

Interspecific competition has been dealt with in connection with niche relationships (pp. 45-49), and will only be treated briefly here. There is a vast literature on interspecific competition among plants that can be considered for an exhaustive treatment of the subject. Interspecific competition occurs with various intensities (Yodzis 1986). In order of increasing intensity, we may distinguish (1) competition for empty space, (2) competition for space, and (3) competition for resources in short supply.

The inclusion of competition for empty space as a kind of interspecific competition can be questioned. A typical example of this kind of competition occurs during the invasion of bryophytes and lichens on fallen, decorticated spruce logs in boreal forests (Söderström 1988). Another example is the colonization of patches of naked peat in bogs (R. Økland 1989b, 1990b), early stages of recolonization of such patches are characterized by species with efficient means of attachment, able to endure periods of drying-up and burial in redistributed peat, and that are able to spread rapidly on such a substrate. A third example is the colonization of small cavities in the boreal forest floor by small species of mosses and hepatics (the "pocket species of R. Økland & Bendiksen 1985). Interactions between species (actually between individuals) will eventually occur at later stages of colonization. The niche shifts of some *Sphagnum* species (occupation of different vertical intervals relative to the depth to the water table gradient in different transects) in a boreal mire observed by Rydin (1986) are likely, at least in part, to be a result of so-called **pre-emptive competition** (Werner 1976): when the first colonizer has established on a patch well before the competitors arrive, it will maintain itself for a very long time because of the difficulties for new *Sphagnum* species to establish within a closed *Sphagnum* carpet. Rydin (1986) considers this kind of competition as the most important structuring process in bogs. Pre-emptive competition is likely to be widespread among bryophytes and lichens, as establishment is easier on naked soil patches than in dense moss cushions (cf. Schuster 1966). A classical example of pre-emptive competition is provided by the dense cushions of *Leucobryum glaucum*, that may reach diameters up to 50 cm. In intitial stages of cushion development, the close spacing of shoots and the high growth-rates of the moss prevent intruders from getting established. In later stages, however, the structure of the cushion slowly disintegrates due to density-independent mortality processes, the killing of parts of the cushion by accumulating litter, the drying-out of some parts, and the creation of an uneven surface due to unequal growth, thus increasing the probability of establishment of other bryophytes and vascular plants (cf. Vallin 1974, Bates 1989). Pre-emption of space by *Leucobryum glaucum* thus continues for some years, until the whole population (or individual; one cushion mostly derives from one individual by branching) senesces.

Competition between plants for space occurs as neighbour interactions (Turkington et al. 1977, Turkington & Harper 1979b) or localized competition (Shmida & Ellner 1984). As previously mentioned, there is no clear distinction between inter- and intraspecific competition of this kind. Competition for space between many species along many gradients has been termed **diffuse competition** (MacArthur 1972). The term is currently used in a more inclusive sense; S. Wilson and Keddy (1986) define diffuse competition as competition with a constellation of species in varoius combinations and densities. Diffuse competition occurs in all vegetation, but its importance as a structuring factor and its relationship to other kinds of interspecific competition is unclear. In the broad sense, diffuse competition is used to encompass all kinds of interactions that are not explicable in terms of resource competition. S. Wilson and Keddy (1986) approached the importance of diffuse competition in Canadian lakeshore vegetation experimentally. They selected a number of plots along transects at right angle to the lakeshore, divided each plot in two, cleared one half for all vegetation, and transplanted ramets (shoots) of each of the three species into cleared as well as uncleared plots. Diffuse competition was estimated for each site by an index expressing the proportional decrease in dry weight from the cleared plot to the uncleared control. Diffuse competition, measured in this way, was shown to be highest in the more productive environment, that is, where standing crop was highest, and in locatities sheltered from stress (exposed shores) and disturbance (wave action).

Competition for resources in short supply has been demonstrated for several plant groups in laboratory experiments, e.g. for diatoms (Tilman 1982). The importance of this kind of competition in natural vegetation is hard to assess. A species may be absent from a site within its fundamental niche because it is an inferior competitor for resources, but may more often be absent from marginal sites for other reasons, e.g. low density of propagules (low probability of arrival at the site), low tolerance for diffuse competition in sub-optimal sites, etc.

Facilitation is the phenomenon that the occurrence of one species encreases the probability of occurrence of another. The occurrence of *Sphagnum balticum* in bog hummocks in the presence of *Sphagnum fuscum* is an illustrative example (Rydin 1985, R. Økland 1989b). In pure patches, *S. balticum* is unable to inhabit high hummocks, even in the absence of competition, because of low physiological tolerance to drought. However, *S. balticum* can ascend to the top of high hummocks as single individuals in dense cushions of *S. fuscum*; the latter provides support and water. Another example from bogs is the occurrence of small, slow-growing hepatics, for instance *Calypogeia sphagnicola*, growing over the *Sphagnum* capitula (R. Økland 1989b, 1990b). Because of its small size and its firm attachment to the capitulum (well above the zone of intense length growth of the peat-moss) by rhizoids, the hepatic escapes burial between the fast-growing *Sphagnum* shoots despite its far lower growth rate.

Destabilizing factors: disturbance and fluctuations

Destabilizing factors may be divided into two categories: disturbance and fluctuations. Both kinds of destabilizing factors are included in the concept of disturbance applied by several authors, e.g. Grime (1979). The term **ruderal** is used for plants with high tolerance to disturbance (Grime 1979). Ruderals share a lot of characteristics: short life-span, high frequency of sexual reproduction, large proportion of annual production devoted to vegetative growth, perennation by dormant diaspores, and a potentially high photosynthetic activity, coincident with periods of high potential productivity.

Disturbance encompasses sudden events impacting the vegetation by increasing the density-independent mortality. Examples of disturbance of different magnitudes are the sudden extrusion of decomposed peat in bog mud-bottoms accompanying methane release (Aario 1932), causing burial and high risk of death of nearby bryophytes; the creation of gaps in forests by windfall and root uplift of trees (Schaetzl et al. 1989); and forest fires and avalances leaving behind larger areas more or less devoid of vegetation.

Disturbance affects the intensity of competition by increasing the density-independent mortality (Peet et al. 1983), and promotes coexistence of plant species without niche differentiation (Connell 1978, Silvertown 1983, Shmida & Ellner 1984). Huston (1979) has shown that the introduction of density-independent mortality in Lotka-Volterra models postpones competitive exclusion.

Fluctuations are used to denote more or less predictable variation in environmental factors affecting density-independent mortality. Important factors are climatic parameters (temperature and precipitation), and predation by herbivores with cyclic changes in population density. One example is the harmful effect of extreme drought on vegetation; after dry years large patches in pine forests on shallow soil (particularly overlying rock outcrops) may be devoid of vascular plants. Fluctuations in climate are thought to influence the fine balance between hepatics, lichens and *Sphagnum* of bog hummocks (the small-scale succession; cf. Tolonen 1971, Økland 1989a, 1989b). Fluctuations are shown to affect the relative growth rates of co-occurring *Sphagnum* species (Lindholm 1979) and thus the outcome of competition (Wallén et al. 1988). Temporary variability in the environment promotes coexistence by preventing establishment of an equilibrium (Chesson & Warner 1981) and by periodic reversal of competitive superiority (Hutchinson 1961).

Stress

Stress is a constantly occurring environmental impact on vegetation that adversely affects production, mortality or establishment. Grime (1979: 21) defines stress as "the external constraints which limit the rate of dry matter production of all or part of the vegetation." As opposed to disturbance and fluctuation, stress constantly impacts the plants. **Stress-tolerators** (Grime 1979) are characterized by: long or very long life spans, long-lived, often perennial leaves (or other photosynthetic parts), evergreenness, small proportion of annual production devoted to reproduction, slow growth, and opportunistic photosynthesis.

Stress is connected with end-points of environmental gradients: temperature stress increases towards high altitudes in the mountains, leading to gradual reduction in species number with increasing altitudes; toxicity stress may occur near the high-pH end of a nutrient gradient, e.g., associated with ultramafic (e.g., serpentine) rocks; and litterfall stress, moisture stess and light deficiency stress may occur in spruce forests close to the stem of large trees.

Stress reduces competition by inhibiting dominants from monopolizing critical resources (Grime 1979, Pickett 1980), by reducing shading and probably also by reducing diffuse competition.

Chance

The importance of chance, that is random processes in vegetation, is probably strongly underestimated. However, when species responses to environmental gradients are recorded, only 50-90 % of the variation in species abundances are normally accounted for as response to gradients. The rest represents random or apparently random variation, often termed **noise** (cf. pp. 96-97). Factors contributing to randomness are: the intraspecific genetic variability, manifest in differences in life history parameters (flowering, biomass, reproduction), and for instance, success of pollination and dispersal. Randomness also occurs in the variation of environmental factors, but random effects of the environment are rather considered as destabilizing factors if affecting vegetation. The importance of randomness increases towards finer spatial scales (Schafale & Christensen 1986) and towards earlier successional stages

(Rogers 1983, Silvertown 1983, O'Connor & Aarssen 1987).

Examples of effects of random processes in vegetation are numerous. Naked peat patches in bog hummocks may be colonized by small *Cladonia* spp. At N. Kisselbergmosen some 15 *Cladonia* species, apparently more or less without niche differentiation, may occur in such habitats. Their local distribution among available habitats on N. Kisselbergmosen shows few interpretable patterns apart from some indications of aggregations, that is clumped distributions. Chance is a major factor determining the local distribution of such species.

Community theories

Chesson and Case (1986) present an overview of current theories in community ecology. The main types of theories relevant to vegetation will be reviewed in the following. The main distinction is between **equilibrium theories** and **non-equilibrium theories.** Equilibrium theories focus on system properties at the equilibrium point, disregarding variation in time and space due to environmental heterogeneity, fluctuation, stress, and other factors leading to density-independent mortality. Non-equilibrium theories focus on variation in time and properties of the system.

Equilibrium theories

Classical competition theory keeps a central position among the equilibrium theories. It can be summarized in the following five points (Chesson & Case 1986: 230): "(1) The life history characteristics of species can be adequately summarized by the population's per capita growth rate. (2) Deterministic equations can be used to model population growth; in particular, environmental fluctuations can be ignored. (3) The environment is spatially homogeneous, and migration is unimportant. (4) Competition is the only important biological interaction. (5) Coexistence requires a stable equilibrium point." It follows that coexistence requires a limiting similarity (p. 46). We have previously seen why the concept of limiting similarity, and hence the principle of competitive exclusion, is inappropriate to most vegetation systems. This does not, however, imply that interspecific competition is not important for plants, but rather that non-equilibrium elements should be part of any theory of vegetation. An extension of the classical equilibrium theory is the introduction of the stable, patchy environment, where some species survive better in some kinds of patches, others in other kinds. The view of Grubb (1977) that community composition is structured by between-species differences in requirements for germination and establishment (the regeneration niche) may also be considered an extension of the classical equilibrium theories by introduction of new niche dimensions. In fact, this is merely an inclusion of more niche dimensions by allowing for simultaneous niche separation on several spatial scales.

Non-equilibrium theories

The agreement on non-equilibrium models as the most appropriate for explaining patterns in vegetation is perhaps the most important outcome of more than ten years of intense debate on vegetation theory and models. The non-equilibrium situation is characterized by species densities not remaining constant over time at each point in space (Chesson & Case 1986). This definition of non-equilibrium is not dependent on scale, but make all theories allowing for small-scale variation with time non-equilibrium theories. There is no contradiction between equilibrium at a broad scale and non-equilibrium at a fine scale

(Chesson & Case 1986, Williamson 1987). At this point, the concept of **stability** is useful. A stable community is characterized by a tendency to approach its equilibrium (at some scale). With the definition of non-equilibrium here adopted, a non-equilibrium theory do not have to be a non-stability theory (Williamson 1987). Stable communities may show cyclical or any sort of local non-equilibrium variation, but the broad-scale result is stability. Thus there is a gradual transition from fine-scale equilibrium theories via theories predicting a combination of non-equilibrium at a fine scale and broad-scale equilibrium to broad-scale non-equilibrium theories.

Chesson and Case (1986) perform a classification of non-equilibrium theories into categories along a gradient from broad-scale equilibrium stability to non-stability theories:

(1) *Fluctuations and continuous competition.* This is a fine-scale non-equilibrium group of theories, including fine-scale non-equilibrium as an explanation to coexistence of species, but maintaining interspecific competition as an important and continuously operating factor. Fluctuations may occur in populations (due to differences in demographic properties), environmental variables etc. These theories share many properties with equilibrium theories, but allow for coexistence of species without niche differentiation.

(2) *Fluctuations and discontinuous competition (density-dependence).* This category leads one step further away from the classical equilibrium theories by emphasizing fluctuations in species densities and/or environmental factors as the dominant process. Fluctuations occur on ecological time-scales and population dynamics are density-independent much of the time. The environmentally induced reduction in population densities (density-independent mortality) reduces competition and promotes coexistence of species without niche differentiation.

The importance of patchiness of the environment and environmental fluctuations (or disturbance) for creation of gaps is central to the **gap dynamics theories** or **patch dynamics theories** (cf. Whittaker & Levin 1977, Pickett 1980, Grubb 1986). The importance of chance recruitment to unfilled gaps is central to the **lottery models** (Sale 1977, 1982, Chesson 1986), but stochasticity may apply to any critical stage in the life cycle. The difference between gap dynamics and lottery models is only one of relative emphasis on process, as models of type (2) are likely to incorporate elements of both.

Pickett (1980) points to three important conditions to be satisfied for competitive exclusion to be prevented by gap dynamics: (a) efficient disturbance favours species with low competitive ability, (b) intensitity of disturbance is high enough for the expected time until gap creation to be less the than expected time to competitive exclusion, and (c) the spatial distribution of patches have to suit the poor competitors. As formulated by Pickett (1980), the patch dynamics theory involves: "(1) pattern of patch (= gap) creation in time and space, (2) patch size and structure, and (3) the changes in individual patches of a cohort and size class due to species availabilities, adaptations, and interactions."

Shmida and Ellner (1984) have shown that the incorporation of random access to vacant sites ("lottery") may lead to coexistence between, for instance, a species with superior reproductive capacity and a species with superior vegetative competitive ability, without habitat niche differentiation. Furthermore, they stress the importance of **mass effects**, that is, (1) the input of diaspores from nearby habitats (spatial mass effect), and (2) differences in demographic responses to environmental fluctuations (temporal mass effect), as factors promoting the increase of species richness in the absence of further niche differentiation. For example, lottery models thus also account for persistence of species in a community offering them no immediate opportunity for recruiment by the presence of strong cohorts established in occasional good recruitment years (due to climatic fluctuation), cf. Chesson and Warner (1981).

Huston (1979) incorporates stress, disturbance and productivity into a model predicting

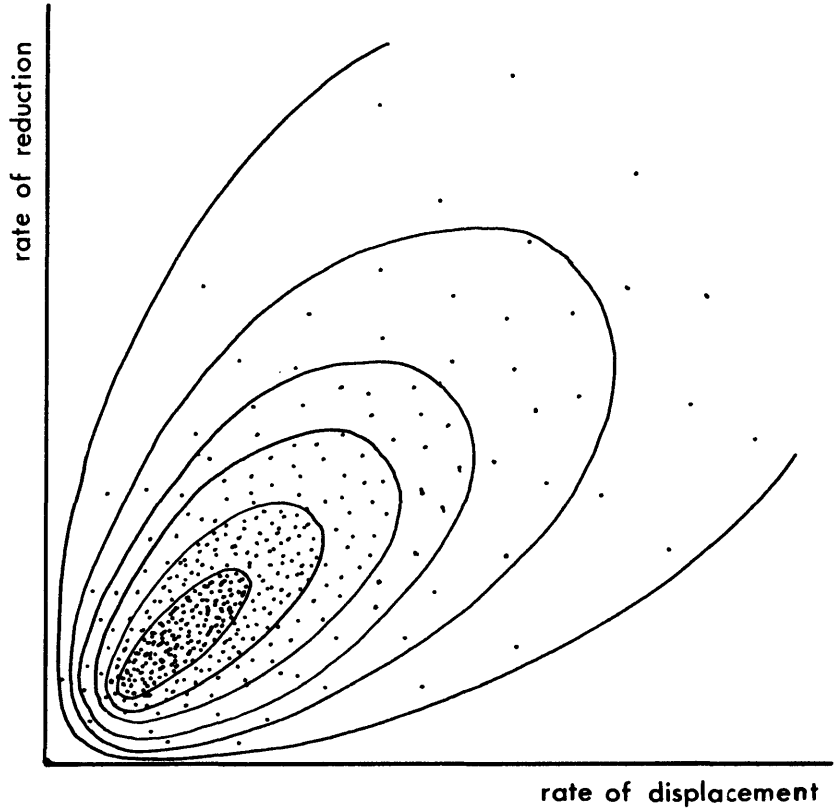


Fig. 55. Huston's model of relationship between rate of displacement and rate of frequency of population reduction. The displacement rate expresses population growth rate, and hence, the stress, or the density-dependent mortality in the population. The rate of reduction expresses the intensity of disturbance, or the density-independent mortality in the population.

α diversity (Fig. 55). Highest species richness is predicted in habitats with moderate productivity (low stress) and moderate disturbance. Low productivity implies nutrient stress, and leads to low species richness. Very high potential productivity (high rate of displacement) may involve toxic nutrient levels, superoptimal temperatures for growth, etc., also leading to reduced species richness. Low disturbance leads to low species richness due to interspecific competition, moderate disturbance promotes coexistence by reducing the importance of competition, while high disturbance prevents establishment and leads to reduced species richness. The model is applied to grasslands by During & Willems (1985). A model of this kind is coarse, and cannot be expected to be strictly applicable to all systems (cf. Yodzis 1986).

(3) *Changing environmental mean.* If we expand the time scale to allow for variation in mean and variance of climatical parameters like annual mean temperatures, annual precipitation etc., theory types (1) and (2) are changed into non-stability theories. This type of theories does not necessarily demand very long time scales. One may assume year-to-

year fluctuations in climate to influence community composition so strongly that the criteria for stability are violated. The operating time scales will depend on the lifetime expectancies of individuals (shoots) in the vegetation and on the spatial scales considered. Time scales will be broad for long-lived plants and for large regions.

(4) *Slow competitive displacement* (Hubbell & Foster 1986). This theory was originally put forward to explain the observations that many tropical rain forest trees are ecologically identical. The argument is that the competitive displacement in such a system is so slow that it approaches time for speciation. In such systems, fluctuation in numbers results from death and recruitment of individuals, and will show random variation.

Relevance of theories to some Northern systems

The investigation of pattern and process in vegetation has mostly played a subordinate role in the Northern tradition of vegetation (as will be addressed in the next chapter). Although considerations of these topics have occasionally been made in connection with descriptive investigations, there are large gaps in our knowledge. This chapter is no attempt to give an exhaustive treatment; rather it is meant as a brief introduction to the major questions of tomorrow's vegetation ecology.

Mires

Backéus (1985) has studied the biology of vascular plants on Skattlösbergs Stormosse, a C Swedish bog, Rydin (1985, 1986) has investigated interactions between *Sphagnum* at Ryggmossen, an E Swedish bog, and Økland (1990b) has studied habitat niche relationships at N Kisselbergmosen, SE Norway. Several examples from some of these studies have been quoted above. It is well documented that vascular plants of bogs experience a harsh environment; they show the characteristics of stress-tolerators. *Sphagnum* species, hepatics and lichens show a more diverse spectrum of strategies than previously assumed, thus violating the traditional view that hepatics are mainly ruderals or fugitive species (Schuster 1957, 1966, Slack 1977, During 1979), and lichens stress-tolerators (Grime 1979). The above-mentioned studies emphasize the importance of destabilizing factors in the structuring of the bog community. Density-independent mortality is an important process at the population level, e.g. due to extrusion and redistribution of peat (p. 51), occasional extreme drought, and water and ice erosion (Økland 1989b). Creation of new gaps (naked peat patches of variable size) occurs sufficiently frequent to prevent competitive exclusion between catastrophes, but sufficiently rare to allow interspecific interactions to occur. Bogs (and fens) in those parts of Fennoscandia where erosion is unimportant are likely to have reached an equilibrium between growth and decomposition, while bogs in more humid areas are unlikely to escape erosion (R. Økland 1989a). On an ecological time-scale and a broad spatial scale these bogs may be considered as stable, and unstable, respectively. On a fine spatial scale, non-equilibrium theories of the patch dynamics type appear well suited (R. Økland 1990b).

Towards richer fen sites, productivity of vascular plants increases as a result of reduced environmental stress. The bottom layer dominants change from *Sphagnum* in bogs and poor fens to mosses in rich fens. However, the importance of naked peat does not decrease, again pointing to high importance of destabilizing factors. The high descomposition rate of peat in rich fens and the lack of a firm moss carpet increases the danger of redistribution of peat at high water tables or high water throughflow rates. Furthermore, the increased productivity of vascular plants increases the litterfall and hence also the density-independent mortality in the bottom layer.

Boreal forests

Because of the immense economical importance of the boreal spruce and pine forests, the patterns and processes in the tree layer are well known. At moderate altitudes, the dynamics of the tree species are governed by storms and fires (Hytteborn et al. 1987), that is by disturbance factors causing density-independent mortality. Seed production is abundant and seedlings are randomly dispersed (Leemans 1989). Recent studies (e.g., Hytteborn & Packham 1985, 1987, Hytteborn et al. 1987) have corroborated the storm-gap regeneration theory of Sernander (1936) for spruce forests; spruce seedlings suffer higher mortality in the shade under mature trees than in the gaps between, and they can persist in gaps as small, slow-growing trees for a long time, eventually to be recruited into the canopy when a gap is produced by storm felling (often following fungal attack or other diseases, or weakening of a tree for other reasons). Towards the forest limit, temperature stress increases and regeneration becomes a major problem for recruitment (Steijlen & Zachrisson 1987).

The knowledge of pattern and process in the field and bottom layers of the boreal forest is remarkably poor. Despite the fact that these vegetation types are the quantitatively most important over most of Fennoscandia, they have not attracted much interest. The field layer is mostly dense or almost closed, in submesic to xeric sites dominated by dwarf shrubs like *Vaccinium myrtillus*, *V. vitis-idaea*, *Calluna vulgaris*, and *Empetrum nigrum*. These species appear to compete intensely, at least for water. The concentration of spruce saplings to decomposed logs and boulders has been ascribed to lower root competition in these sites (Hytteborn & Packham 1987). Other species are also likely to show clumped distributions reflecting competitive effects. The density (total cover) of the field layer and hence probably also interspecific competition increase from the xeric, lichen-dominated forests to the submesic, *Vaccinium myrtillus*-dominated forests (Kielland-Lund 1981, R. Økland & Bendiksen 1985). Water stress, on the other hand, increases from the submesic to the xeric forests (R. Økland & Eilertsen in prep.). The importance of competition is consequently likely to decrease strongly towards xeric sites. Light stress (perhaps also water stress) may prevent vascular plants from occurring underneath large trees. The importance of disturbance is probably low, but fire and uprooting associated with storm felling also affects the field layer. Bonan and Shugart (1989) present a simplified (and probably incomplete) model of large-scale environmental factors in boreal forests and the way the control vegetation patterns. Our knowledge of structuring factors, and hence, of processes, descreases from the tree, via the field, to the bottom layer.

The development of the bottom layer varies from a closed carpet to few, scattered individuals with low vitality. Litterfall from trees, dwarf shrubs and even herbs is a most important disturbance factor, leading to a high danger of burial and thus contributing strongly to density-independent mortality (T. Økland 1989, R. Økland & Eilertsen in prep.). There seems to be a link between litterfall, water balance and development of the bottom layer: development of the bottom layer is favoured by reduced litterfall and improved water availability. Thus stress (water balance) and disturbance (litterfall) both contribute to reduce competition in the bottom layer. Other disturbance factors affecting the bottom layer are trampling, excretion and urination of large mammals, and the occasionally very strong predation and tramling disturbance of bryophytes by rodents in years of high population density (Ericson 1977). The latter effect increases towards the mountains, and may lead to cyclic patterns in vegetation with a lagged response to the impact of rodents (Ericson 1977). A population study of *Hylocomium splendens* in boreal *Vaccinium myrtillus*-dominated forests (R. Økland, in prep.) shows high importance of density-independent mortality factors, while inter- and intraspecific competition appears to be of minor importance. Pre-emptive competition for vacant microsites (cavities, stone walls etc.) is likely to be important (R. Økland & Bendiksen 1985). The presence of a marked microtopographic variation strongly increases species richness by increasing the number of microsites and the diversity of microsite types.

Maslov (1989) demonstrates a connection between the patterns of occurrence of species, their vegetative strategy, and environmental heterogeneity in boreal forests in the USSR. He found that vegetatively mobile herbs like *Convallaria majalis*, *Maianthemum bifolium* and *Trientalis europaea* more closely approached a random distribution (in Maslov's terminology, they were low-contagious) than did the bryophytes of the bottom layer, e.g., *Hylocomium splendens*, *Polytrichum commune*, and *Sphagnum girgensohnii*. This is likely to be a response to the environmental heterogeneity of the forest floor, strengthened by pre-emptive competition. Maslov (1989) hypothesizes random (and low-contagious) distribution to result from low vegetative mobility and/or homogeneity at the scale of the environment to which the species reacts. Conversely, high-contagious distribution is hypothesized to result from high vegetative mobility and/or environmental heterogeneity at appropriate scale. Interspecific competition may add to complicate this simple picture, which nevertheless seems to apply rather well to the boreal forest floor.

Boreal forests seem to be impacted by several structuring factors; disturbance and stress are important, but their relative and absolute importance varies between layers and along major environmental gradients. Interspecific competition is probably highest in the field layer of mesic and submesic forests, and probably plays a minor role in the bottom layer. The stability of boreal forests is likely to be turned into instability because of the impact of airborne pollutants, "acid rain" (Hallbäcken & Tamm 1986, Falkengren-Grerup et al. 1987, Persson et al. 1987, Aune et al. 1989), potentially also by climatic change.

Alpine heaths

Temperature stress increases towards the mountains, and affects the population dynamics of plants in several ways (Resvoll 1917, Dahl 1957, Baadsvik 1971, Wijk 1986). Climatic fluctuations leading to frost damage in spring and summer, and physiological drought in winter further increases the density-independent mortality. Disturbance by rodents occurs. The importance of interspecific competition is hard to assess, but probably varies considerably. It is likely to be highest in moderately snow-covered sites. The often high cover in the field layer may indicate significant interactions. The positive effects of absence of a tree layer may partially outweigh the increased stress in this respect. The bottom layer varies strongly with local ecological conditions, but the reduced litter fall relative to the forests imply a relatively lower disturbance. The importance of climatic fluctuations for species in the bottom layer is not known, but may be considerable.

To sum up, alpine heaths are characterized by high climatic stress and strong impact of climatic fluctuations. Both of these factors increase in importance with altitude. Fine-scale non-equilibrium is probably the reality in a majority of alpine vegetation types, but the importance of interspecific interactions may be higher than presently assumed.

THE TRADITIONS: APPROACHES TO DESCRIPTION OF VEGETATION

INTRODUCTION

The multiplicity of approaches and theories in contemporary vegetation science can only be understood by knowledge of its past. The history of vegetation ecology before 1960 is intimately connected with description of vegetation, for which classification has been the major tool. The history of classification shows an early divergence into several schools, and many of the schools later became fragmented into minor branches. Whittaker (1962: 3) commented upon this "remarkable fragmentation of the study of plant communities into schools": "Probably in no other field of natural science has there been such proliferation of local schools with distinctive viewpoints and techniques." There are several reasons for the development of traditions, differences in scientific traditions in general, and differences of the vegetation and its developmental history between regions ("the ecology of ecological traditions"; Whittaker 1962). Two of the seven major "traditions" recognized by Whittaker (1962); the Braun-Blanquet approach (the Southern tradition) and the two branches of the Northern tradition have influenced Fennoscandian vegetation ecology strongly. These will be treated in some detail. Furthermore, the basis for classification and the development of numerical techniques in vegetation ecology will be briefly commented.

Phytosociology - art or science?

All descriptive traditions except the British and American share some fundamental principles: subjective classification into units, **plant communities**, and filing of these communities into a formal hierarchy. These are the fundamental tenets of the branch of vegetation ecology known as **phytosociology**. The term **association** has been coined for the fundamental unit of most of these schools, but the definition of this unit varies between (and within) schools.

Done the traditional way, description of vegetation involves several steps (cf. Westhoff & van der Maarel 1978): (1) **the analytic phase**, subjective selection of homogeneous stands of vegetation (homogeneity judged subjectively or, more rarely, by some statistical method), subjective selection of one or more sample plots within the stand, and analysis of the vegetation within these plots, (2) **the synthetic phase**, arrangement of sample plots into tables showing similarities and differences in species composition, and (3) **the syntaxonomical phase**, the abstraction (in the investigator's mind) of plant communities (hierarchically arranged) from the ordered tables of sample plots in accordance with the rules of the tradition in question.

The phytosociological method is inductive; knowledge of the nature emerges from a general-purpose descriptive investigation. No hypothesis is formulated initially, and no testing occurs. Whittaker (1962: 124) made a valuation of the phytosociological method from a scientific point of view: "It is, in any case, questionable whether classification of natural communities should be termed "science". Science and art are not mutually exclusive, and there may be more art in science than first meets the eye. This account has emphasized features of classification - subjective balancing of values, translation of experience into varied, personally satisfactory classificatory designs, the influence of culture and personal factors and self-influence by precedent and tradition, the rise and fall of "schools" with different views and techniques - more generally associated with arts than sciences. For the preponderance of such features in problems of community classification, one may consider that this is less a science than an art instrumental to other aspects of ecological science." However, the importance of the ecological knowledge emerging from the effort put into description of vegetation should not be underestimated. This inductive phase has provided most of the hypotheses that are now being tested by more rigorous methods.

Vegetation models and the basis of classification

Acceptance of the continuum concept of vegetation, i.e. the more or less continuous variation in species composition along continuous environmental gradients, has important implications for the classificatory approaches. The multidimensional continuous structure of vegetation makes all appoaches involving classification artificial, because they involve drawing boundaries where no or few boundaries exist. No classification can claim exclusive merit, and no classification can be considered as natural. Evaluation of classifications must be by comparison with known gradient structure or by its suitability for applied purposes. The inherent arbitrariness of classification does not prevent classification from being a useful tool for structuring variation in vegetation. A recurrent argument in favour of the classificatory approach is that classification is a fundamental mental activity.

Vegetation models and the hierarchy

As mentioned, a common feature of the traditions of classification is the arrangement of vegetation types or "**plant communities**" into a hierarchy. A hierarchical classification of a multidimensional continuum cannot do justice to natural conditions, as recognized by several early 20th century scientists (e.g., Gams 1918, Nordhagen 1928). Turning a network of multidimensional relationships into a hierarchy inevitably implies a loss of information (Goodall 1978b) owing to the unidimensionality of the hierarchy. On a regional scale, further problems are added: species often show different responses to local environmental gradients in different regions, thus when the studied area increases, a hierarchic system "becomes more and more divorced from reality and will be in still greater danger of becoming a useless end in itself" (Kalela 1960: 42). The hierarchy has mostly been justified by analogies to human perception, but such a justification is doubtful when the hierarchical structure does not do reflect the inherent structure of vegetation. Rather than being a help for the comprehension of complicated relationships, the hierarchy can be considered an unnecessary and undesirable strait-jacket; an obstacle for the mind to understand the gradient structure of vegetation.

THE BRAUN-BLANQUET APPROACH

European phytosociology has its roots in early 19th century vegetation description. Among the many regional schools emerging at the start of the 20th century, one should soon stand out as the leading approach, gaining support from most of Europe. This was the approach named after its founder, J. Braun-Blanquet (1884-1980), developing in Zürich (Switzerland) and Montpellier (France) during the 1900s and 1910s. In his 1921 textbook (Braun-Blanquet

1921), the essence of the system was fully developed. Further developments have occurred, but most of the fundament is still retained. The development of the approach is characterized by some tendency to segregate into "subschools", but without causing a disintegration of a distinctive school as such. During most of this century, the development of the Braun-Blanquet approach has been characterized by increasing geographical spread of the ideas of the school. Now, there is almost no part of the world that has not been described by the methods of the Braun-Blanquet approach.

The Braun-Blanquet approach is also called "the floristic-sociological approach", "the Zürich-Montpelier school", and "the Middle European-Mediterranean school".

Several reviews and textbooks describe the approach; e.g., Whittaker (1962), Braun-Blanquet (1964), Shimwell (1972), Mueller-Dombois & Ellenberg (1974) and Westhoff & van der Maarel (1978). The following account is in accordance with the latter.

Basic principles

The essence of the school may be summarized in three ideas (Westhoff & van der Maarel 1978: 289): "(1) Plant communities are conceived as types of vegetation, recognized by their *floristic composition*. The full species compositions of communities better express their relations to one another and environment than any other characteristic. (2) Amongst the species that make up the floristic composition of a community, some are more sensitive expressions of a given relationship than others. For practical classification (and indication of environment) the approach seeks to use those species whose ecological relationship make them most effective indicators; these are *diagnostic species* (character-species, differential species, and constant companions). (3) Diagnostic species are used to organize communities into a *hierarchical classification* of which the association is the basic unit. The vast information with which phytosociologists deal must, of necessity, be thus organized; and the hierarchy is not merely necessary but invaluable for the understanding and communication of community relationships that it makes possible."

Description of vegetation according to the Braun-Blanquet approach proceeds through the three phases described at p. 59. We will consider them in turn.

The analytical phase

Initially, the region studied and the range of vegetation to be included in the study is decided upon. After an initial survey of the area, including getting preliminary ideas of major vegetation types, vegetation stands (**phytocoenoses**) are selected subjectively for analysis. In each stand, (at least) one sample plot, the **relevé**, is selected subjectively to be representative, homogeneous (mostly judged subjectively), complete (with respect to species composition) and stable. The size of the relevé is not to be below the **minimal area** for the stand analyzed. The minimal area of the stand is the least representative area, i.e., the smallest area containing most species regularly occurring in the stand (p. 80). Several more or less objective methods for determination of the minimal area have been proposed (e.g., Dahl 1957, Dietvorst et al. 1982), but as the concepts of a discrete stand and homogeneity are burdened with problems due to the continuity of vegetation, pragmatical solutions are usually chosen.

The vegetation of the relevé is divided into four **strata**; (1) tree layer (> 2 m, or > 4 m), (2) shrub layer (woody species of a certain height, e.g. 0.8 < h < 2.0 m), (3) field layer (all herbs and woody species below a certain height), and (4) bottom layer

Tab. 3. The cover-abundance scale of Braun-Blanquet (1928) with later amendments, and its ordinal transform (Westhoff & van der Maarel 1978, van der Maarel 1979). BB - value on the Braun-Blanquet scale. OT - ordinal transformation.

Cover-abundance	BB	OT
one or a few individuals	r	1
occasional and less than 5 % of total plot area	+	2
abundant and with very low cover, or less abundant but with higher cover; in any case less than 5 % cover	1	3
very abundant and less than 5 % cover	2m	4
5-12.5 % cover	2a	5
12.5-25 % cover	2b	6
25-50 % cover	3	7
50-75 % cover	4	8
75-100 cover	5	9

(bryophytes and lichens). The percentage cover of each stratum is recorded as descriptors of structure.

All vascular plant taxa, mostly also bryophytes and lichens, are recorded. Species quantities are assigned by a combination of cover and abundance estimation. The two most common cover-abundance scales are those of Braun-Blanquet (1928; expanded by Barkman et al. 1964; transformed to a 1-9 ordinal scale by Westhoff & van der Maarel 1978, van der Maarel 1979) and Domin (Evans & Dahl 1955), see Tabs 3-4. In addition, the **sociability**, that is a measure of the degree of clustring of individuals of each species, and the **vitality** and **fertility** of the species may be noted.

The synthetical phase

After completion of the field work, the relevés are tabulated in a primary table. The major task of the synthetical phase is to rearrange the relevés into structured tables from which distinct plant communities (**phytocoenoses**) emerge. This is a process of successive approximation in which the primary table is rearranged several times.

Table rearrangement involves several judgments and calculation of some community descriptors. **Constancy** is the percent occurrence of a species in a table, provided that the sample plot size is constant. Constancy is often expressed in classes; Class I - 1-20 %, II - 21-40 %, III - 41-60 %, IV - 61-80 %, and V - 81-100 %. **Homotoneity** is an expression of the homogeneity of a vegetation table (Nordhagen 1943). Several indices exist to judge for homotoneity, e.g. the "Raunkiær law of frequency" (Raunkiær 1918), stating that the number of species in constancy class V is to be higher than the number of species in class IV, and "Dahl's index of uniformity" (Dahl 1957, 1960). None of these indices (or others) give entirely unambiguous answers; the former is the less reliable of the two (R. Økland & Bendiksen 1985).

Next, the species are judged for their value as **diagnostic species** for the plant communities. According to Westhoff & van der Maarel (1978), diagnostic species are of

Tab. 4. The Domin cover-abundance scale (e.g. Evans & Dahl 1955). DO - cover-abundance value.

Cover-abundance	DO
one individual with reduced vigour	+
rare	1
sparse	2
less than 4 % cover, frequent	3
5-10 %	4
11-25 %	5
26-33 %	6
34-50 %	7
51-75 %	8
76-90 %	9
91-100 %	10

three types; **character-species**, **differential species**, and **constant companions**. Character-species show preference for one vegetation unit (phytocoenon); the degree of restiction to this unit is termed **fidelity**. Three degrees of fidelity is recognized among character-species: **exclusive character-species** (completely or almost completely restricted to one phytocoenon), **selective character-species** (clear preference for one unit, but present also in others), **preferential character-species** (slight preference for one unit). Differential species show preference for one unit (or one group of units) relative to another, thus useful for differentiation between the two. No regard is paid to presence in other units. Constant companions are species constantly occurring (constancy class V) in a unit.

After judgment of the fidelity, differentiating value and constancy of the species, a local phytocoenon table may be arranged. In this, the species are arranged with character-species first, then differential and constant species, and with the remaining species at the bottom.

The syntaxonomical phase

The final phase of phytosociological work is to fit a phytocoenon (a local vegetation unit) into the formal hierarchy of **syntaxa**, that is plant communities described and named according to the Code of phytosociological nomenclature (Barkman et al. 1976). Three questions (at least) are to be addressed during this phase (Westhoff & van der Maarel 1978: 329): "(1) Which already described association can be recognized in the characteristic taxon combination of the phytocoenon; (2) which lower units could be recognized on the basis of the established differentiating taxa; (3) which taxa can be recognized as character- or differential-taxa from units already distinguished?" The syntaxonomical phase proceeds through consultation of syntaxonomical literature. After the three questions have been answered, the restructured phytocoenon table has become a syntaxon table.

The syntaxonomical hierarchy deserves special consideration. The fundamental unit is the **association**, defined as a phytocoenon having a characteristic species combination, including character-species, differential species and constant companions (Braun-Blanquet 1921, Meijer Drees 1951). The possession of character-species as an absolute constraint on the association has been emphasized by many workers within the tradition (e.g., Braun-Blanquet 1921, Oberdorfer 1968, Dierschke 1971), while others (a less orthodox branch) have allowed associations to be defined by a characteristic species combination not including character-species (e.g., Ellenberg 1954, Braun-Blanquet 1964, Westhoff & van der Maarel 1978). Considerable effort has been put into discussions on this topic, but no general agreement has been achieved. Anyway, the weakening of the demand for character-species has led to a considerable inflation in number of associations, and an accompanied narrowing of the association concept. Naming of associations is by the adding the suffix **-etum** to one or two characteristic species, e.g. Eu-Piceetum abietis is the name of the northern bilberry-fern spruce forests (Kielland-Lund 1981).

Higher units in the hierarchy are, in order of increasing rank, alliance (suffix **-ion**), order (suffix **-etalia**) and class (suffix **-etea**). The bilberry-fern spruce forests have been classified to the alliance Vaccinio-Piceion, order Vaccinio-Piceetalia, class Vaccinio-Piceetea. Formal definitions of these higher units have not been agreed upon (cf. Pignatti 1968, Dierschke 1971, Westhoff & van der Maarel 1978). These higher units are characterized by having a characteristic species combination, in which species characteristic to syntaxa of lower rank are included.

Units of lower rank than the association are, in order of decreasing rank, subassociation (suffix **-etosum**), variant, and facies. The latter two are named after a prominent species. Several proposals for definitions of the lower syntaxa have been proposed. Commonly, variants are characterized by differential species, facies by dominance of a normally occurring species. Some authors separate geographical variation by use of "geographic races", not formally included in the hierarchy.

The outcome for the approach and some problems

The history of 20th century phytosociology is, to a large extent, the history of the spread of the Braun-Blanquet approach over most of the world. From C Europe the approach rapidly spread into E Europe, and still dominates vegetation ecology over most of the European continent. Furthermore, the approach has a strong position in Japan and several other Asian countries, as well as in S America. Through several reviews (e.g., Poore 1955a, 1955b, 1955c, 1956, Becking 1957), the Braun-Blanquet approach also got a foothold on the British Isles and in N. America. The spread of the Braun-Blanquet approach northwards will be dealt with in the next chapter.

The proponents of the Braun-Blanquet approach have stressed the applicability of phytosociology to practical purposes. Vegetation mapping is perhaps the most important of these applications.

The increasing interest in data-processing methods from the 1960s has also spread to the Braun-Blanquet approach. Several program packages for computerized tabular arrangement (the synthetical phase) have been made (e.g., the TABORD package, van der Maarel et al. 1978), and it is now customary to use numerical classification and ordination techniques as a part of the synthetical table work, for identification of relevé groupings, for elucidation of relationships between groups, etc.

Some problems: the local scale. Returning to the vegetational continuum, there is a deep cleft between reality on one hand and the syntaxonomic hierarchy on the other. Even on a local scale, not including climatical variation, there is impossible to incorporate the natural relationships in the vegetation into a hierarchy. Furthermore, contemporary phytosociology is burdened with a tremendous (and increasing) literature on questions relating to the nomenclature and delimitation of syntaxa. This seems a waste of effort when nature is continuous and no classification is natural. The formalization of the hierarchy thus appears to be one of the main disadvantages of the approach, bound to tie up more and more research effort into syntaxonomical problems with doubtful relevance to the understanding of patterns and processes in vegetation.

Some problems: the regional scale. The ambitious goal of the Braun-Blanquet approach is the expansion of the syntaxonomic hierarchy to include most of the earth's vegetation. The step from the local to the regional scale, crucial to this expansion, involves two major problems: (1) the intergradation of phytocoena along regional gradients, and (2) the lack of geographic consistency of species fidelity. These problems have been known from before 1920, but still have not got satisfactory solutions.

As a solution to the second problem, Westhoff & van der Maarel (1978) recognized character-species of three kinds: **local character-species** (fidelity restricted to part of the area of the syntaxon), **regional character-species** (fidelity in whole area of syntaxon, but distribution of the species exceeding that of the syntaxon), and **general character-species** (fidelity in whole area of syntaxon, areas of species and syntaxon coincident).

The problem of building local and geographic variation into one hierarchy has been discussed by several authors (e.g., Knapp 1948, Meijer Drees 1951, Westhoff & van der Maarel 1978). In fact, these two kinds of variation has led the authors to consider two different principles applicable to the construction of the hierarchy: **the horizontal classification** with a geographic, and **the vertical classification** with an edaphic-ecological basis. Several practical solutions have been proposed to accomodate these two principles into one hierarchy: Most authors allow the description of narrowly defined "regional" and "local" associations if they possess regional or general character-species. Local or regional associations occupying similar habitats in different areas are termed **vicariant associations** (Meijer Drees 1951), examples are the bilberry-herb forests of S Fennoscandia; the spruce forests of this kind is classified to Eu-Piceetum, intergrading continuously into the W Norwegian birch forests classified as Corno-Betuletum (Aune 1973). Proposals for restriction of some hierarchical levels to one kind of variation have been made, e.g., by Meijer Drees (1951), following Braun-Blanquet (1928). They restricted the variant to horizontal classification, while the subassociation was used for vertical classification. This has not gained common acceptance, and Westhoff and van der Maarel (1978) suggest vertical and horizontal classification at each level of the hierarchy. The practice on this matter differs from one investigator to another, and no general solution to the problem of regional variation seems to be within reach.

Assessment. The major problems of the Braun-Blanquet approach today emerge from the inconsistency between properties of the vegetation and the system used for its description. Furthermore, the Braun-Blanquet approach is based on a inductive method, heavily burdened with subjectivity in all phases of the classificatory process. Although helpful in an initial phase of vegetation ecological research, aiding the process of structuring variation, other methods are needed to test the claimed relationships for their objective validity and their relative importance.

THE NORTHERN TRADITION: SCANDINAVIAN PHYTOSOCIOLOGY

The northern European approaches to description of vegetation are easily divided on two schools; the Scandinavian (Uppsala) school and the Finnish school. These will be treated separately. Several outlines of history and basic concepts of the Uppsala school of phytosociology exist, e.g., R. Fries (1950), Whittaker (1962), Trass & Malmer (1978), and R. Økland & Bendiksen (1985).

The Uppsala school before 1930

Late 19th century phytosociology using widely circumscribed formations based on life-forms of dominating species as units (e.g., Hult 1881, 1887) formed the origin of the Northern tradition. The 1910s was the start of modern Scandinavian phytosociology, with a strong increase in the effort put into description of vegetation. The fundamental vegetation unit, the association, was defined by T. Fries (1913: 47) as a vegetation-type with largely uniform physiognomy and floristic composition. The concept of the association as well as a whole theory of vegetation (cf. Trass & Malmer 1978) was further developed by G.E. Du Rietz (1895-1967) and co-workers (e.g., Du Rietz et al. 1918, 1920, Du Rietz 1921), redefining the association by replacing "floristic composition" with "having its own set of constants". A **constant** was defined as a species occurring in more than 90 per cent of the sample plots classified to an association (Du Rietz et al. 1920). Nordhagen (1928) amended the definition of the association again, emphasizing floristic-physiognomic uniformity as well as constant and dominant species (note the similarity to, and difference from the characteristic species combination of the Braun-Blanquet approach).

The analytical phase in the work of the early Uppsala school differed considerably from the Braun-Blanquet approach. In each homogeneous stand, five or more small sample plots, often 1 m^2 or less, were placed subjectively. The term **frequency** was used for the percentage of sample plots within a stand containing a species, while **constancy** was used for the percentage of a species in a synthetic material (several stands). Species abundances were estimated by use of the Hult-Sernander-Du Rietz cover scale (Du Rietz 1921, cf. Tab. 5). The associations were often delimited in the field. By intention, they should be applicable to the investigation area only; thus the synthetical phase was far less time-consuming than in the Braun-Blanquet approach and a syntaxonomical phase was irrelevant. A distinctive feature of the early history of the Uppsala school was the strong parallel interest in taxonomy: Du Rietz has published on the taxonomy of bryophytes and lichens and Nannfeldt was a renowned mycologist. This strong taxonomic tradition made the inclusion of cryptogams in the survey of the small sample plots not only natural, but an obligatory and obvious part of the analysis. This strong taxonomic tradition has continued till today.

The association concept of the Uppsala school around 1920 was extremely narrow, as readily apparent from some of the monographs. In a monographic study of the mire Komosse, S. Sweden, Osvald (1923) described 164 associations! In addition, variants were used for types at a lower level. When a hierarchy was needed, it was obtained by using formations based on life-forms of the dominating species (mostly of upper strata).

Tab. 5. The Hult-Sernander-Du Rietz cover scale (Du Rietz 1921). HSD - value according to the scale.

Cover	HSD
< 1/16	1
1/16 - 1/8	2
1/8 - 1/4	3
1/4 - 1/2	4
1/2 - 1/1	5

The Uppsala school after 1930

The use of constants for defining the association, and the sharp limit between constants and accidental species claimed by Du Rietz et al. (1920) and Du Rietz (1921) provoked strong criticism by most contemporary Scandinavian plant ecologists and many others as well (e.g., Nordhagen 1920, 1924, Arrhenius 1921, Braun-Blanquet 1921). This criticism led Du Rietz (1930, 1932, 1936) to shift to uniform dominance in each layer as the diagnostic feature of the fundamental unit, now renamed sociation. The following definitions were given: "A **sociation** is a stable phytocoenose of essentially homogeneous species composition, that is at least with constant dominants in each layer" (Du Rietz 1930: 307, translation after Trass & Malmer 1978). "A consocion is a relatively homogenous plant population of species that all belong to the same layer, dominated by a certain species or a few species together. Such a consocion can, either alone or with one or more consocions of other layers, form a sociation - that is, the plant community forming the whole vegetation of its site and formed by either a certain consocion or a combination of certain consocions of different layers" (Du Rietz 1932: 63-64, translation by Trass & Malmer 1978). Despite its new name, the sociation was largely equivalent to the old association of the early Uppsala school. Sociations have been widely used for description of mountain vegetation (e.g., Fægri 1934, Nordhagen 1937, 1943, Gjærevoll 1949, 1956), but have not commonly been used for forest and mire vegetation. Mire vegetation has been extensively described by the methodology of the Uppsala school (e.g., Sjörs 1948, Malmer 1962), but the name association has been retained for the fundamental unit and the concept of the association broadened relative to the old one (Sjörs described 24 associations from Skattlösbergs Stormosse, a mire with a range of environmental variation comparable to Osvald's Komosse).

The analytical methods of the Scandinavian workers did not change along with the change in the theoretical framework; the analysis of small sample plots distributed within stands has continued till today (cf. R. Økland 1989b).

Merging of the Braun-Blanquet and Uppsala schools

From the 1920s, the development of the Braun-Blanquet approach attracted the interest of the leading Norwegian phytosociologist Rolf Nordhagen (1894-1979). The alliance concept appears to have appealed to him quite early (cf. Nordhagen 1924, 1928), but the poverty of species in the northern, formerly glaciated parts of Europe, made an association-concept involving character-species apparently unsuitable for Scandinavian vegetation. After some years of some approximation of the two approaches, the 6th International Botanical Congress in Amsterdam in 1935 sanctioned a formal merger of the two schools: sociations and associations were regarded as alternative basic units to be fitted into the Braun-Blanquet hierarchy of higher units (Du Rietz 1936).

Applications of the combined approach soon appeared; already in 1937 Nordhagen (1937) made a classification of S. Norwegian mountain vegetation in which sociations were grouped into alliances and orders. Later on, sociations were combined into associations by means of differential and preferential species (character-species in a very weak sense), as in the monumental "Sikilsdalen og Norges fjellbeiter" (Nordhagen 1943), and "The plant communities of the Scandinavian alpine snow-beds" (Gjærevoll 1956), the highlights of this combined approach. The alliance maintained its position as the most important among the higher units.

The situation today and the outcome for the Uppsala school

The merger of the Uppsala school and the Braun-Blanquet approach continued. The shift in emphasis from sociations to associations (Nordhagen 1955, Dahl 1957) made the merger complete, as demonstrated by the last classical mountain vegetation monograph, "Rondane: mountain vegetation in South Norway and its relation to the environment" (Dahl 1957). Since that time, much phytosociological work has been carried out in Scandinavia within the Braun-Blanquet approach (e.g., Hallberg 1971, Olsson 1974, Kielland-Lund 1981), including an attempt to compile a list of Norwegian syntaxa within the Braun-Blanquet system (Vevle 1983). Thus the Uppsala school has nearly been included in "the expanding sphere of the school of Braun-Blanquet", as stated by Trass & Malmer (1978). The outcome for the Uppsala school was described by Trass & Malmer (1978: 217) as follows: "There is no longer a school of Uppsala as such; Swedish phytosociology now represents more a tradition than a well-defined method. A persistent feature of this tradition is the stress on small-scale variation in vegetation and the interest in vegetation units of low rank, ... This emphasis may be ascribed not only to the tradition and its methods, but also to a flora rather poor in number of species and therefore including many vegetation types with few and poorly specialized species. It is often difficult to find species fulfilling the requirements for character-species, at least on the level of associations."

THE NORTHERN TRADITION: THE FINNISH AND OTHER SITE-TYPE APPROACHES

The history and principles of the forest site-type approaches are outlined by Malmström (1949), Whittaker (1962), Frey (1978) and R. Økland & Bendiksen (1985).

The Finnish site-type approach

The Finnish school of forest site-types was founded by the Finnish botanist and statesman A.K. Cajander (1879-1943). The basic principles were worked out in a series of papers (Cajander 1909, 1913, 1921 etc.). Like the founders of the Uppsala school, Cajander stressed the value of the species of the bottom and field layers as indicators of **site** properties. The site concept is central, comprising the vegetation as well as its environment (soil, etc.). Sites are classified into **site-types**, comprising all stands which at maturity have more or less identical floristic composition and ecologic-biological nature (cf. Cajander 1926). The site-types thus comprise all successional stages. Site-types are characterized by the use of dominant, constant, differential, and character-species. Naming is based on dominant's names, e.g. "The Myrtillus-Type", comprising the bilberry forests.

The analytical phase proceeds through selection of homogeneous stands (sites) for analysis, positioning on one large (or in mire, several smaller) sample plots within the stand, and recording of percentage cover for all species. Emphasis is put on total species composition as within the Uppsala school.

The site-types of more recent applications (e.g., Kalela 1961, Hämet-Ahti 1963, Haapasaari 1988), are narrow units, corresponding to variants and subassociations in the Braun-Blanquet system. The units have occasionally been grouped in **site-type classes**, the higher units in this system.

A major difference from the phytosociological approaches is that emphasis has been

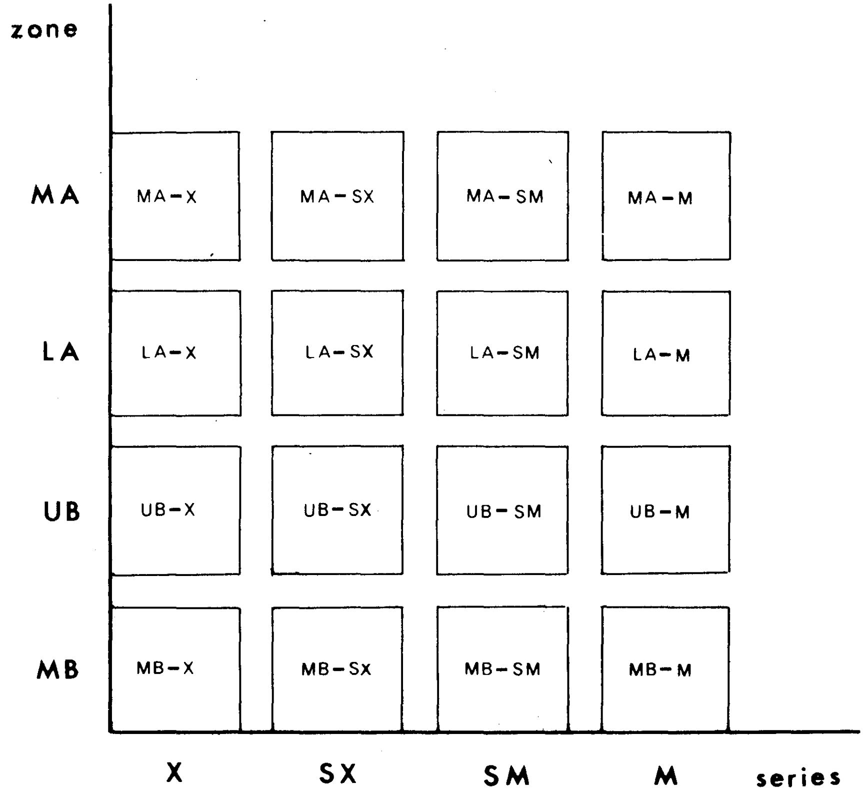


Fig. 56. The direct gradient approach to classification of vegetation. Division of the forest-alpine transition in Grunningsdalen, SE Norway, into 16 site-types by R. Økland & Bendiksen (1985). The site-types are shown as squares in a two-gradient system. Series along the complex-gradient topographic moisture-snow cover are shown along the abscissa; X - xeric, SX - subxeric, SM - submesic, M - mesic. Zones along the ordinate are MB - middle boreal, UB - upper boreal, LA - low alpine, MA - middle alpine.

on gradient relationships rather than on hierachies. Already in one of the pioneering works, the ecological gradient relationships of the site-types were expressed by arrangement of the site-types in **ecological series** (Cajander 1903). These series correspond to coenoclines (intentionally ecoclines) in the terminology of Whittaker (cf. p. 17). For instance, relationships along the gradient from poor and dry to rich and more mesic in boreal forests are normally expressed in the forest site-type series. Description of **parallel site-type series** in different regions, consisting of **vicariant site-types** (e.g., Kujala 1936), has been useful for differentiation of forest vegetation regions (Kujala 1938, Hämet-Ahti 1963, Ahti et al. 1968). Similar approaches have been used for regional differentiation of Finnish mire vegetation (Ruuhijärvi 1960, Eurola 1962).

Direct gradient approaches to classification

The interest in gradient relationships in the Finnish school was also evident in theoretical contributions to vegetation science. In 1942, Tuomikoski proposed an approach to classification (Tuomikoski 1942) that has later been adopted independently by vegetation ecologists in several parts of the world, **the direct gradient approach to classification** (e.g., Whittaker 1956, 1967). An account of history and concepts is given by R. Økland and Bendiksen (1985). The essence of this approach is in many ways similar to the site-type approach, aiming at a simultaneous classification of vegetation and site (ecoclines). Assuming that the major ecoclines (or coenoclines) are known, the direct gradient approach to vegetation converts the multidimensional pattern into a classification by a division of the gradient axes, thus providing a reticulate, non-hierarchic classification (Tuomikoski 1942, Webb 1954). Each gradient-segment combination then becomes a type (site-type) in this system. One example is the system of forest- and alpine site-types in Grunningsdalen, SE. Norway, described by R. Økland and Bendiksen (1985). Two gradients; topographic soil moisture-snow cover (4 segments) and elevation (4 segments) were considered, giving a total of 16 site-types (Fig. 56).

An early venture in gradient analysis is the system of N. Swedish forest site-types proposed by Eneroth (1931, 1934, 1937), developed further by Arnborg and Ebeling (1978). In this system forest site-types are displayed in a two-dimensional system with the moisture and nutrient gradients as axes. Strong influence from Tuomikoski's ideas can also be traced in the Swedish approach to mire classification (Sjörs 1948, Malmer 1962a, Fransson 1972, see also Økland 1989b). These works combine the small sample plots of the Uppsala school with a reticulate classification system, in which units represent one particular position in a three- or four-gradient system.

Arguments in favour of the direct gradient approach to classification are given by R. Økland and Bendiksen (1985), emphasizing consistency with the continuum concept and suitability for comparisons between regions. They emphasize that a **local reference-frame**, that is a set of local ecoclines divided into a reticulate system, is suitable for regional comparison by making recognition of **ecologically corresponding vegetation types** in different regions possible.

OTHER APPROACHES TO CLASSIFICATION OF VEGETATION

The reviews of approaches to classification by Whittaker (1962) and several contributors to "Classification of natural communities" (e.g., Whittaker 1978b) show that the number of more or less distinct approaches to classification is far higher than the four treated here. The Anglo-American tradition with its classification into **dominance-types** (Whittaker 1978c), the Russian tradition (Aleksandrova 1978) and others could be mentioned. These traditions have, for many reasons, played less important roles on the international scene, or have become parts of other traditions (e.g., the direct gradient approach mentioned above). They will not be considered further here.

Synusial approaches. Within most schools, the study of single layers of the vegetation, **synusiae**, have been widespread. Within the Braun-Blanquet school (see Barkman 1978) a separate hierarchy was erected to accomodate synusiae, with the **associon** as the basal unit corresponding to the association of the full syntaxonomical hierarchy. In the Uppsala school, the **union** was the main unit. The synusial approach has been widely criticized for its lack of attention to the interdependence of layers, and has mostly been used for description of sociological relationhips of bryophytes and lichens.

TODAY'S SITUATION: THE DEVELOPMENT OF NUMERICAL TECHNIQUES AND WEAKENING OF TRADITIONS

The primary aim of phytosociology as a branch of vegetation ecology is classification and description of vegetation. The concluding remarks of R. Økland and Bendiksen (1985: 198) are relevant for assessment of the role of phytosociological approaches within vegetation science: "In our opinion the multidimensional structure of vegetation makes all approaches involving classification artificial, because they involve drawing boundaries in a basically continuous environment with its correspondingly more or less continuous vegetation. The numerous classificational approaches that have been, and are still in use, for the understanding of the structure of vegetation are per se a proof that no single correct classification exists. It thus does not seem profitable for vegetation ecology, as a branch of science, that so much effort is spent on discussions concerning details of classifications. Such discussions actually lead away from the real task of vegetation ecology - to understand the relationships between vegetation and environment. At this point we must emphasize the urgent need for integrated studies treating variation in vegetation and ecological factors simultaneously, without attaching too much importance to either component of the ecosystem." A first conclusion is that the main role of phytosociological approaches should be in the intitial (α) phase of vegetation ecological exploration, for generation of hypotheses for more intensive studies (cf. Harper 1982). A rapid scrutiny of major ecological journals will reveal a strong increase during the 1980s in the number of studies treating the relationships between vegetation patterns, environmental conditions, vegetation models, structuring factors and processes. Phytosociology still has a central position on the European continent with satellites over the world, but the general impression that the share of the total effort in vegetation ecology that is devoted to phytosociology is declining, can hardly be contested. Vegetation ecology no doubt is in touch to enter a next, "post-descriptive" phase (cf. Harper 1982).

From the late 1950s, the phytosociological approaches have been complemented, and challenged, by multivariate (numerical) techniques. The early period (till ca. 1975) was characterized by lots of methods launched on the international arena. Most of these methods proved to be of low value. After 1975 there has been more attention to development of models for vegetation-gradient relationships (cf. pp. 22-33), thorough testing of methods for consistency with these models, and eventually abandonment of inferior methods. Today, the number of numerical techniques have been reduced drastically. The investigator can choose among two or three ordination methods and a somewhat higher number of numerical classification techniques as alternatives to phytosociological approaches with their inherent subjectivity. Crucial to the multivariate appoaches is the possibility for generating hypotheses that may be tested by use of independent ecological data sets. In order to retain the possibility of using statistical methods, the sampling procedure is essential. In the following, we will examine some of the prospects for analysis of vegetation-environment relationships offered by multivariate numerical techniques. For reasons that will become apparent, one should carefully select the best of the old for incorporation in the new approach. Two essential features of the analytical phase of the Uppsala school should be particularly stressed: the use of small sample plots and the emphasis on the full species composition of the vegetation.

METHODS: COLLECTING DATA

SAMPLING DESIGNS

Almost all problems in vegetation ecology are approached by sampling, selecting a small subset of the vegetation we are interested in. Subsequently, the properties of this subset are investigated in the belief that they reflect important properties of the vegetation itself. Obviously, the way the sampling is carried out implies a strong filtering of the numerous inherent properties of vegetation. While vegetation is continuous over large areas, with almost no pair of sites completely identical, our sample plots are discrete with a fixed size. Any choice of sampling design implies restrictions on properties of vegetation we are able to detect. The nature of these restrictions determines the degree of realism in the results, and severely limits the scope of the analysis. From this introduction, it follows that sampling considerations are among the most important subjects of vegetation ecology. The literature on sampling methods is extensive. A recent review is provided by Kenkel et al. (1989).

Sampling of vegetation proceeds through three phases: (1) placement of sample plots, (2) determination of sample plot size (and shape), and (3) determination of number of sample plots.

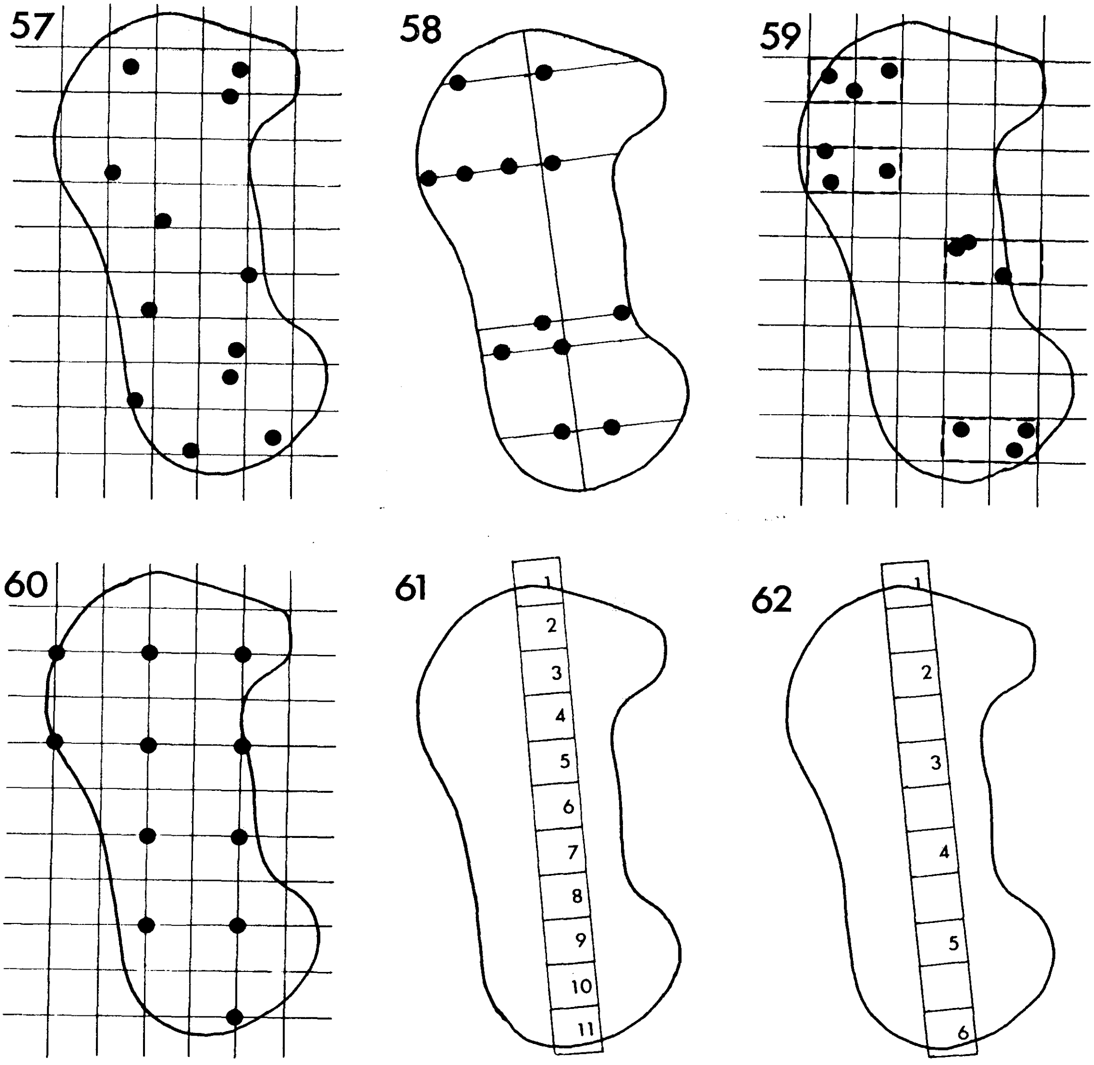
Placement of sample plots

The sampling designs to be described below differ in many respects. The most important are: (1) Statistical properties; whether the sample plots can be assumed independent of each other, and hence whether formal statistical tests will be valid. (2) Representation of dominant versus rare species, species combinations, and combinations of environmental conditions (and vegetation types). (3) Practical considerations, e.g. time needed in the field for placement of sample plots. The sampling designs will be discussed with respect to these (and other) aspects.

Selective sampling

When the purpose of a study is description of selected stands as in phytosociology, **selective** (or subjective, or preferential) **sampling** is a natural choice. Plots which are sampled selectively according to the Braun-Blanquet approach, are called **relevés**. By this method, subjectivity will constrain all subsequent analyses, as pointed out in the treatment of phytosociological approaches. The demands for independence of plots are, of course, not satisfied, and tests of species abundances, areal importance of vegetation types, etc., are not valid. This kind of sampling is inappropriate if exploration of vegetation-environment relationships are aimed at. The representation of rare species and vegetation types is often good, as they can be overrepresented relative to their frequency in the investigation area. Furthermore, the time necessary in the field for plot selection is minimal.

Selective sampling has not only been common within the phytosociological traditions, but has been the most common sampling design for most kinds of ecological studies. Most studies by the direct gradient approach (e.g., Whittaker 1956, R. Økland & Bendiksen 1985) used subjectively placed sample plots to represent the variation within each combination of



Figs 57-62. Different methods for placement of sample plots applied to a hypothetic investigation area. Fig. 57. Random sampling (12 sample plots); random numbers are taken as coordinates for points relative to a grid. Fig. 58. Stratified random sampling (12 sample plots); a baseline is placed along the long axis of the investigation area, transverse lines are randomly placed along the baseline, and sample plots are located on the transverse lines by random numbers, the number of sample plots along each transverse line proportional to the length of the line. Fig. 59. Stratified random sampling (12 sample plots); four blocks of fixed size are randomly placed within the investigation area, within each block three sample plots are randomly distributed. Fig. 60. Systematic sampling (11 sample plots) in a 2-dimensional grid. Fig. 61. Systematic sampling (11 sample plots) in a closed transect (1-dimensional grid). Fig. 62. Systematic sampling (6 sample plots) in an open transect (1-dimensional grid).

segments along major gradients. The subjective bias is as in the phytosociological approaches, and there is a great danger of circular reasoning: vegetation used as indicator of ecological conditions, samples placed accordingly, and species distributions along the assumed gradients considered as if the underlying gradients were documented.

The only situations where selective sampling is unavoidable, is in autecological studies. When the ecological relationships of one species, or a group of related species, is the object of our study, all kinds of randomization will be impractical unless the species are abundant or very abundant in the studied region. Normally, this is not the case. Autecological studies covering a broad geographical area, or addressing rare species regardless the area studied, use **synedria** (Lid 1964); sample plots placed subjectively to include the species in question. The method is subjectively biased, but inclusion of ecological measurements from each sample plot improves environmental interpretation. It should, however, be remembered that the amplitudes and optima of species, as estimated from synedria, may be strongly biased by the subjectivity of the sampling. Synedria used for population studies often show a marked decline of the analyzed species during the first year(s) due to inadvertent selection of plots in which the species shows particular vigour when sample placement was performed.

Random sampling

From a statistical point of view, **random sampling** (Fig. 57) is optimal. If plots are positioned at random, there are no restrictions on statistical testing. The most common method for random sampling, is by imposing a co-ordinate system (a grid) on the investigation area, and indicate this in the field. Co-ordinates for sample plot positions are chosen as pairs of random numbers. Random sampling has not been used in many Fennoscandian studies. One recent example is the study by R. Økland (1989b) of the mire N. Kisselbergmosen. Eight hundred sample plots were randomly distributed on a 0.3 km^2 mire by the procedure described above (R. Økland 1989b: Fig. 3).

Random sampling is optimal if the research purposes include estimation of abundance of species and types (Greig-Smith 1964, Smartt & Grainger 1974), independent tests of classifications, or identification and relative ranking of coenoclines (R. Økland 1990a). By random sampling, the quantitative optimum of a species is found, reflecting the relative frequency in the investigation area of different ecological conditions. Rare combinations of environmental factors or rare species are poorly represented in the data set. This impacts the subsequent analysis, mostly in an unwarranted way: (1) Considerable redundancy results for a few, dominant types, while many rare but ecologically distinctive types (or species) are poorly represented or lacks altogether. In the study of N. Kisselbergmosen (R. Økland 1989b), 32 site-types were distinguished by a direct gradient approach to classification using four complex-gradients. In the set of 800 randomly placed sample plots, 77 per cent of the sample plots were classified to one of the nine site-types with the highest areal importance. Two site-types were not represented at all, while eleven site-types were represented by four sample plots or less (R. Økland 1990a). Several species were so rare in the material that no conclusions about their autecology in the material could be drawn. (2) Much time is spent on collecting redundant information. (3) Most often the rare combinations of ecological factors are associated with gradient extremes. Thus random sampling often results in a strong redundancy with respect to mid-gradient conditions, while extremes are poorly represented or not represented at all. This affects the study of species responses to known gradients (direct gradient analysis), coenocline identification by numerical techniques, niche studies etc. (R. Økland 1986c, 1990a). In the study of N. Kisselbergmosen (R. Økland 1989b), species responses to a gradient in depth to the water table would have been improved by proportional overrepresentation of the (rarely occurring) gradient extremes. (4) Unless the sampling intensity is very high, random sampling often results in spatial clumping of plots and an uneven coverage of the investigation area (Pielou 1984). This is, however, mostly not very serious. (5) Identification of sample plot positions in the field is often claimed to be time-consuming.

The disadvantages of random sampling mostly outweigh the advantages. In most cases, strict independence of sample plots are not desired as statistical testing of abundances are not of interest. Relaxation of the demands for strict randomness is advocated by most authors (e.g., Greig-Smith 1964, Gauch 1982a, Austin 1987).

Stratified random sampling

Several ways of restricting randomness have been proposed. Thereby some subjectivity is introduced into the sampling designs, but subjective placement of individual sample plots is avoided. Two possible sampling designs are shown in Figs 58-59. Four examples will be given to illustrate **stratified random sampling**, often termed **restricted random sampling**.

Matthews (1979a) studied the vegetation of the Storbreen gletschervorfeld, Jotunheimen, C. Norway. He imposed a grid with 7 x 13 squares upon an aerial photograph of the investigation area. Eight points were allocated at random to each of the squares. In the field, sample plots positions were found by measurement of distances and directions from of identifiable details on the aerial photo, boulder stones, etc. By this sample placement strategy, a more even spacing of sample plots over the area was ensured than would have been obtained by random placement.

Halvorsen (1980) studied the vegetation of shell-beds at Akerøya, Hvaler, SE Norway. At Akerøya, shell-beds occur as disjunct patches. Sampling was approached by a first mapping of shell-beds. A total of 32 shell-beds, each larger than ca. 300 m^2, were found (Halvorsen 1980: Fig. 2). Each of these were provided with a co-ordinate system with mesh width 20 m, and 2-8 sample plots were positioned within each shell-bed by use of pairs of random numbers as co-ordinates. The number of sample plots per shell-bed was proportional to the area of the shell-bed.

In an investigation of the Fritzøehusparken beech forest, Brunlanes, SE Norway, T. Økland (1988) used a **baseline approach** (T. Økland 1988: Fig. 1, cf. also Fig. 58). Two discontinuous valley sides made up her investigation area. They were carefully delimited and one baseline was measured and marked in the field in each of the two compartments. The positions of transverse lines were determined by use of random numbers, referring to distance along the baselines. The number of sample plots to be placed along each of the transverse lines was proportional to the length of the line. The sample plots were randomly positioned along the transverse lines.

The three examples all include some subjectivity in the decisions (the number of sample plots per unit distance along the baseline, the number of sample plots per unit area in the former two designs), but still satisfy the demands for independence of sample plots. All points in the investigation areas have the same probability of being sampled. Thus the statistical properties of these restricted random sampling designs are about the same as for random sampling. Strategies involving **randomization within random blocks** (Fig. 59) maintain statistical properties when the number of blocks and/or the total area of the blocks relative to the area of the investigation area are high.

The examples of stratified random sampling so far considered do not improve the disadvantages (1)-(3) of random sampling procedures, but may improve points (4) and (5). A more even spacing of sample plots over the investigation area is likely to result from randomization within blocks, all blocks used for sampling (as in Matthews' and Halvorsen's studies), but the baseline and the block approaches result in stronger clumping of plots when the percentage of the investigation area included in the blocks (or the number and total length of transverse lines relative to the baseline) is reduced. The main advantage of the stratified random sampling procedures described over random sampling are on the practical part (point (5)).

Restricted random sampling also includes strategies with stronger relaxation of the demands for randomness. One example is the study of variation in bilberry-dominated spruce forest in Rausjømarka, Enebakk, SE Norway by T. Økland (1989). In order to span the macro-scale variation in ecological conditions (moisture, aspect, slope etc.), ten macro sample plots, each 5 x 10 m, were selected. Within each of these plots, five meso-scale sample plots (each 1 m^2) were positioned at random. Analysis of vegetation was performed at the meso scale. This sampling design can be termed **randomization within selected blocks**. By randomization within each block, this procedure maintains randomness at the fine scale, and avoids the potentially important role of the human factor in selection of individual sample plots. Randomization within selected blocks efficiently resolves all five problems of strictly random sampling techniques. The problems (1)-(3) of random sampling techniques can only be removed by relaxation of the demands for randomness, thereby sacrificing the independence of sample plots in the strict statistical sense. Most studies do not involve tests based on these assumptions, and the loss is then of no importance. In such cases, randomization within selected blocks is often a natural choice of sample placement strategy.

Systematic sampling

Systematic sampling (Figs 60-62) implies that a grid in one or two dimensions is superimposed upon the investigation area or a part of the investigation area. Sample plots are regularly placed in the grid.

Sampling by use of a two-dimensional grid is often referred to as **grid sampling**. Galten (1987) used grid sampling in his study of the vegetation of the mire Åsenmyra, Engerdal, C. Norway. He imposed a grid with mesh width 50 m in the N-S direction, 25 m in the W-E direction, on the investigation area. He sampled every point on the grid except every third point in the W-E direction, giving a total of 390 sample plots. Grid sampling is particularly appealing for biogeographical studies. Andersson (1988) studied gradients in the flora of Dalsland, W. Sweden, by division of the province into 271 contiguous squares, each 5 x 5 km.

One-dimensional grids are termed **transects**. They are of two kinds; **closed transects** (Fig. 61), with sample plots contiguously placed along the transect, and **open transects**, with regular or random positioning of sample plots along the transects. Closed transects are often used to display vegetational variation along sharp gradients, e.g., the hummock-carpet gradient in mires (the standard example from Rønnåsmyra), and the ridge-snow bed gradient in mountains (Dahl 1957). Open transects are used for less sharp gradients, for instance the topography-moisture gradient in boreal forests. The study of R. Økland and Eilertsen (in prep.) of the variation in forest vegetation of the Solhomfjell area, Gjerstad, Aust-Agder, S Norway, used this method (Fig. 63). They selected 8 transects assumed to cover most of the local variation due to other factors (aspect, altitude, slope, etc.). The number of sample plots along each transect was proportional to the length of the transect. Every tenth meter along the transect was marked in the field as a potential sampling site. The desired number of sample plots were selected by use of random numbers.

Systematic sampling techniques involve some subjectivity, as the origin of the grid

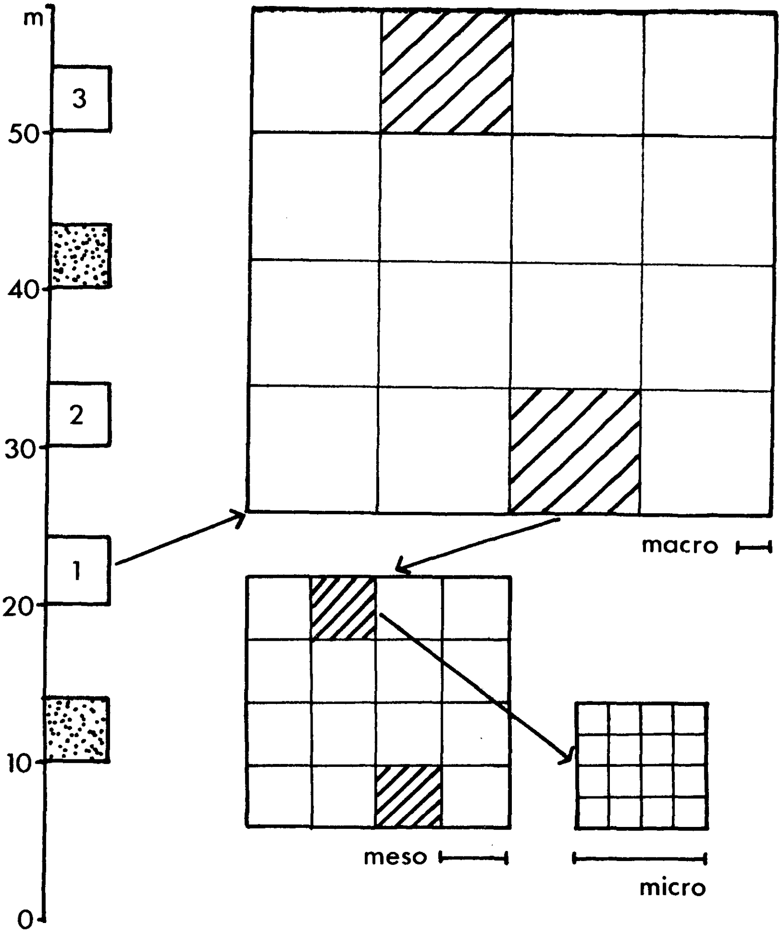


Fig. 63. The sampling design used in the study of boreal forest vegetation in Gjerstad, Aust-Agder (R. Økland & Eilertsen, in prep.). Transects from hilltop to valley bottoms are demarcated in the field (left). Every tenth meter along the transect is a potential site for a macro sample plot. Rejection of plots is done by reference to a set of criteria. The macro sample plots, each 16 m^2, are divided into 16 subplots, 1 m^2 each. Two of the subplots (at fixed positions) were taken as meso sample plots, 1 m^2 each, and divided into 16 subplots (each 0.0625 m^2). Two of the subplots (at fixed positions), termed micro sample plots, were divided again into 16 subplots. Presence/absence of all species was recorded in subplots at the meso and micro plot scales.

or the end-points of the transects are selected subjectively. This subjectivity is unimportant for the grid sampling, but may be quite important for the transect techniques. The demand for independence of sample plots is well satisfied with grid sampling provided the mesh width is much smaller or much larger than recurrent structures of vegetation (e.g., regular hummock-hollow patterns in a unilaterally sloping mire). In most cases, this condition is easily satisfied. Galten (1987) used different mesh widths in each of the two dimensions of his grid in order to reduce this probability. Demands for independence of sample plots are generally not satisfied with transect sampling; in this respect transects are similar to randomization within selected blocks.

The disadvantages of random sampling are reduced to some extent by the systematic sampling approaches. Grid sampling shares the disadvantages (1)-(3) of random sampling, but resolves the uneven coverage of the investigation area (4), partly also point (5), the time-demandingness of sample plot localization in the field. As mentioned above, disadvantages (1) to (3) of random sampling techniques can only be resolved by incorporating elements of subjectivity into the sampling design. The transect techniques may partly correct for point (3); by placing transect end-points at gradient extremes a far better representation of rare species and quantitatively unimportant combinations of environmental factors may be achieved. However, this problem is mostly only resolved only to some degree, as the mid-gradient positions will be represented more or less in proportion to their areal importance. Thus problems (1) and (2) will not be solved except in the exceptional cases when all steps along a dominant gradient have almost the same quantitative importance. Then a transect method will be close to optimal for general-purpose sampling of vegetation.

Systematic sampling designs with elements of stratified randomness may also be constructed. One could, for instance, perform a stratification of a transect according to an environmental variable, and perform a stratified randomized sampling within each compartment. For instance, a transect in a boreal forest ranging from a hilltop with lichen-dominated pine forest, via mixed spruce-pine forest and bilberry-dominated spruce forest on the slope, to fern-dominated spruce forest in the valley bottom, could be divided into compartments according to terrain form (hilltop, convex slope, plane slope, concave slope, valley bottom). This would reduce the redundancy in the data set and more or less reduce (or remove) problems (1)-(3).

Assessment and recommendations

Methods for placement of sample plots make up a series from purely randomized to purely selective techniques, associated with variation from strictly objective to strictly subjective positioning of individual sample plots. Each end of this series is connected with a set of advantages and disadvantages, as discussed in detail above. The disadvantages of the randomized techniques can only be ameliorated by incorporation of an element of subjectivity into the sampling design; the disadvantages of the selective techniques are only ameliorated by choice of another strategy. The following questions should be considered when strategy for sample plot placement is decided upon: (1) Are estimation of quantitative characteristics (species abundances, areal importance of types etc.) an important purpose of the study? If yes, either of random, stratified random or grid sampling should be chosen. (2) If not, and if the purpose of the study does not specifically call for a selective sampling technique, transect sampling or, perhaps more often, randomization within selected blocks, will mostly be optimal compromises. They avoid the strong subjectivity of selective methods, while reducing or avoiding the redundancy and the poor representation of rare combinations in many randomized or systematic methods. If a major gradient is present, transect sampling is often appropriate, and if all stages along the transect have almost the same quantitative importance, closed or open transects are suitable. If, however, this is not the case, randomization within selected blocks or randomization within segments of transects may be useful.

Sample plot size

The use of square sample plots for vegetation analysis has a long tradition. It is practical and convenient, and allows comparison with most previous studies. The effect of sample plot shape is unimportant as compared to effects of size, and sample plot shape will not be further discussed.

All sample plots in a study should have the same size (or sizes, as each plot may allow analysis of subplots of several sizes) in order to be directly comparable (Greig-Smith 1964, Westhoff & van der Maarel 1978, Gauch 1982a). The main problem is to decide *which* size to choose. Selection of sample plot size is to make a compromize between (1) **homogeneity**, suggesting small plots, and (2) **representativity**, suggesting large plots. We will consider each of these two important demands in turn, ending with some recommendations.

Homogeneity

Sample plot or stand homogeneity can be defined as follows (Dahl 1957: 29): "A plant species is said to be homogeneously distributed over an area if the mean number of individuals or the mean plant mass of the species in question within a sample plot of given size is the same in all parts of the area. A plant community is said to be homogeneous if the plant species of the community are homogeneously distributed." Probable, the reference to "plant communities" refers to concrete stands of vegetation. Ecological homogeneity can be defined in a similar way, by specifying a range of variation along each complex-gradient that should not be exceeded within a sample plot in order for the plot to be considered homogeneous. Despite explicit definitions, homogeneity remains a difficult concept. This has several reasons:

(1) In a continuous nature, increasing area inevitably implies increasing environmental heterogeneity, increasing number of micro-scale habitat niches, and increasing range of variation along micro-scale (and to a lesser degree also other) gradients. Most ecological and vegetational parameters usually show continuously increasing variance when the size of individual sample plots is increased and the number of plots is kept constant (Goodall 1961, Matthews 1979b). Homogeneity in a strict sense (following Dahl's definition), is unattainable, what we can imagine is different degrees of homogeneity.

(2) Different complex-gradients vary on different spatial scales (Poore 1962, Gauch 1982a). In the study of the mire N. Kisselbergmosen, R. Økland (1989b) recognized four gradients, operating on two scales: broad-scale gradients, mire expanse - mire margin, and ombrotrophic - poor minerotrophic; and fine-scale gradients, depth to the water table, and the coenocline associated with peat-producing ability of the vegetation. Only the broad-scale gradients were recovered by 16 m^2 sample plots, while all gradients were recovered by sample plots sized 0.25 m^2. This observation can be generalized to most ecosystems.

(3) In boreal forests the presence of small cavities in the forest floor, stone walls, rock outcrops, etc., on scales below 0.25 m are necessary for the occurrence of a lot of weakly competitive bryophytes (e.g., *Tetraphis pellucida, Calypogeia integristipula, C. neesiana, Cephalozia* spp., *Lophozia ventricosa* agg.). Vascular plants react to complex-gradients operating on somewhat larger scales, e.g., fine-scale (1-2 m) topographic variation influencing moisture, soil depth, etc. Trees react to broad-scale variation in these factors (5-20 m). How fine-scaled environmental variation a species is able to respond to is dependent on the size of the plant, as demonstrated by the boreal forest example (above). By their long and deep rooting systems, the trees are overriding the fine-scale variation in environmental factors. Thus the problem of scale not only concerns variation along

complex-gradients at more spatial scales (the mire example, point 2), but in many cases different components of the vegetation (plants growing together) respond to variation at different scales.

(4) Vegetation may consist of a more or less recurrent pattern of similar patches (**mosaic**). Whether a mosaic is to be judged homogeneous or heterogeneous is a question of the scale on which homogeneity is judged, relative to the size of the individual patches. For instance, R. Økland (1989a) recognized five different kinds of mire part types, on different scales. A hummock-hollow area is obviously heterogeneous at a scale including one hollow and the adjacent hummock, but may be a homogeneous mosaic at the scale of the entire bog synsegment.

Several statistical tests for homogeneity have been proposed (e.g., Fisher et al. 1943, Dahl 1957, Greig-Smith 1964), but if analysis of homogeneity is not the main purpose of the investigation, such are not recommendable for two reasons: (1) formulation of the statistical properties of vegetation is extremely difficult (Gauch 1982a), and (2) collecting material for such tests are extremely time-consuming.

Considerations of homogeneity are important for the initial choice of sample plot size. In most sample plots, the variation along most (or all) the complex-gradients of interest has to be small compared to the overall variation along these gradients in the data set.

Representativity

In general-purpose vegetation ecological studies, aiming at extraction of the major structure in vegetation (for instance by ordination or classification methods to be discussed in later chapters), each sample plot has to be representative for the combination of environmental conditions at its site. **Representativity** may be defined as the degree to which one can predict the site conditions from the species composition of a sample plot. Representativity in this sense does not directly correspond to **the minimal area concept** in phytosociology. The minimal area is defined to be the smallest area in which the species composition of a vegetation type is adequately represented (Mueller-Dombois & Ellenberg 1974). The minimal area has been approached in several ways, but still no unambiguous way to determine it exists (Dietvorst et al. 1982).

The minimal area concept has been referred to concrete stands (**the analytical minimal area**; Westhoff & van der Maarel 1978) as well as abstract plant communities (**the synthetic minimal area**; Westhoff & van der Maarel 1978). We will consider the former. Furthermore, the concept can be referred to qualitative (presence/absence of species) or quantitative species composition.

Dietvorst et al. (1982) quote five approaches to determination of the minimal area:

(1) *Species-area curves* (Braun-Blanquet 1964, Mueller-Dombois & Ellenberg 1974, Dahl 1980). In a stand judged homogeneous, a small sample plot is selected and its species composition recorded. The plot size is increased step-wise, each plot including all plots of smaller size. The species composition is recorded at each scale. The number of species is graphed as a function of sample plot size. Ideally, this graph first increases steeply and then, at some point, levels rapidly off. The plot size at which the graph levels off is the minimal area. The problem with this method is that the graph mostly levels off very gradually or does not level off at all (Hopkins 1955, Peet 1974).

(2) *Frequency-area curves* (Du Rietz et al. 1920, Du Rietz 1932). Similar to (1), but based on number of species in different frequency classes as a function of sample plot size. Leading to similar problems as (1) and not in current use.

(3) *Quantitative representativity*. Dietvorst et al. (1982) quote several studies in which the minimal area is taken as the sample plot size by which a fixed fraction (varying from 50 to 80 per cent) of the species occurring in the stand are, on aveerage, included in the sample plots. This method is burdened with the problem of delimiting homogeneous stands and the arbitrariness of the choice of a threshold fraction.

(4) *Sample plot similarity* (Moravec 1973, Roux & Rieux 1981, Dietvorst et al. 1982). Several series of sample plots with increasing size are obtained from one stand. Mean similarity between sample plots (see p. 106) of the same size is calculated, and graphed as function of sample plot size. Moravec (1973) presents a model of the plant community as consisting of **coenotic molecules**. A coenotic molecule is the minimal part

of the plant community that includes the fundamental species, more or less regularly repeated throughout the stand. The minimal area is the least area including at least one coenotic molecule. Dietvorst et al. (1982) used mean sample plot similarity as a function of sample plot size to identify the size of coenotic molecules. This approach does, however, not solve the fundamental problems of the minimal area concept. The threshold similarity used for defining the size of the coenotic molecule will have to be a technical limit. Furthermore, there are no reasons to expect similar limits to be reasonable for different vegetation types. Different results can be obtained by different choices of similarity index, among others reflecting whether this index expresses quantitative or only qualitative variation.

(5) *Analysis of patterns*, that is, identifying scales of variation in vegetation. Several techniques exist (e.g., Greig-Smith 1979, Burrough 1987, Legendre & Fortin 1989). They cannot be used for determination of minimal area directly, but are relevant for making sound judgments of representativity.

There are no objective methods for determination of the smallest possible sample plot size which maintains representativity. The concept of representativity is diffuse, but can be defined somewhat more precisely with respect to multivariate methods for data analysis. In this case, a sample plot is representative for the site if the ecological conditions of the site can be predicted from the species composition of the sample plot. This condition can be satisfied in two different ways: (a) by the presence of some species with narrow amplitude (high indicator potential), or (b) by presence of many species with wider amplitude, or by a combination. One example will illustrate the problem of representativity. In the study of the Fritzøehusparken beech forest, sample plots from the poor forest on morainic material included 4-10 species with wide tolerance. These sample plots did not characterize the site adequately, and were removed before further analysis. Sample plots with less than 5-8 species will mostly behave poorly when subjected to ordination. Representativity can be enhanced in two ways: (1) By including the full species composition of the vegetation; vascular plants, bryophytes, and lichens, with identification down to the species level (or even lower) whenever possible. (2) By increasing the sample plot size. Point (1) implies that one should always include as much of the vegetational information as possible. This will reduce the least representative sample plot size.

Assessment and recommendations

As no exact methods for determining the ideal sample plot size exist, plot size must be decided in each case by considering a set of crucial questions:

(1) On which scale(s) are the variation I want to study? The sample plots must be so small that each plot comprises little variation along the most finely-grained gradient of interest, compared to the total variation along this gradient. Thus a study of the variation in depth to the water-table gradient in bogs should use sample plots not spanning more than, say, a 5-8(-10) cm difference in relative level (compared to the total of ca. 40 cm along the gradient). When a detailed study of species' responses to a complex-gradient (without invoking multivariate methods) is planned, the demands for representativity can by relaxed in order to increase sample plot homogeneity. Tyler (1981) used sample plots of 3 x 3 cm (in closed transects) for studying species' responses to a tussock - interspace gradient in Swedish calcareous fens. However, if our interest is rectricted to variation along the broad-scale gradient in nutrient availability, more representative sample plots with respect to this gradient is achieved by increasing the sample plot size considerably. Determination of sample plot size implies considerable **filtering** of the data, as variation on scales below the sample plot size is sifted out.

(2) What if the scale of variation is unknown, or variation occurs at several scales? Often this situation calls for a pilot study using a small number of sample plots, their size based on an educated guess. This is one example of the principle of **successive refinement** in ecology (Poore 1956), the gradual impovement of methods and the gradual accumulation and refinement of results. An alternative solution is to use a combination of several sample

Tab. 6. Suggested sample plot size for identification of major gradients in some northern ecosystems by use of multivariate techniques.

Ecosystem	Layer	Sample plot size (m^2)
Forests	Tree layer	25-100
	Field layer	(0.5-)1(-4)
	Bottom layer	(0.01-)0.1-0.25(-1)
Grasslands	Field and bottom layers	0.25-1(-4)
Alpine heaths and snow-beds	Field and bottom layers	(0.1-)0.25-1
Mires: bogs and poor fens	Field layer	0.25
	Bottom layer	(0.01-)0.04-0.25
Mires: rich fens	Field layer	0.25-1
	Bottom layer	(0.01-)0.04-0.25
Cryptogamic vegetation		0.01

plot sizes. **Nested plots** (cf. Austin 1981) is the most commonly used combined approach, implying that each sample plots is divided into subplots according to specified rules. The nested plots are congruent, each smaller sample plot lying within the larger. An example is provided by a sample plot (1 m^2) divided into 16 subplots (Figs 2, 63). A series of four nested plots can be constructed, including the lower left subplot (0.0625 m^2), the four subplots down left (0.25 m^2), the nine subplots down left (0.5625 m^2), and the whole sample plot (1 m^2). Matthews (1979a) used nested plots from 1 m^2 to 16 m^2 in the study of patterns in vegetation of the Storbreen gletschervorfeld. Two examples related to nested plots, but not satisfying the demand for congruence, are provided by the studies of boreal forest vegetation in Rausjømarka, Enebakk, SE Norway, by T. Økland (1989) and Solhomfjell, Gjerstad, S Norway, by R. Økland & Eilertsen (in prep.), see Fig. 63. T. Økland (1989) used randomization within selected blocks to place meso sample plots, 1 m^2 each (cf. p. 76). In the latter study, macro scale sample plots, each 16 m^2, were positioned at random within transects. The macro scale sample plots were divided into 16 subplots, 1 m^2 each. The vegetation of two meso scale sample plots, 1 m^2 each, at fixed positions within the macro plot, was analyzed. Each meso plot was divided into 16 subplots, and presence/absence of all species recorded in all subplots. Two subplots at fixed positions were taken as micro sample plots, 0.0625 m^2 each, and divided into 16 subplots the same way as the meso sample plots. This design also allows analysis at several intermediate sample plot sizes, e.g. 9/16 m^2, and 1/4 m^2 (use of 9 and 4 of the meso subplots, respectively), and 9/256 m^2, and 1/64 m^2 (use of 9 and 4 of the micro subplots), thereby representing an extension of the nested plot approach.

(3) What sample plot sizes have previously been used for analysis of similar vegetation? If comparability with other studies is important, this will be strongly enhanced by use of the same sample plot size. The resolving power with one sample plot size can

often be judged fairly well from the gradients identified in previous studies using this sample plot size.

The final determination of sample plot size must be done by skilled judgment. For general-purpose ecological analysis, with gradient identification by multivariate techniques as one of the main purposes, the best sample plot size is the smallest which is representative (Green 1979, R. Økland 1990a). This calls for a continuation of the small-square techniques of the Uppsala school of phytosociology, as contrasted to the large relevés mostly used within the Braun-Blanquet approach (R. Økland 1990b). When a tree layer is present (forests), it cannot be included in the same data set as the field and bottom layers, if major gradients for the understory shall possibly be identified. Instead, the influence of the tree layer should be taken into account as ecological factors like light, litterfall, etc., as in T. Økland (1989). Similar considerations may apply to the field layer if variation in the bottom layer is the primary concern.

Appropriate sample plot sizes for some northern ecosystems are suggested in Tab. 6. Corresponding tables based on different assumptions and different methods for data treatment have been proposed by other authors, e.g. Westhoff & van der Maarel (1978). These are not comparable to Tab. 6.

Number of sample plots

As with sample plot size, objective criteria for determination of the minimum number of sample plots necessary for a particular study do not exist. Statistical considerations are presented in several textbooks (e.g., Greig-Smith 1964, Green 1979), but again the basis for such considerations is doubtful.

For descriptive purposes, each type to be described should be represented by an adequate number of plots. Determination of this number depends on sample plot size, whether intra-type variation is to be represented, etc. The smaller plots used, the higher number of plots is necessary to represent the species composition of the type. R. Økland & Bendiksen (1985) used 25 m^2 sample plots for analysis of forest- and alpine vegetation in the Grunningsdalen area. Each vegetation type was represented by 3-15 sample plots. To the contrary, R. Økland (1989b) used 10-117 sample plots per type for description of vegetation types on the mire N. Kisselbergmosen. Suggestions in the literature differs considerably. For instance, Green (1979) holds the view that 3 samples plots per type may suffice for descriptive purposes, while Greig-Smith (1964) recommends 10-50. As demonstrated above, the number is strongly dependent on purpose and sample plot size.

The purpose of the study and the method chosen for placement of sample plots also strongly impact the optimal number of sample plots. If random or systematic sampling is used, a very high number of sample plots will mostly be necessary to recover rare species or rare combinations of ecological factors because of strong redundancy. A compromize between what is ideal and what is practically possible is necessary. The study of N. Kisselbergmosen (R. Økland 1989b, 1990a, 1990b) using 800 randomly placed sample plots is illustrative (cf. p. 74). Even this high number of sample plots was far from sufficient for an adequate representation of all combinations of states of the four main gradients, and the sampling design was therefore judged suboptimal for studying species responses to gradients and habitat niche relationships. Similar results have been reached for systematic sampling (cf. Galten 1987). Relaxation of the demands for randomness is often beneficial. One of the most important gains will be the considerable reduction in sample plot number necessary to represent the variation in the investigation area adequately.

If statistical tests, estimation of characteristics for types, etc., are aimed at, the variance of the estimators decrease proportionally with the square root of n, the number of sample plots (Green 1979). Thus, when the number of sample plots referable to a type or a combination of environmental factors is increased from 4 to 16, the variance is decreased by 50 percent. To reduce the variance another 50 percent, the number of sample plots must be increased to 64. This calls for a compromise between time spent in the field and accuracy in estimation.

In the final judgment, the following points should be taken into consideration for determination of sample plot number: (1) the expected variation in ecological conditions and vegetation in the investigation area, (2) the method used for sample plot positioning, (3) the sample plot size, (4) the desired representation of each combination of complex-gradients or vegetation type, and (5) time available for field work.

Some practical considerations

When the sampling design is chosen, the sample plot size is fixed and the number of sample plots determined, some practical considerations still have to be made. We shall discuss some of these briefly.

Rejection of sample plots

If random, restricted random or systematic sampling designs are used, there is a risk at including sample plots which, for some reasons, do not fall within the scope of the analysis. If these sample plots can be identified before they are analyzed in the field, much time can be saved for more constructive work. In order not to get into a circular reasoning with rejection of sample plots not fitting one's preconceived ideas (like arguments against selective sampling), the criteria for rejection should be stated explicitely before sample plot positions are fixed in the field. Criteria should relate to environmental conditions directly rather than properties of the vegetation. For instance, in studies of boreal forests using plots of 1 m^2, the following set of criteria have been used (T. Økland 1989, R. Økland & Eilertsen in prep.): no tree (defined as a woody species with height above 2.0 m) is allowed to be rooted in the plot, no vertical wall above 25 cm shall occur in the plot, and not more than 25 per cent of the plot can be covered by naked rock, stones, etc.

Permanent plots

The vegetation of a site is not constant over time, but varies as a consequence of changing environmental conditions, biotic factors and chance factors. One of the main reasons for the poor knowledge of dynamics in vegetation, vegetation of the Northern regions in particular, is lack of a tradition with permanent marking of sample plots. **Permanent plots**, sample plots marked in the field in a way ensuring they can be exactly recovered later, is the basis for long-term studies (Austin 1981). Examples of studies in Fennoscandian vegetation using permanent plots are few (e.g., Persson 1984, Falkengren-Grerup 1986, Dahl 1988, cf. also Sunding 1985). One of the major challenges of future vegetation ecology is the monitoring of changes in vegetation caused by pollution, man-induced climatic change, etc. Monitoring is necessary to understand the mechanisms involved and to model future effects.

In the field, sample plots have to be marked by subterranean markers and their positions carefully mapped in order for the plots to be "permanent". Visible (above-ground) markers may aid recovering the positions, but the use of such markers must be judged against the danger of attracting attention from man and animals and thereby increasing local disturbance. Subterranean markers should be made from non-corrosive materials allowing detection by metal detectors.

RECORDING SPECIES ABUNDANCE

Terminology

An important aspect of vegetation sampling is the recording of species abundance. The variation in vegetation is of two principally different kinds: **qualitative**, that is variation in presence/absence of species, and **quantitative**, that is variation in species amounts (biomass, frequency in subplots, cover etc.). Approaches to measuring abundance differ in their emphasis on either of these two components. The weight attributed to quantitative variation can expressed in the **range** of the abundance scale (r; R. Økland 1986a). The range is defined as the ratio of the largest value and the smallest value recorded for presence of a species. For instance, the range of the Hult-Sernander-Du Rietz cover-abundance scale (Tab. 5) is 5/1 = 5, the range of the ordinal transform of the Braun-Blanquet scale (Tab. 3) is 9/1 = 9.

Four conceptually different approaches to recording abundance are frequently in use:

(1) *Presence/absence.* No actual quantification occurs, range of the scale is 1.

(2) *Cover estimation.* The vertical projection of all living phytomass of a species can be given as percentage cover (e.g., on a 1-100 scale; r = 100) or by use of cover- or cover-abundance scales (cf. pp. 62, 66, Tabs 3-5).

(3) *Frequency in subplots.* The sample plot is divided into subplots, and presence/absence of each species is recorded in each subplot. Abundance is expressed as the frequency of each species in the subplots. The range of the scale equals the number of subplots. Frequency in subplots is used in the study by T. Økland (1988), using sample plots of 25 m^2 divided into 25 subplots, the studies of boreal forests by T. Økland (1989) and R. Økland & Eilertsen (in prep.), using two sample plot sizes, 1 m^2, and 0.0625 m^2, both divided into 16 subplots (Fig. 63), and the standard example from Rønnåsmyra, using sample plots of 0.25 m^2 divided into 16 subplots (Fig. 2).

(4) *Point frequency.* A regular or random arrangement of pins are set up in the sample plot. All species touching each pin are recorded. Abundance of a species is the frequency of touches. The range of the scale cannot be defined, as species may be present in the sample plot without touching any pin. Sometimes point frequency is combined with presence/absence registration, so as to include all species that are present without touching pins as well. Such species are given a minimum value. The range of the scale is then the number of pins divided by this minimum value.

Other ways of recording species abundance have also been proposed, e.g. by estimation of biomass (Smartt et al. 1974, 1976) and production, but these have not been much used and will not be considered further.

Evaluation

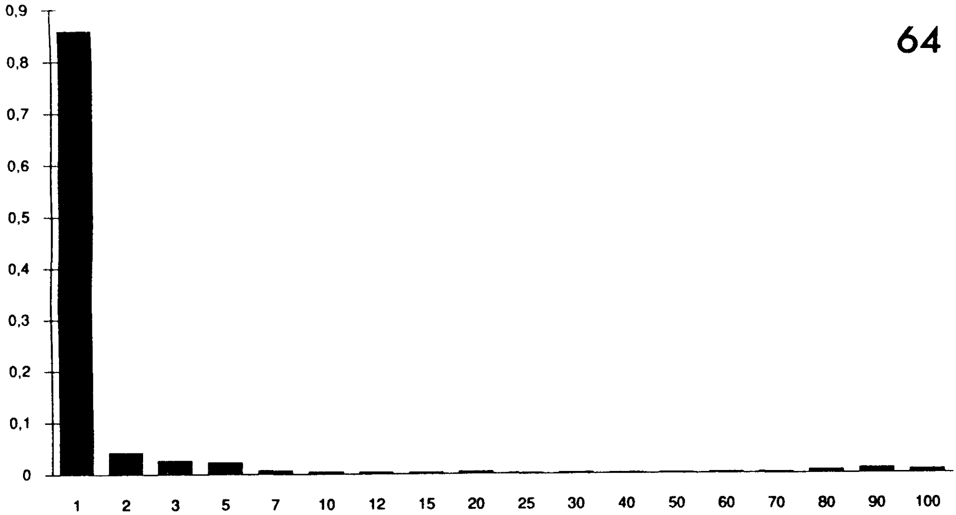
The range of the scale determines the weight we attribute to qualitative and quantitative variation in the subsequent data analysis. There is a quite simple relationship between ratio of quantitative and qualitative variation in a data set and the ß diversity of the data set

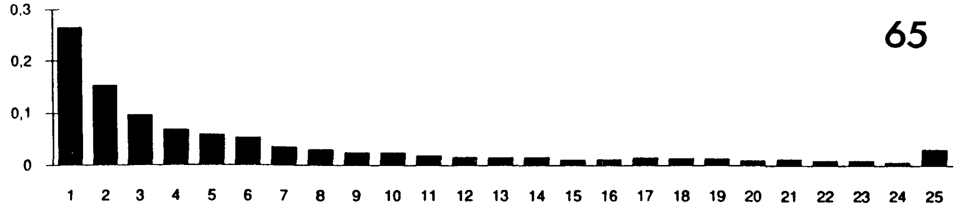
(Jensén 1978, van der Maarel 1979, R. Økland 1986a): the higher the beta diversity (and the higher the number of gradients with high ß diversity), the higher the proportion of qualitative variation in the data set. For example, it is quite easy to tell bog hummocks from hollows by a list of species present, but to separate relative levels within hummocks or hollows should take advantage of knowledge of abundances of species. It follows that by only recording presence/absence, much potentially important information is lost. An exception may be when the sample plots are very small or the ß diversity very high.

Cover and frequency in subplots are two conceptually different approaches to quantification of species amounts, with point frequency in an intermediate position (T. Økland 1988). When the points used for point frequency determination are "without area", point frequency will be an estimate of percentage cover. The accuracy of the estimates will depend on the number of points. With increasing area of the points, point frequency gradually approaches frequency in subplots. Frequency in subplots can be conceived as a point frequency method using contiguous, square points. Point frequency has very rarely been used in Scandinavia, but one example is provided by Lindquist (1931) in a study of beech forests. The point frequency method provides objective estimation of cover. When the pins are virtually not occupying any area, the properties of the point frequency method comes close to those of cover estimation. Disadvantages of the method are: (1) Recovering a reasonable proportion of the species present in a sample plot by touch of pins puts heavy demands on pin number and thereby makes the method very time-consuming. (2) A high number of pins makes the method practically difficult. (3) There is a great danger of damaging the vegetation during analysis. (4) Scoring of touches involves several subjective judgments. (5) The results by the point frequency method will be strongly dependent on the season. (6) Like other cover-recording method, the point-frequency method will discriminate species with long, narrow leaves. These points dissuade the use of the point frequency method.

Two strategies, cover estimation and frequency in subplots, remain. Several points relevant to the choice between the two will be discussed (cf. T. Økland 1988).

(1) *Frequency distribution of abundance values and the dispersion problem.* A data set consists of abundances for a set of species in a set of sample plots. Abundance is usually recorded on a discrete scale, in practical application percentage cover can be considered a discrete scale due to the inability to separate more than ca. 25 cover classes (e.g., 1, 2, 3, 5, 7, 10, 12, 15, 20, 25, 30, 40, 45, 60, 70, 80, 90, 95, 100). , The **frequency distribution** of each cover or frequency in subplots class, that is, the number of abundance values in each of the classes of the scale (e.g. Figs 64-65), expresses the ability of the abundance scale to recover differences in abundance. In the Subset A data set of T. Økland (1988), consisting of 74 sample plots from the Fritzøehusparken beech forest frequency in subplots give a far better separation of relative amounts than percentage cover (Figs 64-65). In fact, 85 % of the cover values were 1; the lowest value for presence. Many of the species with low cover were, however, distributed over the sample plots, as evident from the low number of observations in the lowest frequency in subplots class. Species with low cover but regular distribution, poorly recovered by use of cover, cause the **dispersion problem** (Nordhagen 1928, Du Rietz 1930, Lindquist 1931, T. Økland 1988). The dispersion problem may be considerable in vegetation with high importance of grasses and/or small species with regular distribution, and is generally high in vegetation where only a few species reach high cover values. Frequency distributions of percentage cover and frequency in subplots for two more data sets are presented by Eilertsen et al. (1990). The data set of 125 sample plots, each 1 m^2, of O. Eilertsen (in prep.) from shell-beds at Akerøya, Hvaler, SE. Norway as well as the data set of 181 *Teucrium scorodonia* synedria, each 1 m^2, from southernmost Norway (mostly meadow and deciduous forest





Figs 64-65. Frequency distributions of abundance on abundance scale classes, for 74 sample plots in the Fritzøehusparken beech forest, Brunlanes, SE Norway (subset A of T. Økland 1988, after T. Økland 1988: Figs 5-6 and Eilertsen et al. 1990: Figs 4-5.) Fig. 64. Abundance measured as percentage cover. Fig. 65. Abundance measured as frequency in subplots (25 subplots).

vegetation) by O. Pedersen (in prep.) both show more equal distributions of frequency in subplots than of percentage cover, supporting the results of T. Økland (1988) that frequency in subplots is generally a more sensitive method for recording abundance than cover, even when cover is estimated as percentage. This sensitivity is also expressed in the better separation of sample plots in ordination (T. Økland 1988). The opposite conclusion may be reached for vegetation with few, but dominating species, where cover may provide a more sensitive measure of abundance, or where the number of subplots has to be high (higher than 16 or 25) for frequency in subplots to give equally good results (E. Bendiksen, pers. medd.).

(2) *Seasonal variation.* T. Økland (1988) points to the strong variation in cover of many species during the season, and mentions the problem of geophytes like *Anemone nemorosa* in beech forest as an example. Based on cover estimation, the spring and summer aspects of the beech forest (as most other southern deciduous forests) are most dissimilar. Based on frequency, however, the early-flowering species have their quantities only slightly

reduced from spring till summer. When vegetation analysis is aiming at identification of gradients, its optimal development should be recorded. In many cases, this can be done satisfactorily without reanalysis when abundance is recorded by use of the frequency in subplots method. The seasonal variation reduces the accuracy of the cover estimates. In some open vegetation types like recently cleared forests, the incoming radiation is so strong that the spring-flowering species disappear early (E. Bendiksen, pers. comm.). Separate recording of frequency in subplots for these species at the appropriate time resolves this problem, which is even larger if cover estimation is used. A problem related to that of seasonal variation is the arbitrariness involved in recording frequency in subplots merely by considering the horizontal projection of living plant material. Whether a species will be recorded as present in a subplot or not, will to some extent be influenced by season, damage to the vegetation caused by analysis, broken stems, or any other process giving a shoot another orientation. These problems are easily resolved by recording a species as present in a subplot only when it is rooted in the subplot, or recording rooting in adition to presence based on cover.

(3) *Nested plots.* The use of frequency in subplots for quantification of species amounts opens for the use of the data as a series of nested plots (cf. p. 82), with species quantity recorded as presence/absence in each plot (Matthews 1979a, 1979b, cf. T. Økland 1988). This possibility is considered desirable for permanent plots (Austin 1981), as the appropriate scales for recording future changes in the vegetation are essentially unknown.

(4) *Time demands for field work.* The main objection to frequency in subplots is the time necessary for field work. Obviously, the time for analysis of one sample plot increases with the number of subplots. My own experience with the two methods (in mire and forest vegetation) indicates that the frequency in subplots method using 16 subplots is about four times as time-consuming as cover, using the same sample plot size.

(5) *The human factor.* While cover estimation is a subjective method (can be objectivized by use of point frequency, as explained above), frequency in subplots is objective in the sense that every skilled field ecologist should ideally reach the same result (T. Økland 1988). Kennedy & Addison (1987) estimated the uncertainty (standard error) in cover estimates due to the human factor to amount to ca. 20 %. This complicates comparisons between sample plots analyzed by different persons, between sample plots from similar vegetation and different stations, and, perhaps the most important, between the same sample plots analyzed at different times (Kennedy & Addison 1987, T. Økland 1988, 1989). The observer-independence make frequency in subplots a more sensitive instrument than cover estimates for detection of small changes in vegetation in space and over time, and have considerable advantages over cover estimates for monitoring of vegetation (T. Økland 1988, 1989).

Of the five points discussed, the only one favouring cover estimation is the practical one, demand for time to be spent on field work. Smartt et al. (1974, 1976) made extensive comparisons of different methods for quantification of species amounts, and concluded that this disadvantage is not outweighted by the theoretical advantages of frequency methods. I cannot agree with this conclusion. If sample plots are permanently marked and future reexamination for monitoring purposes is under consideration, frequency in subplots is definitely the better method. Even if reanalysis is not planned, the advantages of frequency in subplots are considerable. Only if there are serious problems involved in carrying out the necessary field program should cover estimation be considered as an alternative to frequency in subplots. On the other hand, supplementary information on cover is easily recorded when the frequency analysis is made, almost without extra costs. In particular, dominance relationships in the subplots may be informative. A discrete cover scale may be used for this, e.g., the Hult-Sernander-Du Rietz cover scale or a less detailed scale (e.g., > 50 %, 10-50 %, and < 10 %; E. Bendiksen, pers. comm.).

ENVIRONMENTAL DATA

Sampling of vegetation is only one part of the ecological analysis. The vegetational data have to be related to environmental data in order to provide an **interpretation** of the vegetational patterns, or an understanding of the vegetational variation along recognized environmental gradients. When the sampling design is fixed, this is used for vegetation sampling and collection of environmental data. Of course, destructive sampling of environmental data (e.g., collection of soil samples), must be performed outside the sample plots if these are intended for later reanalysis. The choice of environmental variables restricts the potential of the subsequent analysis. It is beyond the scope of this book to enter the different abiotic factors and their impact on plants. Some general points relevant to selection of environmental variables may, however, be noted: (1) Variables should be measured in such ways that they are *representative for the plot* and *relevant for the vegetation* studied. For instance, it is not obvious that the mean of ten measurements of soil depth in or around a sample plot is a more representative soil depth parameter than the median depth. Furthermore, the maximum or minimum value may be more important for the vegetation, and hence a more relevant parameter for the analysis, than either the median or the mean. Due consideration is necessary when parameters are seleced. Selection of environmental variables will differ from one study to another because of differences in scale, research purpose and differences between the systems studied. (2) Knowledge of the within sample plot *variation* in the parameters is useful. This can be estimated by use of replicate sampling of the environmental parameters. (3) The factors often recorded in the vegetation under consideration are often useful for comparison with other studies. Furthermore, previous studies of comparable vegetation may provide valuable suggestions for variables to be measured. (4) Variables associated with layers above the uppermost layers included in the analysis (e.g., cover. litterfall etc.) should be included as environmental variables (T. Økland 1989). (5) One environmental factor may influence the vegetation in different ways on different scales. One example is the topography of boreal forests; variation in topography occurs on several, continuously intergrading scales, and affects water availability in different ways. (6) Always try to figure out new measurable environmental variables. (7) All observed impacts on the vegetation that are not possible to quantify (e.g., grazing pressure and subterranean flush effects) should be registered. (8) All environmental variables should be measured for all sample plots. Environmental variables operating on scales larger than the plot size may attain the same value in several plots.

It is not possible to compile a generally applicable list of important variables to be measured in all studies of particular ecosystems. However, suggestions for variables are readily apparent from examples to be given below.

Boreal forests. A study strongly emphasizing environmental relationships is the study of variation in the field and bottom layer vegetation of *Vaccinium myrtillus*-dominated spruce forest vegetation in Rausjømarka by T. Økland (1989). Her sample plot sizes were 50 m^2 (macro scale), 1 m^2 (meso scale), and 0.0625 m^2 (micro scale). Emphasis was put on the meso scale. As the study is a part of an integrated monitoring programme, environmental parameters had to be recorded without causing any damage to the sample plots. T. Økland distinguished between macro and meso scale parameters. Macro scale parameters were: **slope**, measured by a clinometer; **aspect**, measured by a compass; **soil depth**, subjectively judged on a 1-4 scale; **topography**, rigde, convex valleyside, plane valleyside, concave valleyside, valley bottom, etc; **unevenness**, subjectively judged on a 1-4 scale; **macro scale relascope sum**, an expression of tree density; **macro scale**

light index; estimated from the total cover of trees in the sample plots; **tree production estimates** ("bonitet"); and the **age of the tree stand.** Several parameters were measured for all trees coevering the 50 m^2 macro sample plot. Some of these were used for estimating meso scale envcironmental parameters, e.g., height, diameter at breast height, crown perimeter, crown density and cover, etc. Meso scale parameters used for interpretation of patterns in vegetation were: **aspect**, measured by compass and converted to a linear scale expressing favourability or relative incoming radiation; taking 225° as the most favourable aspect, 25° as the least favourable. Difference from these extremes are taken as the aspect parameter, scored on a 0-200 scale (Dargie 1984); **slope**; **microtopography**, used to estimate indices for **convexity** and **unevenness**; **litterfall**, estimated by use of the tree parameters and the position of the meso sample plot relative to the crowns of the nearest trees; **soil moisture** at one particular occation, on a volumetric basis; **soil depth**, measured in 6 positions around the sample plot, minimum, meadian and maximum values used as environmental variables; chemical and physical characteristics of the humus layer (0-5 cm), based on samples collected around the sample plot. Each soil sample consisted of minimum 5 soil cores, in order to ensure representativity for the sample plot. Parameters measured in soil samples were **loss on ignition**, an easily obtained estimate of the organic content of the humus layer; **pH**, and the amounts of several elements, given as ppm (parts per million), as fraction of the organic content (estimated by loss on ignition). These elements were Ca, Mg, K, Na, H, Al, Fe, Mn, Zn, P, N, and S.

In spite of the high number of variables included in the list given above, several other factors could have been included, and several among the recorded variables are complex. Soil moisture is one of the most complex variables. It is generally accepted that soil moisture should be recorded on a volumetric basis (F. Andersson & Ericson 1963, Zhang 1983, Jeffrey 1987). This does not, however, solve the problem that soil moisture varies strongly throughout the season (F. Andersson & Ericson 1963, F. Andersson 1970). Furthermore, it is not known which parameter of water availability which is the most relevant to plants. A group of parameters not included in the study of T. Økland (1989) are those of the mechanical composition of the soil, i.e. the distribution of soil on size classes. Though perhaps not of utmost importance in forests with rather homogeneous parent material (cf. T. Økland 1988), it may be important in systems different ion this respect (cf. F. Andersson 1970).

Mires. Perhaps the most important single environmental variable in mires is the depth to the water table (Malmer 1962a, R. Økland 1989b, 1990a). Several parameters of the relationship between vegetation (the surface of the bottom layer) and water table can potentially be used as environmental variables; for instance the absolute maximum distance to the water table during some period, the median distance, the mimimum distance (the maximum water table), and the point exceeded by water 10 % of the period. R. Økland (1990a) found the minimum depth to the water table to explain the variation in vegetation the best among these parameters. Chemical parameters may be measured in mire water or directly in the peat. Malmer (1962b) showed the variation in peat parameters during the season to be considerably lower than the variation in mire water. Other parameters of importance are **oxygen content**, **electric conductivity**, and **redox potential**.

Alpine heaths. Above the tree limit, parameters of the tree layer are of course no longer relevant. Instead, the depth, duration and stability of the snow cover becomes one of the most important factors (cf. Dahl 1957, etc.). As with soil moisture, characteristics of the snow cover are not easily converted into environmental parameters. Soil stability and seasonal flush effects are other parameters of potentially great importance, that are not easily quantified.

Sea-shore vegetation. The set of relevant environmental parameters for seashore vegetation is quite different from the terrestrial systems. One example of relevant environmental variables is provided by the study of Siira (1970), of seashore meadows in Liminka, Oulu county, C Finland. Parameters relating to the water level have the same importance as in mires. In tidal areas, absolute and relative tidal levels strongly structure vegetation below the highest tide levels. Above the level of direct influence by water, soil salinity, for instance measured by electric conductivity or by **chloride** concentrations, is one of the most important factors. Mechanical and chemical composition of soil, distance from the sea, and altitude are other factors of importance.

The human impact on vegetation is often considerable, but hard to concentrate into environmental variables. For instance, the cultural landscape can only be understood in terms of management regimes, time elapsed since abandonment of management, frequency of haymaking, etc. Appropriate variables must be chosen with care. Grazing pressure and other factors relating to cultural landscapes are equally hard to quantify.

So far, only environmental parameters operating on local scales (fine-scale variation) have been considered. Appropriate environmental factors for use in studies with a regional perspective, are those which make up the regional complex-gradients (see Ahti et al. 1968, R. Økland & Bendiksen 1985). Two regional complex-gradients explain most of the regional variation in Fennoscandian vegetation; one is associated with warmth (temperature sum in the growing-season, etc), the other associated with humidity and oceanicity (precipitation surplus, annual temperature amplitude, etc).

The examples given above do not pretend to be exhaustive for the ecosystems mentioned; from the literature it can easily be seen that this list can be extended and that potentially important variables have not even been mentioned here. The choice of environmental variables will remain a subjective, and a most critical part of the ecological analysis.

METHODS: THE DATA SETS AND DATA MANIPULATION

MATRIX REPRESENTATION OF DATA SETS

A matrix is a tabular arrangement of numbers or **matrix elements**, denoted y_{ij}, arranged in m **rows** and n **columns**. The element y_{ij} is the matrix element in row i and column j. A matrix including m rows and n columns is termed a m x n-matrix and denoted $\mathbf{Y} = \{y_{ij}\}$. A data set consisting of abundance values for m species (species number denoted i; i = 1,...,m) in n sample plots (sample plots denoted j; j = 1,...,n) can be given a matrix representation. In the **species-sample plot matrix**, element y_{ij} is the abundance of species i in sample plot j. The rows are termed **species vectors**. A species vector contains the abundances of species i in all sample plots j = 1,...,n. Actually each species vector is a 1 x n-matrix. The columns are termed **sample plot vectors**, m x 1-matrices containing abundances of all species i = 1,...,m in sample plot j.

The occurrence of 52 species in 51 virgin sample plots at Rønnåsmyra, the standard example (pp. 10-16, cf. Tab. 1), can be represented as a 52 x 51 matrix; the species-sample plot matrix for this data set. A more suitable matrix to use as an example is obtained from the observations of frequency in subplots for the seven *Sphagnum* species occurring in the eleven sample plots in T1. This 7 x 11 matrix **Y** can be compiled from Tab. 1:

$$\mathbf{Y} = \begin{bmatrix} 16 & 16 & 16 & 16 & 16 & 16 & 14 & 4 & 0 & 0 & 0 \\ 16 & 16 & 15 & 16 & 11 & 8 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 11 & 16 & 16 & 16 & 16 \\ 0 & 0 & 0 & 0 & 0 & 16 & 16 & 0 & 0 & 0 & 0 \\ 16 & 16 & 16 & 16 & 14 & 7 & 0 & 0 & 0 & 0 & 0 \\ 2 & 10 & 0 & 0 & 8 & 14 & 12 & 16 & 16 & 12 & 7 \\ 16 & 16 & 16 & 16 & 16 & 16 & 8 & 0 & 0 & 0 & 0 \end{bmatrix}$$

The seven rows, i = 1,...,7 represent the *Sphagnum* species in the order *S. balticum*, *S. cuspidatum*, *S. fuscum*, *S. magellanicum*, *S. majus*, *S. rubellum*, and *S. tenellum*. The species vector $\mathbf{Y}_{1.}$ for *Sphagnum balticum* is:

$$\mathbf{Y}_{1.} = \begin{bmatrix} 16 & 16 & 16 & 16 & 16 & 16 & 14 & 4 & 0 & 0 & 0 \end{bmatrix}$$

The eleven columns represent the eleven sample plots in ascending order. The column vector $\mathbf{Y}_{.1}$ for sample plot 1 is:

$$\mathbf{Y}_{.1} = \begin{bmatrix} 16 \\ 16 \\ 0 \\ 0 \\ 16 \\ 2 \\ 16 \end{bmatrix}$$

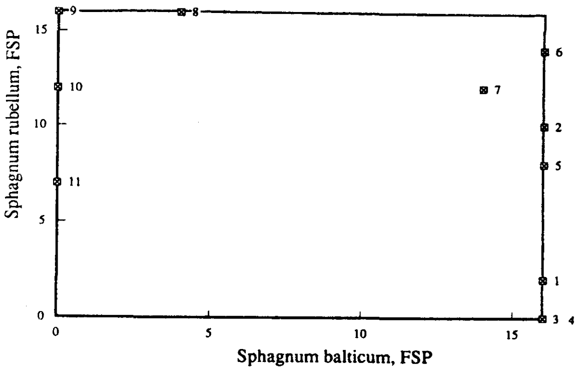
The rows and columns of a matrix is often referred to as the **variables** and the **objects**, respectively. For most ecological studies, relationships of the vegetation (the sample plots) are the main objects of study, and it is natural to consider the sample plots as objects and species as variables as implied by the matrix representation. If, however, we are rather interested in relationships between species (e.g., niche overlap, etc.), the species should be treated as objects, the sample plots as variables. The corresponding matrix representation is the **transposed matrix**, $\mathbf{Y}^t = \{y_{ji}\}$, where the rows of matrix $\mathbf{Y}$ is turned into columns of $\mathbf{Y}^t$, and vice versa:

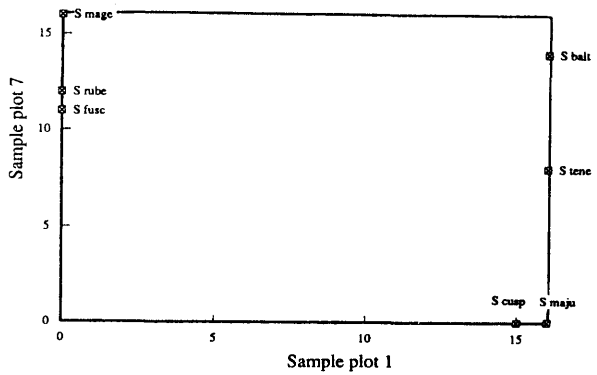
$$\mathbf{Y}^t = \begin{bmatrix} 16 & 16 & 0 & 0 & 16 & 2 & 16 \\ 16 & 16 & 0 & 0 & 16 & 10 & 16 \\ 16 & 15 & 0 & 0 & 16 & 0 & 16 \\ 16 & 16 & 0 & 0 & 16 & 0 & 16 \\ 16 & 11 & 0 & 0 & 14 & 8 & 16 \\ 16 & 9 & 0 & 16 & 7 & 14 & 16 \\ 14 & 0 & 11 & 16 & 0 & 12 & 8 \\ 4 & 0 & 16 & 0 & 0 & 16 & 0 \\ 0 & 0 & 16 & 0 & 0 & 16 & 0 \\ 0 & 0 & 16 & 0 & 0 & 12 & 0 \\ 0 & 0 & 16 & 0 & 0 & 7 & 0 \end{bmatrix}$$

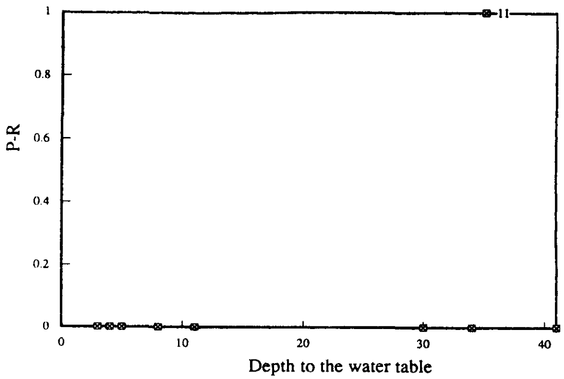
The **environmental variable-sample plot matrix**, $\mathbf{Z} = \{z_{kj}\}$, is the p x n matrix with observations of p environmental variables in n sample plots as matrix elements. The observation of environmental variable k ($k = 1,...,p$) in sample plot j is the matrix element z_{kj}. The use of rows for environmental variables, the *variables* of the matrix, and sample plots as columns, or objects, is logical. The 2 x 11 matrix for explanatory variables (depth to the water table and assumed peat-producing ability of the vegetation) can be compiled from Tab. 1:

$$\mathbf{Z} = \begin{bmatrix} 4 & 3 & 3 & 4 & 5 & 8 & 11 & 30 & 34 & 41 & 35 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

The matrices of primary data (observations in plots) are the **primary matrices**. A second type of matrix is the **secondary matrices** (McIntosh 1978), containing derived data. The term secondary matrix is most often used to mean a matrix of distances (or dissimilarities or similarities) between sample plots, or between the species. The secondary matrices are always square (number of rows equals number of columns). For instance, a







Figs 66-68. Geometric models of three conceptual spaces. Material from the Rønnåsmyra, Grue, SE Norway (the standard example). Fig. 66. The species-dimensional space with *Sphagnum balticum* and *S. rubellum* as axes, and points defined by frequency in subplots of the 11 sample plots of T1 (cf. Tab. 1, matrix Y' at p. 95). Fig. 67. The sample-dimensional space with sample plots 1 and 7 of T1 as axes, and points defined by

matrix, a secondary matrix of distances between the seven *Sphagnum* species is a 7 x 7 matrix.

GEOMETRIC MODELS

Matrices are central to linear algebra, the branch of mathematics dealing with linear spaces. Any matrix can be represented as points in a hyperdimensional, euclidean space. The number of dimensions of the space equals m, the number of variables (rows). In linear algebra these variables are considered independent and represented geometrically as **orthogonal** axes (at right angles to each other). The objects are represented as points in the m-dimensional space with the variables as axes.

Several geometric models are relevant to vegetation ecology. In the **species-dimensional space** (Orlóci 1978, Gauch 1982a) of dimension m each species defines one axis, and the sample plot vectors are represented as points. In the **sample-dimensional space** (Orlóci 1978) of dimension n each sample plot defines one axis, and the species vectors are represented as points. These two spaces are geometric representations of the species-sample plot matrix and its transpose, respectively.

If we consider the quantities of the two *Sphagnum* species *S. balticum* and *S. rubellum* in the 11 sample plots of T1 from Rønnåsmyra, corresponding to the first and the sixth row in the matrix **Y** at p. 92, the following matrix representation is obtained:

$$\mathbf{Y}' = \begin{bmatrix} 16 & 16 & 16 & 16 & 16 & 16 & 14 & 4 & 0 & 0 & 0 \\ 2 & 10 & 0 & 0 & 8 & 14 & 12 & 16 & 16 & 12 & 7 \end{bmatrix}$$

The geometric representation of the species-dimensional space defined by this matrix is given in Fig. 66.

If we consider the seven *Sphagnum* species as objects, and restrict our attention to two of the sample plots, for instance plots 1 and 7 (the first and seventh row of the transposed matrix $\mathbf{Y}^t$ at p. 93, the following matrix representation is obtained:

$$\mathbf{Y}'' = \begin{bmatrix} 16 & 16 & 0 & 0 & 16 & 2 & 16 \\ 14 & 0 & 11 & 16 & 0 & 12 & 8 \end{bmatrix}$$

The geometric representation of the sample-dimensional space defined by this matrix is given in Fig. 67.

An **environmental variables space** have environmental variables as axes, and the sample plots are represented as points. An example of such a geometric representation is provided by Fig. 68, using the two explanatory variables recorded at Rønnåsmyra as axes.

frequency in subplots of the seven *Sphagnum* species occurring in any of these plots (cf. Tab. 1, matrix **Y''** at p. 95). Fig. 68. The ecological space with the two environmental variables recorded at Rønnåsmyra as axes, and points defined by the recorded value of these two variables in the 11 sample plots of T1 (cf. Tab. 1, matrix **Z** at p. 93).

The 11 sample plots of T1 are shown. This is the geometric representation of the matrix Z at p. 93. If the major complex-gradients of an investigation area are known, we can make these the axes of an **ecological space** (Whittaker 1967, Austin 1976a, Gauch 1982a). The number of important complex-gradients in an area of restricted size is usually low, and the ecological space therefore differs from the environmental variables space by being low-dimensional (Gauch & Whittaker 1981, Austin et al. 1984). The major aim of many ecological studies is to reconstruct the axes of the ecological space and to relate sample plots, species optima etc. to these axes. We will return to this in the section on gradient analysis.

Two more geometric models may be mentioned. Secondary matrices of sample plot dissimilarities can be represented geometrically as a **sample dissimilarity space** in which dissimilarity to each of the n sample plots make up the n axes and sample plots are located in the space according to their dissimilarities to the other sample plots. A **species dissimilarity space** of dimension m is the geometric representation of a secondary matrix of species dissimilarities.

TYPES OF VARIATION IN VEGETATION DATA SETS

Variation in a vegetational data sets are of several kinds. Perhaps the most important way to divide this variation into types is the division into **co-ordinated variation in species abundance** (Poore 1956), termed **structure** by Gauch (1982a, 1982b), and **unco-ordinated variation in species abundance**, termed **noise** in the terminology of Gauch.

Co-ordinated variation in species abundance

The reaction of all or nearly all species growing together to the same, relatively few complex-gradients, is the main reason for co-ordiated variation in species abundance, but co-ordinated variation also results from the interactions between species. Co-ordinated variation gives rise to **redundancy** (Gauch 1982a) in data sets; the presence of variables which can be predicted (more or less exactly) from the remaining variables. This redundancy causes **relationships** (Gauch 1982a) in the data sets; reflected in close positions along the major underlying complex-gradients (and hence, in the ecological space) of sample plots with similar species composition. One of the main purposes of multivariate methods applied to vegetation data is to extract the co-ordinated variation in species abundances, that is, to extract the structure of the data set. The co-ordinated variation in abundance is the variation that is **potentially predictable** from (1) ecological conditions of the site, and (2) knowledge of presence and abundance of interacting species. As previously discussed, the structure may be divided technically into qualitative and quantitative variation (p. 85).

Unco-ordinated variation in species amounts

Variation in species amounts predictable neither from site conditions nor from amounts of other species, has often been referred to as noise (Poore 1956, Gauch 1982a, 1982b). Due to this kind of variation, two sample plots from sites completely identical with respect to environmental conditions (if two such sites exists, confer the discussions of homogeneity) differ in species composition. The amount of uncoordinated variation in a data set may be predicted from knowledge of the difference between replicate sample plots (cf. the internal association, p. 112).

According to Gauch (1982a), the aim of multivariate techniques in vegetation ecology is selective summarization of the structure of the data, eliminating "noise". The lack of attention to noise in ecological literature is almost complete, only brief comments may be found. In my opinion, the use of the word noise itself, and the rejection of this noise as "uninteresting" (Gauch 1982a: 7), is most unfortunate. In a situation when the fundamentals of structure and function of vegetation is not or only very imperfectly known (cf. pp. 49-58), to discard the unpredictable variation in data sets as uninteresting appears most unfortunate, not to say unwise. It is possible, perhaps likely, that understanding of unco-ordinated variation in species quantities is an important key to understanding the properties of the individual species, and the system as a whole. It is also possible that the amount of unco-ordinated variation in a particular data set has bearings on the structure and function of this system, relative to other systems.

Noise, or variation in the abundance of one species not co-ordinated with variation in other species' abundance, may have many causes, the most plausible being (cf. also Gauch 1982a): random events in dispersal and establishment of individuals, species-specific effects of predation, grazing etc., environmental heterogeneity on scales below the sample plot size, and effects of micro-scale disturbance and patch dynamics. None of these are uninteresting from a biologist's point of view. In addition, the observational error resulting from the subjectivity of abundance recording, effects of season etc. (cf. pp. 87-88) are potential sources of (mostly less interesting) unco-ordinated variation. The major aim of vegetation ecology is to explain as much as possible of the co-ordinated as well as the unco-ordinated variation in species abundances. Multivariate methods are excellent tools for the former while the latter calls for fine-scale analysis, and reductionistic approaches (cf. Harper 1982); analyses at the population and individual levels.

With respect to the application of multivariate methods to analysis of vegetation, some aspects of noise deserve particular attention. So far, we have considered unco-ordinated variation in each matrix element. However, the lack of co-ordination of abundances may apply to species, sample plots, groups of species or groups of sample plots. Deviant sample plots and species have been termed **outliers** (Gauch 1980, 1982a), deviant groups have been termed **disjunctions** (Gauch 1982a). The most frequently occurring kind of outliers are sample plots very poor in species, and species occurring in one or very few sample plots. Outliers and disjunctions are problematic in gradient analysis as their relationship to the rest of the material is not or only poorly deducable from the data. As the available methods are mostly not suited for handling outliers and disjunctions (they are coined for extraction of structure), the outliers should be identified and removed (or the weight attributed to them considerably reduced) before analysis, and disjunct data sets divided and analyzed separately (Gauch et al. 1977, 1981, Noy-Meir & Whittaker 1977, Gauch 1982a).

Disjunct data sets often correspond to **disjunct data matrices**. A disjunct matrix is characterized by the possibility of regrouping sample plots and species so that some square blocks along the diagonal of the matrix contain high proportions of nonzero entries, while the rest of the matrix has high proportions of zeros. The blocks occur due to the existence of one group of species more or less confined to one group of sample plots, the sample plots containing few other species.

Tab. 7. Numerical properties of the data set from virgin bog vegetation at Rønnåsmyra, Grue, SE. Norway. Definitions in text.

Numerical characteristic	Value		
number of sample plots	n	=	51
number of species	m	=	52
number of elements in the data matrix (maximum possible number of observations)	o_t	=	2652
number of nonzero elements in the data matrix (number of observations)	o_0	=	764
mean number of species per sample plot	m_m	=	14.98
number of species with frequency above 20	m_{20}	=	25
proportion of frequent species	m_{20}/m	=	0.48
proportion of nonzero matrix elements	o_0/o_t	=	0.29
number of elements corresponding to frequent species	o_{20}	=	661
proportion of elements corresponding to frequent species	o_{20}/o_0	=	0.87
median frequency of species	F_m	=	19.6

NUMERICAL PROPERTIES OF VEGETATION DATA SETS

Eilertsen et al. (1990) show that species-sample plot matrices can be characterized by a set of numerical properties. The most important of these are as follows (* - not intended as a characterizing parameter, merely a component of other expressions):

Number of sample plots (n). The total number of sample plots in the data set.

Number of species (m). The total number of species in the data set.

* *Number of elements in the data matrix* (o_t), that is the product of n and m.

* *Number of nonzero elements in the data matrix* (o_0), that is the number of observations of species in sample plots.

Mean number of species per sample plot (m_m), that is the quotient o_0/n, giving information of the representativity of the plots (low number, low representativity, cf. pp. 83-84).

* *Number of species with frequency above 20* (m_{20}). The definition of frequent species by Eilertsen et al. (1990), including species with total frequency in the material above 20 %, is arbitrary.

Proportion of frequent species (m_{20}/m), that is the fraction of the species with frequency above 20. Low fraction of frequent species implies that the material has high noise, high β diversity, or both.

Proportion of nonzero matrix elements (o_0/o_t), an important characteristic relating to the density of the data matrix; the lower proportion of nonzero matrix elements, the more sparse are the matrices. Such sparse matrices may offer a problem to subsequent numerical analyses because of the danger of poorly described relationships (outliers, disjunctions).

* *Number of elements corresponding to frequent species* (o_{20}).

Proportion of elements corresponding to frequent species (o_{20}/o_0). Strongly correlated with number of frequent species.

Median frequency of species (F_m) is a robust expression of the distribution of species frequencies in the material. Low median frequency of species (i.e., below 5 %), indicates that the proportion of accidental species in the material is high.

Values for more important numerical properties in the standard example data set from Rønnåsmyra are given in Tab. 7. Eilertsen et al. (1990) show that all derived characteristics (except n and m) are correlated, and that they express different facets of matrix density. The magnitude of the correlation will differ from data set to data set. Knowledge of the numerical properties of data sets relating to matrix density is important for several reasons: (1) as an aid for choice of multivariate method, (2) as an aid for setting some options of this method, and (3) as an aid for interpretation of results. We will return to these points several times.

DATA MANIPULATION: THE SPECIES-SAMPLE PLOT MATRIX

Definitions

Data manipulation (Wildi 1980, van der Maarel 1982) includes all operations performed on the primary data matrix $\mathbf{Y} = \{y_{ij}\}$, and is an important initial step in data treatment. There are three kinds of operations under this heading: (1) **Weighting** (van der Maarel 1979, Clymo 1980), operations on single elements of the data matrix. The terms **transformation** (Jensén 1978, van der Maarel 1979) and **element transformation** (Brochmann 1987) are often used synomymous with weighting, but transformation is more frequently used as a synonym of data manipulation (e.g., Noy-Meir et al. 1975, Gauch 1982a). (2) **Standardization** (van der Maarel 1979, Clymo 1980) comprises operations on rows (variables) or columns (objects) of the data matrix. **Vector transformation** (Brochmann 1987) is a synonym. (3) **Adjustment** (Clymo 1980) is used for operations involving all matrix elements. They have theoretical interest only, and will not be considered further.

Weighting

Weighting functions

The different scales for estimation of cover used within different phytosociological traditions, and the different approaches to recording of abundance have been treated before. The different abundance measures differ in the relative weight given to qualitative and quantitative variation, as expressed by the range of the scale. The range is, however, also possible to modify *a posteriori* by weighting.

During the late 1970s, there was a vigourous debate on the influence of different weighting of quantitative variation on the results of multivariate analysis. Several different transformations (weighting functions) of the traditional cover and cover-abundance scales were proposed. These included arcsin transformations (cf. van der Maarel 1979), logarithmic transformations (Jensén 1978), root transformations (Halvorsen 1980), ordinal transformations (van der Maarel 1979), and transformation to octave (logarithmic) scales (Gauch 1982a).

The discussions of the relative merit of different scales and their transformations got a new dimension in 1979, as van der Maarel (1979) and Clymo (1980) showed that all cover scales and weighting functions can be approached by a power function with two variables;

$$y_{ij}' = f(y) = a*y_{ij}^{w} \qquad (9)$$

where y_{ij} is the original cover of species i in sample plot j, w is the weighting parameter (specifying the weight atributed to dominance), a is a ranging scalar determining the absolute limits for abundance after weighting, and y_{ij}' is the weighted abundance values. The formula is, of course, applicable to frequencies in subplots, point frequencies, etc. as well as percent cover values.

If, for instance, y_{ij} represents percent cover and we want the maximum of the scale (after weighting) to be 100, then

$$f(100) = 100,$$

that is

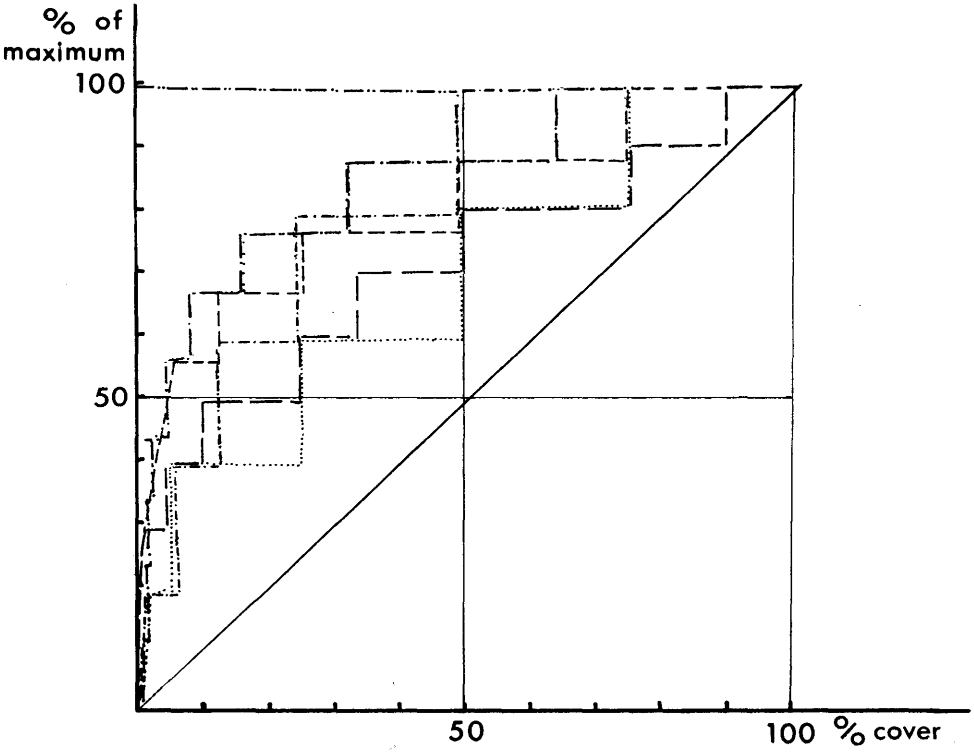


Fig. 69. The relative weight given to species quantity in each of some commonly used cover-abundance scales. For each scale, % of scale maximum is given as a function of percent cover. ———— - percent cover. —·—·—·- - presence/absence. —·—·— - octave scale (logarithmic; Gauch 1982a). – – – - ordinal transformation of the Braun-Blanquet scale (van der Maarel 1979). –·–·– - Hult-Sernander-Du Rietz (5-degree) scale (Du Rietz 1921). ······ - Braun-Blanquet scale (Braun-Blanquet 1921). —— - Domin scale (Evans & Dahl 1955).

$$a*100^w = 100$$

$$a = 100^{1-w} \qquad (10)$$

Then a is fixed, and all cover scales can be approached by a function with only one variable. If (10) is substituted in (9), we obtain:

$$y_{ij}' = f(y_{ij}) = 100^{1-w} y_{ij}^{w}. \qquad (11)$$

As $f(1) = 100^{1-w}$ and $f(100) = 100$, the range of the scale is

$$r = f(100)/f(1) = 100^{1-1+w} = 100^{w}, \qquad (12)$$

provided 1 % is the lowest cover value originally registered.

Fig. 69 shows the weight attributed to quantity and presence in some traditional cover-abundance scales. The stronger displacement towards the upper left of the figure, the stronger emphasis on presence. Fig. 70 shows weighting of percent cover by a power function with different values of the weighting parameter w. By varying w from 0 to 1, one spans the range from presence/absence to an unaltered percent cover scale.

A comparison of Figs 69 and 70, reveals that w = 0.5 gives r = 10 (and a scale approaching the ordinal

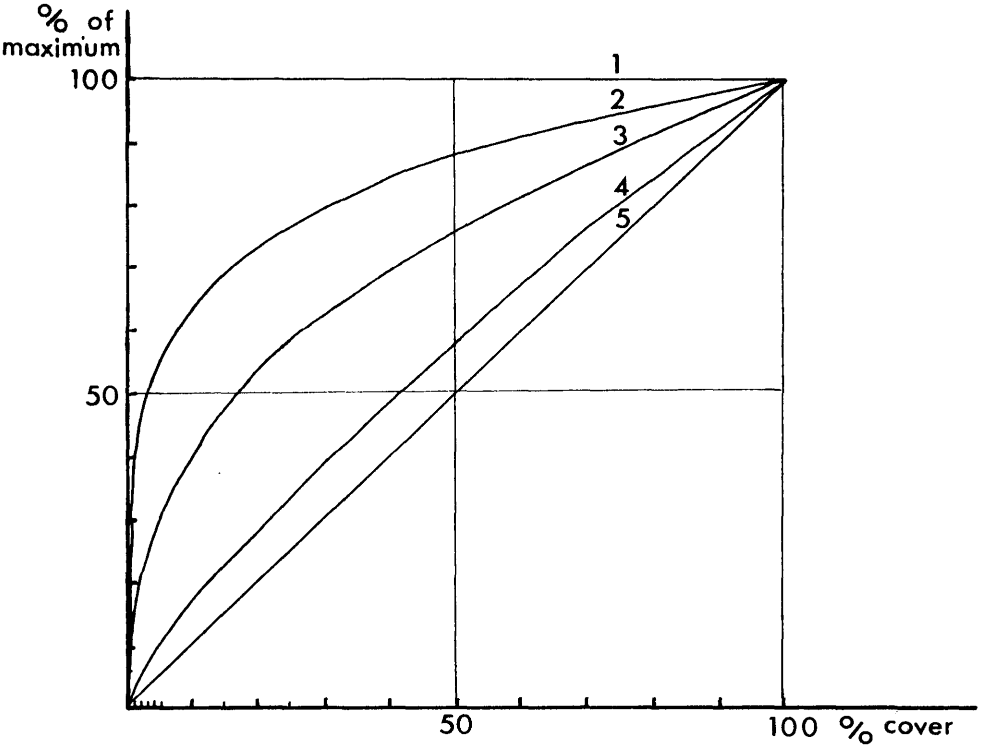


Fig. 70. The power function, $y = 100^{1-w}x^{w}$, of percent cover, ranged to a 0-100 scale with lowermost value indicating presence being 100/r. The five graphs are: (1) presence/absence; w = 0, r = 1 (y is defined to be 0 for x = 0), (2) w = 0.2, r = 2.5, (3) w = 0.4, r = 6, (4) w = 0.8, r = 40, and (5) percent; w = 1, r = 100.

transformation of the Braun-Blanquet scale, the Domin scale, or the octave scale), while w = 0.35 gives r = 5 (and a scale approaching the Braun-Blanquet or Hult-Sernander-Du Rietz scales).

Discussion

Discrete cover scales are too coarse (there are too few steps on the scale) to be weighted by the power function. Consequently, assessment of percent cover or frequency in subplots (for a choice between the two, see pp. 86-89) should be preferred to the use of discrete scales. However, the uncertainty involved in subjective assessment of cover makes a very detailed cover scale out of place. A scale consisting of the value 1, 2, 3, 5, 7, 10, 15, 20, 25, 30, 40, 50, 60, 70, 80, 90, 100 is sufficient. The results of multivariate analysis will not be influenced by one class errors in the judgment of cover (Smartt et al. 1976, Gauch 1982a). Reanalysis of permanent plots for assessment of vegetational change does, however, put strong demands for exactness in abundance recording.

The choice of weighting function influences the results of multivariate analysis to a strong degree (Jensén 1978, van der Maarel 1979, Clymo 1980). As most biological processes are of an exponential nature (cf. Preston 1948, van der Maarel 1979, Skre 1979), i.e., the response increases exponentially as a function of some determining factor, a logarithmic abundance scale should be natural. A logarithmic scale has r about 5. However, the choice of the weighting function should take advantage of knowledge of data set properties and inherent properties of the multivariate techniques to be used subsequently. If the ß diversity of the data set is small, the majority of the variation in the data set is quantitative variation, and dominance should be upweighted. Conversely, by large total variation, presence/absence should be upweighted (Williams et al. 1973, Smartt et al. 1976, Campbell 1978, Jensén 1978, van der Maarel 1979). Generally, intermediate weighting gives the best results (r = 5-10, w = 0.35-0.5 based on a percent cover scale), cf. R. Økland (1986a) and T. Økland (1988). It appears that frequency in subplots give better results with higher r (r = 16-25). Resemblance measures and ordination and classification methods (with built-in resemblance measures) often alter the original weighting, a fact that should be taken into account in the initial choice of weighting function.

Standardization

Standardizations, that is, operations on rows (variables) or columns (objects) of the data matrix, can be made during the initial step of data treatment as a part of the data manipulation procedure. Standardizations are often implicit in resemblance measures (sample dissimilarity measures, etc.) and in algorithms for multivariate techniques. The geometric interpretation of the standardizations (relative to the sample- and species-dimensional spaces) will not be treated here (see Noy-Meir et al. 1975). A survey of equations for main standardizations is given in Tab. 8.

No standardization

Most of the currently used multivariate techniques use the raw (or weighted) data as input. The relative weight given to species with various abundance and to sample plots differing with respect to species richness is then fixed.

Sample plot standardization

Omission of sample plots. Omission of species, sample plots or both from the primary matrix prior to multivariate analysis can also be considered as a kind of standardization, whereby all elements in specified columns or rows are set equal to zero. The detrimental effects of outliers to multivariate analysis has been mentioned before (p. 97). If the purpose of the analysis is to elucidate relationships between sample plots, omission of sample plots with poorly defined relationships to the other sample plots is particularly important (Gauch et al. 1977, Gauch 1982a).

Sample plot centering only has theoretical interest it is not in use.

Sample plot normalization. The length of all sample plot vectors is set equal to 1. The length, or norm of a vector is defined by the formula

$$y_{.j}' = [\mathrm{SUM}_{i=1,\ldots,m} (y_{ij})^2]^{0.5}. \qquad (13)$$

Sample plot normalization makes all sample plots get the same weight in the analysis. The weight attributed to species-poor sample plots and plots with low total abundance of species will be increased relative to other sample plots.

Sample plot relativization. As with normalization, but with total abundance set equal to 1 instead of using the norm. Effects as above.

Sample plot centering followed division with standard deviation only has theoretical interest; not used.

Species standardization

Omission of species. The relationships of species occurring in less than, say 5 sample plots, to other species are unlikely to be adequately described, and such species may therefore act as outliers *in a multivariate* treatment of the data. In species-oriented work (e.g., estimation of relationships between species), such species are usually removed prior to numerical treatment (cf. Tyler 1979, Halvorsen 1980, Jonasson 1981, Gauch 1982a, T. Økland 1988, R. Økland 1989b). Techniques based on a secondary matrix of sample plot resemblance (like most ordination and classification methods) do not attribute much weight to such species, and these species therefore do not influence the analysis to any strong extent. Other methods, like the ordination techniques CA and DCA have in-built options for downweighting of rare species (CA and DCA), see Eilertsen and Pedersen (1989) and p. 155.

Species centering. The mean abundance of a species over all sample plots is subtracted from all abundance values of the species. Species centering has a considerable effect on subsequent analyses. By centering, abundances are replaced by the deviation from mean abundance for the species. Thus the species

Tab. 8. Mathematical formulas for standardization processes. $Y = \{y_{ij}\}$ is the primary data matrix with species are the m rows and sample plots as the n columns; $i = 1,...,m$, and $j = 1,...,n$. $y_{i.}$ - the sum of y_{ij} over all j (the species total). $y_{i.}/n$ - the mean y_{ij} value for species i. $y_{i,max}$ - the maximum abundance for species i. $y_{.j}$ - the sum of y_{ij} over all i (the sample plot total). $y_{.j}/m$ - the mean y_{ij} value for sample plot j.

Type	Name	Formula
No stand.		y_{ij}
Sample plot	Centered	$y_{ij} - (y_{.j}/m)$
	Normalized	$y_{ij}/[SUM_{i=1,...,m} (y_{ij}^2)]^{0.5}$
	Relativized	$y_{ij}/y_{.j}$
	Centered and divided by standard deviation	$[y_{ij} - (y_{.j}/m)]/\{SUM_{i=1,...,m} [y_{ij} - (y_{.j}/m)]^2\}^{0.5}$
Species	Centered	$y_{ij} - (y_{i.}/n)$
	Normalized	$y_{ij}/[SUM_{j=1,...,n} (y_{ij}^2)]^{0.5}$
	Relativized	$y_{ij}/y_{i.}$
	Divided by max. abund.	$y_{ij}/y_{i,max}$
	Centered and divided by standard deviation	$[y_{ij} - (y_{i.}/n)]/\{SUM_{j=1,...,n} [y_{ij} - (y_{i.}/n)]^2\}^{0.5}$

with the largest spread on the abundance scale are most heavily weighted. Species centering most strongly emphasizes occationally high abundance of otherwise rare or quantitatively unimportant species, or occasionally low abundance of otherwise abundant species, thus emphasizing deviant sample plots. This is not in accordance with most purposes of multivariate analysis.

Species normalization. As with sample plot normalization, species normalization equalizes the weight attributed to all species. Thus infrequent species and species with low quantities, and hence, species with few, infrequent species (often outliers) are upweighted. This may be in accordance with the purpose of species-oriented studies, but is not generally desired for sample-plot oriented studies.

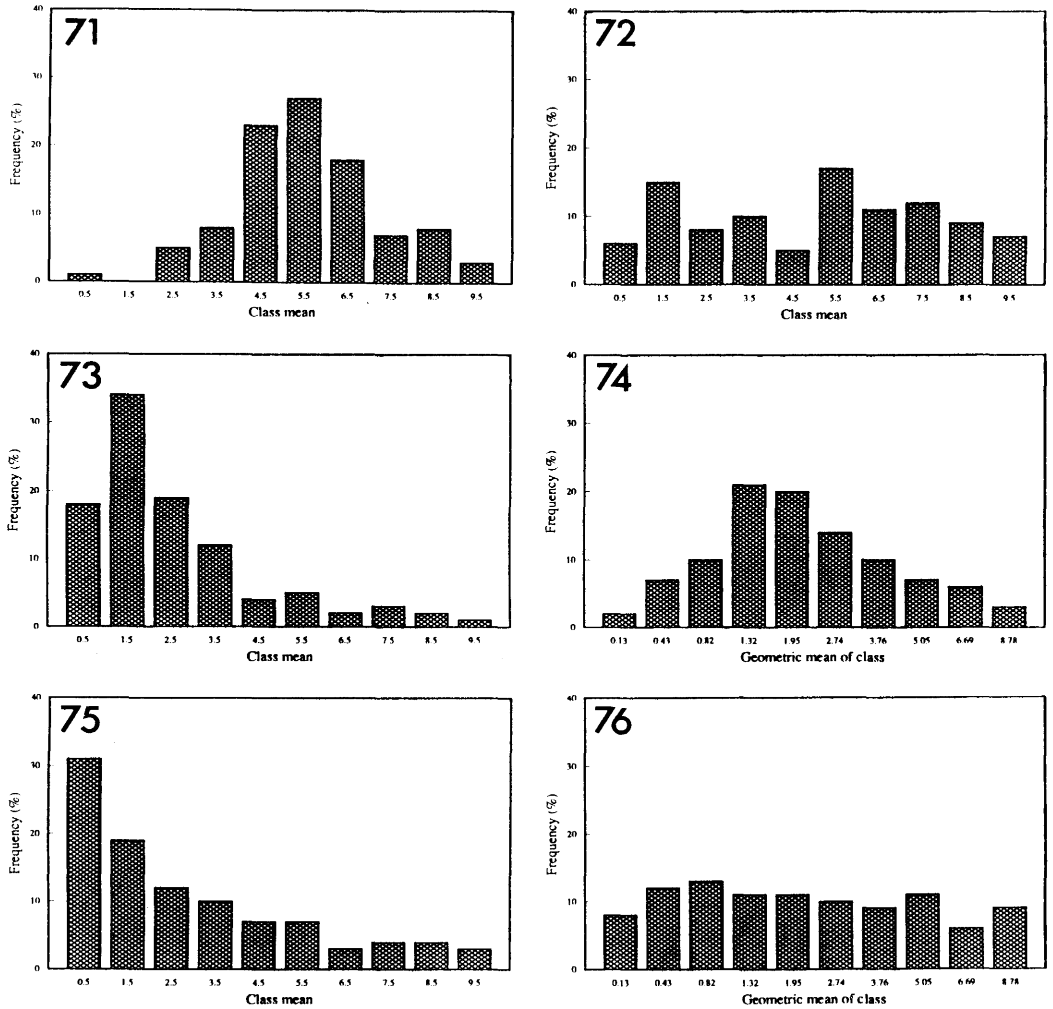
Species relativization can be interpreted as species normalization.

Division by species maximum. This standardization equalizes the maximum abundance of all species, thereby reducing the effects of abundant species without altering the relative weight given to quantity versus presence within a species. By this standardization all species get the same weight regardless of their abundance. Such a standardization is ecologically sound as it assumes that species have the same value as indicators of site conditions regardless of being dominant or not. There is, however, a danger of upweighting rare and deviant species (outliers) and sample plots with high proportion of such species.

Species centering followed by division with standard deviation (normalization of centered species vectors). After this standardization all species have zero mean and unit standard deviation. This standardization is like species centering, but followed by equalization of the weight attributed to all species. This implies weighting of rare species occurring in unusually high amounts and frequent species occurring in unusually small amounts. This standardization method then conflicts common sense in vegetation ecology by emphasizing deviant species and, hence, sample outliers, and cannot be generally recommended (Webb et al. 1967, Noy-Meir et al. 1975).

Double standardization

Double normalization or *double relativization* has often been used in North Americal ecology (cf. Bray & Curtis 1957, Gauch & Whittaker 1972b, Gauch 1973a, Beals 1984). Species quantities are divided by species maxima, whereafter samples are relativized. This actually is an adjustment method. The largest weight is



Figs 71-76. Frequency distributions of hypothetical environmental variables with different statistical distributions, with and without transformations. Four each variable and transformation, the range is divided into ten equal intervals, the mean of which is indicated along the abscissa. Fig. 71. Normal distribution. Fig. 72. Uniform (random) distribution, Fig. 73. Lognormal distribution. Fig. 74. Lognormal distribution (as in Fig. 73), but each value weighted by the ln (1+x) formula. Fig. 75. Lograndom distribution. Fig. 76. Lograndom distribution (as in Fig. 75), but weighted by the ln (1+x) formula.

given to species occurring in species-poor sample plots, and to sample plots with few species or uneven distribution of species abundance. Double standardization has often been recommended (e.g., Cottam et al. 1978, Whittaker & Gauch 1978), but is hard to defend from a theoretical viewpoint and hard to interpret ecologically (Noy-Meir et al. 1975).

DATA MANIPULATION: THE ENVIRONMENTAL VARIABLE-SAMPLE PLOT MATRIX

The primary matrix of p environmental variables in n sample plots, $\mathbf{Z} = \{z_{kj}\}$, offers other demands for data manipulation than the species-sample plot matrix. In most cases, the environmental variables are measured on different scales (pH on a logarithmic scale, soil depth in cm, slope in degrees, etc.). In order to compare the variation of these variables over the sample plots, some sort of data manipulation has to be made.

Ranging (Gower 1967, Sokal & Sneath 1973) is the standardization process transforming all variables onto a 0-1 scale, without altering the relative positions of observations along the scale:

$$z_{kj}' = (z_{kj} - z_{k,min})/(z_{k,max} - z_{k,min}), \tag{14}$$

where z_{kj}' is the ranged value, $z_{k,min}$ is the lowest value of variable k encountered over the n sample plots, and $z_{k,max}$ is the highest value of the variable. Ranging is frequently used in numerical taxonomy to make different characters comparable. By ranging, all variables are given the same weight, regardless the variability relative to the original scaling.

Logarithmic transformations. However, the environmental variables may differ considerably with respect to frequency distribution, thus hardly comparable in a statistical sense even after ranging. Commonly encountered frequency distributions of environmental variables are the **normal distribution** (Fig. 71), the **uniform (random, rectangular) distribution** (Fig. 72), the **lognormal distribution** (Fig. 73), and the **lograndom distribution** (Fig. 75). The latter two are transformed into normal and uniform distributions, respectively, by logarithmic transformation (the ln $(1+z_{kj})$ function, see Figs 74, 76). Variables conforming to a normal or uniform distribution (if necessary, after transformation) are suited for statistical analysis by robust techniques assuming normally distributed variables (Dahl et al. 1967, Dahl 1980, 1981).

Centering. Centering of variables is the process of subtracting the mean from each observation. Centering is often combined with *standardization by division with standard deviation.* Each variable is then transformed to zero mean and unit variance. This transformation increases the weight of the less variable variables relative to the more variable ones, and increases the weight put on strongly deviant observations. Neither of these effects are particularly desirable from an ecological point of view, and the justification for centering of environmental variables and division by standard deviation is questionable.

RELATIONSHIPS BETWEEN SAMPLE PLOTS

Basic concepts

The term relationship is used in a broad sense to include all kinds of indices expressing similarity, dissimilarity or distance between objects or variables. Relationships are of two principally different kinds (R. Økland 1986a): (1) **Floristic relationships**, relationships between sample plots in species space (summarizing differences in species composition), and (2) **ecological distance**, referring to relationships of sample plots in ecological space (relative to the underlying complex-gradients).

Floristic relationships

Two main kinds of measures of floristic relationships are often separated: (1) **Similarity**, a high value indicates high degree of similarity. Similarity is most often expressed on a 0-1 scale. The similarity of sample plots j and l will be denoted s(j,l). (2) **Dissimilarity**, a low value indicates high degree of similarity Dissimilarity is often expressed on a 0-1 scale. The dissimilarity of sample plots j and l will be denoted δ(j,l). Any expression of similarity on a 0-1 scale can be converted into dissimilarity by the equation

$$\delta(j,l) = 1 - s(j,l). \tag{15}$$

Measures of floristic relationships expressing similarity or dissimilarity are termed **floristic resemblance measures** (R. Økland 1986a). Most often floristic resemblance is expressed as dissimilarity. We will use floristic dissimilarity and dissimilarity measure as synomymous terms. Measures of floristic relationships may also be grouped according to other criteria: They may express **quantitative relationships**, that is, they use species abundances as input, or they may express **qualitative relationships**, using presence/absence data only. Furthermore, they may be grouped according to built-in standardizations (cf. Faith et al. 1987).

In more mathematically minded texts, a third kind of measures of floristic resemblance are often separated from similarity and dissimilarity measures, namely **distance** measures (e.g., Rørslett 1982). In its strict meaning, distance is related to Euclidean space, and used exclusively for **metric** relationship measures, by definition satisfying a set of four mathematical axioms (Orlóci 1978). However, except for these mathematical properties, there are no practical differences between dissimilarity and distance measures. We therefore follow the practice in recent ecological literature to use **dissimilarity** as a collective term for dissimilarity (in the strict sense) and distance.

The metric axioms, relating to the species space, are:

(1) $r(j,l) > 0,\ r(j,j) = r(l,l) = 0$
(2) $r(j,l) = r(l,j)$
(3) $j \neq l \Rightarrow r(j,l) > 0$
(4) $r(j,m) \leq r(j,l) + r(l,m)$

The fourth axiom is the triangular inequality, demanding that the distance between two sample plots shall be shorter than the indirect path through a third sample plot. The term **semimetric** is used for measures violating (3). **Non-metrics** violate both (3) and (4).

Metric properties of distance measures were considered important in the early period of multivariate techniques (e.g., Williams & Dale 1965, Sneath & Sokal 1973). However, the lack of ecological realism of the Euclidean species-dimensional space, makes the demand on metric properties in species-dimensional space largely irrelevant to ecological applications (Beals 1973, Austin 1976a, 1976b, Gauch et al. 1977, 1981). There is now an increasing tendency not even to mention metric properties of dissimilarity measures (in the collective sense) in connection with evaluation of measures (e.g., Webb et al. 1967, Goodall 1978a, Hajdu 1981, Hubálek 1982, Faith et al. 1987).

The set of metric distance measures in Euclidean space called **Minkowski metrics**, have the general formula:

$$d_r(j,l) = [\mathrm{SUM}_{i=1,\ldots,m} (y_{ij} - y_{il})^r]^{1/r} \tag{16}$$

where r is the order of the Minkowski metric. The Minkowski metric of 2nd order is the Euclidean distance;

$$d_2(j,l) = [\mathrm{SUM}_{i=1,\ldots,m} (y_{ij} - y_{il})^2]^{0.5}; \tag{17}$$

the Minkowski metric of 1st order is the absolute value function;

$$d_1(j,l) = \mathrm{SUM}_{i=1,\ldots,m} |y_{ij} - y_{il}|. \tag{18}$$

Distance can be defined more generally on the basis of any similarity index s(j,l), cf. Gower 1967, Cormack

1971, Orlóci 1978). A **general distance function of 2nd order** is

$$d_2(j,l) = [s(j,j) + s(l,l) - 2*s(j,l)]^{0.5} \tag{19}$$

and a **general distance function of 1st order** is

$$d_1(j,l) = s(j,j) + s(l,l) - 2*s(j,l). \tag{20}$$

If $s(j,j) = 1$, the similarity measure varies on a 0-1 scale, and (19) reduces to

$$d_2'(j,l) = [2(1 - s(j,l))]^{0.5} = (2*\delta(j,l))^{0.5} \tag{21}$$

and (20) reduces to

$$d_1'(j,l) = 2(1 - s(j,l)) = 2*\delta(j,k). \tag{22}$$

We also see that $s(j,j) = 1$ gives $0 \leq d_2(j,l) \leq 2^{0.5}$ and $0 \leq d_1(j,l) \leq 2$.

Closely associated with metric distance measures are the **scalar products**, a group of similarity measures that can be interpreted geometrically relative to the Euclidean species-dimensional space. Generally, the scalar product (inner product) of two vectors $\mathbf{Y}_{.j}$ and $\mathbf{Y}_{.l}$ can be expressed

$$\mathbf{Y}_{.j} * \mathbf{Y}_{.l} = \mathrm{SUM}_{i=1,\ldots,m} y_{ij} * y_{il}. \tag{23}$$

A matrix of scalar products between all pairs of sample plots (objects) or between all pairs of species (variables) is a secondary matrix. This secondary matrix can be given a geometric interpretation in the species-dimensional space. Three relevant cases can be recognized, dependent on the standardization of data (Orlóci 1978, Matthews 1979b, Gauch 1982a): (1) ***Dispersion matrix*** (Noy-Meir 1973a, Gauch 1982a); scalar products between sample plots (any standardization except centering) or between non-standardized species. If sample plot normalization is applied, a matrix of scalar products between sample plots can be interpreted as the cosines between pairs of sample plot vectors in species-dimensional space. (2) **Variance-covariance matrix**; scalar products between species, based on species-centered data. In this case the scalar product of a species with itself is the variance of the species, the scalar product of two species their covariance. (3) ***Correlation matrix***; scalar products between centered species, standardized by division with the species' standard deviation. The scalar product is the Pearson product-moment correlation coefficient between species (cf. Sokal & Rohlf 1969, Orlóci 1978, pp. 113-114), and is 1 for a species with itself.

Criteria for evaluation of floristic dissimilarity measures

Floristic dissimilarity measures must be evaluated with reference to some underlying model. Hajdu (1981) proposed the following criteria for evaluation of floristic dissimilarity measures: (1) linear response to linear floristic changes (changes in the composition of vegetation), (2) balanced sensitivity to qualitative and quantitative information (cf. Campbell 1978), and (3) high resolving power (use the full scale). The first criterion is intuitively sound, giving prevalence to measures preserving the scale of species importance values chosen by the investigator during the phase of data manipulation (weighting). Thus the second criterion is redundant; given linearity, quantitative and qualitative variation is balanced in accordance with the investigator's preferences. Failure to use the whole scale may be overcome by ranging (Gower 1971, cf. also p. 105), and is not important. Linearity remains the only important criterion (R. Økland 1986a). One point does, however, need to be considered. The usefulness of floristic dissimilarity measures as such in ecology can be questioned (R. Økland 1986a, Faith et al. 1987). In most cases, floristic dissimilarity measures are used to measure ecological distance, and criteria for evaluation then becomes entirely different.

Ecological distance

If we use the term ecological distance, we are not longer interested in the floristic differences between sample plots, rather we intend to assess the ecological significance of the differences in species composition. Our aim is now to measure relationships in the underlying ecological space. Ecological distance should be expressed as distance, referring to metric distance in ecological space (R. Økland 1986a). The term ecological distance was defined by Whittaker (1952) as "degree of community separation, expressed in change of community composition in response to environmental change". Gauch (1973b) used the term in a wider sense to mean any (floristic) dissimilarity index calculated to compare sample plots along a recognized coenocline. The terms floristic and ecological relationships are often confused in the literature (e.g., Green 1980).

In a previous section on ß diversity measures, several ecological distance measures were evaluated (pp. 35-36). When ecoclines are scaled in units of compositional turnover, an estimate of ecological distance is the distance along the scaled gradient or Euclidean distance in the space of scaled ecoclines.

Criteria for evaluation of floristic dissimilarity measures used to measure ecological distance

Most multivariate techniques use floristic dissimilarity measures for estimation of ecological distance. The reliability of such methods will, to a large extent, depend on the properties of the distance measure. It is therefore of considerable importance to know the ecological distance properties of floristic dissimilarity measures. A good measure of ecological distance must satisfy two criteria (R. Økland 1986a, Faith et al. 1987): (1) linear response to separation along the ecocline (Beals 1973, van Groenewoud 1976), that is, metric properties in an ecological space with axes scaled in units of compositional turnover, and (2) robustness (Gauch 1982a), that is, giving good estimates of ecological distance with high noise levels in the data set (large proportion on variation in species abundances not co-ordinated with variation in abundances of other species, cf. pp. 96-97), and with considerable variation in the underlying community models.

Tab. 9. Mathematical formulas for some floristic resemblance measures, given as dissimilarity or distance. Both the quantitative and presence/absence forms of the measures are given. Y = $\{y_{ij}\}$ is the primary data matrix with species as the m rows and sample plots as the n columns; i = 1,...,m, and j = 1,...,n. A second sample plot is referred to as y_{il}, l = 1,...,n. $y_{i.}$ - the sum of y_{ij} (or y_{il}) over all j (or l), the species total. $y_{i.}/n$ - the mean y_{ij} value for species i. $y_{i,max}$ - the maximum abundance for species i. $y_{i,min}$ - the minimum abundance for species i. $y_{.j}$ - the sum of y_{ij} over all i (the sample plot total). $y_{.j}/m$ - the mean y_{ij} value for sample plot j. $y_{.l}$ and $y_{.l}/m$ are defined similarly. Variables of presence/absence expressions of the measures are: m_{jl} - number of sample plots occurring in both compared sample plots sample plots j and l, m_j - number of species only occurring in sample plot j, m_l - number of species only occurring in sample plot l, m_- - number of species occurring in neither sample plot, n_i - number of sample plots containing species i.

Name	Quantitative form	Presence/absence form
Euclidean distance	$[\mathrm{SUM}_{i=1,\ldots,m}(y_{ij} - y_{il})^2]^{0.5}$ (24)	$(m_j + m_l)^{0.5}$ (25)
Chord distance	$\{\mathrm{SUM}_{i=1,\ldots,m}[y_{ij}/(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}^2)^{0.5} - y_{il}/(\mathrm{SUM}_{i=1,\ldots,m}y_{il}^2)^{0.5}]^2\}^{0.5}$ $= \{(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}^2)/(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}^2) + (\mathrm{SUM}_{i=1,\ldots,m}y_{il}^2)/(\mathrm{SUM}_{i=1,\ldots,m}y_{il}^2)$ $- 2*(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}*y_{il})/[(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}^2)^{0.5}*(\mathrm{SUM}_{i=1,\ldots,m}y_{il}^2)^{0.5}]\}^{0.5}$ $= \{2*[1-(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}*y_{il})/[(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}^2)^{0.5}*(\mathrm{SUM}_{i=1,\ldots,m}y_{il}^2)^{0.5}]]\}^{0.5}$ (26)	$\{2[1-m_{jl}/(m_{jl}+m_j)(m_{jl}+m_l)^{0.5}]\}^{0.5}$ (27)
Complemented similarity ratio	$1 - \{(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}*y_{il})/[(\mathrm{SUM}_{i=1,\ldots,m}y_{ij}^2) + (\mathrm{SUM}_{i=1,\ldots,m}y_{il}^2)$ $- (\mathrm{SUM}_{i=1,\ldots,m}y_{ij}*y_{il})]\}$ (28)	$(m_j + m_l)/(m_{jl} + m_j + m_l)$ (29)
Percentage dissimilarity (Bray-Curtis)	$1 - 2*(\mathrm{SUM}_{i=1,\ldots,m}\min(y_{ij},y_{il}))/$ (30) $= (\mathrm{SUM}_{i=1,\ldots,m}\lvert y_{ij} - y_{il}\rvert)/(y_{.j} + y_{.l})$ (32)	$1 - [2*m_{jl}/(2*m_{jl} + m_j + m_l)]$ (31) $= (m_j + m_l)/(2*m_{jl} + m_j + m_l)$ (33)
Quantitative symmetric (Kulczynski)	$1 - 0.5*[(\mathrm{SUM}_{i=1,\ldots,m}\min(y_{ij},y_{il}))/y_{.j} + (\mathrm{SUM}_{i=1,\ldots,m}\min(y_{ij},y_{il}))/y_{.l}]$ (34)	$1 - 0.5*(m_{jl}/m_{jl} + m_j) + m_{jl}/m_{jl} + m_l)$ (35)
Chi-square	$[\mathrm{SUM}_{i=1,\ldots,m}(1/y_{i.})(y_{ij}/y_{.j} - y_{ij}/y_{.l})^2]^{0.5}$ (36)	$\{\mathrm{SUM}_{i=1,\ldots,m}(1/n_i)[y_{ij}/(m_j + m_{jl})$ $- y_{ij}/(m_l + m_{jl})]^2\}^{0.5}$ (37)

Evaluation of some floristic dissimilarity measures

Presentation, discussion and evaluation of formulas

Some of the most frequently used measures of floristic dissimilarity are given in Tab. 9. The number of available floristic resemblance measures is very high, and more complete treatments are available, for instance, in Goodall (1978a), Orlóci (1978), Hajdu (1981), Hubálek (1982), and Faith et al. (1987). The measures shown in Tab. 9 will be treated in some detail.

Euclidean distance (equation 24 in Tab. 9) is one of the most widely used floristic distance measures (cf. Orlóci 1972, 1978, van der Maarel et al. 1978, Gauch 1982a). In its original form, it measures distance in the Euclidean species-dimensional space and has no upper bound. The metric properties of this measure in species-dimensional space are ecologically irrelevant (Beals 1973). Euclidean distance implies a multiplication and squaring of abundance values, and therefore strongly emphasizes dominants (van der Maarel 1979). Thus, the linearity criterion for floristic resemblance measures is violated and the measure is vulnerable to random variation in dominance relationships (Gauch 1973b, 1982a, Kessell & Whittaker 1976, Noy-Meir & Whittaker 1977). The lack of an upper bound of the scale makes the Euclidean distance of two sample plots without any species in common potentially less than the distance between two sample plots with many species, all shared, but with considerable differences in quantities of individual species (Orlóci 1967, Campbell 1978). These disadvantages make Euclidean distance unsuited as a floristic resemblance measure.

The problem of an unbound scale may partly be overcome by division by the square root of the number of species present in one or both of the compared sample plots. The scale will then be bounded by y_{max}, the largest single observation of any species (Orlóci 1974, Jensén 1978). If all variables are scored on a 0-1 scale, the upper bound is 1. This variant has been much used in numerical taxonomy under the name of *taxonomic distance* (Sokal 1961, Sneath & Sokal 1973).

Chord distance (equation 26 in Tab. 9) is another variant of Euclidean distance, in which the sample plot vectors are normalized. Thus chord distance may be interpreted as the length of the chord between two points (sample plot vectors) on the unit hypersphere in the species-dimensional space. The upper bound of this measure then becomes $2^{0.5}$. The chord distance may also be expressed as a function of the cosine separating the species vectors;

$$CD(j,l) = [2(1 - \cos x)]^{0.5}. \qquad (38)$$

This interpretation rests on the fact that the inner sum in equation (26) is the mathematical expression of the cosine between two vectors in m-dimensional space (cf. p. 95). Chord distance (and the cosine, as a similarity measure) share the disadvantages of the Euclidean distance resulting from multiplication and squarring of abundances, strongly emphasizing dominance. The square root-transformation implicit in chord distance improves the situation somewhat (compared to Euclidean distance and the cosine measure). The weight given to dominance in the family of derivatives of Euclidean distance can be reduced by weighting of the data with a low value of the weighting parameter, w (Campbell 1978, Jensén 1978, van der Maarel 1979).

Complemented similarity ratio (equation 28 in Tab. 9), has been rather recently introduced into vegetation ecology (as a similarity index; van der Maarel et al. 1978, Westhoff & van der Maarel 1978, van der Maarel 1979). The measure is non-metric and emphasizes quantity (Campbell 1978), but to a lesser degree than Euclidean distance (Hajdu 1981). This is due to the subtraction of the scalar product of the sample plot vectors in the nominator. The upper bound of the scale is 1. The binary variant of the index is known as Jaccard's index of similarity (Jaccard 1901). The linearity of the measure with linear floristic changes is reasonably good (Hajdu 1981).

Percentage dissimilarity (equation 32 in Tab. 9) has been widely used in vegetation ecology, mostly in its similarity form (equation 30). It is known by several names, e.g., percentage similarity (Gauch & Whittaker 1972a, Gauch 1973b, 1982a), Czekanowski's index of similarity (cf. Goodall 1978a), and the Bray-Curtis coefficient (Faith et al. 1987, cf. also Bray & Curtis 1957). It was first used by Czekanowski (1909), and introduced into phytosociology by Dahl & Hadač (1941). The scale is bounded (0-1). With binary data the equation (32) reduces to (33), known as Sørensen's index of similarity (Sørensen 1948), also known as coefficient of community (Gauch 1973b, 1982a). No multiplication or squaring of abundances is made, consequently the measure gives a linear response to linear floristic variation (Hajdu 1981). Its mathematical simplicity and good linearity makes percentage dissimilarity one of the best, or perhaps the best floristic resemblance measure.

Quantitative symmetric index (equation 34 in Tab. 9), first proposed by Kulczynski (1928), differs from percentage dissimilarity by being symmetric with respect to the two sample plots compared, thus equalizing the contributions of the two to the dissimiliarity. Percentage dissimilarity, on the other hand, emphasizes the plot with the higher species total. However, the difference is unimportant and the properties of the quantitative symmetric index closely resembles percentage dissimilarity (Hajdu 1981).

Chi-squared distance (equation 36 in Tab. 9) has not been used as a measure of floristic dissimilarity, but is implicit in the family of CA ordination techniques (Chardy et al. 1976, Faith et al. 1987, Minchin 1987a). From the equation, it is evident that the measure gives weights to species inversely proportional to their abundance (division with $1/y_i$) Sample plots are weighted inversely proportional to their total abundance. High abundances of infrequent species in sample plots with low totals (species-poor sample plots, or sample plots without or with a few dominants only) are particularly strongly emphasized (cf. also Minchin 1987a). Multiplication of abundances strengthens the weight given to dominants. A very poor floristic linearity is expected to result.

Floristic dissimilarity measures as ecological distance measures

Figs 77-78 illustrate the three faults of floristic dissimilarity measures, used as measures of ecological distance (R. Økland 1986a):

(1) Owing to noise in the data set, replicate sample plots will never have identical species compositions. Thus sample plots will not reach the theoretical lower limit of zero floristic dissimilarity when their ecological distance is zero. Over short ecological distances, measures of floristic relationships will therefore lack robustness (Gauch 1973b, Gauch & Whittaker 1981). The real lower bound of the scale of the floristic dissimiliarity measure (the internal association, cf. p. 112) can hardly be determined exactly.

(2) Sample plots separated by more than ca. 4 S.D. units along the coenocline have few or no species in common (p. 35), and thus 0 floristic similarity (Swan 1970, Gauch & Whittaker 1972b). Floristic dissimilarity measures are therefore indeterminate for coenocline distances above ca. 4 S.D. units (Swan 1970, Clymo 1980).

(3) All floristic measures of ecological distance show a characteristic S-shaped curve in Fig. 78. Floristic separation increases slightly between 0 and 0.5 S.D., then increases more rapidly to an inflexion point about 2 S.D. separation, and levels off gradually between 2 and 4 S.D. This curve shape is shared by all measures of floristic dissimilarity (cf. Whittaker 1960, 1967, Gauch 1973b, 1982a, Gauch & Whittaker 1981), and is due to the non-linear relationships between the species-dimensional and ecological spaces, that is the fact that the species quantities do not increase or decrease monotonously along the complex-gradients (Swan 1970, Austin 1976a, Gauch 1973b, 1982a).

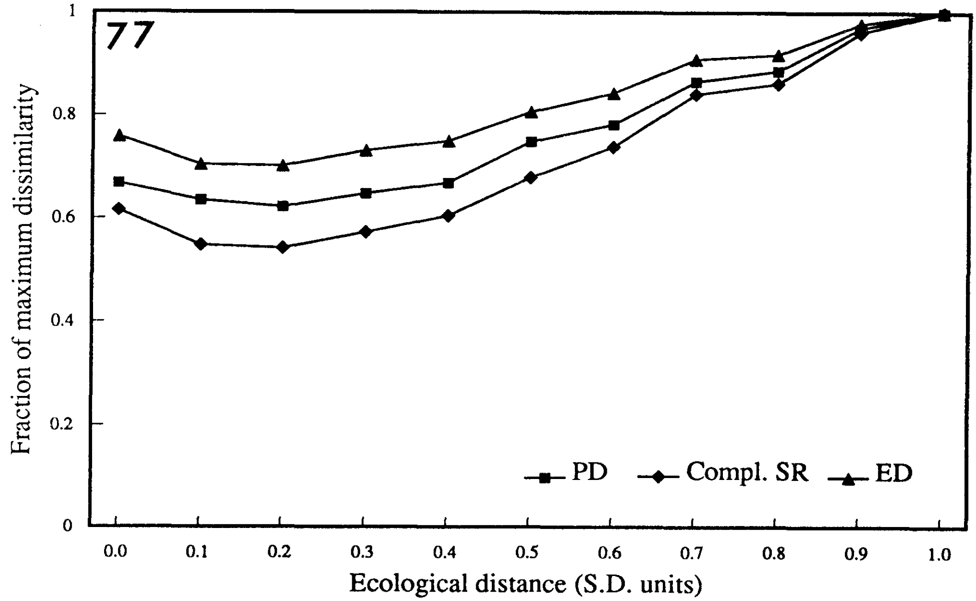
Tests of floristic resemblance measures as measures of ecological distance have been performed by R. Økland (1986a) and Faith et al. (1987). R. Økland (1986a) tested the performance of four indices (Euclidean distance, chord distance, complemented similarity ratio, and percentage dissimilarity) with four simulated coenoclines. Test criteria were (1) linearity of dissimilarity measure with ecological distance, and (2) robustness; vulnerability to noise. Faith et al. (1987) combined linearity and robustness by testing 29 indices (or variants of indices) for linear and rank correlation with ecological distance on more than 500 data sets, and used mean correlation coefficients for each index over a set of models as a test statistic.

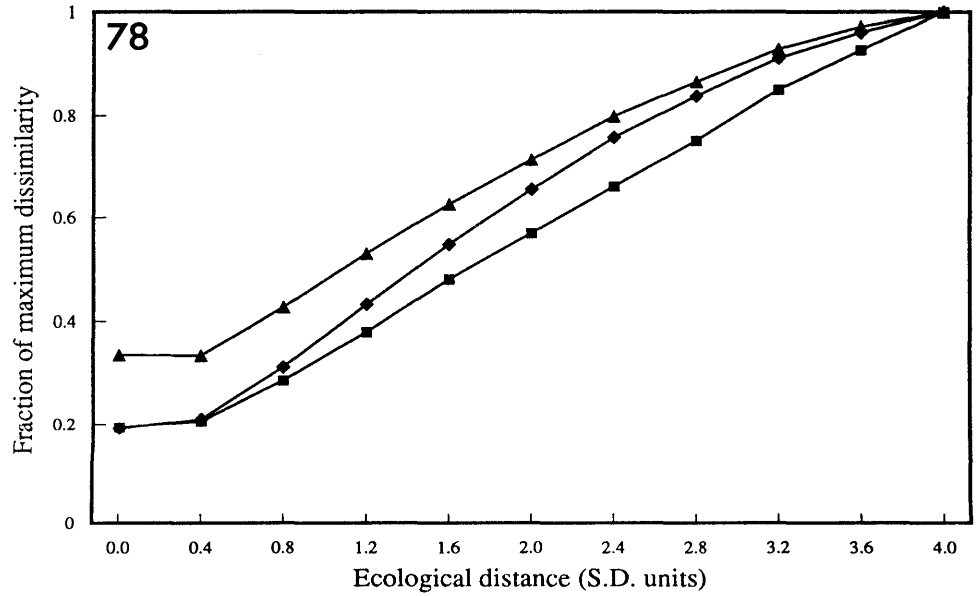
Although the three general faults and shortcomings of floristic measures used to describe ecological distance are shared by all indices, there are considerable differences in detail. R. Økland (1986a) showed percentage dissimilarity to have the best linearity and in general also the best robustness among the measures compared. Euclidean distance generally showed the poorest linearity and the lowest robustness, similarity ratio was intermediate. In their extensive test, Faith et al. (1987) found the quantitative symmetric index, used on data standardized by division with species maxima to have the best performance, closely followed by several other indices, among them percentage dissimilarity, standardized similarly. The same measures without standardization showed intermediate performance, while chi-square and the different variants of euclidean distance showed the poorest performance. Abundance was scored on a scale with of range of 10,000 (P. Minchin, pers. medd.). This explains the improvement by standardization by division with species maxima. By use of scales with far lower ranges, as recommended at pp. 101-102, the differences between the unstandardized and species maximum-standardized indices are likely to be smaller. Anyway, the tests give unequivocal evidence that the floristic measures with best linearity in species-dimensional space are also the best estimators of ecological distance.

Approaches to amend the faults of floristic dissimilarity measures as measures of ecological distance

Several attempts have been made to reduce or eliminate the faults of floristic dissimilarity measures as measures of ecological distance:

(1) The problem with low robustness (and low linearity) at small ecological distances has been approached by trying to estimate the internal association, the distance between replicate sample plots (Bray





Figs 77-78. Relative ecological distances (in per cent of distances between sample plots 1, respective, 4 S.D. apart) as functions of coenocline separation. Percentage cover data weighted to range 2.5 (after R. Økland 1986a). PD - percentage dissimilarity, Compl. SR - complemented similarity ratio, ED - Euclidean distance divided with the number of species in the two compared sample plots. Fig. 77. Simulated coenocline with length 2 S.D. Fig. 78. Simulated coenocline with length 8 S.D.

& Curtis 1957, Gauch 1973a). If the internal association was known, the floristic resemblance measures could be "corrected" as follows:

$$s'(j,l) = s(j,l) + 1 - IA,$$
$$\delta'(j,l) = IA - s(j,l),$$

where $s'(j,k)$ and $\delta'(j,k)$ are the corrected similarity and dissimilarity values, respectively, IA is the internal association and the floristic dissimilarities are given on a 0-1 scale (cf. Bray & Curtis 1957, Gauch & Whittaker 1972b, Gauch 1973a, 1973b). However, the noise, the cause of the problem, is a stochastic component. Thus estimation of the internal association will not overcome the problem with robustness (Gauch 1982a, R. Økland 1986a). The magnitude of stochastic variation in natural data sets is normally so large that the similarity of replicate sample plots will vary considerably. Underestimation of IA leads to corrected similarities above the upper bound of the scale (and corrected dissimilarities or distances below zero). As the problems with underestimation are more serious than the problems with overestimation (Gauch 1973a, 1982a), one usually have to set IA = 1 or equal to the maximum floristic similarity encountered in the secondary matrix. In a large material this maximum is close to one. There is consequently no satisfactory solutions to the first problem.

(2) The problem of undefined or unreliable dissimilarities associated with large coenocline separation has been approached by introducing measures of "degree of absence" (Swan 1970). Clymo (1980) outlines three such methods, all based on the principle of replacing unreliable distance estimates by new, more reliable values. These are found as the "shortest path" between two sample plots through reliable dissimilarities. The "step across" algorithm of Williamson (1978) may serve as an example. Consider three sample plots, A, B, and C. Floristic dissimilarity between all pairs of sample plots is calculated on a 0-1-scale. These distance estimates are d(A,B) = 0.6, d(B,C) = 0.7, and d(A,C) = 1.0. Distance estimates larger than, say, 0.95 are considered unreliable. A new distance estimate calculated by step across is d'(A,C) = d(A,B) + d(B,C) = 1.3, the shortest path from A to C via reliable dissimilarities. Approaches like step across solve the problem of unreliable relationships, but the new distance estimates are less robust than the individual dissimilarities they are based on. A stochastic variable formed by addition has higher variance than any of its addend variables (cf. Sverdrup 1973). There is also a danger of overestimation of distances by "shortest path" procedures, particularly when the number of sample plots in the data set is small.

(3) The non-linearity problem has been approached by transformation of resemblance measures (cf. R. Økland 1986a). However, none of the transformations give considerable improvements of linearity, and none improve robustness (Gauch 1973b, Noy-Meir & Whittaker 1977). The approach now appears to have been abandoned.

Assessment

The fundamental problems of floristic dissimilarity measures for estimation of ecological distance are inherent in the approach, and cannot be circumvented. Floristic resemblance measures are incorporated into multivariate methods, and knowledge of the properties of the various dissimilarity measures is of utmost importance for evaluation of multivariate methods and interpretation of results (Faith et al. 1987, Minchin 1987a). Percentage dissimilarity and the quantitative symmetric index are recommended as the floristic dissimilarity measures with best linearity and highest robustness, thereby best suited for estimation of ecological distance.

Alternative approaches to the measurement of ecological distance are needed. In a previous section, we have discussed ß diversity measures, and made an evaluation of some alternative approaches. R. Økland (1986a) argues that at least for single ecoclines, non-linear rescaling (by the option available in DCA, detrended correspondence analysis) is a far more reliable method for gradient rescaling (estimation of ecological distances between sample plots) than the use of floristic dissimilarity measures.

RELATIONSHIPS BETWEEN SPECIES

Relationships between species may be calculated from the primary data matrix just as the relationships between sample plots. However, the variation in species abundances along complex-gradients gives relationships between species a different meaning than relationships between sample plots, each representing a point in ecological space. We may distinguish between floristic and ecological relationships between species, just as in the case of relationships between sample plots. In addition, statistical tests of association between species have frequently been used. We will consider each of these three approaches in turn.

Floristic relationships

Floristic relationships between species express the degree of similarity in species distributions in a set of sample plots. Such measures do not take the optima and amplitude of species relative to the underlying gradients into account, they are strongly influenced by differences in species abundances, and hence, they will not give much information of ecological value. If, for some reason, floristic measures of relationships between species are to be used, the indices corresponding to percentage dissimilarity (or the quantitative symmetric index) are likely to be favourable because of their linearity properties, but the approach as such is not recommended.

Ecological relationships

Ecological relationships between species implies comparing species abundance data relative to underlying complex-gradients, appropriately scaled (cf. pp. 33-34). Parameters of species responses curves relevant for comparison, are distance between modes, overlap between species, and the gradient intervals spanned by the compared species. These topics belong to niche breadth and overlap calculation (pp. 43-45). The use of multivariate techniques for identification of the major ecoclines in the material prior to studying ecological relationships of species is recommended.

Species association and correlation coefficients

Statistical approaches to species association use the data (quantitative or qualitative) for two species, h and i, in a set of n sample plots. The null hypothesis tested is that the species are randomly distributed on the sample plots. The species are **positively associated** if the null hypothesis is rejected, and the species co-occur more frequently than expected from their frequencies in the material. Similarly, **negatively associated** species have a significantly lower degree of association than expected. Tests of this kind rest on several assumptions (Greig-Smith 1964, Goodall 1978a), the most important being independence of sample plots. The degree to which this demand is satisfied depends on the sampling design. Among the numerous approaches to species association (cf. Goodall 1978a, Sokal & Rohlf 1981), we will consider the approaches by correlation in some detail. Correlation coefficients provide estimates of the degree of co-ordination of the variation in two variables over n observations. If the variables are uncorrelated, the value of the correlation coefficient is 0. If the correlation is perfect (as judged relative to a statistical model), the value of the coefficient is 1, and if there is a perfect negative correlation, the value of the coefficient is -1. Several correlation coefficients are in use, assuming different statistical models. The most widely used is the **Pearson product-moment correlation coefficient** (cf. Sokal & Rohlf 1981), expressing the linear relationship between variables. This correlation coefficient assumes that the observations are independent with normally distributed error functions. For quantitative data, the correlation between two variables h and i is

$$r(h,i) = [SUM_{j=1,...,n}(y_{hj} - n^*y_{h.})(y_{ij} - n^*y_{i.})]/\{[SUM_{j=1,...,n}(y_{hj} - n^*y_{h.})^2][SUM_{j=1,...,n}(y_{ij} - n^*y_{i.})^2]^{0.5} \quad (39)$$

where y_{ij} is the observation of variable i in sample j, and $y_{i.}$ is the sum of y_{ij} over the n samples. Terms with h instead of i are defined similarly. Equation (39) has been proposed for testing the association between species pairs. The approach is burdened with several pitfalls. Let us consider a set of sample plots representing the variation along a coenocline of some length (at least 4 S.D. units). Fig. 79 shows the correlation coefficient between two species as a function of separation of the species modes along a coenocline, assuming

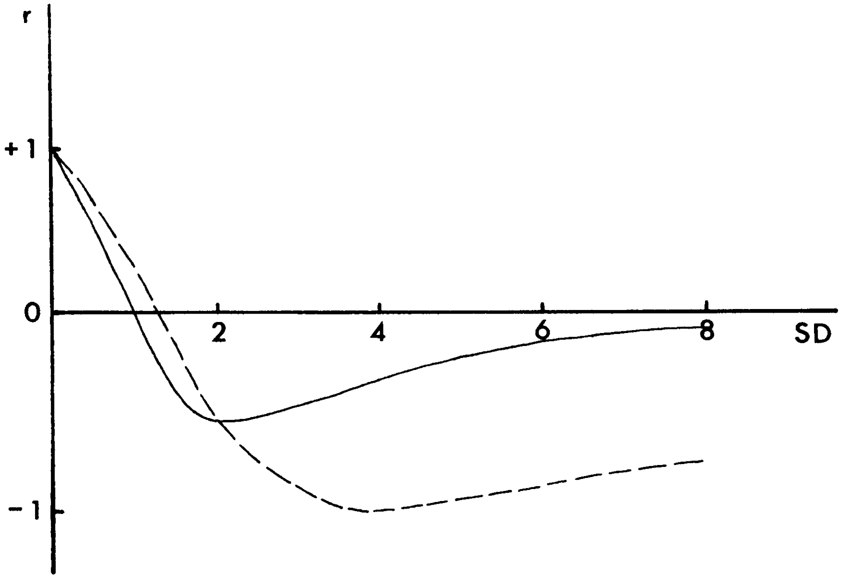


Fig. 79. Pearson's product-moment correlation coefficient between a pair of species, expressed as a function of separation of the modes of the two species along an underlying coenocline (scaled in S.D. units). The graphs are tentative (after Groenewoud 1976). Continuous line - quantitative data. Broken line - qualitative (presence/absence) data. All intermediates between the two graphs can be produced by a choice of appropriate weighting functions.

bell-shaped distribution of species response curves and no noise. Due to the non-linear relationships of species to the complex-gradients, the correlation between two species decreases rapidly from 1 when the modes coincide, to a minimum below zero, and then rises again. This shows that the correlation coefficient is inappropriate as a measure of association if the ß diversity is unknown (van Groenewoud 1976). The problem is somewhat reduced when qualitative (presence/absence) data is used. Then the formula is reduces to:

$$r(h,i) = (n_{hi}*n_{-} - n_{h}*n_{i})/[(n_{hi} + n_{h})(n_{hi} + n_{i})(n_{h} + n_{-})(n_{i} + n_{-})]_{0.5} \qquad (40)$$

where n_{hi} is the number of sample plots containing both species, n_h is the number of sample plots containing species h, n_i is the number of sample plots containing species i, and n_{-} the number of sample plots in which neither species occur.

Non-parametric or distribution-free correlation coefficients assess the correlation by only taking the rank order of the observations into account. They are less sensible to non-linear variation, but still assume that the variables have a monotonous relationship (steady increase or decrease) to the underlying complex-gradients. The most widely used non-parametric correlation coefficients are **Spearman's rank correlation coefficient** and **Kendall's rank correlation coefficient** (cf. Sokal & Rohlf 1981). As the assumption of monotonous species response to complex-gradients is violated, non-parametric correlation coefficients offer no solution to the problem of testing for species association in data sets of moderate, high or unknown beta diversity.

Tests of species association tests should be restricted to situations of very low beta diversity. In such cases, the association patterns have important bearings on the structure and function of vegetation; e.g., the importance of interspecific interactions for community structure, and assessment of the scale on which the interactions occur (e.g., Turkington & Harper 1979a, Pentecost 1980, Rogers 1983, Mahdi & Law 1987, O'Connor & Aarssen 1987, John 1989). The number of different available tests is high. Testing for correlation may be performed using one of the correlation coefficients mentioned above. As an example, we will take the simple testing of species association using qualitative data for two species. We count the number of samples in which both, one, or none of the species is present, and create a 2 x 2 contingency table:

		Sp. h		Total
		+	-	
Sp. i	+	n_{hi}	n_i	$n_{hi} + n_i$
	-	n_h	n_-	$n_h + n_-$
Total		$n_{hi} + n_h$	$n_i + n_-$	n

A chi-square test for association is carried out by calculating the chi-square test statistic (with Yates' (1934) correction)

$$r(h,i) = n(|n_{hi}*n_- - n_h*n_i| - 0.5*n)^2/[(n_{hi} + n_h)(n_{hi} + n_i)(n_h + n_-)(n_i + n_-)]. \qquad (41)$$

This statistic is chi-square distributed with one degree of freedom. This approach is used, for instance by Williams & Lambert (1959), Elven (1978) and Halvorsen (1980).

RELATIONSHIPS BETWEEN ENVIRONMENTAL VARIABLES

One of the major goals of ecological analysis is to identify complex-gradients, that is groups of correlated environmental gradients. Analysis of correlation between measured environmental variables is an important initial step in ecological analysis. The Pearson product-moment correlation coefficient (equation 39) is useful for testing linear correlation between variables, but requires that the variables are checked for statistical distribution in advance, and that appropriate transformations are made if necessary. Rank correlation coefficients are invariant of distribution, and give the same result with all monotonous transformations of data. Rank correlation have only slightly lower test power than the product-moment correlation coefficient when the distribution of the variable is normal, but considerably higher test power when the distribution is deviant. Thus rank correlation coefficients are recommended for use with environmental variables. Kendall's rank correlation coefficient (Kendall 1938) is often rated highest among the two most commonly used coefficients (Fenstad et al. 1977).

Relationships in the secondary matrix of relationships between ecological variables (e.g., a secondary matrix of correlation coefficients) can be visualized by use of **plexus diagrams** (McIntosh 1978). The variables are displayed as points, and the relationships between the points are shown by lines. Usually, strong positive and strong negative correlations are shown by lines of different thickness, broken lines, etc. Strongly positively correlated variables are grouped together in order to make the relationships more clearly comprehensible from the diagram. Examples of plexus diagrams of ecological variables are given by T. Økland (1988, 1989).

METHODS: GRADIENT ANALYSIS

INTRODUCTION AND BASIC CONCEPTS

The gradient structure of vegetation has been emphasized throughout this book. Species respond to environmental factor complexes; each species occupying a limited range along each of the major complex-gradients. Consequently, the methods for studing species-gradient relationships, **gradient analysis**, make up one of the most important, or perhaps the most important, group of techniques in vegetation ecology. The term gradient analysis will be used here in the widest sense, in accordance with ter Braak & Prentice (1988: 272), to comprise "techniques that assist the interpretation of community composition in terms of species' responses to environmental gradients in the broadest sense".

Most multivariate techniques in use for gradient analysis in vegetation ecology are actually general methods, applicable in many branches of science. Ter Braak and Prentice (1988) recognize four kinds of gradient analysis techniques. With reference to vegetation ecology, these can be briefly described as follows: (1) **direct gradient analysis** or **regression**, the study of species' responses to measured environmental gradients, (2) **inverse direct gradient analysis** or **calibration**, the inference of environmental variables from the species composition of the vegetation, (3) **indirect gradient analysis** or **ordination**, the ordering of sample plots and/or species along axes of variation in vegetational composition (the term indirect refers to the interpretation of axes, which is made as a second, ibndependent step), and (4) **constrained ordination**, the ordering of sample plots and/or species along axes of variation in vegetational composition, optimizing the fit to measured environmental data.

REGRESSION

Regression techniques are statistical curve-fitting methods. Using regression, we aim at finding the function that, relative to a given model, most closely fits the observations of species abundances (**the response variable** or **the dependent variable**) to one or more environmental variables (the **predictor**, or **explanatory**, or **independent variables**), cf. Austin (1971) and ter Braak and Prentice (1988). Regression as here defined includes **direct gradient analysis** in the sense of Whittaker (1967, 1978b). Regression may serve the following purposes in vegetation ecology (ter Braak & Looman 1987): (1) estimating parameters of species response functions, e.g., the ecological amplitude (or tolerance), the mode (or optimum), and the modal abundance, and (2) predicting species' responses from knowledge of environmental conditions at a site.

A comprehensive survey of regression techniques relative to a variety of statistical models is given by ter Braak and Looman (1987). We will describe some of these models and the associated regression methods briefly, as knowledge of them is necessary for understanding other gradient analysis techniques.

The linear model

The **linear model** assumes a linear relationship between species abundances and the environmental gradients. Elsewhere (pp. 26-33) we have shown that species response curves are mostly unimodal. Hence, linear models are only appropriate when very short gradient segments are considered (ß diversities < (1.0-)1.5-2.0 S.D. units).

A statistical response model consists of two parts, a systematic part describing the way the expected response depends on the environmental variable, and an error part describing the way the observed response deviates from the expected response. The systematic part is specified as an equation, the error part is specified as the distribution of ε, the error in single observations. The linear model is

$$y = a_1z + a_0 + \varepsilon \qquad (42)$$

where y is the abundance of a species, z the environmental (explanatory) variable, and a_1 and a_0 are coefficients. The systematic part, represented by the expected response, Ey, is

$$Ey = a_1z + a_0. \qquad (43)$$

Fig. 80 gives a geometric interpretation of the parameters of the linear model.

Assuming that the recorded abundances are independent and that the error is normally distributed with a mean equal to the expected values Ey, we can use the least-squares principle to estimate the parameters a_1 and a_0. Our aim is to find those estimators for the coefficients, $a_1{}^\wedge$ and $a_0{}^\wedge$, that give the best overall correspondence between the observed abundances for the species in question in sample plot j, $j = 1,\ldots,n$, x_j, and the fitted values, $a_1{}^\wedge z_j + a_0{}^\wedge$, where z_j is the value for the environmental variable in sample plot j. According to the least-squares principle the correspondence is best when the quadrat sum

$$Q = SUM_{j=1,\ldots,n}\ (y_j - a_1z_j - a_0)^2 \qquad (44)$$

reaches its minimum. We introduce the notation $y_.$ for the sum of the y_j values and $z_.$ for the sum of the z_j values, and introduce the parameter a_p by the equation

$$a_p = a_1z/n + a_0$$

$$a_0 = a_p - a_1z/n \qquad (45)$$

Equation (44) can then be rewritten as

$$Q = SUM_{j=1,\ldots,n}\ [y_j - a_p - a_1(z_j - z/n)]2 \qquad (46)$$

The estimators $a_p{}^\wedge$ and $a_1{}^\wedge$ (and hence $a_0{}^\wedge$) are estimated from the equations

$$dQ/da_p{}^\wedge = 0 \qquad (47)$$

$$dQ/da_1{}^\wedge = 0 \qquad (48)$$

From (47) we obtain

$$SUM_{j=1,\ldots,n}\ [y_j - a_p{}^\wedge - a_1{}^\wedge(z_j - z/n)] = 0$$

$$SUM_{j=1,\ldots,n}\ y_j - na_p{}^\wedge - a_1{}^\wedge * SUM_{j=1,\ldots,n}\ (z_j - z/n)] = 0$$

$$a_p{}^\wedge = y/n + a_1{}^\wedge(z_. - nz/n)$$

$$a_p{}^\wedge = y/n \qquad (49)$$

Inserting (49) in (48) we obtain

$$SUM_{j=1,\ldots,n}\ [y_j - y_. - a_1{}^\wedge(z_j - z/n)](z_j - z/n)$$

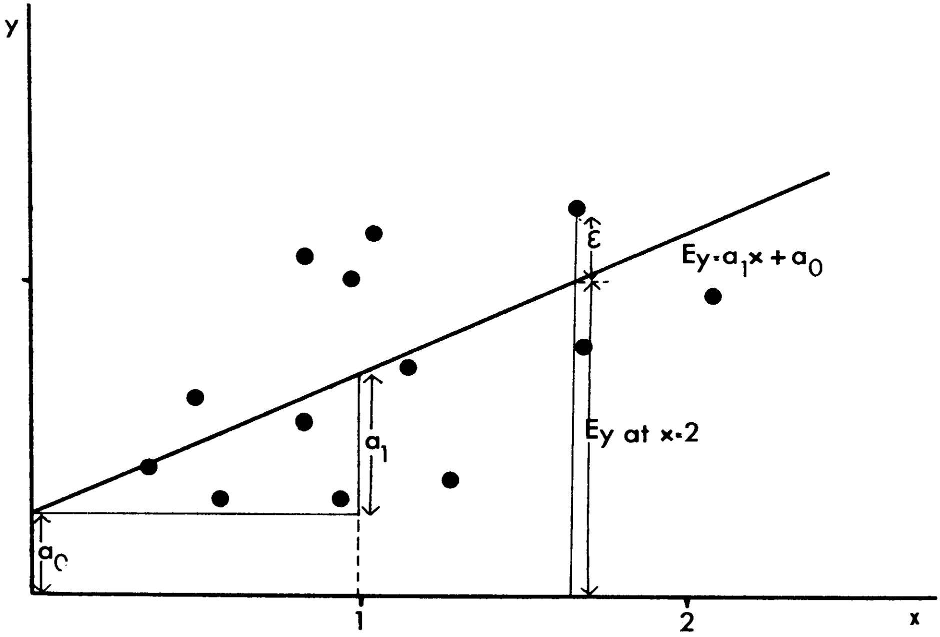


Fig. 80. Geometric interpretation of the parameters of the linear response model. Ey is the systematic part of the model, ε represents the error. a_0 and a_1 are parameters of the regression. For further information, see text.

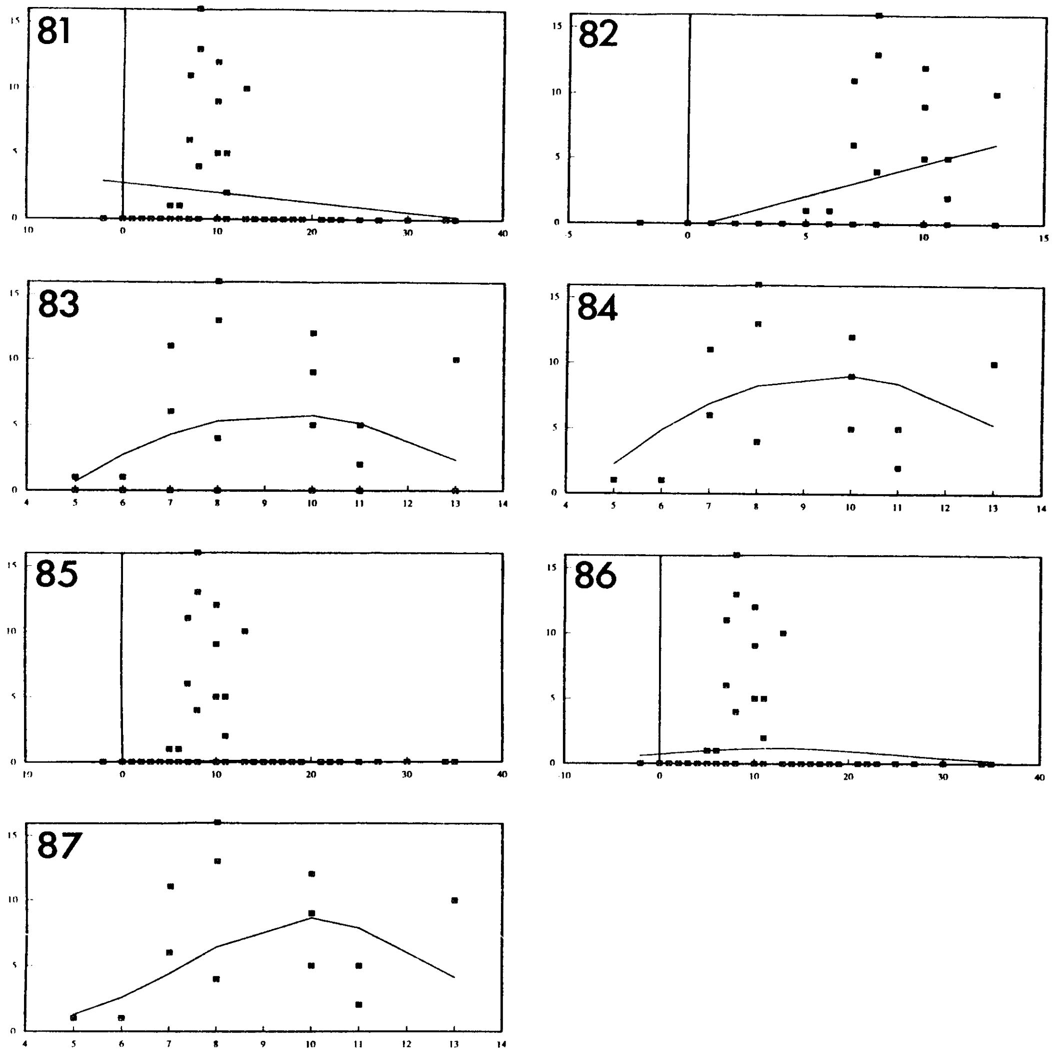
$$SUM_{j=1,...,n}\ (y_j - y/n)(z_j - z/n) - a_1\hat{}*SUM_{j=1,...,n}\ (z_j - z/n)^2 = 0$$

$$a_1\hat{} = [SUM_{j=1,...,n}\ (z_j - z/n)(y_j - y/n)]/[SUM_{j=1,...,n}\ (z_j - z/n)^2] \qquad (50)$$

Inserting equation (49) in equation (44) then gives

$$a_0\hat{} = y/n - a_1\hat{}z/n \qquad (51)$$

As an example, we take the abundance of *Scirpus cespitosus* in virgin mire sites at Rønnåsmyra, cf. Tab. 1. In this case, the number of observations is n = 51, z_j denotes the depth to the water table, and y_j denotes the frequency in subplots of the species in sample plot j. The values of the estimators (using equations (50) and (51)) are a_1^ = - 0.0726 and a_0^ = 2.7457. The correlation coefficient for the regression (Pearson's correlation coefficient between observed and fitted values for y, describing the goodness-of-fit of the data to the model), is r = - 0.1631, indicating that the model is inadequate for the data (r = 1 indicates perfect fit, r = -1 indicates perfect negative fit, and r = 0 indicates no linear trend in the data). Fig. 81 shows the data and the fitted regression. The unimodal response of *Scirpus cespitosus* to the environmental variable is the reason for the inadequacy of the linear model. However, if we restrict our attention to a part of the gradient in depth to the water table, say DEPT ≤ 13 cm, a more close fit to a linear model might be expected. In this case, n = 33, and the estimators are a_1^ = 0.4943 and a_0^ = - 0.3716. The correlation coefficient now becomes r = 0.4069, indicating a moderately good fit to the model (cf. Fig. 82). This demonstrates the point made above, that the linear model is only appropriate when the ß diversity is low.



Figs 81-87. Regression: fitting curves to *Scirpus cespitosus* frequency in subplots data from Rønnåsmyra, Grue, Hedmark (as function of depth to the water table), by several response models. Original observations are shown by symbols. Parameters of the fitted curves are given in text. Fig. 81. Linear model, all observations included (n = 51). Fig. 82. Linear model, observations corresponding to depth to the water table (DIST) less or equal to 13 cm included (n = 33). Fig. 83. Second order polynomial model, all observations corresponding to 5 ≤ DIST ≤ 13 included (n = 23). Fig. 84. Second order polynomial model, all nonzero observations included (n = 13). Fig. 85. Gaussian model, all observations included (n = 51). Zero abundance replaced by the value 0.01. Fig. 86. Gaussian model, all observations included (n = 51). Zero values replaced by the value 0.5. Fig. 87. Gaussian model, all nonzero observations included (n = 13).

The polynomial model

The linear response model is a special case of the general **polynomial model**

$$Ey = a_n z^n + \ldots + a_i z^i + \ldots + a_0. \qquad (52)$$

The unimodal response of *Scirpus cespitosus* to depth to the water table (the species is restricted to the interval $5 \leq z \leq 13$), suggests that the response of the species to the environmental variable could perhaps be fitted more closely by a parabola; a polynomial function of power 2:

$$Ey = a_2 z^2 + a_1 z + a_0 \qquad (53)$$

The parameters a_2, a_1, and a_0 can be estimated by the least-squares principle, just as in the case of the linear model.

As an example, we take all abundances of *Scirpus cespitosus* in the range $5 \leq \text{DEPT} \leq 13$, including the zeros (absences). In this case, n = 23, and the least-squares estimators are a_2^ = - 0.2665, a_1^ = 5.0074, and a_0^ = -17.7034. The correlation coefficient is r = 0.3382, indicating a moderate fit to observations (Fig. 83).

Obviously, the zero values represent qualitative noise strongly reducing the fit of the parabola to the abundance values. Minchin (1987b, 1989b), in his comprehensive simulation model for ecological data, generates the data in three steps: (1) generation of (physiological) species response curves, (2) generation of a sampling pattern, and (3) generation of species-in-sample plot data, incorporating noise. Noise is of two kinds, qualitative and quantitative. Zero values within the range along the gradient where the species occurs, are caused by qualitative (presence/absence) noise. Qualitative noise increases with decreasing sample plot size, by reduction in matrix density (cf. p. 98; R. Økland et al. in prep.). An alternative to the regression procedure above is therefore the elimination of qualitative noise at the onset by restricting attention to the nonzero abundance values. Fitting a response curve to the nonzero abundance values is equivalent to a reduction of quantitative noise, assuming that the error part of the regression always has the expected value of zero.

The fitting of a parabola to *Scirpus cespitosus* abundance values was repeated, but this time only the 13 nonzero frequency in subplots values were included. Estimators for the regression parameters were a_2^ = - 0.3232, a_1^ = 6.2011, and a_0^ = - 20.6681, giving a correlation coefficient of r = 0.4174 (Fig. 84). The mode of the fitted response curve is at DIST = 9.59 (estimated from the regression by setting dy/dz = 0).

The Gaussian model

The **Gaussian model** assumes that the species' response to environmental gradients is adequately described by the Gaussian curve, as given by equation (4), also see Fig. 23. The Gaussian model is acceptable for ecological data only as a course generalization (cf. pp. 32-33). In the notation used here, the systematic part of the Gaussian model is:

$$Ey = a^* \exp\,[-0.5(z-\mu)^2\sigma^{-2}], \qquad (54)$$

where μ is the mode, σ is the tolerance, and a is the modal abundance. The parameters of the Gaussian curve can be estimated directly by the least-squares principle, but this is most complicated. A much simpler approach is to fit a parabola to log-transformed abundances; the regression model then becomes

$$E(\ln y) = \ln a - 0.5(z-\mu)^2/\sigma^2$$

$$E(\ln y) = -0.5z^2/\sigma^2 + \mu z/\sigma^2 + \ln a - 0.5\mu^2/\sigma^2 \qquad (55)$$

We substitute for a, σ, and μ in (55) to get the regression model

$$E(\ln y) = a_2 z^2 + a_1 z + a_0, \qquad (56)$$

where

$$a_2 = - 1/(2\sigma^2) \qquad (57)$$

$$a_1 = \mu/\sigma^2 \qquad (58)$$

$$a_0 = \ln a - \mu^2/(2\sigma^2). \qquad (59)$$

The parameters a_2, a_1 and a_0 are estimated by parabolic regression using ln x as the dependent variable. The parameters of the Gaussian curve are estimated from (57)-(59) by solving the equations for a, σ and μ:

$$\mu{\wedge} = -\ a_1/(2a_2) \qquad (60)$$

$$\sigma{\wedge} = (-2a_2)^{-0.5} \qquad (61)$$

$$c{\wedge} = \exp\ (a_2\mu{\wedge}^2 + a_1\mu{\wedge} + a_0) \qquad (62)$$

The presence of zeros in the abundance data matrix is a serious problem as the logarithm of zero is undefined. One way of overcoming this problem is by adding a small, positive number to all abundance values (or to the zeros), but this approach has the disadvantage that the result is dependent on the value chosen for addition.

As examples, we consider the abundance of *Scirpus cespitosus* at Rønnåsmyra. First, we replace all zeros in the data with 0.01, then we fit a parabola to log-abundances as outlined above. We obtain the following estimators: a_2^ = - 0.00846, a_1^ = 0.1976, a_0^ = - 3.4829, giving estimators for the mode μ^ = 11.68, for the tolerance σ^ = 7.69, and for the modal abundance a^ = 0.9743. The original and back-transformed fitted values are shown in Fig. 85. It can be noticed that the high proportion of zeros and the low value added to the abundances give rise to a very low estimator for the modal abundance. The correlation between the original and the fitted abundance values is r = 0.4208. Second, we make a new trial, by adding the value 0.5 to all zeros. Now the estimators become a_2^ = - 0.00344, a_1^ = 0.08385, and a_0^ = - 0.3260, and μ^ = 12.19, σ^ = 12.06, and a^ = 1.203. The correlation is r = 0.3565. We observe (cf. also Fig. 86) that the estimator for the mode is almost unchanged, the tolerance estimators strongly increased, and the modal abundance slightly increased. As a third approach to fit a Gaussian curve to the abundances, we consider the presences only, thereby omitting the qualitative noise. The number of samples is n = 13. Regression is performed as above, giving the estimators a_2^ = - 0.07844, a_1^ = 1.5574, a_0^ = - 5.5710, and hence μ^ = 9.93, σ^ = 2.52 and a^ = 8.66 (Fig. 87). The correlation (between original and fitted, back-transformed values) is r = 0.3071.

Other models, e.g., the beta function (p. 22), are also relevant, but will not be considered in detail here.

Weighted averages

One points of major interest is the estimation of a species' mode along an environmental gradient. Tentative estimates of species modes are often termed **ecological indicator values** (Ellenberg 1979). An intuitively sound, heuristic method for estimating species modes from a set of observations of the abundance y_{ij} of species i in sample plot j, j = 1,...,n, relative to an environmental variable k that has the value z_{kj} in sample plot j, is the mean of the environmental variable over all sample plots, weighted by species abundance:

$$u_i = (\mathrm{SUM}_{j=1,...,n}\ y_{ij}z_{kj})/(\mathrm{SUM}_{j=1,...,n}\ y_{ij}). \qquad (63)$$

A simple example is provided by abundance data for *Scirpus cespitosus* on Rønnåsmyra (Tab. 1). Zero abundance values do not contribute to either of the denominator or the numerator of equation (63), thus this reduces to

$$u_i = (2*11 + 4*11 + 1*5 + 1*6 + 11*7 + 6*7 + 13*8 + 10*13 + 12*10 + 16*8 + 9*10 + 5*10 + 4*8 + 5*11)/(2 + 4 + 1 + 1 + 11 + 6 + 13 + 10 + 12 + 16 + 9 + 5 + 4 + 5)$$

$$u_i = 905/99$$

$$u_i = 9.14$$

Disregarding species absences, estimation of modes by weighted averaging is strongly influenced by sample plot distribution along the environmental gradient.

Weighted averaging has the advantage of being computationally much simpler than estimation of parameters of the Gaussian model. Furthermore, the model is not so restrictive, merely demanding that the species show unimodal responses to the environmental variable. Ter Braak & Looman (1986) compared the relative efficiency of weighted averaging and Gaussian (logit) regression, concluding that the mode of a species can be estimated efficiently provided that the site scores are evenly (homogeneously) distributed over the range of the species along the environmental variable.

CALIBRATION

Calibration is the inverse of regression, i.e. techniques that address the problem of estimating site conditions from the species composition at a site, provided that relationships of the species to the environmental variable are known. Several statistical models can be used for calibration. Calibration rests on the assumption that the species composition is a good predictor of site conditions. This is the case when (1) the response model is realistic, (2) the data used for establishment of relationships between species and environmental gradients are adequate, (3) the tolerance of the species is low (species with narrow ecological amplitudes are better predictors of site conditions), and (4) the number of species occurring at the site, for which knowledge of environmental relationships is available, is high (cf. also ter Braak 1987b).

Several methods for calibration are available. We will restrict our attention to two of these; for a more detailed treatment is referred to ter Braak (1987b).

The linear model

Let us assume that the relationship between the abundance of a number of species i, i = 1,...,m, and an environmental variable z is known to be linear (recall that this only holds true for short segments of gradients, cf. p. 117). Also assume that the parameters of the linear response functions have been estimated, that is that the parameters a_1 and a_0 of equation (43) are known. Then the expected value for the abundance y_{ij} of species i, given a value $z = z_j$ for the environmental variable, is:

$$Ey_{ij} = a_{1i}z_j + a_{0i} \tag{64}$$

If the error is normally distributed with zero mean, we can obtain an estimate for z, $z_i{}^\wedge$, based on one species i by solving (64) for z:

$$z_{ij}{}^\wedge = y_{ij}/a_{1i} + a_{0i}/a_{1i} \tag{65}$$

An estimator for z_j by the least-squares principle based on all species can be obtained by minimizing the sum of squared differences between the observed and estimated abundances y_i (cf. equation 64), that is, by minimizing

$$Q = \mathrm{SUM}_{i=1,...,m}\,(y_{ij} - Ey_{ij})^2$$

$$Q = \mathrm{SUM}_{i=1,...,m}\,(y_{ij} - a_{1i}z_j{}^\wedge - a_{0i})2. \tag{66}$$

Equation (66) is minimized by solving

$$dQ/dz_j{}^\wedge = 0$$

$$\mathrm{SUM}_{i=1,...,m}\,a_{1i}(y_{ij} - a_{1i}z_j{}^\wedge - a_{0i}) = 0$$

$$z_j\hat{}*(\mathrm{SUM}_{i=1,...,m}\ a_{1i}^2) = \mathrm{SUM}_{i=1,...,m}\ a_{1i}(y_{ij} - a_{0i})$$

$$z_j\hat{} = [\mathrm{SUM}_{i=1,...,m}\ a_{1i}(y_{ij} - a_{0i})]/(\mathrm{SUM}_{i=1,...,m}\ a_{1i}^2) \qquad (67)$$

The estimator is good when the species are independent and have equal error variances (ter Braak 1987b). These requirements are unrealistic, as is the linear model.

Weighted averages

If all species' indicator values relative to an environmental gradient (estimates for the modes), u_i, are known, an estimate for the position of a sample plot along the gradient conditions, $z_j\hat{}$, can be obtained by averaging the indicator values for the species occurring in the sample plot (for which the indicator value is known). It is intuitively sound to use the species abundances as weights, thus obtaining the following formula for weighted averaging calibration:

$$z_j\hat{} = (\mathrm{SUM}_{i=1,...,m}\ y_{ij}u_{kj})/(\mathrm{SUM}_{i=1,...,m}\ y_{ij}) \qquad (68)$$

In principle, the Gaussian model can also be used for calibration. This is, however, computationally complicated. Ter Braak and Barendregt (1986) have shown (for Gaussian logit curves) that estimates by weighted averaging calibration approximate estimates based on a Gaussian model provided the species optima are evenly (homogeneously) distributed along the environmental gradient, and the species have equal tolerances and equal maxima.

Ellenberg (1979) provides estimates of indicator values for a large number of Middle European species relative to some ecological factors, e.g. soil acidity, light and nitrogen. Vevle & Aase (1980) compare pH measurements (from several Norwegian phytosociological investigations) with estimates based on Ellenberg's indicator values, and found a relatively good correspondence. There are, however, good reasons to use calibration with care as any bias (sampling bias, subjective bias, etc.) in the data used for establishing the indicator values will be reflected in the site estimates. Therefore calibration should only be used when environmental measurements cannot be achieved (e.g., for palaeoecological data). An example of calibration is the reconstruction of past pH in lakes from the composition of diatoms, based on the present environmental relationships of the species (Flower 1986, Stevenson et al. 1989).

ORDINATION

Basic principles

At the start of most general-purpose vegetation ecological studies, there are several fundamental questions, the answers of which are unknown; which environmental factors are the most important, how do gradients in single environmental variables make up complex-gradients, and how can the complex-gradients be ranked according to importance for determining vegetation structure? The intrinsic dimensionality of the species-in-sample plot data matrix equals the minimum of m, the number of species, and n, the number of sample plots. In all terrestrial systems, the number of complex-gradients with major impact on the vegetation is low. The sample plots and species modes of all data-sets are therefore possible to order along coenoclines. Ordination is the process of reducing the dimensionality of a data matrix by extracting (coenocline) axes, without involving external variables. The interpretation of these axes (in ecological terms) has to follow as an separate procedure.

Conceptually, there are at least three ways to approach ordination techniques:

(1) *Geometrically*, as **scaling methods** (Prentice 1977), ordination methods are conceived as summarizing vegetation data by producing a low-dimensional ordination space in which the dissimilarities between sample plots in the data matrix are preserved as well as possible; optimality judged by some objective criterion (cf. Gauch 1982a, Minchin 1987a, ter Braak & Prentice 1988). The ordination space can be conceived as a low-dimensional subspace of the species-dimensional space. The intention of ordination is to produce an ordination space with axes closely approaching the axes of the ecological space. It appears intuitively sound that pairs of sample plots with low floristic dissimilarity should be placed close to each other in an ordination diagram (a plot of sample plot positions relative to 2 or 3 ordination axes). The high dimensionality of data matrices makes a perfect correspondence between the original dissimilarities and fitted distances (in the ordination) impossible. The goodness-of-fit is measured by a **stress function** (Prentice 1977). As scaling methods, ordination techniques can be characterized by the combination of (a) dissimilarity measure (fixed, or chosen by the investigator), and (b) stress function. Ordination techniques can be divided into **metric scaling techniques**, using the numerical values of the dissimilarities for calculation of the stress, and **non-metric scaling techniques**, only using the rank order of the dissimilarities. **Hybrid scaling techniques** (Faith et al. 1987) combine properties of metric and non-metric scaling techniques by partly using the numerical values of dissimilarities, partly the rank order. Each ordination technique may appear in several varieties depending on standardizations and other options.

(2) *Statistically*, "ordination axes can be considered as latent variables, or hypothetical environmental variables, constructed in such a way as to optimize the fit of the species data to a particular (linear or unimodal) statistical model of how species abundance varies along gradients" (ter Braak & Prentice 1988: 272; ter Braak 1985, 1987a). We will consider this viewpoint in some detail. First, let us assume that for a given data set, one statistical model describes the relationship between species abundance and environmental variables appropriately. Then we can fit response curves for all species i relative to environmental variables k by regression. Normally, some species will show best fit to one variable, other species will show better fit to other variables. Several statistical techniques can be used to measure the overall fit of the species to an environmental variable (e.g., ter Braak 1987c). The task of ordination is to construct the hypothetical environmental variable giving the theoretically best overall fit of the species data, given this response model. This hypothetical variable is taken as the first ordination axis. A second axis can be found by correcting the data matrix for the variation accounted for by the first axis, repeating the process of axis extraction, and so on.

Ter Braak and Prentice (1988) explain metric ordination methods as iteration processes with cycles of regressions and calibrations, relative to a specified statistical model. Initially, the sample plots are given random scores (positions relative to a trial vector for the first ordination axes). The relationships of the species abundances to this hypothetical variable is determined by regression. Secondly, we use calibration to infer new trial site scores from the observed species abundances. In almost all cases, this second trial vector shows better fit to the species data than the first. Then the process of regression followed by calibration is repeated again, the fit of the third trial vector tested, and so on until the fit is not improved by further iterations. Then the first ordination axis is found. The process is repeated after correction of the data matrix for the variance now accounted for, and so on until no more ordination axes are to be extracted.

(3) *Algebraically*, metric ordination techniques can be explained as techniques for obtaining the **eigenvectors** (latent variables) and the corresponding **eigenvalues** (measures of the goodness-of-fit of the data to the latent variables) of the data matrices (or derived secondary matrices). We will not consider the matrix algebra of ordination methods in

further detail (see, for instance Pielou 1977, 1984, Orlóci 1978, ter Braak 1987c).

The three approaches express different aspects of ordination, and also indicate that computationally, there are several equivalent ways to obtain the results for one ordination method (characterized by a particular combination of scaling method and dissimilarity measure). The three viewpoints therefore complement each other, and are equally valid. We will emphasize the first two, describing those among the presently available techniques that are most relevant to vegetation data.

Evaluation of ordination methods

Principles of evaluation

The usage of ordination techniques has increased steadily since they were introduction to ecology in the 1950s and early 1960s (Kent & Ballard 1988). Following the increased interest in ordination, the number of different techniques and variants of techniques has also increased strongly. This has called for evaluation strategies in order to sort out the generally preferrable methods. Several different approaches to evaluation of the relative merit of ordination techniques have been attempted. These can be divided into three main strategies: (1) by means of simulated data, (2) by means of real data, and (3) by theoretical reasoning.

(1) *By means of simulated data.* Simulated data sets (cf. p. 120) are computed on basis of a model with explicitely formulated properties. Thus, they have the obvious advantages that their properties are exactly known (Gauch et al. 1981, Kenkel & Orlóci 1986), which can be varied independently in order to study their effects on ordination (Minchin 1987a). One of the properties that can be controlled is the noise level (Minchin 1987a, 1987b). The expected ordination result (**target configuration**) can be specified precisely as sample co-ordinates in the simulated ecological space (Minchin 1987b). Objective comparison is therefore possible by use of simulated data (Kenkel & Orlóci 1986). However, the validity of the evaluation results is completely dependent on the realism of the simulated models (Austin 1980, Gauch 1982a, Kenkel & Orlóci 1986). All simulated models used so far in published evaluations of ordinations, are open to the criticism that they are based on too simplified assumptions and thereby lack realism (cf. Oksanen 1983, R. Økland 1990a). Minchin (1987a) proposed to compensate for this by using the **robustness** of ordination methods over a large number of models spanning the range of current possibilities, as an optimality criterion. This approach may overcome some of the problems with the simulation approach, but does not fully remove the danger of lack of realism in one or many properties in a larger part of the data sets used for evaluation. Furthermore, the overall test statistic (goodness-of-fit) of ordinations relative to the target configurations may be significantly influenced by data sets with unrealistic properties or unrealistic combinations of properties.

Several indices may be used for comparison of an ordination and a target configuration (review by Podani (1989)). Most simply, one-dimensional comparisons may be made by calculating correlation coefficients between sample positions along the target gradient and ordination scores. In the case of more than one gradient in the simulated ecological space (and several ordination axes), this method is less applicable. One can still make pairwise comparisons of axes in the target configuration and ordination axes, but there is a great risk that the target configuration is rotated in the ordination, thereby reducing all correlations and invalidizing the comparison.

Comparison may be done by **matrix correlation techniques** (Sneath & Sokal 1973, see Gauch et al. 1981 for an example), by which the corresponding distances (e.g., euclidean distances in ecological space and in ordination space) are used for calculating an overall dissimilarity or correlation between ordination and target.

The best way of assessing the goodness-of-fit of an ordination to a target configuration is by use of Procrustean analysis (Schönemann & Carroll 1970, see Fasham 1977, Kenkel & Orlóci 1986, Digby & Kempton 1987, Minchin 1987a). Minchin (1987a) gives the following brief explanation of the rationale of the method: "This technique fits one configuration to another using a combination of [1] origin translation, [2] rigid rotation and [3] reflection of reference axes and [4] uniform central dilation or contraction of scaling. The combination of transformations is found analytically, so as to minimize the sum of the squared distances between each point in the target configuration. The RMS [residual mean square] average of these displacements may be used as a measure of the discrepancy between the configurations (i.e. lower values indicate better fit)." The numbered transformations imply (1) moving of the origin (centroid) of the ordination to the origin (centroid) of target, (2) rotation of ordination axes (without any other adjustments) to maximize correspondence between the configurations, (3) replacement of an axis with its mirror image, and (4) stretching or contracting whole ordination axes without changing the position of the origin (centroid), to maximize the fit to the target configuration.

(2) *By means of real data.* No simulated data sets have yet met the realism of field data. However, as the true structure of real data cannot be known (Oksanen 1983, Minchin 1987a), this strategy "suffers from the major limitation that there is no precise statement of the underlying gradient structure which a successful ordination is expected to recover. The ordination results are assessed on the basis of preconceptions about the major environmental relationships derived from previous work. It is seldom possible to make quantitative statements about sample positions on the underlying environmental gradients which are sufficiently precise to allow a sensitive comparison of the performance of different ordination methods and independent of the biases of the formal or informal methods of vegetation analysis used in previous work" (Minchin 1987a: 89-90). Thus real data do not satisfy the criteria usually set for a test in the statistical sense of this concept, and the use of this word in this connection (e.g., Hill & Gauch 1980, Gauch et al. 1981, Ezcurra 1987) is inappropriate. However, real data can, and should, be used for evaluations in a less rigorous meaning. Such exploratory types of evaluation (Podani 1989) have shown to be extremely useful; much of our present knowledge of the functioning of ordination methods has actually appeared from the critical judgment of results from ordinations of field data. Observational analysis of the behaviour of ordination methods on field data is a necessary supplement to evaluation by means of simulated data-sets, but with a hypothesis-generating rather than a hypothesis-testing function.

Evaluation by real data mostly proceeds by visual inspection of ordination diagrams and comparison with previous knowledge, e.g. previous classifications (e.g., Oksanen 1983), previously recognized gradient structure (e.g., Hill & Gauch 1980, Gauch et al. 1981), and correlations with environmental variables (e.g., Ezcurra 1987, Peet et al. 1988).

(3) *By theoretical reasoning*; evaluation of the relevance of the underlying statistical model to known model properties of ecological data (e.g., Minchin 1987a, ter Braak 1987c). Such evaluation should be made pragmatically (Goodall & Johnson 1987), with clear reference to realistic models. Theoretical reasoning relative to ecologically uninteresting mathematical properties (cf. Beals 1973) or relative to unrealistic, or even pathological models (e.g., Wartenberg et al. 1987), is not relevant.

Examples used for illustration and evaluation

Four data-sets, one field data-set and three simulated data-sets are used for comparison and illustration of the properties of ordination techniques in this book.

(1) The field data-set is from virgin bog vegetation at Rønnåsmyra, the standard example (pp. 10-16). From the 51 sample plots of Tab. 1, sample plot No. 17 is removed to give a new data-set of 50 sample plots with a total of 52 species. This removal is frequency distribution (cf. Figs 71-72, cf. p. 105), the linear model is suitable. In order to in several of the ordinations.

(2) Three simulated data-sets with closely similar properties in terms of species distributions, noise levels, etc. (cf. Tab. 10) were simulated by COMPAS, Version 1.0 (Minchin 1988). With a range of the abundance scale of 10, the data-set accords to recommendations by, for instance, van der Maarel (1979) and R. Økland (1986a), also see pp. 101-102. The three data-sets (a-c) primarily differ with respect to dimensions of the simulated coenoplane: (a) The 6 x 1.5 S.D. data-set has one long, prominent gradient, and one short, minor gradient. This combination of gradient lengths may be encountered in nature for instance along sea-shores, or in boreal forests or alpine heaths when the whole length of the ridge-valley (topographic moisture-snow cover) gradient is included, and the variation in nutrient availability is low. (b) The 5 x 2 S.D. data-set resembles the 6 x 1.5 S.D. data-set, but with the prominence of the longer gradient somewhat reduced. (c) The 2.4 x 2 S.D. data-set is typical of situations when the ß diversity is low, e.g. where there are several species occurring throughout the material, as in the studies of the Fritzøehusparken beech forest by T. Økland (1988), a herb-rich spruce forest in Velfjord, Nordland, C Norway, by Rydgren (1989), and **Vaccinium myrtillus**-dominated spruce forest in Rausjømarka by T. Økland (1989).

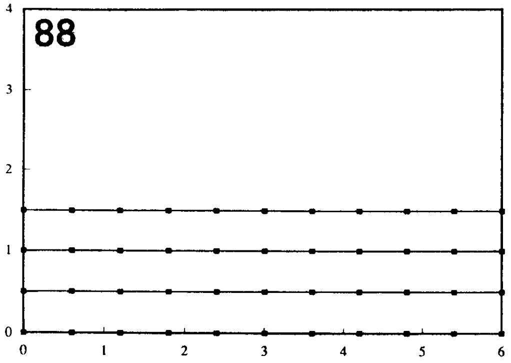
The field data set is used merely for illustration of some general features of the methods. The simulated data sets are for an introductory test of the performance of the ordination methods. As none of the ordinations rotated the target configuration (or hardly did so), ordination axes were compared to each of the target configuration gradients (separately) by calculating the product-moment correlation coefficients between sample plot positions along the compared axes/gradients.

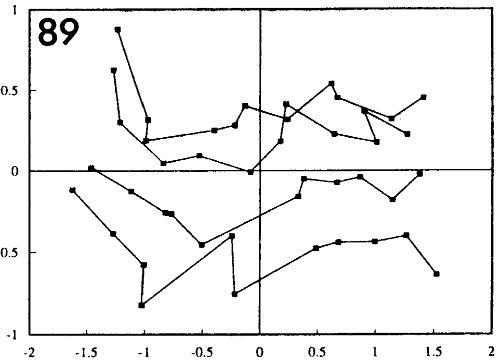
Tab. 10. COMPAS parameter settings and some data-set properties of simulated data sets used for evaluation of ordination techniques.

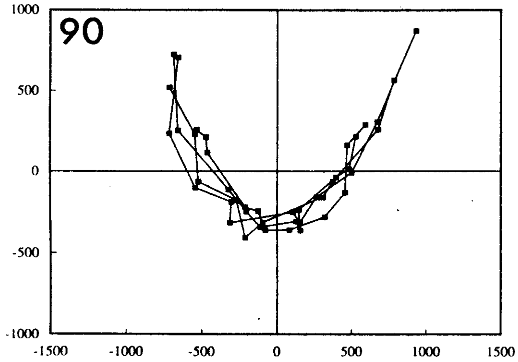
Property/parameter	Model (coenoplane dimension in S.D. units)		
	6 x 1.5 S.D.	5 x 2 S.D.	2.4 x 2 S.D.
Parameter settings of species distributions			
Number of species in model	120	120	100
Modal abundance (A)	lograndom, 1-100 scale	lograndom, 1-100 scale	lograndom, 1-100 scale
Ranges of species distrib. (grad. 1/grad. 2)	normal (μ = 100/400; σ = 25/100)	normal (μ = 120/300; σ = 30/75)	normal (μ = 250/300; σ = 62.5/75)
Coordinates for modes	random	random	random
Parameters α and τ	uniform random, 0.2-5.0	uniform random, 0.2-5.0	uniform random, 0.2-5.0
% of major species with modes adjusted	20	20	20
Parameter settings of the sampling pattern			
Number of sample plots (grad. 1 * grad. 2)	44 (11*4)	45 (9*5)	42 (7*6)
Parameter settings of the data-set generation			
Species interactions	no	no	no
α diversity trend	no	no	no
Qualitative noise	uniform random, 0.65-1.0	uniform random, 0.65-1.0	uniform random, 0.65-1.0
Quantitative noise	uniform random, $\approx A^{-1}$	uniform random, $\approx A^{-1}$	uniform random, $\approx A^{-1}$
Range of abundance scale	10	10	10
Properties of the data-set			
Number of species	102	100	100
Number of species pr. sample plot (min)mean(max)	14-(21)-29	16-(23)-32	16-(23)-30
Gradient length in R units (grad. 1/grad. 2)	0.96/0.24	0.78/0.32	0.38/0.33
Gradient length in S.D. units (by DCA ordination)	4.91/1.84	4.13/1.98	2.61/2.28

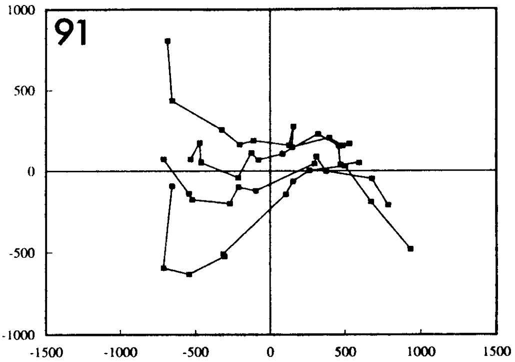
Principal component analysis (PCA)

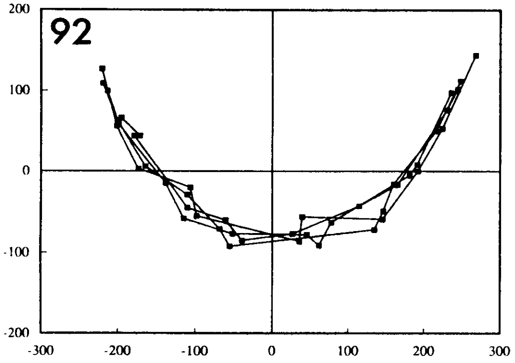
As an algebraic method, principal component analysis or PCA has been known since the beginning of the century; invented by Pearson (1901). It was the first ordination method to be applied to a vegetation data set (Goodall 1954a). Its mathematical properties have been described by several authors, including Pielou (1977), Orlóci (1978), Rørslett (1982) and ter Braak (1987c). As a standard mathematical technique with nice algebraic properties, it has always fascinated ecologists. We will focus its properties in relation to vegetation models.

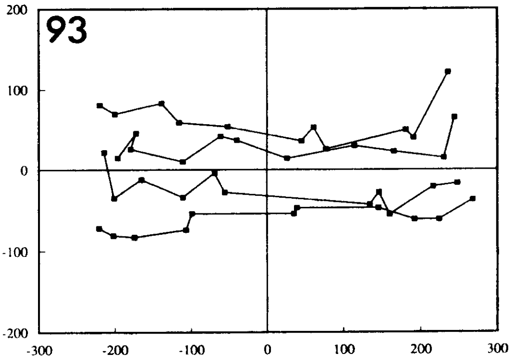








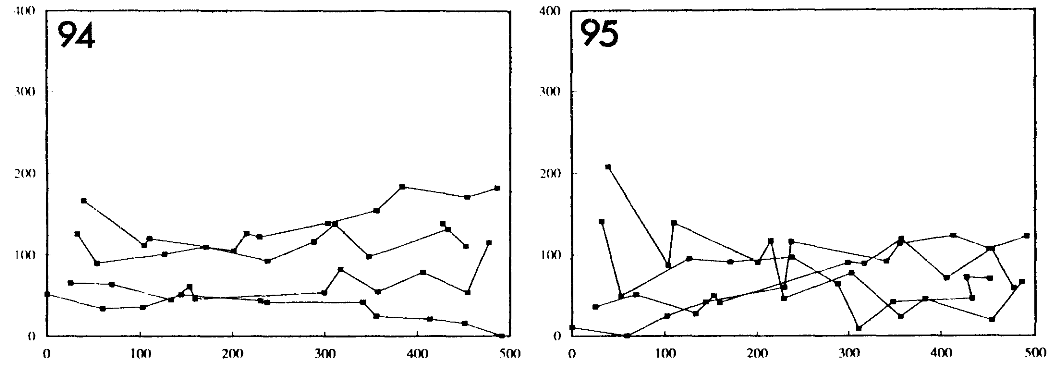




The method: model and iteration algorithm

Statistically, PCA can be described as a metric scaling method fitting species abundance data to latent variables (the hypothetical, underlying variables) by optimizing the overall fit to a *linear model*. PCA assumes that the species abundances can be adequately described as a linear function of position along the latent variables. The distance measure used in PCA is euclidean distance (equation 24).

The first axis, or the first **principal component**, is the hypothetical variable that minimizes the total residual sum of squares of linear least-squares regressions of the species abundances (ter Braak 1987c, cf. p.



Figs 88-95. Ordination of the 6 x 1.5 S.D. simulated coenoplane. Fig. 88. Target configuration, gradients 1 and 2. Fig. 89. LNMDS-BS, axes 1 and 2. Fig. 90. PCA-CS, axes 1 and 2. Fig. 91. PCA-CS, axes 1 and 3. Fig. 92. CA, axes 1 and 2. Fig. 93. CA, axes 1 and 3. Fig. 94. DCA, axes 1 and 2. Fig. 95. DCA, axes 1 and 3. Scaling of axes in Fig. 88 in S.D. units, in Figs 94-95 in S.D. units *100, otherwise scaling arbitrary.

00). The total residual sum of squares, the stress function in PCA, is the sum of the residual sum of squares from the regressions of each of the species abundances on the hypothetical variable. The complement of the stress (the stress subtracted from one) equals the eigenvalue of the ordination axis. The fraction of the variance in the data matrix accounted for by an axis is the ratio of the eigenvalue of this axis and the sum of the eigenvalues of all axes. The sum of eigenvalues is the total sum of squares in the data matrix, i.e.

$$\mathrm{SUM}_{i=1,\dots,m}\ [\mathrm{SUM}_{j=1,\dots,n}\ y_{ij}^2]$$

where y_{ij} is the abundance of species i in sample plot j (after standardization of the data). PCA ordinates species and sample plots simultaneously, i.e. it is a dual technique (e.g., Gower 1966, Orlóci 1978). The species score, often termed **loading**, indicates the direction of steepest increase in abundance of a species relative to an axis. The loadings relative to several ordination axes define a vector in the ordination space. This vector is the result of the linear regression of the abundance for this species on the axis (equation 43; estimators for parameters, equations 50 and 51). The sample scores result from a linear calibration, using the abundances of all species in a sample plot and the regression coefficients to predict the position of the sample along the axis (equation 67).

Among the numerous algorithms available for PCA, we will follow ter Braak (1987c) and ter Braak and Prentice (1988), describing the iterative algorithm termed the power method (Gourlay & Watson 1973), which illustrates the repeated cycles of regressions and calibrations leading to the ordination result (Tab. 11). An example using data for seven *Sphagnum* species in the 11 sample plots of Transect 1 at Rønnåsmyra (cf. Tab. 12) is given in Tab. 13. The iteration process starts with arbitrary initial sample scores. In the example, we used the depths to the water table for this purpose, but it can be shown that the final solution does not depend on the initial scores. Before the iteration process commences, the raw data are standardized (Step 1.2). Major variants of PCA can be separated according to the standardization method used. If no standardization is used, **non-centered PCA** (Noy-Meir 1973a, Noy-Meir et al. 1975, Ezcurra 1987) is obtained. In this case, the regression parameters are estimated by the unmodified equations 50 and 51. The vector defined by the regression of species i on the latent variable is the vector from an origin defined by the hypothetical sample plot with abundance 0 of all species. Another name of this variant is **PCA performed on a dispersion matrix**. If the abundance data are species-centered, equation 43 is simplified, $a_0 = 0$ (equation 51), and equation (50) reduces to (69). In this variant, **species-centered PCA**, the origin of all species vectors have been moved to the centroid, i.e., the mean abundance for all species. On convergence, the regression (equation 69) indicates the direction of steepest increase in the abundance of the species. Another name of this variant is **PCA performed on a covariance matrix**. An equation equivalent to (69) is obtained when the species abundance values are both centered and standardized by division with the standard deviation; **species-centered and standardized PCA**. The position of the origin is as in centered PCA. This variant is also termed **PCA**

Tab. 11. Iterative algorithm for PCA (species-centered) by the power method (cf. ter Braak 1987c, ter Braak & Prentice 1988).

Step 1. Getting started.

Step 1.1. Choose arbitrary initial sample scores $\{x_i\}$, not all equal.

Step 1.2. Perform a centering of the abundance values for all species:

$$y_{ij,\,new} = y_{ij,\,old} - y_{i.}/n$$

where

$$y_{i.} = SUM_{j=1,\ldots,n}\, y_{ij}$$

and $y_{i.}/n$ is the mean abundance of species i over all sample plots.[*]

Step 1.3. Center the sample scores $\{x_j\}$ and divide by the standard deviation:

$$x_{j,\,new} = (x_{j,\,old} - x_{.}/n)/[SUM_{j=1,\ldots,n}\,(x_j - x_{.}/n)^2]^{0.5}$$

where

$$x_{.} = SUM_{j=1,\ldots,n}\, x_j.$$

Step 2. Calculate new species scores $\{a_i\}$ by weighted summation of the sample scores;

$$a_i = SUM_{j=1,\ldots,n}\, y_{ij}x_j. \qquad (69)$$

Step 3. Calculate new sample scores $\{x_j\}$ by weighted summation of species scores;

$$x_i = (SUM_{i=1,\ldots,m}\, y_{ij}a_i)/(SUM_{i=1,\ldots,m}\, a_i^2). \qquad (70)$$

Step 4. The orthogonalization step; just by calculation of axes 2, 3 etc. By calculation of axis 1, go to step 5.

Step 4.1. Denote sample scores relative to previous axis $\{f_j\}$, sample scores relative to this axis $\{x_j\}$.

Step 4.2. Calculate

$$v = SUM_{j=1,\ldots,n}\, x_j f_j.$$

Step 4.3. Calculate

$$x_{j,\,new} = x_{j,\,old} - v{*}f_j$$

Step 4.4. Repeat 4.1-4.3 for all previous axes.

Step 5. The standardization procedure.

Step 5.1. Calculate the sum of squares of sample scores;

$$s^2 = SUM_{j=1,\ldots,n}\, x_j^2.$$

Step 5.2. Calculate new sample scores

$$x_{j,\,new} = x_{j,\,old}/s.$$

Step 6. Stop on convergence, that is when the new sample scores are sufficiently similar to the old ones, else go to step 2 and repeat the iteration.

---

[*] PCA, species-centered and standardized by division with the standard deviation is obtained by performing both centering and standardization in Step 1.2. Non-centered PCA is obtained by omitting Step 1.2.

performed on a correlation matrix. Ter Braak (1987c) gives a lucid survey of PCA variants and further details of their interpretation. We will not treat this in more detail, instead returning to the iteration procedure for centered PCA. After standardizing the abundance values, the trial sample scores are centered and standardized to unit standard deviation (Step 1.3). This considerably simplifies the following calculations. Step 2 is the regression step, step 3 is the calibration step. Step 4 is the **orthogonalization** step, by which an axis is made uncorrelated with all axes of lower rank. This step is, of course, not active when the first axis is extracted. The PCA axes are orthogonal (ay right angles) in the multidimensional ordination space. In the last step, the sample scores are standardized to zero mean and unit standard deviation to make them comparable to the sample scores of the previous iteration cycle. After a few iteration cycles, sample scores no longer change, and convergence has been reached. The value of s (Step 5) on convergence, the square root of the sum of squares of the sample scores (cf. Tab. 11), is the eigenvalue of the axis. Further axes may be extracted by the same procedure, invoking the orthogonalization step.

Biplot interpretation and scaling of axes

The sample scores and the species scores may be used for preparing a **biplot** (ter Braak 1985, 1987c); a joint plot displaying two kinds of information. In two dimensions, the species scores define an arrowhead (vector) pointing in the direction of strongest increase in abundance of this species, while the sample score is a point indicating the position of the sample along the axis. As seen from Tab. 13, the scalings of the species and sample plot axes are not strictly comparable. However, a biplot may be obtained by multiplying all species scores by a constant that enables the joint plotting of all scores. The species vectors can be used to read the fitted species abundances (a proportionality factor depending on the scaling may have to be taken into consideration). In species-centered PCA, this is simply done by finding the orthogonal projection of a point representing a sample plot on the species vector. Thus, a species is generally more abundant than the mean of its abundance in sites lying on the same side of the origin as the direction of the species vector.

PCA axes can be scaled in several ways. The most commonly applied scaling is the Euclidean Distance biplot scaling (ter Braak 1983, 1987c): the species scores are standardized to unit sum of squares;

$$a_i' = a_i/(\mathrm{SUM}_{i=1,\dots,m}\ a_i^2),$$

and the sample scores are standardized so that their sum of squares equal the eigenvalue (see Step 5 in Tab. 11). Then the sample scores are the weighted sum of the species scores. This scaling gives the best preservation of the Euclidean distances of the original species-dimensional space in the ordination space. If the species and sample scores a_{ki} and x_{kj} relative to axis k are rescaled according to the equations

$$a_{ki}' = a_{ki} * \varepsilon_k^{0.5}$$

Tab. 12. *Sphagnum* species of sample plots in Transect 1; virgin bog vegetation at Rønnåsmyra, Grue, Hedmark. For each species and sample plot, frequency in subplots is shown on a 0-16 scale. DIST - distance to the water table.

Plot No. DIST	1 4	2 3	3 3	4 4	5 5	6 8	7 11	8 30	9 34	10 41	11 35
Sphagnum balticum	16	16	16	16	16	16	14	4	.	.	.
Sphagnum cuspidatum	16	16	15	16	11	8	.	.	.	.	.
Sphagnum fuscum	.	.	.	.	.	.	11	16	16	16	16
Sphagnum majus	16	16	16	16	14	7	.	.	.	.	.
Sphagnum magellanicum	.	.	.	.	.	16	16	.	.	.	.
Sphagnum rubellum	2	10	.	.	8	14	12	16	16	12	7
Sphagnum tenellum	16	16	16	16	16	16	8	.	.	.	

Tab. 13. Calculations involved in extracting the first axis of species-centered PCA by the iterative algorithm of Tab. 11. The data-set used is the abundances of the seven *Sphagnum* species occurring in the 11 sample plots of Transect 1 at Rønnåsmyra, Grue, SE Norway (cf. Tab. 1). Species names are abbreviated by the first 2 or three letters of the specific epithet.

Iteration cycle	Step	Parameter	Sample plot											Species							Value
			1	2	3	4	5	6	7	8	9	10	11	ba	cu	fu	mag	maj	ru	te	
1	1.1	x_j	4	3	3	4	5	8	11	30	34	41	35								
	1.2	y_i												10.36	7.45	6.73	2.91	7.73	8.73	9.45	
	1.3	$x_{.}$																			16.18
		$x_{j,\,new}$	-0.252	-0.272	-0.272	-0.252	-0.231	-0.169	-0.107	0.286	0.368	0.513	0.389								
	2	a_i												-23.5	-20.4	23.8	-4.4	-21.2	10.2	-24.0	
	3	x_j	-856	-774	-856	-876	-650	-450	318	1001	1095	1053	992								
	5	s																			51.45
		$x_{j,\,new}$	-0.305	-0.276	-0.305	-0.313	-0.232	-0.160	0.113	0.357	0.391	0.376	0.354								
2	2	a_i												-22.5	-22.7	24.8	-0.8	-23.6	12.5	-24.6	
	3	x_j	-925	-825	-927	-950	-689	-394	417	1049	1138	1089	1014								
	5	s																			54.30
		$x_{j,\,new}$	-0.314	-0.280	-0.315	-0.322	-0.234	-0.133	0.142	0.356	0.386	0.369	0.344								
3	2	a_i												-22.2	-23.0	24.7	0.2	-23.9	12.9	-24.4	
	3	x_j	-933	-830	-936	-959	-693	-377	436	1050	1139	1087	1010								
	5	s																			54.45
		$x_{j,\,new}$	-0.315	-0.280	-0.316	-0.323	-0.234	-0.127	0.147	0.354	0.384	0.367	0.341								
4	2	a_i												-22.0	-23.0	24.6	0.3	-23.9	13.0	-24.3	
	3	x_j	-932	-828	-934	-958	-691	-373	438	1048	1136	1084	1006								
	5	s																			54.32
		$x_{j,\,new}$	-0.316	-0.281	-0.317	-0.325	-0.234	-0.126	0.149	0.355	0.385	0.367	0.341								

and

$$x_{kj}' = x_{kj}/\varepsilon_k^{0.5},$$

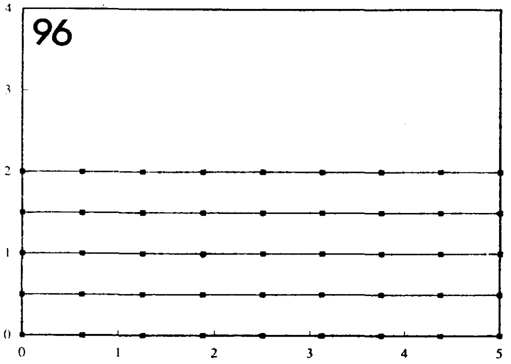
where ε_k is the eigenvalue of axis k, we obtain a covariance biplot (ter Braak 1983, 1987b). In this plot, the angle between species vectors approximates the pair-wise correlation between species; positively correlated species are represented by arrows pointing in the same direction.

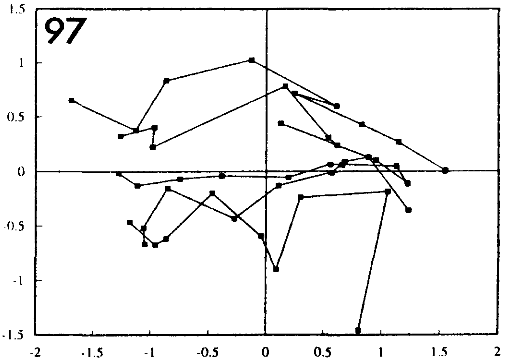
Performance with simulated and real data

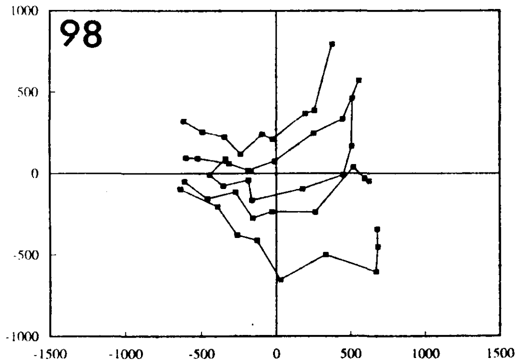
Simulated data. Figs 90-91 show the performance of species-centered and standardized PCA (PCA-CS) with the 6 x 1.5 S.D. coenoplane. The longest gradient was well recovered along the first ordination axis (Tab. 14), but the second axis did not reflect any of the underlying gradients (Fig. 90). Actually, position along the second axis was merely a quadratic function of position along the first axis. The true second gradient was moderately well recovered along the third axis (Fig. 91, Tab. 14). With the 5 x 2 S.D. coenoplane, the target

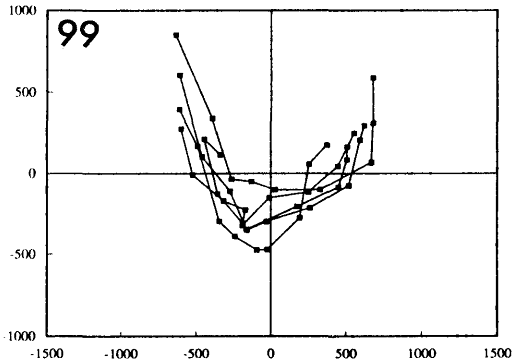
Tab. 14. Evaluation of ordination methods by use of the three simulated data-sets (see Tab. 10 for properties and parameter settings). Product-moment correlation coefficients between sample plot scores and target configuration, gradient 1 (TCG 1) and 2 (TCG 2) are given for each ordination axis. Recovery of target configuration indicated by boldface types. LNMDS variants: -BS - with percentage dissimilarity (the Bray-Curtis measure), species standardized by division with species maxima; -B - as above, without standardization; -QS - with the quantitative symmetric (Kulczynski) measure, standardized by division with species maxima. PCA variants: - CS - species-centered and standardized by division with species maxima; C - species-centered; NC - non-centered. CA and DCA with non-linear rescaling of axes and the option for downweigting of rare species invoked; DCA with detrending by segments.

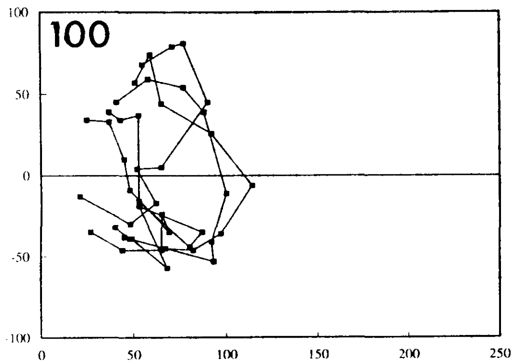
Data-set (S.D.)	Ordination (ranked performance)	Ordination axis 1		Ordination axis 2		Ordination axis 3		Ordination axis 4	
		TCG 1	TCG 2	TCG 1	TCG 2	TCG 1	TCG 2	TCG 1	TCG 2
6 x 1.5	DCA	**.991**	.014	.113	**.900**	.012	.088	.148	.060
	LNMDS-BS	**.986**	.021	.037	**.887**				
	LNMDS-KS	**.983**	.023	.037	**.871**				
	LNMDS-B	**.983**	.029	.029	**.768**				
	CA	**.984**	.011	.027	.097	.018	**.921**	.134	.077
	PCA-CS	**.978**	.018	.049	.140	.024	**.776**	.021	.231
5 x 2	LNMDS-BS	**.983**	.080	.010	**.931**				
	LNMDS-KS	**.980**	.061	.010	**.924**				
	DCA	**.978**	.153	.182	**.899**	.036	.017	.046	.144
	CA	**.981**	.107	.189	**.852**	.103	.160	.021	.311
	LNMDS-B	**.961**	.084	.107	**.831**				
	PCA-CS	**.954**	.188	.180	**.826**	.080	.354	.038	.207
	PCA-NC	.004	.280	**.849**	.305	.282	.303	.218	**.675**
2.4 x 2	LNMDS-BS	.094	**.980**	**.970**	.108				
	LNMDS-KS	.121	**.977**	**.966**	.134				
	LNMDS-B	.013	**.973**	**.968**	.027				
	PCA-CS	**.949**	.110	.159	**.939**	.183	.119	.060	.148
	DCA	**.900**	.334	.330	**.916**	.053	.057	.112	.069
	CA	**.885**	.352	.334	**.916**	.061	.054	.153	.102
	PCA-C	.431	**.809**	**.819**	.450	.045	.031	.215	.104

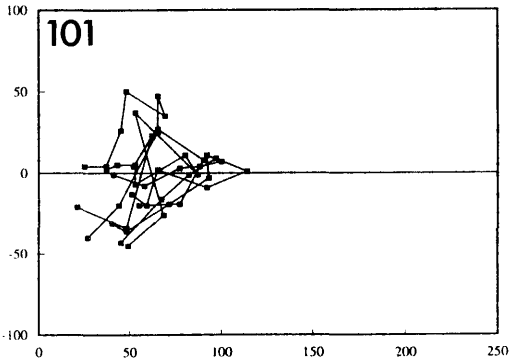










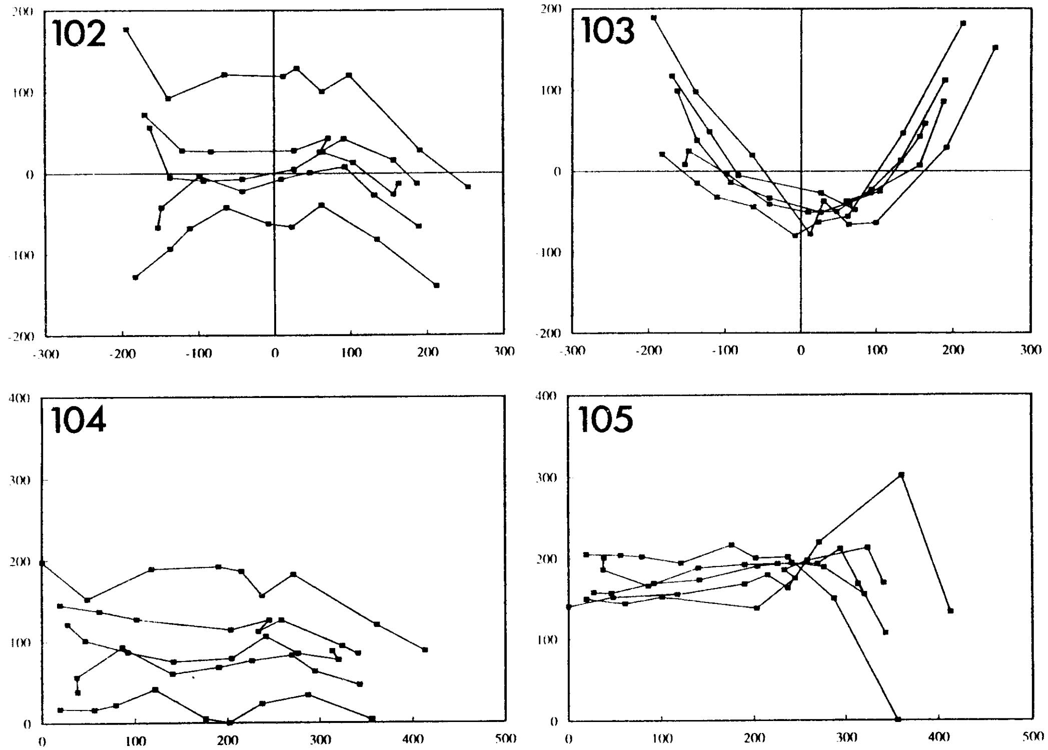


configuration was recovered as a slightly arched structure (Fig. 98). The third ordination axis was interpretable as a function of position along the first axis (Fig. 99), just as axis two of the 6 x 1.5 S.D. coenoplane. With the 2.4 x 2 S.D. coenoplane (Fig. 108), the target configuration was well recovered on the first two PCA axes.

Non-centered PCA (PCA-NC) and species-centered PCA without standardization (PCA-C) performed more poorly than PCA-CS; cf. Figs 98-101 and Tab. 14.

For the coenoclines with one long and one short gradient, PCA invariably showed the poorest performance among the compared ordination techniques. With two short coenoclines, PCA-CS performed better than DCA and CA, but poorer than all variants of MDS.

Real data. The ordination of the 50 sample plots from virgin bog vegetation at Rønnåsmyra by PCA-CS reminded of the diagrams with the 6 x 1.5 and 5 x 2 S.D. coenoplanes. Variation according to depth to the water table was reasonably well recovered along axis 1 (Fig. 111), while axis 2 was a strongly arched



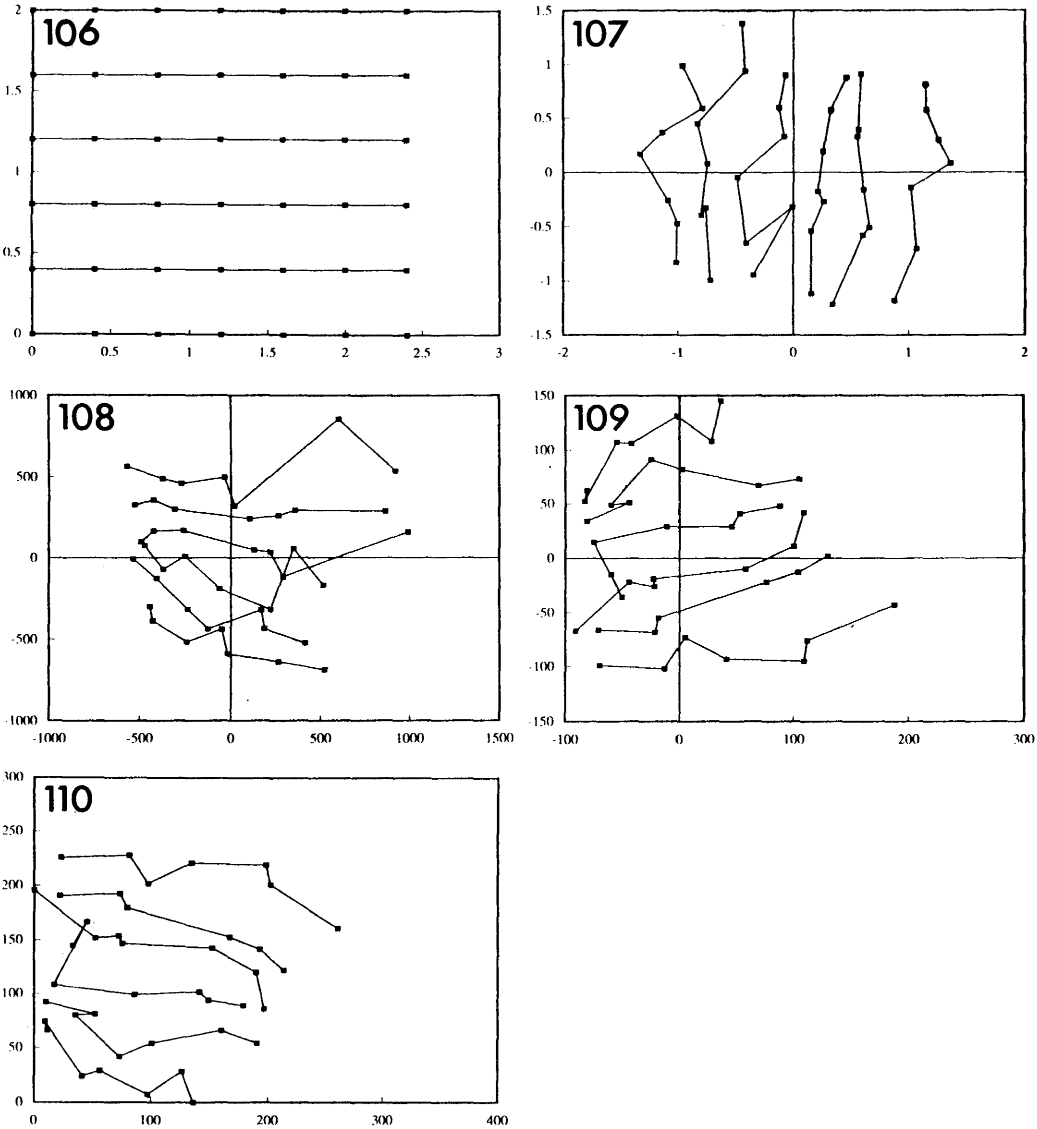
Figs 96-105. Ordination of the 5 x 2 S.D. simulated coenoplane. Fig. 96. Target configuration, gradients 1 and 2. Fig. 97. LNMDS-BS, axes 1 and 2. Fig. 98. PCA-CS, axes 1 and 2. Fig. 99. PCA-CS, axes 1 and 3. Fig. 100. PCA-NC, axes 1 and 2. Fig. 101. PCA-NC, axes 1 and 3. Fig. 102. CA, axes 1 and 2. Fig. 103. CA, axes 1 and 3. Fig. 104. DCA. axes 1 and 2. Fig. 105. DCA, axes 1 and 3. Scaling of axes in Fig. 96 in S.D. units, in Figs 104-105 in S.D. units *100, otherwise scaling arbitrary.

function of axis 1. Axis 3 separated the five sample plots most close to the dry (hummock) end of axis 1.

Summary. The results of PCA with simulated and real data sets illustrate the problems of PCA when applied to vegetation data-sets. Already in the first application of PCA to vegetation data, Goodall (1954) observed that the relationship between the underlying gradient and the ordination axes was non-linear. This phenomenon, that the underlying gradient appears in the ordination diagram as a curved structure, in extreme cases with the ends of the underlying gradient inflexed and thereby approaching each other, has been termed the **horseshoe effect**. It has been noticed several times (e.g., Swan 1970, Austin & Noy-Meir 1971, Jeglum et al. 1971, Austin 1976b, Gauch et al. 1977), and is present in ordination diagrams based on field data sets presented by Jensén (1978) and van der Maarel (1979), among many others. A clear horseshoe effect is evident in Figs 90 and 111.

Theoretical considerations and assessment

The poor performance of PCA with simulated data sets including a long major gradient, and with the Figs



106-110. Ordination of the 2.4 x 2 S.D. simulated coenoplane. Fig. 106. Target configuration, gradients 1 and 2. Fig. 107. LNMDS-BS, axes 1 and 2. Fig. 108. PCA-CS, axes 1 and 2. Fig. 109. CA, axes 1 and 2. Fig. 110. DCA, axes 1 and 2. Scaling of axes in Fig. 106 in S.D. units, of Fig. 110 in S.D. units *100, otherwise scaling arbitrary.

Rønnåsmyra data-set, is due to the non-linear response of species to ecological gradients (Beals 1973, Gauch et al. 1977, Gauch 1982a). PCA is based on the statistical model that species abundances has a linear relationship to the underlying gradients. With long gradients in the material, this assumption is certainly not true, probably not for any species! Thus the regression step, fitting straight lines to the species abundances, will predict species-axis relationships that poorly fits the observed abundances (cf. Fig. 81, pp. 117-119). The sample scores fitted by calibration become unreliable as well, and the ordination gives a poor representation of the underlying gradient structure.

Viewed geometrically, PCA attempts at extracting the ordination axes giving the best possible recovery of the original Euclidean distances between sample plots (in the species-dimensional space). However, Euclidean distance is a poor measure of ecological distance (cf. p. 109, R. Økland 1986a, Faith et al. 1987). It can be seen from Figs 77-78 that Euclidean distance will proportionally overestimate ecological distances between sample plots closely spaced along the gradient, while the distance between sample plots far apart will be strongly underestimated. The effect of this is clear from Fig. 90: we see that adjacent sample plots along the major gradient are separated proportionally more strongly than sample plots further apart, just as the Euclidean distance indicates. A horse-shoe is the inevitable result of the non-linearity of Euclidean distance as a function of gradient separation.

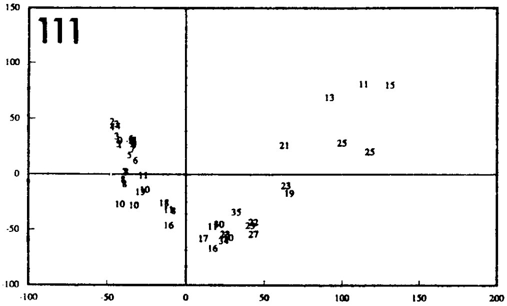
The same lines of reasoning can also explain the relatively better performance of PCA with short gradients. In this case a larger part of the species will show monotonous response to the underlying gradients (cf. pp. 117-119), and the fit of the data to a linear model will be increasingly better as the length of the longest gradient decreases. When the longest gradient is below 2 S.D. units, most species will show monotonous response functions, and their abundances can mostly be accurately predicted by linear regression. Then sample plot scores are confidently estimated by linear calibration. This ß diversity level also corresponds to the most linear part of the curve for euclidean distance as function of gradient separation (Figs 77-78).

The performance of PCA variants can also be understood by theoretical reasoning. By non-centering, the point of reference (the origo in the ordination) is the sample plot with abundance 0 for all species. The species vectors will point in the directions of maximum abundance of the species, assuming linear relationships to the underlying gradient. This model is clearly inadequate for ecological situations, and the ordinations mostly show more distinct horseshoe effects than do the centered variants (cf. Figs 100-101). This variant is therefore not recommended for gradient identification (for an opposite view, see Ezcurra 1987). The weight given to each species in the PCA ordination is proportional to the variance of the abundance of this species (ter Braak 1987c). In species-centered PCA the species with the strongest variation in species abundance will be the most heavily weighted; this will mostly be the most frequent ones (unless they show high abundance in all or almost all sample plots). Minor species will influence the ordination less strongly. With standardization by division with standard deviation, all species are given the same weight. There is then a danger that rare species occurring in deviant sample plots will influence the ordination strongly. In the case of the 2.4 x 2 S.D. simulated coenoplane (a coenoplane near-optimal for the PCA model), PCS-CS performed far better than PCA-C. In ordinations of real data sets with short gradients, Oksanen (1983) observed that PCA-C results were strongly dominated by few, dominant species, giving relatively poor performance (relative to CA and DCA). Minchin (1987a) performed extensive tests of PCA variants on simulated data, clearly showing that PCA-CS was preferential for gradient identification. This supports the indication here that PCA-CS should be preferred when PCA is, for some reason, applied to vegetation data. Ter Braak (1987c) recommends the species-centered version.

The usefulness of PCA to vegetation data is limited; Tab. 14 clearly shows that there are always ordination methods with considerably better gradient recovery. Thus the use of PCA for vegetational ordination should be terminated. However, PCA is still frequently used for this purpose (cf. Kent & Ballard 1988) despite the clear indications from comparative studies that the method is burdened with fundamental shortcomings. It has been argued that the curvilinear distortion in PCA does not invalidate its use, as the possibility that artifacts may occur can be taken into consideration when diagrams are interpreted (e.g., Feoli & Feoli Chiapella 1980). Minchin (1987a) gives examples of diagrams in which the separation of ecologically based structure and mathematical artifacts are virtually inseparable, and concludes his judgment of PCA as follows: "There is little justification for the continued application of linear ordination methods to community data *for the purpose of indirect gradient analysis*". To this conclusion I fully subscribe.

If, however, we want to study the interrelationships between measured environmental variables and their grouping into complex-gradients, PCA may be an effective tool. If all variables show reasonably well fit (eventually after transformation) to a normal or uniform frequency distribution (cf. Figs 71-72, cf. p. 00), the linear model is suitable. In order to make the environmental variables comparable and with equal weight, they must be centered and divided with their standard deviation.

The ordination scores of environmental variables are interpreted as vectors showing the direction of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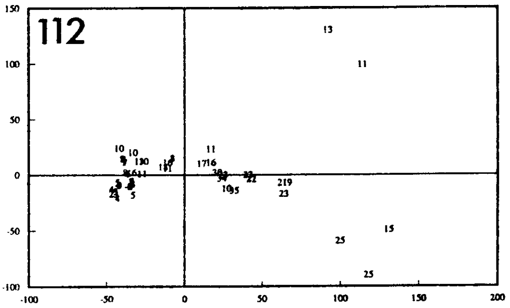
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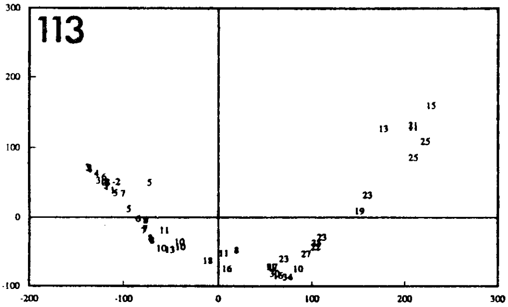
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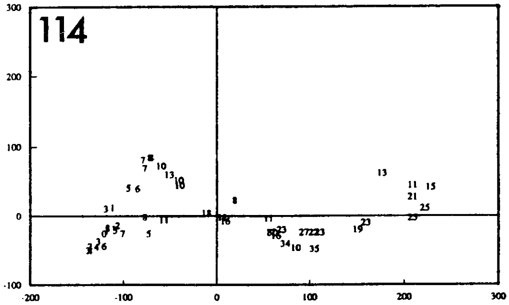
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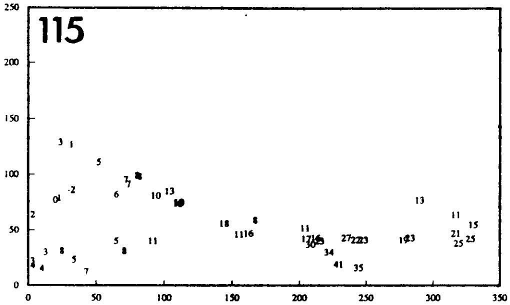
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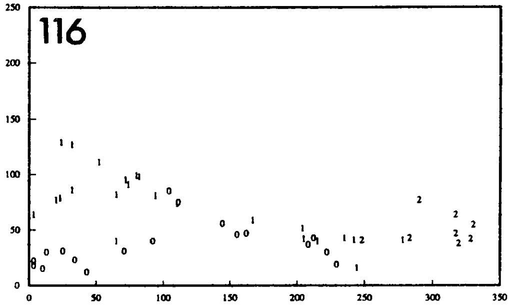
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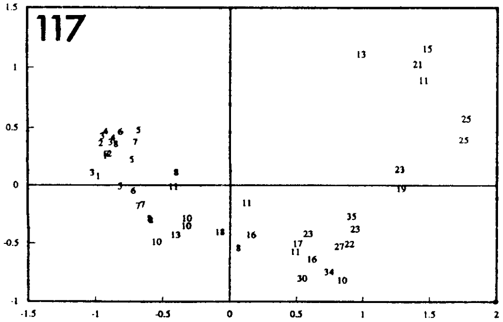
117
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-1
-1.5
-1
-0.5
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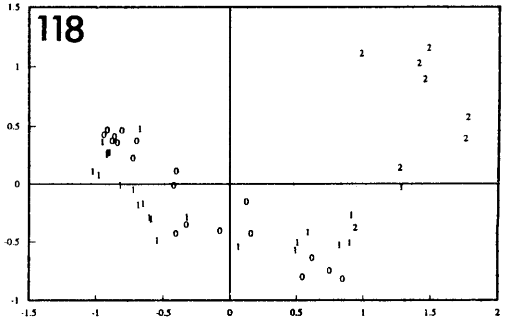
1
1.5
2


118
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2

their strongest change. The length of the vectors indicate the rate of change along each vector. Thus the relatively longer the vector, the higher is the correlation between the variable and the biplot axes. The projection of a vector on an axis indicates the correlation between the variable and the axis. Vectors pointing in the same direction tend to indicate highly correlated variables, making up complex-gradients. It should be noticed that the direction of a vector is reversed by change of the sign of the variable. Thus vectors pointing in opposite directions tend to be strongly negatively correlated, and are to be considered as making up one complex-gradient.

Applications

Jensén (1978) shows PCA diagrams of South Swedish lake vegetation, with clear horseshoe distortions. R. Økland (1989b) used PCA for analysis of transformed and standardized environmental variables in order to identify complex-gradients at N Kisselbergmosen. A similar approach to complex-gradients in *Vaccinium myrtillus*-dominated spruce forest in Rausjømarka was made by T. Økland (1989).

Principal co-ordinate ordination (PCO)

The poor performance of PCA on vegetation data, partly attributable to the inadequacy of the distance measure, led to the development of a more general ordination technique. This technique, termed principal co-ordinate ordination or PCO, is a metric scaling technique in which Euclidean distance can be replaced by any dissimilarity measure. PCO is described by Gower (1966, 1967), also see Pielou (1977), Orlóci (1978) and Williamson (1978). Computationally, the latent variables (axes) are found by performing eigenanalysis on a secondary matrix of sample plot dissimilarities (or species dissimilarities). The technique is thus not dual. Furthermore, it cannot be formulated as a simple iteration process of regressions and calibrations as in the case with PCA.

Although PCO with the best among the floristic dissimilarity measures (e.g., percentage dissimilarity, cf. p. 109) has been shown to give results little better than PCA when applied to the same data (e.g., Clymo 1980, Minchin 1987a), the results produced by the two methods do not differ strongly. Compared to CA, DCA and MDS, PCO with percentage dissimilarity almost invariably shows less successful gradient recovery (Brown et al. 1984, Kenkel & Orlóci 1986, Minchin 1987a).

The reason for the failure of PCO to amend the faults of PCA is the lack of linearity between any of the floristic dissimilarity measures and ecological distance (cf. p. 110), inevitably leading to the horseshoe effect (or similar curvilinear distortions) for all metric scaling techniques. PCO will therefore not be considered in further detail.

R. Økland & Bendiksen (1985) applied PCO in an analysis of the forest-alpine transition in Grunningsdalen. Many of their ordination diagrams show curvilinear distortions.

Gaussian ordination (GO)

From 1970 there was a growing awareness that PCA was not well suited for use with vegetation ecological data-sets. Methods based on more realistic statistical models were needed. The Gaussian model (Gauch & Whittaker 1972a) appeared attractive as an alternative underlying statistical model for ordination. An ordination method based on this model, **Gaussian ordination** (GO), was proposed by Gauch et al. (1974), and has been

Figs 111-118. Ordination of 50 sample plots from virgin bog vegetation at Rønnåsmyra, Grue, Hedmark, SE Norway (all except sample plot No. 17 in Tab. 1). Fig. 111. PCA-CS, axes 1 and 2. Fig. 112. PCA-CS, axes 1 and 3. Fig. 113. CA, axes 1 and 2. Fig. 114. CA, axes 1 and 3. Figs 115-116. DCA, axes 1 and 2. Figs 117-118. LNMDS-BS, axes 1 and 2. Numbers plotted on sample plot positions are depth to the water table (Figs 111-115 and 117) or peat-producing ability, subjectively judged (0 - strongly peat-producing, 2 - slightly peat-producing, 1 - intermediate, cf. p. 16; Figs 116 and 118). Scaling of axes in Figs 115-116 in S.D. units *100, otherwise arbitrary.

discussed in several later papers (see ter Braak & Prentice 1988 for review and references).

Gaussian ordination can be formulated as an iteration process; Gaussian curves are fitted to the species abundances and sample scores are later on estimated by Gaussian calibration. The process is computationally complicated, and most available programs for Gaussian ordination just find the first axis of the ordination. Minchin (1987a) shows that GO give good results with relatively long simulated coenoclines with low levels of quantitative noise, but performs poorly with higher noise levels and/or other combinations of underlying gradients in the data-set. When GO performs the best, several other techniques (DCA, MDS) perform equally well. Minchin (1987a) reviews GO and other "curve-fitting" approaches to ordination, and demonstrates their sensitivity to noise and deviating response curves. It seems that GO and other curve-fitting methods (e.g. the techniques of Goodall & Johnson 1982 and Fewster & Orlóci 1983) represent a dead end in ordination methodology, and they will not be considered further.

Correspondence analysis (CA)

The correspondence analysis (CA) concept, first developed by Hirschfeld (1935) and Fisher (1940), was used in some ecological studies around 1970, but became generally known to ecologists by the works of Hill (1973, 1974). CA and derived techniques have dominated quantitative vegetation ecology during the last half of the 1970s and the 1980s. The properties of this group of methods therefore merit detailed consideration.

CA is used under a variety of names, the most frequently used are "correspondence analysis" (Hill 1974, ter Braak 1987c, 1987d, ter Braak & Prentice 1988) and "reciprocal averaging" (cf. Hill 1973, Gauch et al. 1977, Gauch 1982a).

The method: model and iteration algorithm

Statistically, CA is a metric scaling method fitting the species abundance data to latent variables (the hypothetical, underlying variables) by choosing the sample scores that optimize the dispersion of species scores (ter Braak 1987c, ter Braak & Prentice 1988). This is done by an iterative process including cycles of weighted averages regressions and calibrations. The species scores are estimates for species optima. CA is a method optimizing the dispersion of species optima, estimated by weighted averages. Thus CA assumes a **unimodal model**. Sample scores are found from the species scores (optima) by weighted averages calibration.

CA is a metric scaling method, and can be formulated as a principal coordinate ordination using the Chi-square distance measure (equation 36, p. 110), see Chardy et al. (1976) and Minchin (1987a).

The iteration algorithm for CA is described in Tab. 15, and an example using the data for seven *Sphagnum* species in the 11 sample plots of Transect 1 at Rønnåsmyra (cf. Tab. 12) is given in Tab. 16. The iteration starts with giving the sample plots arbitrary scores $\{x_j\}$, not all identical. For convenience, the values for depth to the water table were used for this purpose, but the process always converges to a unique solution (ter Braak 1987c). These trial sample scores are used to estimate species optima, $\{u_i\}$, by weighted averages regression (step 2, equation 71). In the example of Tab. 16, these species scores are the u_i values in the second line. New sample scores are estimated by weighted averages calibration (step 3, equation 72), given as x_j values in line 3 in Tab. 16. We see that the range of the sample scores has been reduced from 38 (maximum - minimum depth to the water table, cf. Tab. 16, line 1) to 26.5 (Tab. 16: line 3) during one iteration cycle. This is typical of the CA iteration process; the range of the sample scores becomes smaller every turn of the iteration cycle. A technical standardization step (step 5) is added to the algorithm to counteract the reduction of the range of scores. In this step, the site scores are standardized to mean 0 and variance 1. In the example, the new sample scores (after standardization) are given in line 8. We can see that the process eventually converge; from

Tab. 15. Iterative algorithm for CA by the power method (cf. ter Braak 1987c, ter Braak & Prentice 1988).

Step 1. Choose arbitrary initial sample scores $\{x_i\}$, not all equal.

Step 2. Calculate new species scores $\{u_i\}$ by weighted averaging of the sample scores;

$$u_i = (\mathrm{SUM}_{j=1,\dots,n}\ y_{ij}x_j)/(\mathrm{SUM}_{j=1,\dots,n}\ y_{ij}) \qquad (71)$$

Step 3. Calculate new sample scores $\{x_j\}$ by weighted averaging of species scores;

$$x_i = (\mathrm{SUM}_{i=1,\dots,m}\ y_{ij}u_i)/(\mathrm{SUM}_{i=1,\dots,m}\ u_i) \qquad (72)$$

Step 4. The orthogonalization step; to be used for calculation of axes 2, 3 etc. By calculation of axis 1, go to step 5.

Step 4.1. Denote sample scores relative to previous axis $\{f_j\}$, sample scores relative to this axis $\{x_j\}$.

Step 4.2. Calculate

$$v = (\mathrm{SUM}_{j=1,\dots,n}\ y_{.j}x_jf_j)/y_{..}$$

where

$$y_{.j} = \mathrm{SUM}_{i=1,\dots,m}\ yij$$

and

$$y_{..} = \mathrm{SUM}_{j=1,\dots,n}\ (\mathrm{SUM}_{i=1,\dots,m}\ y_{ij})$$

Step 4.3. Calculate

$$x_{j,\ new} = x_{j,\ old} - v*f_j$$

Step 4.4. Repeat 4.1-4.3 for all previous axes.

Step 5. The standardization procedure.

Step 5.1. Calculate the centroid c of the sample scores $\{x_j\}$,

$$c = (\mathrm{SUM}_{j=1,\dots,n}\ y_{.j}x_j)/y_{..}$$

Step 5.2. Calculate the dispersion s^2 of the sample scores

$$s^2 = \mathrm{SUM}_{\ j=1,\dots,n}\ y_{.j}(x_j - c)^2/y_{..}$$

Step 5.3. Calculate

$$x_{j,\ new} = (x_{j,\ old} - c)/s$$

Step 6. Stop on convergence, that is when the new sample scores are sufficiently similar to the old ones, else go to step 2 and repeat the iteration.

Tab. 16. Calculations involved in extracting the first CA axis by the iterative algorithm of Tab. 14. The data-set used is the abundances of the seven *Sphagnum* species occurring in the 11 sample plots of Transect 1 at Rønnåsmyra, Grue, SE Norway (cf. Tab. 1). Species names are abbreviated by the first 2 or three letters of the specific epithet.

Iteration cycle	Step	Parameter	Sample plot											Species							Value
			1	2	3	4	5	6	7	8	9	10	11	ba	cu	fu	mag	maj	ru	te	
1	1	x_j	4	3	3	4	5	8	11	30	34	41	35								
	2	u_i												8.6	4.1	35.0	9.5	4.1	23.5	5.0	
	3	x_j	6.0	7.9	5.5	5.4	7.8	9.9	15.7	27.0	29.3	30.1	31.9								
	5.1	$y_{.j}$	66	74	63	64	65	77	60	36	32	28	22								
		$y_{..}$																			587
		c																			12.50
	5.2	s																			8.93
	5.3	x_j	-0.73	-0.52	-0.78	-0.80	-0.53	-0.29	0.36	1.62	1.88	1.97	2.17								
2	2	$y_{i.}$												114	82	74	32	85	96	104	
		u_i												-0.50	-0.64	1.60	0.03	-0.64	0.75	-0.59	
	3	x_j	-0.55	-0.41	-0.59	-0.59	-0.42	-0.22	0.23	0.99	1.18	1.24	1.37								
	5.1	c																			-0.07
	5.2	s																			0.660
	5.3	x_j	-0.73	-0.52	-0.79	-0.79	-0.54	-0.23	0.45	1.61	1.89	1.98	2.18								
3	2	u_i												-0.39	-0.67	1.55	0.11	-0.64	0.87	-0.52	
	3	x_j	-0.51	-0.36	-0.55	-0.56	-0.37	-0.14	0.30	1.03	1.21	1.26	1.36								
	5.1	c																			0
	5.2	s																			0.655
	5.3	x_j	-0.78	-0.55	-0.84	-0.84	-0.56	-0.21	0.46	1.57	1.85	1.92	2.08								
4	2	u_i												-0.42	-0.67	1.67	0.13	-0.68	0.84	-0.55	
	3	x_j	-0.54	-0.39	-0.58	-0.58	-0.39	-0.15	0.31	1.07	1.26	1.32	1.45								
	5.1	c																			0
	5.2	s																			0.688
	5.3	x_j	-0.78	-0.57	-0.84	-0.84	-0.57	-0.22	0.45	1.56	1.83	1.92	2.11								
5	2	u_i												-0.43	-0.68	1.67	0.12	-0.68	0.84	-0.55	
	3	x_j	-0.54	-0.39	-0.59	-0.59	-0.40	-0.16	0.30	1.07	1.26	1.31	1.44								
	5.1	c																			0
	5.2	s																			0.688
	5.3	x_j	-0.78	-0.57	-0.84	-0.84	-0.57	-0.22	0.45	1.56	1.83	1.92	2.11								
Scores after rescaling			-0.80	-0.57	-0.88	-0.88	-0.59	-0.24	0.45	1.59	1.87	1.95	2.14	-0.93	-1.47	3.60	0.36	-1.47	1.81	-1.18	

the fourth to the fifth iteration cycle there is almost no change in the species or sample scores. At convergence, the species scores relative to this first CA axis are calculated by step 2, and the sample scores are calculated as the weighted averages of the species scores.

The dispersion of the sample scores along the axis, weighted by total abundance in the samples, s in Tab. 15, is the eigenvalue of the axis. The eigenvalue measures the relative importance of the axis. Eigenvalues in CA always lie between 0 and 1. The contraction of the sample scale in one iteration cycle at convergence equals the eigenvalue.

Further axes may be extracted by introducing an orthogonalization step (step 4 in Tab. 15), ensuring that all axes are made uncorrelated to axes of lower rank.

If the sample plots and species are both reordered in the data matrix according to increasing score along the first CA axis, high abundance values will be concentrated along the diagonal of the matrix (for instance, try to rearrange the samples and species in the example!). Maximizing the correlation between species and site scores is a typical feature of CA.

Interpretation of plots and scaling of axes

After convergence, species scores may be calculated by weighted averaging of sample scores, or sample scores may be calculated as weighted averages of species scores. Intuitively, the latter appears the more sound. This way the range of the sample scores becomes fully contained within the range of the species scores, thus allowing for species optima outside the sampled portion of the gradient.

The standardization of sample scores to mean 0 and variance 1 disregards the important fact that the ordination axes differ in importance. Rather than scaling all sample axes as if they were equally important, several other ways of scaling CA biplots have been proposed (cf. Hill 1979a, ter Braak 1987c, 1987d, Oksanen 1987).

One possibility is to perform a **linear rescaling** of the axes (Hill 1979a, ter Braak 1987c, 1987d): For each species the variance of the scores of the samples containing the species (weighted by species abundance in the sample plot) is calculated. These variances, weighted by species totals, are then averaged over all species. The weighted average of the variance of the species along the axis is given by

$$s^2 = \mathrm{SUM}_{i=1,\dots,m}\ y_{i.}\ [\mathrm{SUM}_{j=1,\dots,n}\ y_{ij}(x_j - u_i)^2]/y_{..} \qquad (73)$$

where y_{ij} is the abundance of species i in sample plot j, x_j is the score of sample j, u_i is the score of species i, $y_{i.}$ the sum of abundances of species i over all sample plots, and $y_{..}$ the total abundance over all species and all sample plots. If all scores along an axis were divided with s, the lengths of the axes obtained reflected the amont of compositional turnover along the axis. One s unit corresponds to the standard deviation of species response curve widths, estimated by equation (73). This is one way of estimating ß diversity in S.D. units (cf. p. 35). However, the estimates obtained this way are not robust and an alternative **non-linear rescaling** approach (Hill 1979, Hill & Gauch 1980) performs considerably better in this respect (R. Økland, unpubl., also see Knox 1989). The above linear rescaling, often referred to as Hill's scaling (ter Braak 1987c), can be obtained from the scores at convergence by the following equations:

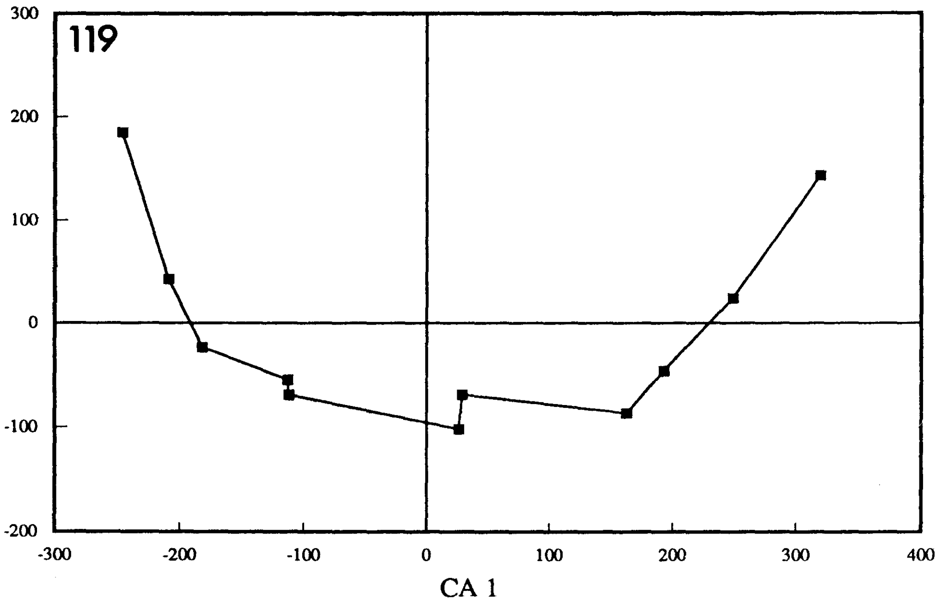
$$x_j' = (1 - \varepsilon)^{0.5}/\varepsilon^{0.5} \qquad (74)$$

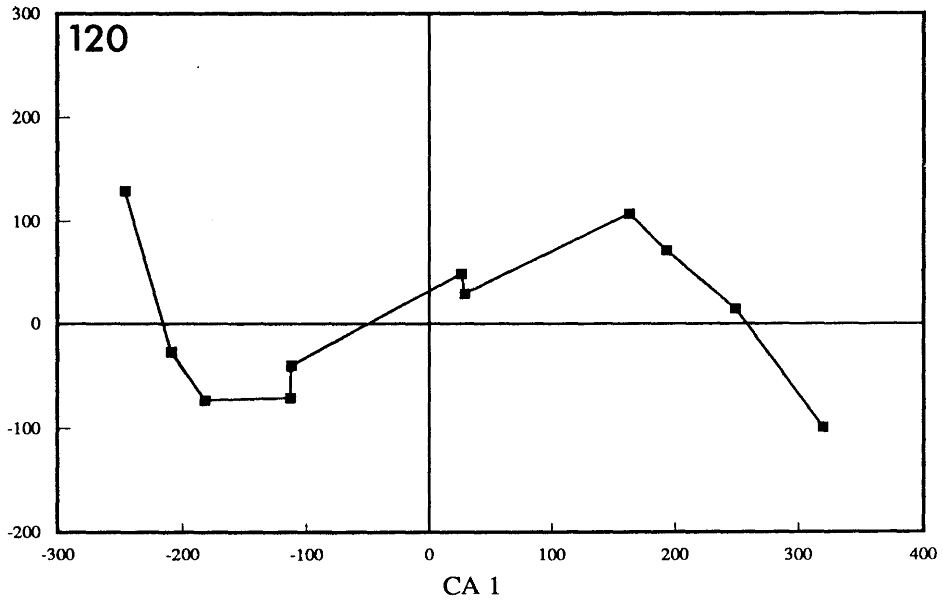
$$u_i' = \varepsilon^{0.5}(1 - \varepsilon)^{0.5} \qquad (75)$$

where ε is the eigenvalue of the axis. The standardization of equation (74) is applied to the sample scores at step 3 in the iteration process. The interpretation of S.D. units in terms of species response curve parameters is explained on pp. 149-150.

Performance with simulated and real data

Simulated data. Figs 92-93 show the performance of CA with the 6 x 1.5 S.D. coenoplane. The recovery of the major gradient along the first ordination axis was very good (Tab. 14). However, the second axis was merely a quadratic function of position along the first axis, and essentially uncorrelated with the underlying gradient structure (Fig. 92, Tab. 14). The true second gradient of the target configuration was well recovered along the third ordination axis (Fig. 93, Tab. 14). With the 5 x 2 S.D. coenoplane, the two first gradients of the target configuration were recovered along the first two ordination axes (Fig. 102, Tab. 14), but the recovery of the second gradient was not good. The samples aligned onto a slightly arched curve in Fig. 102, indicating that the second axis was also influenced by the first gradient. The third CA axis was a quadratic





Figs 119-120. CA ordination of a simulated 6 S.D. coenocline, showing the arch effect. Fig. 119. Axes 1 and 2; position along axis 2 is a quadratic function of position along axis 1. Fig. 120. Axes 1 and 3: positions along axis 3 is a cubic function of position along axis 1.

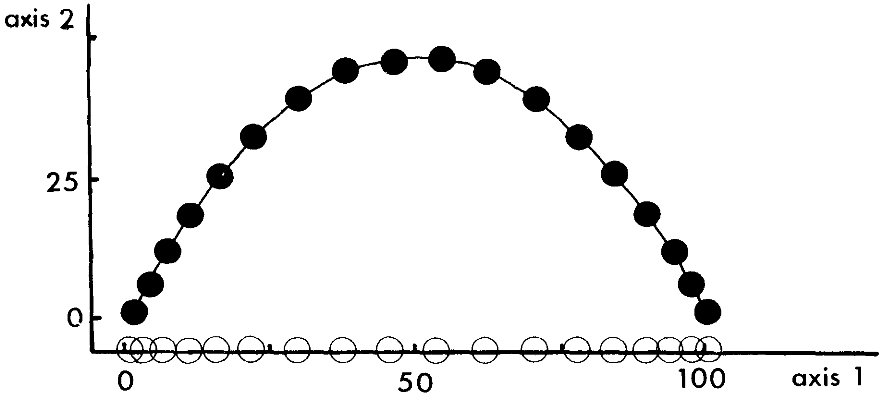


Fig. 121. Schematic diagram showing axes 1 and 2 of a hypothetical CA ordination of a simulated coenocline with symmetric and unimodal species response curves and regular spacing of sample plots. Sample positions are indicated by dots, aligning on a perfect arch. The sample scores with respect to CA axis 1 are indicated by circles on the first axis, clearly indicating the compression of sample scores near the axis ends (the edge effect). Redrawn from Hill and Gauch (1980).

function of the first axis (Fig. 103). With the 2.4 x 2 S.D. coenoplane, the two gradients of the target configuration were recovered on the first two ordination axes, but with only moderately good fits (Fig. 109, Tab. 14).

Further testing of CA was done on a data-set including 11 sample plots from the 6 x 1.5 S.D. data set, including only sample plots with similar position along the second underlying gradient. The CA ordination of this data-set is shown in Figs 119-120. The first axis recovered the gradient well; the second axis was a quadratic function of the first axis, and the third axis was a cubic function of the first axis.

Real data. The CA ordination of the 50 virgin bog sample plots from Rønnåsmyra is shown in Figs 113-114. The first axis reflected variation according to depth to the water table. The second axis was a quadratic function of position along the first axis, and the third axis was a cubic (third order) function of position along the same axis.

The performance of CA with the simulated and real data sets referred above clearly show that the method has two grave faults: (1) **The arch effect** (Hill 1973, Austin 1976b, Gauch et al. 1977, etc.); the appearance of ordination axes that are polynomial functions of one or more axes of lower rank. Most frequently, it is the first ordination axis that reappears as an arch or a more complex curvilinearly distorted structure. The term "arch effect" originally refers to the quadratic function most frequently appearing, but is inadequate for most other structures of this kind. A better, collective term for this type of distorted axes is **polynomial distortion axis** (Gauch et al. 1977). A simple visualization of the arch effect is given in Fig. 121. (2) **The edge effect** (Hill 1979a, Hill & Gauch 1980); the phenomenon that regular coenoclines with regular spacing of sample plots are distorted by CA so that scores of samples and species near the gradient end-points are strongly compressed (Figs 121-122). These faults have long been recognized and have been demonstrated in studies by Gauch et al. (1977), and Kenkel and Orlóci (1986), among others.

Theoretical considerations and assessment

The shortcomings of CA are due to inconsistencies between the method and the underlying model. These inconsistencies may be explained in at least two different ways; (1) by consideration of the statistical model;

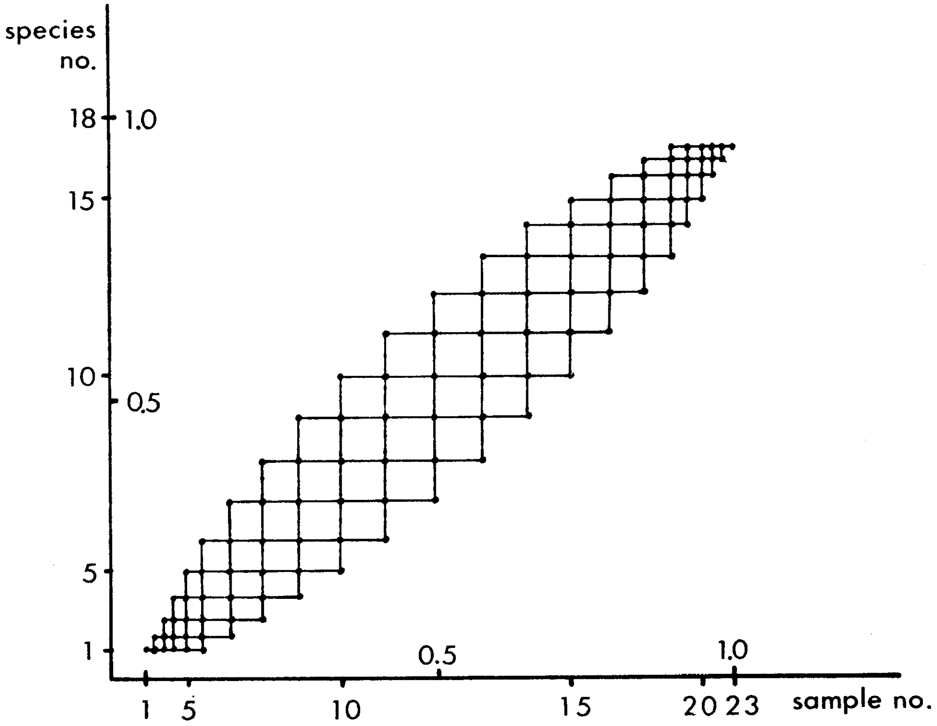


Fig. 122. Schematic diagram showing the compression of sample scores and species scores near the axis ends by CA ordination. The hypothetical coenocline contains 23 species (symmetric and unimodal species response curves) and 18 regularly spaced sample plots; the species modes extending outside the sampled portion of the gradient. The vertical bars indicate species scores along CA axis 1, the horizontal bars indicate sample scores along the same axis. Redrawn from Hill and Gauch (1980).

the efficiency of weighted averaging regression and calibration, and (2) by consideration of the geometrical aspects of the method; first of all the scaling metricity and the distance measure used. We will do both, starting with the statistical aspects. Finally, we will consider mathematical properties of the orthogonalization procedure in CA.

Statistical considerations. Ter Braak and Looman (1986) showed that estimates for species optima obtained by weighted averages regression approximate maximum likelihood estimates (statistically optimal estimates by Gaussian logit regression) provided that the following condition is satisfied (ter Braak & Prentice 1988):

(1) The sample scores $\{x_j\}$ are closely spaced over the whole range of the species along the gradient.

Ter Braak and Barendregt (1986) showed that the sample scores obtained by weighted averages calibration approximate maximum likelihood estimates provided

(2) The species' optima $\{u_i\}$ are closely spaced along the gradient over an interval extending for a sufficient distance in both directions from the true value of the site score.

(3) The species have equal tolerances.

(4) The species have equal maximum values.

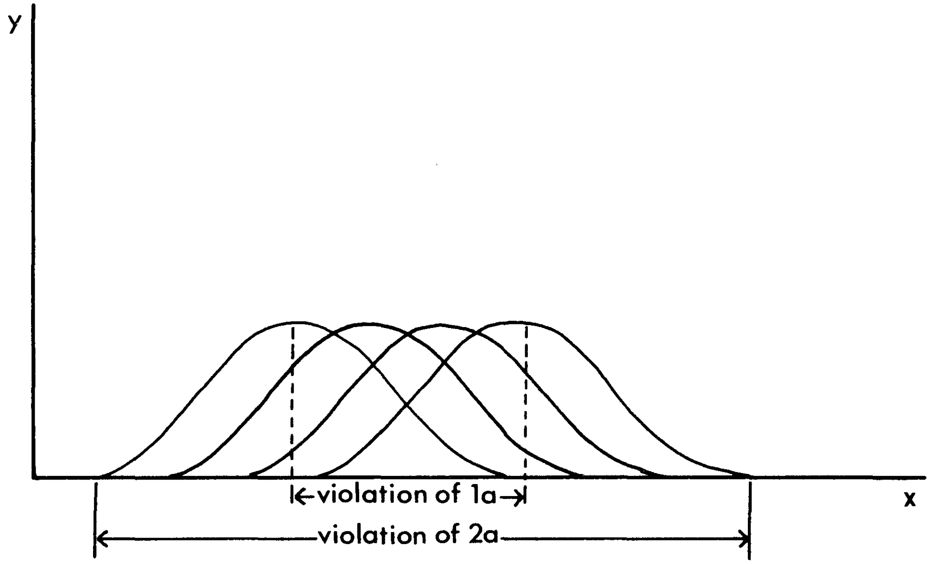


Fig. 123. The species packing model and the faults of CA. Two different ranges of sample positions relative to the gradient (x) are indicated; the wider violate condition 2a for weighted averages calibration, the narrower violate condition 1 for weighted averages regression (see text for further explanation). y - species abundance.

The model defined by these requirements has been called **the species packing model** (Whittaker et al. 1973, ter Braak & Prentice 1988); species have unimodal responses to the underlying gradient, with equal tolerances, equal spacing and equal modal abundances. Relaxation of some conditions do not necessarily affect the estimates strongly, cf. ter Braak & Prentice (1988).

It is obvious from Fig. 123 that conditions 1 and 2 cannot be satisfied simultaneously. This adversely affects the weighted averages estimates, bringing about a compression of sample and species scores in those regions of the sampled gradient where the conditions are violated. Obviously, good estimates for optima of species appearing near the gradient end-points would require sample plots placed outside the sampled end (condition 1). As this condition is violated, the estimated optima fall *within* the sampled gradient instead of without. The result is the edge effect, as shown in Fig. 122.

Geometrical considerations. As a metric scaling method, CA extracts ordination axes by optimizing the recovery of Chi-squared distances between sample plots. As other floristic dissimilarity measures, Chi-squared distance has a non-linear relationship to ecological distance (cf. p. 110), and like other metric scaling techniques CA is therefore bound to overestimate distances between closely spaced samples. This results in the now well-known arch effect. Ordinarily, the gradient end-points are not involuted in CA (unlike PCA, where involution of gradient end-points is common). However, it is possible to produce data-sets that will lead to involuted axes in CA (Austin 1976b, Wartenberg et al. 1987).

Chi-squared distance has several undesirable properties previously commented upon (p. 110, cf. Faith et al. 1987). Species are weighted inversely proportional to their total abundance, and sample plots are weighted inversely proportional to the sum of the abundances of species occurring in them. Furthermore, the measure is unbounded, thereby giving particularly poor estimates of ecological distance for sample plots with few species in common (Faith et al. 1987, Minchin 1987a). These properties of the distance measure may explain the sensitivity of the method to deviating species, deviating sample plots and, in particular, sample plots with few, deviating species (cf. Gauch 1982a, Oksanen 1983, ter Braak 1987c). This results in a strong tendency of the method to exaggerate the distinctiveness of species with low totals and sample plots with low totals and high importance of rare species (Gauch 1982a). CA axes tend to be strongly influenced by such species and samples. The method is therefore vulnerable to disjunctions (ter Braak 1987c).

Considerations of the orthogonality of axes. The occurrence of polynomial distortion axes in CA has challenged theoretically minded ecologists for many years (e.g., Gauch et al. 1977, Gauch 1982a, 1982b, ter Braak 1987c, ter Braak & Prentice 1988), but still the phenomenon is considered as "not well-understood" (ter Braak & Prentice 1988: 291). Although the arch effect is not easily understood from the statistical point of view, it is easy to understand why the polynomial distortion axes appear by consideration of the orthogonalization step in the CA algorithm (Tab. 15). The demand on the second (and further) axes that they are orthogonal to axes of lower rank, implies that they have to be ***uncorrelated*** to lower ranked axes. After extraction of the first axis, a candidate for the second axis is the first axis, folded in the middle. It can easily be seen that the second axis in Fig. 121 has no linear correlation with the first axis. If the eigenvalue of the first axis is ε, the eigenvalue of this folded axis is claimed to be approximately ε^2 (Peet et al. 1988). As the axes are extracted in order of decreasing eigenvalues, the arch is taken as the second ordination axis if there are no coenoclines in the data-set that leads to a higher dispersion of sample scores (and hence, to higher eigenvalues) than the arch (Gauch et al. 1977, Fasham 1977, Hill & Gauch 1980). In practical applications, a second axis shorter than half the length of the first (gradient length measured in ß diversity units) will normally be overruled by the arch. This is the situation with the 6 x 1.5 S.D. coenoplane, but with the 5 x 2 S.D. coenoplane (gradient lengths are modified by inclusion of noise, in this case estimated by non-linear rescaling to be 4.13 and 1.98 S.D., respectively) the second gradient of the target configuration is expressed on the second ordination axis. The eigenvalues of the second ($\varepsilon_2 = 0.2983$) and third ($\varepsilon_3 = 0.2804$) axes are closely similar in this case. This example indicates that there is no straightforward relationship between the eigenvalue of an axis and the eigenvalues of its potential polynomial distortions: the eigenvalue of the first axis is $\varepsilon_1 = 0.5752$, while $\varepsilon_1^2 = 0.3309$. The considerations above can therefore only serve as course indications of expected eigenvalues of polynomial distortion axes. One more candidate for an ordination axis, uncorrelated with the first axis and its arch, is the third order polynomial distortion of the first axis. This is expressed on the fourth axis of the CA ordination of the 5 x 2 S.D. coenoplane with eigenvalue $\varepsilon_4 = 0.2204$ ($\varepsilon_1^3 = 0.1903$). More candidates for ordination axes of higher order can be found as higher polynomial functions of the first axis and, eventually, of all subsequent structure axes as well as of combinations of structure axes. Gauch (1982b) claims that the axes reflecting true structure in the data-set and the polynomial distortion axes tend to keep separate, but the observation in Fig. 102 that the second axis is a slightly arched representation of the target gradient questions this claim. No apparent mathematical justification for a clear-cut separation of ecologically based structure axes and polynomial distortion axes have been made. As the eigenvalues gradually diminishes, a third type of ordination axes, **noise axes** (Gauch 1982b) also come into action. Ordination of random numbers also result in first axes with eigenvalues larger than expected if no relationships at all existed in the data matrices (Gauch 1982b). The problems addressed in this section makes interpretation of ordination axes of higher rank than three, or at most four, impossible.

Most comparative studies, including the observations referred to above, support the view that CA performs better than PCA (Austin 1976b, Gauch et al. 1977, Clymo 1980, Kenkel & Orlóci 1986). However, the performance of CA relative to other ordination techniques (DCA, MDS) is generally inferior (Tab. 14, also see Hill & Gauch 1980, Gauch et al. 1981, Kenkel & Orlóci 1986) and the continuated use of CA (as any other unmodified metric scaling technique) for ordination of vegetation data, is strongly dissuaded.

Applications

From 1975 onwards, CA has frequently been used for ordination of vegetation data, and the method is still popular (Kent & Ballard 1988). Examples of studies using CA for ordinating Fennoscandian vegetation are Pakarinen & Ruuhijärvi (1978) and Tyler (1979) with data from mire vegetation, and Bjørndalen (1981) on data from basiphilous pine forest vegetation.

Detrended correspondence analysis (DCA)

Soon after CA became available to the ecological community, its faults became apparent and the search for alternative techniques started. One path to improved ordinations could be by *a posteriori* corrections for the conspicuous faults of CA. This is what is done by detrended correspondence analysis (DCA; Hill 1979a, Hill & Gauch 1980). The method was implemented in the program DECORANA (Hill 1979a), which rapidly spread around the world. In very few years, the method became the state-of-the-art method for ordination, stated not to be far from the theoretical optimum for ordination methods (Gauch 1982a, 1982b). Its popularity has increased steadily during the 1980s (Kent & Ballard 1988). A closer look at DCA starts with a description of the adjustments made to alleviate the faults of CA.

The method: correction of the faults of CA

DCA is a modification of CA, a metric scaling method based on a unimodal statistical model for the relationship between species abundance and underlying gradients. The implied distance measure is Chi-squared distance. By the inclusion of *a posteriori* corrections, DCA becomes a heuristic method, with ill-defined statistical properties (Wartenberg et al. 1987). We now consider the amendments to CA, starting with the detrending procedure.

Detrending: removal of the arch effect. The arch effect occurs because the demand that axes of higher order are to be uncorrelated with axes of lower order is not sufficient to preclude the occurrence of polynomial distortion axes. Hill (1979a; Hill & Gauch 1980) therefore replaced the orthogonalization step of CA (Step 4 of Tab. 15) with a stronger criterion: that the axes shall have no systematic relationship to axes of lower order.

To achieve this, Hill (1979a) designed the **detrending-by-segments** procedure. After obtaining the trial vector for an axis (for instance a second axis, as in Fig. 124) by Step 3 of the CA procedure (Tab. 15), the sample scores with respect to the trial vector are adjusted to zero mean in each (running) segment along the first axis, as illustrated in Fig. 124. For axes of higher order, detrending is made with respect to all previous axes. The result is that any polynomial function of any axis of lower rank is removed before the iteration process proceeds. This new Step 4 is performed at each iteration cycle, until convergence is reached.

Hill and Gauch (1980) suggested another method of detrending; **detrending-by-polynomials**, that might be more suitable for theoretical reasons because it addresses the specific shape of the distortion functions. Ter Braak (1987c, 1987d), also see ter Braak and Prentice (1988), implemented detrending-by-polynomials into the program package CANOCO for correspondence analysis with variants. This was done by extending Step 4 of CA so that trial sample scores were made uncorrelated not only with previous axes but also with polynomial functions of these axes up to a specified degree (2, 3, or 4).

Non-linear rescaling: removal of the edge effect. The edge effect manifests itself in a lowered tolerance of species (with respect to the scaling of axes in CA) towards the axis end-points (see Figs 121-122). Hill (1979a) deviced a method for non-linear rescaling of the axes, that is, for stretching and narrowing portions along the axis, in order to achieve uniform mean tolerances of species all along the axes. The non-linear rescaling method does this in such a way as to make the mean tolerance of all species approximately 1 for all segments of the axis. The resulting unit is the S.D. unit of ß diversity (cf. p. 35).

We have previously described the linear rescaling of CA axes, which also estimates gradient length in S.D. units. The non-linear rescaling procedure differs in several respects, most fundamentally in not preserving relative distances of sample plots (and species optima) along the axes.

Species differ considerably in their tolerances, and an approach to rescaling based directly on the species abundances is likely to be burdened with several sources of error; the most important being the lack of data on the extension of ranges of species occurring near the axis ends (Hill 1979a). Instead, Hill (1979a) assumed equivalence of (1) the variance of the optima (scores) of species present in a sample plot, and (2) the average squared tolerance of these species (also see ter Braak 1987c). This assumption is met when all species occurring in the sample plot are randomly distributed with equal variances (Hill 1979a), but the validity of this assumption when these demands are not met, is not known. As there are no problems involved in calculating the within-sample plot variance of species scores, weighted by species abundance,

$$v_j = [\mathrm{SUM}_{i=1,\ldots,m}\ y_{ij}(u_i - x_j)^2]/y_{.j}, \tag{76}$$

where y_{ij} is the abundance of species i in sample plot j, u_i the trial score of species i (before rescaling), x_j the trial score of sample j, and $y_{.j}$ the total abundance in sample j, this equation was used for rescaling the axes. When $v/n = 1$, $v_. = \mathrm{SUM}_{j=1,\ldots,n}\ v_j$, the mean (weighted) species tolerance is 1 if the assumptions above are satisfied. In order to achieve this, the ordination axis was divided into a number of small segments, the

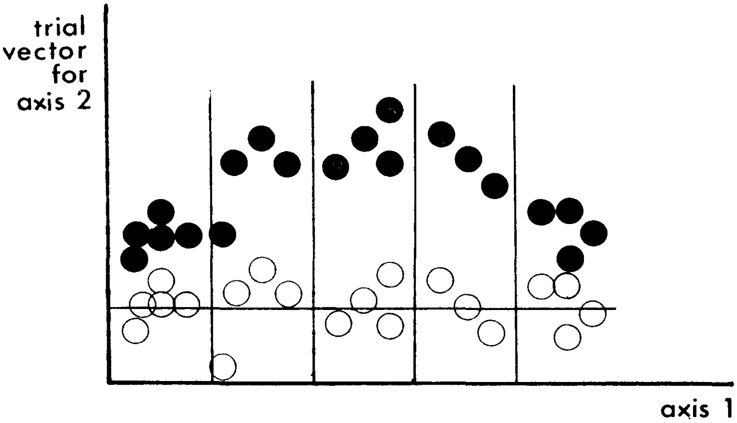


Fig. 124. Detrending by segments in DCA, somewhat simplified. Dots indicate scores for 20 hypothetical sample plots along DCA axis 1 and along a trial vector for axis 2. Detrending is done by dividing the first axis into a number of (overlapping) segments, and adjusting the trial scores for axis 2 to zero mean for each segment. The new scores (after detrending) are indicated by circles. The illustration is oversimplified as detrending in DCA is effected by averaging sample scores produced by several independent segmentations of the axis, but nevertheless explains the principle. Redrawn from Hill and Gauch (1980).

(running) mean of v_j was calculated for all of these segments, and the species ordination was expanded or contracted accordingly. After a specified number of iterations, the process is stopped and the species scores are used to calculate sample scores as the weighted averages of species scores. Then the sample scores are standardized (linearly) so that $v/n = 1$. Setting the lowest sample score equal to 0, the gradient length is measured in S.D. units. Rescaling by Hill's non-linear rescaling procedure (Hill 1979a) is implemented in the DCA algorithm as a separate step 6 after convergence of the iteration cycle. The properties of non-linear rescaling in DCA as a measure of ß diversity is further discussed on p. 153.

Performance with simulated and real data

All DCA ordinations were run on CANOCO (ter Braak 1987d), using default options (detrending-by-segments and non-linear rescaling), except that the option for downweighting of rare species was used.

Simulated data. The DCA ordination of the 6 x 1.5 S.D. coenoplane is shown in Figs 94-95. The recovery of the major gradient on the first axis was almost perfect (Tab. 14). The length of the first axis, 4.91 S.D., is an estimate of the length of the major gradient in S.D. units. The second gradient was satisfactorily recovered on the second axis, the length of which was 1.84 S.D. units. The third axis was not correlated with any of the underlying gradients, but its length amounted to 2.09 S.D. units. There was a considerable drop in eigenvalue from axis 2 ($\varepsilon = 0.1841$) to axis 3 ($\varepsilon = 0.1146$), indicating that the variation accounted for by axis 3 was significantly lower than axis 2. Higher gradient length of a lower-ranked axis is often an indication that the latter is determined by outliers (cf. R. Økland 1990a) or random effects of high noise levels.

DCA showed good recovery of the major gradient of the 5 x 2 S.D. coenoplane on the first axis and relatively good recovery of the second gradient on the second axis (Fig. 104, Tab. 14). However, axes 1 showed some correlation with gradient 2 and axis 2 was slightly correlated with axis 1. Towards the right-hand side of Fig. 104, the range of sample scores along axis 2 was gradually reduced; the sample plots made up a tongue in the diagram. The length of axis 1 was 4.13 S.D. units, axis 2 measured 1.98 S.D. units. Axis 3 was associated with a considerable drop in eigenvalue (0.1210 vs 0.2124 for axis 2), but the length of the third axis was 3.01 S.D. The same explanations as for the 6 x 1.5 S.D. data set may be applicable. The third axis was not correlated with any of the gradients (Fig. 105).

DCA recovered the gradients of the 2.4 x 2 S.D. coenoplane reasonably well on the first two axes, but relatively high correlations of axis 1 with gradient 2 and of axis 2 with gradient 1 indicated a slight rotation in the diagram (Fig. 110, Tab. 14). The length of the axes were 2.61 and 2.28 S.D. units, respectively. The eigenvalue and the axis length both dropped strongly from axis 2 to axis 3 (eigenvalues 0.2616 and 0.0844; axis lengths 2.28 and 1.63 S.D. units, respectively), showing that only two underlying gradients were present in the data-set. The third axis should be interpreted as a noise axis.

Real data. The DCA ordination of the 50 bog sample plots from Rønnåsmyra is shown in Figs 115-116. The first ordination axis separated sample plots according to their depth to the water table; sample plots from carpets (low depths) to the left, sample plots from hummocks to the right in the diagram (Fig. 115). The second axis separated sample plots with low depth to the water table (the left part of the diagram) according to assumed peat-producing ability (Fig. 116).

The results presented above support the results of other tests on simulated data (e.g., Hill & Gauch 1980, Kenkel & Orlóci 1986, Minchin 1987a), that DCA is a generally more reliable ordination method than either of PCA or CA. The application of DCA to the three simulated data-sets presented above, gives some indications of the strengths and weaknesses of DCA in relationship to coenoplane dimensions. These suggestions are supported by the extensive studies of Minchin (1987a): DCA recovers one single coenocline very well, although being somewhat sensitive to high noise and species response functions considerably deviating from symmetric, unimodal curves. DCA usually shows good recovery of a coenoplane with one gradient much longer than the other (e.g., similar to the 6 x 1.5 or 5 x 2 S.D. coenoplanes), but occasionally flattens out the variation along the minor gradient so that this appears as a tongue in the ordination diagram (cf. Fig. 104). This apparent fault of DCA was termed **the tongue effect** by Minchin (1987a). Furthermore, he shows poorer, sometimes rather poor, performance of DCA on complex models such as quadratic coenoplanes or models with T- or X-shaped sampling designs (only part of the models sampled). The results of the less comprehensive study by Kenkel and Orlóci (1986) largely give the same indications. Oksanen (1988) demonstrates that DCA may be unstable under random variation when the eigenvalues of the first two axes are very close. We will consider this as **the instability problem**.

Studies using DCA for ordination of field data often conclude that the method is well suited for extraction of ecologically interpretable axes (e.g., Gauch 1982a, Kent & Ballard 1988, T. Økland 1988, Peet et al. 1988). Unlike most other ordination methods, practical applications of DCA has often resulted in three interpretable axes (e,g., Hill & Gauch 1980, van der Maarel et al. 1985, R. Økland 1990a).

Theoretical considerations and assessment

While DCA has become a most valuable tool for the field ecologist, the method has received much criticism from statistically and mathematically minded ecologist for its heuristic, "brute force" approach to correct the faults of CA (Pielou 1984, Kenkel & Orlóci 1986, Minchin 1987a, Wartenberg et al. 1987). Three representative examples of critical views are the following: "..., DCA manipulates the data to reflect specific, preconceived notions and expectations, implying a systematic modification of the underlying data structure" (Pielou 1984, Kenkel & Orlóci 1986: 921); "... there is no empirical justification for the method, since the DCA model is not consistent with the structure of the data (given simplistic but routine assumptions), and that there is no theoretical justification for the method, since DCA is, as Hill and Gauch (1980) pointed out, an ad hoc adjestment of CA." (Wartenberg et al. 1987: 438); "DCA seems pointless, except for making plots that hide the presence of the curvilinear arch in the actual data. The problem of interpreting this curvature has been resolved by disguising its presence. The deception does not enhance our understanding of the data or help identify the cause of the observed distribution." (Wartenberg et al. 1987: 439). This criticism relates to the fact that the adjustments in DCA deliberately removes some unwarranted features of the CA results, (1) at the risk of introducing new distortions onits own (Pielou 1984, Minchin 1987a), and (2) at the cost of an underlying model with well-defined statistical properties. CA can be formulated as a scaling method with an explicit measure of distance, but such a model formulation is not really possible for DCA: a model has to be viewed in the light of the *a posteriori* adjustments. Minchin (1987a) discusses DCA in relation to the unfavourable properties of the Chi-squared distance measure, but in addition opens for the possibility that poor performance may be attributable to the behaviour of either or both of detrending and rescaling. The performance of DCA, and in particular its faults, deserve detailed consideration.

R. Økland (1990a) examined more than one hundred published applications of DCA for presence of the faults noted above. He found that the two major types of faults, the tongue effect and the instability, could be divided into several types, occurring under more or less predictable circumstances:

The tongue effect. According to R. Økland (1990a), tongues can be classified as follows:

(1) Separation of sample plots near the end of the first axis; five indistinctly separated subtypes: (a) separation of sample plots in the species-rich end of axis 1 (e.g., Vitt et al. 1986, R. Økland 1990a), (b) separation of sample plots in the extremely species-poor end of axis 1 (e.g., Lieffers 1984), (c) a secondary gradient only expressed along a part of the first axis (e.g., Carleton 1982, Gibson & Kirkpatrick 1985), (d) tongue caused by instability of the method (e.g., the tongue appearing in the simulation studies by Minchin (1987a), and the tongue changing from one end of the ordination to the other upon a minor change of options for the program (Eyre et al. 1986)), and (e) tongue caused by large gaps in the sampling of the underlying ecological space (Chang & Gauch 1986).

(2) Separation of sample plots near the middle of the first axis; two-sided tongues (e.g. Bernard et al. 1983, Robertson et al. 1984).

Several explanations are likely to account for the occurrence of tongues:

(1) The tongues represent true structure in the data-set, more or less distorted by the detrending procedure. It is well-known that CA and DCA are vulnerable to large disjunctions (cf. p. 147). Disjunctions with respect to the second gradient (e.g., like 1e above) inevitably results in a tongue, because the mean of axis 2 sample scores is equalized all along axis 1 in the detrending process. This is particularly well illustrated in the study of Tibetanian mountain vegetation by Chang and Gauch (1986). The first DCA axis was interpreted as corresponding to an altitudinal gradient, the second axis as corresponding more or less to a moisture gradient. However, towards low altitudes, there are disjunct zones along the moisture gradient, separated along the altitudinal gradient (medium altitude combined with high moisture, low altitude combined with low moisture). The second gradient will not be able to separate the low to medium altitude samples according to moisture, they are aligned on a straight line by detrending-by-segments. In situation 2 above, the two-sided tongues may represent "true structure" of the data; beta diversity may be high in the middle portion of a long gradient (reflected on the first axis). However, the alignment of the ends of the first axis to the mean axis 2 sample score, may be inappropriate. The distorted nature of the ordinations exhibiting sample plots aligned on a straight line is evident from many studies with type 1c tongues. When the second gradient only results in vegetational variation along part of the first gradient, the detrending procedure will produce a straight tongue regardless the similarity of the sample plots on the tongue with plots on the lower or the upper part of the second axis, near the opposite end of axis 1. This means that a rectangular coenoplane with a long and a shorter gradient will result in the same ordination diagram regardless whether we remove sample plots from the upper right or lower right triangle. This distortion is evidently caused by the detrending process alone.

(2) The tongues represent artifacts produced by the distance measure. Chi-squared distance overemphasizes species with low totals, and hence, sample plots with a high proportion of the total abundance allocated to such species. Overemphasis on such sample plots and species is likely to be responsible for the situations 1a and 1b above, separating the deviant sample plots and species rather than vegetational variation relevant to the higher number of species and sample plots without these features. The distorted nature of these situations is obvious.

(3) The tongue represents instability of the detrending procedure. This is the only likely explanation to situation 1d. The rescaling procedure affects relative positions of segments *within* axes, and operates on one axis in turn. Defects in this procedure will not be able to produce a tongue, as opened for by Minchin (1987a) and ter Braak and Prentice (1988).

The tongue effect thus can be ascribed to properties of the data-set (mostly inappropriately handled by the detrending-by-segments procedure), poor properties of the distance measure, and instability/inappropriateness of the detrending-by-segments procedure (R. Økland 1990a).

The instability problem. The most probable explanation of the instability of DCA in situations with more or less equal eigenvalues of subsequent axes is shortcomings of the detrendings-by-segments procedure (Oksanen 1988, R. Økland 1990a). This type of instability also explains the poor performance of DCA with simulated quadratic coenoplanes (Kenkel & Orlóci 1986, Minchin 1987a), in particular with incorporation of random noise (Minchin 1987a).

The two empirical adjustments of DCA have jointly been made responsible for the occasional poor performance of the method (Pielou 1984, ter Braak 1987c, Minchin 1987a, Wartenberg et al. 1987, ter Braak & Prentice 1988). DCA users have therefore been advised to use these options with precaution, or apply the detrending-by-polynomials option now available in CANOCO (ter Braak 1987d, ter Braak & Prentice 1988). We will consider these advices in some more detail.

Detrending. The shortcomings of the detrending-by-segments procedure are evident from the discussion above. Between one third and one half of the DCA ordination diagrams published before 1989 are burdened with a tongue effect that most probably is an artifact. However, the new options for detrending-by-polynomials do not resolve the problem of tongue effects, they merely reshape the tongues (O. Eilertsen, R.H. Økland, T. Økland, and O. Pedersen, unpubl., O. Eilertsen, in prep.) and make them less easily recognized. Knox (1989) showed that the detrending-by-segments procedure was preferential to the detrending-by-polynomials procedure available in CANOCO, resulting in generally more accurate and more stable solutions. Detrending also improves the accuracy of ordination solutions in comparison with the orhogonalization procedure of CA, but at some cost of the stability (Knox 1989). Detrending-by-segments as originally implemented in DECORANA is therefore the best available method for eliminating the arch effect in CA, despite its obvious defects.

Non-linear rescaling. Ter Braak (1987c) and ter Braak and Prentice (1988) advice against the routine use of the non-linear rescaling option in DCA. The thorough examination of the faults of DCA given above did not result in any indications of responsibility of the rescaling procedure for the occasional poor performance of DCA. Indeed, Knox (1989) found non-linear rescaling to give more stable and more accurate ordination results than linear rescaling. Oksanen (1988) found the non-linear rescaling procedure to increase the stability of solutions. The linear rescaling procedure (p. 143) estimates the length of the axis in S.D. units by equation (73), using the mean weighted variances of the species. Low variance of sample scores containing species occurring near the axis end-points (caused by the edge effect in CA) leads to low mean variance (over all species), and hence, strongly overestimated axis lengths (O. Eilertsen, R. Økland, T. Økland, O. Pedersen, unpubl., O. Eilertsen, in prep.). In contrast, the non-linear rescaling approach (equalizing the weighted within-sample variance of species scores, cf. equation (76)) is much more robust and therefore give axis lengths that are in good accordance with expectations from simulated models, at least when the model properties are near-optimal for correspondence analysis (ter Braak 1985, 1987c, R. Økland 1986a, cf. pp. 146-147). It is likely, yet has to be proven, that the non-linear rescaling is robust to noise and deviations from symmetric unimodal response curves. There are still no indications of unfavourable properties of the non-linear rescaling method.

Thus non-linear rescaling of recognized gradients in S.D. units of compositional turnover (as can be done by rescaled canonical correspondence analysis (pp. 169-170), using positions relative to the recognized gradient as the constraining variable) appears to have favourable properties as a measure of ß diversity or compositional turnover (cf. R. Økland 1986a, 1986c, 1990a, 1990b, Peet et al. 1988, Eilertsen et al. 1990). The measure is, however, dependent on the settings of several parameters and on aspects of data manipulation. These topics are discussed by R. Økland (1986a) and Eilertsen et al. (1990). Factors influencing the gradient length estimates by non-linear rescaling are: (1) the measure of abundance used (indirectly influencing the shape of species response curves), (2) the range of the scale used for weighting species abundances; altering the scale range by a power function changes the kurtosis of the species response curves (high r implies more leptocurtic (sharp-peaked) curves and hence, increases the estimated gradient length), (3) removal of rare species; equivalent to removal of species with narrow tolerances, and hence, leads to increased mean species tolerances, and to reduced estimates for gradient length, (4) sample plot size; reduced size implies lower frequency of species in the material, narrower tolerances, and hence, increased gradient length estimates (R. Økland et al. 1989, in prep.), and (5) downweighting of rare species by the downweighting option in the DECORANA/CANOCO programs; effect not predictable. The comparison of estimates for gradient lengths by the non-linear rescaling approach therefore necessitates that comparability is ensured (R. Økland 1986a, Eilertsen et al. 1990).

The rating of DCA ranges from the profuse adherence to the hostile antagonism. Present knowledge of the performance of the method must lead to an intermediate standpoint. There is no doubt that the characterization of the method as close to the theoretical optimum for ordination methods (e.g., Gauch 1982a) is, at best, premature. This does, however, also apply to the strong advise against using the method by Wartenberg et al. (1987). It cannot be denied that DCA has been the basis for a considerable number of successful studies in gradient analysis. The method is simple in use, and has the favourable properties of ordinating samples and species simultaneously, and providing a scaling of axes that is interpretable as a robust measure of compositional turnover (ecological distance). Its shortcomings are in touch to become better known; the most important of these, the tongue effect is easily identified by visual inspection. The occurence of a tongue warrants a careful analysis of the data in order to identify the reason for the appearance of the tongue (R. Økland 1990a). A division of the material and subsequent separate ordinations of one or both of the subsets as suggested by Peet (1980) and done, for instance, by White and Glenn-Lewin (1984), Palmer (1986), T. Økland (1988, 1989) and R. Økland (1990a), is often informative. In particular, division of the material is useful when one gradient is relevant to a subset of the data-set only, and when poor performance is caused by outliers.

The relative efficiencies of DCA and MDS will be discussed by treatment of the latter (pp. 159-160).

Applications

Fennoscandian applications of DCA include the study of Oksanen (1983) of dry, boreal pine forests in Finland; the study of T. Økland (1988) of the Fritzøehusparken beech forest, with two interpretable axes; the study of T. Økland (1989) of *Vaccinium myrtillus*-dominated spruce forest in Rausjømarka, also giving two interpretable axes; and the studies of mire vegetation by Heikilä (1987), Singsaas (1989) and R. Økland (1990a), with two, two and three interpretable axes, respectively. Applications of the non-linear rescaling procedure for estimation of gradient length are provided by Cramer and Hytteborn (1987) and Rydin and Borgegård (1988), in the context of niche studies by R. Økland (1986c, 1990b).

Some practical considerations

Computer programs for principal component analysis and correspondence analysis are available in the CANOCO package (ter Braak 1987d). Some advice regarding choice of options in the program, as well as recommendations with respect to the data-set are appropriate.

Number and size of sample plots. DCA is vulnerable to outliers; sample plots with few species and disjunct groups of sample plots (with species more or less confined to this group). All ordination axes are found by extracting the co-ordinated variation in species responses to underlying, hypothetical gradients. Therefore, the number of sample plots must be sufficient for adequately describing the relationships of the species to the underlying gradients, and for the relationships of the sample plots to become apparent. This minimum number is dependent on the ß diversity in the data-set (cf. discussion on pp. 83-84). If only one gradient is present (this is rarely the case), a minimum of ca. 20 sample plots appears sufficient. If there are reasons to believe there are more than one gradient present, or the number of gradients are unknown, 50 sample plots should be a minimum. The statistical significance of estimates (relating to species responses (e.g., species optima), relative positions of sample plots, change in vegetation over time, etc.) always increases with increasing number of sample plots.

Number of sample plots must be viewed in connection with size. The most important demand on sample plot size is that each sample plot has a species composition that is representative for the conditions at the site (for reliable calibration of site conditions from the abundance data). As previously discussed (pp. 83-84), the lower limit of species number per sample plot for the sample plot to be representative for the site conditions is dependent on the tolerance of species. In general, data-sets from species-poor vegetation (e.g., the macrophyte vegetation of lakes), will be better suited for ordination than data-sets with a strong variation in species richness. In practice, sample plots with less than, say, 5 species will rarely be representative. Judgments of representativity must preceed the choice of sample plot size. The smaller the sample plots (and lower the number of species per sample plot), the higher number of sample plots is generally needed.

Choice of abundance scale. Data manipulation. T. Økland (1988) demonstrated for the Fritzøehusparken beech forest that the use of frequency in subplots rather than percentage cover resulted in better separation of sample plots in DCA ordination. Similar results have been reached in other studies, but there are also examples of the opposite pattern (S. Flatby, in prep.). The choices of abundance scale and ordination method do not depend on each other.

R. Økland (1986a) showed that the gradient length estimates by non-linear rescaling, relative to a Gaussian model, were best with a moderate weighting of abundance (range of the abundance scale 10-30). The preference for intermediate weighting (cf. pp. 101-102) is also valid for DCA.

Downweighting of rare species. As rare species were known unduly to influence the gradient recovery by CA (and DCA), Hill (1979a) included an option for downweighting of rare species in DECORANA.

The downweighting procedure replaces the abundance values of infrequent species in the data-set, y_{ij}, with new values, y_{ij}'. A species is defined to be infrequent if its frequency in the data-set, f_i, is lower than $f_{i,max}/5$, where $f_{i,max}$ is the maximum frequency of any species. For the infrequent species, the new abundances are

$$y_{ij}' = y_{ij}*[f_i/(f_{i,max}/5)]. \qquad (77)$$

Eilertsen and Pedersen (1989) and Eilertsen et al. (1990) evaluated this downweighting option, and concluded that a too high proportion of the species are normally downweighted. Instead, they suggested to define infrequent species relative to the median frequency in the material, f_m. Species less frequent than the median frequency are considered infrequent and hence subjected to downweighting by the equation

$$y_{ij}'' = y_{ij}*(f_i/f_m)^n \qquad (78)$$

where n is a parameter determining the degree of downweighting. A value of 1 appear reasonable, but this as well as the relative performance of this alternative downweighting option remains to be tested.

The Chi-squared distance measure weights species inversely proportional to their total abundance. There is therefore reason to believe that downweighting would actually increase the emphasis on rare species and increase the danger of outlier effects. This remains to be tested.

The properties of the downweighting option in DCA is not well known, but some examples (e.g., Eyre et al. 1986), indicate an instability of the downweighting option. It should be used with caution.

Rescaling. The option for non-linear rescaling should be used, as discussed above (p. 153).

Detrending. The option for detrending-by-segments should be used, as discussed above (pp. 152-153). Several options for parameters related to the detrending procedure are available (Hill 1979a, ter Braak 1987d). The effect of deviating from default values are not well known; but Minchin (1987a) did not obtain improved ordinations in a limited experiment on simulated data sets. There are no reason to deviate from the defaults unless particular indications should suggest so.

The use of covariables. CANOCO includes a possibility for removing the variation in the data-set that can be explained by a particular set of variables of known or uninteresting effect, termed **covariables**, (e.g., a group of environmental variables), before ordination (ter Braak 1987d). This is done by detrending with respect to the specified variables at each turn of the iteration cycle, thereby to obtain ordination axes without any systematic relationship to the covariables.

The inclusion of passive samples. CANOCO allows the inclusion of sample plots in the data-set that are not to be included in the process of axis extraction, but that are passively fit into the ordination after the axes are defined. Such **passive samples** may be outliers, newly obtained samples, reanalyzed sample plots (second, third etc. replicate of a time series), that are to be related to previously published or interpreted ordinations.

Nonmetric multidimenional scaling (NMDS)

All ordination methods treated so far are original or modified versions of metric scaling techniques: they aim at finding a configuration that optimizes the fit of floristic dissimilarities to distances in the ordination space. The stress function, measuring the badness-of-fit, depends on the numerical values of dissimilarities and distances. We have seen that there are fundamental problems with the metric scaling approach, deriving from the non-linearity of floristic resemblance measures as functions of ecological distance, making the metric scaling concept incapable of recovering the underlying structure axes as straight lines in the ordination space. Attempts to correct these faults by empirical adjustments (e.g., DCA) have not been entirely unsuccessful, but will never yield an optimal solution to the ordination problem. Attempts to use nonmetric scaling methods for ordination of ecological data have been made several times (see Austin 1976b, Fasham 1977, Prentice 1977, Gauch 1982a, Minchin 1987a, ter Braak 1987c), but the break-through of these methods still has not come. Anyway, they deserve further consideration.

The method: measure of stress and algorithm

The nonmetric multidimensional scaling (NMDS) techniques "construct a configuration of points in a specified number of dimensions, such that the rank order agreement between the inter-point distances and the resemblance values is maximized" (Minchin 1987a). The main difference from the metric scaling techniques is the use of the rank order of dissimilarities and ordination space distances instead of the dissimilarity values and distances themselves. This is what is referred to by the term "**nonmetric**". The term "multidimensional scaling" do not imply any difference from the previously treated methods; all ordination methods deal with multidimensional matrices, and all are scaling techniques. So far, our approach to nonmetric multidimensional scaling has been a geometrical approach. It is not possible to use a statistical approach to NMDS, as the methods only depend on the secondary matrix of dissimilarities supplied, regardless the response of the species to underlying gradients (Minchin 1987a). NMDS is a concept; in practice there are almost infinitely many ways to perform NMDS. The bewilderingly high number of choices to be made in NMDS has certainly discouraged many ecologists from trying NMDS. Earlier tests of the method (e.g., Gauch et al. 1981, Oksanen 1983) have probably reached the conclusions that NMDS is inferior to, or at least no better than the linear scaling methods on the basis of unfortunate choices of options. Minchin (1987a) gives a lucid survey of NMDS; the concepts, a survey of the choices to be made, and guidelines for performing the optimal choices. We will describe the family of NMDS techniques by considering the different options and the NMDS variants they define.

Like other scaling techniques, NMDS assesses the badness-of-fit of points in the ordination space to the original dissimilarities by use of a stress function, but unlike the metric scaling methods this stress function only express the rank order (monotonous) correspondence between dissimilarities and distances. NMDS can be applied to any kind of objects; sample plots, species, etc., but only one kind at a time. It therefore lacks the duality of PCA, CA, DCA, etc. NMDS techniques use an iterative algorithm (Kruskal 1964b). The following information has to be supplied at the outset:

(1) An initial configuration of points in the desired dimensionality. This dimensionality is chosen by the investigator.

(2) A matrix of dissimilarities between, for instance, sample plots. This implies that a dissimilarity measure and a standardization has to be specified in advance. We will denote the dissimilarity between sample plots j and l by $\delta(j,l)$.

(3) A measure of badness-of-fit of distances in the ordination diagram to the supplied dissimilarities. We denote the distance between samples j and l in the ordination diagram $d(j,l)$.

At each turn of the iteration cycle, $d(j,l)$ is calculated. A diagram, often called a **Shepard diagram**, with distance $d(j,l)$ on the abscissa and dissimilarity $\delta(j,l)$ on the ordinate, is (implicitely) made. Points corresponding to the sample plots are plotted on the diagram, according to corresponding values of $d(j,l)$ and $\delta(j,l)$. The best monotonous (ascending) curve is fitted to the points by monotonous regression. Fig. 125 shows a hypothetical Shepard diagram. By intention, we should only use the rank order of the dissimilarities. An appealing approach to assessment of the badness-of-fit is then to look at the deviations of the distances $d(j,l)$ from the regression curve (Kruskal 1964a, 1964b), i.e. the distance in the Shepard diagram from a point (j,l) to the curve, measured along the abscissa (horizontally in the diagram). This point on the curve is the fitted distance, termed $d^{\wedge}(j,l)$. Kruskal (1964a) suggested the following measure of stress:

$$s = \{[\mathrm{SUM}_{j,l}\ (d_{j,l} - d^{\wedge}_{j,l})^2]/(\mathrm{SUM}_{j,l}\ d_{l,j}^2)\}^{0.5}, \qquad (79)$$

which is simply the square root of the residual sum of squares divided with the total sum of squared distances. The stress function takes on a value of 0 when themonotonousfit is perfect, and increases towards a theoretical

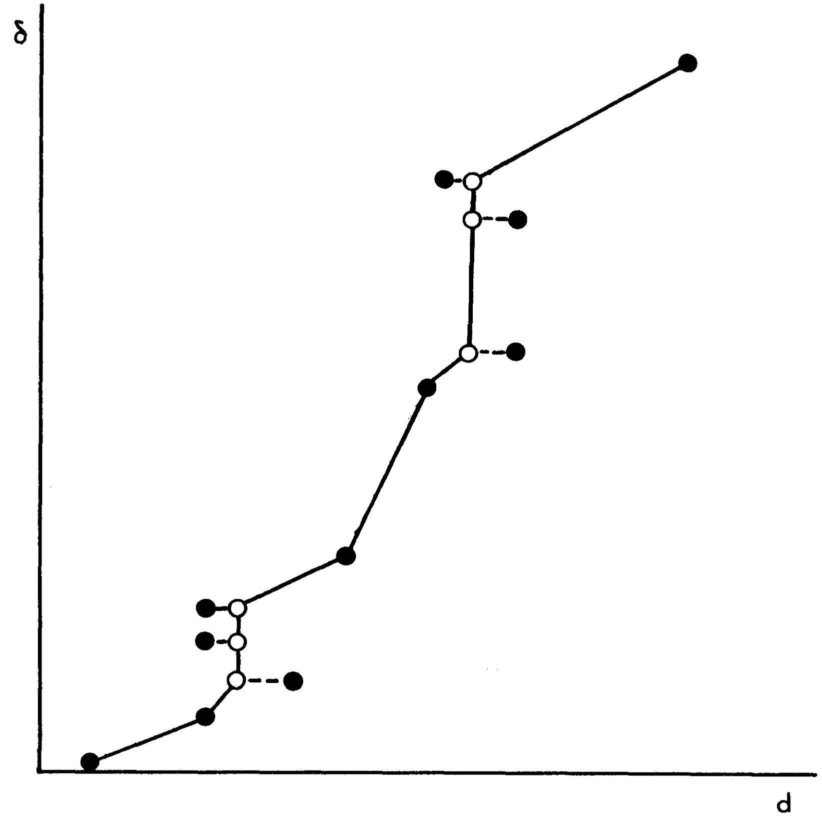


Fig. 125. Hypothetical Shepard diagram. The abscissa expresses distances in the ordination space, d(j,l), the corresponding original dissimilarities δ(j,l) are shown on the ordinate. The monotonic regression curve for δ(j,l) on d(j,l) is shown as a continuous line. The fitted distances d^(j,l) are drawn into the diagram as horizontal, broken lines. The relative length of the broken lines determine the stress in the MDS solution.

maximum of 1. The subscripts j,l are not specified in the equation. This is because there are several ways of treating the dissimilarities and distances. Not all dissimilarities need to be taken account of. For instance, we know that sample plots with no species in common will have a similarity of 0. If the dissimilarity scale has an upper bound, for instance of 1, then this value for the dissimilarities will be indeterminate (cf. p. 112), and hence, should be excluded from the calculation of stress. The number of pairs of sample plots in a set of n samples is n(n-1)/2, thus there are sufficient information left to perform the ordination. Furthermore, tied dissimilarities, i.e. the situation that several pairs of sample plots have the same dissimilarities, can be treated in different ways. Kruskal (1964a) proposed not to demand that equal dissimilarities should imply equal distances in the ordination, and recommended to omit tied dissimilarities from calculation of the stress. D. Kendall (1971a, 1971b) shows that arch effects may arise from too strong conditions on ties. The recommendation of Kruskal has been generally accepted (ter Braak 1987c, Minchin 1987a).

The iteration procedure used in NMDS programs is the method of steepest descent (see Kruskal 1964b), by which each point (sample) in turn is moved around slightly in the ordination space in order to find the direction of change leading to the strongest decrease in stress. Then each point is moved in the direction of steepest descent, the stress calculated again, and so on until a minimum of the stress function is reached. It should be stressed that the minimum is not necessarily the global minimum; NMDS can be trapped in local minima. Kruskal (1964b), followed by later authors, therefore strongly recommends the use of several starting configurations. Minchin (1987a) recommends that one should be based on DCA, perhaps the best of the ordination methods with small computational demands. The solution with the lowest stress is selected for use.

A high number of programs have been deviced for variants of NMDS (e.g., Prentice 1977, Gauch et al. 1981, Minchin 1987a). A thorough examination of the algorithm of these methods and tests of their properties on vegetation data by Minchin, Faith and Belbin (in Minchin 1987a) gave preference to the program KYST by Kruskal et al. (1973), incorporated into the DECODA package (Minchin 1986). This carries out NMDS by the algorithm described above, based on Kruskal's original studies (Kruskal 1964a, 1964b), but with allowance for several optional modifications to be considered below.

The method: variants and options

Having decided upon the measure of stress (and which program to use), still many choices remains to be made. First, we have to decide which measure of dissimilarity measure (and standardization) to use. Obviously, the best measure is the one that shows the best rank correlation with ecological distance (Faith et al. 1987). Faith et al. (1987), also see pp. 108-112, showed that the quantitative symmetric (Kulczynski) measure and percentage dissimilarity (Bray-Curtis), both standardized by division with species maxima, were the two best in this respect, among a number of compared measures of dissimilarity. Furthermore, indeterminate dissimilarity values (1.0) should be disregarded.

The two main variants of NMDS are **global nonmetric multidimensional scaling** (GNMDS) and **local nonmetric multidimensional scaling** (LNMDS). The global variant uses all distances (except the discarded ones) for making the Shepard diagram. On the basis of this, one measure of stress is then calculated. However, Sibson (1972) proposed to make one Shepard diagram for each sample (with dissimilarities and distances to all other samples as points), thereby calculating one value of the stress function for each sample. The n values of the stress function are averaged to give the overall stress. This local variant has the advantage of allowing for the possibility that differences in species number per sample plot and other properties which can potentially influence dissimilarities, vary in the ecological space (Prentice 1977, 1980, Minchin 1987a).

Faith et al. (1987) proposed a variant of NMDS, **hybrid multidimensional scaling** (HMDS), that depends on both the rank order and the linear relationship between original dissimilarities and distances in ordination space, and in this way unites the techniques of metric and nonmetric multidimensional scaling. The procedure is as follows:

(1) Compute a secondary matrix of dissimilarities, based on an optimal dissimilarity measure.

(2) Make two copies of this matrix. Below a threshold value (cf. Fig. 78), the dissimilarity measure approaches a linear function of ecological distance. Set all dissimilarities above this threshold as missing in the first matrix. In the second matrix, keep all values below 1.0.

(3) Subject both matrices to multidimensional scaling. The first matrix is used for metric scaling, using a linear regression of distance on dissimilarity, the second is used for nonmetric scaling. At each step on the iteration process, the stress functions from the two approaches are combined to give an overall stress function.

Performance with simulated and real data

All NMDS ordinations were run on KYST (Kruskal et al. 1973), as implemented in the DECODA program package (Minchin 1986). The local variant (LNMDS) was used, with various dissimilarity coefficients and standardizations. A minimum of ten starting configurations was used for each data-set, and no solution was accepted that had not been reached from at least two different starting configurations, thus likely to be the global minimum. Attention was restricted to the two-dimensional MDS solution.

Simulated data. All three coenoplanes were ordinated by LNMDS, with three different combinations of dissimilarity measure and standardization. In accordance with recommendations by Faith et al. (1987) and Minchin (1987a), we chose the quantitative symmetric (Kulczynski) measure (K) and percentage dissimilarity (Bray-Curtis measure; B), both in the form standardized by division with species maxima (S; cf. p. 103), the latter also without standardization. The relative performance of LNMDS using these three combinations of dissimilarity measure and standardization did not differ between the simulated models (cf. Tab. 14); percentage dissimilarity standardized by division with species maxima always gave the best results, (closely) followed by the standardized quantitative symmetric measure, and with the unstandardized percentage dissimilarity mostly definitely inferior. Attention will be restricted to the results with standardized percentage dissimilarity.

With the 6 x 1.5 S.D. coenoplane, the two underlying gradients were recovered on the first two ordination axis (Fig. 89). The recovery of the first gradient was very good, although somewhat inferior to that of DCA. Also in the case of the second gradient, the correlation of sample scores and gradient positions was lower than for DCA. On the other hand, the second LNMDS axis showed lower correlation with gradient 1 than in DCA. The high value for DCA in this respect is likely to be due to effects of the detrending procedure.

LNMDS showed by far the best gradient recovery for the 5 x 2 S.D. coenoplane (Fig. 97). For the 2.4 x 2 S.D. coenoplane, the gradient recovery of LNMDS was again best, in fact the difference in correlations from the metric scaling techniques were more pronounced than with the other coenoplanes. LNMDS rotated the solution 90°, thus gradient 2 was reflected on axis 1 and vice versa.

Real data. The two-dimensional LNMDS solution for the 50 sample plots from virgin bog vegetation at Rønnåsmyra is shown in Figs 117-118. The first axis reflects the gradient in depth to the water table (Fig. 117), the second axis separates the drier (right) end of the water table gradient according to assumed peat-producing ability (Fig. 118). Thus the second axis differs from the second axis of the DCA ordination. In two dimensions, the solution gives a very good separation of sample plots relative to the two explanatory variables.

The results presented here point in the same direction as the comprehensive simulation approach by Minchin (1987a), that LNMDS is generally superior to DCA for the task of ordination when gradient recovery is used as the only optimality criterion. However, Minchin (1987a) shows that LNMDS does not always give good results; the method does not perform well with complex sampling patterns (and complex models). R. Økland & Eilertsen (in prep.) show that LNMDS solutions in three dimensions may yield spurious axes that are not ecologically interpretable, likely to be distortions of the underlying gradient structure.

The lack of agreement on the merit of NMDS from previous comparative studies (except Minchin 1987a) is mostly due to use of programs with suboptimal stress functions or other suboptimal properties, the use of global instead of local variants (as recommended by Minchin, Faith & Belbin, unpubl., in Faith et al. (1987) and Minchin (1987a)), trapping in local minima, and the use of unsuited or suboptimal dissimilarity measures, or standardizations of dissimilarity measures (cf. Minchin 1987a).

Faith et al. (1987) report the results of extensive tests on simulated data, showing preference for HMDS over LNMDS (in turn considerably better than GNMDS), but the difference in performance is generally not large.

Assessment: NMDS versus DCA

Thanks to the clarifying work of the Australian group (Minchin 1987a, Faith et al. 1987, Minchin, Faith & Belbin, unpubl.), sufficient knowledge has accumulated to sort out the most efficient MDS strategies. A clear recommendation emerging from the above-mentioned studies (and in accordance with simulations shown above), can be given.

The program KYST, modified and incorporated into DECODA (Minchin 1986) contains options for the most efficient MDS variants known today. Percentage dissimilarity, standardized by division with species maxima, is the recommended dissimilarity measure. Local NMDS is preferential to global NMDS. Hybrid MDS gives even better results, but the considerably higher computation time necessary for HMDS may not be justified in simple situations (P. Minchin, pers. comm.). At least ten different starting configurations should be used, one of them based on DCA. No solution should be accepted unless it is reached from more than one starting configuration. The program KYSTPOST in DECODA includes an option for comparing MDS solutions by Procrustean analysis.

One special problem offered by MDS is that the number of dimensions have to be specified in advance (Kruskal 1964a, 1964b, Austin 1976b, Fasham 1977, Gauch et al. 1981). Kruskal (1964a) suggests examination of the minimum stress as a function of number of dimensions, and to choose the dimensionality corresponding to a levelling off of the stress curve. In most cases, the stress levels off gradually (as do eigenvalues of subsequent axes obtained by metric scaling techniques), and this criterion cannot be used. The belief of Sibson (1972) that the dimensionality should be possible to determine by objective criteria is unrealistic. The use of the stress function for this is further complicated by the fact that the stress is a function of n, the number of sample plots, the distribution of the dissimilarities, and the noise level in the data (Kenkel & Orlóci 1986). In practical applications, at least two- and three-dimensional solutions should be tested.

Accepting that LNMDS produces generally more reliable ordinations than do other ordination methods, the choice of ordination method should be simple. When this is not so, the reason is that there are several properties of the ordinations other than the configuration of points as such, that affect the usefulness of an ordination. In addition, neither LNMDS nor DCA can guarantee a good and reliable result with all realistic data-sets. Several other properties of the methods may influence the choice of method:

(1) The lack of uniqueness of LNMDS solutions with different dimensionalities, and the danger of

trapping in local minima. These problems are, however, not critical. The first can partly be overcome by finding the best solution in several dimensions, and interpret these separately by use of external data, the second can be almost fully circumvented by using a high number of initial configurations.

(2) MDS do not ordinate species and sample plots simultaneously (cf. Gauch et al. 1981). The duality of metric scaling techniques may enhance interpretability.

(3) MDS provides an arbitrary scaling of the gradients. The usefulness of such a scaling is inferior to the scaling of DCA, which is in S.D. units reflecting compositional turnover, and which can be related to species turnover along the axis (cf. p. 35).

Inter-sample distances in NMDS ordination diagrams reflect the optimal fit of the point configuration in ordination diagram, relative to sample dissimilarities. Thus a nonlinear rescaling of axes is not desired. On one hand, it might destroy the optimality of the ordination, on the other it should be unnecessary as the inter-point distances in the ordination diagram should reflect compositional turnover rather well. The units used for scaling the NMDS axes are arbitrary. Furthermore, a comparison of the scalings of LNMDS and DCA applied to the same simulated data sets showed that the lengths of the LNMDS axes (in the arbitrary units) and the corresponding DCA axes were only weakly correlated, although the same target gradient were confidently recovered in both cases. Improved interpreatbility of MDS diagrams can be obtained by a **linear** recaling of the axes in S.D. units. Such a scaling can be obtained from a rescaled canonical correspondence analysis (rCCA; cf. pp. 169-170), using sample scores with respect to the MDS axes as constraining variables (Eilertsen et al. 1990). The sample scores which are linear combinations of the constraining variables are the rescaled MDS scores. For practical reasons, they should be adjusted to zero minimum for each axis.

(4) MDS has high demands on computation time (cf. Gauch et al. 1981). This point is decreasing in importance parallel with the development of more powerful processors.

(5) The availability of the program package CANOCO (ter Braak 1987d), containing an integrated set of tools for gradient analysis based on the same underlying model, including ordination and constrained ordination (cf. pp. 167-174), that for many applications will be more useful than each of the techniques, viewed separately. No such integration of different approaches are yet available based on the MDS concept.

The decision, DCA or LNMDS (or HMDS), must take advantage of the fact that the pros and cons of the different approaches are now reasonably well known. Ordination may fruitfully be approached by using *both* DCA and LNMDS. Congruent configurations are a strong indication that a realistic ordination has been achieved.

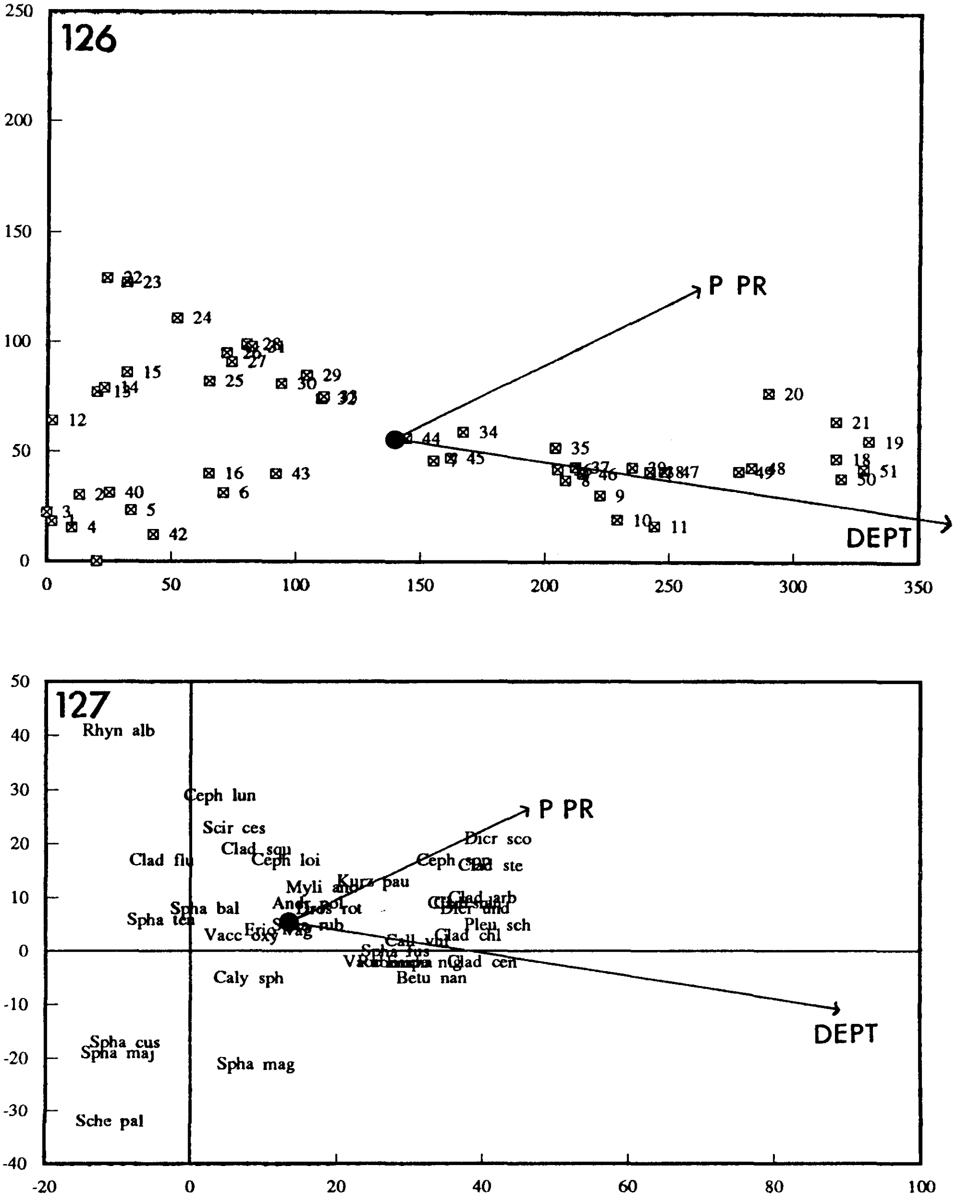
Applications

NMDS has been used by Oksanen (1983) for ordination of Finnish pine forests. LNMDS was used by Rydgren (1989) for ordination of herb-rich spruce forests in Nordland.

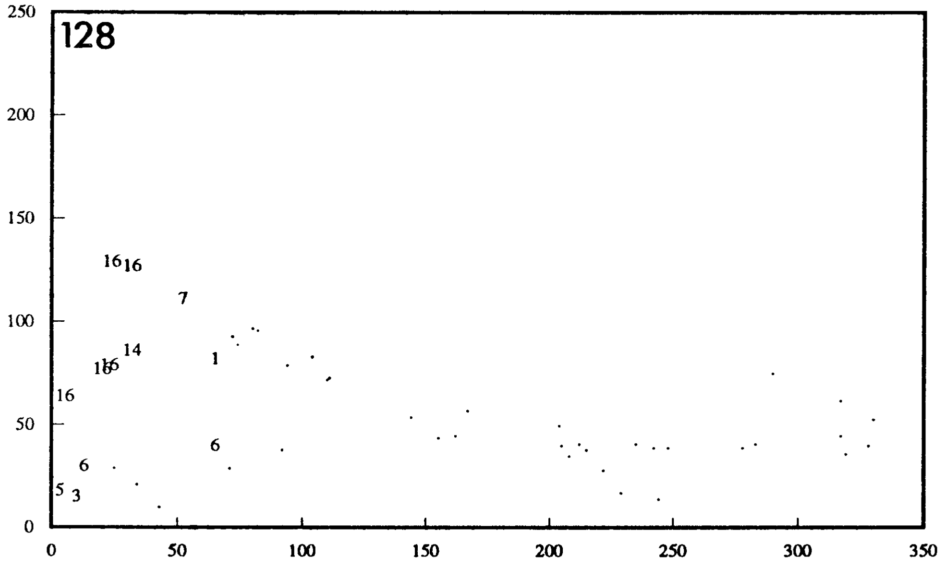
Interpretation of ordination results

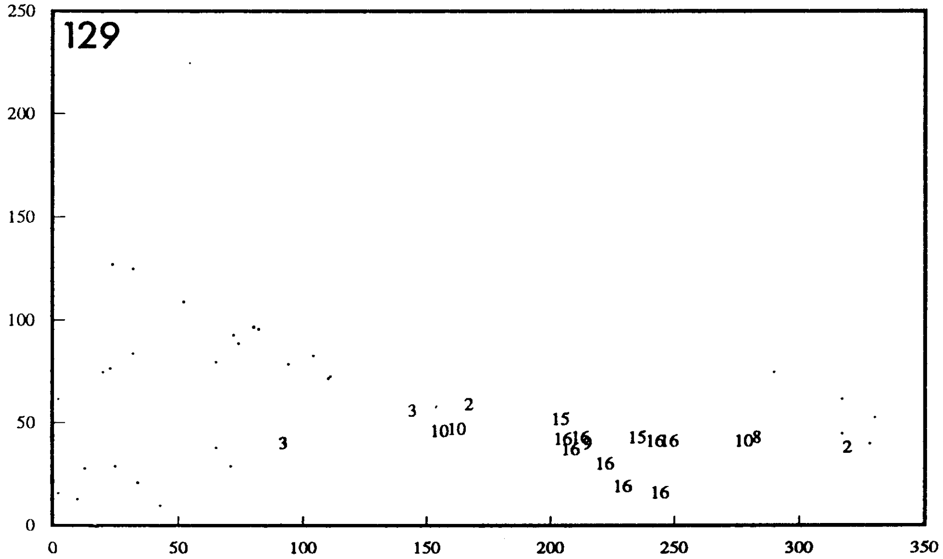
Ordination is indirect gradient analysis; the extraction of axes in vegetational variation (coenoclines). The interpretation of these axes must follow as a separate step. Several approaches to interpretation are possible (see, for instance Gauch (1982a) and ter Braak (1987c)). We will give a short account of the most useful among them, and give examples from the literature (with particular reference to the study of beech forests based on DCA by T. Økland (1988)) the application of the interpretative devices to the DCA ordination of the 50 sample plots from Rønnåsmyra (Figs 115-116).

(1) *Comparison of species and sample ordinations*. Ordinarily, ordination diagrams show (numbered or labelled) sample plots (Fig. 126) and, when available, species optima (Fig. 127). Species and sample plots may be displayed in the same ordination diagrams (a biplot), but such diagrams will often suffer from a lack of clarity due to overcrowding of information. The species plot may aid interpretation of the sample plot ordination (the axes) in environmental terms by use of "general knowledge" of the ecological requirements of the species. This informal way of interpretation may give good indications of complex-gradients underlying the ordination axes, but the subjectivity of this approach may lead to an interpretation that is unduly favoured by preconceived ideas. Thus other approaches,

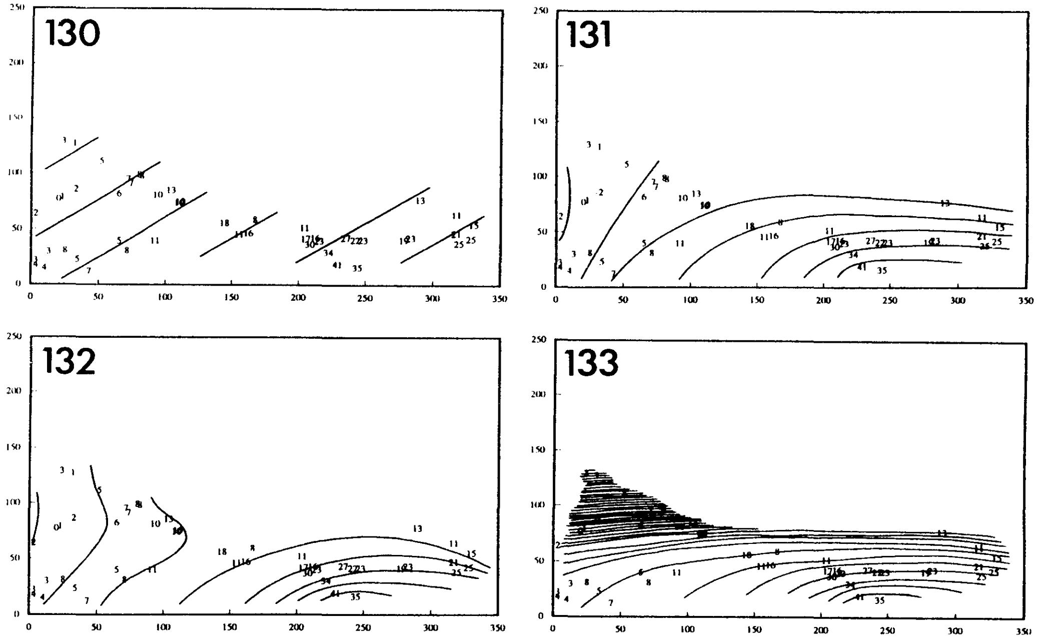


Figs 126-127. DCA ordination of 50 sample plots from virgin bog at Rønnåsmyra, Grue, SE Norway, axes 1 and 2. Vectors indicating the directions of steepest descent of the two explanatory variables, DEPT (depth to the water table, in the direction of higher depth) and P PR (assumed peat-producing ability, in the direction of lower productivity), are shown. Scaling of axes in S.D. units *100. Fig. 126. Numbers of sample plots indicated. Fig. 127. Names of species (abbreviated, cf. Tab. 1) indicated. Only the more frequent species shown.





Figs 128-129. DCA ordination of 50 sample plots from virgin bog at Rønnåsmyra, Grue, SE Norway, axes 1 and 2. Frequency in subplots shown onto the sample plot positions. Scaling of axes in S.D. units *100. Fig. 128. *Rhynchospora alba*. Fig. 129. *Sphagnum fuscum*.



Figs 130-133. DCA ordination of 50 sample plots from virgin bog at Rønnåsmyra, Grue, SE Norway, axes 1 and 2. Depth to the water table indicated on the sample positions, as well as isolines of trend surfaces, contour interval 5 cm. Scaling of axes in S.D. units *100. Fig. 130. Trend surface of order 1. Multiple correlation coefficient r = 0.8172. Fig. 131. Trend surface of order 2. r = 0.9309. Fig. 132. Trend surface of order 3. r = 0.9544. Fig. 133. Trend surface of order 4. r = 0.9590.

more independent of the interpreter, should be favoured.

(2) *Plotting species abundances on the sample ordination.* As an informal approach to interpretation, species abundances may be plotted onto the sample plot positions in the ordination (Figs 128-129). The use of symbols of increasing size to indicate increasing abundance (T. Økland 1988: Figs 12-14) can be illustrative. Any biotic variable that may aid interpretation, for instance the number of species per sample plot (T. Økland 1988: Fig. 4), and importance of different taxocenes (taxonomic groups) or phytogeographical groups (R. Økland 1989b), may be plotted.

(3) *Plotting values for explanatory variables on the sample ordination.* Figs 115-116 show two explanatory variables plotted onto the sample plot positions in the DCA ordination of the Rønnåsmyra data. Similar plots are shown by T. Økland (1988: Figs 16-18). Visual inspection of trends in the plotted variables will give indications of the nature of the underlying complex-gradients.

(4) *Trend surface analysis* (e.g., Burrough 1987). One step away from visual interpretation is the fitting of **trend surfaces** to the environmental variables. A trend surface is a three-dimensional surface (like the contours of a map), which is fitted to environmental variables plotted on the ordination.

Trend surface analysis is a regression problem. If the environmental variable has been transformed to an approximate normal distribution (cf. p. 105), the fitting of a surface to the "landscape" which "altitudes" over the plane of the ordination diagram are defined by the values of the environmental variable, can be done by polynomial regression, using the least-squares principle. The order p of the polynomial is called **the order of the trend surface**. For two ordination axes, the regression model is

$$z = \mathrm{SUM}_{r+s \leq p}\, a_{rs} x_1^r x_2^s + \varepsilon, \qquad (79)$$

where z is the environmental variable, p is the order of the polynomial, x_1 is sample plot position along the first ordination axis and x_2 position along the second axis, and the a's are coefficients to be estimated. The error, ε, is assumed to be normally distributed with zero mean. We will not go into the problem of estimating the coefficients (this is shown for p = 1 in the one-variable case on pp. 117-118). The number of coefficients in the equation is

$$(p + 1)(p + 2)/2,$$

the constant included. The number of coefficients to be estimated are 1 for p = 1, 3 for p = 2, 6 for p = 3, and 15 for p = 4. The systematic parts of the regression models ($p \leq 4$) are:

$$z = a_2x_1 + a_1x_2 + a_0 \quad (p = 1) \qquad (80)$$

$$z = a_5x_1^2 + a_4x_1x_2 + a_3x_2^2 + a_2x_1 + a_1x_2 + a_0 \quad (p = 2) \qquad (81)$$

$$z = a_9x_1^3 + a_8x_1^2x_2 + a_7x_1x_2^2 + a_6x_2^3 + a_5x_1^2 + a_4x_1x_2 + a_3x_2^2 + a_2x_1 + a_1x_2 + a_0 \quad (p = 3) \qquad (82)$$

$$z = a_{14}x_1^4 + a_{13}x_1^3x_2 + a_{12}x_1^2x_2^2 + a_{11}x_1x_2^3 + a_{10}x_2^4 + a_9x_1^3 + a_8x_1^2x_2 + a_7x_1x_2^2 + a_6x_2^3 + a_5x_1^2 + a_4x_1x_2 +$$
$$a_3x_2^2 + a_2x_1 + a_1x_2 + a_0 \quad (p = 4) \qquad (83)$$

There are several problems associated with using polynomial regression for trend surface analysis (cf. Ripley 1981, Burrough 1987). The number of sample plots has to be much higher than the number of parameters in the polynomial, otherwise the surface will be an exact fit. Trend surfaces are strongly vulnerable to edge effects; this particularly applies to high-order surfaces. The goodness-of-fit of the surface is measured by a least sum-of-squares criterion. The correlation coefficient, r, between the observed and the fitted values, gives indications of this goodness of fit, but may be an inappropriate measure of fit if the number of points is low. Statistical tests of the goodness of fit of a trend surface are discussed by Burrough 1987 (also see Sokal & Rohlf 1981, ter Braak 1987b).

Examples of trend surface analysis applied to the DCA ordination of the 50 sample plots from Rønnåsmyra, are given in Figs 130-133.

(5) *Other approaches to response surface smoothening*. Rather than using polynomial regression, a surface can be fitted to the plot of explanatory variables onto the sample ordination by **moving weighted averages** and a suite of other statistical techniques based on spatial pattern analysis (e.g., Burrough 1987). The principle is to calculate new values for the explanatory variable at each point (x_1, x_2) in the two-dimensional ordination diagram. This can be done by averaging the values for the variable for the points most close to (x_1, x_2) and replace the original value by the average value in the diagram. The smoothened values are corrected for noise to a great degree, and make overall trends more clearly visible in the diagram. The general formula for weighted moving averages smoothening is

$$z^{\wedge}(x_0) = [\mathrm{SUM}_{j=1,\ldots,s}\, w_j z(x_j)]/(\mathrm{SUM}_{j=1,\ldots,s}\, w_j) \qquad (84)$$

where x_j is a point in the two-diomensional ordination diagram, x_0 is the point for which the explanatory variable is to be estimated,$z(x_j)$ is the value of the explanatory variable at point x_j, and w_j is the weight attributed to point j. The weights may be chosen in several different ways; as a function of distance between x_j and x_0, constant weights applied to the s points most close to x_0, etc.

T. Økland (1988: Figs 16-18) applied weighted moving averages smoothening of three environmental variables in an ordination diagram and subsequent hand-fitting of isolines as an aid to interpretation.

(6) *Calculation of correlation coefficients between sample scores and explanatory variables* is a simple means of approaching the question of statistically reliable relationships between the explanatory variables and sample scores. The higher the correlation, the higher is the probability that the variable is part of a complex-gradient underlying the axis. Calculation of correlation coefficients between sample scores and axes is a standard initial

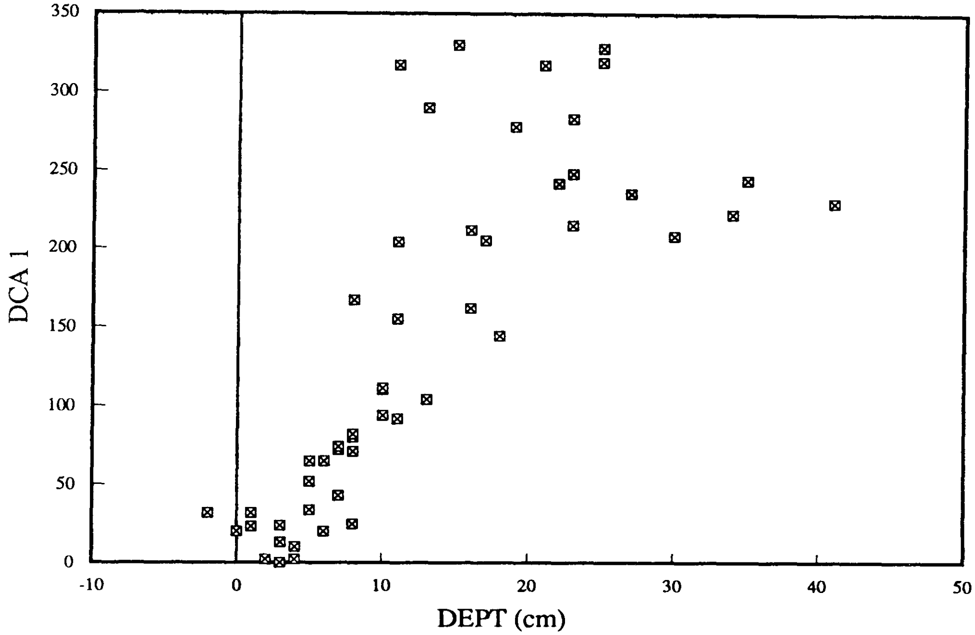


Fig. 134. DCA ordination of 50 sample plots from virgin bog at Rønnåsmyra, Grue, SE Norway. Sample scores relative to axis 1 as a function of depth to the water table. Scaling of axes in S.D. units *100.

step in interpretation of axes, and frequently used, for instance, by T. Økland (1988: Tab. 10). In the Rønnåsmyra example, the product-moment correlation coefficient between depth to the water table and axis 1 sample score is r = 0.7964, with axis 2 r = -0.3723. If the distribution of the explanatory variable is unknown, or assumed to deviate strongly from normal, distribution-free or nonparametric, rank correlation coefficients, should be used.

(7) *Multiple regression analysis between sample scores and a set of explanatory variables.* Several variants of multiple regression analysis (see for instance Hull & Nie 1981, Nie et al. 1975) may be used for ranking of explanatory variables according to their ability to explain the variation in sample scores along an ordination axis. In the regression model, sample scores are taken as the dependent variable, all explanatory variables as independent variables. An example using stepwise deletion multiple regression is presented by T. Økland (1988: Tab. 11).

(8) *Constructing a sample plot-explanatory variable biplot.* So far, the interpretative aids have been directed at interpretation of one axis in turn. The axes do, however, not necessarily have specific ecological significance; all directions in the ordination diagrams can, in principle, be interpreted as representing variation along underlying complex-gradients. A helpful interpretative device is to indicate explanatory variables in the ordination diagram as arrows pointing in the direction of strongest change in the variable (Dargie 1984, Bowman & Minchin 1987, ter Braak 1987c). This **vector fitting** is a regression problem, solved by two-variable least-squares regression of the explanatory variable z_j on the sample scores x_{1j} and x_{2j} relative to the two first ordination axes; i.e. by estimating the coefficients a_2, a_1, and a_0 in the equation

$$Ez = a_1x_1 + a_2x_2 + a_0. \qquad (85)$$

When the centroid of the ordination diagram is at the origin, $a_0 = 0$, the environmental variable should be indicated as an arrow from the origin to (a_1, a_2). The multiple correlation coefficient r indicates the maximum correlation between z and x_1 and x_2. When the centroid is not at the origin, but at the point (c_1, c_2), as in

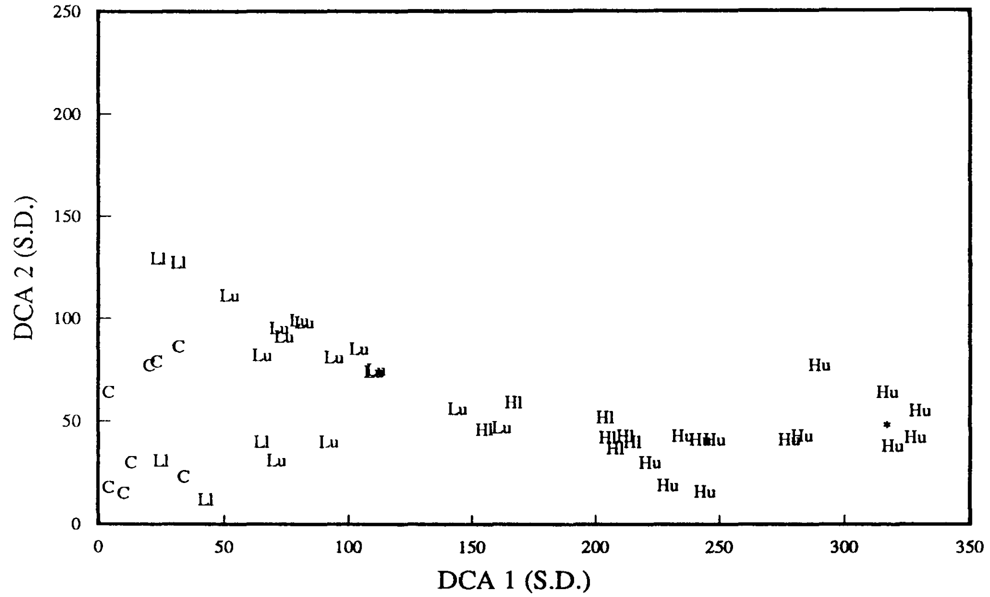


Fig. 135. DCA ordination of 50 sample plots from virgin bog at Rønnåsmyra, Grue, SE Norway, axes 1 and 2. A classification of vegetation into series reflecting differences attributable to the depth to the water table gradient is plotted onto the sample positions: C - carpet, Ll - lower lawn, Lu - upper lawn, Hl - lower hummock, Hu - upper hummock. Scaling of axes in S.D. units *100.

DCA, the regression may be carried out on centered sample scores (which is equal to moving the centroid to the origin):

$$Ez = a_1(x_1 - c_1) + a_2(x_2 - c_2). \qquad (86)$$

The arrows representing the explanatory variables are plotted in the sample ordination as vectors from the centroid (c_1, c_2) to (a_1, a_2). The program package CANOCO provides options for fitting explanatory variable vectors to PCA, CA, and DCA ordination diagrams (cf. ter Braak 1987d). Fitting of vectors in MDS ordination space by use of DECODA (Minchin 1986) is also possible (Bowman & Minchin 1987, Kantvilas & Minchin 1989).

Examples explanatory variables vectors plotted onto a DCA ordination diagram are shown for the ordination of 50 sample plots from Rønnåsmyra in Figs 126-127.

(9) *Plotting a classification on the sample plot ordination.* If a classification of the sample plots is available, it can be used as an informal aid to interpretation of ordination diagrams. T. Økland (1988: Fig. 11) performed a classification of soil types and topographic conditions in the Fritzøehusparken beech forest into four main types (and several transitional types). The types were plotted onto the sample plot ordination, clearly showing that major trends in the ordination could be explained by the environmental conditions used for classification. A similar approach was used by R. Økland, who performed a classification of the vegetation of the mire N Kisselbergmosen into 32 site-types by means of the direct gradient approach to classification (R. Økland 1989b, cf. p. 70). This classification was used for interpretation of ordinations by R. Økland (1990a). A similar approach applied to the vegetation of the virgin part of Rønnåsmyra implies a classification into 5 series, each

characterized by species indicating a specific interval along the gradient in depth to the water table (R. Økland 1989b): C - carpet, Ll - lower lawn, Lu - upper lawn, Hl - lower hummock, and Hu - upper hummock. The series codes are then plotted on the sample positions in the diagram of DCA axes 1 and 2 (Fig. 135).

In conclusion, the interpretation of ordination diagrams should be aided by use of all available external data. More interpretative devices can be added to the list above by reviewing recent ecological literature.

CONSTRAINED ORDINATION

Basic principles

The relationships between species abundance and single environmental variables are studied by means of regression analysis. Regression analysis can also be used to find the environmental variable that best explains the variation in species abundance in a data-set (cf. pp. 116-121). In ordination, the axes are the hypothetical environmental variables that optimize the fit of the species abundance data to an underlying statistical model. However, the interpretation of ordination results is not always easy, as no information about environmental variables is incorporated in the analysis. A question, somewhat "intermediate" between those posed in regression and ordination is the following: "Which (linear) combination of environmental variables explains the variation in species abundances best (relative to a given statistical model of species response to gradients)?" This question is answered by **constrained ordination** (ter Braak & Prentice 1988), also termed **canonical ordination** (ter Braak 1986, 1987a, 1987c, 1987d). Constrained ordination thus optimizes the fit of the species abundance data to supplied environmental data (ter Braak 1986, ter Braak & Prentice 1988).

Just as regression, calibration and ordination, constrained ordination can be combined with different statistical models of species-gradient relationships. Well-known methods for constrained ordination are the constrained counterpart of PCA, termed **redundancy analysis** (RDA; Rao 1964, ter Braak 1987c, ter Braak & Prentice 1988) and the constrained counterpart of CA **canonical correspondence analysis** (CCA; ter Braak 1986, 1987a, 1987c, 1987d). A detrended version of the latter is known as **detrended canonical correspondence analysis** (DCCA; ter Braak 1987a). The principles of constrained ordination do, however, not depend on the model, and can therefore be explained in general terms. No constrained variant of nonmetric multidimensional scaling is yet available, but the construction of such variants is theoretically possible (P. Minchin, pers. comm.).

The metric scaling ordination methods (PCA, CA, DCA) were introduced as iteration processes with alternate regressions and calibrations (cf. Tabs 11, 15). Upon convergence, the axis defined by sample and species scores maximized the fit of the species abundances to the underlying model, in one dimension. In constrained ordination, a constraint is put on this solution: instead of searching for the ordination axis as the best hypothetical variable, we are now interested in extracting the variation in abundances that can be explained by a set of environmental variables. This is a multiple regression problem. Given trial sample scores in Step 3 of the iteration process for PCA or CA (or DCA), cf. Tabs 11 and 15, $\{x_j\}$, we want these sample scores to satisfy the equation

$$Ex_j = SUM_{k=1,...,s} c_k z_{kj} \qquad (87)$$

where the c's are regression coefficients to be estimated (actually they are weights indicating the contribution of each environmental variable to the explanation of the dependent variable). All environmental variables z_k are centered and standardized to unit variance (cf. p. 105) in order to make the set of variables comparable and for technical reasons (ter Braak 1986, 1987a). Also for technical reasons (ter Braak 1986, 1987d), total abundance in sample plots is used as weights in CCA. Such a multiple regression step is included in the iteration procedure as a Step 3'. After some turns of the iteration cycle, the process converges, and the resulting sample scores define the first constrained ordination axis. The scores of samples and species relative to this **constrained axis** are interpreted much the same way as the unconstrained (ordination) axes. For instance, the (constrained) axes in CCA still consist of sample scores that are weighted averages of the species scores, and the sample scores are weighted average of species scores. The species scores represent the estimated optima along the constrained axes. The difference from ordination is that the axes are now linear combinations of environmental variables; thus only the fraction of variation in vegetation which can be attributed to variation in the supplied environmental variables is expressed (ter Braak 1987a, 1987c).

CCA: technical details and biplot interpretation

The technical details of constrained ordination are rather complex. We will explain the most important terms below, with particular reference to CCA. For details, the reader is referred to ter Braak (1986, 1987a, 1987c, 1987d).

The score of sample j along the constrained ordination axis h (which is a linear combination of the species scores), is denoted $\{x_{hj}\}$. The systematic part of the multiple regression defining the constraint upon sample scores is given in equation (87). When the regression coefficients (the c's in equation (87)) have been estimated, the fitted values of x, $\{x_{hj}^*\}$, i.e. **sample scores which are linear combinations of environmental variables** can be determined from the equation:

$$x_{hj*} = \mathrm{SUM}_{k=1,...,s}\, c_{hk}z_{kj}. \qquad (88)$$

The correlation coefficient between the sample scores $\{x_{hj}\}$ and the fitted values $\{x_{hj}^*\}$, the **species-environment correlation**, $r_{se,h}$, tells something about the goodness-of-fit of the abundance data to the underlying environmental variables. However, like other multiple correlation coefficients, it should be interpreted with care. When the number of environmental variables used to constrain the ordination, s, approaches the number of sample plots, n, the correlation will become better and better and eventually be perfect. In this case, the environmental variables will not constrain the axes at all, and the analysis reduces to ordinary ordination. Thus the species-environment correlation is only informative when s is much lower than n. Even in this case it may be problematic, as the relative importance of the axes may vary independently of r_{se}. A better measure of the relative importance of an axis is the eigenvalue.

The estimated coefficients of (87), the c's, are termed **canonical coefficients**. They are partial correlation coefficients; i.e. c_{hk} indicate the degree of vegetational change occurring per unit of change in the centered and standardized environmental variable k along axis h, given that all other variables are constant. They are dependent of the other variables in the analysis, and may therefore be misleading if we want information of the relationship between axes and variables as such.

Two other sets of correlation coefficients may also be calculated. The correlation between the sample scores $\{x_{hj}\}$ and environmental variable $\{z_{kj}\}$, the **inter-set correlation** between axis h and environmental variable k, r_{hk}^*, do not depend on the environmental variables (as the canonical coefficients do). The correlation between the fitted sample scores $\{x_{hj}^*\}$ and environmental variable $\{z_{kj}\}$ is the **intra-set correlation**, $r_{hk}^\wedge$. There is a simple relationship between the inter-set correlation, the intra-set correlation and the species-environment correlation with respect to axis h and environmental variable k:

$$r_{hk}^* = r_{se,h} * r_{hk}^\wedge. \qquad (89)$$

The principles for biplot interpretation in the cases of RDA and (D)CCA are discussed by ter Braak (1986, 1987a, 1987c, 1987d). In the case of CCA, species scores are estimates for species optima, and can be plotted as points a diagram with the constrained ordination axes as axes. Sample-species biplots require considerations of scaling (cf. p. 143 for CA). Sample- or species-environmental variables biplots may be constructed just as with CA or DCA (cf. pp. 149-150); environmental variables are indicated as vectors in the ordination diagram, originating from the centroid (coinciding with the true origin in CCA).

Theoretical and practical considerations

Constrained ordination has become available rather recently, and only few applications have yet been published. As the method includes environmental variables as well as species abundance data, evaluation is far more complicated than in the case of ordination. Realistic simulated data are exceedingly difficult to make, as the number of environmental variables, their combination into complex-gradients, and the strength of the relationship between these complex-gradients and the vegetation has to be specified in the model. No simulation studies have been made for evaluation of constrained ordination methods. The considerations presented below are therefore based on theoretical reasoning and the works of ter Braak (1986, 1987a, 1987c, 1987d) and ter Braak and Prentice (1988), supplied with results from practical applications (e.g., Cramer & Hytteborn 1987, R. Økland 1990a).

Constrained ordination (RDA and (D)CCA) with several variants and combinations of options are available in the program package CANOCO (ter Braak 1987d).

Choice of method. The choice between RDA and CCA is a choice between a linear and a unimodal model for species' responses to underlying complex-gradients. Recommendations will follow those for ordination methods; the linear method should be applied with care. For very short gradients, the matter may not be easily settled; for data with the longest coenoclines longer than 2.0-2.5 S.D., CCA is likely to be superior (cf. ter Braak 1987c). Further considerations therefore concerns (D)CCA.

Scaling of axes. Linear rescaling (as in CA) seems natural, as the addition of a rescaling step after the iteration process has converged, implies a destruction of the optimal dispersion of samples with respect to linear combinations of the environmental variables. However, the introduction of nonlinear rescaling provides an opportunity to obtain a reliable scaling in ß diversity units (cf. p. 35). Thus, the loss of optimality may be more than compensated for in situations where species turnover along gradients shall be considered (e.g., Cramer & Hytteborn 1987).

Detrending. Just as nonlinear rescaling, detrending will destroy the optimal dispersion of sample plots. In cases with few and not very highly correlated environmental variables, CCA does not have any arch problem (ter Braak 1987c), and no detrending is necessary. The danger of appearance of polynomial distortion axes increases as the number of environmental variables and their correlation increases. Such situations may be approached by detrending or by exclusion of environmental variables from the analysis (ter Braak 1987a).

Hybrid ordination/constrained ordination. The maximum number of constrained ordination axes possible to extract equals the number of environmental variables supplied. There is, of course, not necessary to extract more than a specified number, s_c, of constrained axes. After the desired number of constrained axes are extracted, a number, s_u, of unconstrained axes may be found by the ordinary iteration procedure, not including a constraining step. These unconstrained axes have been termed **partial ordination axes** (ter Braak 1987d). They represent the major directions of residual variation in the data-set, after the variation attributable to the environmental factors (s_c equals the number of environmental variables) has been extracted, or after a fraction of the variation attributable to the environmental factors has been extracted (s_c lower than the number of environmental variables). The opportunity to extract such "residual axes" is most useful, as it can give good indications whether the supplied environmental variables are important for explaining the variation in the data-set or not, and whether there are prominent coenoclines in the material that are caused by complex-gradients not included among the environmental data. According to ter Braak and Prentice (1988: 302), "terrestrial community data commonly give a residual eigenvalue as large as the first constrained eigenvalue, however carefully the environmental variables are chosen." Interpretation of the unconstrained residual axes must follow the same lines as the interpretation of ordination axes (cf. pp. 160-167).

Monte Carlo permutation test for significance of constrained axis. CANOCO includes an option for testing the significance of axis-environment relationships. Sample numbers are permuted randomly in the sample-environmental variable data matrix, and the eigenvalues of the first constrained ordination axis relative to the new, random environmental variables are obtained. The exact significance of a Monte Carlo permutation test, p, is given from the equation

$$p = (x + 1)/(n + 1) \quad (90)$$

where x is the number of random data-sets for which the eigenvalue of the first constrained axis is higher than the eigenvalue of the axis to be tested, and n is the number of permutations.

The recommendations for other options discussed unter treatment of DCA (cf. p. 155), such as passive samples, covariables, downweighting of rare species, etc. do not differ for (D)CCA, except that the problem of outliers is lower than for CA/DCA if the sample plots with deviating species composition are included in the normal variation of the environmental variables (cf. ter Braak 1987a).

An example

Constrained ordination has a considerable potential for practical purposes, as many of the technical details mentioned above can be successfully turned into advantages for applied use. Hopefully, this will be apparent from an example with canonical correspondence analysis applied to the full material from Rønnåsmyra (standard example; Tabs 1-2). The material consists of frequency in subplots data for 69 species in 95 sample plots; 44 of which are situated in the mire part that has been drained and where a reclamation experiment is now going on. Depth to the water table is measured in all plots. Several questions relevant to judgment of the success of the reclamation experiment can be approached by constrained ordination. Among them are: (1) How strongly have the drainage attempt influenced the vegetation? (2) Is this influence the same in all vegetation types? Furthermore, it is of interest to predict future development under different hypotheses: What direction(s) will future development take? Can vegetational short-term vegetational changes be used to predict

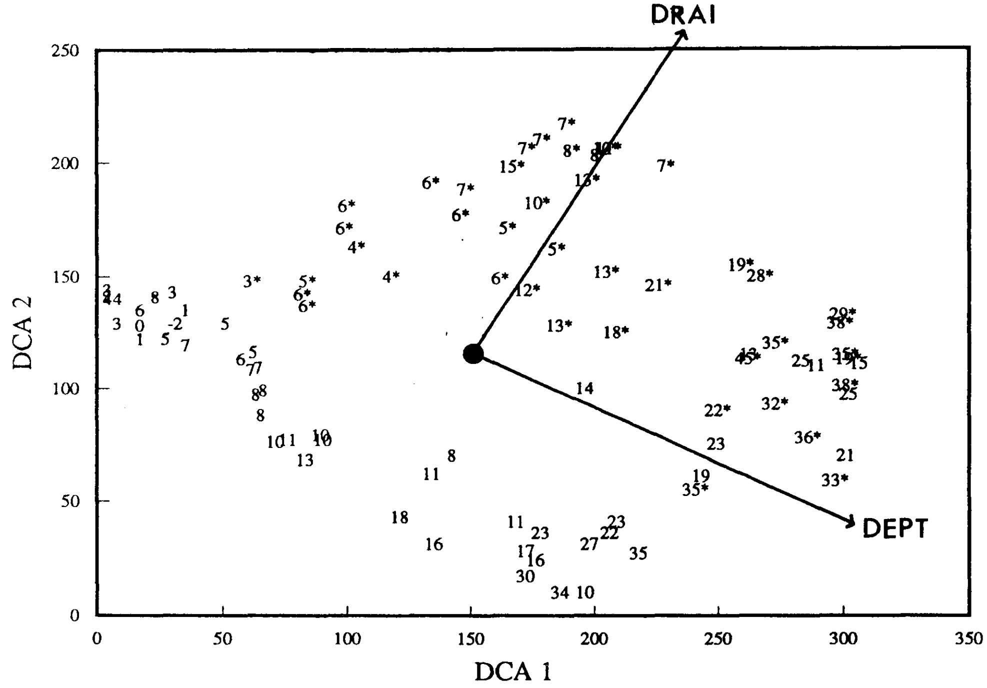


Fig. 136. First two axes of DCA ordination of 95 samples from Rønnåsmyra, Grue, SE Norway. Depth to the water table is plotted onto the sample positions. An asterisk indicates drained site. Arrows indicate directions of strongest change of environmental variables. DEPT - depth to the water table (cm). DRAI - drainage (0 - undrained, 1 - drained). Scaling of axes in S.D. units *100.

the success of the reclamation experiment?

As we have already seen, CCA may be run with or without nonlinear rescaling and with or without detrending. In our analysis, only two environmental variables were included; depth to the water table (in cm), and drainage status (0 - undrained, 1 - drained). With constrained ordination relative to these two variables, there is no danger of any arch effect as in CA, and no detrending is made. As one of our major concerns is about species turnover along the constrained gradients, CCA was used with nonlinear rescaling of axes. With only two constraining variables, only two constrained axes could be extracted. The remaining two axes given by CANOCO were unconstrained residual axes, and the analysis a rescaled hybrid CCA (rhCCA). A separate DCA run was carried out to compare the variation along the constrained ordination axes with the overall vegetational structure of the data. Rare species were downweighted by use of the downweighting option.

Data on the first two axes of the DCA ordination and the first three rhCCA axes (two constrained axes and the first residual, unconstrained axis) are given in Tab. 17. Fig. 136 shows axes 1 and 2 of the DCA ordination. Values for depth to the water table are plotted onto the sample positions to aid interpretation. Drained sample plots are indicated by an asterisk. The corresponding constrained ordination diagram is shown in Fig. 137. The very high overall similarity between the two diagrams is striking, showing that the two environmental variables account well for the vegetational variation. This is substantiated by the eigenvalues of corresponding axes (cf. Tab. 17); although not as high in rhCCA as in DCA, the CCA axes have relatively high eigenvalues. The first unconstrained axis in the hybrid CCA had only slightly higher eigenvalue than the second (constrained) axis (compare statement by ter Braak & Prentice 1988, above). The lengths of the first axes was almost equal in the two analyses. The (inter-set) correlations between axes and environmental

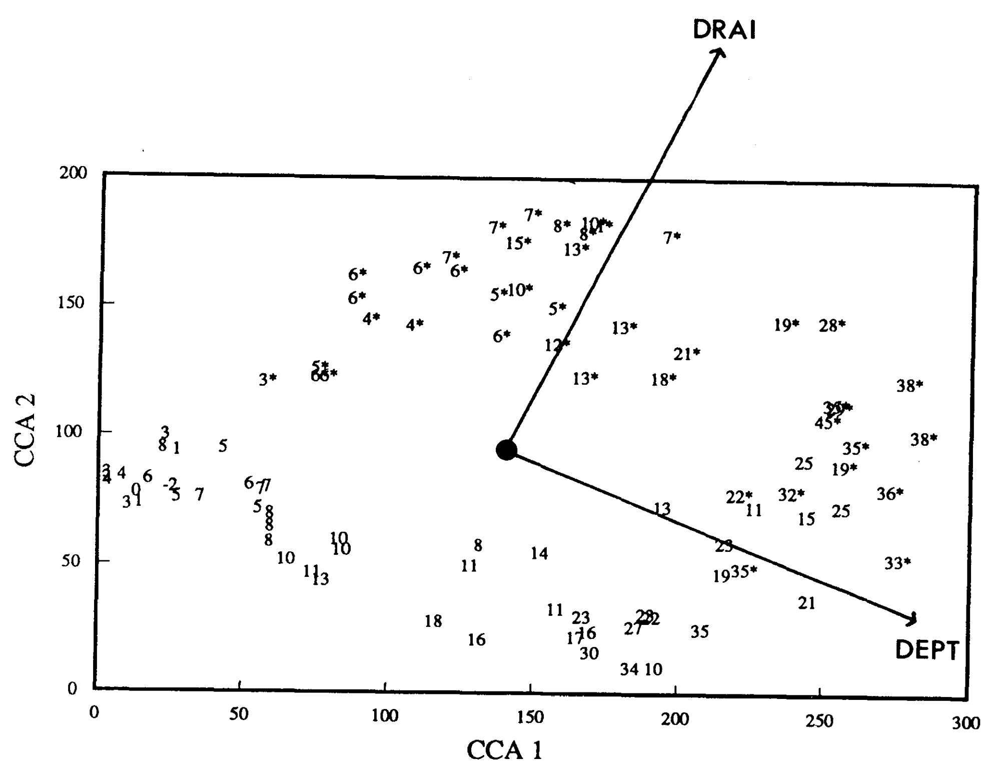


Fig. 137. First two (constrained) axes of rescaled CCA analysis of 95 samples from Rønnåsmyra, Grue, SE Norway. Depth to the water table is plotted onto the sample positions. An asterisk indicates drained site. Arrows indicate directions of strongest change of environmental variables. DEPT - depth to the water table (cm). DRAI - drainage (0 - undrained, 1 - drained). Scaling of axes in S.D. units *100.

variables were also roughly similar, although there was a tendency to a stronger concentration of variation with respect to depth to the water table along CCA 1, while a corresponding tendency for drainage was observed along CCA 2 (Tab. 17). The species-environment correlation was slightly higher in the constrained ordination. We can conclude with confidence that depth to the water table is the most important single factor for determining vegetational composition, and that drainage is also important, although less important than depth to the water table. Several important points should be noted: The (product-moment) correlation coefficient between depth to the water table and drainage is only 0.1136 (not significant). As both the undrained and drained mire parts were sampled by use of transects from hummock to hollow, this indicates that the original water-table of the drained mire part has been successfully restored by plugging the ditches. Two possible effects of draining still visible six years after plugging the ditches can be conceived: (1) The drainage led to a new, lower water table. The vegetation rapidly adjusted to this new level by invasion of more drought-tolerant species and exclusion of species with optima in wet habitats. (2) The drainage not only caused the water table to sink, but imposed irreversible structural changes to the peat, followed by a specific drainage-dependent contribution to the vegetation. In both cases, but more so as a consequence of (1), drainage should be correlated with depth to the water table in the ordination and contrained ordination diagrams. This is only the case to some degree (Figs 136-137, Tab. 17). The correlations of drainage and depth to the water table with the first constrained axis both indicate some adjustment of the vegetation to drier conditions. However, the long second axis of the constrained ordination indicates a strong, specific contribution of drainage to the vegetation. The displacement of CCA 1 scores for drained sample plots relative to undrained ones in a

Tab. 17. The DCA and rescaled hybrid CCA (rhCCA) analyses (2 constrained axes) of 95 sample plots from Rønnåsmyra, Grue, Hedmark: eigenvalues, length of axes in S.D. units, secies-environment correlation, inter-set correlations (correlations between standardized environmental variables and sample scores (that are linear combinations of species scores), and canonical correlations (for the constrained ordination axes only; is the coefficients of the regression of sample scores on the environmental variables). DEPT - depth to the water table (cm), DRAI - drainage (0 - undrained, 1 - drained and reclaimed).

		DCA		rhCCA		
		DCA 1	DCA 2	CCA 1	CCA 2	CCA 3*
Eigenvalue		0.465	0.249	0.320	0.198	0.226
Length of axis (S.D. units)		3.06	2.17	3.17	1.55	2.38
Species-environment corr.		0.80	0.85	0.85	0.90	
Inter-set correlations	DEPT	0.734	- 0.468	0.792	- 0.315	
	DRAI	0.403	0.651	0.385	0.801	
Canonical coefficients	DEPT			0.586	- 0.212	
	DRAI			0.231	0.437	

* unconstrained axis

diagram of CCA 1 score as a function of depth to the water table (Fig. 138) demonstrates that the composition of vegetation (sample score along CCA 1) in drained sample plots is generally indicating drier conditions (higher sample scores) than samples from virgin bog. This indicates that drainage led to a drying-up of the vegetation as an adjustment to lower water tables, *and* that drainage had a specific impact on the vegetation that cannot be explained by adjustment to lower water tables alone. The displacement shown in Fig. 138 indicates that the vegetation of the reclaimed mire part had not yet (1988) adjusted to the restored (high) water table.

Tab. 18. Means and standard deviations of the two environmental variables used for the rescaled hybrid CCA (rhCCA) analyses (2 constrained axes) of 95 sample plots from Rønnåsmyra, Grue, Hedmark. DEPT - depth to the water table (cm), DRAI - drainage (0 - undrained, 1 - drained and reclaimed).

	mean	S.D.
DEPT	13.87	10.19
DRAI	0.44	0.50

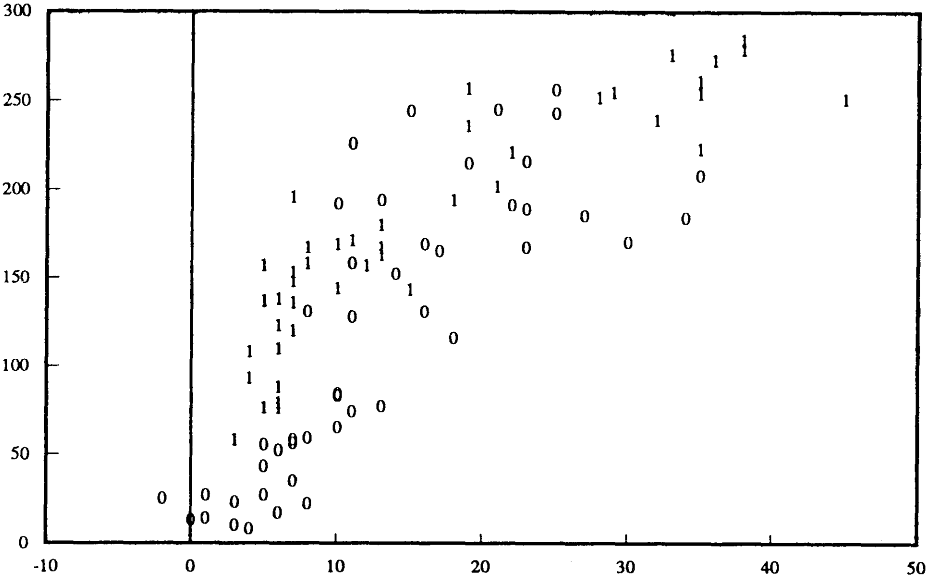


Fig. 138. Rescaled CCA analysis of 95 sample plots from Rønnåsmyra, Grue, SE Norway: position along the first constrained ordination axis (CCA 1), scaled in S.D. units *100, as function of depth to the water table (cm). 0 - undrained sample plot, 1 - drained.

We may now approach the questions asked initially. A visual inspection of Fig. 137 gives indications of the answers to questions (1) and (2). The relatively high eigenvalue of the second constrained axis (most strongly correlated with drainage), significant at $p < 0.01$ (Monte Carlo permutation test), and the considerable length of this axis, 1.55 S.D, indicate that drainage has influenced the vegetation considerably. The variation in CCA 2 score as a function of CCA 1 adds details to this picture: At low CCA 1 score (< 0.5 S.D.), only undrained samples occur. The first drained samples encountered from left to right in the diagram, are not considerably displaced along CCA 2 relative to the adjacent undrained samples. This is an indication that the vegetation of the wettest parts of the mire has not received much of the specific drainage effect, but that the vegetation has adjusted to drier conditions. The strongest drainage effect is encountered at intermediate positions along the depth to the water table gradient (1-2 S.D.), while the displacement along CCA 1 as well as the separation along CCA 2 is reduced again in the high hummocks. We can then conclude that drainage has had different effects in different parts along the hummock-hollow gradient.

The constrained ordination gives an opportunity to estimate the *magnitude* of the drainage effect and the lag of the drained vegetation relative to the present water table. The canonical axes are constrained to be linear combinations of the environmental variables. If we denote the standardized variables z_1^* (depth to the water table) and z_2^* (drainage) and the scores relative to the two constrained ordination axes x_{1j} and x_{2j}, then we obtain from (86):

$$x_{1j} = 0.586 * z_{1j}^* + 0.231 * z_{2j}^* + 1.40$$
$$x_{2j} = - 0.212 * z_{1j}^* + 0.437 x_{2j}^* + 0.93.$$

Introducing the unstandardized variables z_{1j} and z_{2j} using data from Tab. 18, we get

$$x_{1j} = 0.586(z_{1j} - 13.87)/10.19 + 0.231(z_{2j} - 0.44)/0.50$$
$$x_{2j} = - 0.212(z_{1j} - 13.87)/10.19 + 0.437(z_{2j} - 0.44)/0.50,$$

$$x_{1j} = 0.058 z_{1j} + 0.462 z_{2j} + 0.40 \quad (91)$$

$$x_{2j} = - 0.0212z_{1j} + 0.874z_{2j} + 0.83 \qquad (92)$$

The first CCA axis reflects the main direction of variation in vegetation, attributable to the two variables. The effect of drainage on vegetation (change from $z_2 = 0$ to $z_2 = 1$), given constant depth to the water table, can be estimated from (90) setting $z_{1j} = c$:

$$x_0 = 0.058*c + 0.462*0 + 0.40$$
$$x_1 = 0.058*c + 0.462*1 + 0.40$$

from which we obtain

$$x_1 - x_0 = 0.462 \text{ S.D. units.}$$

Similarly, the change in vegetation as response to a 1 cm change in depth to the water table can be estimated to be 0.058 S.D. units. The drainage effect thus corresponds to a change in the depth to the water table of 0.462 S.D./(0.058 S.D./cm) = 7.97 cm. Assuming that the water table has been restored, the vegetation lags behind by ca. 8 cm in 1988. This should be reduced to zero over time for the reclamation to have been totally successful.

The specific drainage effect can be estimated from (90) and (91): It is 0.874 S.D. along CCA 2, and 0.462 S.D.along CCA 1. The overall length of the drainage vector, i.e. the total effect of drainage, is

$$d = (0.462^2 + 0.874^2)^{0.5} = 0.989 \text{ S.D.}$$

Successful reclamation is dependent on a gradual disappearance of the specific drainage effect (the contribution of drainage to CCA 2). If this will not be the case, it is likely that irreversible changes of the peat has occurred. These matters can be settled by reanalysis and inspection of changes of the constrained ordination. A time axis can be included as a separate variable.

Assessment: the role of constrained ordination in gradient analysis

The development of constrained ordination, particularly constrained variants of correspondence analysis, has added a new, potentially powerful tool to the ecologist's toolkit. Constrained ordination provides an opportunity to test the significance of vegetational variation attributable to specified environmental variables. Furthermore, the joint effects of environmental varables on vegetation may be sorted out. The opportunities for removing effects of specified variables (covariables) and the inclusion of passive samples (and species) in the analysis, makes CCA useful for many applied purposes, such as testing the effects of particular management regimes (ter Braak 1987d, example in this book), and successional processes (Cramer & Hytteborn 1987).

The relationship between constrained ordination and ordination deserves some more consideration. Ter Braak and Prentice (1988: 308) conclude as follows: "Often, community-environment relationships have been explored by "indirect gradient analysis" - ordination, followed by interpretation of the axes in terms of environmental variables. But if the environmental data are to hand, constrained ordination ("multivariate direct gradient analysis") provides a more powerful means to the same end." To this I cannot subscribe. Rather than emphasizing the superiority of constrained ordination, one should regard the two strategies as complementary (Cramer & Hytteborn 1987, ter Braak 1987c, R. Økland 1990a). Ordination is necessary to reveal the major coenoclines in the data-set. Constrained ordination will overlook variation associated with environmental factors not measured, and hence preclude unknown gradients from being identified. An example of a case where such an "unexpected" coenocline could be hypothesized by ordination, is provided by Kantvilas and Minchin (1989), who also warned about this limitation of constrained ordination. Thus constrained ordination should not be used for explaratory gradient analysis without simultaneous (unconstrained) ordination. The hybrid option, enabling extraction of unconstrained axes of residual variation, is potentially useful for detecting such poorly known coenoclines and for rating the importance of the extracted axes (cf. Machena 1987, R. Økland 1990a). Constrained ordination also has a potential for studying variation relative to gradients of low, but significant impact on the vegetation. The potentials of constrained ordination will be fully demonstrated by applications within few years.

CONCLUSIONS AND PERSPECTIVES FOR THE FUTURE

The span of techniques presently available for gradient analysis; the study of vegetation-gradient relationships, is wide. Four basic categories of gradient analysis have been presented; regression, calibration, ordination and constrained ordination. The former two are concerned with single species or single environmental variables, and are useful for application to specific hypotheses about species responses to environmental gradients and the inference of environmental conditions from species abundances. The latter two concern the whole vegetation and the environmental factors; in turn or simultaneously. Ordination differs from the other strategies by dealing with relationships in the species-sample plot data-set alone, thereby being an indirect gradient analysis strategy. The others all use environmental data for the analysis (in calibration more indirect; as the species-environment relationships are assumed to be known). The choice of strategy must depent on the purpose of the investigation.

This chapter has considered gradient analysis without reference to the spatial aspects of vegetation, thus disregarding the position of samples and the variation in environmental factors across the landscape. The study of **spatial processes** is a separate field of gradient analysis that may be important for several kinds of applications. Interested readers are referred to works by Greig-Smith (1979), Gibson and Greig-Smith (1986), Burrough (1987), Galiano et al. (1987), Dale and MacIsaac (1989), and Legendre and Fortin (1989).

The ecologist's tools for gradient analysis have been gradually improved during the last 20 years. Gradually, improved knowledge of the relative merits of different strategies, techniques, variants and options has emerged. Presently, our understanding of the pros and cons of the immense number of combinations of techniques for gradient analysis is, apart from some uncertainties, sufficient to make choices motivated by sound biological reasoning. A considerable rationalization among available techniques is possible, reducing the number of recommendable approaches to few.

Improvements in the field of regression analysis are likely to include the application of more sophisticated statistical models to species abundance data, in order to obtain more detailed knowledge of species-environment relationships and species response curves. The Generalized Linear Model offers interesting perspectives (cf. Austin et al. 1984, Austin 1985). In turn, better insights into species-environment relationships can improve vegetation models and hence, improve the basis for evaluation of ordination techniques. Improvements in ordination methodology are most likely to occur by improvements of nonmetric multidimensional scaling techniques, as the metric scaling approach seems to have inherent limitations that can hardly be overcome. A realistic statistical model for ordination is likely to be too complex to be used in alternate regressions and calibrations, as is even the case with the quite simple (but hardly appropriate) Gaussian model. It is likely that the most robust metric scaling ordination and constrained ordination techniques will be those based on weighted averaging, with empirical, a posteriori, corrections of faults. The detrending procedures hitherto proposed for DCA can probably be improved. Programs for nonmetric multidimensional scaling so far available lack the high number of options and accessories that make CANOCO so valuable to the user. Improvements in ordination methodology are likely to come from improvements to the NMDS concept and by the availability of flexible microcomputer programs. Suggested improvements include refined ordination methods (e.g., based on the hybrid multidimensional scaling principle; Faith et al. 1987), improved scaling of axes in ß diversity units (cf. p. 00), options for inclusion of covariables, passive samples and species, and constrained variants.

METHODS: NUMERICAL CLASSIFICATION

INTRODUCTION

Acceptance of the idea of vegetation as a multidimensional continuum has important implications for the classificatory approach (cf. p. 60): All approaches involving classification are artificial in the sense that no classification reflects natural properties of vegetation, and there is no theoretical justification for the hierarchy of vegetation types. On this background, the use of a classificatory approach must be motivated by practical purposes (description of vegetation, or, perhaps, as an aid to interpretation of ordination diagrams). Although the favourability of combining ordination and classification has often been emphasized (e.g., Gauch 1982a, Kent & Ballard 1988), gradient analysis has the advantage of addressing the relationships between vegetation (or directly, the species) and the underlying complex-gradients (through measured environmental variables). In this sense, gradient analysis is the all-important fundament of vegetation ecological analysis, while classification can be used in addition when motivated by practical or other specified purposes. Only a brief survey of major classificatory strategies will be given here. The interested reader is referred to more exhaustive texts, e.g., Sneath & Sokal (1973), Gordon (1981), Dunn & Everitt (1982) and Gauch (1982a).

The availability of computers to the ecologist rapidly raised the quest for objectivization of the classificatory process that had for a long time been the subjective fundament of vegetation ecology. **Numerical classification** techniques were deviced for this purpose. After attracting considerable interest in the 1960s and 1970s, leading to a proliferation of techniques, there has been a considerable rationalization among methods in the 1980s, combined with decreasing interest in the field as a whole. Several strategies are possible for the purpose of classification; the reduction of a data-set from n objects to n* clusters (cf. Cormack 1971). We will first consider critieria for judging goodness of classifictions, then consider main types of classification methods, and finally give some examples of much used methods.

OPTIMALITY CRITERIA AND EVALUATION OF NUMERICAL CLASSIFICATION METHODS

Optimality criteria

Evaluation of classification methods is in many respects more complicated than evaluation of ordination methods. Simulated data-sets may be used (e.g., Gauch & Whittaker 1981), but the heuristic nature of classification methods (van Tongeren 1987) in a continuous vegetation, makes tests of optimality hard to design. Some simple optimality criteria can, however, be designed. Apart from general demands of efficiency, relevance etc. (Gauch 1982a), a favourable classification method should satisfy the following criteria:

(1) The clusters should be as homogeneous as possible (for instance, judged by the average dissimilarity between members of the same cluster; Popma et al. 1983).

(2) The clusters should be as well separated as possible (for instance, judged by the

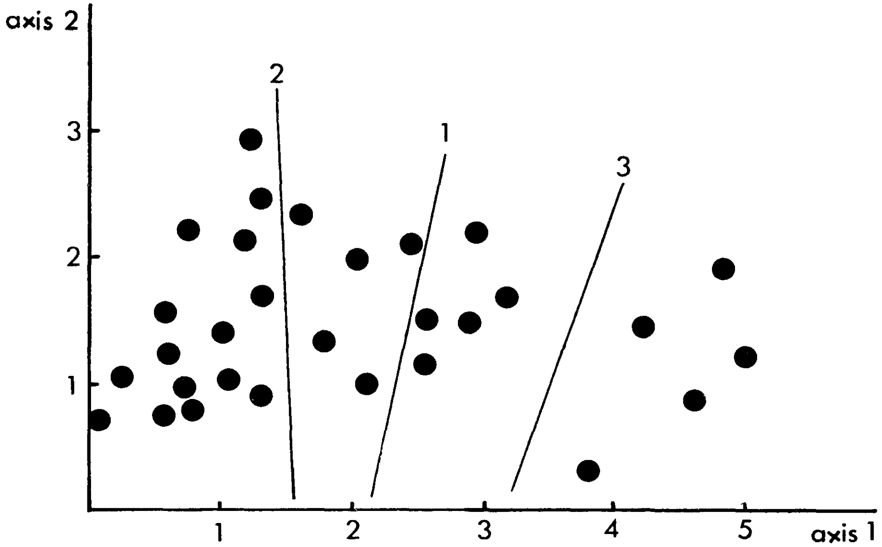


Fig. 139. The three criteria for division of a continuous sample set into two clusters, applied to division of a hypothetical ordination space. 1 - division into equal volumes (spread of ordination scores more or less equal in both clusters). 2 - division into equal numbers. 3 - division in sparse regions.

average dissimilarity between members of neighbouring clusters; Popma et al. 1983).

These criteria imply that groups in a naturally clustered data-set should be identified by the method. In case no such groups are present, all divisions are arbitrary. Divisions may then be done in three different ways, all desirable (cf. Fig. 139), cf. Gauch & Whittaker (1981), Gauch (1982a): (1) A division into *equal volumes* (a division at right angles to the long axis of a point swarm (e.g., in an ordination space), to optimize a measure of cluster compactness). (2) A division into *equal numbers* of samples. (3) A division *through sparse regions* (relative discontinuities).

Intuitively, (2) is unimportant, reflecting properties of the sampling strategy rather than propeties of the vegetation itself; (3) is most important (cf. above; and Williams & Dale 1965, Cormack 1971), while some weight may be attributed to (2) (Williams & Dale 1965, Orlóci 1978, Gauch & Whittaker 1981).

Evaluation of numerical classification methods

Evaluation of classification methods can be done by (1) observations on real data, (2) tests on simulated data, and (3) theoretical reasoning (Gauch & Whittaker 1981, Gauch 1982a, Podani 1989).

Several indices for assessment of the optimality (and comparison) of classifications relative to the demands for cluster homogeneity and separation have been proposed (e.g., Sneath & Sokal 1973, Farris 1973, Gauch & Whittaker 1981, Podani 1989). A few examples of such indices will be given.

Comparison of dendrograms, or between a dendrogram and a secondary matrix of dissimilarities. Hierarchical relationships between clusters are visualized in **dendrograms** (e.g., Figs 140-142). The relationship (similarity or dissimilarity) between two clusters in a dendrogram can be defined as the level of the dendrogram where the two clusters join. The correlation coefficient between similarities of sample plots in the dendrogram and in the secondary matrix has been proposed as a measure of clustering efficiency under the name **cophenetic correlation coefficient** (Sokal & Rohlf 1962). This measure can also be used for pair-wise comparison of dendrograms. This, as well as other indices expressing dendrogrammatic similarity in one single value are burdened with several problems (Farris 1973, Gauch & Whittaker 1981).

Comparison of groups in two or more classifications. The "overall similarity" between two classifications (j and k) of a data-set into n groups can be judged by the proportion of mutual matches (cf. Gauch 1980);

$$\mathrm{PMM}\ (j,k) = 2{*}a_{jk}/(a_j + a_k), \tag{93}$$

where a_{jk} is the number of sample pairs classified to the same cluster in both classifications, a_j and a_k the number of pairs classified to the same cluster in each of the classifications. PMM varies on a 0-1 scale.

Optimality tests. Ordination diagrams can be used to test the homogeneity and separation of clusters by analysis of variance.

The problems involved in formal testing of the efficiency of a classification (see, however, the attempts by Gauch & Whittaker 1981) have given preference to theoretical reasoning and results in practical application as basis for evaluation (cf. van Tongeren 1987).

CLASSIFICATION STRATEGIES

Definitions

Classification techniques can be classified according to clustering strategy. Three main strategies may be discerned (Lance & Williams 1967, Sneath & Sokal 1973, Orlóci 1978, Goodall 1978b, Gauch & Whittaker 1981, Gauch 1982a):

(1) ***Hierarchical** or **non-hierarchical**.* All classificatory techniques group objects into clusters. Hierachical techniques in addition arranges the clusters in a hierarchy.

(2) ***Divisive or agglomerative**.* Divisive methods start with the whole sample set, dividing it into successively smaller clusters. Agglomerative methods start with the individual sample plots, uniting them into successively larger clusters. The end of the process is one cluster containing all samples.

(3) ***Monothetic or polythetic**.* Monothetic methods use one criterion to perform each division (e.g., the occurrence or non-occurrence of a single species); polythetic methods use several properties, most often the whole species composition of the data-set.

Furthermore, **dual** methods classify samples and species at the same time, **single** methods do not. Several classifications produce **overlapping clusters**, most do not.

Evaluation

Hierarchical or non-hierarchical

Four points deserve to be mentioned:

(1) Hierarchical techniques show the relationships between groups, non-hierarchical do not (Gauch & Whittaker 1981, Gauch 1982a).

(2) Non-hierarchical methods cluster similar samples together without being constrained by hierarchical relationships; it is therefore likely to produce a more near-optimal classification (with respect to cluster compactness and separation), given a fixed number of clusters (Cormack 1971, Sneath & Sokal 1973, Gauch 1980, 1982a, van

Tongeren 1987).

(3) Establishment of a hierarchy involves numerous compromises. Non-hierarchical methods are consequently more appropriate at the level of raw data, summarizing relationships and reducing noise in the species abundance data (Gauch 1982a). When the number of objects has been reduced, for instance by initial non-hierarchical clustering, relations can be shown by hierarchical classification.

(4) Hierarchies give a unidimensional representation of objects by placing them side by side along the baseline of the dendrogram. A hierarchical representation of sample plots representing an ecological space with more than one complex-gradient will inevitably lead to loss of information and distortion of real relationships (Tuomikoski 1942, Whittaker 1962, Gauch & Whittaker 1981, R. Økland & Bendiksen 1985). The performance of non-hierarchical methods does not depend on the dimensionality of the data matrix.

The choice must be based upon the purpose of the study. Non-hierachical methods are natural choices for initial data reduction; summarizing of redundancy, reduction of noise and identification of outliers (Gauch 1980, 1982a, van Tongeren 1987). The use of hierarchical classification techniques to represent relationships among samples or clusters should take notice of the inherent limitations of the hierarchical approach.

Divisive or agglomerative

Non-hierarchical techniques optimize clustering at a specified level, i.e. with a given number of clusters. The algorithms are mostly complex, and not easily classified as divisive or agglomerative, although closer to the agglomerative than to the divisive approach.

For hierarchical techniques, this question is most important. Agglomerative techniques build a hierarchy starting with the small differences between objects, potentially with high noise. This makes agglomerative techniques less robust than divisive (Orlóci 1978, Gauch & Whittaker 1981, Gauch 1982a). On the contrary, divisive techniques start with the whole material, and thereby have the potential to make the first, critical divisions in a way that reflect broad lines of the material (Lambert et al. 1973, Orlóci 1978). Only divisive techniques can be used to obtain an ecologically based numerical classificatiobn, based on division of ecological gradients. Divisive techniques are generally considered superior to agglomerative for classification of vegetation ecological data (Williams & Dale 1965, Hill et al. 1975, Gauch & Whittaker 1981).

Monothetic or polythetic

Polythetic techniques are generally preferred over monothetic (using presence/absence of single species as criteria for divisions) for the following reasons:

(1) Monothetic techniques have high misclassification rates due to noise; the occasional presence/absence of the dividing species (Williams & Lambert 1959, Noy-Meir et al. 1970, Hill et al. 1975, Goodall 1978b, Halvorsen 1980, Gauch 1982a). The rate of misclassifications will equal the qualitative noise of the dividing species.

(2) In situations with low ß diversity or low species or sample numbers, the disadvantages of the monothetic criterion is strengthened (Noy-Meir et al. 1970, Hill 1977).

(3) In situations with high ß diversity relative to one (or more) gradients, the use of a monothetic criterion is ecologically nonsense: Dividing species with optima near the gradient middle, absent from both ends, separate samples from the gradient middle from samples from both gradient ends, inferring that the gradients ends have more in common than does each of the gradients ends have with the gradient middle.

Monothetic techniques can only be divisive, polythetic techniques can be divisive or agglomerative.

Now monothetic techniques merely have historical interest.

Combinations of strategies

Four combinations of techniques are frequently encountered. These are the major types of classification techniques: (1) Hierarchical agglomerative (always polythetic), (2) Hierarchical monothetic divisive, (3) Hierarchical polythetic divisive, and (4) Non-hierarchical (always polythetic). We will consider some examples of these major types.

HIERARCHICAL METHODS

Agglomerative methods

Despite the drawbacks of building a hierarchy upon the individual, noisy sample plots, agglomerative hierarchical clustering methods have maintained their popularity among numerical classification techniques up to present, and they are often recommended for use in ecology. Kent and Ballard (1988) found the usage of agglomerative polythetic methods in vegetation ecology steadily increasing from 1960 to 1985. In the early days of numerical analysis in ecology, they were preferred for their computational efficiency; they can easily be carried out by a desk calculator! The simplicity of the methods, their long tradition, and the fact that they mostly give reliable results on data-sets where the noise has been reduced, for instance by non-hierarchical clustering, are the main reasons why they are still popular.

Types of agglomerative methods

We will consider the agglomerative (polythetic) hierarchical strategy in some detail. All methods start with a secondary matrix of (between-object) similarities or dissimilarities. Let us denote a secondary matrix of dissimilarities between n objects (for instance, samples)

$$D = \{\delta_{jk}\},\ j,k = 1,\ldots,n.$$

Based on this matrix, the objects are united to clusters until all objects in one cluster. The methods can be divided into several groups according to the criteria used for fusion (cf. Lance & Williams 1967, Cormack 1971, Sneath & Sokal 1973, Orlóci 1978). Let us denote three clusters (at any level in the process) by p, q, and r. These clusters contain n_p, n_q, and n_r objects, respectively. The dissimilarity between two groups p and q is denoted $\delta(p,q)$, and the dissimilarity between one group pq made by fusion of p and q, and another group r, is denoted $\delta(pq,r)$. Lance & Williams (1967) divided agglomerative techniques by the following criteria:

(1) **Combinatorial** or **non-combinatorial**. Combinatorical methods only depend on the matrix D; calculation of $\delta(p,q)$ and $\delta(pq,r)$ is done arithmetically on the basis of original dissimilarities $\delta(j,k)$. Non-combinatorical methods calculate new dissimilarities from the species-sample plot matrix during the fusion process, for instance by replacing the objects with cluster **centroids** (a hypothetical object with the cluster mean as variable values; e.g. a sample with the cluster mean abundance for each species), for calculation of

inter-group dissimilarities.

(2) The dissimilarity measure and standardization used. Choice of dissimilarity measure should follow recommendations on p. 112, thus the most robust and linear measures (percentage dissimilarity (equation 32, Tab. 9) and the quantitative symmetric measure (equation 34, Tab. 9)) should be preferred. No standardization, or division by species maxima (Faith et al. 1987) is recommended. Weighting of abundances must be decided by consideration of the ß diversity of the data-set (pp. 101-102).

(3) **Space-dilating, space-conserving** or **space-contracting.** Agglomerative classification methods define new dissimilarities d(j,k) between objects, that can be read from the dendrogram as the fusion dissimilarity when the two objects become members of the same cluster. If the original dissimilarities tend to be conserved ($\delta(j,k) \approx d(j,k)$), the method is space-conserving. If $\delta(j,k) << d(j,k)$, the objects have been moved more apart by the classification method, and this is therefore space-dilating. A space-contracting method is characterized by $\delta(j,k) >> d(j,k)$. The spaces referred to here are the floristic spaces, e.g. the species-dimensional space in the case that sample plots are objects.

(4) Weighted or unweighted methods. The groups p and q can be given equal or different weights in the calculation of $\delta(pq,r)$, or their weights can be proportional with the number of objects in the groups.

We will concentrate on the combinatorial methods. Essentially non-combinatorial methods like **Ward's method** (Ward 1963, Orlóci 1967, 1978, van Tongeren 1987) and different **centroid clustering methods** have been used by several authors (e.g., Matthews 1979a), but as the results do not differ strongly from those obtained by the more simple combinatorial methods, or are inferior (Gauch & Whittaker 1981), the methods will not be considered further. The representativity of the centroid for a cluster is questionable. The centroid becomes increasingly richer in species, with lower and lower abundance of each species, when the cluster grows in size (cf. Noy-Meir 1973a, Noy-Meir et al. 1975).

In combinatorial methods, $\delta(pq,r)$ is a function of $\delta(p,r)$, $\delta(q,r)$, $\delta(p,q)$, n_p and n_q. The three most frequently used combinatorial methods will be considered.

Single linkage clustering (SL)

In the **nearest-neighbour method** or **single linkage clustering** method (Lance & Williams 1967, Sneath & Sokal 1973), the dissimilarity between two clusters is defined as the lowest dissimilarity between any pairs of objects, one in each cluster. Thus two clusters are as dissimilar as the least dissimilar pair of objects, one element in each cluster. A published example of its use, is found in Pakarinen (1976).

We will illustrate the method by an example; the frequencies in subplots for the 7 *Sphagnum* species in the 11 sample plots of T1 at Rønnåsmyra (cf. Tab. 12). The species-sample plot data matrix for the data-set is shown on p. 92. We generate a secondary matrix of dissimilarities, using percentage dissimilarity (equation 32). This matrix D is:

$$\left[\begin{array}{ccccccccccc}
000 & 057 & 023 & 015 & 084 & 315 & 622 & 941 & 980 & 979 & 978 \\
057 & 000 & 080 & 072 & 065 & 245 & 526 & 873 & 906 & 902 & 928 \\
023 & 080 & 000 & 008 & 109 & 329 & 645 & 949 & 1 & 1 & 1 \\
015 & 072 & 008 & 000 & 116 & 333 & 648 & 960 & 1 & 1 & 1 \\
084 & 065 & 109 & 116 & 000 & 225 & 508 & 881 & 918 & 914 & 920 \\
315 & 245 & 329 & 333 & 225 & 000 & 275 & 841 & 872 & 886 & 930 \\
622 & 526 & 645 & 648 & 508 & 275 & 000 & 443 & 505 & 483 & 571 \\
941 & 873 & 949 & 960 & 881 & 841 & 443 & 000 & 059 & 125 & 220 \\
980 & 906 & 1 & 1 & 918 & 872 & 505 & 059 & 000 & 067 & 164 \\
979 & 902 & 1 & 1 & 914 & 886 & 483 & 125 & 067 & 000 & 098 \\
978 & 928 & 1 & 1 & 920 & 930 & 571 & 220 & 164 & 098 & 000
\end{array}\right]
\begin{array}{l}
1 \\ 2 \\ 3 \\ 4 \\ 5 \\ 6 \\ 7 \\ 8 \\ 9 \\ 10 \\ 11
\end{array}$$

For convenience, the sample numbers are given outside the matrix, to the right. The columns could have been numbered from left to right, similarly. Dissimilarities are given as $1000{*}\delta(j,k)$, except for 1, indicating no species in common ($\delta(j,k) = 1$). The dissimilarity between samples 3 and 4 is, for instance, $\delta(3,4) = 0.015$. Clustering starts with finding the smallest dissimilarity in the matrix. This is 0.015, between samples 3 and 4. These two samples are therefore fused to make cluster 3(2) (clusters are named according to the lowest sample number occurring in them). The number in brackets is the number of samples in the cluster. We now generate a new matrix of dissimilarities by replacing the rows and columns 3 and 4 by a new one, 3(2) for the new cluster. The similarity between, for instance, sample 6 and the new cluster is then the smallest of $\delta(3,6) = 0.329$ and $\delta(4,6) = 0.333$, which is the former. Doing this for all samples, we obtain the new matrix:

$$\left[\begin{array}{cccccccccc}
000 & 057 & 015 & 084 & 315 & 622 & 941 & 980 & 979 & 978 \\
057 & 000 & 072 & 065 & 245 & 526 & 873 & 906 & 902 & 928 \\
015 & 072 & 000 & 109 & 329 & 645 & 949 & 1 & 1 & 1 \\
084 & 065 & 109 & 000 & 225 & 508 & 881 & 918 & 914 & 920 \\
315 & 245 & 329 & 225 & 000 & 275 & 841 & 872 & 886 & 930 \\
622 & 526 & 645 & 508 & 275 & 000 & 443 & 505 & 483 & 571 \\
941 & 873 & 949 & 881 & 841 & 443 & 000 & 059 & 125 & 220 \\
980 & 906 & 1 & 918 & 872 & 505 & 059 & 000 & 067 & 164 \\
979 & 902 & 1 & 914 & 886 & 483 & 125 & 067 & 000 & 098 \\
978 & 928 & 1 & 920 & 930 & 571 & 220 & 164 & 098 & 000
\end{array}\right]
\begin{array}{l}
1 \\ 2 \\ 3(2) \\ 5 \\ 6 \\ 7 \\ 8 \\ 9 \\ 10 \\ 11
\end{array}$$

The process is repeated again: Sample 1 joins the cluster 3(2) to give the new cluster 1(3), and the matrix now becomes

$$\left[\begin{array}{ccccccccc}
000 & 057 & 084 & 315 & 622 & 941 & 980 & 979 & 978 \\
057 & 000 & 065 & 245 & 526 & 873 & 906 & 902 & 928 \\
084 & 065 & 000 & 225 & 508 & 881 & 918 & 914 & 920 \\
315 & 245 & 225 & 000 & 275 & 841 & 872 & 886 & 930 \\
622 & 526 & 508 & 275 & 000 & 443 & 505 & 483 & 571 \\
941 & 873 & 881 & 841 & 443 & 000 & 059 & 125 & 220 \\
980 & 906 & 918 & 872 & 505 & 059 & 000 & 067 & 164 \\
979 & 902 & 914 & 886 & 483 & 125 & 067 & 000 & 098 \\
978 & 928 & 920 & 930 & 571 & 220 & 164 & 098 & 000
\end{array}\right]
\begin{array}{l}
1(3) \\ 2 \\ 5 \\ 6 \\ 7 \\ 8 \\ 9 \\ 10 \\ 11
\end{array}$$

Once again, we find the lowest value in the matrix. This is δ(1(3),2) = 0.057, giving a new cluster 1(4) with similarities with the other samples given by

$$\left[\begin{array}{cccccccc}
000 & 065 & 245 & 526 & 873 & 906 & 902 & 928 \\
065 & 000 & 225 & 508 & 881 & 918 & 914 & 920 \\
245 & 225 & 000 & 275 & 841 & 872 & 886 & 930 \\
526 & 508 & 275 & 000 & 443 & 505 & 483 & 571 \\
873 & 881 & 841 & 443 & 000 & 059 & 125 & 220 \\
906 & 918 & 872 & 505 & 059 & 000 & 067 & 164 \\
902 & 914 & 886 & 483 & 125 & 067 & 000 & 098 \\
928 & 920 & 930 & 571 & 220 & 164 & 098 & 000
\end{array}\right]
\begin{array}{l}
1(4) \\ 5 \\ 6 \\ 7 \\ 8 \\ 9 \\ 10 \\ 11
\end{array}$$

The most similar samples are 8 and 9, with δ(8,9) = 0.059, giving a new cluster 8(2) and a new matrix

$$\left[\begin{array}{ccccccc}
000 & 065 & 245 & 526 & 873 & 902 & 928 \\
065 & 000 & 225 & 508 & 881 & 914 & 920 \\
245 & 225 & 000 & 275 & 841 & 886 & 930 \\
526 & 508 & 275 & 000 & 443 & 483 & 571 \\
873 & 881 & 841 & 443 & 000 & 067 & 164 \\
902 & 914 & 886 & 483 & 067 & 000 & 098 \\
928 & 920 & 930 & 571 & 164 & 098 & 000
\end{array}\right]
\begin{array}{l}
1(4) \\ 5 \\ 6 \\ 7 \\ 8(2) \\ 10 \\ 11
\end{array}$$

The smallest dissimilarity in the matrix is δ(1(4),5) = 0.065. The dissimilarity between clusters now becomes

$$\left[\begin{array}{cccccc}
000 & 225 & 508 & 881 & 914 & 920 \\
225 & 000 & 275 & 841 & 886 & 930 \\
508 & 275 & 000 & 443 & 483 & 571 \\
881 & 841 & 443 & 000 & 067 & 164 \\
914 & 886 & 483 & 067 & 000 & 098 \\
920 & 930 & 571 & 164 & 098 & 000
\end{array}\right]
\begin{array}{l}
1(5) \\ 6 \\ 7 \\ 8(2) \\ 10 \\ 11
\end{array}$$

This time, the lowest value in the matrix is δ(8(2),10) = 0.067, giving av new cluster 8(3) and a new matrix

$$\left[\begin{array}{ccccc}
000 & 225 & 508 & 873 & 920 \\
225 & 000 & 275 & 841 & 930 \\
508 & 275 & 000 & 443 & 571 \\
873 & 841 & 443 & 000 & 098 \\
920 & 930 & 571 & 098 & 000
\end{array}\right]
\begin{array}{l}
1(5) \\ 6 \\ 7 \\ 8(3) \\ 11
\end{array}$$

Repeating the process again, we find that δ(8(3),11) = 0.098 is the lowest value;

$$\begin{array}{cc} \begin{bmatrix} 000 & 225 & 508 & 873 \\ 225 & 000 & 275 & 841 \\ 508 & 275 & 000 & 443 \\ 873 & 841 & 443 & 000 \end{bmatrix} & \begin{matrix} 1(5) \\ 6 \\ 7 \\ 8(4) \end{matrix} \end{array}$$

Now the lowest value is δ(1(5),6) = 0.225, giving the new cluster 1(6) and the new matrix

$$\begin{array}{cc} \begin{bmatrix} 000 & 275 & 841 \\ 275 & 000 & 443 \\ 841 & 443 & 000 \end{bmatrix} & \begin{matrix} 1(6) \\ 7 \\ 8(4) \end{matrix} \end{array}$$

The lowest dissimilarity is now δ(1(6),7) = 0.275. The dissimilarity between the two remaining clusters, δ(1(7),8(4)), is 0.443. The resulting dendrogram is shown in Fig. 140. Interpretation is aided by performing an initial DCA ordination of the data-set (eigenvalue of first axis 0.686, length of axis 3.00 S.D. units; eigenvalue of second axis 0.009, length of axis 0.53 S.D.), for the purpose of ordering sample plots along the baseline of the dendrogram. We observe that there is a strong tendency to **chaining** in Fig. 140, the tendency of clusters already formed to fuse with single samples (or other clusters) rather than for single samples to form a new, small cluster (cf. Lance & Williams 1967, Sneath & Sokal 1973, Gauch 1982a). In fact, only two clusters were formed by fusion of two samples. We also see that dissimilarities is the dendrogram are lower than the original dissimilarities; thus the method is space-contracting.

Complete linkage clustering (CL)

The **farthest-neighbour method** or **complete linkage clustering** (Lance & Williams 1967, Sneath & Sokal 1973) defines the dissimilarity between two clusters as the highest dissimilarity between any pairs of objects, one in each cluster. Thus two clusters are as dissimilar as the most dissimilar pair of objects, one object in each cluster.

The method is illustrated by application to the same data-set as above. The initial secondary matrix and the first step in the agglomerative process is the same as for single linkage. The second step again fuses sample 1 with cluster 3(2), but δ(1,3(2)) = 0.023, the dissimilarity between 1 and 3. The following steps follow different lines; samples 8 and 9 fuse to 8(2) at dissimilarity 0.059; 2 and 5 fuse to 2(2) at 0.065; 10 and 11 fuse to 10(2) at 0.098; 1(3) fuse with 2(2) to 1(5) at 0.116; 8(2) and 10(2) fuse to 8(4) at 0.220; 6 and 7 fuse to 6(2) at 0.275; 6(2) and 8(4) fuse to 6(6) at 0.571, and 1(5) and 6(6) finally fuse at 1.000. The complete linkage dendrogram for the example is shown in Fig. 141. We see that complete linkage gives small, compact clusters bacause of the higher liability of small clusters (or single samples) to form clusters, than for large clusters to fuse with smaller. The method is space-dilating; the dissimilarities in the dendrogram (Fig. 141) are larger than the original ones.

Group average clustering (GA)

The **group average** or **unweighted pair-group method using arithmetic averages** (UPGMA; Sokal & Michener 1958, Lance & Williams 1967) is by far the most frequently used agglomerative classification method, in vegetation ecology as well as numerical taxonomy. An example is provided by R. Økland & Bendiksen (1985). The dissimilarity betwen two groups is defined as the average of all pair-wise dissimilarities between objects, one in each cluster. Using the notation of the introduction to this chapter (p. 180),

$$\delta(p,q) = [\mathrm{SUM}_{j \in p, k \in q}\ \delta(j,k)]/n_p n_q \qquad (94)$$

and the dissimilarity between a cluster formed by fusion and a third cluster is

$$\delta(pq,r) = [n_p/(n_p + n_q)]*[\mathrm{SUM}_{j \in p, k \in r}\ \delta(j,k)] + [n_q/(n_p + n_q)]*[\mathrm{SUM}_{j \in q, k \in r}\ \delta(j,k)] \qquad (95)$$

We use the same example as above to illustrate the method. The first four fusions are the same as in complete linkage, but except for the fist step, the fusion dissimilarities differ: in the second step, sample 1 and cluster 3(2) fuse to 1(3) at dissimilarity 0.019; at the third step samples 8 and 9 form 8(2) at 0.059; next samples 2 and 5 form 2(2) at the fusion dissimilarity 0.065. We then obtain the matrix of dissimilarities

$$\left[\begin{array}{ccccccc}
000 & 087 & 325 & 649 & 972 & 993 & 993 \\
087 & 000 & 235 & 517 & 895 & 908 & 924 \\
325 & 235 & 000 & 275 & 857 & 886 & 930 \\
649 & 517 & 275 & 000 & 474 & 483 & 571 \\
972 & 895 & 857 & 474 & 000 & 096 & 197 \\
993 & 908 & 886 & 483 & 096 & 000 & 098 \\
993 & 924 & 930 & 571 & 197 & 098 & 000
\end{array}\right]
\begin{array}{l}
1(3) \\ 2(2) \\ 6 \\ 7 \\ 8(2) \\ 10 \\ 11
\end{array}$$

We find that the lowest dissimilarity in the matrix is $\delta(1(3),2(2)) = 0.087$. The new dissimilarities between cluster 1(5) and other clusters are found by use of the formula (94), inserting $n_p = 3$, $n_q = 2$. For instance,

$$\delta(1(5),6) = (3/5)*\delta(1(3),6) + (2/5)*\delta(2(2),6) = 0.6*0.325 + 0.4*0.235 = 0.289$$

and

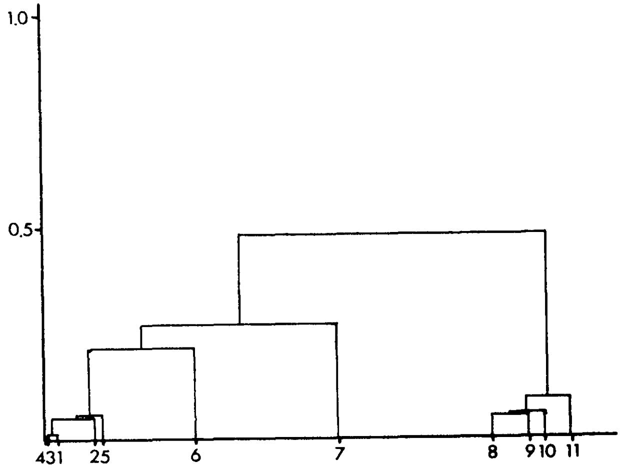
$$\delta(1(5),8(2)) = 0.6*0.972 + 0.4*0.895 = 0.941.$$

The new matrix eventually becomes

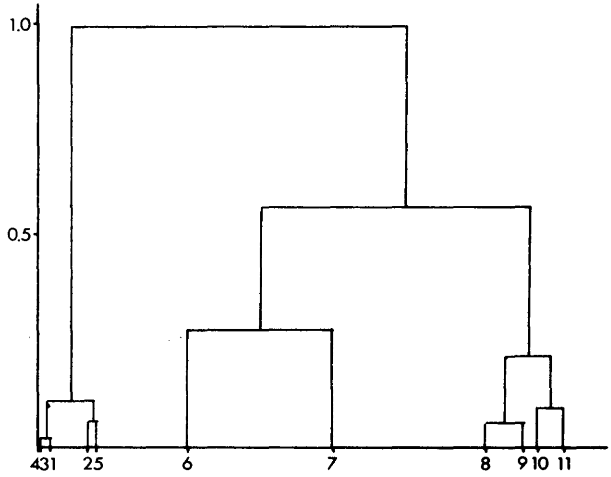
$$\left[\begin{array}{cccccc}
000 & 289 & 588 & 941 & 959 & 965 \\
289 & 000 & 275 & 857 & 886 & 930 \\
588 & 275 & 000 & 474 & 483 & 571 \\
941 & 857 & 474 & 000 & 096 & 197 \\
959 & 886 & 483 & 096 & 000 & 098 \\
965 & 930 & 571 & 197 & 098 & 000
\end{array}\right]
\begin{array}{l}
1(5) \\ 6 \\ 7 \\ 8(2) \\ 10 \\ 11
\end{array}$$

The next fusion occurs between 8(2) and 10 at level 0.096, to give the new cluster 8(3). The last divisions are as follows: 8(3) and 11 join to form 8(4) at 0.163; 6 and 7 fuse to 6(2) at 0.275; 1(5) and 6(2) fuse to 1(7) at 0.439, and in the last step 1(7) and 8(4) join to form 1(11) at 0.878. The group average dendrogram is shown in Fig. 142. It is

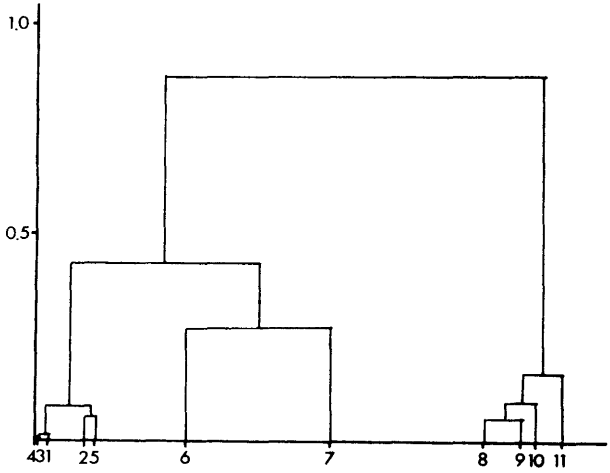
140


1.0
0.5
431
25
6
7
8
910
11

141


1.0
0.5
431
25
6
7
8
910
11

142


1.0
0.5
431
25
6
7
8
910
11

intermediate between the single linkage and complete linkage methods; the averaging of dissimilarities makes the fusion process independent of cluster size. Thus the group average method is a space-conserving technique.

Assessment

Provided the dissimilarity measure used for agglomerative classification is a fairly linear function of ecological distance (as for instance, percentage dissimilarity), the space-conserving property of the group average method is desired. The group average method is also preferable from a statistical point of view. Estimation of between-cluster dissimilarity on the basis of all available between-object dissimilarities gives more robust estimates than estimates based on extreme values (as in single linkage and complete linkage). Therefore, the group average method is more robust than either of the two latter (cf. Gauch & Whittaker 1981). The disadvantages of methods using centroids are mentioned before. The group average method with percentage dissimilarity performed the best in tests of agglomerative classification methods by Gauch & Whittaker (1981). Agglomerative clustering by minimization of within-group variance (e.g., Ward's method, cf. p. 181) has been advocated from a mathematical point of view, by arguments similar to those used in favour of Euclidean distance in species-dimensional space as a measure of sample dissimilarity and PCA as an ordination method (e.g., Orlóci 1978, Wishart 1978). Gauch and Whittaker (1981) found minimization of within-group variance less robust than the group average method. The group average method has been recommended by Lance and Williams (1967), Sneath and Sokal (1973), Campbell (1978), Orlóci (1978), and Gauch and Whittaker (1981).

Monothetic divisive methods

As the first numerical classification methods to come into common usage, techniques of this suboptimal strategy deserves mention because of their historical interest. Their present-day function is to provide initial classifications for non-hierarchical classification methods. Two main groups of techniques were widely used in the 1960s, 1970s (and early 1980s), with a peak around 1970 (Kent & Ballard 1988): **association-analysis** and **information analysis**.

Association-analysis (Goodall 1953, Williams & Lambert 1959, 1960). The method uses qualitative data (presence/absence of species in sample plots). The pair-wise association is tested for all species pairs by calculating the chi-square (equation 41) or some derived statistic. A significance level, most frequently $p = 0.05$, is chosen. For each species, the sum of all chi-square values significant at the specified level is summarized, and the species with the highest sum is used for the first monothetic division. One group consists of sample plots containing the species, and group is negatively characterized group. The process is repeated for each group, and so on until a specified **stopping-rule** comes into action. Such stopping-rules may be that no more significant associations occur (Goodall 1953), that the sum of chi-square values drops below a specified limit (Williams & Lambert 1959), or based on the ratio of within- and between-group variances (Ratliff & Pieper 1981). The use of negative associations is questionable. The resulting classification may be improved by relocation of resulting samples (Orlóci 1978, Halvorsen 1980). Association-analysis is used for analysis of Norwegian vegetation by Elven (1978) and Halvorsen (1980).

Divisive information-analysis (Williams et al. 1966, Lance & Williams 1968). The principle of information-analysis is analogous to association-analysis. The information content ("entropy") in a data-set with

Figs 140-142. Dendrograms from agglomerative clustring methods applied to the 7 *Sphagnum* species in 11 samples at Rønnåsmyra, Grue, SE Norway (data of Tab. 12). Samples are ordered along the first DCA axis. Fig. 140. Single linkage. Fig. 141. Complete linkage. Fig. 142. Group average.

m species in n samples, the number of samples containing species i being n_i, is defined as

$$I = m*n*\ln n - \mathrm{SUM}_{i=1...m} [n_i \ln n_i - (n - n_i)\ln(n - n_i)] \qquad (96)$$

At the start of the divisive process, I is calculated for the whole data-set and in addition, I is calculated for all 2m subsets derived by using presence/absence of the species to perform a bipartition. The value of I for the subset containing species i is termed I_{i+}, the corresponding value for the subset without i I_{i-}. For all species, the value

$$\delta I_i = I - I_{i+} - I_{i-} \qquad (97)$$

is calculated. Presence/absence of the species giving the highest δI_i is used to perform the first division. A stopping-rule is used to end the process. Divisive information has been applied to the study of Norwegian vegetation by Matthews (1979a) and Galten (1987).

Polythetic divisive methods

Polythetic divisive methods have repeatedly been recommended as the optimal strategy to classification (pp. 178-180, also see Sneath & Sokal 1973, Hill et al. 1975, Gauch & Whittaker 1981, Gauch 1982a, Kershaw & Looney 1985, Digby & Kempton 1987, van Tongeren 1987). This stems from the theoretical advantages of using information on the whole data-set for performing the initial, critical divisions, the advantages of making first divisions according to the major lines of variation in the data-set, and the preference of many investigators for hierarchical classification.

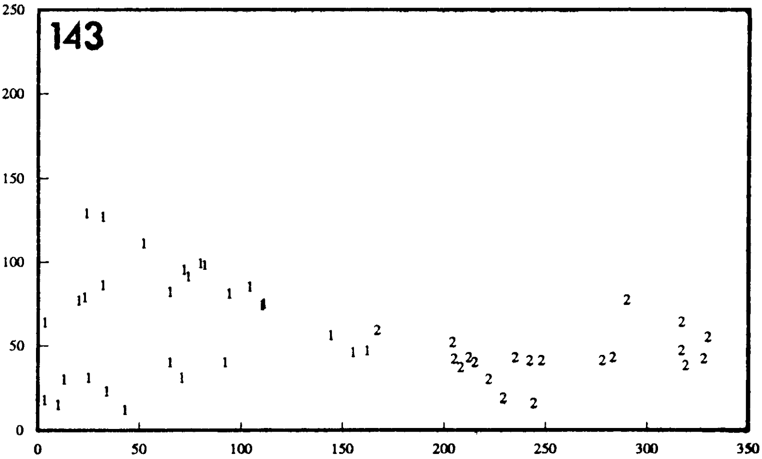
The computational difficulties associated with polythetic divisive methods (large computational demands) hindered progress within this strategy until the 1970s. At present, one method stands out as the state-of-the-art in numerical classification (Kershaw & Looney 1985, Digby & Kempton 1987, van Tongeren 1987): **two-way indicator species analysis**, TWINSPAN. We will consider this method in some detail. In addition we will consider **ordination space partitioning** (Gauch & Whittaker 1981, Gauch 1982a); a "substrategy" more than a defined method.

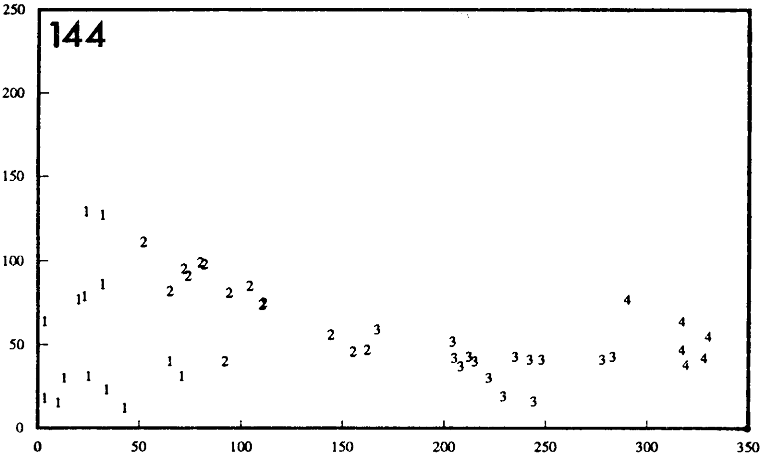
Two-way indicator species analysis (TWINSPAN)

The method was developed by Hill (1979b), based on a previous method (indicator species analysis), deviced by Hill et al. (1975). The immense increase in popularity of the method during the 1980s makes it deserve particular consideration. Descriptions of the method follow Hill (1979b).

TWINSPAN is a dual technique, classifying both samples and species. It also reorganizes the species-sample plot data matrix into an ordered two-way table. The basic idea is that a group of samples should be characterized by a characteristic species combination, or at least a group of differential species (as in phytosociological classification according to the Braun-Blanquet approach, cf. pp. 60-65). The qualitative concept of a differential species is transferred to quantitative data by use of **pseudospecies** (*Hill* et al. 1975). A pseudospecies is defined by a minimum abundance of a species. This minimum is called the **cut level**. The main features of a species' response to a gradient is maintained

Figs 143-145. TWINSPAN sample classification of the virgin bog samples from Rønnåsmyra, Grue, SE Norway, plotted onto sample positions in with respect to the first two DCA axes (Fig. 126), scaled in S.D. units *100. Fig. 143. 2-cluster level. Fig. 144. 4-cluster level. Fig. 145. 8-cluster level.


143
250
200
150
100
50
0
0
50
100
150
200
250
300
350


144
250
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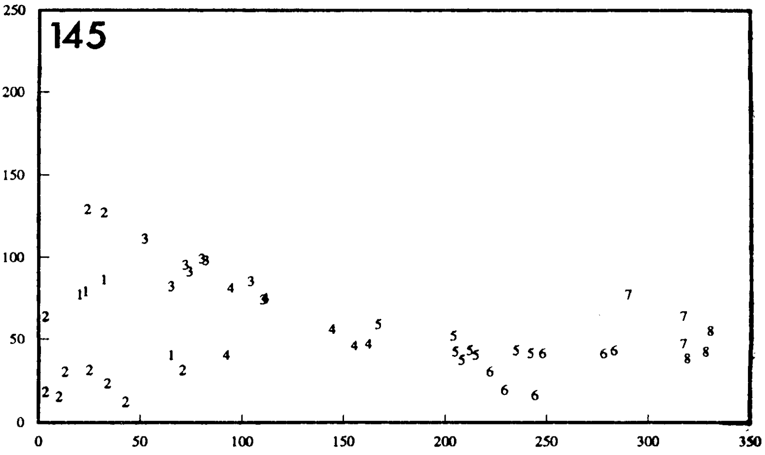
145
250
200
150
100
50
0
0
50
100
150
200
250
300
350

Tab. 19. Output from TWINSPAN classification of 7 *Sphagnum* species (names to the left, abbreviated) in the 11 sample plots (numbers at top) of transect 1 at Rønnåsmyra, Grue, SE. Norway (data of Tab. 12). Sample classification at the bottom, each dichotomy indicated by 0 or 1 in consecutive lines, starting from the top. Species classification to the right.

```
                       11
              34152678901

2 Spha  cus   444342-----  00
5 Spha  maj   444342-----  00
7 Spha  ten   4444442----  0100
1 Spha  bal   44444431---  0101
4 Spha  mag   -----44----  011
6 Spha  rub   --123334432  10
3 Spha  fus   ------34444  11

              00000001111
              00000010011
              000001 0101
              00011
              00101
```

by the pseudospecies. This is easily illustrated by an example: Assume that species abundance has been measured as frequency in 16 subplots. Cut-levels 0, 5, 10, and 15 are used. Pesudospecies 1 is present in all samples including the species; pseudospecies 2 is present in all samples where the frequency in subplots is equal to or higher than 5; pseudospecies 3 is present in all samples with frequency 10 or more, and pseudospecies 4 present in all samples with frequency 15 or 16. Thus all pseudospecies will be present near the mode of the species, and all pseudospecies will maintain the unimodal response to the gradient (van Tongeren 1987).

The sample classification in TWINSPAN uses the first axis of a CA ordination to order the samples, and an initial dichotomy into two groups, 0 and 1, is performed near the axis middle. This classification is refined in two more steps by a first identification of **indicator species** for each axis pole, assessment of the indicator value of each pseudospecies (calculation of a **preference score** for each species). The weighted average of the preference scores is calculated for each sample, and this is taken as the basis for a reordering of samples (**refined ordination**) and for making an improved dichotomy. This process is repeated once more, to produce an **indicator ordination**. When the dichotomy is fixed, the main clusters 0 and 1 are determined. The process is repeated on each cluster, to produce clusters 00 and 01 from 0, and 10 and 11 from 1, and so on until a maximum number of hierarchical levels is reached or the number of samples in a group has dropped below a specified minimum. (The clusters are also numbered in another way; 1 (whole material), 2-3 (two-group level), 4-7 (three-group level), etc. (Adding a "1" as the first digit to the first numbering, the first becomes a binary representation of the second). The ordering of clusters at each hierarchical level is done with reference to orderings at higher levels, thus clusters at all hierarchical levels are ordered along the major gradient in the material.

Tab. 20. Output from TWINSPAN classification of 52 species (names to the left, abbreviated) in the 51 sample plots (numbers at top) from virgin bog at Rønnåsmyra, Grue, SE. Norway (data of Tab. 1). Sample classification at the bottom, each dichotomy indicated by 0 or 1 in consecutive lines, starting from the top. Species classification to the right.

```
                1111 2 124  4  422222323 44334333 3334 114441122155
                534643322012156245786192734035456878969017897801901

  9 Dros   ang  -------2-------------------------------------------  000000
 12 Care   lim  ----------43---------------------------------------  000000
 15 Sche   pal  ----4-4---32344------------------------------------  000000
 23 Spha   cus  44444-44-4444444---------4------------------4------  000001
 26 Spha   maj  34444-44-4444444---------3------------------2------  000001
 14 Rhyn   alb  444444444-44----42---------------------------------  00001
 20 Drep   flu  ---2-----------------------------------------------  00001
 25 Spha   mag  -2------------4---------4--------------------------  0001
 28 Spha   ten  44444444444444444444444444-44-4-------------2-2----  0001
 35 Clad   flu  444444444444444444444444444444-------2------3------  0001
 22 Spha   bal  44444444444444444444444444444444444444------4-2----  0010
 30 Caly   sph  24442-------2344---3223232-444--24-2-324-----------  0010
 16 Scir   ces  ----------------224444443--44-44-------------------  0011
 33 Ceph   lun  3-232-----------4-4444-------------422-------------  0011
 49 Clad   squ  ------------------223--2---34-32-------------------  0011
  1 Andr   pol  444444444444444444444444444444444444444444444444444  0100
  7 Vacc   oxy  4444444444444444444444444444444-4444444444444---243  0100
 13 Erio   vag  444444444444444444444444444444444444444444444444422  0100
 10 Dros   rot  334----2---2--4-23-424444344444444444444-2-4-------  0101
 27 Spha   rub  -----3----3424444444444444444444444444444424-------  0101
 32 Ceph   loi  ------------------4--2-----442423--------2--2------  011
 37 Myli   ano  444444-------44-44444444444444444444444444444242-32  011
  6 Vacc   mic  ---------------3-----24444443444444444444444-----42  100
 11 Rubu   cha  -------------244--323234444-44444444444444443444244  100
  3 Call   vul  -----------------------24--244444444444444442244-44  1010
  4 Empe   nig  ---4--------------------4---3444424444444--4-434444  1010
 36 Kurz   pau  ---------------------------4-3-23-423------3-------  1010
 24 Spha   fus  ------------------------444--434444444444444-----3-  1011
  5 Pinu   syl  -------------------------------2----24---4---------  1100
 17 Dicr   lei  ------------------------------------------4--------  1100
 51 Clad   sul  -----------------------------------232----------33-  11010
 43 Clad   chl  ------------------------------22--2444--2444-443444  110110
 48 Clad   ran  ------------------------------344-3444--44444444444  110110
 39 Clad   arb  -----------------------2------322--424---4444444444  110111
 42 Clad   cen  -----------------------------------3------24----342  110111
 19 Dicr   und  ---------------------------------4-2------4-2244444  11100
 21 Pleu   sch  ------------------------------------2---4-444444444  11100
 34 Ceph   spp  -------------------------------3-----------43-42---  11100
  8 Vacc   uli  -------------------------------------------------24  111010
 18 Dicr   sco  ----------------------------------------------442--  111010
 29 Caly   nee  ----------------------------------------------44---  111010
 31 Ceph   con  --------------------------------------------2-44---  111010
 38 Ptil   cil  -----------------------------------------------32--  111010
 40 Clad   bot  ------------------------------------------------4--  111010
 41 Clad   car  ------------------------------------------------2--  111010
 44 Clad   cor  -----------------------------------------------34--  111010
 45 Clad   cya  ------------------------------------------------222  111010
 46 Clad   def  -------------------------------------------------43  111010
 47 Clad   gra  -----------------------------------------------2---  111010
 52 Clad   unc  ----------------------------------------------2----  111010
 50 Clad   ste  -----------------------2-----------44-------44444-2  111011
  2 Betu   nan  4--4--------------------4------------24444444444444  1111

                000000000000000000000000000000111111111111111111111
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                011100000000011100000011000111000111110001110111
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The species classification by TWINSPAN is derived in much the same way as the sample classification. Further details of TWINSPAN is given by Hill (1979b).

Two examples will be presented, using the material from Rønnåsmyra (Tabs 1, 12). In both cases, four pseudospecies were defined, corresponding to cut-levels 0, 5, 10, and 15 for frequency in subplots at a 0-16 scale. Otherwise, default options were used throughout. The first example used the 7 *Sphagnum* species in 11 sample plots in Transect 1 (Tab. 12). The classification of species and sample plots is shown in Tab. 19. Abbreviated species names are shown to the left, sample plot numbers at the top, the sample plot classification to the right and the species classification at the bottom. The TWINSPAN sample plot classification is intermediate between classifications by the group average and complete linkage clustering methods (cf. Figs 141-142), agreeing with the former in the major dichotomies, with the latter in the lower level divisions. The second example used the 52 species in 51 sample plots from virgin bog vegetation (Tab. 1). The ordered two-way table and sample plot and species classifications are shown in Tab. 20. The sample plot classification (2-, 4-, and 8-cluster levels) are plotted onto the DCA ordination of 50 sample plots in Fig. 126, in order to judge the correspondence between classification and ordination results (Figs 143-145). The 2 major divisions correspond well with separation along the first DCA axis, the third division is made according to other criteria.

An application of TWINSPAN to Finnish mire vegetation is provided by Heikilä (1987).

Ordination space partitioning (OSP)

The possibility of performing classification in ordination diagrams has been mentioned several times (e.g., Noy-Meir 1973b, Noy-Meir & Whittaker 1977, Peet 1981, Gauch 1982a). Gauch and Whittaker (1981) suggested subjective partitioning of a DCA diagram as a classification method under the name **DCA space partitioning** (DCASP). There are, however, several ways to objectivize ordination space partitioning, for instance by agglomerative clustering from on a matrix of distances in ordination space. Ordination used for the purpose of classification is termed **taxometric ordination**. Distortions in the ordination configuration will influence the resulting classification. This disadvantage must be judged against the noise-reducing power of ordinations (cf. Gauch 1982b), obviously advantageous for classification. Direct gradient approaches to classification (p. 70) are conceptually related to OSP, as both aim at dividing the ecological space into units with a well-defined ecological basis that is reflected in the species composition.

Assessment

Gauch & Whittaker (1981) compared several classification methods, and found TWINSPAN and DCASP both to give results that were generally interpretable. As TWINSPAN is also based on ordination, this polythetic divisive method can be considered an improved OSP method where the criteria for division have been objectivized. Such an objectivization is desirable in itself. As the ordering of sample plots and species along the first CA axis optimizes the correlation of species optima and sample positions, TWINSPAN is likely not to be far from the theoretical optimum for polythetic divisive, hierarchical numerical classification techniques. It is likely that the popularity of TWINSPAN will continue to increase.

NON-HIERARCHICAL METHODS

This strategy of polythetic techniques optimize the **homogeneity** within clusters (equal volume, cf. p. 177), when the number of clusters is specified. Several programs have been proposed, differing in computer requirements and several details of algorithm, e.g., TABORD (van der Maarel et al. 1978), the **iterative relocation procedure** in CLUSTAN (Wishart 1978), CLUSLA (Louppen & van der Maarel 1979), COMPCLUS (Gauch 1980), and FLEXCLUS (van Tongeren 1986). Differences in computer requirements are reflected in the allowed departure from the theoretical optimum solution. We will describe the strategy in general, without special reference to any of the programs mentioned above.

Iterative relocation proceeds, as the name says, as an iteration process.

(1) The final number of clusters is specified.

(2) All samples plots are assigned to n clusters; randomly (Wishart 1978), by use of an initial classification; by picking up a sample x_j at random (or simply, taking number one), specifying a maximum dissimilarity (the **radius** of the cluster), and assign subsequent samples to the same group as x_j if the dissimilarity to this sample is lower than the specified radius, else erect a new cluster (variants of this procedure is used in the other programs). The latter approach specifies radius instead of final number of clusters.

(3) All samples plots are judged for dissimilarity with all clusters, using a favourable dissimilarity measure (cf. p. 112). The dissimilarity between a sample plot and a cluster can be calculated as the dissimilarity between the sample plot and the centroid of the cluster, (Wishart 1978, van der Maarel et al. 1978), by using average dissimilarity between the sample plot and all members of the cluster, or by comparison with one member of the cluster, e.g., the site first entered to the cluster.

(4) Samples more similar to another cluster than the cluster to which it belongs at present, are relocated to the new cluster.

(5) The cycle (3)-(4) is repeated until stability is reached. There is a danger that some objects never reach a stable position, but rather oscillate between two clusters infinitely. This can be avoided by specifying a maximum number of iteration cycles to be performed.

Several programs include an option for placing outliers (defined as samples with dissimilarity to all clusters larger than a specified limit) in a **residual group**. This mostly increases the optimality of the method considerably (Cormack 1971). A minimum number of samples per cluster can also be specified, thereby also allowing for rejection of outlying groups.

The advantages of non-hierarchical clustering methods are the possibility of optimizing within-group homogeneity given the number of clusters, the opportunity to identify outliers, and the opportunity to reduce the noise of the data-set by converting n sample plots to n^* clusters that can be subjected to further analysis (Gauch 1982a, van Tongeren 1986). Relationships between clusters produced in non-hierarchical classification may be found by subsequent application of agglomerative, hierarchical clutering methods (see, for instance R. Økland 1989b).

INTERPRETATION OF CLASSIFICATION RESULTS

The division gradient analysis techniques into direct (regression, constrained ordination) and indirect (ordination), can be paralleled for numerical classification. The direct gradient approach to classification and other approaches to classification, using the vegetation *and* environmental factors jointly as basis for classification, parallel the direct gradient analysis techniques (compare the Finnish site-type approach to classification, cf. pp. 68-69). Most classification methods, including all numerical classification techniques described here are indirect in this sense. Thus a subsequent step of environmental interpretation is necessary. We will consider some interpretative devices.

Displaying the vegetational variation

(1) *Display of vegetational variation in ordered tables.* This is a first step in cluster interpretation. Ordered tables may be like the TWINSPAN output (Tabs 19-20), showing the assigment of samples to clusters and the preference of species for these clusters in a two-way table. Alternatively, simple descriptive statistics, such as the mean abundance and constancy (frequency in a table; cf. p. 62) of all species may be tabulated. Such tables are found in almost all works using classification, both by traditional and numerical approaches (e.g., Elven 1978, Tyler 1979, Halvorsen 1980, Kielland-Lund 1981, R. Økland & Bendiksen 1985, R. Økland 1989a). As they show the contents of groups rather than between-group relationships, they are useful both for hierarchical and non-hierarchical classifications.

(2) *Dendrograms.* Hierarchical classifications may favourably be displayed by use of dendrograms (e.g. Figs 140-142). The readability of a dendrogram can be enhanced by a rational ordering of objects along the horizontal axis (e.g., by an initial ordination as in Figs 140-142), and indication of between-cluster dissimilarity (e.g., fusion levels in agglomerative clasification) along the vertical axis. Dendrograms are shown in almost all previously mentioned works using hierachical classification techniques.

Environmental interpretation of classifications

Non-hierarchical classification allows for comparison of the resulting clusters, pair-wise or simultaneously, with environmental data. Hierarchical classifications allows for such comparisons at each dendrogrammatic level. We will consider a few devices for environmental interpretation of classifications.

(1) *Calculation of descriptive statistics.* If the environmental variables are transformed to approach the Gaussian distribution (cf. p. 105), the mean and standard deviation can be calculated for each environmental variable and cluster at a specified hierarchical level. When the distribution of variables is expected to be highly skewed or the distribution is unknown, parameters like the median, the range (difference between minimum and maximum), and percentiles (the value superseeded by a given percentage of the observations) are more informative.

(2) *Statistical tests for two clusters.* Given environmental variables with Gaussian distribution, the significance of differences between two clusters with respect to one environmental factor, can be tested by **Student's T-test**. With deviant or unknown distributions of the environmental variable, an non-parametric test is recommended. The

Wilcoxon (Mann-Whitney) text is only based on the ranks of the environmental variables. These tests are described in detail, for instance by Sokal & Rohlf (1981). T. Økland (1988) used the Wilcoxon test to explore the differences between two distinct clusters in an ordination diagram.

(3) *Statistical tests for several clusters.* Analysis of variance (ANOVA) can be used to test the hypothesis of departures from a random distribution of the environmental variable on the clusters. The test criterion is based on the ratio of between-cluster to within-cluster variance, and assumes a normal distribution of errors.

(4) *Discriminant analysis* (Dahl et al. 1967, Sokal & Rohlf 1981, ter Braak 1987c) selects the (linear) combination of environmental factors which best predicts a specified classification. Dahl et al (1967) used this method on data from E Norwegian coniferous forest types, finding that the best predictor variables (for the phytosociological classification of Kielland-Lund (e.g., 1981)) were loss on ignition and base saturation.

Interpretation by gradient analysis

Ecologically interpreted ordination diagrams can be used for display of relationships between clusters and for environmental interpretation of classifications. Several uses of ordination methods in this respect can be imagined:

(1) *Plotting of a classification onto an ordination diagram.* Examples are given in Figs 143-145. Conversely, classifications are often plotted onto ordinations for interpretation of ordinations (e.g., Fig. 135). A circular reasoning; using a classification for interpretation of ordinations, that are in turn used for interpretation of a classification, must be avoided. The circle must be broken by including environmental information. In most cases, classifications are used for interpretation of ordinations (pp. 166-167).

(2) *Ordination of clusters.* Clusters resulting from non-hierarchical classification methods can be ordinated in order to show relationships between clusters and enhance environmental interpretation (Gauch & Whittaker 1981, Gauch 1982a). As input data for ordination, the centroid of each cluster may be used (see, however p. 181 for a criticism of the use of centroids). Examples of this approach are given by Matthews (1979b), and R. Økland and Bendiksen (1985).

CONCLUSIONS AND PERSPECTIVES FOR THE FUTURE

The conceptual limitations of classification as an approach to structure variation in an essentially continuous vegetation (and a continuous environment) are obvious. This at once seems to be at odds with the consensus that gradient analysis and classification are complementary approaches (see, for instance, Gauch 1982a, Kent & Ballard 1988). However, there is nothing to prevent classification in a continuum, as long as one appreciates the inherent limitations of the classificatory approach. However, one can argue that gradient analysis is the more fundamental of the two approaches as it is likely to give information more relevant to understanding vegetation-environment relationships (cf. R. Økland 1989a).

A brief summary of recommendations with respect to numerical classification methods can be given: Non-hierarchical classification can be used for initial structuring of large datasets, and for obtaining optimal classifications relative to a given resolution level. When the hierarchy is desired, divisive polythetic techniques based on ordination is the strategy most likely to be optimal. Among the methods so far available, TWINSPAN appears the best.

There have been remarkably few developments in numerical classification methodology during the 1980s. I think there are at least two reasons for this; the proportionally higher interest in gradient analysis and other types of approach (cf. Kent & Ballard 1988), and the fact that the best techniques within each classification strategy are close to the theoretical optima, and hence, that the potentials for improvements are low. Future developments in numerical classification are likely to come in better devices for interpretation, integrated with the vegetational classification (compare the development of constrained ordination), and minor improvements in the polythetic divisive approach following improvements in ordination methodology.

REFERENCES

Aario, L. 1932. Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. - Fennia 55: 1: 1-179.

Abrams, P. 1980. Some comments on measuring niche overlap. - Ecology 61: 44-49.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. - Annls bot. fenn. 5: 169-211.

Alatalo, R. 1981. Problems in the measurement of evenness in ecology. - Oikos 37: 199-204.

Aleksandrova, V.D. 1978. Russian approaches to vegetation. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 167-200.

Alley, T.R. 1982. Competition theory, evolution, and the concept of an ecological niche. - Acta biotheor. 31: 165-180.

Andersson, F. 1970. Ecological studies in a Scanian woodland and meadow area, Southern Sweden. I. Vegetational and environmental structure. - Opera bot. 27: 1-190.

- & Ericson, J. 1963. Soil moisture in relation to heath and meadow vegetation. I. Principles and methods. - Bot. Not. 116: 257-266.

Andersson, P.-A. 1988. Ordination and classification of operational geographic units in Southwest Sweden. - Vegetatio 74: 95-106.

Arnborg, T. & Ebeling, F. 1978. Nordsvenska skogstyper. - Sver. Skogsvårdsförb. Tidskr. 76: 339-381.

Arrhenius, A. 1921. Species and area. - J. Ecol. 9: 95-99.

Aune, E.I. 1973. Forest vegetation in Hemne, Sør-Trøndelag, Western Central Norway. - K. norske Vidensk. Selsk. Mus. Miscellanea 12: 1-87.

- , Dahl, E. & Løes, A.-K. 1989. Soil acidification in spruce forests in Norway and West Germany. - Stud. Pl. Ecol. 18: 13-15.

Austin, M.P. 1971. Role of regression analysis in plant ecology. - Proc. ecol. Soc. Aust. 6: 63-75.

- 1976a. On non-linear species response models in ordination. - Vegetatio 33: 33-41.
- 1976b. Performance of four ordination techniques assuming three different non-linear species response models. - Vegetatio 33: 43-49.
- 1980. Searching for a model for use in vegetation analysis. - Vegetatio 42: 11-21.
- 1981. Permanent quadrats: an interface for theory and practice. - Vegetatio 46-47: 1-10.
- 1985. Continuum concept, ordination methods, and niche theory. - A. Rev. Ecol. Syst. 16: 39-61.
- 1986. The theoretical basis of vegetation science. - Trends Ecol. Evol. 1: 161-164.
- 1987. Models for the analysis of species' response to environmental gradients. - Vegetatio 69: 35-45.
- & Austin, B.O. 1980. Behavior of experimental communities along a nutrient gradient. - J. Ecol. 68: 891-918.
- & Cunningham, R.B. 1981. Observational analysis of environmental gradients. - Proc. ecol. Soc. Aust. 11: 109-119.
- , Cunningham, R.B. & Good, R.B. 1983. Altitudinal distribution of several eucalypt species in relation to other environmental factors in New South Wales. - Aust. J. Ecol. 8: 169-180.
- , Cunningham, R.B. & Fleming, P.M. 1984. New approaches to direct gradient analysis using environmental scalars and curve-fitting procedures. - Vegetatio 55: 11-

27.
- & Noy-Meir, I. 1971. The problem of non-linearity in ordination: experiments with two-gradient models. - J. Ecol. 59: 763-773.
- & Smith, T.M. 1989. A new model for the continuum concept. - Vegetatio 83: 35-47.

Baadsvik, K. 1971. Om klimaet ved jordoverflaten og de temperaturforhold fjellplantene lever under. - K. norske Vidensk. Selsk. Mus. Miscellanea 3: 1-28.

Backéus, I. 1985. Aboveground production and growth dynamics of vascular bog plants in Central Sweden. - Acta phytogeogr. suec. 74: 1-98.

Barkman, J.J. 1978. Synusial approaches to classification. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 111-165.
- , Doing, H. & Segal, S. 1964. Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. - Acta bot. neerl. 13: 394-419.
- , Moravec, J. & Rauschert, S. 1976. Code of phytosociological nomenclature. - Vegetatio 32: 131-185.

Bates, J.W. 1989. Growth of Leucobryum glaucum cushions in a Berkshire oakwood. - J. Bryol. 15: 785-791.

Beals, E.W. 1973. Ordination: mathematical elegance and ecological naïveté. - J. Ecol. 61: 23-35.
- 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. - Adv. ecol. Res. 14: 1-55.

Becking, R.W. 1957. The Zürich-Montpellier school of phytosociology. - Bot. Rev. 23: 411-488.

Begon, M. Harper, J.L. & Townsend, C.R. 1986. Ecology: individuals, populations and communities. - Blackwell, Oxford.

Bernard, J.M., Seischab, F.K. & Gauch, H.G. 1983. Gradient analysis of the vegetation of the Byron-Bergen swamp, a rich fen in western New York. - Vegetatio 53: 85-91.

Bjørndalen, J.E. 1981. Classification of basiphilous pine forests in Telemark, SE. Norway: a numerical approach. - Nord. J. Bot. 1: 665-670.

Bonan, G.B. & Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. - A. Rev. Ecol. Syst. 20: 1-28.

Bowman, D.M.J.S. & Minchin, P.R. 1987. Environmental relationships of woody vegetation patterns in the Australian monsoon tropics. - Aust. J. Bot. 35: 151-169.

Braak, C.J.F. ter 1983. Principal components biplots and alpha and beta diversity. - Ecology 64: 454-462.
- 1985. Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. - Biometrics 41:859-873.
- 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. - Ecology 67: 1167-1179.
- 1987a. The analysis of vegetation-environment relationships by canonical correspondence analysis. - Vegetatio 69: 69-77.
- 1987b. Calibration. - In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.), Data analysis in community and lanmdscape ecology, Pudoc, Wageningen, pp. 78-90.
- 1987c. Ordination. - In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.), Data analysis in community and landscape ecology, Pudoc, Wageningen, pp. 91-173.
- 1987d. CANOCO - a FORTRAN program for canonical community ordination by (partial)(detrended)(canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). - TNO Inst. appl. Comp. Sci., Stat. Dept.

Wageningen, Wageningen.
- 1987e. Unimodal models to relate species to environment. - Diss., Group Landbouwwiskunde, Wageningen.
- & Barendregt, L.G. 1986. Weighted averaging of species indicator values: its efficiency in environmental calibration. - Math. Biosci. 78: 57-72.
- & Looman, C.W.N. 1986. Weighted averaging, logistic regression and the Gaussian response model. - Vegetatio 65: 3-11.
- & Looman, C.W.N. 1987. Regression. - In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.), Data analysis in community and landscape ecology, Pudoc, Wageningen, pp. 29-77.
- & Prentice, I.C. 1988. A theory of gradient analysis. - Adv. ecol. Res. 18: 271-317.

Braun-Blanquet, J. 1921. Prinzipien einer Systematik der Pflanzengessellschaften auf floristischer Grundlage. - Vjschr. naturf. Ges. Zürich 70: 122-149.
- 1928. Pflanzensoziologie. Grundzüge der Vegetationskunde, ed. 1. - Springer, Berlin.
- 1964. Pflenzensoziologie. Grundzüge der Vegetationskunde, ed. 3. - Springer, Wien.

Bray, J.R. & Curtis,. J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. - Ecol. Monogr. 27: 325-349.

Brochmann, C. 1987. Evaluation of some methods for hybrid analysis, exemplified by hybridization in Argyranthemum (Asteraceae). - Nord. J. Bot. 7: 609-630.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. - Am. Nat. 124: 255-279.

Brown, M.J., Ratkowsky, D.A. & Minchin, P.R. 1984. A comparison of detrended correspondence analysis and principal co-ordinates analysis using four sets of Tasmanian vegetation data. - Aust. J. Ecol. 9: 273-279.

Burrough, P. 1987. Spatial aspects of ecological data. - In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.), Data analysis in community and landscape ecology, Pudoc, Wageningen, pp. 213-251.

Cajander, A.K. 1903. Beiträge zur Kenntnis der Vegetation der Alluvionen des nördlichen Eurasiens. I. Die Alluvionen der unteren Lena-Thales. - Acta Soc. scient. fenn. 32: 1: 1-182.
- 1909. Über Waldtypen. - Acta for. fenn. 1: 1: 1-175.
- 1913. Studien über die Moore Finnlands. - Acta for. fenn. 2: 3: 1-208.
- 1921. Über Waldtypen II. I. Über Waldtypen im allgemeinen. - Acta for. fenn. 20: 1: 1-41.
- 1926. The theory of forest types. - Acta for. fenn. 29: 3: 1-108.

Campbell, B. 1978. Similarity coefficients for classifying relevés. - Vegetatio 37: 101-109.

Carleton, T.J. 1982. The composition, diversity, and heterogeneity of some jack pine (Pinus banksiana) stands in northeastern Ontario. - Can. J. Bot. 60: 2629-2636.

Chang, D.H.S. & Gauch, H.G., Jr. 1986. Multivariate analysis of plant communities and environmental factors in Ngari, Tibet. - Ecology 67: 1568-1575.

Chardy, P., Glenmarec, M. & Laurec, A. 1976. Application of inertia methods to benthic marine ecology: practical implications of the basic options. - Estuarine cstl mar. Sci. 4: 179-205.

Chesson, P.L. 1986. Environmental variation and the coexistence of species. - In: Diamond, J. & Case, T.J. (eds), Community ecology, Harper & Row, New York, pp. 240-256.
- & Case, T.J. 1986. Overview: nonequilibrium theories: chance, variability, history, and coexistence. - In: Diamond, J. & Case, T.J. (eds.), Community ecology, Harper & Row, New York, pp. 229-239.
- & Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. - Am. Nat. 117: 923-943.

Christensen, N.L. & Peet, R.K. 1984. Convergence during secondary forest succession. - J. Ecol. 72: 25-36.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. - Carnegie Instn Wash. Publ. 242: 1-512.

Clymo, R.S. 1980. Preliminary survey of the peat-bog Hummell Knowe Moss using various numerical methods. - Vegetatio 42: 129-148.

Cody, M.L. 1986. Structural niches in plant communities. - In: Diamond, J. & Case. T.J. (eds), Community ecology, Harper & Row, New York, pp. 381-405.

Colwell, R.K. & Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. - Ecology 52: 567-576.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. - Science 199: 1302-1310.

- 1980. Diversity and the coevolution of competitors, or the ghost of competition past. - Oikos 35: 131-138.

Cormack, R.M. 1971. A review of classification. - J. r. statist. Soc. Ser. A 134: 321-353.

Cottam, G., Goff, F.G. & Whittaker, R.H. 1978. Wisconsin comparative ordination. - In: Whittaker, R.H. (ed.), Ordination of plant communities, Junk, The Hague, pp. 185-213.

Cramer, W. & Hytteborn, H. 1987. The separation of fluctuation and long-term change in vegetation dynamics of a rising seashore. - Vegetatio 69: 157-167.

Curtis, J.T. & McIntosh, R.P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. - Ecology 32: 476-496.

Czekanowski, J. 1909. Zur differential Diagnose der Neandertalgruppe. - Korrespondenzbl. dt. Ges. Anthrop. 40: 44-47.

Dahl, E. 1957. Rondane: mountain vegetation in South Norway and its relation to the environment. - Skr. norske Vidensk.-Akad. Oslo mat.-naturvid. Klasse 1956: 3: 1-374.

- 1960. Some measures of uniformity in vegetation analysis. - Ecology 41: 805-808.

- 1980. Modeller av plantesamfunn, vurdering av plantesosiologiske tabeller og bearbeiding av økologiske målinger. - Norg. Landbrukshøgsk., Ås, mimeogr.

- 1981. Økologisk analyse. - Norg. Landbrukshøgsk., Ås, mimeogr.

- 1988. Acidification of soils in the Rondane mountains, South Norway, due to acid precipitation. - Økoforsk Rapp. 1988: 1: 1-53.

- , Gjems, O. & Kielland-Lund, J. 1967. On the vegetation types of Norwegian conifer forest in relation to the chemical properties of the humus layer. - Meddr norske SkogforsVesen 85: 505-531.

- & Hadač, E. 1941. Strandgesellschaften der Insel Ostøy im Oslofjord. Eine pflanzensoziologische Studie. - Nytt Mag. Naturvid. 82: 251-312.

Dale, M.R.T. & MacIsaac, D.A. 1989 New methods for the analysis of spatial patterns in vegetation. - J. Ecol. 77: 78-91.

Dargie, T.C.D. 1984. On the integrated interpretation of indirect site ordinations: a case study using semi-arid vegetation in south-eastern Spain. - Vegetatio 55: 37-55.

Daubenmire, R. 1966. Vegetation: identification of typal communities. - Science 151: 201-298.

Dierschke, H. 1971. Stand und Aufgaben der pflanzensoziologischen Systematik in Europa. - Vegetatio 22: 255-264.

Dietvorst P., van der Maarel, E., & van der Putten, H. 1982. A new approach to the minimal area of a plant community. - Vegetatio 50: 77-91.

Digby, P.G.N. & Kempton, R.A. 1987. Multivariate analysis of ecological communities. - Chapman & Hall, London.

Dunn, G. & Everitt, B.S. 1982. An introduction to mathematical taxonomy. - Camb. Univ. Press, Cambridge.

Du Rietz, G.E. 1921. Zur metodologischen Grundlage der modernen Pflanzensoziologie. - Holzhausen, Wien.

- 1930. Classification and nomenclature of vegetation. - Svensk bot. Tidskr. 24: 489-503.

- 1932. Vegetationsforschung auf soziationsanalytischer Grundlage. - In: Abderhalden, E. (ed.), Handbuch der biologischen Arbeitsmethoden, XI, 5, Urban & Schwarzenberg, Berlin, pp. 293-480.

- 1936. Classification and nomenclature of vegetation units 1930-1935. - Svensk bot. Tidskr. 30: 580-589.

- , Fries, T.C.E., Osvald, H. & Tengwall, T.Å. 1920. Gesetze der Konstitution natürlicher Pflanzengesellschaften. - Vetensk. prakt. Unders. Lappl. Flora Fauna 7: 1-47.

- , Fries, T.C.E. & Tengwall, T.Å. 1918. Vorschlag zur Nomenklatur der Soziologischen Pflanzengeographie. - Svensk bot. Tidskr. 12: 145-170.

During, H.J. 1979. Life strategies of bryophytes: a preliminary survey. - Lindbergia 5: 2-18.

- & Willems, J.H. 1985. Diversity models applied to a chalk grassland. - Vegetatio 57: 103-114.

Eilertsen, O., Økland, R.H., Økland, T. & Pedersen, O. 1990. The effects of scale range, species removal and downweighting of rare species on eigenvalue and gradient length in DCA ordination. - J. Veg. Sci. in press.

- & Pedersen, O. 1989. Virkning av nedveiing og artsfjerning ved DCA-ordinasjon av vegetasjonsøkologiske datasett. - Univ. Trondheim VitenskMus. Rapp. bot. Ser. 1988: 1: 5-18.

Ellenberg, H. 1954. Über einige Fortschritte der kausalen Vegetationskunde. - Vegetatio 5-6: 199-211.

- 1979. Zeigerwerte der Gefässpflanzen Mitteleuropas. - Scr. geobot. 9: 1-121.

Elven, R. 1978. Association analysis of moraine vegetation at the glacier Hardangerjøkulen, Finse, South Norway. - Norw. J. Bot. 25: 171-191.

- 1980. The Omnsbreen glacier nunataks - a case study of plant immigration. - Norw. J. Bot. 25: 171-191.

Eneroth, O. 1931. Om skogstyper och föryngringsförhållanden inom Lappmarken. I. Norrl. Skogsvårdsförb. Tidskr. 1931: 113-182.

- 1934. Om skogstyper och föryngringsförhållanden inom Lappmarken. II. Norrl. Skogsvårdsförb. Tidskr. 1934: 49-83.

- 1937. Om skogstyperna och deras praktiska betydelse. - K. Lantbr.-Akad. Handl. Tidskr. 75: 821-837.

Ericson, L. 1977. The influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. - Wahlenbergia 4: 1-114.

Ernst, W. 1978. Discrepancy between ecological and physiological optima of plant species. A re-interpretation. - Oekol. pl. 175-188.

Eurola, S. 1962. Über die regionale Einteilung der südfinnischen Moore. - Annls bot. Soc. zool.-bot. fenn. Vanamo 33: 2: 1-243.

Evans F.C., & Dahl, E. 1955. The vegetational structure of an abandoned field in Southeastern Michigan and its relation to environmental factors. - Ecology 36: 685-706.

Eyre, M.D., Ball, S.G. & Foster, G.N. 1986. An initial classification of the habitats of aquatic Coleoptera in north-east England. - J. appl. Ecol. 23: 841-852.

Ezcurra, E. 1987. A comparison of reciprocal averaging and noncentered principal component analysis. - Vegetatio 71: 41-47.

Fægri, K. 1934. Über die Längenvariationen einiger Gletscher des Jostedalsbre und die dadurch bedingten Pflanzensukzessionen. - Bergens Mus. Årb. naturvid. Rekke 1933: 7: 1-255.

Faith, D.P., Minchin, P.R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. - Vegetatio 69: 57-68.

Falkengren-Grerup. U. 1986. Soil acidification and vegetation changes in deciduous forest in southern Sweden. - Oecologia (Berlin) 70: 339-347.

- , Linnermark, N. & Tyler, G. 1987. Changes in acidity and cation pools of south Swedish soils between 1949 and 1985. - Chemosphere 16: 2239-2248.

Farris, J.S. 1973. On comparing the shapes of taxonomic trees. - Syst. Zool. 22: 50-54.

Fasham, M.J.R. 1977. A comparison of non-metric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines and coenoplanes. - Ecology 58: 551-561.

Fenstad, G.U., Walløe, L. & Wille, S.Ø. 1977. Three tests for regression compared by stochastic simulation under normal and heavy tailed distribution of errors. - Scand. J. Statist. 4: 31-34.

Feoli E. & Feoli Chiapella, J. 1980. Evaluation of ordination methods through simulated coenoclines: some comments. - Vegetatio 42: 35-41.

Fewster, P.H. & Orlóci, L. 1983. On choosing a resemblance measure for non-linear predictive ordination. - Vegetatio 54: 27-35.

Fisher, R.A. 1940. The precision of discriminant functions. - Ann. Eugenics 10: 422-429.

- , Corbet, A.S. & Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. - J. Anim. Ecol. 12: 42-58.

Flatberg, K.I. 1984. A taxonomic revision of the Sphagnum imbricatum complex. - K. norske Vidensk. Selsk. Skr. 1984: 3: 1-80.

- 1986. Taxonomy, morphovariation, distribution and ecology of the Sphagnum imbricatum complex with main reference to Norway. - Gunneria 54: 1-118.

Flower, R.J. 1986. The realtionship between surface sediment diatom assemblages and pH inn 33 Galloway lakes: some regression methods for reconstructing pH and their application to sediment cores. - Hydrobiologia 143: 93-103.

Fransson, S. 1972. Myrvegetation i sydvästra Värmland. - Acta phytogeogr. suec. 57: 1-133.

Frey, T.E.A. 1978. The Finnish school and forest site-types. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 81-110.

Fries, R.E. 1950. A short history of botany in Sweden. - Almqvist & Wiksell, Uppsala.

Fries, T.C.E. 1913. Botanische Untersuchungen in nördlichsten Schweden: Ein Beitrag zur Kenntnis der alpinen und subalpinen Vegetation in Torne Lappmark. - Vetensk. prakt. Unders. Lappl. Flora Fauna 2: 1-361.

- 1925. Über primäre und sekundäre Standortbedingungen. - Svensk bot. Tidskr. 19: 49-69.

Galiano, E.F., Castro, I. & Sterling, A. 1987. A test for spatial pattern in vegetation using a Monte-Carlo simulation. - J. Ecol. 75: 915-924.

Galten, L. 1987. Numerical analysis of mire vegetation at Åsenmyra, Engerdal, Central Southern Norway and comparison with traditional Fennoscandian paludicology. - Nord. J. Bot. 7: 187-214.

Gams, H. 1918. Prinzipienfragen der Vegetationsforschung. - Vjschr. naturf. Ges. Zürich 63: 293-493.

Gauch, H.G. 1973a. A quantitative evaluation of the Bray-Curtis ordination. - Ecology 54: 829-836.
- 1973b. The relationship between sample similarity and ecological distance. - Ecology 54: 618-622.
- 1980. Rapid initial clustering of large data sets. - Vegetatio 42: 103-111.
- 1982a. Multivariate analysis in community ecology. - Camb. Stud. Ecol. 1: 1-298.
- 1982b. Noise reduction by eigenvector ordinations. - Ecology 63: 1643-1649.
- , Chase, G.B. & Whittaker, R.H. 1974. Ordination of vegetation samples by Gaussian species distributions. - Ecology 55: 1382-1390.
- & Whittaker, R.H. 1972a. Coenocline simulation. - Ecology 53: 446-451.
- & Whittaker, R.H. 1972b. Comparison of ordination techniques. - Ecology 53: 868-875.
- & Whittaker, R.H. 1976. Simulation of community patterns. - Vegetatio 33: 13-16.
- & Whittaker, R.H. 1981. Hierarchical classification of community data. - J. Ecol. 69: 537-557.
- , Whittaker, R.H. & Singer, S.B. 1981. A comparative study of nonmetric ordinations. - J. Ecol. 69: 135-152.
- , Whittaker, R.H. & Wentworth, T.R. 1977. A comparative study of reciprocal averaging and other ordination techniques. - J. Ecol. 65: 135-152.

Gibson, D.J. & Greig-Smith, P. 1986. Community pattern analysis: a method for quantifying community mosaic structure. - Vegetatio 66: 41-47.

Gibson, N. & Kirkpatrick, J.B. 1985. Vegetation and flora associated with localized snow accumulation at Mount Field West, Tasmania. - Aust. J. Ecol. 10: 91-99.

Gjærevoll, O. 1949. Snøleievegetasjonen i Oviksfjellene. - Acta phytogeogr. suec. 25: 1-106.
- 1956. The plant communities of the Scandinavian alpine snow-beds. - K. norske Vidensk. Selsk. Skr. 1956: 1: 1-405.

Gleason, H.A. 1926. The individualistic concept of the plant association. - Bull. Torrey bot. Club 53: 7-26.

Glime, J.M. & Vitt, D.H. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. - Can. J. Bot. 65: 1824-1837.

Goldberg, D.E. & Werner, P.A. 1983. Equivalent competitors in plant communities: a null hypothesis and a field experimental approach. - Am. J. Bot. 70: 1098-1104.

Goodall, D.W. 1953. Objective methods for the classification of vegetation. II. The use of positive interspecific correlation. - Aust. J. Bot. 1: 39-63.
- 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. - Aust. J. Bot. 2: 304-324.
- 1961. Objective methods for the classification of vegetation. IV. Patterns and minimal area. - Aust. J. Bot. 9: 162-196.
- 1963. The continuum and the individualistic association. - Vegetatio 11: 297-316.
- 1978a. Sample similarity and species correlation. - In: Whittaker, R.H. (ed.), Ordination of plant communities, Junk, The Hague, pp. 99-149.
- 1978b. Numerical classification. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 247-286.
- & Johnson, R.W. 1982. Non-linear ordination in several dimensions. A maximum likelihood approach. - Vegetatio 48: 197-208.
- & Johnson, R.W. 1987. Maximum likelihood ordination - some improvements and further tests. - Vegetatio 73: 3-12.

Gordon, A.D. 1981. Classification. Methods for the exploratory analysis of multivariate data. - Chapman & Hall, London.

Gourlay, A.R. & Watson, G.A. 1973. Computational methods for matrix eigen problems. - Wiley, New York.

Gower, J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. - Biometrika 53: 325-338.

- 1967. Multivariate analysis and multidimensional geometry. - Statistician 17: 13-28.
- 1971. A general coeffcient of similarity and some of its properties. - Biometrics 27: 857-871.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. - Wiley, New York.

- 1980. Multivariate approaches in ecology: the assessment of ecological similarity. - A. Rev. Ecol. Syst. 11: 1-14.

Greig-Smith, P. 1964. Quantitative plant ecology, ed. 2. - Butterworth, London.

- 1979. Pattern in vegetation. - J. Ecol. 67: 755-769.

Grime, J.P. 1973. Control of species density in herbaceous vegetation. - J. env. Mgmt 1: 151-167.

- 1979. Plant strategies and vegetation processes, Wiley, Chichester.
- & Lloyd, P.S. 1973. An ecological atlas of grassland plants. - Arnold, London.

Groenewoud, H. van. 1976. Theoretical considerations on the covariation of plant species along ecological gradients with regard to multivariate analysis. - J. Ecol. 64: 837-847.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. - Biol. Rev. Camb. phil. Soc. 52: 107-145.

- 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. - In: Diamond, J. & Case, T.J. (eds), Community ecology, Harper & Row, New York, pp. 207-225.

Haapasaari, M. 1988. The oligotrophic heath vegetation of northern Fennoscandia and its zonation. - Acta bot. fenn. 135: 1-219.

Hämet-Ahti, L. 1963. Zonation of the mountain birch forest in northernmost Fennoscandia. - Annls bot. Soc. zool. bot. fenn. Vanamo 34: 4: 1-127.

Hajdu, L.J. 1981. Graphical comparison of resemblance measures in phytosociology. - Vegetatio 48: 47-59.

Hallbäcken, L. & Tamm, C.O. 1986. Changes in soil acidity from 1927 to 1982-84 in a forest area of southwest Sweden. - Scand. J. For. Res. 1: 219-232.

Hallberg, H.P. 1971. Vegetation auf den Schalenablagerungen in Bohuslän, Schweden- . Acta phytogeogr. suec. 56: 1-136.

Halvorsen, R. 1980. Numerical analysis and successional relationships of shell-bed vegetation at Akerøya, Hvaler, SE Norway. - Norw. J. Bot. 27: 71-95.

Harper, J.L. 1977. Population biology of plants. - Academic Press, London.

- 1982. After description. - Br. ecol. Soc. spec. Publs Ser. 1: 11-25.

Heikilä, H. 1987. The vegetation and ecology of mesotrophic and eutrophic fens in western Finland. - Annls bot. fenn. 24: 155-175.

Hill, M.O. 1973. Reciprocal averaging; an eigenvector method of ordination. - J. Ecol. 61: 237-249.

- 1974. Correspondence analysis: a neglected multivariate method. - J. r. statist. Soc. Ser. C 23: 340-354.
- 1977. Use of simple discriminant functions to classify quantitative phytosociological data. - In: Diday, E., Lebart, L., Pages, J.P. & Tomassone, R. (eds), First international symposium on data analysis and informatics, Institut de recherche d'informatique et d'automatique, Le Chesnay, pp. 181-199.
- 1979a. DECORANA - A Fortran program for detrended correspondence analysis and

reciprocal averaging. - Cornell Univ., Ithaca, New York.
- 1979b. TWINSPAN - A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. - Cornell Univ., Ithaca, New York.
- , Bunce, R.G.H. & Shaw, M.W. 1975. Indicator species analysis, a divsive polythetivc method of classification, and its application to a survey of native pinewoods in Scotland. - J. Ecol. 63: 597-613.
- & Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. - Vegetatio 42: 47-58.

Hirschfeld, H.O. 1935. A connection between correlation and contingency. - Proc. Camb. phil. Soc. 31: 520-524.

Hopkins, B. 1955. The species-area relations of plant communities. - J. Ecol. 43: 409-426.

Hubálek, Z. 1982. Coeffcients of association and similarity, based on binary (presence-absence) data: an evaluation. - Biol. Rev. Camb. phil. Soc. 57: 669-689.

Hubbell, S.P. & Foster, R.B. 1986. Biology, chance, and history of the structure of tropical rain forest tree communities. - In: Diamond, J. & Case, T.J. (eds), Community ecology, Harper & Row, New York, pp. 314-329.

Hull, C.H. & Nie, N.H. 1981. SPSS. Update 7-9. New procedures and facilities for releases 7-9. - McGraw-Hill, New York.

Hult, R. 1881. Försök till analytisk behandling av växtformationerna. - Meddn Soc. Fauna Flora fenn. 8: 1-155.
- 1887. Die alpinen Pflanzenformationen des nördlichsten Finnlands. - Meddn Soc. Fauna Flora fenn. 14: 153-228.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. - Ecology 52: 577-586.

Huston, M. 1979. A general hypothesis of species diversity. - Am. Nat. 113: 81-101.
- & Smith, T. 1987. Plant succession: life history and competition. - Am. Nat. 130: 168-198.

Hutchinson, G.E. 1957. Concluding remarks. - Cold Spring Harbor Symp. quantve Biol. 22: 415-427.
- 1961. The paradox of the plankton. - Am. Nat. 95: 137-145.

Hytteborn, H. & Packham, J.R. 1985. Left to nature: forest structure and regeneration in Fiby urskog, central Sweden. - Arboricult. J. 9: 1-11.
- & Packham, J.R. 1987. Decay rate of Picea abies logs and the storm gap theory: a re-examination of Sernander plot II, Fiby urskog, central Sweden. - Arboricult. J. 11: 299-311.
- , Packham, J.R. & Verwijst, T. 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of Vallibäcken, northern Sweden. - Vegetatio 72: 3-19.

Jaccard, P. 1901. Distribution de la flora alpine dans le bassin des Dranses et dans quelques régions Voisines. - Bull. Soc. Vaudoise Sci. Nat. 37: 241-272.

Jeffrey, D.W. 1987. Soil-plant relationships. An ecological approach. - Croom Helm, London.

Jeglum, J.K., Wehrhahn, C.F. & Swan, J.M.A. 1971. Comparisons of environmental ordinations with principal component vegetational ordinations for sets of data having different degrees of complexity. - Can. J. For. Res. 1: 99-112.

Jensén, S. 1978. Influences of transformation of cover values on classification and ordination of lake vegetation. - Vegetatio 37: 19-31.

John, E. 1989. An assessment of the role of biotic interactions and dynamic processes in the organization of species in a saxicolous lichen community. - Can. J. Bot. 67:

2025-2038.

Jonasson, S. 1981. Plant communities and species distribution of low alpine Betula nana heaths in northernmost Sweden. - Vegetatio 44: 51-64.

Kalela, A. 1960. Classification of the vegetation, especially the forests, with particular reference to regional problems. - Silva fenn. 105: 40-49.

- 1961. Waldvegetationszonen Finnlands und ihre klimatischen Paralleltypen. - Archvm Soc. zool. bot. fenn. Vanamo 16: Suppl. 65-83.

Kantvilas, G. & Minchin, P.R. 1989. An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforest. - Vegetatio 84: 99-112.

Kendall, D.G. 1971a. Abundance matrices and seriation in archaeology. - Z. Wahrscheinlichkeitstheor. 17: 104-112.

- 1971b. Seriation from abundance matrices. - In: Hodson, F.R., Kendall, D.G. & Tautu, P. (eds), Mathematics in the archeological and historical sciences, Edinburgh Univ. Press, Edinburgh, pp. 215-252.

Kendall, M.G. 1938. A new measure of rank correlation. - Biometrika 30: 81-93.

Kenkel, N.C. & Orlóci, L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. - Ecology 67: 919-928.

- , Juhász-Nagy, P. & Podani, J. 1989. On sampling procedures in population and community ecology. - Vegetatio 83: 195-207.

Kennedy, K.A. & Addison, P.A. 1987. Some considerations for the use of visual estimates of plant cover in biomonitoring. - J. Ecol. 75: 151-157.

Kent, M. & Ballard, J. 1988. Trends and problems in the application of classification and ordination methods in plant ecology. - Vegetatio 78: 109-124.

Kershaw, K.A. & Looney, J.H.H. 1985. Quantitative and dynamic plant ecology, ed. 3. - Arnold, London.

Kessell, S.R. & Whittaker, R.H. 1976. Comparisons of three ordination techniques. - Vegetatio 32: 21-29.

Kielland-Lund, J. 1981. Die Waldgesellschaften SO-Norwegens. - Phytocoenologia 9: 53-250.

Knapp, R. 1948. Einführung in die Pflanzensoziologie. I. Arbeitsmethoden der Pflanzensoziologie und Eigenschaften der Pflanzengesellschaften. - Ulmer, Stuttgart.

Knox, R.G. 1989. Effects of detrending and rescaling on correspondence analysis: solution stability and accuracy. - Vegetatio 83: 129-136.

Korsmo, M. 1980. Myrvegetasjonen på Rønnåsmyra, Grue kommune, Hedmark. - Cand. real. Thesis, Univ. Trondheim, unpubl.

Kruskal, J.B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. - Psychometrika 29: 1-27.

- 1964b. Nonmetric multidimensional scaling: a numerical method. - Psychometrika 29: 115-129.

- , Young, F.W. & Seery, J.B. 1973. How to use KYST, a very flexible program to do multidimensional scaling an unfolding. - Bell Labs, Murray Hill, New Jersey, unpubl.

Kujala, V. 1936. Tutkimuksia keski-ja Pohjoissuomen välisestä kasvillisuus rajasta. - Communtnes Inst. for. fenn. 22: 4: 1-95.

- 1938. Metsätyyppien parallelisuudesta. - Communtnes Inst. for. fenn. 27: 1: 1-17.

Kulczynski, S. 1928. Die Pflanzenassoziationen der Peininen. - Bull. int. Acad. pol. Sci. Lett. Classe Sci. mat. nat. Sér. B. Sci. nat. Suppl. 2: 53-203.

Lambert, J.M., Meacock, S.E., Barrs, J. & Smartt, P.F.M. 1973. AXOR and MONIT: two new polythetic-divisive strategies for hierarchical classification. - Taxon 22: 173-176.

Lance, G.N. & Williams, W.T. 1967. A general theory of classificatory sorting strategies.

I. Hierarchical systems. - Computer J. 9: 373-380.

- & Williams, W.T. 1968. Note on a new information-statistic classificatory program. - Computer J. 11: 195.

Leemans, R. 1989. Regeneration and establishment patterns of spruce (Picea abies L.) in two southern boreal forests in Sweden. - Stud. Pl. Ecol. 18: 153-155.

Legendre, P. & Fortin, M.-J. 1989. Spatial pattern and ecological analysis. - Vegetatio 80: 107-138.

Levins, R. 1968. Evolution in changing environments. - Princeton Univ. Press, Princeton.

Lid, J. 1964. The flora of Jan Mayen. - Norsk Polarinst. Skr. 130: 1-107.

Lieffers, V.J. 1984. Emergent plant communities of oxbow lakes in northeastern Alberta: salinity, water-level fluctuation, and succession. - Can. J. Bot. 62: 310-316.

Lindholm, T. 1979. Keidasrämeen mätässammalten vuotuinen pituuskasvu Lamilla (EH). - Suo 30: 13-16.

Lindqvist, B. 1931. Den skandinaviska bokskogens biologi. - Svenska Skogsvårdsför. Tidskr. 1931: 179-532.

Louppen, J.W.M. & van der Maarel, E. 1979. CLUSLA: a computer program for clustering of large phytosociological data sets. - Vegetatio 40: 107-114.

Maarel, E. van der. 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. - Vegetatio 39: 97-114.

- 1982. On the manipulation and editing of phytosociological and ecological data. - Vegetatio 50: 71-76.

- Boot, R., Dorp, D. van & Rijntjes, J. 1985. Vegetation succession on the dunes near Oostvoorne, The Netherlands; a comparison of the vegetation in 1959 and 1980. - Vegetatio 58: 137-187.

- , Janssen, J.G.M. & Louppen, J.M.W. 1978. TABORD, a program for structuring phytosociological tables. - Vegetatio 38: 143-156.

MacArthur, R.H. 1972. Geographical ecology. - Harper & Row, New York.

- & Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. - Am. Nat. 101: 377-385.

McCune, B. & Antos, J.A. 1981. Correlations between forest layers in the Swan Valley, Montana. - Ecology 62: 1196-1204.

Machena, C. 1987. Zonation of submerged macrophyte vegetation in Lake Kariba, Zimbabwe and its ecological interpretation. - Vegetatio 73: 111-119.

McIntosh, R.P. 1967. The continuum concept of vegetation. - Bot. Rev. 33: 130-187.

- 1978. Matrix and plexus techniques. - In: Whittaker, R.H. (ed.), Ordination of plant communities, Junk, The Hague, pp. 151-184.

Mahdi, A. & Law, R. 1987. On the spatial organisation of plant species in a limestone grassland community. - J. Ecol. 75: 459-476.

Malmer, N. 1962a. Studies on mire vegetation in the Archaean area of Southwestern Götaland (South Sweden). I. Vegetation and habitat conditions on the Åkhult mire. - Opera bot. 7: 1: 1-322.

- 1962b. Studies on mire vegetation in the Archaean area of Southwestern Götaland (South Sweden). II. Distribution and seasonal variation in elementary constituents on some mire sites. - Opera bot. 7: 2: 1-67.

Malmström, C. 1949. Studier över skogstyper och trädslagsfördelning inom Västerbottens län. - Meddn St. SkogsförsInst. 37: 1-231.

Maslov, A.A. 1989. Small-scale patterns of forest plants and environmental heterogeneity. - Vegetatio 84: 1-7.

Matthews, J.A. 1979a. The vegetation of the Storbreen gletchervorfeld, Jotunheimen, Norway. - I. Introduction and approaches involving classification. - J. Biogeogr. 6:

17-47.
- 1979b. The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. II. Approaches involving ordination and general conclusions. - J. Biogeogr. 6: 133-167.

May, R.M. 1973. Stability and complexity in model ecosystems. - Princeton Univ. Press, Princeton.
- 1975. Some notes on measurements of the competition matrix, α. - Ecology 56: 737-741.

Meijer Drees, F. 1951. Capita selecta from modern plant sociology and a design for rules of phytosociological nomenclature. - Rapp. Bosbouwproefstation Bogor 52: 1-68.

Metsävainio, K. 1931. Untersuchungen über das Wurzelsystem der Moorpflanzen. - Annls bot. Soc. zool.-bot. fenn. Vanamo 1: 1-422.

Minchin, P. 1986. How to use ECOPAK: an ecological database system. - CSIRO Inst. biol. Res. Div. Wat. Land Res. techn. Mem. 86: 6: 1-138.
- 1987a. An evaluation of the relative robustness of techniques for ecological ordination. - Vegetatio 69: 89-107.
- 1987b. Simulation of multidimensionl community patterns: towards a comprehensive model. - Vegetatio 71: 145-156.
- 1989a. Montane vegetation of the Mt. Field massif, Tasmania: a test of some hypotheses about properties of community patterns. - Vegetatio 83: 97-110.
- 1989b. COMPAS - COMmunity PAttern Simulator. Version 3.0. - Dept. Biogeogr. Geomorph., Aust. natn. Univ., Canberra, unpubl.

Moral, R. del 1985. Competitive effects on the structure of subalpine meadow communities. - Can. J. Bot. 63: 1444-1452.

Moravec, J. 1973. The determination of the minimal area of phytocoenoses. - Folia geobot. & phytotax. 8: 23-47.

Mueller-Dombois, D. & Ellenberg, H. 1974. Aims and methods of vegetation ecology. - Wiley, New York.

NAVF, 1988. International evaluations: terrestrial ecology and systematics in Norway. - Council for natural Science Research, Norwegian Research Council for Science and the Humanities, Oslo.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. 1975. SPSS. Statistical package for the social sciences, ed. 2. - McGraw-Hill, New York.

Nordhagen, R. 1920. Om nomenklatur og begrepsdannelse i plantesociologien. - Nyt Mag. Naturvid. 57: 17-128.
- 1924. Om homogenitet, konstans og minimiareal. - Nytt Mag. Naturvid. 61: 1-51.
- 1928. Die Vegetation und Flora des Sylenegebietes. - Skr. norske Vidensk.-Akad. Oslo mat.-naturvid. Klasse 1927: 1: 1-612.
- 1937. Versuch einer neuen Eintilung der subalpinen-alpinen Vegetation Norwegens. - Bergens Mus. Årb. naturvid. Rekke 1936: 7: 1-88.
- 1943. Sikilsdalen og Norges fjellbeiter. - Bergens Mus. Skr. 22: 1-607.
- 1955. Kobresieto-Dryadion in Northern Scandinavia. - Svensk bot. Tidskr. 49: 63-87.

Noy-Meir, I. 1973a. Data transformations in ecological ordination. I. Some advantages of non-centering. - J. Ecol. 61: 329-341.
- 1973b. Divisive polythetic classification of vegetation data by optimized division on ordination components. - J. Ecol. 61: 753-760.
- & Maarel, E. van der 1987. Relations between community theory and community analysis in vegetation science: some historical perspectives. - Vegetatio 69: 5-15.
- , Tadmor, N.H. & Orshan, G. 1970. Association analysis of desert vegetation. - Israel J. Bot. 19: 561-591.

- , Walker, D. & Williams, W.T. 1975. Data transformation in ecological ordination. II. On the meaning of data standardization. - J. Ecol. 63: 779-800.
- & Whittaker, R.H. 1977. Continuous multivariate methods in community analysis: some problems and developments. - Vegetatio 33: 79-98.

Oberdorfer, E. 1968. Assoziation, Gebietsassoziation, Geographische Rasse. - In: Tüxen, R. (ed.), Pflanzensoziologische Systematik. Bericht über das internationale Symposium in Stolzenau/Weser 1964, der Internationalen Vereinigung für Vegetationskunde, Junk, Den Haag, pp. 124-131.

O'Connor, I. & Aarssen, L.W. 1987. Species association patterns in abandoned sand quarries. - Vegetatio 73: 101-109.

Økland, R.H. 1986a. Rescaling of ecological gradients. I. Calculation of ecological distance between vegetation stands by means of their floristic composition. - Nord. J. Bot. 6: 651-660.
- 1986b. Rescaling of ecological gradients. II. The effect of scale on symmetry of species response curves. - Nord. J. Bot. 6: 661-670.
- 1986c. Rescaling of ecological gradients. III. The effect of scale on niche breadth measurements. - Nord. J. Bot. 6: 671-677.
- 1989a. Hydromorphology and phytogeography of mires in inner Østfold and adjacent part of Akershus, SE Norway, in relation to SE Fennoscandian mires. - Opera bot. 97: 1-122.
- 1989b. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. I. Introduction, flora, vegetation and ecological conditions. - Sommerfeltia 8: 1-172.
- 1990a. A phytoecological study of the mire Northern Kisselbergmosen, Rødenes, SE Norway. II. Identification of gradients by detrended (canonical) correspondence analysis. - Nord. J. Bot. 10: in press.
- 1990b. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. III. Diversity and habitat niche relationships. - Nord. J. Bot. 10: in press.
- & Bendiksen, E. 1985. The vegetation of the forest-alpine transition in the Grunningsdalen area, Telemark, SE Norway. - Sommerfeltia 2: 1-224.

Økland, T. 1988. An ecological approach to the investigation of a beech forest in Vestfold, SE Norway. - Nord. J. Bot. 8: 375-407.
- 1989. Program "Overvåking av skogens sunnhetstilstand": Vegetasjonsøkologisk overvåking av boreal barskog i Norge. I. Rausjømarka i Akershus. - Norsk Inst. for Jord- og Skogkartlegging, Ås.

Oksanen, J. 1983. Ordination of boreal heath-like vegetation with principal component analysis, correspondence analysis and multidimensional scaling. - Vegetatio 52: 181-189.
- 1987. Problems of joint display of species and site scores in correspondence analysis. - Vegetatio 72: 51-57.
- 1988. A note on the occasional instability of detrending in correspondence analysis. - Vegetatio 74: 29-32.

Olsson, H. 1974. Studies on South Swedish sand vegetation. - Acta phytogeogr. suec. 60: 1-170.

Orlóci, L. 1967. An agglomerative method for the classification of plant communities. - J. Ecol. 55: 193-206.
- 1972. On objective functions of phytosociological resemblance. - Am. Midl. Nat. 88: 28-55.
- 1974. On information flow in ordination. - Vegetatio 29: 11-16.
- 1978. Multivariate analysis in vegetation research, ed. 2., Junk, The Hague.

Osvald, H. 1923. Die Vegetation des Hochmoores Komosse. - Svenska växtsociol. Sällsk.

Handl. 1: 1-436.

Pakarinen, P. 1976. Agglomerative clustering and factor analysis of south Finnish mire types. - Annls bot. fenn. 13: 35-41.

- & Ruuhijärvi, R. 1978. Ordination of northern Finnish peatland vegetation with factor analysis and reciprocal averaging. - Annls bot. fenn. 15: 147-157.

Palmer, M.W. 1986. Pattern in corticolous bryophyte communities of the North Carolina piedmont: do mosses see the forest or the trees? - Bryologist 89: 59-65.

Pearson, K. 1901. On lines and planes of closest fit to systems of points in space. - Phil. Mag., 6. Ser. 2: 559-572.

Peet, R.K. 1974. The measurement of species diversity. - A. Rev. Ecol. Syst. 5: 285-307.

- 1980. Ordination as a tool for analyzing complex data sets. - Vegetatio 42: 171-174.
- 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. - Vegetatio 45: 3-75.
- , Glenn-Lewin, D.C. & Wolf, J.W. 1983. Prediction of man's impact on plant species diversity: a challenge for vegetation science. In: Holzner, W., Werger, M.J.A. & Ikusima, I. (eds), Man's impact on vegetation, Junk, The Hague, pp. 41-54.
- , Knox, R.G., Case, J.S. & Allen, R.B. 1988. Putting things in order: the advantages of detrended correspondence analysis. - Am. Nat. 131: 924-934.

Pentecost, A. 1980. Aspects of competition in saxicolous lichen communities. - Lichenologist 12: 135-144.

Persson, S. 1984. Vegetation development after the exclusion of grazing cattle in a meadow area in the south of Sweden. - Vegetatio 55: 65-92.

- , Malmer, N. & Wallén, B. 1987. Leaf litter fall and soil acidity during half a cenury of secondary succession in a temperate deciduous forest. - Vegetatio 73: 31-45.

Pianka, E.R. 1973. The structure of lizard communities. - A. Rev. Ecol. Syst. 4: 53-74.

Pickett, S.T.A. 1980. Non-equilibrium coexistence of plants. - Bull. Torrey bot. Club 107: 238-248.

Pielou, E.C. 1977. Mathematical ecology. - Wiley, New York.

- 1984. The interpretation of ecological data. - Wiley, New York.

Pignatti, S. 1968. Die Inflation der höheren pflanzensoziologischen Einheiten. - In: Tüxen, R. (ed.), Pflanzensoziologische Systematik. Bericht über das internationale Symposium in Stolzenau/Weser 1964, der Internationalen Vereinigung für Vegetationskunde, Junk, Den Haag, pp. 85-88.

Platt, N.J. & Weis, I.M. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. - Am. Nat. 111: 479-513.

Podani, J. 1989. Comparison of ordinations and classificatuions of vegetation data. - Vegetatio 83: 111-128.

Poore, M.E.D. 1955a. The use of phytosociological methods in ecological investigations. I. The Braun-Blanquet system. - J. Ecol. 43: 226-244.

- 1955b. The use of phytosociological methods in ecological investigations. II. Practical issues involved in an attempt to apply the Braun-Blanquet system. - J. Ecol. 43: 245-269.
- 1955c. The use of phytosociological methods in ecological investigations. III. Practical application. - J. Ecol. 43: 606-631.
- 1956. The use of phytosociological methods in ecological investigations. IV. General discussion of phytosociological problems. - J. Ecol. 44: 28-50.
- 1962. The method of successive approximation in descriptive ecology. - Adv. ecol. Res. 1: 35-68.

Popma, J., Mucina, L. & van Tongeren, O. & van der Maarel. E, 1983. On the determination of optimal levels in phytosociological classification. - Vegetatio 52: 65-

76.

Prentice, I.C. 1977. Non-metric ordination methods in ecology. - J. Ecol. 65: 85-94.

Preston, F.W. 1948. The commonness, and rarity, of species. - Ecology 29: 254-283.

Ramensky, L.G. 1930. Zur Methodik der vergleichenden Bearbeitung und Ordnung von Pflanzenlisten und anderen Objekten, die durch mehrere, verschiedenartig wirkende Faktoren bestimmt werden. - Beitr. Biol. Pfl. 18: 269-304.

Rao, C.R. 1964. The use and interpretation of principal components analysis in applied research. - Sankhya A 26: 329-358.

Ratliff, D. & Pieper, R.D. 1981. Deciding final clusters: an approach using intra- and intercluster distances. - Vegetatio 48: 83-86.

Raunkiær, C. 1918. Recherches statistiques sur les formations vegétales. - Biol. Meddr k. danske Vidensk. Selsk. 1: 3: 1-80.

Resvoll, T.R. 1917. Om planter som passer til kort og kold sommer. - Arch. Math. Naturvid. 35: 6: 1-224.

Ripley, B. 1981. Spatial statistics. - Wiley, New York.

Robertson, P.A., MacKenzie, M.D. & Elliot, L.F. 1984. Gradient analysis and classification of the woody vegetation for four sites in southern Illinois and adjacent Missouri. - Vegetatio 58: 87-104.

Rørslett, B. 1982. Ordinasjon - hvorfor går det galt? - K. norske Vidensk. Selsk. Mus. Rapp. bot. Ser. 1982: 8: 154-165.

Rogers, R.S. 1983. Small area coexistence of forest vernal herbs: does functional similarity of plants matter? - Am. Nat. 121: 835-850.

Root, R. 1967. The niche exploitation pattern of the blue-grey gnatcatcher. - Ecol. Monogr. 37: 317-350.

Roux, C. & Rieux, R. 1981. L'aire minimale des peuplements lichèniques saxicoles-calcicoles. - Vegetatio 44: 65-76.

Ruuhijärvi, R. 1960. Über die regionale Einteilung der nordfinnischen Moore. - Annls bot. Soc. zool. bot. fenn. Vanamo 31: 1: 1-360.

Rydgren, K. 1989. Urterike granskoger i Brønnøy kommune, Nordland. En vegetasjonsøkologisk undersøkelse med vekt på metodiske aspekter. - Cand. scient. Thesis, Univ. Oslo, unpubl.

Rydin, H. 1985. Effect of water level on desiccation of Sphagnum in relation to surrounding Sphagna. - Oikos 45: 374-379.

- 1986. Competition and niche separation in Sphagnum. - Can. J. Bot. 64: 1817-1824.

- & Borgegård, S.O. 1988. Plant species richness on islands over a century of primary succession: Lake Hjälmaren. - Ecology 69: 916-927.

Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. - Am. Nat. 111: 337-359.

- 1982. Stock-recruit relationships and regional coexistence in a lottery competitive system: a simulation study. - Am. Nat. 120: 139-159.

Schaetzl, R.J., Burns, S.F., Johnson, D.L. & Small, T.W. 1989. Tree uprooting: review of impacts on forest ecology. - Vegetatio 79: 165-176.

Schafale, M. & Christensen, N.C. 1986. Vegetational variation among old fields in Piedmont North Carolina. - Bull. Torrey bot. Club 113: 413-420.

Schönemann, P.H. & Carroll, R.M. 1970. Fitting one matrix to another under choice of a central dilation and a rigid motion. - Psychometrika 35: 245-255.

Schuster, R.M. 1957. Boreal Hepaticae, a manual of the liverworts of Minnesota and adjacent regions. II. Ecology. - Am. Midl. Nat. 57: 203-299.

- 1966. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. 1. - Columbia Univ. Press, New York.

Sernander, R. 1936. Granskär och Fiby urskog. - Acta phytogeogr. suec. 8: 1-232.

Shannon, C.E. & Weaver, W. 1949. The mathematical theory of communication. - Univ. Ill. Press, Urbana, Ill.

Shimwell, D. 1971. The description and classification of vegetation. - Sidgwick & Jackson, London.

Shipley, B. & Keddy, P.A. 1987. The individualistic and community-unit concepts as falsifiable hypotheses. - Vegetatio 69: 47-55.

Shmida, A. & Ellner, S. 1984. Coexistence of plants with similar niches. - Vegetatio 58: 29-55.

- & Wilson, M.V. 1985. Biological determinants of species diversity. - J. Biogeogr. 12: 1-20.

Sibson, R. 1972. Order invariant methods for data analysis. - J. r. statist. Soc. Ser. B 34: 311-349.

Siira, J. 1970. Studies in the ecology of the sea-shore meadows of the Bothnian Bay with special reference to the Liminka area. - Aquilo Ser. bot. 9: 1-109.

Silvertown, J.W. 1983. The distribution of plants in limestone pavements: tests of species interaction and niche separation against null hypotheses. - J. Ecol. 71: 819-828.

- & Law, R. 1987. Do plants need niches? Some recent developments in plant community ecology. - Trends Ecol. Evol. 2: 24-26.

Singsaas, S. 1989. Classification and ordination of the mire vegetation of Stormyra near Tynset, S Norway. - Nord. J. Bot. 9: 413-423.

Sjörs, H. 1948. Myrvegetation i Bergslagen. - Acta phytogeogr. suec. 21: 1-299.

Skre, O. 1979. The regional distribution of vascular plants in Scandinavia with requirements for high summer temperatures. - Norw. J. Bot. 26: 295-318.

Smartt, P.F.M. & Grainger, J.E.A. 1974. Sampling for vegetation survey: some aspects of the behaviour of unrestricted, restricted and stratified techniques. - J. Biogeogr. 1: 193-206.

- , Meacock, S.E. & Lambert, J.M. 1974. Investigations into the properties of quantitative vegetational data. - J. Ecol. 62: 735-759.

- , Meacock, S.E. & Lambert, J.M. 1974. Investigations into the properties of quantitative vegetational data. II. Further data type comparisons. - J. Ecol. 64: 47-78.

Sneath, P.H.A. & Sokal, R.R. 1973. Numerical taxonomy. - Freeman, San Fransisco.

Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. - Nord. J. Bot. 8: 89-97.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of the vegetation on Danish commons. - Biol. Skr. k. danske Vidensk. Selsk. 5: 4: 1-34.

Sokal, R.R. 1961. Distance as a measure of taxonomic similarity. - Syst. Zool. 10: 70-79.

- & Michener, C.D. 1958. A statistic method for evaluating systematic relationships. - Univ. Kansas Sci. Bull. 38: 1409-1438.

& Rohlf, F.J. 1962. The comparison of dendrograms by objective methods. - Taxon 11: 33-40.

- & Rohlf, F.J. 1981. Biometry, ed. 2. - Freeman, New York.

Steijlen, I. & Zachrisson, O. 1987. Long-term regeneration dynamics and successional trends in a northern Swedish coniferous forest stand. - Can. J. Bot. 65: 839-848.

Stevenson, A.C., Birks, H.J.B., Flower, R.J. & Battarbee, R.W. 1989. Diatom-based pH reconstruction of lake acidification using canonical correspondence analysis. - Ambio 18: 228-233.

Sunding, P. 1985. Faste analyseruter og vegetasjonsforandringer - hva er gjort i SØ-Norge?

- K. norske Vidensk. Selsk. Mus. Rapp. bot. Ser. 1985: 2: 74-78.

Sverdrup. E. 1973. Lov og tilfeldighet. I. - Universitetsforlaget, Oslo.

Swan, J.M.A. 1970. An examination of some ordination problems by use of simulated vegetation data. - Ecology 51: 89-102.

Tilman, 1982. Resource competition and community structure. - Princeton Univ. Press, Princeton.

Tolonen, K. 1971. On the regeneration of Northeuropaean bogs. I. Klaukkalan Isosuo in S. Finland. - Acta agr. fenn. 123: 143-166.

Tongeren, O.F.R. van 1986. FLEXCLUS, an interactive program for classification and tabulation of ecological data. - Acta bot. neerl. 35: 137-142.

- 1987. Cluster analysis. - In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.), Data analysis in community and landscape ecology, Pudoc, Wageningen, pp. 174-212.

Trass, H. & Malmer, N. 1978. North European approaches to classification. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 201-245.

Tuomikoski, R. 1942. Untersuchungen über die Untervegetation der Bruchmoore in Ostfinnland. I. Zur Methodik der pflanzensoziologischen Systematik. - Annls bot. Soc. zool.-bot. fenn. Vanamo 17: 1: 1-203.

Turkington, R., Cavers, P.B. & Aarssen, L.W. 1977. Neighbor relationships in grass-legume communities. I. Interspecific contacts in four grassland communities near London, Ontario. - Can. J. Bot. 55: 2701-2711.

- & Harper, J.L. 1979a. The growth, distribution and neighbour relationships of Trifolium repens in a permanent pasture. I. Ordination, pattern and contact. - J. Ecol. 67: 201-218.

- & Harper, J.L. 1979b. The growth, distribution and neighbour relationships of Trifolium repens in a permanent pasture. II. Inter- and intra-specific contact. - J. Ecol. 67: 219-230.

Tyler, C. 1979. Schoenus vegetation and environmental conditions in South and Southeast Sweden. - Vegetatio 41: 155-170.

- 1981. Soil acidity and distribution of species on tussocks and interspaces in Schoenus vegetation of South and Southeast Sweden. - Vegetatio 44: 25-35.

Vallin, H. 1974. Vegetation changes in a moss cushion during 50 years. - Svensk bot. Tidskr. 68: 169-191.

Vevle, O. 1983. Norwegian vegetation types. A preliminary survey of higher syntaxa. - Tuexenia 3: 169-178.

- & Aase, K. 1980. Om bruk av økologiske faktortall i norske plantesamfunn. - K. norske Vidensk. Selsk. Mus. Rapp. bot. Ser. 1980: 5: 178-201.

Vitt, D.H., Glime, J.M. & LaFarge-England, C. 1986. Bryophyte vegetation and habitat gradients of montane streams in western Canada. - Hikobia 9: 367-385.

- & Slack, N.G. 1984. Niche diversification of Sphagnum relative to environmental factors in northern Minnesota peatlands. - Can. J. Bot. 62: 1409-1430.

Wallén, B., Falkengren-Grerup, U. & Malmer, N. 1988. Biomass, productivity and relative rate of photosynthesis of Sphagnum at different water levels on a South Swedish peat bog. - Holarct. Ecol. 11: 70-76.

Ward, J.H. 1963. Hierarchical grouping to optimize an objective function. - Am. statist. Ass. J. 58: 236-244.

Wartenberg, D., Ferson, S. & Rohlf, F.J. 1987. Putting things in order: a critique of detrended correspondence analysis. - Am. Nat. 129: 434-448.

Watson, M.A. 1980a. Patterns of habitat occupation in mosses - relevance to considerations of the niche. - Bull. Torrey bot. Club 107: 346-372.

- 1980b. Shifts in patterns of microhabitat occupation by six closely related species of mosses along a complex altitudinal gradient. - Oecologia (Berlin) 47: 46-55.
- 1981. Patterns of micro habitat occupation of six closely related species of mosses along a complex altitudinal gradient. - Ecology 62: 1067-1078.

Watt, A.S. 1947. Pattern and process in the plant community. - J. Ecol. 35: 1-22.

Webb, D.A. 1954. Is the classification of plant communities either possible or desirable? - Bot. Tidsskr. 51: 362-370.

Webb, L.J., Tracey, J.G., Williams, W.T. & Lance, G.N. 1967. Studies in the numerical analysis of complex rain forest communities. II. The problem of species-sampling. - J. Ecol. 55: 525-538.

Werner, P.A. 1976. Ecology of plant populations in successional environments. - Syst. Bot. 1: 246-248.

Westhoff, V. & van der Maarel, E. 1978. The Braun-Blanquet approach. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 287-399.

White, J.A. & Glenn-Lewin, D.C. 1984. Regional and local variation in tallgrass prairie remnants of Iowa and eastern Nebraska. - Vegetatio 57: 65-78.

Whittaker, R.H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. - Ecol. Monogr. 22: 1-44.

- 1956. Vegetation of the Great Smoky Mountains. - Ecol. Monogr. 26: 1-80.
- 1960. Vegetation of the Siskiyou Mountains, Oregon and California. - Ecol. Monogr. 30: 279-338.
- 1962. Classification of natural communities. - Bot. Rev. 28: 1-239.
- 1967. Gradient analysis of vegetation. - Biol. Rev. Camb. phil. Soc. 42: 207-264.
- 1969. Evolution of diversity in plant communities. - Brookhaven Symp. Biol. 22: 178-196.
- 1972. Evolution and measurement of species diversity. - Taxon 21: 213-251.
- 1977. Evolution of species diversity in land communities. - Evol. Biol. 10: 1-67.
- 1978a. Direct gradient analysis. - In: Whittaker, R.H. (ed.), Ordination of plant communities, Junk, The Hague, pp. 7-50.
- 1978b. Approaches to classifying vegetation. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 1-31.
- 1978c. Dominance-types. - In: Whittaker, R.H. (ed.), Classification of plant communities, Junk, The Hague, pp. 65-79.
- & Gauch, H.G., Jr. 1978. Evaluation of ordination techniques. - In: Whittaker, R.H. (ed.), Ordination of plant communities, Junk, The Hague, pp. 277-336.
- & Levin, S.A. 1977. The role of mosaic phenomena in natural communities. - Theor. Pop. Biol. 12: 117-139.
- , Levin, S.A. & Root, R.B. 1973. Niche, habitat and ecotope. - Am. Nat. 107: 321-338.

Wielgolaski, F.E. 1978. Planter og omgivelser. - Universitetsforlaget, Oslo.

Wiens, J.A. 1977. On competition and variable environments. - Am. Sci. 65: 590-597.

Wijk, S. 1986. Performance of Salix herbacea in an alpine snow-bed gradient. - J. Ecol. 74: 675-684.

Wildi, O. 1980. Management and multivariate analysis of large data sets in vegetation research. - Vegetatio 42: 175-180.

Williams, W.T. & Dale, M.B. 1965. Fundamental problems in numerical taxonomy. - Adv. bot. Res. 2: 35-68.

- & Lambert, J.M. 1959. Multivariate methods in plant ecology. I. Association-analysis in plant communities. - J. Ecol. 47: 83-101.
- & Lambert, J.M. 1960. Multivariate methods in plant ecology. II. The use of an

electronic digital computer for association-analysis. - J. Ecol. 48: 689-710.
- , Lambert, J.M. & Lance, G.N. 1966. Multivariate methods in plant ecology. V. similarity analyses and information-analysis. - J. Ecol. 54: 427-445.
- , Lance, G.N., Webb, L.J. & Tracey, J.G. 1973. Studies in the numerical analysis of complex rain-forest communities. VI. Models for the classification of quantitative data. - J. Ecol. 61: 47-70.

Willamson, M.H. 1978. The ordination of incidence data. - J. Ecol. 66: 911-920.
- 1987. Are communities ever stable? - In: Gray, A.J., Crawley, M.J. & Edwards, P.J. (eds), Colonization, succession and stability, Blackwell, Oxford, pp. 353-371.

Wilson, M.V. & Mohler, C.L. 1983. Measuring compositional change along gradients. - Vegetatio 54: 129-141.

Wilson, S.D. & Keddy, P.A. 1986. Species competitive ability and position along a natural stress/disturbance gradient. - Ecology 67: 1236-1242.

Wishart, D. 1978. CLUSTAN user manual, ed. 3. - Edinburgh Univ., Edinburgh.

Yates, F. 1934. Contingency tables involving small numbers and the χ^2 test. - J. r. statist. Soc. Suppl. 1: 217-235.

Yodzis, P. 1986. Competition, mortality, and community structure. - In: Diamond, J. & Case, T.J. (eds), Community ecology, Harper & Row, New York, pp. 480-491.

Zhang, L. 1983. Vegetation ecology and population biology of Fritillaria meleagris L. at the Kungsängen Nature Reserve, Eastern Sweden. - Acta phytogeogr. suec. 73: 1-96.

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