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11

R.H. Økland (ed.)

Evolution in higher plants: patterns and processes

Papers and posters presented on a symposium
arranged on occasion of the 175th anniversary
of the Botanical Garden in Oslo,
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1990

sommerfeltia

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CONTENTS

MYOSOTIS BALTICA - A QUESTIONABLE TAXON

K. Apelgren

Apelgren, K. 1990. *Myosotis baltica* - a questionable taxon. - Sommerfeltia 11: 5-11. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

Some problems in the *Myosotis laxa* group are surveyed. The relationship between *M. baltica* Sam. and *M. caespitosa* C.F. Schulz in the Baltic land-uplift area is particularly addressed. Studied aspects include morphological variation, chromosome numbers, reproductive system, and ecology. In the studied area, the "*M. baltica* type" and the "*M. caespitosa* type" seem to be connected through complex series of intermediate forms. It is not unlikely that the "*M. baltica* type" has evolved from the "*M. caespitosa* type", one or several times, as an adaptation to coastal conditions.

Keywords: Baltic land-uplift area, Clinal variation, *Myosotis*, Taxonomy.

Karin Apelgren, Department of Systematic Botany, Uppsala University, Box 541, S-751 21 Uppsala, Sweden.

INTRODUCTION

Many botanists have noticed the large amount of variation within the *Myosotis laxa* group. This variation seems to be particularly pronounced in the Baltic land-uplift area. The Finnish botanist Harald Lindberg was the first to notice a special form in this area, identified by him as the North American taxon *Myosotis laxa* (Lindberg 1915). This identification was not generally accepted. Samuelsson (1926) stressed that this form was distinct from *M. laxa*, and he described it as a new species, *Myosotis baltica.* Lindberg (1933) later accepted that his *M. laxa* from the SW Finnish archipelago corresponded to Samuelsson's *M. baltica* from the Swedish side of the Baltic Sea.

I am studying the *Myosotis laxa* group in the Baltic land-uplift area. This study is part of an investigation of groups of species which occur in different forms on sea-shores and inland habitats in the Baltic area. In addition to the *M. laxa* group, the *Valeriana officinalis* complex and *Galium palustre* s.lat. are included in the investigation (Apelgren 1983, 1986, 1987).

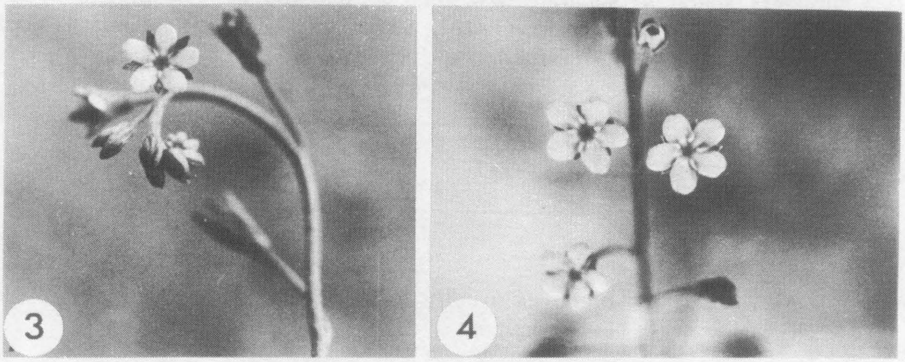
The *Myosotis laxa* group is usually considered to consist of three taxa: *M. laxa* Lehm., *M. caespitosa* C.F. Schulz, and *M. baltica* Sam. *M. laxa* occurs in North America and perhaps also in Europe (Grau & Merxmüller 1972, Hultén & Fries 1986). *M. caespitosa* is distributed throughout Europe and in Asia (Hultén & Fries 1986). It is fairly common in the Nordic countries. *M. baltica* has been recorded from the Baltic land-uplift area. Forms which have been attributed to *M. baltica* have also been found on the Swedish west coast and in Norway (Hultén 1971, Alm et al. 1987). An important question is whether the "*M. baltica* type" has evolved one or several times (Apelgren 1986, Jonsell 1988).

The purpose of this paper is to give a brief survey of the results of the study of the *Myosotis laxa* group. The study was presented as a poster at the symposium "Evolution in higher plants: patterns and processes".

MATERIALS

This paper is based on a study of 48 populations of *M. laxa* s. lat. collected in the Baltic land-uplift area in Sweden and on Åland, Finland. The material was collected in 1984-1988. At least five individuals from each population were cultivated in the Botanic Garden in Uppsala. Herbarium specimens of *M. laxa* s. lat. from GB, H, LD, S, TUR, TURA, UME, and UPS were also studied.

Figs 1-2. *Myosotis laxa* s. lat., whole plants. Fig. 1. The "*M. baltica* type", collected on a sea shore meadow on Åland, Finland. Fig. 2. The "*M. caespitosa* type", collected on a lake shore in E Central Sweden.



Figs 3-4. Corollas of *Myosotis laxa* s. lat. Notice how much of the calyx that is visible from above. Fig. 3. The "*M. baltica* type". Fig. 4. The "*M. caespitosa* type".

RESULTS AND DISCUSSION: COMPARISON OF *M. CAESPITOSA* AND *M. BALTICA*

Ecology and distribution

In the Nordic countries, the "*M. caespitosa* type" usually grows in damp inland sites, less often on sheltered sea-shores. The "*M. baltica* type" is mostly restricted to the coast, growing among *Phragmites australis*, on drift-lines, or close to rock-pools. They often grow on fairly nitrogen-rich soils, associated with *Galeopsis bifida*, *Atriplex* spp. and *Chenopodi-*

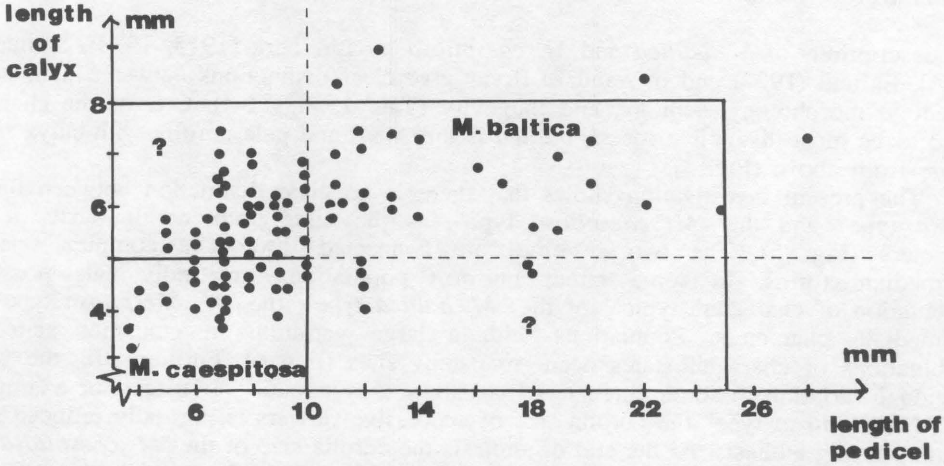


Fig. 5. Variation in calyx and pedicel lengths in 100 herbarium specimens of *Myosotis laxa* s. lat. from Åland, Finland. The lines represent the largest value for each character for *M. caespitosa* and *M. baltica* respectively, referred to in the literature (see Tab. 1).

Tab. 1. Characters stated to separate *Myosotis baltica* and *M. caespitosa*, according to Lindberg (1915, 1933), Samuelsson (1926), Eklund (1927) and standard floras. The chromosome numbers refer to Merxmüller and Grau (1963), Przywara (1978), and Uotila & Pellinen (1985).

Character	*M. baltica*	*M. caespitosa*
longevity	annual	biennial
branching	branches usually in the lower half	branches usually in the upper half
corolla size	< 4 mm	4-5 mm
corolla colour	pale blue - white	(sky) blue
calyx length	elongating after anthesis, up to 8 mm	< 5 mm
pedicel length	elongating after anthesis, up to 25 mm	< 10 mm
fruit size	< 2.5 x 1.4 mm	< 1.5 x 1.0 mm
chromosome number	2n = 88	2n = (22, 44), 88

um spp. (Apelgren 1986). This distribution indicates dispersal by birds and/or sea currents.

Morphology

The descriptions of *M. baltica* and *M. caespitosa* by Lindberg (1915, 1933), Samuelsson (1926), Eklund (1927) and in standard floras give clear distinctions between them with respect to morphology, ecology, and longevity (Tab. 1, Figs 1-4). One of the characters stated to be most distinctive for *M. baltica* is the small and pale corolla with calyx readily visible from above (Fig. 3).

The present investigation shows that there is no clear distinction between the "*M. baltica* type" and the "*M. caespitosa* type", as they intergrade continuously in most characters (Fig. 5). The two extremes are connected through a complex series of intermediate forms. In some rather uniform populations the individuals possess a combination of characters typical of the "*M. baltica* type", the "*M. caespitosa* type", and intermediate characters. Populations with a large variation in character states and combinations of character states occur in patchy sites (Fig. 6). Furthermore, the within-individual variation in some characters may show a systematic variation. For example, in the "*M. caespitosa* type" the corolla size of successive flowers is normally reduced ca. 40 per cent during anthesis. At the end of anthesis the corolla size of the "*M. caespitosa* type" is the same as in the "*M. baltica* type" (Fig. 7). A reduction in flower size during anthesis also occurs in the "*M. baltica* type" as well as in several other *Myosotis* species.

Fig. 6. The "*Myosotis baltica* type" (to the left), the "*M. caespitosa* type" (to the right), and intermediates, in one sea shore collection from Åland, Finland. All individuals were growing within 1 m^2.

Life history, cytology and reproduction

M. caespitosa is stated to be biennial, *M. baltica* to be annual (Lindberg 1915). In cultivation the "*M. baltica* type" started flowering about two weeks earlier than the "*M. caespitosa* type". Both types completed their life-cycles within the first year. All individuals of the "*M. caespitosa* type" and only a few of the "*M. baltica* type" survived until the next year. Thus the "*M. caespitosa* type" is perennial, the "*M. baltica* type" is mostly annual.

The chromosome number is 2n = c. 88 for both types in the Baltic land-uplift area.

Both types are fully self-fertile and self-pollination is probably common. In spite of this, hybridization may play a role in sustaining the pattern of variation. Autogamic annuals are able to differentiate fairly rapidly (Jonsell 1988). The "*M. baltica* type" fits well into this model.

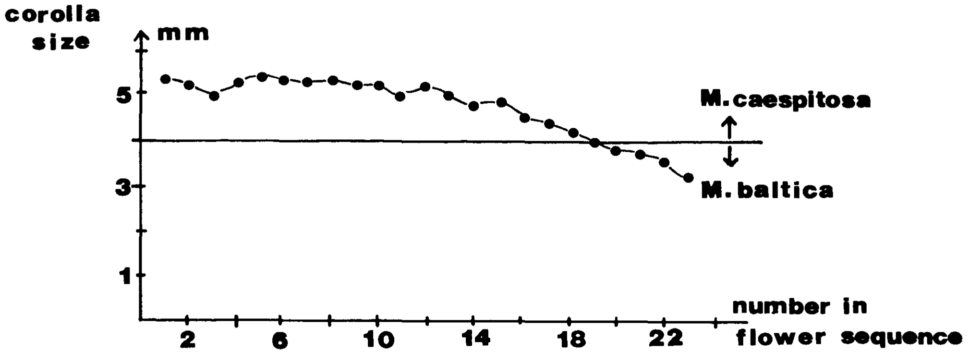


Fig. 7. Reduction in corolla size of successive flowers during the anthesis in one individual of *Myosotis caespitosa*.

CONCLUSIONS

The "*M. baltica* type" may have evolved from the "*M. caespitosa* type", one or several times as an adaptation to the instable, fluctuating conditions of the coastal ecosystem in the Baltic land-uplift area. Adaptations may include: (1) flowers at nodes in the lower parts of the plant, (2) anthesis starting soon after germination, (3) fruits ripening quickly, (4) annual life cycle, (5) autogamy, and (6) rather large fruits. A plausible conclusion is that the name *Myosotis baltica* refers to some extreme populations growing in coastal areas.

The taxonomic treatment of the *M. laxa* group, especially the "*M. baltica* type" will be discussed in detail in forthcoming papers concerning *M. laxa* s. lat. in the Baltic land-uplift area (Apelgren, in prep.).

ACKNOWLEDGEMENTS

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DIFFERENTIATION OF FLOWERS AND INFLORESCENCES OF URTICALES IN RELATION TO THEIR PROTECTION AGAINST BREEDING INSECTS AND TO POLLINATION

C.C. Berg

Berg, C.C. 1990. Differentiation of flowers and inflorescences of Urticales in relation to their protection against breeding insects and to pollination. - Sommerfeltia 11: 13-34. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

The inflorescences of Urticales are very diverse, ranging from simple to highly complex as a result of various processes: condensation, change from bisexual to unisexual, and fusion and reduction of flowers and floral parts. This diversity can be partly related to protection of inflorescences, flowers, and floral parts against phytophagy by breeding insects. A broad array of features which can be regarded as playing a role in such protection is found in Urticales. It comprises among others sexuality of inflorescences and flowers, separation of staminate and pistillate flowers, fusion of floral parts and flowers, "peltation" of perianths and bracts, various types of indumentum and bracts. These are listed, discussed, and compared with traits in other plant groups. Moreover, this protection appears to be related to pollination based on insects breeding in staminate inflorescences.

Keywords: Differentiation, Pollination, Protection, Urticales.

C.C. Berg, Botanical Institute, Arboretum and Botanical Garden (ARBOHA), University of Bergen, N-5067 Store Milde, Norway.

INTRODUCTION

The inflorescences of the Urticales, in particular those of the Moraceae, are very diverse, ranging from simple and branched to complex and condensed ones. The latter represent some of the most advanced types of inflorescences encountered among angiosperms.

The patterns and pathways in the morphological differentiation of inflorescences and flowers of Urticales can be ± precisely indicated (cf. Berg 1977a, 1989a). Certain patterns and traits of this differentiation can be related to anemophily (cf. Berg 1989a) and/or less clearly to certain modes of dispersal (cf. Berg 1983). But these relations between morphology and function are so limited that one could wonder whether the morphological differentiation of inflorescences and flowers in Urticales is the result of ± "autonomous" processes (cf. Berg 1977a) in a spacious "patio ludens" of evolution (van Steenis 1981). However, a more satisfactory and overall explanation of the functional significance of the morphological differentiation of Urticalean flowers and inflorescences may be achieved by including two related matters I touched upon in two previous papers (Berg 1989a, 1989b): protection against phytophagy by insects breeding in inflorescences and pollination by breeding insects.

These two subjects will be treated and discussed in more detail in the present paper.

RESULTS AND OBSERVATIONS

Main lines in the morphological differentiation of inflorescences and flowers

Flowers

The main lines of the floral differentiation in the order are presented in Fig. 1.

The flower of Urticales is commonly unisexual, 4- and 5-merous with simple tepaloid perianth, and has a uniovular pseudomonomerous gynoecium. In some Ulmaceae (e.g., *Ampelocera*) and in a few Urticaceae (e.g. *Parietaria* spp.) the flowers are bisexual. The number of fully developed tepals may be reduced to two. The perianth may become abortive or entirely suppressed, both in staminate flowers (e.g., in *Brosimum*) and pistillate flowers (e.g., in *Phenax* and *Treculia*). The number of stamens may be reduced to one (e.g., in *Coussapoa* and *Forsskaolea*).

Inflorescences

The inflorescence of the Urticales appears to be basically: cymose, bisexual (mostly with unisexual flowers), bracteate, and "dorsi-ventrally" flattened with the flowers pointing upwards.

Condensation into glomerules, spikes (or spadices), ± globose-capitate or discoid-capitate heads is a general trend in the differentiation of the inflorescences of Urticales. It is more pronounced in pistillate inflorescences than in staminate ones. However, there appears to be a less common opposite trend in pistillate inflorescences with fleshy fruits and/or fleshy fruiting perianths: isolation of pistillate flowers by spacing, usually in combination with the occurrence of pedicels or by uniflory of the inflorescence.

Another common trait is the frequent change from the bisexual to the unisexual state of the inflorescence.

Connation of pistillate flowers and fusion of such flowers with the receptacle is only found in Moraceae and appears to be correlated with macrospermy (cf. Berg 1983). Connation of perianths of staminate flowers or fusion of perianths of such flowers with the receptacle is exceptional (occurring in some species of *Naucleopsis* and in *Cecropia purpurascens*).

The inflorescences of Ulmaceae are mostly unisexual and simple, shortly branched or glomerate. Those of Cannabaceae are unisexual and ± loosely branched, but catkin-like condensed in pistillate inflorescences of *Humulus*. In Urticaceae the inflorescences are more diverse, bisexual or unisexual, ranging from richly branched with the flowers loosely arranged (as in *Pilea* spp.) or in terminal globose heads (as in *Debregeasia*) to ± condensed ones: spicate (as in *Myriocarpa*), glomerate (as in *Phenax*), globose-capitate (as in *Leucosyce*), discoid-capitate, whether or not (sub)involucrate (as in *Elatostema* and *Procris*), or with an urceolate receptacle (in *Elatostema ficoides*).

More condensed and complex inflorescences occur to a greater extent in the two following mainly entomophilous families than in the former three anemophilous families.

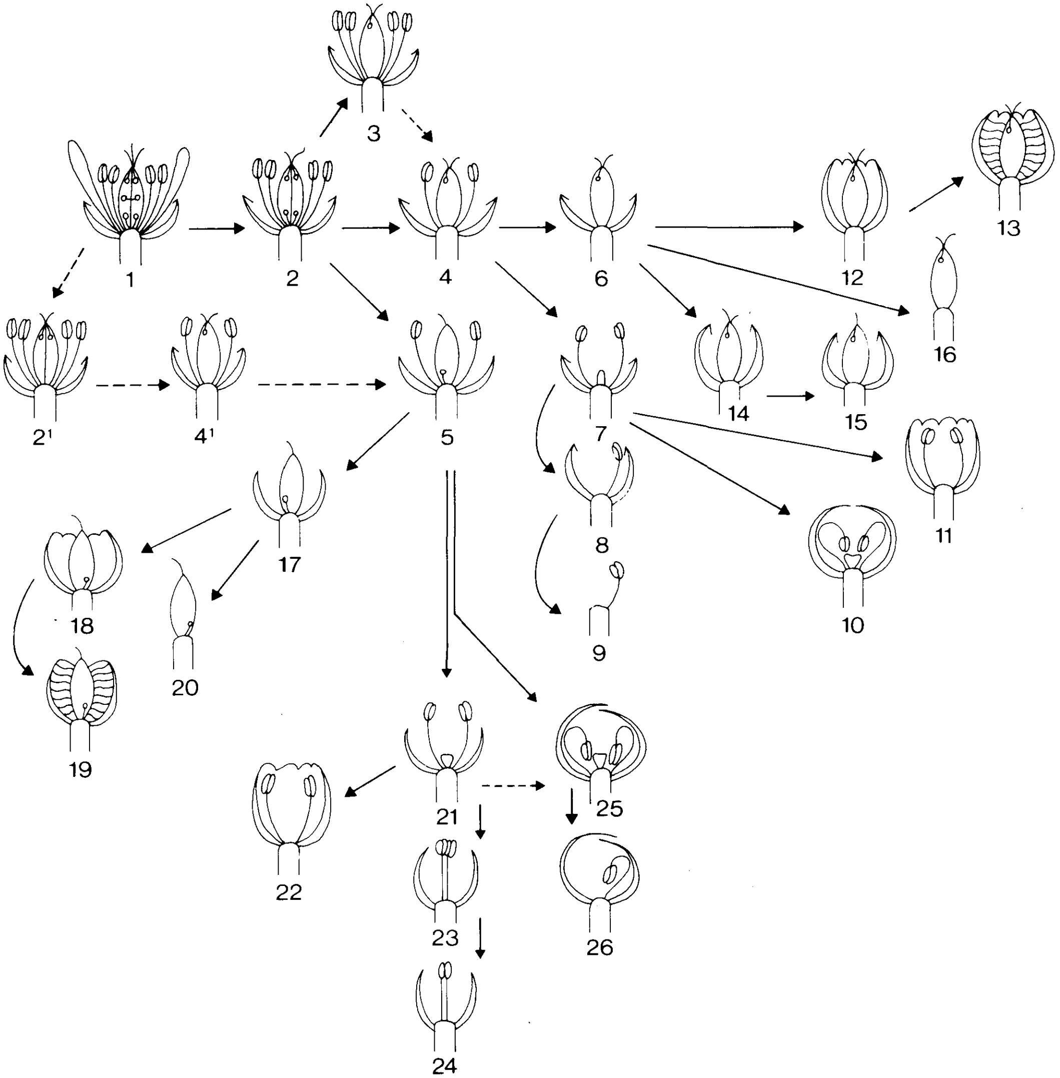

Fig. 1. Schematic drawings of flowers of Urticales, showing main trends of differentiation. (1-2) hypothetical; (2') Ulmaceae occasionally; (3) Ulmaceae p.p.; (4 and 4') Ulmaceae and *Ficus* sect. *Svcidium* p.p.; (5) some Urticaceae; (6-7) Ulmaceae p.p., Moraceae p.p. and Cannabaceae; (8-9) Moraceae p.p.; (10) Moraceae: Moreae p.p.; (11) Moraceae p.p.; (12-16) Moraceae p.p.; (17) Urticaceae p.p.; (18) Urticaceae p.p. and Cecropiaceae p.p.; (19) Urticaceae p.p. and Cecropiaceae: *Myrianthus*; (20) Urticaceae p.p.; (21-22) Cecropiaceae p.p.; (23) Cecropiaceae: *Coussapoa* p.p. and *Pourouma napoensis*; (24) *Coussapoa* p.p.; (25) Urticaceae p.p.; (26) Urticaceae: Forsskaoleae. (With permission of Oxford University Press, see acknowledgements).

The main lines of the differentiation in the inflorescences of Cecropiaceae are presented in Figs 2-4. In all taxa of this family the staminate inflorescences are branched

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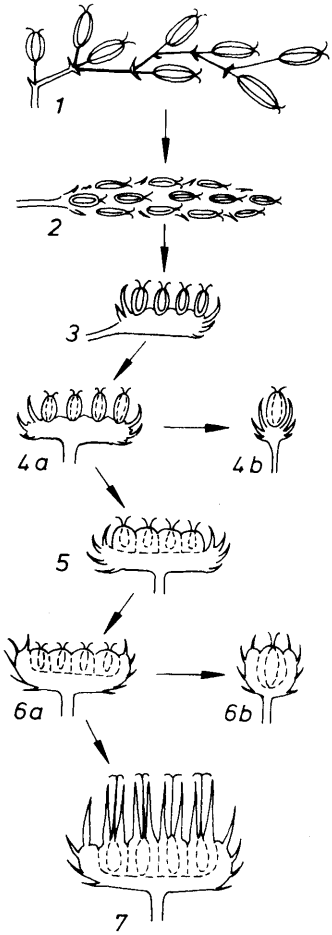

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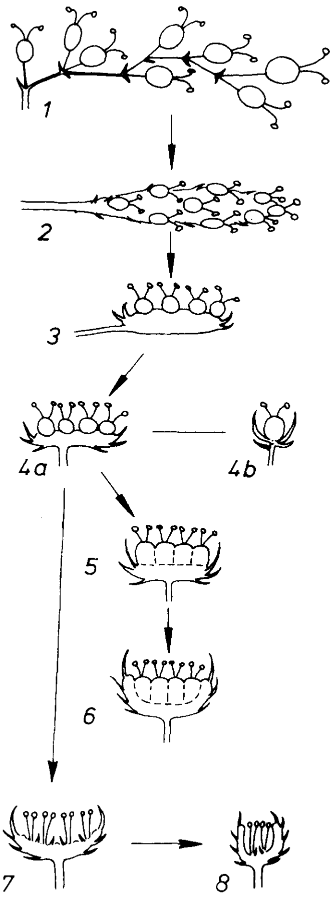


Figs 2-3. Schematic drawings of inflorescences of Castilleae (Moraceae), showing some trends of differentiation. Fig. 2. Pistillate inflorescences. (1-3) hypothetical; (4a) *Perebea, Helicostylis*, etc.; (4b) *Pseudolmedia, Perebea*, etc.; (5) *Perebea, Castilla*, etc.; (6a) *Castilla*; (6b) *Antiaris* and *Mesogyne*; (7) *Naucleopsis*. Fig. 3. Staminate inflorescences. (1-3) hypothetical; (4a) *Perebea, Maquira*, etc.; (4b) *Perebea humilis*; (5) *Helicostylis*; (6) *Naucleopsis*; (7) *Pseudolmedia*; (8) *Castilla*. (With permission of Springer-Verlag and Oxford University Press, see acknowledgements).

with the flowers ± loosely arranged or in spicate or globose-capitate partial inflorescences. With the exception of *Pourouma*, the pistillate flowers are crowded in spicate or globose-capitate inflorescences or in partial inflorescences.

The greatest diversity of inflorescences is found in the Moraceae. The inflorescences are either bisexual or unisexual. Branched inflorescences, mostly racemes, are not common. The majority of the Moraceae have ± strongly condensed inflorescences: spikes, globose-capitate (or subspicate) heads, discoid heads, involucrate or not and with receptacle varying

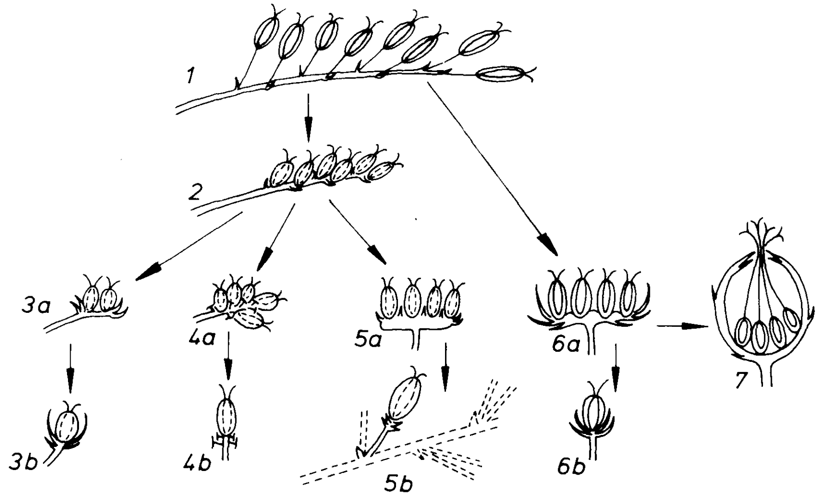


Fig. 4. Schematic drawings of pistillate inflorescences of Artocarpeae and Moreae (Moraceae), showing some trends of differentiation. (1) *Trophis*, *Sorocea*, etc.; (2) *Trophis*, *Streblus*, etc.; (3a) *Trophis involucrata*; (3b) *Trophis caucana*; (4a) *Sorocea sprucei*; (4b) *Sorocea duckei*; (5a) *Clarisia ilicifolia*; (5b) *Clarisia racemosa*; (6a-6b) *Antiaropsis*; (7) *Sparattosyce*. (With permission of Springer-Verlag and Oxford University Press, see acknowledgements).

from saucer-shaped to cup-shaped to urceolate. Pistillate flowers are often fused with adjacent flowers and/or with the receptacle. Main lines of the differentiation of (1) basically racemose and unisexual and (2) basically cymose and bisexual inflorescences are presented in Figs 5 and 6, respectively (cf. Berg 1977a).

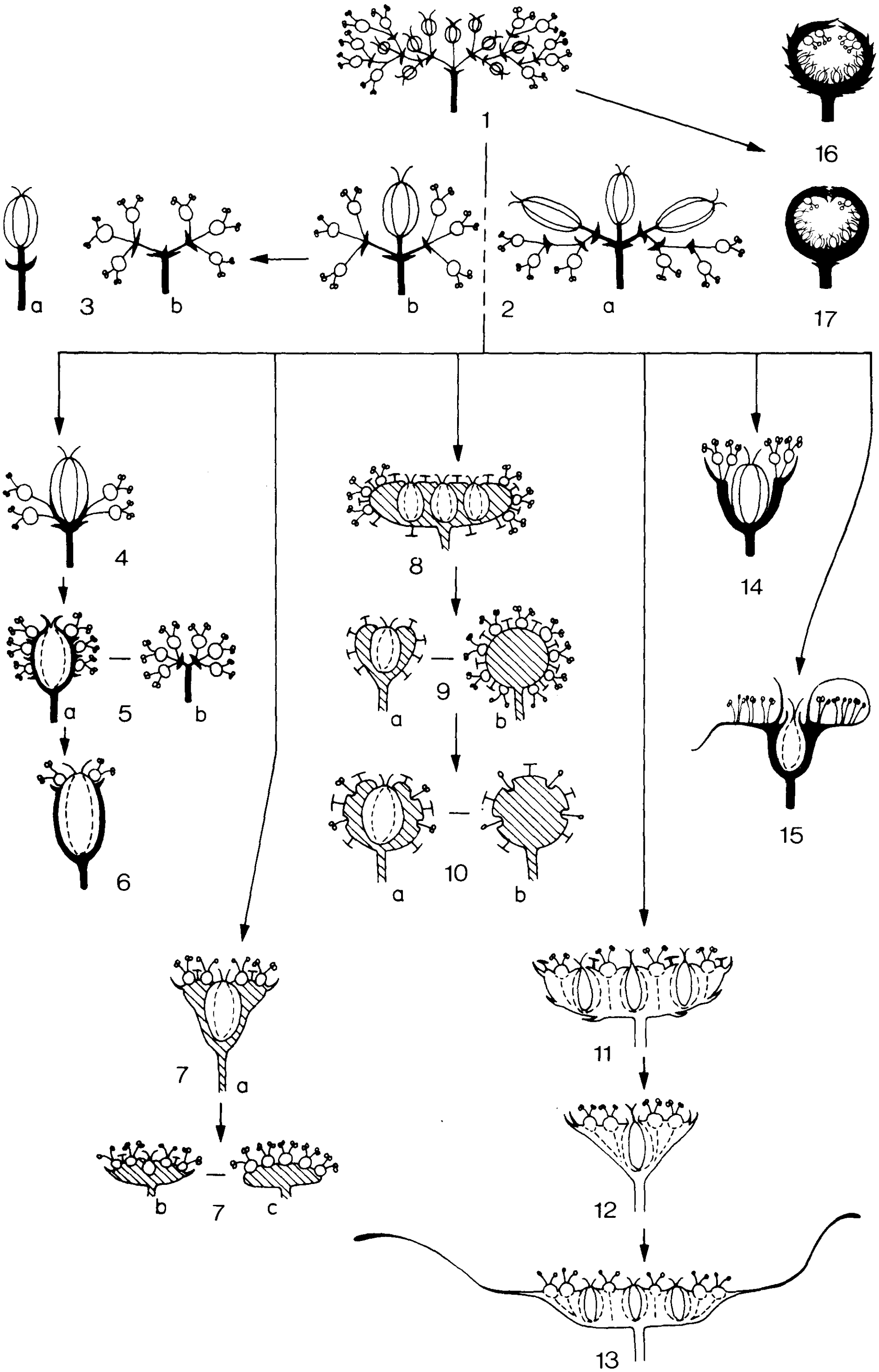
Breeding insects in staminate inflorescences

Cecropia

The unisexual inflorescences of *Cecropia* consist of a cluster of spikes (or spadices) with closely set flowers. In all species (except *C. hololeuca*) the spikes are fully enclosed by a spathe up to anthesis. The inflorescences of *C. hololeuca* and young inflorescences of the other species are enveloped by the cover of large terminal buds, formed by connate stipules.

Within the spikes of the staminate inflorescences one can usually find numerous insect larvae (of drosophilid flies and beetles, cf. Wheeler 1942). Fiebrig (1909) noted the frequent occurrence of certain curculionid beetles (similar to those often present in palm inflorescences) on inflorescences of *Cecropia*, and Andrade (1984) reported that larvae of a curculionid beetle often destroy rachises of the spikes of the staminate inflorescences. Insect larvae are, however, usually absent within the spikes of pistillate inflorescences.

The difference between staminate and pistillate inflorescences with regard to the occurrence of insect larvae can be explained by morphological differences between staminate and pistillate flowers.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In most species the perianth of the staminate flower is tubular with a ± thickened apical part with a narrow, slit-shaped aperture. At anthesis the anthers are pushed through the aperture. In most species there are open slits among the flowers. Insect larvae are able to penetrate the spikes through the aperture of the perianth and/or via the slits among the flowers.

The perianth of the pistillate flowers is also tubular with a thickened apical part often containing tannin (Fig. 17). In most species the aperture is usually circular and very narrow, just allowing the passing of the style. The style is often shortly setose. In all species the outer surface of the perianth bears a dense arachnoid indumentum, that of adjacent flowers being interwoven and occluding the slits among the flowers. Arachnoid indumentum often also occurs on the inner surface of the perianth tube, just below the aperture, which contributes to the closing of the slits between perianth and style in addition to the indumentum of the style. Most *Cecropia* species have rather narrow, ± penicillate to comose stigmas which can be pushed through the aperture of the perianth just before anthesis (Fig. 17). However, in a number of species (e.g., *C. pachystachya* and *C. peltata*) the stigmas are broad and peltate and already outside the perianth long before anthesis (Fig. 18).

In summary, the structure and indumentum of the perianth, features of the style and stigma, and the ontogeny of the pistillate flower can be related to the protection of the developing fruits/seeds.

Both staminate and pistillate inflorescences and flowers are protected by the stipules and the spathe against penetration by insects until anthesis.

Artocarpus heterophyllus

The inflorescences of this species are unisexual, cylindrical to subclavate, with densely set flowers.

Van der Pijl (1953) reported that insects breed within the staminate inflorescences. Insect larvae are able to penetrate the inflorescences at anthesis through the apertures of the perianth and probably also through the slits among the flowers. However, the surface of the pistillate inflorescence is closed by fusion of the upper parts of the perianths (with each other and often with interfloral bracts as well) and by the very narrow tubular aperture in the thickened apex of the perianth that just allows the style through (Fig. 8).

Treculia africana

The inflorescences of this species are (usually) unisexual, (sub)globose, with the flowers occurring scattered among numerous bracts with peltate apices (Figs 9, 24-25).

Breeding insects have been found within the staminate inflorescences (cf. Berg 1977b). Insect larvae can penetrate at anthesis through the open apices of the perianths and possibly also through slits beside the flowers. The surface of the pistillate inflorescence is

Fig. 5. Schematic drawings of inflorescences of Moraceae, showing of the main trends of differentation in groups with bisexual inflorescences - mainly Dorstenieae and *Ficus*. (1) hypothetical; (2a-2b) *Bleekrodea* (Moreae); (3a-3b) *Bleekrodea madagascariensis*; (4) *Utsetela*; (5a-5b) *Helianthostylis*; (6) *Trymatococcus*; (7a-7c) *Bosqueiopsis*; (8) *Brosimum* sp.; (9a-9b) *Brosiumum lactescens*; (10a-10b) *Brosimum utile*; (11) *Dorstenia djettii*; (12) *Dorstenia africana*; (13) *Dorstenia barteri*; (14) *Scyphosyce*; (15) *Trilepisium*; (16-17) *Ficus*. (With permission of Springer-Verlag and Oxford University Press, see acknowledgements).

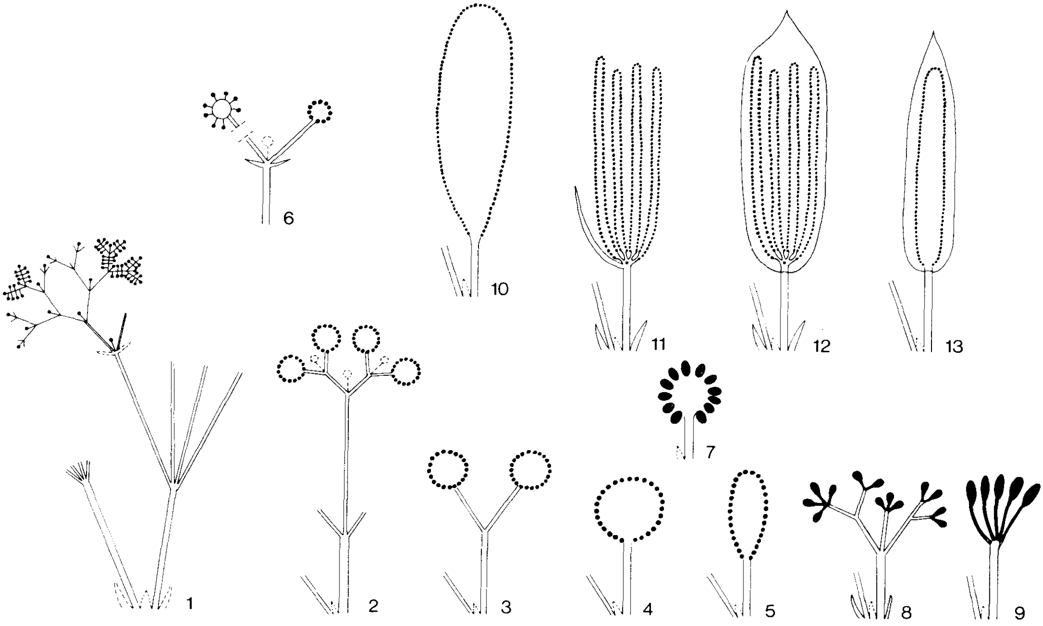


Fig. 6. Schematic drawings of inflorescences of Cecropiaceae. (1) *Myrianthus* and *Pourouma* (staminate), basic type of ramification and floral arrangement; (2) *Coussapoa* (staminate and pistillate), *Musanga* (staminate), *Pourouma* (staminate); (3-5) *Coussapoa* (pistillate); (6) *Poikilospermum* (pistillate and staminate); (7) *Myrianthus* (pistillate); (8-9) *Pourouma* (pistillate); (10) *Musanga* (pistillate); (11-12) *Cecropia* (staminate and pistillate); (13) *Cecropia* (pistillate). (With permission of Oxford University Press, see acknowledgements).

closed off by the imbricate tips of the bracts. The peltate parts of the bracts are cili(ol)ate; the rather stiff hairs at the margin bar the narrow slits between overlapping bract apices. The cover of bract apices just allows the slender styles (of the naked flowers) through; the styles are shortly setose.

Features that can be related to protection of floral structures in other taxa of the Urticales

The three taxa treated above show distinct morphological differences between staminate and pistillate inflorescences which can be related to permission or prevention of penetration and phytophagy by breeding insects.

Phytophagy by insects (imagines and larvae) is a general threat for plant parts including flowers, and, in particular, essential floral parts like anthers, ovaries, ovules, and developing fruits and seeds (cf. Zwölfer 1978). Condensed inflorescences with densely set flowers will be particularly attractive for breeding, because they can provide the larvae with both food (various tender tissues) and shelter.

Traits which can be interpreted as devices for protecting inflorescences, flowers, and floral parts against penetration and damage by breeding insects not only occur in the three taxa discussed above but can also be found in other Urticales.

Staminate flowers and inflorescences

In these flowers defence against the threat of insect attacks is only important up to anthesis, and a well-developed perianth can apparently fend off this threat. The perianth of the staminate flower of most Urticales consists of four or five, free or partly connate tepals. The tepals or perianth lobes are mostly imbricate or valvate. In the former case the margins of the tepals (or lobes) are usually cili(ol)ate: the stiff hairs on the margin close the slits between the overlapping perianth parts. In the latter case the margin usually bears thin, crinkled hairs. The strips of indumentum of opposite margins interlace. This interwoven indumentum closes off the slits between adjacent perianth parts.

In several genera of Moraceae (e.g., *Brosimum*, *Castilla*, *Pseudolmedia*) the perianth is reduced or lacking. In these cases the stamens are protected in several other ways, e.g., by enclosure of the flowers (stamens) in a ± concave receptacle with imbricate (involucral) bracts (cf. Berg 1972, 1977a). Enclosure of flowers in this way apparently also occurs if the perianth is thin or possibly otherwise insufficient for enclosing and protecting the stamens (e.g., in *Naucleopsis*).

Staminate inflorescences can be protected until anthesis by the terminal bud cover (stipules), as often occurs in Cecropiaceae. This protection will be especially important for species in which the anthers are already exserted before anthesis (as in several *Pourouma* species).

Pistillate flowers and inflorescences

Protection of the interior of the pistillate flower against attacks by insects needs to be extended beyond anthesis.

Features which can be regarded as devices against penetration into the interior of the flowers by insects are:

(1) A narrow tubular aperture in a thickened apex of a tubular perianth, just permitting the passage of the style (or stigmas).

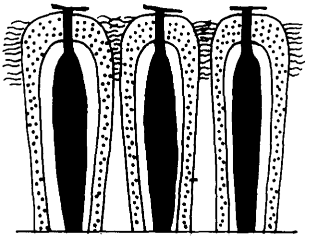
(2) Fusion of the ovary with the perianth (e.g., in *Naucleopsis*, Fig. 14).

(3) Strips of interlocking or interlacing indumentum at opposite margins of the perianth parts (e.g., in *Batocarpus*, Fig. 22) or at the inner surfaces of the tepals (as in *Helicostylis*, Figs 19-21).

(4) Barring of the slits between the style and the perianth with indumentum (e.g., in *Cecropia*, Figs 17-18).

Two types of pistillate inflorescences can be recognized: (1) those with the flowers crowded and sessile, and (2) those with the flowers spatially isolated. In the latter case the flowers are usually pedicellate, at least in the fruiting state. Uniflory of pistillate inflorescences may also be regarded as a mode of isolation.

There are several ways in which slits among flowers in condensed inflorescences can be closed. This is often realized by fusion of the flowers. The fusion may start at the base of the flowers (as in *Castilla*) or at the top (as in *Artocarpus*). It can be realized by contiguity of flattened (subpeltate) apices of perianths (e.g., in *Coussapoa*). Bracts may provide further possibilities for closing the slits among flowers. The lower parts of (± scarous) bracts may occlude the slits among the flowers. Peltate or subpeltate apices of bracts may close the surfaces of the inflorescences. The apices may be imbricate (and ciliate), as in *Treculia*, or they may be equal-levelled and contiguous with interlocking hairs at the margins, as in *Broussonetia* (Fig. 10). In the latter, the perianth of the pistillate



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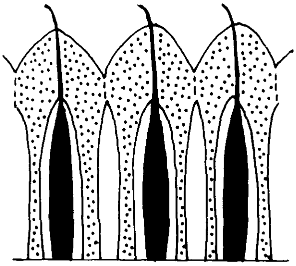

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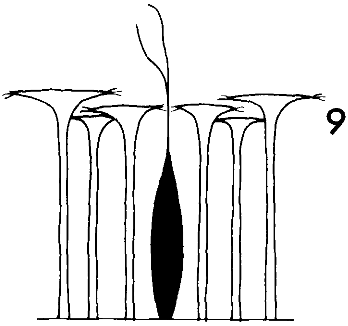

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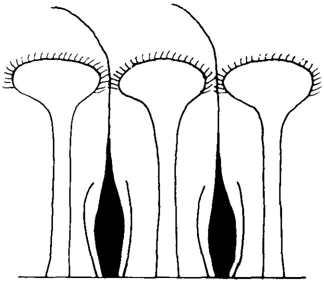

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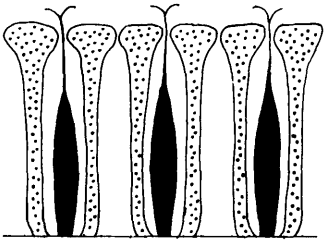

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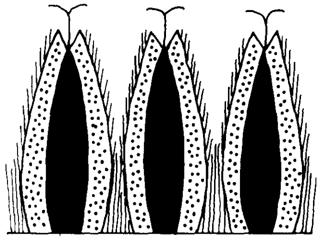

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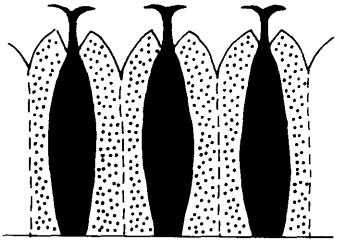

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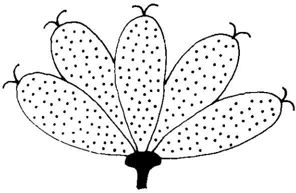

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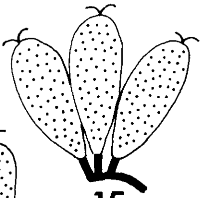

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flower is membranous and small.

Spaces among flowers may be filled with dense bristles (as in *Perebea*, Fig. 12) instead of (the lower parts of ± scarious) bracts.

In *Procris*, with discoid-capitate inflorescences with a fleshy receptacle and the flowers densely set, the long hairs of the stigmas are (partly) interwoven to form a (synstigmatic) cover of the inflorescences (Goebel 1928). This cover may also be regarded as a protective device, as it might have been in ancestral states of the inflorescence of *Ficus* (Berg 1989b).

Open inflorescences, as in *Pourouma* and *Sorocea*, with the flowers more or less separated and mostly pedicellate, at least when fruiting (Figs 27-29), can also be regarded as a device against phytophagy. Shelter (protection against predators, etc.) is excluded in such inflorescences. The same applies to uniflorous pistillate inflorescences. Uniflorous inflorescences are common in Moraceae and found both in groups with condensed (e.g., in *Perebea*) and those with open inflorescences (e.g., *Sorocea* and *Streblus*).

In pistillate inflorescences with free flowers the fruiting perianths are mostly ± closely appressed and the perianths vary from ovoid to obconical and are ± densely hairy, at least in the upper parts (Figs 11-12). However, in a number of taxa (e.g., *Clarisia ilicifolia* and *Maquira costaricana*) the fruiting perianths are less closely packed, ± divergent, and become ellipsoid to broadly spindle-shaped or to obovoid in fruit (Figs 14, 28). In these taxa the surface of the fruiting perianth is (very) smooth and ± lustrous. The opening of the centre of the infructescence will reduce or eliminate shelter for breeding insects. The smooth surfaces may have deterrent properties.

Entire inflorescences may be enveloped until antheses in terminal bud covers (stipules), as in many members of the *Cecropiaceae*, or, in *Cecropia*, the flower-bearing parts are surrounded by a spathe (Fig. 6: 11-13).

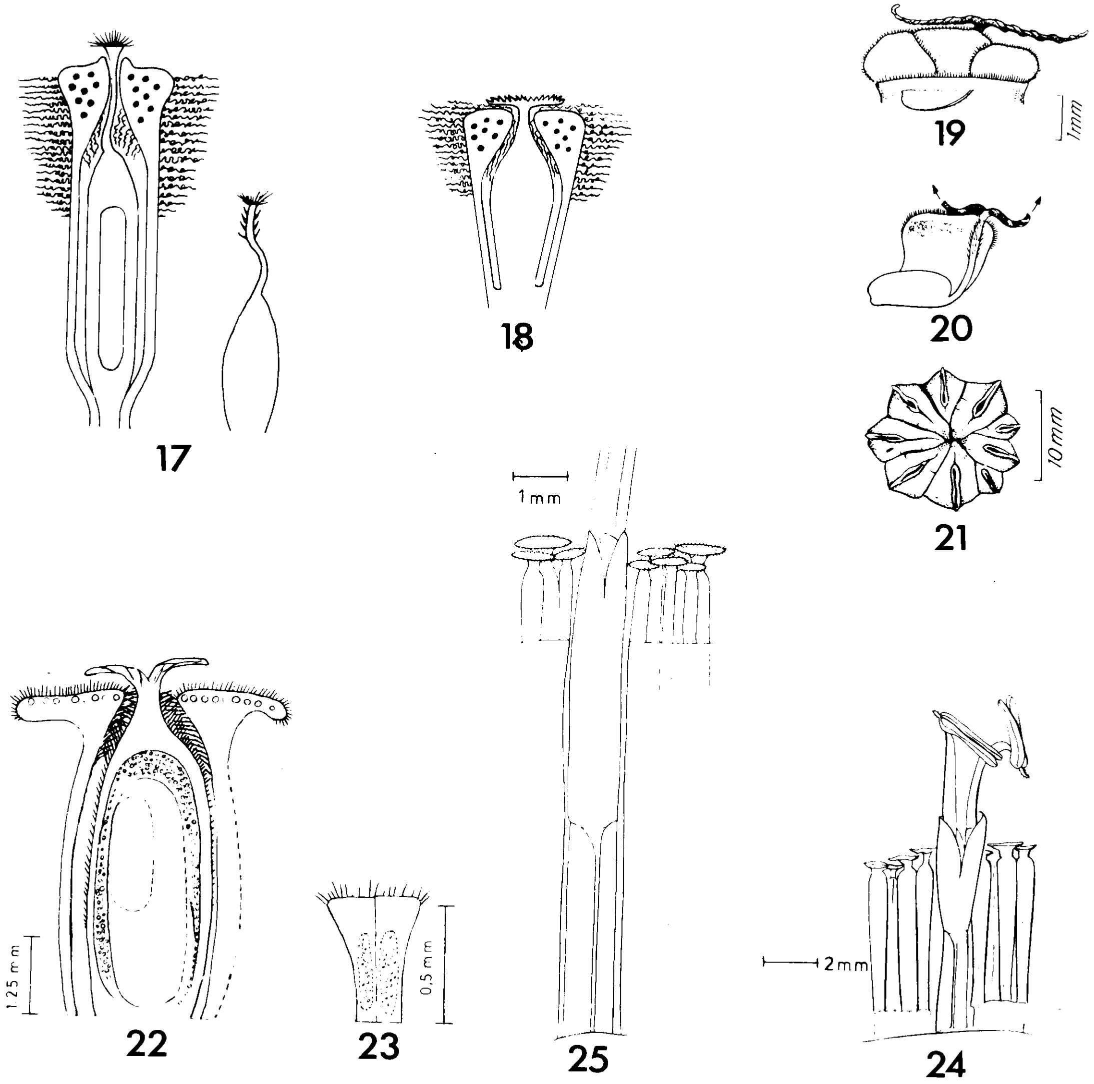
Bisexual inflorescences

In bisexual inflorescences the protection of the pistillate flowers is somewhat more complicated, as the pistillate flowers are basically mixed with staminate flowers, the perianths of which have to open at anthesis and therefore are unable to fuse with the pistillate flowers. In most cases the staminate and pistillate flowers are spatially separate (Fig. 5). In *Dorstenia* the pistillate flowers are sessile and the staminate ones pedicellate; the perianths of the pistillate flowers fuse with the pedicels of the staminate flowers by which the surface of the whole inflorescence may be closed. In other genera (*Brosimum, Helianthostylis*, and *Utsetela*) the single pistillate flower is fused with the urceolate receptacle (and thus embedded in the centre of the inflorescence) and the staminate flowers are borne on the outer surface of the receptacle.

In *Ficus* the numerous free flowers are fully enclosed in an urceolate receptacle the marginal bracts of which occlude the apical entrance (Fig. 5: 16-17).

Entire bisexual inflorescences may be enveloped by terminal bud covers (stipules). In some *Ficus* species young inflorescences are enclosed in lateral, calyptrate bud covers, and in *Trilepisium* young inflorescences are enclosed by two scale leaflets.

Figs 7-16. Schematic drawings of various types of pistillate flowers of Cecropiaceae and Moraceae. Fig. 7. *Cecropia*. Fig. 8. *Artocarpus*. Fig. 9. *Treculia*. Fig. 10. *Broussonetia*. Fig. 11. *Batocarpus*. Fig. 12. *Perebea* Fig. 13. *Naucleopsis*. Fig. 14. *Clarisia ilicifolia*. Fig. 15. *Sorocea*. Fig. 16. *Clarisia racemosa*.



Figs 17-25. Various flowers of Cecropiaceae and Moraceae. Fig. 17. *Cecropia latiloba*, pistillate flower with penicillate stigma and tannin in the upper part of the perianth. Fig. 18. *C. peltata*, pistillate flower with peltate stigma and tannin in the upper part of the perianth. Figs 19-20. *Helicostylis tomentosa*, pistillate flowers, Fig. 20 showing hairs in the inner surface of the perianth. Fig. 21. *H. tomentosa*, infructescence. Fig. 22. *Batocarpus amazonicus*, pistillate flower with immersed glands in the upper part of the perianth. Fig. 23 *B. amazonicus*, interfloral bracts with immersed glands. Figs 24-25. *Treculia africana*, staminate flowers and interfloral bracts.

Summary of putatively protective devices

The previous observations can be summarized as follows:

(1) Fusion of structures by adnation or connation in order to close slits to prevent penetration into the interior of pistillate flowers and pistillate or bisexual inflorescences (Figs 7-16): (a) Fusion of ovary and perianth (e.g., in *Naucleopsis* and *Myrianthus*); perianths become tubular before fusion. In most cases fusion of ovary and perianth is likely to precede the fusion of flowers. (b) Fusion of flowers; mostly pistillate flowers amongst each other: either (i) from the base upward (e.g., *Castilla*) or (ii) from the apex downward (*Artocarpus*). Staminate flowers rarely fuse amongst each other (e.g., in *Cecropia purpurascens*), and pistillate flowers rarely fuse with (pedicels of) staminate flowers (e.g., in *Dorstenia*). (c) Fusion of flowers with the (saucer-shaped, cup-shaped or urceolate) receptacle (e.g., in *Brosimum*).

(2) "Peltation" of bracts and perianths to bar slits in order to prevent penetration into the interior of (pistillate, staminate, and bisexual) inflorescences (Figs 7-16). Two types of peltate bracts can be distinguished: (a) Bracts with the apices imbricate (and with cili(ol)ate margins, e.g., in *Brosimum, Treculia,* and *Coussapoa* spp.). (b) Bracts with the apices uniseriate and touching each other (and with tomentose/tomentellous margins, as in *Broussonetia*). Peltate or subpeltate, touching apices of perianths may cohere, e.g. by interlaced indumentum or indented margins or may be fused (in *Cecropia* spp.). Contiguous (sub)peltate apices of bracts and perianths are often ± distinctly angular.

(3) Indumentum for barring slits leading to the interior of flowers and inflorescences. Several types of indumentum can be distinguished: (a) Short, usually stiff and straight hairs at the margins of imbricate structures: perianth parts and bracts. (b) Short to long, thin and crinkled hairs and those of opposite margins or surfaces interlacing: (i) at margins of valvate structures: perianth parts and bracts, or (ii) at surfaces bordering slits (e.g., inner surface of perianth of pistillate flowers of *Helicostylis* (Figs 19-20) and outer and inner surface of perianth of pistillate flowers of *Cecropia*, Figs 17-18). (c) Stiff hairs, those at opposite surfaces interlocking (e.g., in *Batocarpus*, Fig. 22). (d) Dense indumentum (often consisting of ± setose hairs) among flowers (e.g., in *Perebea*). The bristles among the flowers in some *Ficus* species may be related to protection of early stages of differentiation of the syconium. The scarious bracts in many Urticaceae (and in other *Ficus* species) may have (had) the same protective function.(e) Dense indumentum on (free parts of) persisting (fruiting) perianths (e.g., in *Castilla* and *Perebea*, Fig. 12). This is often found when the pistillate flowers are crowded and the fruits (fruiting perianths) do not diverge (as in *Clarisia ilicifolia*, Figs 14 and 17). In the latter case the fruiting perianths are mostly very smooth and lustrous. (f) Short and often stiff hairs on styles passing through narrow apertures of the thickened apex of the perianth.

(4) Size reduction of apertures of perianths leading to the interior of pistillate flowers. This can be realized by:(a) an apical opening of the perianth so narrow that it just allows the style to pass through; the latter often bears short hairs; or by (b) indumentum on the inner surface or margin of the perianth placed in such a way that the hairs of opposite surfaces or margins are interlaced.

(5) Thickening of apical parts of perianths, in particular of pistillate flowers.

(6) Isolation of pistillate flowers. This can be realized by: (a) ramification of the inflorescence, as in a racemose type; in all cases the fruit-containing perianth is stalked; or by (b) reduction of the number of flowers to one. A stipitate fruit, as occurring in *Ulmus*, can be regarded as serving the same end as the former case.

(7) Separation of staminate and pistillate flowers. As staminate and pistillate flowers do not match structurally with regard to anthesis and in the duration of their functioning,

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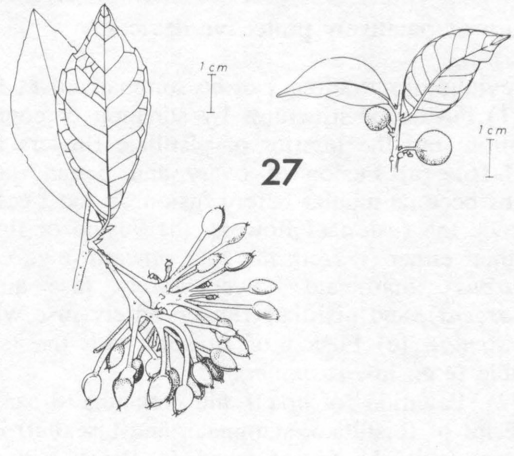

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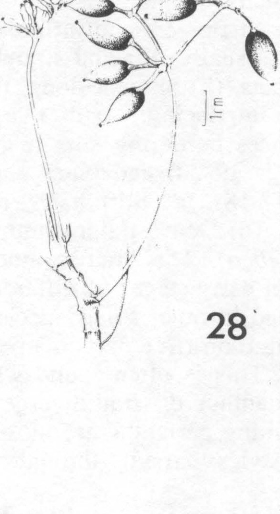

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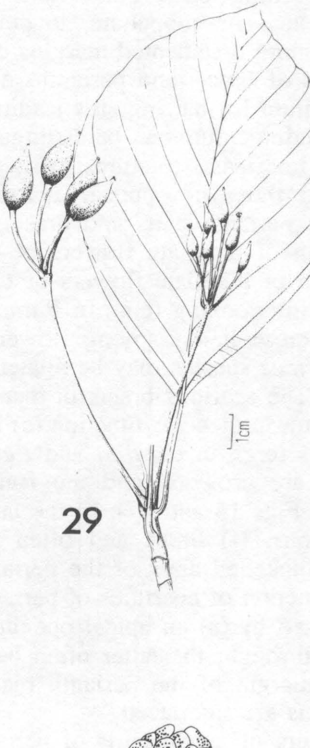

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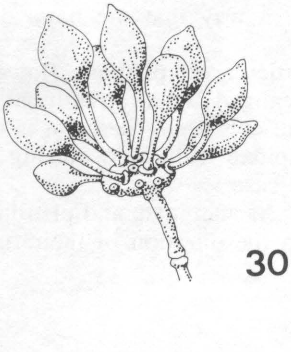

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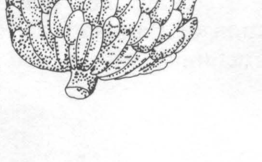

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fusion of both types of flowers on behalf of protection is in most cases not possible. Spatial separation of staminate and pistillate flowers is a solution. This may happen within a bisexual inflorescence or may be achieved by bearing them in separate (unisexual) inflorescences. The remarkable, pronounced (secondary) protogyny in *Ficus* may also have initially been a temporary separation of (the functioning of) staminate and pistillate flowers in connection with protection (cf. Berg 1989b).

(8) Enclosure of (free, staminate and/or pistillate) flowers in receptacles. This can be achieved largely by the receptacle or by both the receptacle and marginal, imbricate bracts. It is mostly correlated with a reduced perianth or a perianth that does not provide sufficient protection. In most cases the inflorescences open at anthesis: the staminate inflorescences of *Elatostema ficoides* and *Sparattosyce* (Fig. 4: 7) by splitting of the receptacle. The urceolate pistillate inflorescence of *Sparattosyce* splits open when the fruits are mature but the bisexual inflorescences of *Ficus* remain (usually) closed.

(9) Enclosure of the entire inflorescence or its flower-bearing parts when juvenile or (nearly) up to anthesis. This is often achieved by (relatively) large stipules forming the cover of the terminal bud, by an enlarged bract forming a spathe (*Cecropia*), by fused and persistent prophylls forming a calyptrate bud cover (*Ficus* spp.), or by coriaceous scale leaves (*Trilepisium*).

(10) In addition other devices may be of importance, such as chemical substances and micro-morphological features of surfaces.The (yellow dye-containing) glands in perianths and/or bracts as occurring in *Maclura* and *Batocarpus* (Figs 22-23), tannin as occurring in the (upper parts of the) perianths of *Cecropia* (Figs 17-18), latex as occurring in parts of flowers and inflorescences of most Moraceae, and bitter mucilaginous sap in parts of flowers and inflorescences of Cecropiaceae could have to do with chemical defence. Very smooth surfaces of fruiting perianths may have deterrent properties (see pp. 00 and 00).

DISCUSSION

Protective devices in Urticales and comparison with other groups of plants

Within the framework of the present study it is not possible (1) to discuss in much detail devices which (may) protect floral parts and seeds and (2) to compare features found in Urticales with those in many other plant groups. Some remarks will be made and comparison will be limited to a few groups.

Endress (1975) described "peltation" in inflorescences, strobili, and flowers in a number of taxa, many of them with unisexual reproductive structures. He related peltation and contiguity of margins of peltate structures to protection.

The connation of pistillate flowers resembles and repeats (the process of) the fusion of carpels to form syncarpous gynoecia, and the adnation of pistillate flowers to the receptacle resembles and repeats (the process of) the fusion of ovaries with hypanthia. Tendencies towards syncarpy, and in polycarpellate groups (like Rosaceae), tendencies

Figs 26-31. Some types of infructescences of Cecropiaceae and Moraceae and multiple fruits of some Annonaceae. Fig. 26. *Clarisia ilicifolia*. Fig. 27. *Sorocea sprucei* (two forms). Fig. 28. *Pourouma tomentosa*. Fig. 29. *P. minor*. Fig. 30. *Cananga*. Fig. 31. *Annona*. (Figs 30-31 from Engler & Prantl, Nat. Pflanzenfam. 3, 2, 1889).

towards epigyny may, therefore, have to do with defence against breeding by insects (involved in pollination or not). The pistillate inflorescence of *Sparattosyce* shows similarities to the perigynous flowers of *Monimia*, *Calycanthus*, and *Rosa*. These types of perigyny (with many free pistils and a dense, setose indumentum among the pistils in the floral cup or hypanthium) may also have originated as a defense against phytophagous insects. In *Sparattosyce* the scarious tepals probably have the same function as the bristles in the floral cups and hypanthia of the other taxa mentioned.

Levin (1973) pointed out the importance of indumentum in connection with protection against phytophagy. Although the cases discussed by Levin refer to vegetative parts of the plants, the principles appear to be applicable to reproductive structures as well. Uhl & Moore (1973) regarded an indumentum of thin, interwoven hairs as one of the defence devices of palm inflorescences and flowers.

Sigmond (1930) gave a survey of several types of closure of flower buds, including the involvement of indumentum for which he recognized two distinct states: valvate and imbricate.

Cecropiaceae and Cannabaceae are strictly dioecious. In other taxa of the Urticales (families, subfamilies, tribes, genera, and even species), however, dioecious and monoecious states occur side by side. Correlations between these states and other features, like modes of pollination, habitat preference, gregarious occurrence, etc. are not evident. This suggests that in Urticales (and probably also in other groups which followed similar evolutionary pathways) dioecy may have had its origin in the need for separation of staminate and pistillate flowers because of dissimilarities in their structure and function in connection with phytophagy, thus being rather an "accidental" change from the monoecious to the dioecious state rather than primarily selected on behalf of advantages of outbreeding (cf. Bawa & Opler 1977).

Large structures which envelop and protect flower-bearing parts of inflorescences, like the spathe of *Cecropia* inflorescences, or entire inflorescences until anthesis, like the large stipules of many Cecropiaceae and some Moraceae (*Artocarpus*), are rare in dicotyledons, in contrast to monocotyledons, e.g., families of the Arecales and Typhaceae. This presence is associated with condensed inflorescences with crowded, reduced, and often unisexual flowers.

In bisexual inflorescences staminate and pistillate flowers often occur on separate parts of the inflorescence (as in Araceae and Typhaceae). The situation in Cyclanthaceae in which the staminate and pistillate flowers occur mixed, the former ones being "elevated" (pedicellate) and the latter "immersed" (sessile), resembles that of the bisexual inflorescences of *Dorstenia*.

Several of the features mentioned and discussed above, such as syncarpy, epigyny, perigyny, stipitation of ovaries, and crowding of flowers, have been pointed out, listed, and discussed by Grant (1950) in connection with the protection of ovules. However, Grant (1950) predominantly considered such structures with regard to complete, well-developed bisexual flowers, visited by animals searching for nectar and/or pollen and likely to damage ovaries and ovules like beetles and birds.

Most features that can be regarded as defence devices in flowers and inflorescences of Urticales as listed and described above are found in many other groups of plants, in particular: (1) in taxa with condensed inflorescences:(a) of bisexual flowers, as in Compositae, Dipsacaceae; Proteaceae, and many Rubiaceae; (b) of unsexual flowers in separate inflorescences; as in "Amentiferae", Arecales, and Pandanales; or (c) of unisexual flowers in bisexual inflorescences (or synflorescences), as in Araceae, Typhaceae, and Cyclanthaceae; (2) in gynoecia of taxa with polycarpellate flowers, as in Magnoliidae and Rosaceae; and (3) in reproductive structures of gymnosperms.

Similarities between Urticales and some of these groups will be indicated or briefly discussed below.

There are striking similarities between fruiting gynoecia of Annonaceae and infructescences of Moraceae, even so that some species of Moraceae (in *Naucleopsis* and *Sorocea*) have been described as Annonaceae (*Duguetia* and *Guatteria*, respectively). The main types of fruiting structures in Annonaceae are:

(1) Those with the carpels completely fused, as in *Duguetia*; such syncarpous gynoecia resemble infructescences with fused pistillate flowers, as occurring in *Naucleopsis*.

(2) Those with free, obconical carpels with flattened apices fitting adjacent carpels, as occurring in *Annona* (Fig. 31): such gynoecia resemble inflorescences of *Batocarpus*.

(3) Those with free, ellipsoid, smooth carpels as in *Artabotrys*; these resemble the infructescences of *Clarisia ilicifolia* (Figs 14 and 26) and *Maquira costaricana*.

(4) Those with free, stipitate (and smooth) carpels as in *Anaxagorea*, *Guatteria*, or *Cananga* (Fig. 30); such gynoecia resemble subumbellate infructescences as occurring in *Pourouma minor* (Fig. 29) and *Sorocea sprucei* (Fig. 27).

(5) Those with a single carpel, as occur in several genera; such gynoecia resemble uniflorous infructescences, as in *Sorocea, Maquira* and several other moraceous genera.

There are striking resemblances between several types of flowers of the Monimiaceae and inflorescences of some Urticales: staminate inflorescences of *Elatostema ficoides*, inflorescences of *Sparattosyce* and *Ficus*.

Endress (1980a, 1980b), Endress & Lorence (1983) and Lorence (1985) described several features of the flowers of Monimiaceae which can be regarded as adaptations for preventing or reducing the premature usage of staminate flowers and breeding in pistillate flowers. Such features are the enclosure of stamens in urceolate flower receptacles (floral cups) splitting open at anthesis to expose the stamens. The enclosure of pistils/ovaries in urceolate floral cups (often remaining closed until maturity of the fruits), the reduction in size of the aperture, which in some genera just allows the styles to pass through, ovaries immersed in the receptacle, indumentum among the ovaries (and near the margin of the floral cup), and probably also the mucilage which may in some cases contribute to the forming of a hyperstigma (cf. Endress 1982).

The urceolate staminate inflorescences of *Elatostema ficoides* and those of *Sparattosyce* (cf. Bureau 1969) split at anthesis and expose the staminate flowers and thus strongly resemble staminate flowers of, e.g., *Tambourissa*.

At anthesis the aperture of the urceolate receptacle of the pistillate inflorescence of *Sparattosyce* just allows the styles to pass through (Fig. 4: 7) and splits open at maturity of the fruits; it resembles the pistillate flowers of, e.g. *Siparuna*.

I have suggested (Berg 1989b) that many features of the inflorescences and flowers of *Ficus* have developed as devices against penetration and breeding by insects (other than in the ovaries by the actual pollinators: fig wasps). Some of these features show distinct similarities to features of flowers in Monimiaceae: an urceolate receptacle, closing of the ostiole, immersed ovaries (as in *Ficus* sect. *Malvanthera*), bristles among the flowers (as in subg. *Ficus*, in other subgenera, e.g. *Urostigma*, substituted by scarious bracts). Even the slightly mucilaginous fluid, as occur in (post-anthesis) receptacles in subg. (or sect.) *Sycomorus*, might be related to the mucilage produced in Monimiaceae flowers.

A comparison of patterns in differentiation of reproductive structures of Urticales can be extended to (recent) gymnosperms as well: (1) to the condensed "male" strobili with peltate sporophylls, (2) to the ovules occurring predominantly in cones with maximal closure of the surfaces, (3) to solitary ovules, or (4) to "clusters" of ± separate ovules as in *Gnetum* (reminiscent of pistillate inflorescences of *Clarisia ilicifolia*).

Protection and pollination

In Urticales two modes of pollination are known: anemophily and entomophily based on breeding. The latter mode links protection of flowers and inflorescences and pollination and places this protection more centrally in the reproduction process.

A considerable number of the Urticales are anemophilous. The adaptations to pollination by wind may be common, such as large anthers on slender filaments (as found in Ulmaceae and Cannabaceae) or long and pendulous staminate catkins (as found in some Moraceae and some species of *Cecropia*), or specialized (two types): an explosive pollen release mechanism (as occurs in all Urticaceae, in one tribe of Moraceae and possibly in some *Celtis* species, cf. Berg 1989a) or abscission of anthers and secondary attachment of them to the flower (as occurs in most *Cecropia* species (Allemão 1860; Berg 1977c, 1989a; cf. Endress 1985).

The assumption that in the Urticales (Moraceae) an extensive reversion from wind pollination to insect pollination has occurred (Stebbins 1974) does not seem to be supported by the evolutionary pathways of differentiation of flowers and inflorescences in this order. Adaptations of the reproductive structures to wind pollination generally appear to be secondary. This seems to be supported by the presumed directions of the differentiation of growth habit/form and leaf. It seems to be likely that shifts towards wind pollination often started in humid tropical environments and that the move to drier or more strongly seasonal conditions was accompanied by improvements of adaptations to wind pollination.

Entomophily appears to be the original state in Urticales and numerous representatives of the Urticales (in the families Cecropiaceae and Moraceae!) do not show adaptations to anemophily. Many of them occur in habitats (like understoreys of rain forest) in which transport of pollen by air currents is not likely to occur (except along streamlets). In most cases one would expect pollen transport by insects, although the attracting devices have not been identified.

Nectar production has only been reported in two taxa: *Artocarpus altilis* by Brantjes (1981) and *Cecropia pachystachya* by Andrade (1984), but in both cases nectar apparently does not play a role in pollination.

In some of the non-anemophilous Urticales (representatives of the tribe Dorstenieae), one might expect some way of pollination based on pollen as an attractant. However, the anthers are often few in number, small and/or inconspicuous. In some cases autogamy may be a way out, in a few other cases (*Dorstenia* spp., cf. Gustafson 1946) it might be apomixis. However, reliable data about pollination in Moraceae with bisexual inflorescences are wanting with the exception of representatives of *Ficus* with bisexual inflorescences. Only in this genus is entomophily established. It is a unique type of pollination to which the inflorescences and flowers show an array of adaptations. However, one may question how many of them are preadaptations related to protection of anthers and ovaries against phytophagy (Berg 1989b).

Another group of non-anemophilous Urticales (most genera of the Cecropiaceae and most representatives of the Moraceous tribes Artocarpeae and Castilleae) have unisexual inflorescences. Data about pollination are again lacking. *Artocarpus heterophyllus*, *A. integer* and *A. dadah* are notable exceptions. In these taxa pollination is carried out by flies and beetles, and is based on breeding by these insects (cf. Jarrett 1959, van der Pijl 1953).

Shelter and brood-places are listed by Fægri & van der Pijl (1979) as primary attractants. The examples mentioned refer to quite different ways of breeding, such as breeding in ovaries employing (direct) predation of developing seeds (as in *Ficus*), oviposition in relation to sapromyophily, and breeding in condensed staminate inflorescences as in *Artocarpus*.

Thanks to the elucidating survey of pollination in palms by Henderson (1986) and the study on *Zamia* by Norstog et al. (1986) many other examples, ± similar to the situation in *Artocarpus*, can be added. They suggest that a mode of pollination largely or partly based on breeding within dense staminate inflorescences (or staminate flowers with numerous stamens) in combination with the absence of (clear) adaptations to pollination by wind and/or occupation of habitats not suitable for wind-pollination may occur and even be common in many non-anemophilous Urticales and in other groups with unisexual blossoms (as Monimiaceae and Pandanaceae) as well. There is, at least, sufficient evidence that unisexual blossoms lacking visual attractants are (with a few acknowledged exceptions) not necessarily anemophilous.

The devices for protecting inflorescences (and flowers) get other dimensions when this type of breeding is involved in pollination. Breeding is then not merely "accidental" but "provoked". This implies improved attraction of breeding insects to staminate inflorescences (or strobili) and well-developed devices against premature occupation of breeding sites. On the other hand, pistillate inflorescences (strobili or flowers) have to be even more thoroughly "armoured" against breeding by morphological and chemical devices.

With the information at hand the (rather complex) "syndrome" of a pollination system based (at least partly) on breeding (not direct seed predation (as in *Ficus*) or in connection with sapromyophily) can be provisionally circumscribed as follows: (1) the entities of pollination are unisexual inflorescences, (2) adaptations to wind pollination are lacking (or are at least not fully developed or deficient), (3) in staminate inflorescences the flowers are crowded, (4) staminate inflorescences provide suitable breeding sites: food and shelter (protection against predators, humidity, etc.), (5) staminate inflorescences (and/or individual flowers) are well protected against premature occupation of the breeding sites, (6) staminate inflorescences emit strong or weak (and to human sense organs imperceptible) olfactory signals for attracting certain breeding insects, (7) the breeding insects are various groups of beetles and flies (cf. Henderson 1986), (8) breeding may be accompanied (or even partly or entirely replaced) by consumption of pollen,(9) pistillate inflorescences have an array of devices for preventing breeding (see above): primarily to prevent penetration of the inflorescence or possibly also to deter from oviposition, (10) attraction of the pollinators to the pistillate inflorescences is predominantly by olfactory signals similar to those emitted by staminate inflorescences or possibly primarily in connection with mating (cf. Pellmyr & Thien 1986), and (11) as a rule the presence and activities of insects are more obvious on staminate inflorescences than on pistillate ones.

One of the important aspects of this mode of pollination is that it ranges from almost full anemophily to full entomophily with traits similar to those of the syndromes of pollination by beetles or flies in bisexual blossoms (Fægri & van der Pijl 1979). The fact that this mode of pollination also occurs in gymnosperms (cf. Norstog et al. 1986) appears to indicate that it is an ancient mode of pollination which angiosperms inherited from gymnosperms. The available data also indicate that there is no sharp distinction between pollination by beetles and flies in unisexual blossoms and in bisexual ones, so that one does not need to focus on bisexual strobili of gymnosperms to postulate the origin of pollination in angiosperms (cf. Leppik 1960, Gottsberger 1988). Analogies not only exist between bisexual gymnospermous strobili and primitive types of bisexual flowers but also between unisexual gymnospermous reproductive structures and unisexual inflorescences of angiosperms (as occurring in Urticales).

Olfactory signals for attracting insects which can play a role in pollination (in particular to pistillate inflorescences) may be quite subtle (not or hardly perceptible to human olfactory organs and resembling those which attract pollinators and many other insects to the inflorescences of *Ficus* in a very selective way).

This mode of pollination may have played an essential role in the transition from entomophily to anemophily through reduction of the dimensions of flowers, reduction of the perianth (and loss of visual attractants), condensation of inflorescences, and the change from the bisexual to the unisexual state. Such changes (to the "amentiferous" state) have apparently occurred quite frequently in the early history of angiosperms (cf. Friis & Crepet 1987). Given the groups of animals available for pollination in that period of angiosperm evolution, not many pathways of evolution were open.

Amphiphily occurs (or can be expected to occur) in connection with this mode of pollination.

This mode of pollination may also have been transitional towards the establishment of some types of trap blossom.

Among the non-anemophilous Urticales with unisexual inflorescences there are two exceptional genera: *Pourouma* and *Sorocea*. In these genera the pistillate inflorescences are not condensed, but the flowers are spaced and pedicellate.

Falcão & Lleras (1980) reported on bees (e.g., *Trigona*) visiting pistillate inflorescences of *Pourouma cecropiifolia* and suggested that these bees play a role in pollination. Common primary attractants like nectar and pollen are not present in these inflorescences. The bees may, however, be attracted by the dense indumentum consisting of pluricellular, brown to purple, granular (and glandular?) trichomes, in dry plant material manifest as a powdery layer. This indumentum, which might be a substitute for pollen, is common on inflorescences of *Pourouma* (and often also present on leafy twigs, leaves, and/or stipules). In the Upper Amazon Basin these young plant parts of several *Pourouma* species are often covered by a mycelium, which suggest that this indumentum provides a substrate and that the trichomes are "nutritious".

It is worth mentioning that on the perianth of pistillate flowers of several species of *Sorocea* also pluricellular ("glandular") trichomes also occur, and that these perianths may also be covered with mycelium.

It is remarkable that the occurrence of the pluricellular trichomes in inflorescences and on the perianth of pistillate flowers is correlated with stalked (pedicellate) fruiting perianths in many-flowered inflorescences: it is a rare character in Cecropiaceae (occurring only in *Pourouma*) and Moraceae (only present in *Sorocea* and in some species of the anemophilous genera, as *Fatoua, Streblus*, and *Trophis*).

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SEED DISPERSAL RELATIVE TO POPULATION STRUCTURE, REPRODUCTIVE CAPACITY, SEED PREDATION, AND DISTRIBUTION IN *EUPHORBIA BALSAMIFERA* (EUPHORBIACEAE), WITH A NOTE ON SCLERENDOCHORY.

R.Y. Berg

Berg, R.Y. 1990. Seed dispersal relative to population structure, reproductive capacity, seed predation, and distribution in *Euphorbia balsamifera* (Euphorbiaceae), with a note on sclerendochory. - Sommerfeltia 11: 35-63. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

Analyses of 25 x 4 m^2 of vegetation of this dioecious species on the S coast of Tenerife indicate establishment as the most critical part of life history, intraspecific competition to cause some mortality, interspecific competition to be insignificant, and populations to be stable with extremely low rates of mortality and recruitment. Specialized dispersal occurs autochorously, by means of a dry explosive capsule. Under optimal conditions maximum dispersal distance somewhat exceeds 20 m. All seeds escape from the mother plant canopy because of the orientation and position of capsules. The seeds constitute a major source of food for rock pigeons (*Columba livia canariensis*). In 1000 m^2 of vegetation, approximately 467,000 seeds were produced in 1988, 10 seeds were needed for recruitment, and about 100,000 were eaten by pigeons. Migration from mainland to islands and from island to island probably occurred by chance endozoochory with rock pigeons as the agent. The term sclerendochory is proposed for endozoochorous dispersal of units that are eaten but have none of the normal endozoochorous attractants.

Keywords: Autochory, Canary Islands, *Columba livia*, Endozoochory, *Euphorbia balsamifera*, Fruit morphology, Granivory, Population structure, Reproduction, Seed predation.

Rolf Y. Berg, Botanical Garden and Museum, University of Oslo, 0562 Oslo 5, Norway.

INTRODUCTION

The relationship between the mechanism of dispersal and the effect of dispersal upon distribution and gene flow is complex. It depends not only upon environment and mechanism, but also upon life history parameters of the species in question, such as size, shape and organization of plant body, life span, reproductive capacity, population structure and competitive behaviour (Stebbins 1971, Berg 1983). This study tries to look at a case of seed dispersal against important parts of its background.

Euphorbia balsamifera Ait. possesses the same autochorous dispersal mechanism as other *Euphorbia* species. Barquin Diez (1973: 66) has described the scattering of seeds from its explosive capsule: "... las semillas pueden separarse varios metros de la planta y

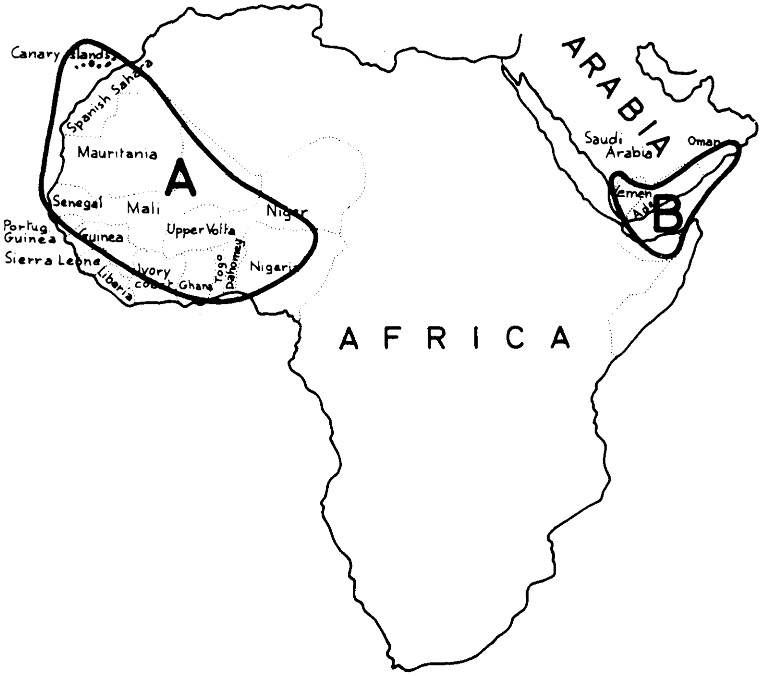


Fig. 1. Distribution of *Euphorbia balsamifera*. a - subsp. *balsamifera*; b - subsp. *adensis* (Defl.) Bally (From Bally 1965).

más en las laderas muy pedientes. Este fenómeno suele suceder a finales de Verano y se reconoce por las continuas crepitaciones de los frutos al abrirse, seguidas por el sonido de las gruesas semillas al caer al suelo." According to Monod (1974) *E. balsamifera* is dispersed by wind in the Western Sahara, as a chamae-anemochorous plant.

Euphorbia balsamifera has obvious dispersal disadvantages compared to other *Euphorbia* species: It is dioecious, which makes impossible the establishment in a new locality through a single incident of successful dispersal. Also, its inflorescences consist of a single cyathium only, while most other *Euphorbia* species have multi-cyathium composite inflorescences. The number of seeds produced per inflorescence, consequently, is lower than in other species.

Despite the short-distance seed dispersal effected by the *Euphorbia* capsule, and despite the added disadvantages of dioecy and one-cyathium inflorescences, *E. balsamifera* is a successful species with large populations and a wide distribution in Arabia, Western Africa and Macaronesia (Fig. 1). Within Macaronesia this species ("Tabaiba dulce") occurs on all of the Canary islands (Hansen & Sunding 1985: 49) as a common, often dominant species of the dry "Piso basal" (Rivas Goday & Esteve Chueca 1964, Gonzales Henríques et al. 1986).

The field work was carried out in the Canary Islands in the spring of 1988, during a Sabbatical Year at the University of La Laguna, Tenerife. It is part of a planned contribution towards the understanding of seed dispersal as it relates to evolution and distribution in oceanic island plants.

MATERIALS AND METHODS

Population structure was studied by direct mapping of position, size and approximate shape of all individuals present in a vegetation plot of 10 x 10 m, subdivided into 25 squares of 4 m^2 each. Simultaneously, maximum height, and largest and smallest diameter of plant were measured, and sex and general condition were recorded.

The plot was selected from within a well-established part of a large population, covering several km^2 on the South Tenerife coast in a site which was subjectively judged as typical with regard to plant density and plant size, without looking for the presence or absence of seedlings or other special features in beforehand. The plot was located at (1) Arico: Abades: S of Montaña Centinela, on a gentle slope NE of Barranco Narices, ca. 100 m a.s. The population structure analyses were made on 4th and 6th February.

Data on fruit set mainly were gathered in (2) Granadilla de Abona: Barranco del Callao (S of Montaña de los Riscos), ca. 150 m a.s., and (3) Granadilla de Abona: in a small barranco directly SE of Montaña de los Riscos, just above Autopista del Sur, 19th January - 2nd February. On smaller plants all capsules/capsule remnants were counted. On larger plants the total number of fruits were calculated from counts made on an estimated fraction of the plant surface.

Autochorous dispersal was studied partly by recording the results of individual capsule explosions in a plant brought from locality No. 1 to a container with water on a plastic-covered terrace in Los Christianos, partly by recording natural seed fall on a large piece of plastic on the ground in locality No. 2.

Observations on seed predation by birds mostly came from (4) Granadilla de Abona: Las Hoyas Blancas (E of San Isidro), where the *E. balsamifera* stands are unusually open. Even so a feeding bird could be observed continuously for only a brief period of time before it again disappeared amongst the plants. The observations were made with field glasses from inside a parked car.

Fruit anatomy was studied on fresh material from locality No. 1, sectioned by hand.

Wind velocities were measured 180 cm above ground, by means of a Lambrecht handcup anemometer.

Voucher specimens are deposited in the Botanical Museum, University of Oslo (O).

RESULTS

Plant body

Together with most of the other Macaronesian species of the genus, *E. balsamifera* belong to section *Tithymalus* Scop., subsection *Pachycladae* Boiss. (Pax & Hoffmann 1931: 218). Characteristic of this subsection are the naked succulent branches as well as the location of leaves, with axillary buds, in terminal pseudo-rosettes (Fig. 2, Kunkel & Kunkel 1978: Fig. 134).

Growth is sympodial, with one branch generation being produced each growing season. Towards the end of the season the leaves wither and fall. The next season one to four axillary buds from each branch tip develop into new branches (Fig. 10).

In plants older than 5-6 seasons most of the ultimate branches are terminated not only

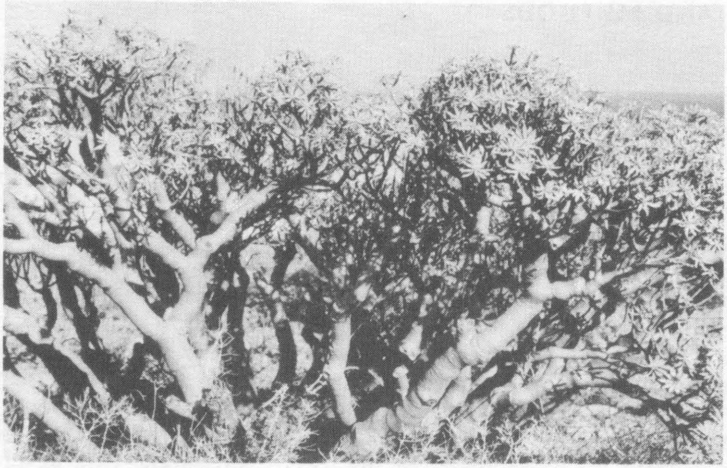


Fig. 2. The naked succulent stems branch sympodially. Leaves are clustered in terminal pseudo-rosettes.

by a leaf rosette but by an inflorescence as well. The inflorescence consists of one cyathium only, either male or female, dioeciously distributed. Since female cyathia possess but one flower, female plants never produce more fruits per year than the number of ultimate branches (Fig. 3), as a rule, considerably fewer. This is an important morphological and reproductive difference against all other succulent Canary Island euphorbs, which

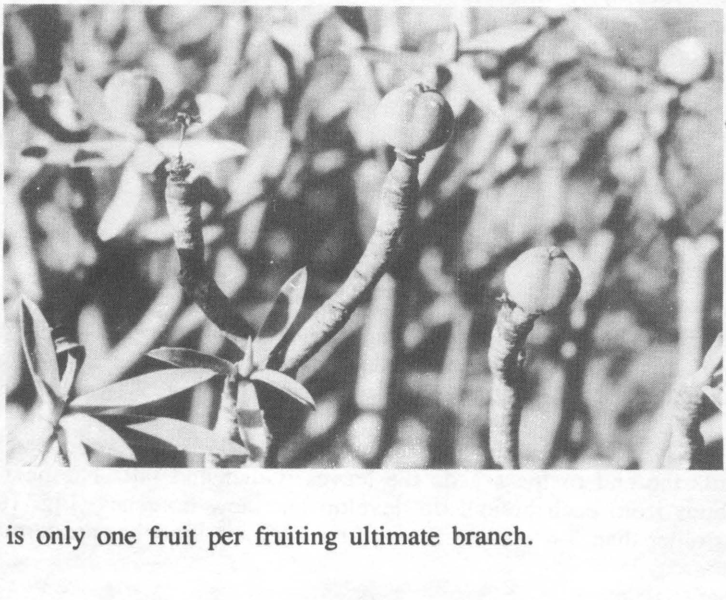


Fig. 3. There is only one fruit per fruiting ultimate branch.

produce several cyathia and, normally, several fruits per fertile branch tip.

The regular growth pattern makes it possible to estimate the age of an individual plant by counting the branch generations. However, this age determination will only be approximate, since branch generations are correlated with growth seasons while growth seasons in this harsh habitat not necessarily correspond exactly with calendar years. Also, the capacity of quite old dormant buds to sprout, sometimes seriously disturbs the regular branch generation pattern.

As the plants mature, their older parts change through self-pruning and coalescence of successive branches and the regular pattern is lost (cf. Gonzales Henríques et al. 1986: 158). The older and larger the plant, the more difficult is the determination of its age. Large plants in the study area must be more than hundred years old. The largest known individuals (Sunding 1972: 66, Kunkel & Kunkel 1978: 82) undoubtedly have an age of several hundred years.

In exposed habitats with open vegetation (cf. Kunkel 1987: Fig. 31) an individual plant will expand in all directions to attain a beautiful dome- or cushion-shape, several metres in diameter, much less in height. In protected habitats plants become taller and less wide. Where plants grow close together they will form a nearly continuous "carpet" over the landscape. Each plant, in this case, will be more erect and less spreading, with branches from different individuals intertwined and reaching to more or less the same level above ground.

Fruit and seed

The capsule of *Euphorbia balsamifera* is of the usual euphorbiaceous type. The three fused carpels form a trilocular ovary with one seed in each locule. The cells adjoining each locule become greatly enlarged and heavily sclerified to form three hard units, the so-called "cocci" (Figs 4-5). Cell orientation and amount of thickening is different in the different parts of a coccus. This accounts for the enormous tensions that build up in the cocci when the mature fruit dries out in the heat of summer (see Berg 1975).

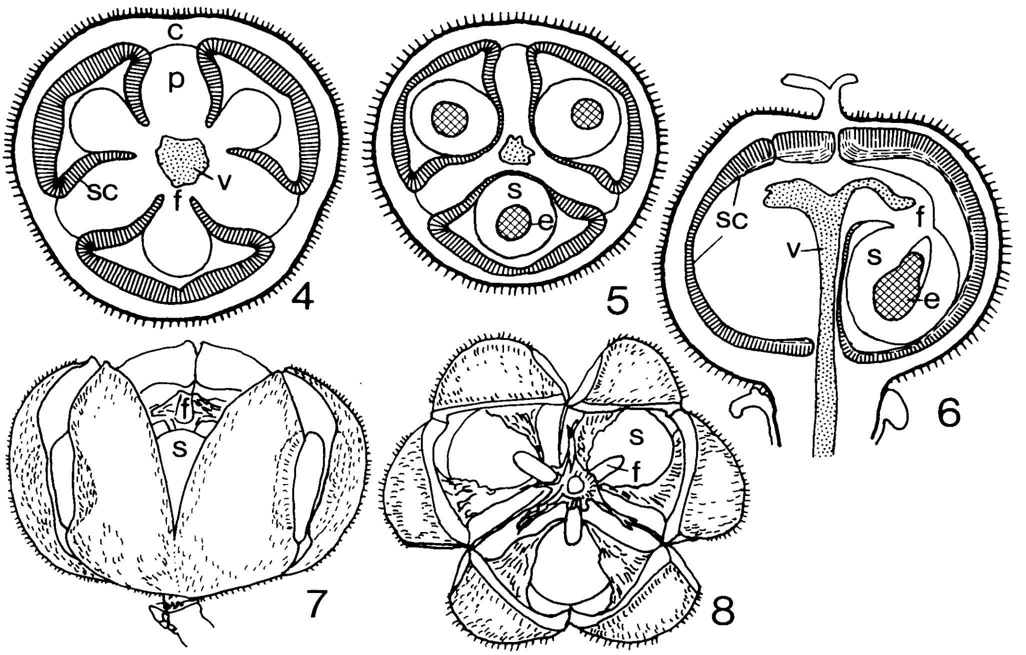
The central part of the fruit, with the vascular strand, will not be included in any coccus, but be left as a column, running vertically through the fruit, from base to just below top. The only opening into a coccus is where a placental knob, or funicle, with its vascular strand, branches off from the longitudinal central column apex (Fig. 6).

As the fully mature fruit dries out and shrinks, three longitudinal fissures open in the pericarp to the outside of the thin-walled parenchyma separating the cocci (Fig. 9). This signalizes the beginning of dehiscence. The cocci now have shrunk away from the central column, the seeds have detached from their funicle, and the stony-hard, ball-shaped capsule easily can be lifted off the plant, like a raspberry from its receptacle.

Suddenly the capsule explodes by splitting violently from the top and downwards. First each coccus begins to split in two at the top; simultaneously the upper part of the cocci move outwards (Figs 7-8) away from each other. As the splitting instantaneously proceeds downwards, the bottom ends of the cocci shoot upwards and the three seeds are propelled upwards and outwards in three opposite directions. The six coccus halves (Fig. 11) fly from the plant also. Only the central column with its six-armed head remains on the plant (Fig. 10).

The seed (Fig. 12, cf. Lid 1967: Fig. 6b) is broadly oviform to round, in cross-section broadly oval to round with the longer axis joining the raphe, 3.5-4.0 mm long, 3.0-3.5 mm broad and 2.5-3.1 mm thick. The average weight, based on 100 seeds, is 16.8 mg.

The seed is hard, smooth, dull and grey. With age most seeds become miscolored:



Figs 4-8. Fruit morphology. Figs 4-6. Sections of immature (green) fruits, showing anatomy (x 4.5). Figs 7-8. Capsule dehiscence (x 3.5). Fig. 4. Cross-section of upper part of fruit. Fig. 5. Cross-section of middle part of fruit. Fig. 6. Longitudinal section of fruit, submedially through right locule. Fig. 7. Side-view of exploding fruit, showing deep split in middle of front coccus. Fig. 8. Top view of exploding fruit, showing central column head made up of three funicles and three projections of collapsed intercoccus tissue. c - chlorenchyma; e - embryo; f - funicle; p - parenchyma; s - seed; sc - sclerenchyma; v - vascular tissue.

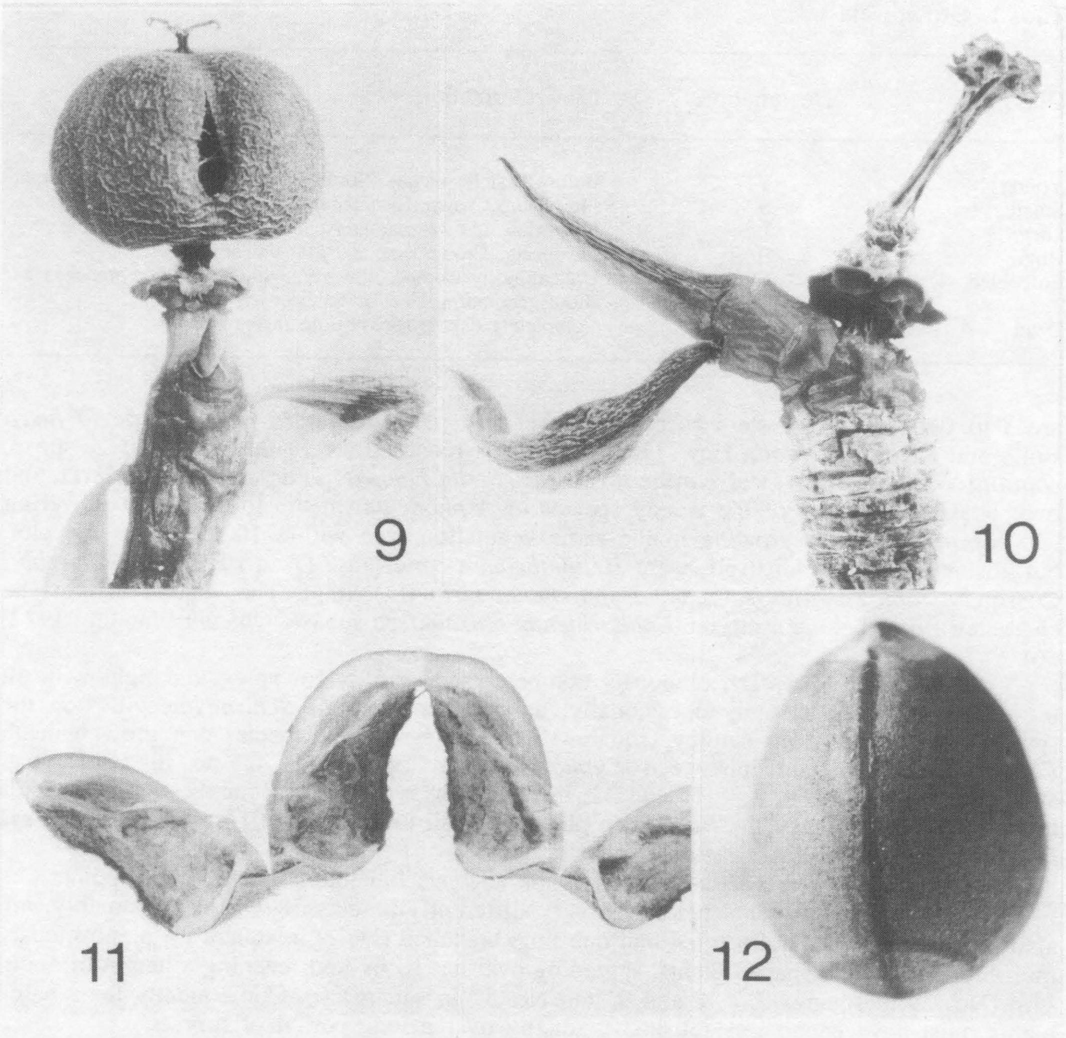
brownish and darkly punctate and spotted. A slightly elevated raphe runs as a sharp, brown line from chalaza to hilum on the proximal side. On top of the seed, the raphe continues in a low ridge onto a small beak- or wart-shaped protuberance. The protuberance is bordered on two sides by semicircular slight depressions. A tiny, sometimes white, scar on the ridge indicates the former point of vascular connection with the placenta. In the chalazal end, the raphe line terminates in the centre of a large roundish sometimes slightly depressed area, characteristically bordered by a low rim.

The embryo is straight, as long as the endosperm, and with cordate cotyledons.

The seed of *E. balsamifera* does not possess a caruncle. A fully mature seed sinks immediately when placed on water.

Population structure

Age composition was recorded by means of six growth classes defined in Tab. 1: Young, Small, Large, Huge, Enfeebled, and Dead.



Figs 9-12. Fruit and seed (Photos by Per Aas). Fig. 9. Fully mature, desiccated fruit, immediately before dehiscence, showing external fissure between two cocci (x 3.1). Fig. 10. The dried up central column with its six-armed head remains on the plant for some time after dehiscence. Axillary bud sprouting (x 4.4). Fig. 11. Two cocci still hanging together, showing last points of attachment between cocci at top, last points of attachment between coccus halves at bottom (x 4.4). Fig. 12. Mature seed (x 13.5).

A map of the analyzed plot is given in Fig. 13, information on individual plants in Tab. 2.

Euphorbia balsamifera is the only dominant species in the plot, with *Schizogyne sericea* (L. fil.) DC. as subdominant. Other shrubs present are *Plocama pendula* Ait., *Neochamaelea pulverulenta* (Vent.) Erdtm. and *Launaea arborescens* (Batt.) Murb. Present

Tab. 1. Growth classes.

Class	Designation	Characterization
Young	Y	Before first flowering. Normally, 1-5(-6) shoot generations.
Small	S	Flowering. Crown diameter up to ca. 100 cm.
Large	L	Flowering. Crown diameter ca. 100-200 cm.
Huge	H	Flowering. Crown diameter 200 cm or more.
Enfeebled	E	Unhealthy, weakened, straggly, with few living branches per shoot generation. Few or no flowers.
Dead	D	Completely dry. No leaves, no milky sap.

are also two species of stem succulents other than *E. balsamifera*, viz. *Ceropegia fusca* Bolle and *Kleinia neriifolia* Haw. Other perennials recorded are *Frankenia laevis* L. subsp. *capitata* Webb et Berth., *Polycarpae nivea* Ait., *Scilla haemorrhoidales* Webb et Berth. and two, possibly all three of the weedy species of *Asphodelus* (in the form of non-flowering leaf rosettes). Species growing in the same vegetation type within 10 metres of the plot, but absent from the plot itself, were *Helianthemum canariense* (Jacq.) Pers., *Seseli webbii* Cosson, *Aizoon canariense* L. and *Hyparrhenia hirta* (L.) Stapf. The vegetation must be characterized as belonging to the *Euphorbietum balsamifera* subass. *typicum* (Sunding 1972: 66).

Euphorbia balsamifera obviously competes successfully for space and light with all the associated species. Only occasionally, a large specimen of *Schizogyne* will stop the spread of the *Euphorbia* canopy (square 10). Most associated species can grow beneath *Euphorbia* crowns and inbetween *Euphorbia* stems with little or no ill effect, e.g. *Schizogyne* in squares 4, 8, 9, 16 and 21. In fact, there is a tendency for these other species to be concentrated under the *Euphorbia* plants (e.g. all individuals of *Ceropegia, Scilla* and *Polycarpae*), possibly as a result of goat grazing.

With regard to *E. balsamifera* itself the analysis illustrates the following points:

(1) The tabaiba plants belong to very different size classes which, presumably, are also age classes, from quite small and one-time branched (No. 9 in square 2) to enormously multibranched dome-shaped giants, spreading over ca. 10 m^2 and reaching a height of about 1 m (No. 29 in squares 3, 4, 8 and 9, and No. 57 in square 20). Consequently the tabaiba plants must have become established gradually over a long period of time.

(2) The plant cover is far from continuous. Large open and irregular spaces exist. In the rocky ground, apparently, safe sites are few and far apart.

(3) Tabaiba plants of approximately equal size will coexist even when they are close together. Over the years their crowns will merge into one large mass of branches, and the group of individuals will look like one single, dome-shaped plant (e.g. Nos. 40, 41, 43 and 51 in square 13, and Nos. 54 and 55 in square 19).

(4) However, plants of considerably different size, and presumably of considerably different age, normally seem to compete when their crowns meet, and the younger one invariably is the loosing part. Plant No. 56 (squares 19-20) is 60 cm tall, but only 40 cm wide, sterile, with long and thin internodes, many dead branches and only a few leaf rosettes. Undoubtedly, it will eventually be killed by the two older plants, Nos. 54 and 55, whose crowns have met and fused over the top of 56. The process takes time, though, to judge from the sequence of older shoot generations with restricted growth present in plant No. 56, and in all other such enfeebled specimens.

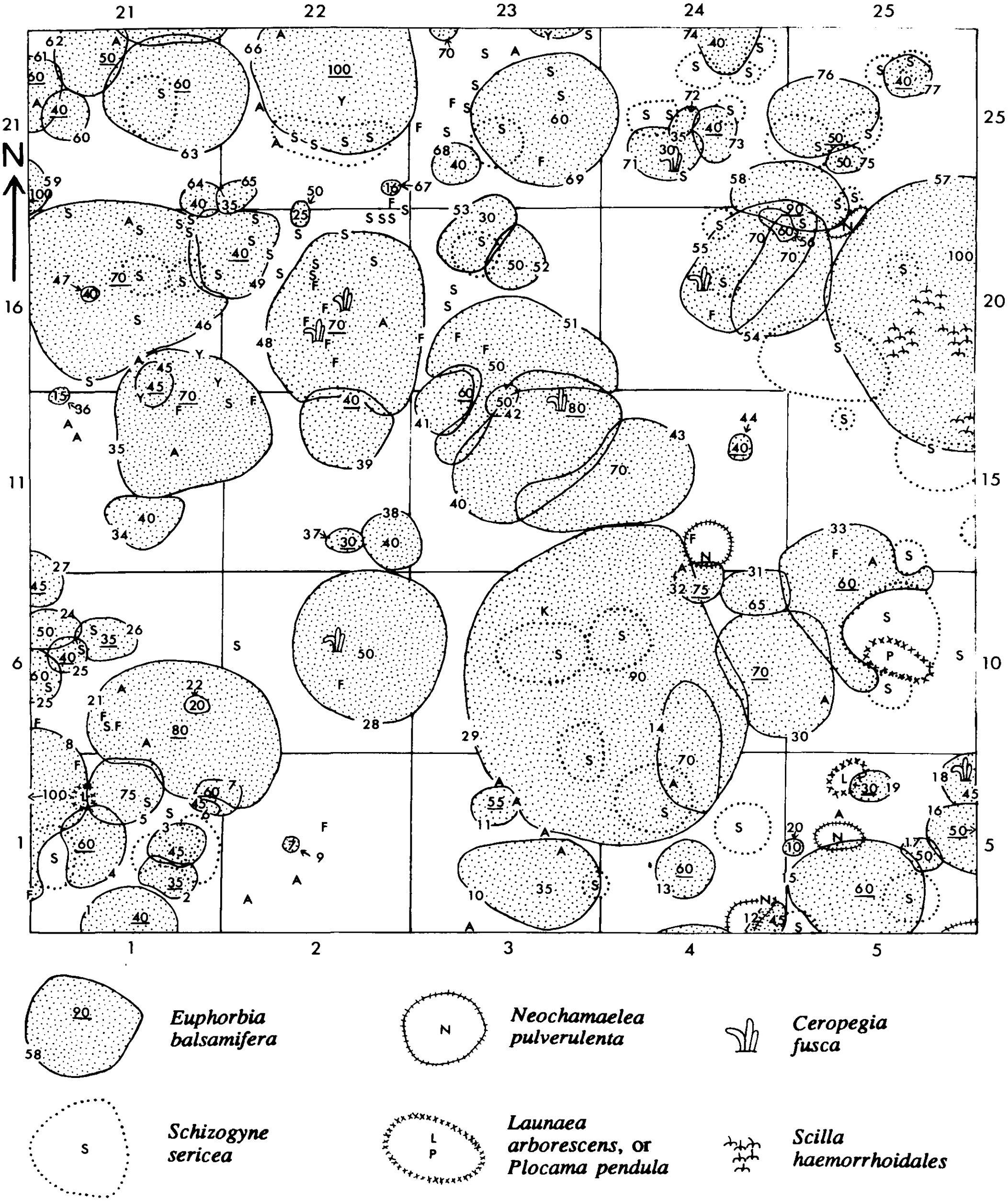


Fig. 13. Population map. Plot of 10 x 10 m, subdivided into 25 squares of 4 m² each (cf. Tab. 2). *Euphorbia balsamifera* plant number is given on, or close to, contour line. Number inside *E. balsamifera* contour is placed at point of inception and gives height of plant and whether pistillate (underlined) or staminate (not underlined). Letters at points of inception: A - *Asphodelus* sp. (leaves only); F - *Frankenia laevis*; K - *Kleinia neriifolia*; L - *Launaea arborescens*; N - *Neochamaelea pulverulenta*; P - *Plocama pendula*; S - *Schizogyne sericea*; Y - *Polycarpae nivea*.

Tab. 2. Individuals of *E. balsamifera* in plot (cf. Fig. 13).

Ind. No.	Sq. No.	♀	♂	Sterile	Height cm	Crown diameter cm	Growth classes						Notes
							Y	S	L	H	E	D	
1	1	x			40	80		x					
2	"	x			35	40 x 30		x					
3	"		x		45	55 x 35		x					
4	"	x			60	55 x 120		x					
5	"		x		75	80 x 60		x					
6	"		x		45	10					x		Nearly dead
7	"		x		60	50 x 70		x					
8	"		x		100	200				x			
9	2			x	7	5	x						2 shoot generations
10	3		x		35	150 x 110			x				
11	"	x			55	40					x		Dying, few terminal rosettes
12	4		x		45	55 x 40		x					One-sided
13	"	x			60	60		x					
14	"		x		70	70 x 100		x					Crown fused with 29
15	5	x			60	160 x 140			x				
16	"	x			50	130 x 100			x				
17	"		x		50	50 x 30					x		Clearly weakened
18	"		x		45	60 x 50		x					
19	"	x			30	40 x 30		x					
20	"			x	10	5	x						2 shoot generations, 2 ultimate branches
21	6	x			80	145 x 120			x				
22	"			x	20	5					x		Dying, 1 leaf rosette + 3 dead ultimate branches
23	"		x		60	60		x					
24	"		x		50	45 x 50		x					
25	"	x			40	40		x					
26	"	x			35	50 x 60		x					
27	"	x			45	70		x					
28	7		x		50	160			x				Compact cushion
29	9		x		90	300 x 330				x			
30	"	x			70	140			x				
31	"		x		65	70 x 60		x					One-sided
32	"	x			75	50 x 30		x					Long internodes. Shaded by 29
33	10	x			60	150 x 180			x				Crowded by *Schizogyne*
34	11		x		40	80 x 60		x					
35	"	x			70	170 x 180			x				
36	"			x	15	10	x						3 shoot generations
37	12	x			30	40 x 30		x					
38	"		x		40	70		x					
39	"	x			40	90		x					One-sided
40	13	x			80	150 x 170			x				One-sided
41	"	x			60	70 x 80		x					One-sided
42	"			x	50	30 x 20					x		Weak. Straggly.
43	14		x		70	170 x 130			x				Compressed
44	"	x			40	20 x 30		x					Partly broken (by sheep trampling?)
45	16	x			45	40 x 50		x					Long internodes, but many ultimate branches
46	"	x			70	240 x 190				x			

Tab. 2 (continued).

Ind. No.	Sq. No.	♀	♂	Sterile	Height cm	Crown diameter cm	Growth classes Y	S	L	H	E	D	Notes
47	16			x	40	10					x		Dying this year? 4 shoot generations. All leaves wilted
48	17	x			70	180 x 220				x			
49	"	x			40	80 x 100		x					
50				x	25	10 x 20	x						4 shoot generations, 16 ultimate branches
51	18		x		50	190 x 120			x				Crown fused with neighbours
52	"		x		50	60		x					Candelabra-shaped
53	"		x		30	70 x 90		x					One-sided
54	19		x		70	160 x 100			x				Completely fused with 55
55	"		x		70	160 x 100			x				" " " 54
56	"			x	60	20					x		2 long ultimate branches, few leaves
57	20		x		100	260				x			
58	"	x			90	100		x					Long internodes, shaded by 57
59	21		x		100	100			x				Candelabra-shaped
60	"	x			40	50		x					One-sided
61	"	x			60	90		x					
62	"	x			50	70 x 80		x					One-sided
63	"	x			60	140 x 130			x				
64	"		x		40	40		x					One-sided
65	22		x		35	40 x 30		x					One-sided
66	"	x			100	190 x 170			x				Dense cushion
67	22			x	16	13	x						3 shoot generations, 9 ultimate branches
68	23		x		40	50		x					
69	23		x		60	160 x 140			x				
70	"			x	50	40	x						6 shoot generations
71	24		x		30	80		x					
72	"	x			35	15 x 30		x					One-sided
73	"	x			40	40 x 70		x					
74	"		x		40	70 x 80		x					
75	25		x		50	40 x 30		x					Long internodes, open
76	"	x			50	110 x 80			x				One-sided
77	"	x			40	40 x 50		x					
Totals		35	32	10			6	41	18	5	7	0	

(5) Not a single dead individual was found within the 100 m^2 plot. The surrounding part of the population finally revealed six dead plants amongst an estimated 300. Four were tall and narrow plants with few branches hidden within the crown of much larger individuals and apparently killed in competition with their larger neighbours. Two were big plants growing side by side which, for some unexplicable reason, had died several years ago and were now heaps of collapsed, dry and partly disintegrated stems. It did not seem as if they had died from natural causes (human interference?). All surrounding plants were healthy and normal. In this area, well established *E. balsamifera*-plants apparently could live

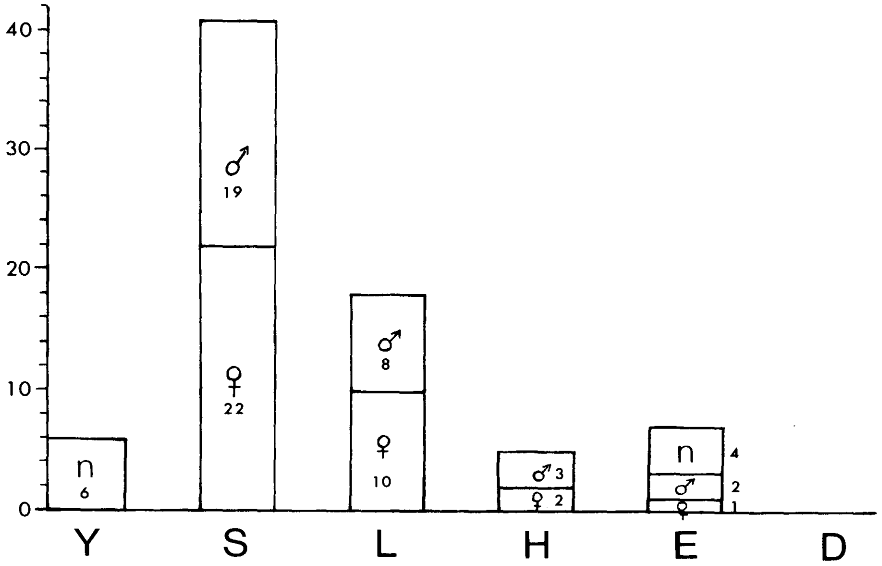


Fig. 14. Number of pistillate, staminate, and non-flowering plants per growth class (cf. Tab. 2). n - non-flowering; ♀- flowering pistillate; ♂- flowering staminate.

forever, excepting accidents and catastrophes. Death rate due to conspecific competition is extremely low, considerably less than one individual per 100 m^2 per year, to judge from my observations.

Predators, including grazing animals, are fended off probably by the milky juice, which occurs in most parts of the plant.

(6) Recruitment rate, too, is extremely low. The analysis plot included only six established young plants. Two of these were two years old, with two shoot generations (Nos. 9 and 20), two were three years old, with three shoot generations and nine ultimate branches (Nos. 36 and 67), one was four years old with four shoot generations and 16 ultimate branches (No. 50) and the last one was six years old with six shoot generations (No. 70). No plant showed seven shoot generations. In other words, during the last seven years, six new plants had been recruited into the plot, i.e. approximatley one per year.

Nearly all newcomers had rooted away from older plants in the vegetation-free openings (squares 2, 5, 11, 17, 22 and 23). The two exceptions (Nos. 42 in square 13 and 47 in square 16) were barely alive, with few and wilted leaves and no chance of survival.

(7) Altogether, the 100 m^2 plot held 77 *E. balsamifera* individuals: 35 pistillate, 32 staminate and 10 non-flowering (Tab. 2). The number of pistillate, staminate and non-flowering plants in each of the six growth classes is shown in Fig. 14. The rate of small plants to large and huge is approximately 6:3:1.

Reproductive capacity

One hundred mature capsules were collected from 30 plants, approximately 3 capsules per plant, and left in a paper bag to explode. Eventually, 298 seeds were released. Seed production, consequently, is very near to three times the capsule production, as indicated

Tab. 3. Seed production per plant and growth class. Sh. cl. - shape class, as follows: K - candelabrum (open on the sides); C - cushion (dense to the ground); I - intermediate (e.g., open on N side, dense on S side). Growth classes in accordance with Tab. 1.

Pl. No.	Sh. cl.	Height	Crown diameter	Growth cl.			Loc. No.	Date	Part counted	Fruits per plant	Seeds per plant (ca.)	Seeds per plant per growth class
				S	L	H						
A	K	40	65	x			1	19-I	1/1	68	204	
B	C	45	80	x			3	31-I	1/1	254	760	510
C	I	45	70	x			"	"	1/1	190	570	
D	C	75	200 x 180		x		"	"	1/1	733	2,200	
E	K	150	200		x		"	"	2/5	ca. 830	2,500	2,290
F	I	70	170		x		"	"	1/2	ca. 720	2,160	
G	K	110	200			x	"	"	1/4	ca. 1,760	5,300	
H	I	105	210			x	"	"	1/4	ca. 2,150	6,450	6,320
I	C	100	200			x	2	2-II	1/4	ca. 2,400	7,200	
J	C	200	400 x 400			x	"	"	1/15	ca. 9,000	27,000	27,000
Total No. of fruits and seeds on 10 plants										18,100	54,300	
Average No. of fruits and seeds per plant										1,810	5,430	

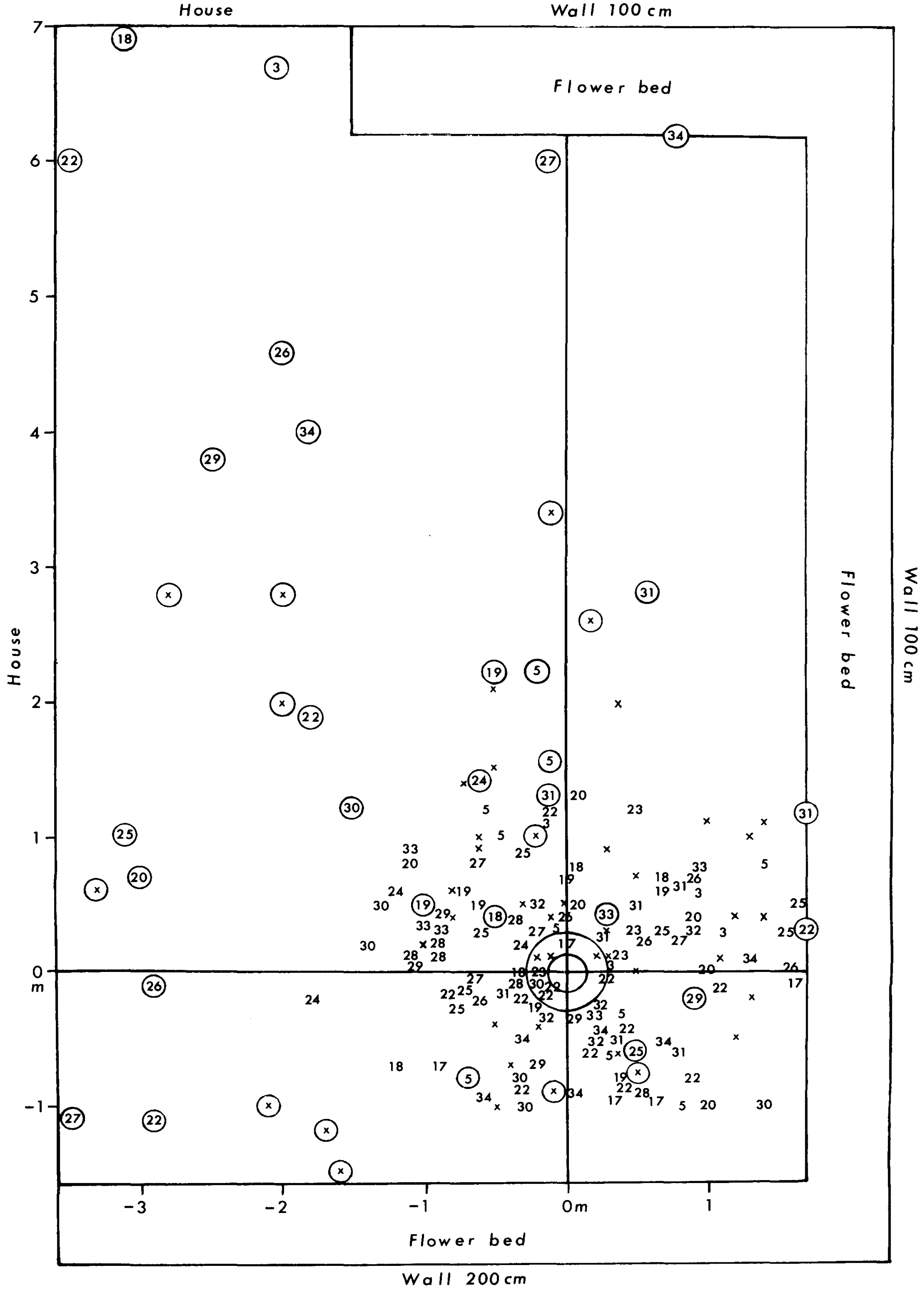
by the number of ovules per ovary.

Capsule production was studied on ten plants subjectively selected as a representative sample. The ten plants had approximately 18,100 fruits altogether, or approximately 54,300 seeds, i.e. about 5,430 seeds per "average fruiting plant" in this area this season (Tab. 3).

This figure is based not only upon plants of different sizes, but also of different

Tab. 4. Estimated seed production per 1000 m^2.

Growth class (cf. Tab. 1)	Number of female plants in plot (cf. Fig. 14)	Seeds per plant (cf. Tab. 3)	Totals
S	22	510	11 220
L	10	2 290	22 900
H	2	6 320	12 640
Seeds produced in 100 m^2			46 760
Seeds produced in 1000 m^2			467 600


House
Wall 100 cm
Flower bed
House
Flower bed
Wall 100 cm
Flower bed
Wall 200 cm
7
6
5
4
3
2
1
0
m
-1
-3
-2
-1
0m
1

Tab. 5. Seeds and fruit valves recovered in experiment (cf. Fig. 15).

Fruit No.	Seeds	Valves	Date	Comments
1	0	6	24-I	Not in Fig. 15
2	0	5	"	"
3	1	4	25-I	
4-5	3	7	"	Marked as 5 in Fig. 15
6-16	12	34	26-I	Marked as x in Fig. 15
17	0	5	27-I	
18	2	4	"	
19	2	6	"	
20	1	6	"	
21-22	4	12	28-I	Marked as 22 in Fig. 15
23	0	5	"	
24	1	3	"	
25	2	6	"	
26	2	5	"	
27	2	4	"	
28	0	6	30-I	
29	2	4	"	
30	1	6	"	
31	3	6	"	All parts!
32	0	5	"	
33	1	6	"	
34	2	6	"	
From target area	41	151		
From container	0	41		
From top of wall	2	0		
Total recovered	43	192		34 fruits give 102 seeds and 204 valves

Fig. 15. Dispersal of seeds and fruit valves in first experiment (cf. text and Tab. 5). Circled number represents a seed, uncircled number represents a valve. Numbers correspond to fruit numbers in Tab. 5. Double circle outlines plant (outer circle) and container.

shapes. Some formed dense dome-shaped cusions with ultimate branches and leaf rosettes over the entire surface down to the ground (Bramwell & Bramwell 1984: Fig. 184, Santos Guerra 1983: 45). Others were candelabrum-shaped with most of the branches in the top one third of the plant (Børgesen 1924: Fig. 12). Typically candelabrum-shaped plants often produce much fewer capsules than typically cushion-shaped plants of approximately the same size. Intermediates of different degrees were as common as the extremes. Also, one of the giants in the study area was included as plant No. J.

A very rough estimate of seed production per growth class is included in Tab. 3, with the giant left out.

On the basis of the estimates in Tab. 3 and the population analysis (Tab. 2, Fig. 14) the approximate seed production per 1,000 m^2 of population can be calculated to roughly 467,600 (Tab. 4).

Autochory

The first experiment (Fig. 15) was performed on a terrace in Los Christianos. The terrace was rectangular, approximately 8 x 5 m, and surrounded by a house on one side, and by flower beds and walls on the other three sides. On 19th January the terrace was covered with a large sheet of plastic and a fruiting plant (No. A in Tab. 3) was brought in from the Montaña Centinela area and placed in a container with water on the terrace, near one corner.

The plant was quite small, and thereby relatively easy to handle, and it was in the beginning of seed discharge activity. Already, 15 of its capsules had exploded leaving behind the characteristic six-armed central columns. Fiftythree capsules remained undehisced, but several showed signs of approaching dehiscence. Some fruits were considerably younger than the majority and probably were from a second burst of flower. All fruits were between 30 and 40 cm above ground, due to the plant's candelabrum shape. The plant remained healthy, with enlarging axillary buds and turgid leaves and stems throughout the experimental period.

Initially, the plant was placed with its fruits between 70 and 80 cm above the terrace floor. However, after the first two capsules had exploded on 24. January, throwing all seeds out of the target area, the plant was lowered so that its fruits were again 30-40 cm above ground.

The process of fruit dehiscence was then followed until 30. January, in the evening, when the experiment was discontinued. Seeds and fruit valves (half cocci) were recovered from the plastic sheet immediately upon dehiscence, tabulated (see Tab. 5) and charted (Fig. 15). Summary records had to be made when two explosions followed in rapid succession (Nos 4 plus 5, and 21 plus 22) and on the day when the plant could not be constantly watched (26. January).

When the plant was cleared away, upon conclusion of the experiment, 41 valves (but no seeds) were found in the container that had housed the plant. Two seeds were detected on top of the 2 m tall part of the surrounding wall. Nineteen capsules were left on the plant unexploded.

The experiment showed, firstly, that the autochorous mechanism of *Euphorbia balsamifera* is unexpectedly forceful. Of the approximately 100 seeds expelled from the 34 dehiscing capsules only 43 were recovered (Tab. 5). More than one half of the seeds had been thrown out of the target area, either into the surrounding flower beds or clear across the surrounding walls.

The impression was gained that most of the recovered seeds had hit the house or one

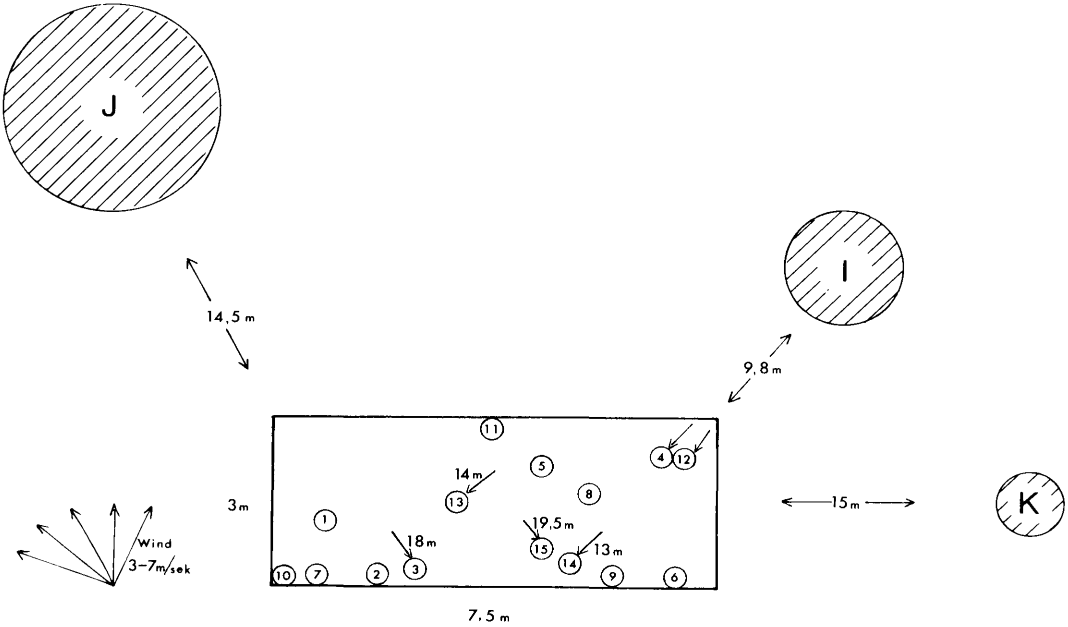


Fig. 16. Diagram of second experiment, showing seed hits (circles with numbers) in target area and distances to the three nearest seed sources. Information about plants I and J in Tab. 3. Arrow on seed points from probable source, in four cases with probable dispersal distance added.

of the surrounding walls before coming to rest. The three seeds of capsule No. 31, for instance, all were deposited on the same side of the mother plant, an accomplishment quite impossible by direct "shots". Possibly all the seeds found near the mother plant had rebounded from the house or the high wall behind the plant.

The experiment did show, however, that the seeds fly much further than the capsule valves. Nearly all the 204 valves produced were recovered, viz. 192 (Tab. 5).

While the "valve rain" is most heavy close to the mother plant, gradually diminishing with distance, the "seed rain" has its maximum a considerable distance away from the mother plant.

It is remarkable that not a single seed ended up under the canopy of the mother plant. Obviously, the combination of a dome-shaped plant body, the position of capsules on ultimate branch tips, and the curved trajectory of the seeds, ascending steeply upwards in the beginning, prevented the flying into the crown of the plant.

Nearly all explosions took part after 12 o'clock, in the hot hours of the afternoon, with a few following into evening and night.

The maximum dispersal distance recorded during this experiment was nearly 8 metres (Fig. 15, seed 18). However, even this seed might have been stopped by the house.

A second experiment was performed in Barranco del Callao on 2. February (Fig. 16). A large sheet of plastic, 7.5 x 3 m, was placed, as a "seed-catcher", on the ground and secured with stones. On one side of the catcher was a gravel road and bare soil, on the

Tab. 6. Wind velocities during period of seed discharge.

Loc. No.	Date	Time of day	Velocity (m/s)
2	2-II	14.00-16.00	3-7
1	3-II	15.30-15.35	10-15(-18)
"	4-II	13.40-13.45	10-15(-20)
"	"	16.00-16.05	15-20
"	"	17.30-17.35	13-18
"	6-II	12.25-12.30	(10-)14-16(-21)
"	"	14.00-14.05	15-20
"	"	16.00-16.05	10-15(-18)

other a gentle slope with scattered individuals of *E. balsamifera*. Most of these were young and non-flowering or staminate. The closest pistillate plants were a giant (J), its periphery 14.5 m away from one corner of the plastic sheet, a huge plant (I) with its periphery 9.8 m from another corner of the sheet and, finally, a small plant (K) about 15 m outside the short end of the sheet.

All pistillate plants in the area were dispersing seeds, as betrayed by the characteristic popping sounds of exploding capsules. The experiment lasted for two hours (14.00-16.00), during which time 15 seeds landed on the plastic sheet. The landings were recorded immediately, before the wind could rustle the plastic and cause seed displacement.

The wind increased from about 3 to about 7 m/sek during the experiment, and influenced both upon dispersal distances and the manageability of the catcher. However, afternoon winds could not be avoided. In fact, incessant afternoon winds prevented experimentation in the Montaña Centinela area (Tab. 6).

Both the strong winds at the time of seed dispersal, the position of the plant, whether on flat ground, on a slope or in a vertical cliff, and the height of the plant, greatly influence upon dispersal distance. In the experiment, plants I and J both were rooted at a level about 2 m higher than the level at which the seed catcher was placed. Also, plant J was unusually tall with the highest capsules 2 m above ground.

When the warning of a popping capsule on plant I resulted in the sighting of an incoming seed from that direction, this seed was assumed to have originated from plant I (Nos. 4, 12, 13, 14). Capsule explosions on plant K, too, could be heard by one of the observers. Seeds which landed on the seed catcher in absolutely quiet periods (Nos. 3, 15) had to come either from plant J or from plants further away.

Seeds caught on the catcher, of course, only represented a small fraction of the seeds that were released by the shrubs I, J and K during the two hours of observation. Two seeds were heard as they hit the ground beyond the catcher.

Measured dispersal distances varied between 11 and 20 metres. For *Euphorbia balsamifera* the maximum autochorous dispersal distance must be well over 20 m under optimal conditions.

Seed predation

Euphorbia balsamifera has few enemies. It is protected against predation by its free-flowing latex. Although non-toxic the latex, when exposed to air, rapidly coagulates into an unpleasant, gluey substance (Gonzales Henríques et al. 1986: 143). No insect attacks were observed on plants or capsules. Even grazing goats do leave *E. balsamifera* alone.

The seeds, however, enjoy no such protection after having left the capsules, and serve as food for rock pigeons (*Columba livia canariensis* Bann.). These birds constantly were present in the tabaibal during the period when seeds were being discharged (Fig. 17), walking about and picking something up from the ground. When undisturbed they only rarely took to the wings, but walked and picked until they disappeared amongst more distant tabaibas. Then a new couple or little band would appear from somewhere else, walking and picking. Occasionally, two or more pigeons would fly in or out of the area.

An attempt at quantifying this seed predation was made at Las Hoyas Blancas East of San Isidro (Tab. 7). A feeding pigeon made an average of 4.4 picking movements per minute.

It should be noted that what the pigeons picked could not be directly observed. However, only two plant species were fruiting in the tabaibal on Las Hoyas Blancas at this time. They were *E. balsamifera* and *Patellarifolia patellaris* (Moq.) S., F.-L. et W. The latter, however, grew mainly along the road while the pigeons most of the time stayed away from the road. The remaining plant species observed in this tabaibal, viz. *Aizoon canariense*, *Argyranthemum frutescens* (L.) Sch. Bip., *Ceropegia fusca*, *Echium bonnetii* Coincy, *Euphorbia obtusifolia* Poir, *Gymnocarpos decander* Forssk., *Helianthemum canariense*, *Heliotropium ramosissimum* (Lehm.) DC., *Herniaria canariensis* Chaudhei, *Ifloga spicata* (Forssk.) Sch. Rip., *Launaea arborescens*, *Lobularia intermedia* Webb in Webb et Berth., *Lotus sessilifolius* DC, *Ononis serrata* Forssk., *Plocama pendula*, *Polycarpaea nivea*, and *Schizogyne sericea* had no seeds at the time of observation, or the species were rare with very small seeds (*Helianthemum* and *Lobularia*). It was assumed,

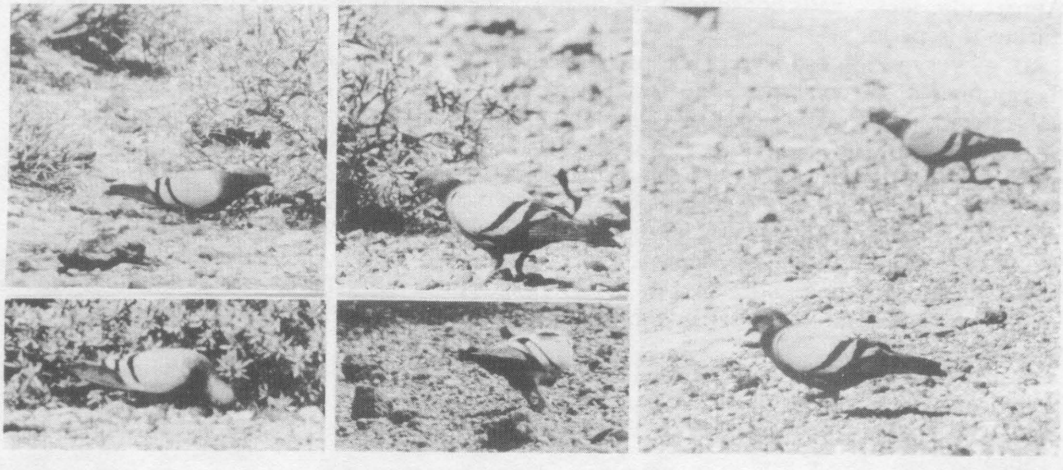


Fig. 17. Rock pigeons searching for seeds amongst *Euphorbia balsamifera* plants. Locality No. 4 on 13. and 14. February.

Tab. 7. Number of picking movements per minute, locality No. 4.

Obs. No.	Date	Time of day (ca.)	Seed discharge activity	Duration (seconds)	Number of movements
A	3-II	11.30	Beginning	260	18
B	"	13.00	Beginning	150	8
C	"	13.30	Beginning	190	8
D	13-II	11.00	Peak	30	7
E	"	13.45	Peak	70	12
F	"	15.40	Peak	230	21
G	"	16.15	Peak	90	6
H	14-II	12.00	Peak	75	6
I	"	12.10	Peak	210	11
J	"	14.15	Peak	60	5
K	"	16.45	Peak	150	9
Total				1 515	111
Duration of each search				1 515/111 = 13.6 s	
Number of picking movements per minute					4.4

therefore, that what the pigeons picked up from the ground were *E. balsamifera* seeds. Apparently, these seeds constituted the main source of food for the local pigeon population during this period.

A very rough estimate of the population of feeding pigeons was obtained by counting the number of pigeons that were frightened away when driving through the area, or when noises were deliberately made (by banging car doors or shouting) during prolonged periods of observation (Tab. 8). It was estimated that the area influenced by such disturbances was on the average about 5,000 m^2, which gave an average of 2.3 feeding pigeons per 1,000 m^2 (Tab. 8).

Pigeons apparently were present in the tabaibal at all hours of the day, during the weeks when *E. balsamifera* capsules were dehiscing. I have no data for when feeding started in the morning and ended in the evening. However, a fairly safe estimate seems to be that pigeons, not necessarily the same individuals all the time, were present in the tabaibal for 8 hours a day.

At each locality intensive seed-scattering lasts for about three weeks, with a varying period of less-instensity dispersal thereafter. This means that pigeons remove on the order of 21 x 8 x 60 x 10.12 = 102,000 seeds from each 1,000 m^2 of tabaibal per fruiting season (Tab. 9).

Since the main seed dispersal period in *E. balsamifera* is closely correlated with the first good rain of the season, occurring about 4 months later, and since the first rain

Tab. 8. Number of pigeons per 1000 m^2.

Obs. No.	Date	Loc. No.	Time of day (ca.)	Seed discharge activity	Number of pigeons frightened away	
1	2-II	2	12.00	Peak	2 + 3 + 5	= 10
2	"	"	16.45	Peak	2 + 2	= 4
3	3-II	"	12.30	Peak	2 + 5 + 3 + 1 + 1	= 12
4	"	4	13.20	Beginning	3 + 2 + 5	= 10
5	4-II	2	10.15	Peak	4	= 4
6	5-II	4	10.00	Beginning	1 + 1 + 2 + 1	= 5
7	6-II	"	11.30	Beginning	2	= 2
8	"	1	12.20	Very end	3	= 3
9	12-II	4	15.00	Peak	6 + 10 + 2 + 2 + 1	= 21
10	13-II	"	11.30	Peak	1 + 2 + 3	= 6
11	"	"	13.00	Peak	12 + 8	= 20
12	"	"	15.20	Peak	13 + 16	= 29
13	14-II	"	16.30	Peak	18 + 4	= 22

Total number in 13 observations	149.0
Average number per observation per 5,000 m^2	11.5
Average number of pigeons per 1,000 m^2	2.3

normally falls at different times in different places, tabaiba seeds in quantity normally could be available to pigeons in one place or another for several months.

Tab. 9. Estimated seed predation per 1000 m^2.

	Number	Reference
Picking movements per pigeon per minute	4.4	Table 7
Seeds removed per minute: 4.4 x 2.3	10.12	Table 8
Seeds removed per 8-hour day: 10.12 x 60 x 8	4857.6	
Seeds removed per 3-week season: 4857.6 x 21	ca. 102,000	

DISCUSSION

Life history

Euphorbia balsamifera is the dominant species of the vegetation type that bears its name, viz. *Euphorbietum balsamifera* (Sunding 1972). Large, continuous areas of the dry lower regions of the Canary Islands have conditions suitable for this species (Voggenreiter 1974, Gonzales Henríques et al. 1986).

Euphorbia balsamifera is long-lived and competes very successfully with its associated species, as deduced from the population analysis, in particular because of its high water storage capacity and resistance to goat grazing. With reference to its dominant position in a stable vegetation type, its longevity, and mode of dispersal, *E. balsamifera* could be classified as a so-called 'K-selected' species (Gadgil & Solbrig 1972). However, other aspects of life history does not fit into the concept of 'K-strategy'. Failure of establishment and mortality apparently is due to harshness of the physical environment more than to density factors and competition, and the vegetation in which this species belongs is an open one, with large areas of bare soil in between the plants. Howe & Smallwood (1982: 221) question the utility of the r-K dichotomy.

The most critical phase in the life history of *E. balsamifera* appears to be establishment, not because of competition amongst siblings, but because of an, as it seems, extreme paucity of safe sites. *Euphorbia balsamifera* grows on rocky ground with a thin soil layer, with most of the soil being washed away by soil erosion (Sunding 1972: 67). Safe sites, apparently, are only those crevices and cracks that lead down to situations in the rock where moisture collects. This is strikingly demonstrated in the outskirts of stable populations. Along the periphery favourable germination microsites are revealed, by a narrow zone of scattered seedlings and young plants. However, these peripheral germination sites are not safe sites, because the plants germinating there regularly die, mostly from drought, before reaching reproductive age. New plants, however, continuously appear because seeds are being shot into this zone every season. If conditions should improve, the young plants of the peripheral zone would grow to maturity and the population would expand its area.

The variable age of plants and the openness of vegetation of most *E. balsamifera* populations might be similarly related to availability of safe sites. If a germination microsite becomes a safe site for growth and reproduction only very rarely, when a particular sequence of seasons with conditions favorable for this particular site occurs, a potentially safe site might remain unfilled for long periods of time.

Seed budget

For each 1,000 m^2 of tabaibal, *E. balsamifera* produces more than 467,000 seeds. With a seed weight of 16.8 mg, this production comes to a total of about 7.86 kg. Under stable conditions only 10 seeds are needed for recruitment, while about 100,000 are eaten by pigeons (Tab. 10).

Obviously, the seed production is sufficient to secure the positioning of 10 seeds in safe sites, where germination and growth do occur. Apparently, an immense seed purplus exists under stable conditions.

Admittedly, due to time available my data on seed production, seed predation, recruitment, population structure etc. are only very approximate and rough and, also,

Tab. 10. Seed account (per 1000 m² per season).

	Credit	Debit	Reference
Number of seeds produced	467,600		Tab. 4
Recruitment		10	p. 00
Predation		102,000	Tab. 9
Not accounted for		365,590	
	467,600	467,600	

Weight of one seed production: 467,600 x 0.0168 g = 7855.68 g
= ca. 7.86 kg

concern one particular place in one particular season only. The data represent no more than an unprecise example of the overall reproductive situation of *Euphorbia balsamifera* populations.

While the individual seed of *E. balsamifera* is relatively large compared to seeds in general (cf. e.g. Brouwer & Stählin 1975), the output of seed in numbers per plant is relatively low (cf. e.g. Salisbury 1942, 1975). Seed production, taken as seed weight per 1.000 m², on the other hand, is considerably higher than for herbaceous species in a temperate forest. Falinska (1968) found the total fresh seed biomass in the herb layer of a *Quercus-Carpinus* forest to be 7.04 kg/1,000 m²/year in the highest yielding areas.

Specialized seed dispersal

Euphorbia balsamifera is among the most efficient autochorous plants with regard to dispersal distance. Only exceptionally do autochores shoot their diaspores more than 10 metres away (Romell 1938: 314). The world record of 45 m is held by *Hura crepitans* (Swaine & Beer 1977), another Euphorbiaceae.

The autochorous dispersal method of *E. balsamifera* is well suited for the maintenance of populations and the gradual expansion of populations into new areas. Because of the relatively dense and locally well distributed seed rain, chances are high for a viable diaspore to be in exactly the right place at exactly the right time (Berg 1983: 18). From a population maintenance point of view, therefore, the general euphorbiaceous dispersal mechanism, with its specific modifications, appears beautifully sufficient for meeting the requirements of *E. balsamifera* - as, of course, one might expect from the specialized dispersal mechanism of a successful species.

The specific modifications in *E. balsamifera*, for instance the dome-shaped growth form and the high number of ultimate branches, as well as longevity, competitive power and other life history traits, have made possible the reduction of number of cyathia, and thereby the number of seeds, per compound inflorescence without ill effects upon reproduction. Important in this connection is also the extreme economy of the *E. balsamifera* dispersal method: every single seed escapes from the canopy of the mother plant but, normally, remains within the ecological niche of the species. It is definitely the opposite of a "wasteful method" in the sense of Salisbury (1975).

Distribution and chance dispersal

Since the expansion of area in a dominating, strongly competitive species can take place gradually, small step by small step, most, if not all, of the distribution of *E. balsamifera* within one island could have come about by autochory, considering time and changing environment. However, autochory definitely is a method for local dispersal only. It is impossible for *E. balsamifera* seeds, even when aided by strong winds and a lofty starting point, to be shot from one Canary Island to another, over stretches of sea varying from 12 km (Lanzarote - Fuerteventura) to 80 km (Fuerteventura - Gran Canaria).

Since the seeds don't float, they cannot be dispersed hydrochorously. Since viable seeds only can be found on living plants, due to the explosive mechanism which is triggered by desiccation, and since living plants and branches sink in water, dispersal by rafting from island to island appears unlikely.

The presence of *E. balsamifera* and other, as it seems, habitually autochorous plants on more than one island, and, in some cases, on the African mainland as well, might be taken as a strong indication of former land connections inbetween the islands and between the islands and Africa. However, most recent research on Canary Island biogeography gives no support to the land bridge hypothesis, but maintains that the Canary Islands, totally or in part, are of oceanic origin, emerging from the sea due to vulcanic activity between 40 (Fuerteventura and Lanzarote) and 0.6 (La Palma) million years ago (Schmincke 1976, Sunding 1979, Araña & Ortiz 1986).

How, then, can the total area of distribution be explained in the case of *E. balsamifera*? The vicariance model of biogeography, which explains disjunctions as resulting from the splitting up of a once continuous area, has little relevance to oceanic islands. The alternative, the dispersalist model, presupposes some kind of dispersal from island to island and from (or to) Africa.

An astronomic number of *E. balsamifera* seeds might be swallowed by rock pigeons in good seed years. The population from which the present data come, stretches for 70 km more or less continuously over a 2 to 10 km wide strip of land, from Costa del Silencio to Fasnia, on the South Coast of Tenerife (see Gonzales Henríques et al. 1986: Fig. 30). In other words, this one population covers an area of about 400 km^2. In the unlikely event that my rough predation figure of ca. 100,000 seeds per 1,000 m^2 represents the average, and that enough pigeons were available, as much as 40,000 millions, or 672 tons, of *E. balsamifera* seeds might have been devoured by rock pigeons on this South Coast of Tenerife in the winter and early spring of 1988.

Also the turtle dove (*Streptopelia turtur turtur* L.) eats *Euphorbia* seeds, according to Nogales Hidalgo (1985: 87). The turtle dove is migatory, arriving in March from the neighbouring continent (Pérez Padrón 1986).

We know that pigeons are excellent fliers (Ridley 1930: 497). We also know that these granivorous birds occasionally pass seeds unharmed (van der Pijl 1982: 31) or are killed with crops full of diaspores by birds of prey (Ridley 1930: 498). We also know (K.W. Emmerson, pers. comm.) that when seeds are plentiful on Tenerife, pigeons are plentiful, too. Furthermore, when seeds are plentiful on La Palma, but not on Tenerife, pigeons are plentiful on La Palma, but not on Tenerife. Outside the breeding season, which lasts from April to July (Pérez Padrón 1986), rock pigeons, apparently, move easily from island to island in search of food. It is my strong belief that long-distance dispersal of *E.*

balsamifera is effected by its seed predator, *Columba livia canariensis*, and possibly by other granivorous birds, as suggested by Bramwell (1985: 10). Unfortunately, the undisputable proof of this speculation is exceedingly difficult to produce.

The dioecy of *E. balsamifera* represents an added complication to successful (Berg 1983: 14) long distance dispersal. However, endozoochory, as opposed to hydrochory and anemochory, has a pronounced tendency towards the deposition of diaspores in aggregates, because the animal dispersal agent normally releases numerous diaspores simultaneously (Fenner 1985: 50, Mendoza-Heuer 1987: 240). Were chance dispersal of *E. balsamifera* to an island due to the death of an incoming pigeon with seeds in its crop, the likelihood is that more than one viable seed would have become released to germinate (see also Baker & Cox 1984: 250).

The numerous species of Canary Island plants classified by Lems (1958, 1960) as "sclerochores" with respect to dispersal mechanism, might very well be dispersed, at least occasionally, by granivorous birds (cf. Bramwell 1985: 14). Lems (1958: 140) regarded his sclerochorous Canary Island plants to have narrow range dispersal only. This may prove not to be true.

Sclerendochory

I propose the term "sclerochorous endozoochory" ("sclerendochory" for short) for endozoochorous dispersal of units that are eaten but have none of the normal endozoochorous attractants: pulp, colour, taste and odour. I feel that a special term is needed for this often neglected type of dispersal, which in adaptive and evolutionary respects differs so strikingly from what is commonly regarded as endozoochory.

Seeds of *E. balsamifera* are such dry dispersal units. Their occasional dispersal by rock pigeons that happen to pass seeds unharmed, or die with viable seeds in their digestive tract, represent cases of sclerendochory.

Sclerendochory is a common phenomenon. Faeces from herbivores, both domesticated and wild, quite regularly contain viable seeds from dry fruits (Heintze 1915, 1916, Müller-Schneider 1954, Heady 1954, Wicklow & Zak 1983, Janzen 1984, Welch 1985). Many birds eat, and sometimes void, dry diaspores (Ridley 1930: 439ff, 488ff, van der Pijl 1982: 31). Savile (1972) considers the grazing of geese during spring migration as one of the two most important dispersal processes in the Arctic.

Sclerendochory has been variously referred to, under headings such as "endozoochory by non-adapted diaspores" (van der Pijl 1982: 31), "accidental endozoochory" (van der Pijl 1982: 46), and "dyszoochory" or "dysochory", i.e. dispersal through chance escape from destruction (van der Pijl 1982: 45, Müller-Schneider 1977: 105).

Dispersal ecologists in the traditional sense naturally have treated sclerendochory only very indifferently, because of the lack of features that could be interpreted as adaptations. Evolutionists, population geneticists and phytogeographers, on the other hand, who are primarily interested in the results of successful dispersal, not so much in the dispersal process itself, should benefit considerably from paying more attention to the phenomenon of sclerendochory.

All endozoochory which is combined with one or more of the normally recognized adaptations for endozoochory, might be termed "pulpendochory", notwithstanding the fact that a pulpy tissue is not always present. Mimetic seeds, for instance, only imitate pulp (van der Pijl 1982: 40).

Basic modes and strategy of dispersal

Most plants are dispersed by most dispersal agents one time or another. It seems important for reasons of evolution and ecology to distinguish between three basic modes of dispersal: specialized, generalized and chance (Stebbins 1971, Berg 1983).

In the case of *E. balsamifera* it might be argued that the effect of the extremely hard capsule is protection of the young seeds against being eaten too early by pigeons, and that the capsule explosion is a mechanism for presentation of the mature diaspore towards its agent. In other words, these charateristics might be interpreted as adaptations for sclerendochory and not for autochory. The evolutionary importance, then, would be attributed not to the short-range dispersal effect caused by capsule explosions, but to the dispersal effect of the few diaspores that survive passage through a pigeon. Sclerendochory, thus considered, would be similar in principle to synzoochory (Sernander 1927: 26), or dispersal by hoarding, in that the majority of diaspores are consumed and destroyed in return for dispersal of a very few (Fenner 1985: 52). Rommel (1938: 284) maintained that, in general, enormous numbers of diaspores are sacrificed in order statistically to enable a distant target hit, through a lucky coincidence of nearly impossible events.

The basic, but often neglected questions are these: Which is the winning seed? And why? Until we understand the problem of success amongst the astronomical number of seeds produced in long-lived plants, questions about gene flow, genetic neighbourhoods, evolution and adaptation can be only inadequately answered.

In the case of *E. balsamifera*, an analysis of the total dispersal mechanism (Berg 1983: 14) seems to indicate that autochory is specialized, sclerendochory is chance. For instance, the positioning of the capsules, namely vertical and peripheral, functions as an adaptation for autochory, since the effect of these characteristics obviously is a better scattering of the seeds, including the escape from mother plant canopy.

Absence of appropriate adaptations for tumbling indicates the nature of the reported chamae-anemochory of this species in Sahara (Monod 1974) to be chance dispersal also.

Plitman (1986) presents evidence of different dispersal agents that distribute the same diaspores and suggests that in most plants dispersal strategy involves two or more agents. In Plitman's way of thinking the strategy of *E. balsamifera* would feature autochory for short-distance dispersal and sclerendochory, and possibly chamae-anemochory, for long-distance dispersal.

In my way of thinking, "dispersal strategy" is "a set of adaptive responses accumulated over evolutionary time, without any teleological implications" (Wilbur et al. 1974), and affecting dispersal. Consequently, in my way of thinking, the dispersal strategy of *E. balsamifera* involves only autochory and no external agent at all.

Designation of every single mode of dispersal observed in a plant species one time or another, as part of the dispersal strategy of that species, contributes little new towards the clarification of the old enigma of dispersal structure versus dispersal mode (see e.g. Sernander 1927: 78, Heintze 1932: 3, Dansereau & Lems 1957: 26, Howe & Smallwood 1982: 203). I agree, however, fully with the notion of Plitman (1986), Herrera (1986), and others that most plant species show dispersal adaptations of such a broad nature that it precludes the idea of one-to-one coevolution between plant and animal species, as well as the idea of a one-to-one functional relationship between plant dispersal structures and details of the present physical environment (see Berg 1983: 20).

Euphorbia balsamifera is an excellent example. Its special kind of explosive capsule is found in thousands of species and hundreds of genera of Euphorbiaceae, representing most growth forms, most environments, most geographical regions and most life strategies. Undoubtedly, this kind of explosive capsule existed in predecessors, and originated long time ago, under conditions unknown to us, at least in detail.

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EVOLUTIONARY PATTERNS IN WILD SPECIES OF HORDEUM

R. von Bothmer

Bothmer, R. von, 1990. Evolutionary patterns in wild barleys. - Sommerfeltia 11: 65-72. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

Despite a similar morphology of the species the evolutionary pattern in the genus *Hordeum* is very complex including diverse reproductive patterns and polyploidy. The genome relationship shows a basic, diploid pattern of four genomes but this pattern becomes more complicated at the polyploid level. The majority of species are rather closely related and show an intricate, reticulate pattern of relationships, which is shown by several methods (C-banding techniques, CpDNA, isoenzymes etc.), There seems to be a certain differentiation between old and new world taxa. The nature of the polyploidy (auto- vs. alloploidy) is difficult to interpret due to the (rapid?) development of genetic systems for meiotic regulation.

Keywords: Evolution, Genome relationships, *Hordeum*, Polyploidy.

Roland von Bothmer, Department of Crop Genetics and Breeding, Swedish University of Agricultural Sciences, S-268 00 Svalöv, Sweden.

INTRODUCTION

The differentiation of plants in nature is a delicate balance between external forces and intrinsic genetic and biological systems. The tools we use for studies of evolutionary patterns and mechanisms are continuously increasing in number and refinements, but still we are far from a general, complete understanding, and no single method can be claimed to be superior to all others. Instead we need a large battery of methods and by combining different sets of data we get an increasingly better understanding of the processes operating in nature.

The present paper is an attempt to visualize some of the complex and intricate variation patterns revealed by different methods. It will not be a complete presentation of all results, but it will merely raise further questions of both biological and technical nature: viz. what do the results actually tell us and is it possible to interpret the data correctly? The project presented is a Swedish-Danish teamwork on the grass tribe, *Triticeae*, and this paper treats the results obtained in the genus *Hordeum*, a group we have studied for more than 10 years.

KARYOTYPES

The morphology of chromosomes may often give good information on relationships of possible pathways of differentiation. In *Hordeum* the karyotype is little differentiated but a few major differentiation lines are evident. On the diploid level all 17 American cytotypes constitute one group with a "basic karyotype" with two satellited pairs and one submetacentric pair as marker chromosomes (Linde-Laursen et al. 1986, 1989). In *H. cordobense* an inversion in one SAT chromosome pair distinguishes this species from the basic karyotype. The karyotype of *H. muticum* has probably developed from the common type through suppression or deletion of the NOR's of the metacentric SAT-chromosomes. Nuclear dominance causing only one visible SAT-chromosome pair occurs in *H. pusillum* or in some populations of *H. brachyantherum*. The old world species are also rather homogeneous having one or two satellited chromosomes. The single clearly differentiated species is *H. brevisubulatum*, the karyotype of which differs conspicuously from all other *Hordeum* species, especially with very large satellites (Linde-Laursen et al. 1980, Linde-Laursen & Bothmer 1984).

There is a general difference between cross- and self-fertilizing species in *Hordeum* reflecting the modes of reproduction. The outbreeder with a self-incompatibility system, *H. brevisubulatum*, has a maximum variation so that it is not possible to identify homologous chromosome pairs, which include both chromosome morphology and C-banding pattern (Linde-Laursen et al. 1980). In contrast, the inbreeders, e.g. the Asiatic diploid species *H. bogdanii* and *H. roshevitzii*, have both distinct homologous pairs and a very moderate variation of C-bands within populations, but a significant variation between populations (Linde-Laursen et al. 1980). Another striking phenomenon is also found in *H. brevisubulatum*, which is a huge species complex covering a distribution from western Turkey to eastern China. It occurs as diploids, tetraploids and hexaploids. Five "morphotypes", treated as subspecies, are recognized (Bothmer 1979). Karyotypes and C-bands differ considerably between populations and taxa. So most populations of subsp. *violaceum* (2x and 4x) have large telomeric heterochromatin similar to those found in rye, whereas the other subspecies have only small amounts of telomeric heterochromatin (Linde-Laursen et al. 1980, Linde-Laursen & Bothmer 1984). All the forms are compatible in crosses and (except for triploids) the hybrids are fertile (Landström et al. 1984).

The fundamental biological questions to be answered are connected with the karyological features and how they perform in nature: (1) Why are karyotypes, including heterochromatic regions, very stable in some species while highly variable in others? (2) Do major chromosomal shifts have evolutionary significance or do they mainly occur at the population level? (3) What biological significance has nucleolar dominance? (4) What biological significance has the constitutive heterochromatin (C-bands)?

GENOME RELATIONSHIPS

The basic concept of genome relationships is that like (homologous) chromosomes pair completely in meiosis, related but not identical chromosomes (homoeologous) pair to a certain extent but not completely and dissimilar chromosomes (non-homologous) do not pair at all (cf. Dewey 1984). Genome relationships are evaluated by analysis of chromosomal pairing in metaphase I in interspecific hybrids, and usually reported as the average number of chiasmata per cell. There are several sources of error in the determination of meiotic pairing, some of which will be treated below. However, provided a fair number of interspecific hybrid combinations are available, valid conclusions of a general pattern can be drawn.

The genus *Hordeum* comprises 30 species (altogether 40 cytotypes) and all species (but not all cytotypes) were included in a crossing programme (Bothmer & Jacobsen 1985, 1986). Altogether ca. 300 interspecific hybrid combinations were produced, the majority of which have been studied for meiotic MI pairing in a recently finished investigation. At the diploid level four "basic" genomes are present. *H. vulgare* and *H. bulbosum* usually have a very high pairing in their hybrids, but there may be variation in chiasma frequency between different hybrid families (Bothmer et al. 1983). The two species have the same genome, called I (Dewey 1984, Bothmer et al. 1986). Despite some morphological similarities *H. marinum* shows no chromosomal homologies to the other *Hordeum* taxa and has thus also a separate genome, provisionally called "X" (Bothmer et al. 1986). As deduced from studies of polyploid hybrids, the diploid *H. murinum* likewise has a separate genome ("Y", Bothmer et al. 1987, 1988). All the remaining 16 diploid species (20 taxa) have intermediate to high pairing in their mutual hybrids, and thus have a common genome, H. There seems to be a certain differentiation between Asiatic and American taxa, thus between species which have been separated for longer periods of time. On the diploid level, there are a few combinations, e.g. *H. patagonicum* (South America) x *H. roshevitzii* (Asia), in which the pairing is affected by specific gene action reducing the pairing.

The patterns at the polyploid levels are of necessity more complicated to interpret than the diploid one, but the major outlines are evident. *H. bulbosum*, 4x (II) and *H. brevisubulatum* (HH and HHH) both behave as true autoploids with an expected, high frequency of multivalents in both the "pure" species and in hybrids. The polyploids of *H. murinum* (4x and 6x) and *H. marinum* (4x) behave curiously, and despite an alloploid behaviour they may in reality be of autoploid origin (see below).

The three tetraploid species *H. secalinum* (Europe), *H. capense* (South Africa), and *H. depressum* (North America) all have the basic genome, H, together with a hitherto unrecognized one, which, in the case of *H. depressum*, may also occur in the genus *Hordelymus*. The remaining polyploids of *Hordeum* (tetra- and hexaploids) are segmental alloploids showing an intricate, reticulate pattern of relationships (Bothmer et al. 1987, 1988, 1989).

Our data on genome relationships coincide well with data from other fields, like isoenzyme electrophoresis (Jørgensen 1986), and CpDNA (Doebley, unpubl.). These data together, however, disagree with the present intrageneric taxonomic delimitation built on morphological variation patterns (Bothmer & Jacobsen 1985) and revaluation of the classification is necessary.

The conclusions for studies of genome relationships are that the concept of genome relationships is generally valid, but there are several sources of error for the interpretations, for example: (1) genetic regulation of meiosis; (2) misinterpretation of meiotic configurations; (3) studies of too restricted material.

GENETIC REGULATION OF MEIOSIS

One of the obstacles to polyploid systems becoming adapted in nature is the meiotic mechanism, leading to gamete formation. Polyploidy, which is almost exclusively a phenomenon occurring in plants, is a "one-step" event. If it takes place in long-lived perennials, it may have a good chance of getting established - the organism may have time during several years to produce a low number of viable, balanced gametes. The situation for short-lived perennial, biennial or annual plants is quite different. They must greatly rely on an even, high rate of viable, balanced gametes. Thus there must be a high selective advantage for the formation of viable gametes, otherwise the material will quickly perish.

It is thus of great importance if a newly formed polyploid (whether auto- or alloploid) is to have an immediate chance of survival that it can more or less directly form a high percentage of viable gametes. For example, a high number of multivalents caused by a combination of identical (homologous chromosomes, autoploidy) genomes or related genomes (homoeologous chromosomes, segmental alloploidy) automatically increases the rate of formation of unbalanced gametes. If pre-adapted or easily modified gene systems for bivalent formation are present, so-called diploidization mechanisms, the chance for immediate survival will increase considerably.

The best known case is the so called *Ph*-system on chromosome 5B in wheat (standing for "pairing homoeologous") and further genes with minor effects have later been detected (Riley & Chapman 1958, Sears 1976). Similar gene systems for regulation of meiosis are probably not uncommon in nature, since they are prerequisites for the establishment of young, newly formed, e.g. polyploid annuals.

In *Hordeum* evidence is accumulating that different gene systems are operating, revealing an intricate balance. Three examples:

(1) The genome of *H. vulgare* or individual barley chromosomes influence the autosyndetic pairing negatively in interspecific hybrids. In many polyploid hybrids with barley a lower autosyndetic meiotic pairing is observed than occurs in haploids of the wild species, which have been obtained through selective chromosome elimination (Bothmer & Subrahmanyam 1988).

The chromosome numbers in interspecific barley hybrids are often variable. The cross with the South American, hexaploid species *H. procerum* should have 28 chromosomes, but in two different families the meiotic number varied between 26-30. The meiotic pairing was observed at each chromosome number. In one family the pairing increased by adding more chromosomes to the complement. However, in the other family the pairing decreased by adding further chromosomes. Similar patterns were also found in other *H. vulgare* crosses, e.g. with *H. brachyantherum* (Bothmer et al. 1983). Hence there are genes on the barley chromosomes which suppress the pairing.

(2) *H. jubatum* is a tetraploid (2n = 4x = 28) perennial species, mainly with a North American distribution. The pure species behaves as an alloploid with almost exclusively bivalents in meiosis. Dihaploids produced after crosses with *H. vulgare* and selective elimination of the barley chromosomes, consequently only show univalents. This is also an indication of non-relation between the two genomes (Bothmer & Subrahmanyam 1988). A similar pattern is also found in hybrids between *H. jubatum* and other *Hordeum* species with no indication of syndesis between the two *jubatum* genomes (Bothmer et al. 1988). However, intergeneric crosses with rye (*Secale*) reveal a high autosyndetic pairing of the two *jubatum* genomes with up to six bivalents (Gupta & Fedak 1985). It is possible to distinguish between pairing including associations with the rye chromosomes due to their larger size and *jubatum* associations. It is quite evident that the two genomes of *H. jubatum* are rather closely related but the action of pairing suppressing genes prevents them from showing the homoeology. Genes in *Secale* thus have the capacity to act as pairing promotors.

(3) The most instructing case is found in *H. marinum*, which is an annual, Mediterranean species. It occurs in two cytotypes, one diploid, predominantly in the western

Mediterranean and one tetraploid, mainly in the eastern Mediterranean region. All evidence has earlier pointed to the tetraploid being of pure alloploid origin, e.g. the isoenzyme pattern (Jørgensen 1986) and the karyotype that has only one pair of satellite chromosomes (Linde-Laursen et al. 1989b). M I of meiosis of the tetraploid shows almost exclusively bivalents, and dihaploids formed after crosses with *H. vulgare* and selective elimination of the barley chromosomes have 14 univalents. However, hybrids between the diploid and the tetraploid cytotypes give a full set of 7 trivalents. Thus all three genomes are homologous and the tetraploid is thus more of an autoploid nature (Bothmer et al. 1989 and unpubl.). Preliminary data show that a single, recessive gene may be the cause of the "alloploid behaviour" of the tetraploid.

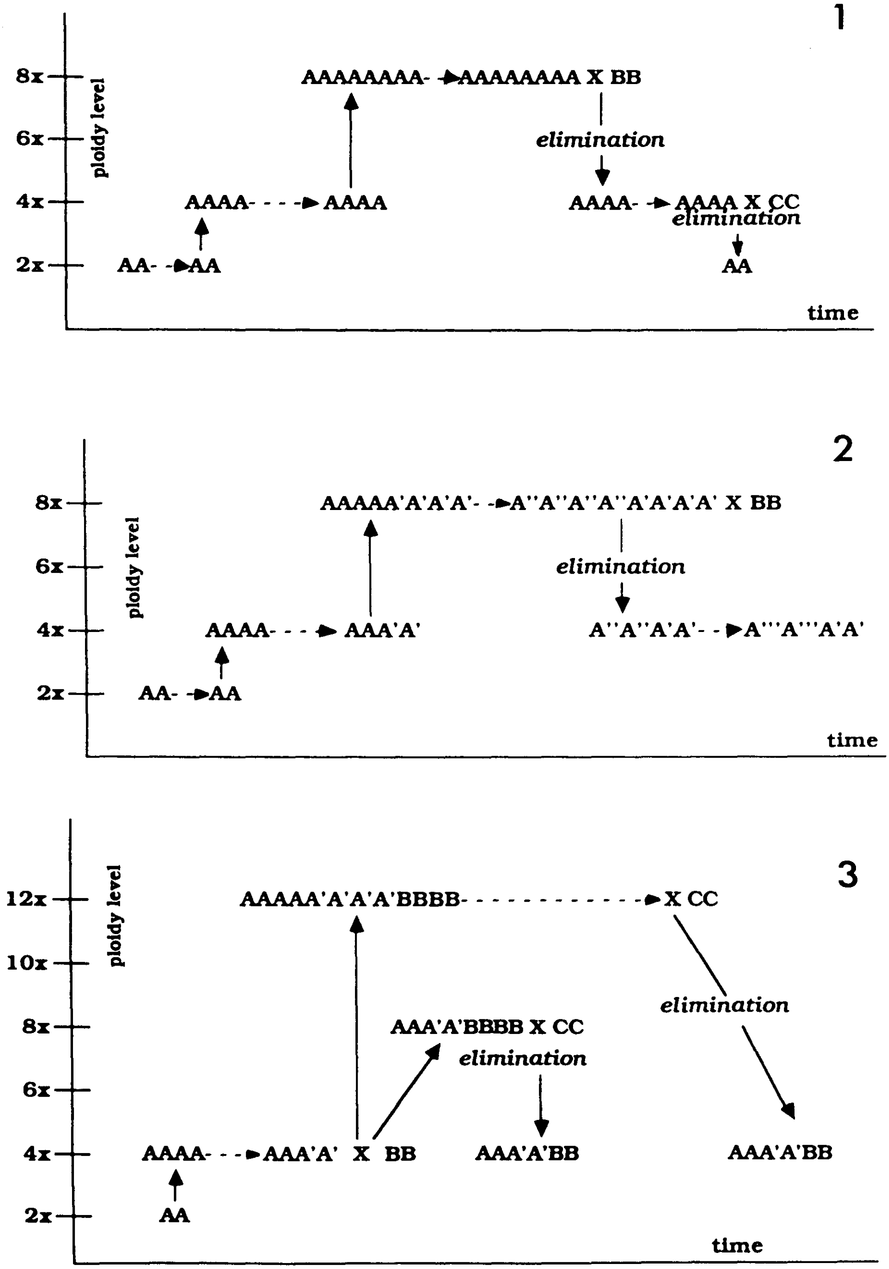
Conclusions: (1) Genetic regulation of meiosis is certainly a widespread mechanism in nature! (2) It may have a strong selective advantage. (3) More cases should be studied.

CHROMOSOME ELIMINATION

In textbooks on evolutionary patterns and mechanisms polyploidy is shown to be a prominent feature in plant speciation (cf. Stebbins 1950, Grant 1971). It is undoubted that different types of polyploidization have been very important, and its significance can certainly not be overestimated. However, higher levels of polyploidy have almost always been regarded as the end product and hence the most advanced forms; that is, change in chromosome numbers of whole genomes is an irreversible process, always being an increase. Sometimes it has been speculated there may be a decrease in chromosome number, or depolyploidization, but there has been no known general mechanism which could explain the phenomenon (Carlbom 1969).

Polyploidization is a very evident process. It is in many cases possible to follow the different steps in the development since the intermediate or end products are available. The reverse process, depolyploidization, is less obvious because: (1) the end product, with a reduced chromosome number has the same ploidy level as intermediate products (this situation is especially difficult when older forms with higher numbers are extinct); (2) formerly no general biological mechanism could be ascribed to cause depolyploidization.

During the last couple of years the cytogenetic principle known as chromosome elimination have been shown to be a more general phenomenon. It was first described in the interspecific cross *Hordeum vulgare* x *H. bulbosum* (Kasha & Kao 1970, Lange 1971). During the first days of embryo development after fertilization the chromosomes of *H. bulbosum* are successively lost and after ca. five days the whole genome is eliminated, leaving a haploid set for barley (Bennett et al. 1976). The cause of chromosome elimination is still not known and several theories hve been presented, e.g. different timing of mitosis of the parental genomes, the faster one being the non-eliminated parent (Lange 1971) and competition of available amino acids in the formation of proteins in the mitotic spindle (Bennett et al. 1976). However, since the discovery of chromosome elimination several interspecific hybrid combinations have been found, first within the *Hordeum* genus (cf. Subrahmanyam & Bothmer 1986), and later in other, intergeneric crosses with *Hordeum* and the genera *Secale, Psathyrostachys, Triticum, Agropyron* and *Elymus* (Fedak 1977, Bothmer et al. 1984, Torbinejad et al. 1987, Sitch & Snape 1986, Wang 1987, Lu et al. 1990). Recently the intergeneric cross *Elymus shandongensis* x *Triticum aestivum* yielded haploids of the female parent (*E. shandongensis*). This is a combination not including a *Hordeum* species and the wheat chromosomes are eliminated (Lu & Bothmer 1990).



Figs 1-3. Some examples of possible pathways of evolution provided chromosome elimination is active in nature as a depolyploidization mechanism.

Is then chromosome elimination a more widespread phenomenon and can it be a general mechanism of depolyploidization in nature? If there actually exists a depolyploidization mechanism in nature, polyploidy is hence not always the end result, but we may face a much more dynamic speciation process than earlier believed and thus an even more complex evolutionary pattern (Figs 1-3). One thus has to be careful in drawing conclusions - a higher chromosome number may not necessarily be a more advanced (more recent) stadium than a lower one. Many more cases must be studied and it will be interesting to follow further investigations in this field.

This study raises the important questions: (1) Is chromosome elimination also operating in nature? (2) Has chromosome elimination an evolutionary significance?

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HIERARCHICAL SELECTION IN CLONAL PLANTS

O. Eriksson & L. Jerling

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Traditional concepts of selection assume that the "individual" is a coherent structural, ontogenetic and genetic unit. This assumption holds for animals such as birds, but it does not hold for plants in general, and especially not for clonal plants. In clonal plants "individuals" occur at several levels of organization. Genets comprise all tissue developed from one zygote, and ramets are potentially independent parts of genets. Ramets are the basic demographic units, while genetic variation mainly occurs at the genet level. Hence, hierarchical models of selection and population dynamics are appropriate for clonal plants. In this paper we present an outline of a hierarchical selection model, and discuss two important consequences for clonal life-histories, implied by the model: (1) within-genet variability in demographic properties of ramets is a potentially important feature of genets, and (2) persistence may be the most relevant measure of genet fitness.

Keywords: Clonal plants, Genet, Population dynamics, Ramet, Selection.

Ove Eriksson & Lenn Jerling, Department of Botany, University of Stockholm, S-106 91 Stockholm, Sweden.

INTRODUCTION

Traditional demographic theory has been developed to deal with "unitary" organisms such as birds, mammals and insects, in which the "individual" is a coherent genetic, ontogenetic, structural and physiological unit. However, as has been thoroughly summarized by several authors in two recent symposium volumes (Jackson et al. 1985, Harper et al. 1986), it is difficult to apply the conceptual and theoretical apparatus of demographic theory to modular organisms, and especially to clonal plants. (The same holds for clonal animals, but these are not discussed here.) The process of selection in clonal plants is not similar to that in, for instance, birds, and fruit-flies. There are two basic reasons for this discrepancy. Firstly, the organizational properties of clonal plants make the concept of individuality ambiguous. Usually at least two levels of organization comprising "individuals" should be recognized; genets (all tissue developed from one zygote) and ramets (potentially independent parts of genets). This organization is inherently hierarchical. The genet level is inclusive in relation to its component ramets. Accordingly, models of population dynamics and selection should account for this hierarchical organization. During recent years, a number of authors have discussed and elaborated general hierarchical models of selection (Sober 1984, Buss 1987, Heisler & Damuth 1987, Damuth & Heisler 1989, Tuomi & Vuorisalo 1989). Wilson & Sober (1989) argued that a hierarchical view of selection eliminates much of the confusion, and possibly also some disagreement, concerning the issue of the most relevant "unit of selection", which has been intensively debated during the last three decades. Secondly, it is doubtful whether genets of clonal plants exhibit senescence (Watkinson & White 1986). Hence, central demographic concepts such as reproductive value and reproductive costs at the genet level become meaningless. Principally, the reproductive value of genets may approach infinity, and, by definition, reproductive costs become infinitesimally small.

In this paper we discuss a hierarchical model of selection applicable to clonal plants. The main purpose is to argue for hierarchical models as such, not to elaborate technical details. Furthermore, we will shortly consider two corollaries of a hierarchical concept of clonal plants: demographic variability among ramets within genets as a feature of genets, and persistence as a general measure of genet fitness.

GENET-RAMET INTERACTIONS

A hierarchy, in the context of the present model, is characterized by four general features. (1) Different kinds of "units" occur at different levels. Higher level units comprise lower level units. (2) Units at each level possess properties that are not "explained" by properties of units occurring at other levels. For instance, in order to describe a certain spatial pattern of growth of a genet one must invoke information on how ramets are placed in relation to each other. Information on such relationships is not contained in the properties of single ramets, but is instead "higher level properties". (3) All units at any level make up a population. Units within such populations may differ with regard to their capacity to survive and "reproduce" (i.e. produce new similar units at the same level of organization). (4) When viewing temporal dynamics of units arranged in a hierarchy, changes normally occur at a higher rate at lower levels than at higher levels.

Two additional features of clonal plants are essential for the construction of the model. Demographic processes, i.e. survivorship, death, and reproduction, as conceived in a "traditional" way, take place at the ramet level. Ramets are the units that conform to the common sense meaning of "individuals". Moreover, most genetic variation occurs at the genet level. Even if intraclonal genetic variation exists (Silander 1985), it seems reasonable to assume that somatic mutations do not create variation of the same magnitude as recombination. However, for clonal plants which almost exclusively reproduce asexually, somatic genetic variation may be of great importance.

The features of clonal plants imply that demographic processes (in the traditional sense), and genetic variation, occur at different levels of organization. This in turn means that it is not only difficult, but perhaps impossible, to combine a demographic analysis of how different environmental factors, e.g. nutrient availability, predators or pathogens, influence survivorship and "reproduction", with an analysis of the genetic response caused by such environmental factors in populations, without taking into account the dynamics at both the genet level and the ramet level simultaneously. Thus, hierarchical models of natural selection are needed. The model we will discuss is schematically illustrated in Fig. 1.

One basic assumption of the model is a distinction between phenotypic selection and, on the other hand, how phenotypic selection "translates" into components of genet fitness and subsequently affects genetic changes in populations. Phenotypic selection (Endler 1986) incorporates the causes behind differential survivorship and "reproduction" of ramets, apart from how ramets vary genetically. The "environment" may specifically influence both the ramet level and the genet level simultaneously. The strength of these influences depends

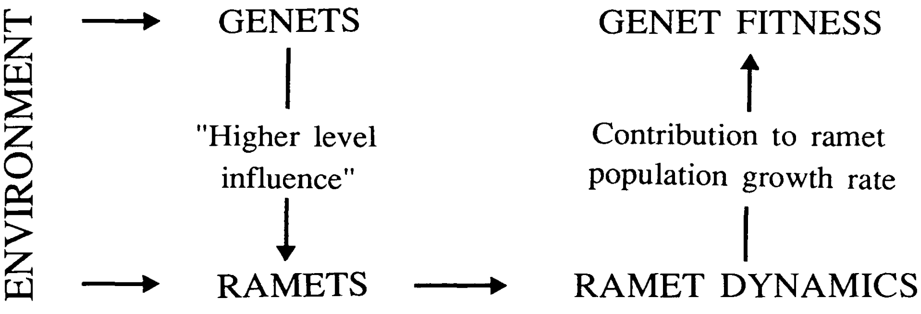

Fig. 1. A schematic illustration of the hierarchical model of selection in clonal plants discussed in the text.

on the properties of genets and ramets, and how these properties are affected by the environmental factors in question. A statistical method for partitioning effects from different hierarchical levels on "fitness" of some chosen lower level unit (i.e. ramets, in the context of the present model) has been developed by Heisler & Damuth (1987). The method implies that one can assess how genet level properties influence variation in reproductive success among ramets, in relation to the influence caused by features of the ramets themselves. This formal "downward" analysis means that all environment/organism interactions are summarized in terms of ramet level dynamics (the left part of Fig. 1). An advantage of this approach is that traditional demographic concepts are unambiguous at the ramet level, and thus can be used in descriptions of ramet dynamics. To our knowledge no studies have been published yet that explicitly address questions of how genet level properties influence ramet level dynamics, and therefore this kind of analysis still awaits empirical evaluation.

The second part of the model concerns how ramet level dynamics are "translated" to components of genet fitness (the right part of Fig. 1). Since a genet may be considered as a population of ramets, it is reasonable to assume that the growth rate of the ramet population comprising the genet is a good measure of genet fitness (the exact meaning of this fitness measure is discussed below). If ramets vary demographically to such an extent that they can be properly grouped into classes, we can analyse how different classes of ramets contribute to ramet population growth rate. The best way to perform such an analysis is to use matrix models combined with sensitivity and elasticity analysis (de Kroon et al. 1986, Eriksson 1988, van Groenendael et al. 1988).

We do not claim that the model shown here is the only possible way to analyse selection in clonal plants. Depending on the nature of the problems addressed, different models, or perhaps different versions of the presented model, might be most appropriate. We do claim, however, that the organizational properties of clonal plants necessitate an extension of the traditional models of selection and population dynamics. One should not assume that a unit at any specific level of organization is *the* unit of selection. Rather selection acts on several levels simultaneously (Buss 1987, Wilson & Sober 1989).

RAMET VARIABILITY AND PERSISTENCE OF GENETS

We will now briefly discuss two corollaries of the proposed model, and point out some issues that would be of interest for field investigations. Most population studies of clonal plants have focused on the ramet level (Cook 1985). This is probably a consequence of the practical difficulties of gathering field data on genets. In some cases, however, ramets as such are considered as the prime objects of life-history analysis (e.g. Fetcher 1983). Empirical information on genet dynamics in clonal plants is mainly of two kinds, either "static" information on size or age of genets (cf. Cook 1985), or information on the early stages of genet development (cf. Eriksson 1989). The conceptual model we present is an attempt to combine these two kinds of information. As a consequence of a hierarchical view of clonal plants, the pattern of variability among ramets within genets becomes a feature of potential evolutionary interest. Recent theories in population and community ecology which consider variability among individuals (not only average performace) as a basic parameter, provide some hypotheses relevant also for clonal plants. Such theories have been developed for coexistence of species (Chesson & Huntly 1988), population dynamics (Lomnicki 1988) and patterns of size structure in populations (Huston et al. 1988). We have proposed that behavioural variability of ramets stabilizes ramet dynamics, promotes genet coexistence, and promotes genet persistence (Eriksson & Jerling 1990). These effects are likely to be especially important for genets living under temporally or spatially variable conditions.

A prerequisite for considering patterns of ramet variability as an ecological "strategy" of genets is that the pattern is to some extent heritable. This assumption has not been evaluated empirically, but it is supported by circumstantial evidence (Eriksson & Jerling 1990). Furthermore, one should expect that different environmental situations select for different kinds of "ramet-variability-strategies". In general, the pattern of variation should function as a "buffer" against adverse conditions of any kind. There are several situations where this function is expected: (1) A size hierarchy among ramets may reduce within-genet competition, and thereby the risk of genet extinction. (2) Variation in flowering behaviour may reduce the risk of complete reproductive failure during one season. (3) Different kinds of ramets may be differently affected by predators or pathogens. If the action of such agents varies temporally and spatially, variability as such may become advantageous. (4) "Foraging" growth of genets, i.e. exploitation of heterogeneous local environments, may depend on ramets differing in their response to local environmental conditions.

In order to evaluate the evolutionary implications of demographic variability among ramets, one must decide how to define and measure fitness of genets. The most commonly held fitness measure in evolutionary biology includes some notion of relative abundance of the unit chosen as object for study (e.g. alleles, genotypes, or phenotypes) (Endler 1986). As mentioned earlier, it is difficult to use reproductive value, or any kind of age-specific measure of reproductive success, for genets. This is due to the fact that a genet is a population of ramets, capable of almost infinite production of offspring, and, as far as known, genets of clonal plants do not exhibit senescence. In many cases it seems most feasible to use persistence (or "expected time to extinction", Cooper 1984) as a general measure of genet fitness. The means of "translation" of ramet dynamics into genets fitness suggested in the hierarchical selection model, i.e. via growth rate of the population of ramets making up the genet, is directly related to genet persistence. The more ramets a genet consists of the smaller becomes its current risk of extinction. This is basically due to the potential independence of ramets, making it increasingly unlikely that a single mortality agent will cause the death of the whole genet, as the genet becomes large. Persistence is probably, but not necessarily, correlated with the number of new genet offspring produced by the genet. If this is so, one may just consider persistence as an operationally more practical measure of "abundance" fitness. However, if persistence is not correlated with production of genet offspring, this implies a conflict between levels of organization, analogous to conflicts between hierarchical levels discussed for other organisms, for instance between workers and queens in some social insects (cf. Wilson & Sober 1989). There is presently no empirical evidence bearing on this issue, but genet-ramet interactions are important aspects of clonal life histories and should be subject to investigations in natural populations of clonal plants.

CONCLUSIONS

Hierarchical models are suggested as necessary tools for analysis of selection and population dynamics in clonal plants. The presented model suggests solutions to both conceptual and practical problems encountered by students of these organisms. A hierarchical concept of clonal plants implies that between-ramet variability, as such, is a potentially important feature of genets, and furthermore that conflicts between the genet level and the ramet level may occur. The most appropriate measure of genet fitness in the context of the presented model is persistence. The suggestions in this paper are speculative, and future studies addressing questions of the hierarchical nature of clonal plants are needed.

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HYBRIDIZATION IN *SYMPHYTUM*: PATTERN AND PROCESS

T.W.J. Gadella

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The restriction endonuclease fragmentation patterns of cpDNA of various *Symphytum*-taxa showed that morphological differentiation and molecular evolution on one hand, and sterility barriers on the other, did not evolve at the same rate. *Symphytum officinale* (2n = 24, 40, 48) and *S. asperum* (2n = 32) differ in their cpDNA pattern, but are able to produce fertile hybrids (*S. x uplandicum*; 2n = 36, 2n = 40).

Pyrrolizidine alkaloids and isobauerenol can be used as chemotaxonomic markers for the identification of these hybrids. Triploid hybrids between diploid and tetraploid plants of *S. officinale* are lacking in mixed populations, possibly because homoploid pollen grows faster than heteroploid. The origin of the 2n = 40 cytotype of *S. officinale* may be explained by a 5 step hypothesis: auto-polyploidization followed by 4 steps of centric fusion.

Introgressive hybridization between the 2n = 40 and 2n = 48 cytotypes of *S. officinale* was studied in a large population along the border of Lake Kinselmeer, The Netherlands. Introgression works in two different directions: towards the 2n = 40 cytotype in the moist bank zone and towards the 2n = 48 cytotype in the dry clayey dike zone. Anderson's hybrid index and Well's distance diagram revealed a close correlation between cytological and morphological variation. A flower colour marker and chromosome number variation indicated that gene flow is strongly restricted by distance.

Keywords: Chemotaxonomy, Cytology, Gene flow, Hybridization, Introgression, *Symphytum*.

T.W.J. Gadella, Department of Plant Ecology and Evolutionary Biology, State University of Utrecht, Padualaan 8, NL-3584 CH Utrecht, The Netherlands.

INTRODUCTION

The genus *Symphytum* (Boraginaceae) contains 41 species, which are classified in the two subgenera, *Symphytum* with 29 and *Tuberosum* with 12 species (J. Sandbrink, unpubl.). Subgenus *Tuberosum* is characterized by the presence of creeping rhizomes.

A phenetic analysis using 69 characters has shown that the species can be divided into 6 geographically differentiated groups (J. Sandbrink, unpubl.). Hybridization studies have demonstrated that morphologically widely different species, belonging to different species groups or subgenera, can be crossed easily (Bucknall 1913, Popov 1953, Gadella 1972, Smejkal 1978, Kurtto 1981, Stearn 1985).

J. Sandbrink (unpubl.) compared the chloroplast DNAs (CpDNA) of 8 *Symphytum* taxa belonging to different species groups and polyploid complexes. He found two types of restriction patterns. The geographical distribution patterns of the species investigated in the CpDNA-tree are congruent within the cpDNA divergences. The European species (including *S. officinale*) can be grouped together, the species of the other branch originate from the Caucasus and NW Turkey and include *S. asperum*.

Apparently the morphological evolution proceeded at a much faster rate than the molecular evolution. Likewise hybridization studies have revealed that the morphological differentiation and sterility barriers did not evolve at the same rate.

This paper is a synthesis of several studies exploring different aspects of hybridization in *Symphytum officinale* and *S. asperum*. In particular the relationship between pattern and process is addressed.

MATERIALS AND METHODS

Plants of *S. officinale* were collected from their natural habitats. Seeds and living plants of *S. asperum*, collected in nature, were provided by various Botanical Gardens.

This material was used for morphological studies as well as for chemotaxonomic analysis. The best results of cytological studies were obtained by fixation of the root tips after a cold night. A combination of the Feulgen and Giemsa methods was used for the study of the karyotype and of the heterochromatic banding patterns of the chromosomes (see Mekki et al. 1987). Voucher specimens and microscopical slides are preserved in the herbarium of the Dept. of Plant Ecology and Evolutionary Biology of the State University of Utrecht.

Pyrrolizidine alkaloid extracts from dried and ground roots and/or shoots were derived according to the method described by Pedersen (1975). All other extractions were performed after a preliminary extraction with n-pentane as described by Huizing & Malingré (1979). The chemotaxonomic methods were described by Huizing (1985). He analysed the pyrrolizidine alkaloids and triterpenoids. A fast method for the isolation of chloroplast DNA (CpDNA), suitable for RFLP analysis, as described by Sandbrink et al. (1989), was applied.

For crossing experiments flower buds were emasculated two or three days before the flowers opened. Two or three days later the desired pollen grains were transferred to the emasculated flower and placed on the stigma. This was repeated two days later. Both the hybrid index method according to Anderson (1949) and the distance diagram method according to Wells (1980) were used for the analysis of the hybrid swarm of Lake Kinselmeer, The Netherlands.

RESULTS AND DISCUSSION

Differentiation of species and cytotypes

Symphytum officinale L. and *S. asperum* Lepech.

In this paper I will treat two species, the European species *S. officinale* L. (including *S. bohemicum* Schmidt, *S. lanceolatum* Weinm. and *S. tanaicense* Stev.) and the Caucasian species *S. asperum* Lepech. *Symphytum officinale* (2n = 24, 40, 48) is a variable lowland

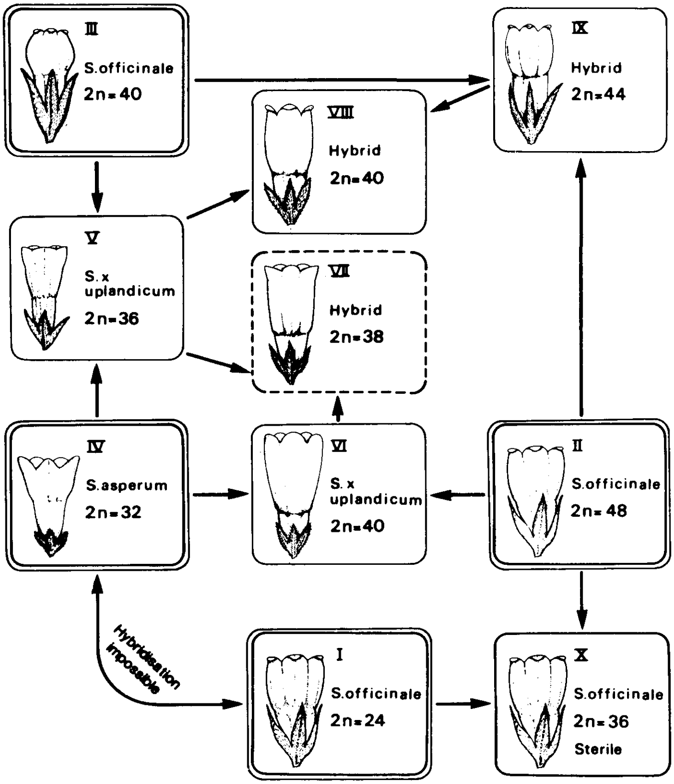


Fig. 1. Crossing experiments between *Symphytum officinale* L. (3 cytotypes) and *S. asperum* Lepech. (2n = 32). The shape of the flowers (calyx and corolla) and the chromosome number of the parental species and hybrids are indicated. Hybrids are single-framed, parental taxa double-framed. All parental cytotypes and species are fertile, except for the intraspecific 2n = 36 hybrid of *S. officinale*.

species with white or purple urceolate flowers, whereas S. asperum (2n = 32) is a montane species with sky-blue campanulate flowers. In *S. officinale* the following cytotypes occur: (1) white-flowered diploids (2n = 24), (2) white- or purple-flowered tetraploids (2n = 48), and (3) purple-flowered plants (2n = 40).

All these races occur in the Netherlands, where they have been studied in detail. *S. officinale* and *S. asperum* differ in their CpDNA restriction pattern (J. Sandbrink, unpubl.). However, 2 cytotypes of *S. officinale* (2n = 40 and 2n = 48) readily cross with *S. asperum* (2n = 32) and produce fertile hybrids. These hybrids are collectively referred to *S. x uplandicum* Nym. and are characterized by the chromosome numbers 2n = 36 and 2n = 40 (Gadella & Kliphuis 1969). After the introduction of *S. asperum* as a fodder plant, many often complicated hybrid swarms were formed (Fig. 1). Pyrrolizidine alkaloids and the triterpenoid isobauerenol can be used as chemotaxonomic markers. *S. officinale* does not contain echimidine, whereas lycopsamine, acetyl-lycopsamine, intermedine and acetyl-intermedine are lacking in *S. asperum*. The hybrids and backcrosses are characterized by

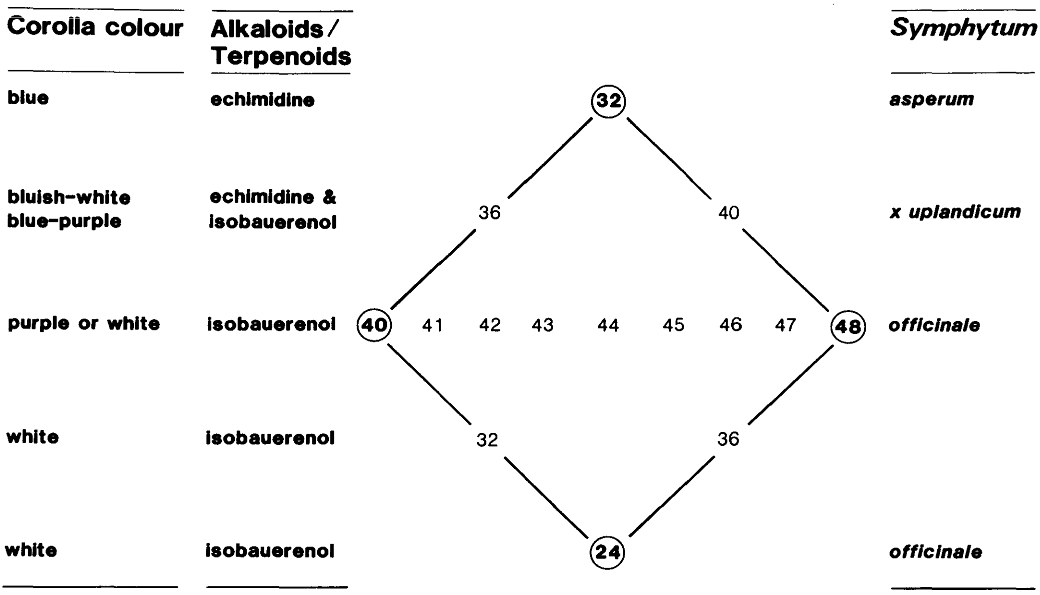


Fig. 2. Intra- and interspecific crosses between *S. officinale* and *S. asperum*. The occurrence of the diagnostic compounds (isobauerenol and pyrollizidine alkaloids) is included.

Pyrrolizidine alkaloids	*S. asperum*	*S. x uplandicum*	*S. officinale*
Echimidine	+	+	−
Lycopsamine	−	+	+
Ac.-lycopsamine	−	+	+
Intermedine	−	+	+
Ac.-intermedine	−	+	+
Symlandine	+	+	+
Symphytine	+	+	+
Echiumine	+	+	+
Myoscorpine	+	+	+

Fig. 3. The distribution of pyrrolizidine alkaloids in *S. officinale*, *S. asperum* and *S. x uplandicum*.

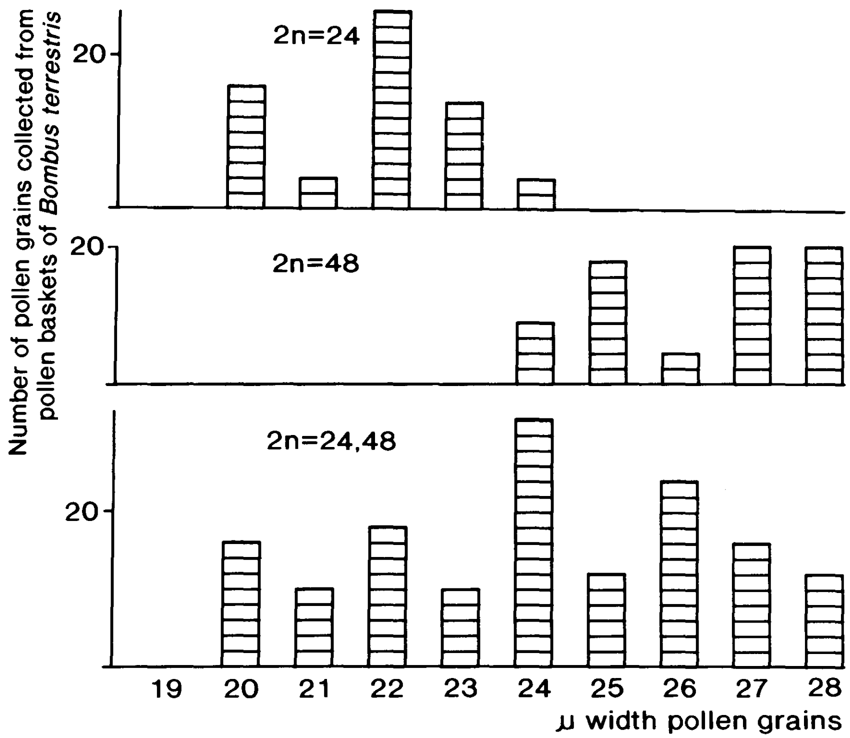


Fig. 4. Diameter of pollen grains (collected from the pollen baskets of the legs of bumble-bees) of diploid (2n = 24) and tetraploid (2n = 48) populations of *S. officinale*. The lower diagram shows the diameter of the pollen grains in a mixed population (2n = 24, 2n = 48).

the presence of all pyrrolizidine alkaloids (Huizing et al. 1982, 1983, Gadella et al. 1983, Huizing 1985), cf. Figs 2 and 3.

Symphytum officinale: 2n = 24 and 2n = 48

The diploids and white-flowered tetraploids are morphologically indistinguishable. Usually they do not grow in mixed populations. In a single population, where many plants of both cytotypes grow in very close proximity, no hybrids were detected. In this population 149 plants were cytologically investigated: 76 plants turned out to be diploid, 73 tetraploid. The diameter of the pollen grains of the diploids and tetraploids differs significantly. Pollen grains, collected from the legs of bumble-bees in pure diploid or pure tetraploid populations showed that two slightly overlapping size distributions were involved. In the mixed population all size classes were represented in the pollen baskets of the bumble-bees, showing that the pollinators visited both cytotypes (Fig. 4). An analysis of the pollinator

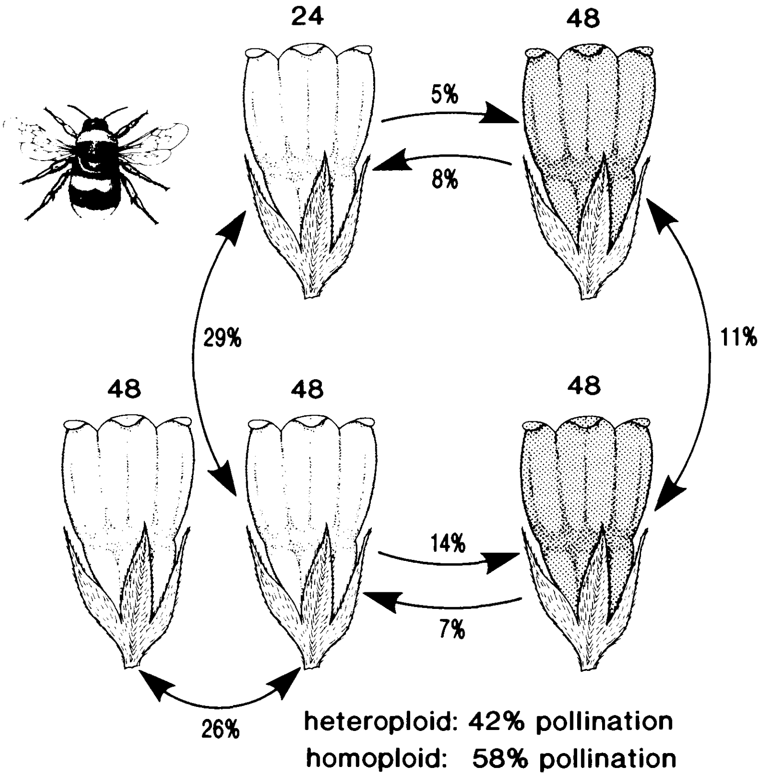


Fig. 5. Pollinator foraging behaviour of a bumble-bee visiting flowers in a mixed population of *S. officinale*, consisting of white-flowered diploid and white-/purple-flowered tetraploid plants.

foraging behaviour demonstrated that bumble-bees did not differentiate between the cytotypes and flower colour. The pollinators cross-pollinated heteroploid plants in 42 % and homoploid plants in 58 % of their visits. In 34 % of the visits the bumble-bees flew to plants with a different colour of the corolla (Fig. 5). Often they stole nectar through a hole bitten in the corolla tube. After emasculation of plants and subsequent heteroploid pollination some completely sterile triploids were obtained. In nature triploids are lacking, presumably because homoploid pollen grows faster than heteroploid.

Symphytum officinale: 2n = 40 and 2n = 48

The plants with 2n = 40 are morphologically slightly different from those with 24 or 48 chromosomes. This is demonstrated by two scatter diagrams (Figs 6 and 7). The cytotypes do not normally hybridize because of differences in ecological requirements. Plants with 40 and 48 chromosomes, however, are interfertile. In disturbed habitats, they produce hybrid swarms consisting of individuals with all chromosome numbers from 2n = 40 to 2n = 48 (Gadella & Kliphuis 1984).

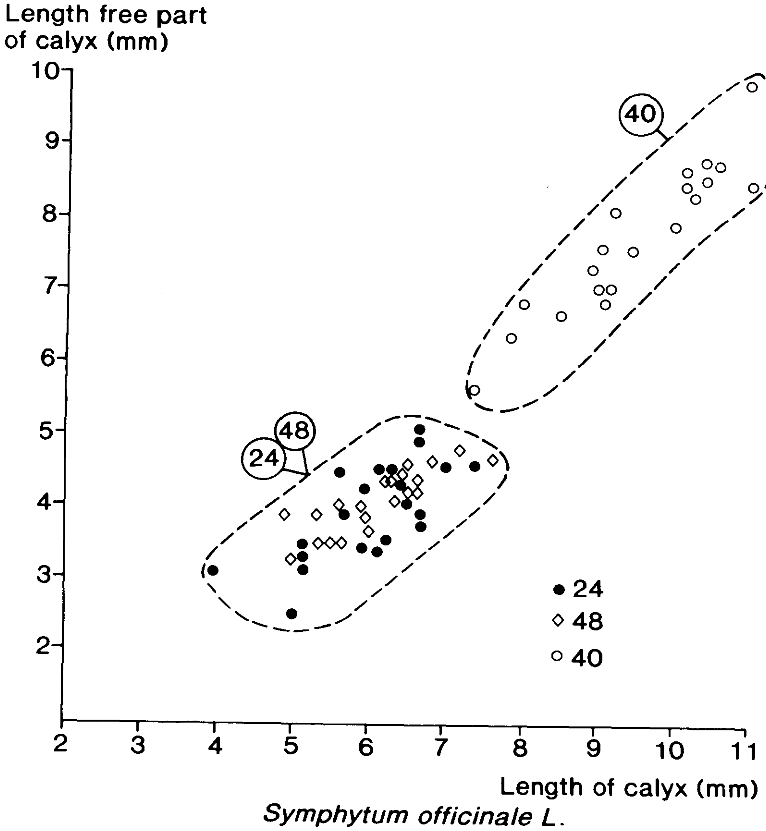


Fig. 6. Scatter diagram showing the relationship between length of the calyx and length of the free part of the calyx of 3 cytotypes (2n = 24, 40, 48) of *S. officinale*.

The origin of the 2n = 48 cytotype

Both morphological characters and the chromosome banding pattern provide evidence for an autoploid origin of the 2n = 48 cytotype. It is remarkable that the E European tetraploid plants are purple-flowered, whereas the W European populations consist of white- and purple-flowered tetraploids. Since all European diploid plants studied so far are white-flowered, it seems likely that the purple flower colour originated after the process of chromosome doubling.

The origin of the 2n = 40 cytotype

Two alternative hypotheses can be formulated for the origin of the 2n = 40 cytotype (Fig. 8): (1) *a three step hypothesis*: the diploid number 24 was reduced to 20 by two steps of centric fusion (Robertsonian translocations), followed by a third step: autopolyploidization,

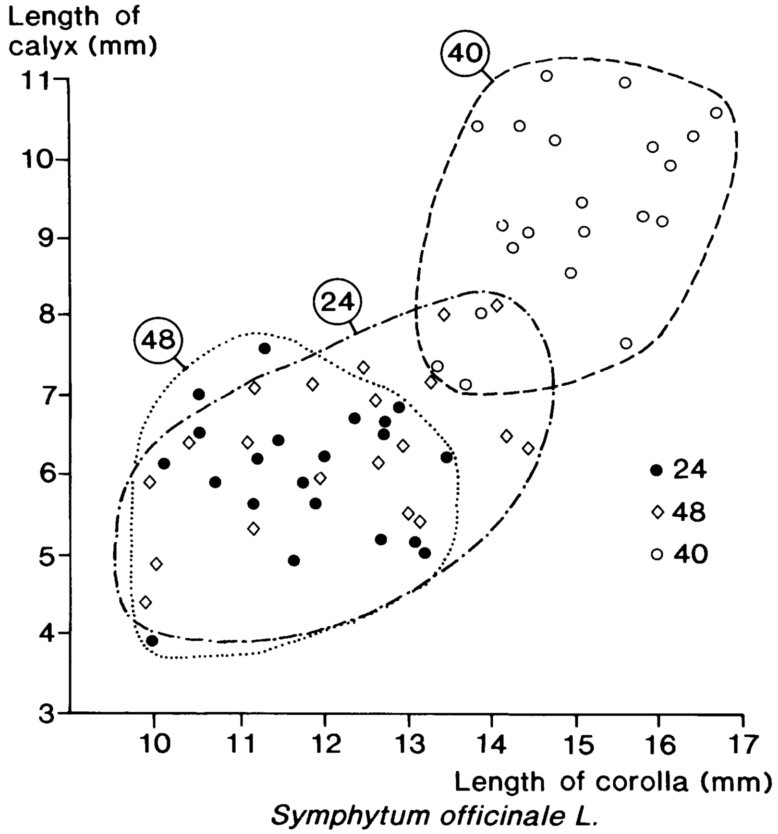


Fig. 7. Scatter diagram showing the relationship between length of the corolla and calyx of 3 cytotypes (2n = 24, 40, 48) of *S. officinale*.

and (2) *a five step hypothesis*: the first step, autopolyploidization, was followed by 4 steps of centric fusion.

The five step hypothesis (2) seems to be favoured by the following evidence:

(1) Crossing experiments revealed that all cytotypes intermediate between 2n = 40 and 48 produce a heterogeneous array of gametes (Fig. 9). The gametes have different chromosome numbers in different but constant proportions. This can only be explained by assuming that polyploidization occurred first and was followed by 4 Robertsonian translocations. If the Robertsonian translocations preceeded the polyploidization, as suggested by the three step hypothesis, only one type of gametes can be produced by a plant with 44 chromosomes. In that case only gametes with 22 chromosomes should be expected, whereas the primary hybrid actually produces 5 types of gametes in the following proportions: n = 20 and n = 24 (6.25 %), n = 21 and n = 23 (25 %), n = 22 (37.5 %). In meiosis, in a heterozygote for a centric fusion, no infertility arises if the centromeres of the two acrocentrics pass to one pole and the centromere of the metacentric to the other.

(2) A second line of evidence was provided by a study of differential staining of

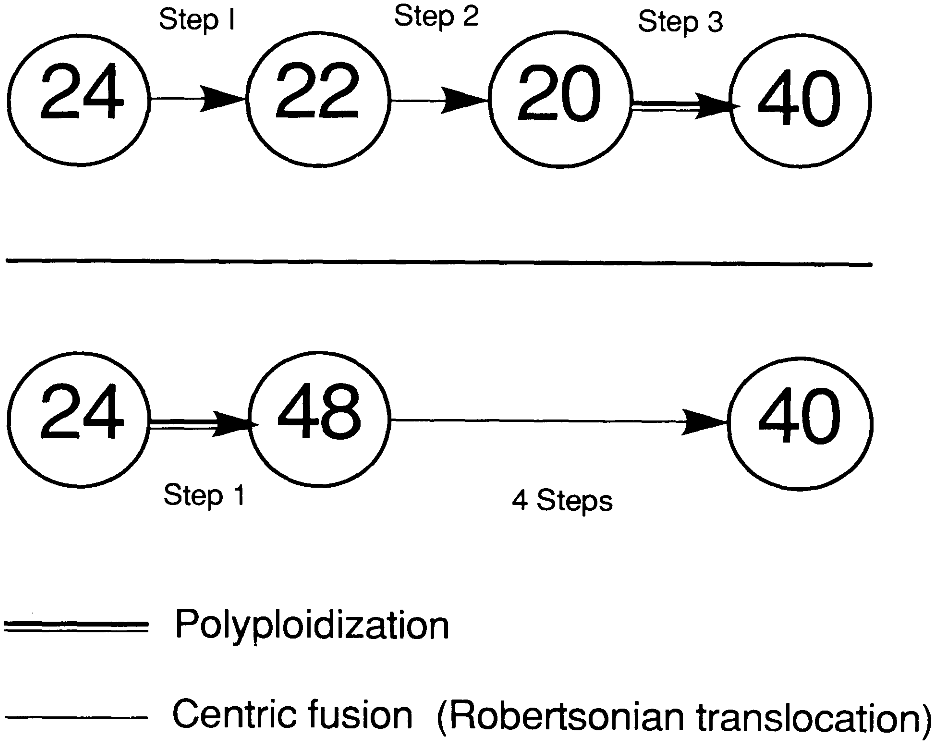


Fig. 8. Two alternative hypotheses explaining the origin of the 2n = 40 cytotype of *S. officinale* (see text).

chromosomes. The combined Feulgen-Giemsa method (Mekki et al. 1987, Mekki 1988) revealed the presence of heterochromatic bands in all the chromosomes of diploids, tetraploids and of the 2n = 40 cytotype. Diploids and tetraploids have only submetacentric or acrocentric chromosomes, whereas the 2n = 40 cytotype has metacentric as well as acro- and submetacentric chromosomes. Giemsa-banding showed that some intercalary heterochromatic bands are present in the two long arms of the metacentric chromosomes of the plants with 40 chromosomes and only in the long arms of the submetacentric chromosomes of the 2n = 48 cytotype (Mekki 1988). This is in favour of chromosome fusions. A comparison of the 20 pairs of chromosomes of the cytotype 2n = 40 with the 24 pairs of the cytotype 2n = 48 showed that always clearly distinguishable pairs of fused metacentric chromosomes were found in the 2n = 40 cytotype. These pairs differed in length and in the position of the centromere. We did not find sets of four identical fused metacentric chromosomes in the cytotype 2n = 40. This supports the five step hypothesis. The 2C-values of DNA of the cytotypes 2n = 40 and 2n = 48 are 6.59 pg and 6.72 pg, respectively. This means that the difference in DNA content between the two cytotypes is only 2 %. Apparently the reduction of the number of chromosomes in the karyotype by the chromosomal fusions involved the loss of a very small amount of DNA.

(3) An additional line of evidence was provided by the study of the base number of the genus *Symphytum*. The only species of the genus *Symphytum* with the chromosome

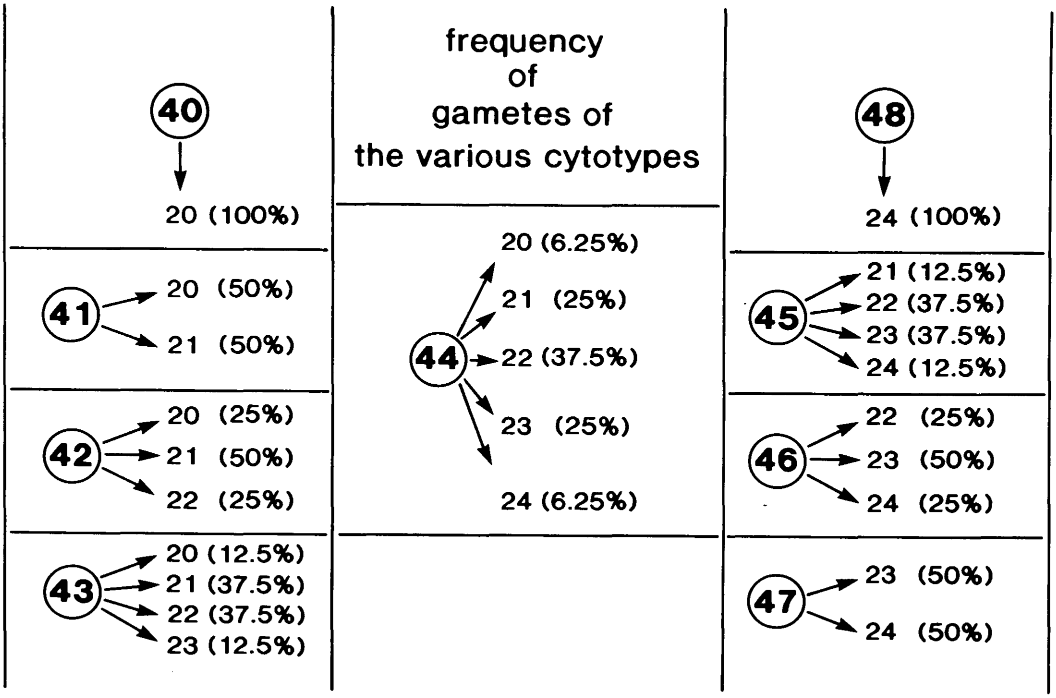
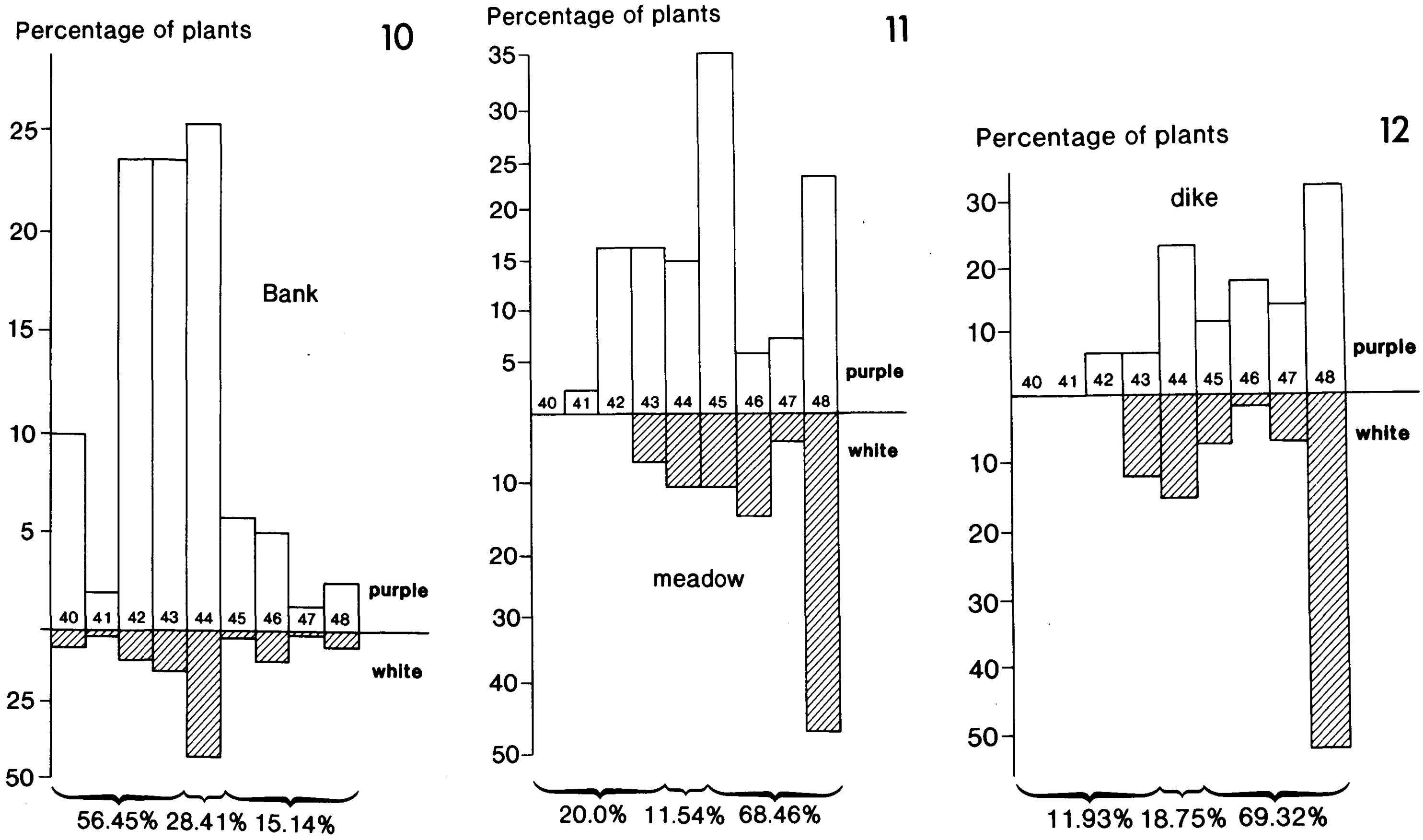


Fig. 9. Frequency of different gametes produced by the intraspecific hybrids between two cytotypes (2n = 40 and 2n = 48) of *S. officinale*.

number 2n = 20 is *S. ottomanum* Friv. (Markowa & Iwanowa 1970). This taxon, however, holds a rather isolated position in the genus and differs from *S. officinale* both in morphological respects and in CpDNA restriction pattern. Hybrids between *S. officinale* and *S. ottomanum* are unknown. They were neither found in areas of sympatric contact, nor could they be produced by experimental hybridization. The most common base number of *Symphytum* is x = 12, which gave rise to a euploid series with chromosome numbers ranging from 2n = 2x = 24 to 2n = 12x = 144, pointing to an ancient origin of this base number. In various species (and species groups) of both subgenera the base number x = 12 occurs. For these reasons it does not seem plausible that x = 10 is the ancient base number. The three lines of evidence suggest that the five step hypothesis provides the best explanation for the origin of the 2n = 40 cytotype. The hypothesis that explains the data in the most parsimonious way (i.e. by 3 steps) seems to be incorrect. The parsimony principle, according to which the shortest pathway that explains the present pattern is considered to be the most likely evolutionary route, apparently does not apply to this special case.

In many taxa chromosome repatterning accompanies race formation or speciation (Stebbins 1950). Also in *S. officinale* (2n = 40 and 2n = 48 cytotypes) the rearrangements involved may serve the function of gene linkage. Because the cytotypes differ in their ecological requirements, a restriction of recombination may have a selective value.



Figs 10-12. Frequency distribution of purple- and white-flowered cytotypes of *S. officinale* along Lake Kinselmeer (N of Amsterdam, The Netherlands). Fig. 10. The moist bank zone. Fig. 11. The drier meadow zone. Fig. 12. The dry clayey dike zone.

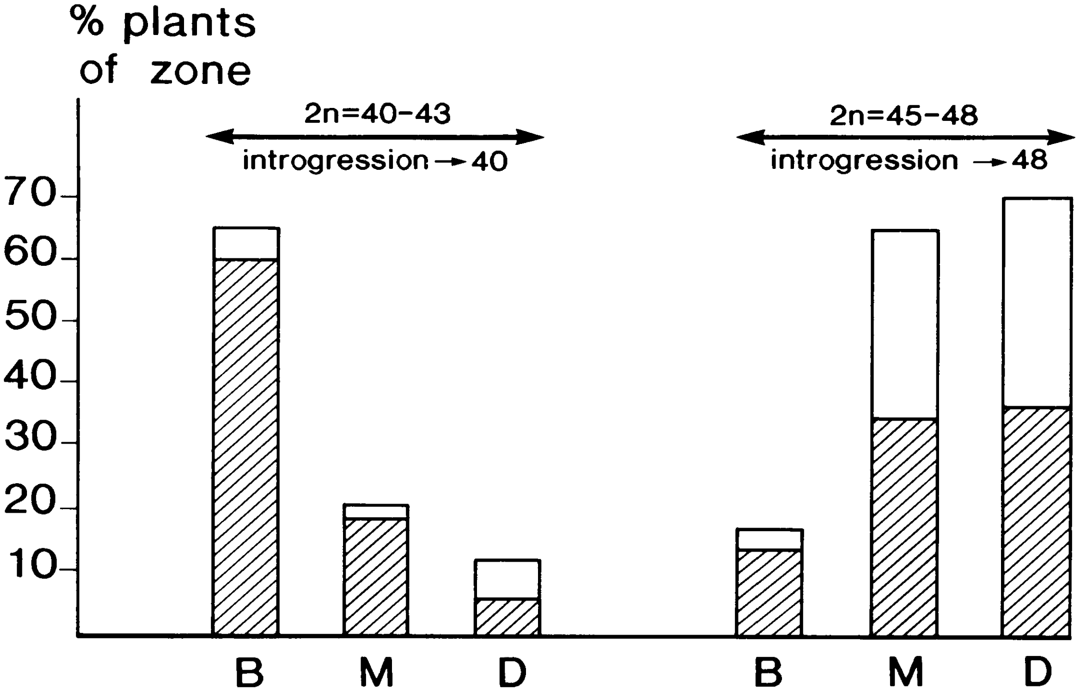


Fig. 13. Introgression towards the 2n = 40 cytotype (left) and towards 2n = 48 (right) in a hybrid swarm along the border of Lake Kinselmeer, N of Amsterdam. Hatched: purple-flowered plants. B - Bank; M - Meadow; D - Dike.

Introgression between the 2n = 40 and 2n = 48 cytotypes

Plants with 40 chromosomes prefer moist and peaty habitats, while plants with 48 chromosomes grow in drier habitats and on sandy or usually clayey soils. This enables these two races to keep their identity, but they are interfertile in areas where they meet, usually as a consequence of man's activities in modifying natural communities or breaking down ecological barriers. The races differ in flower colour (40: dark purple; 48: white or purple) and in the various types of indumentum.

All plants are strictly self-incompatible. Crossing experiments showed that a complete series of more or less fertile hybrids could be formed with chromosome numbers ranging from 2n = 40 to 2n = 48 (Gadella 1972).

Natural hybridization was studied in a large population consisting of about 3000 plants along the border of a small lake (Kinselmeer), North of Amsterdam (Gadella 1987). Along this lake three ecological zones can be recognized: (1) The very moist bank zone with a peaty soil, covered with tall herbs. This ruderal drift zone contains 70 % of the plants of *S. officinale*. (2) A somewhat dryer meadow zone. (3) A dry dike zone with a clayey soil, separating lake Kinselmeer from lake IJsselmeer.

The frequency of white-flowered plants is highest in the dike zone, lowest in the bank zone. This pattern seems difficult to explain, because only purple-flowered individuals

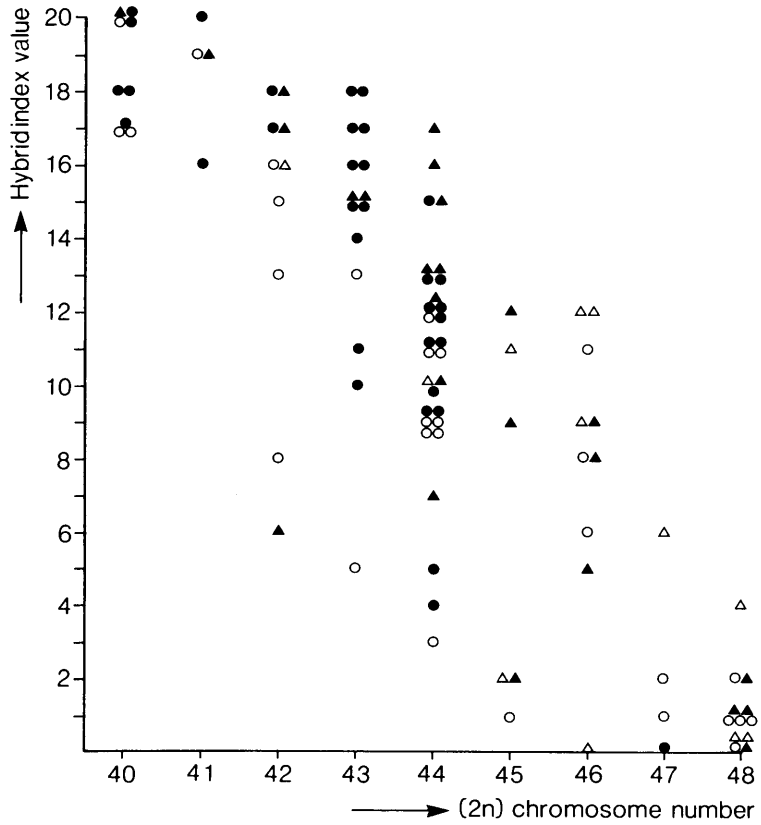


Fig. 14. Anderson's hybrid index and chromosome number of the Lake Kinselmeer population of *Symphytum officinale*. Each dot represents one plant. Solid dot: purple-flowered plant; open dot: white-flowered. The hybrid index is based on ten morphological characters, each character scoring 2 in the 2n = 40 cytotype, 0 in the 2n = 48 cytotype, 1 in an intermediate situation.

with 40 chromosomes occur in comparable localities along borders of ditches and lakes on low-lying peatlands.

Cytological studies demonstrated that the plants of the Kinselmeer have chromosome numbers varying from 40 to 48. Most frequent backcrossing to the 2n = 40 parent seemed likely, since most of the plants have low chromosome numbers. A hypothesis was put forward that genes from the 2n = 48 cytotype had been absorbed by the 2n = 40 cytotype via introgression or unidirectional, repeated hybridization. A careful cytological study of many hybrid plants in this population showed that most plants in the moist bank zone had chromosome numbers ranging from 2n = 40 to 2n = 44, in the intermediate meadow zone the plants had intermediate chromosome numbers, whereas most plants on the dike had chromosome numbers ranging from 2n = 44 to 2n = 48 (Figs 10-13).

Backcross types with intermediate chromosome numbers have partly replaced the pure cytotypes. In such a colony there are apparently genetic and ecological factors promoting

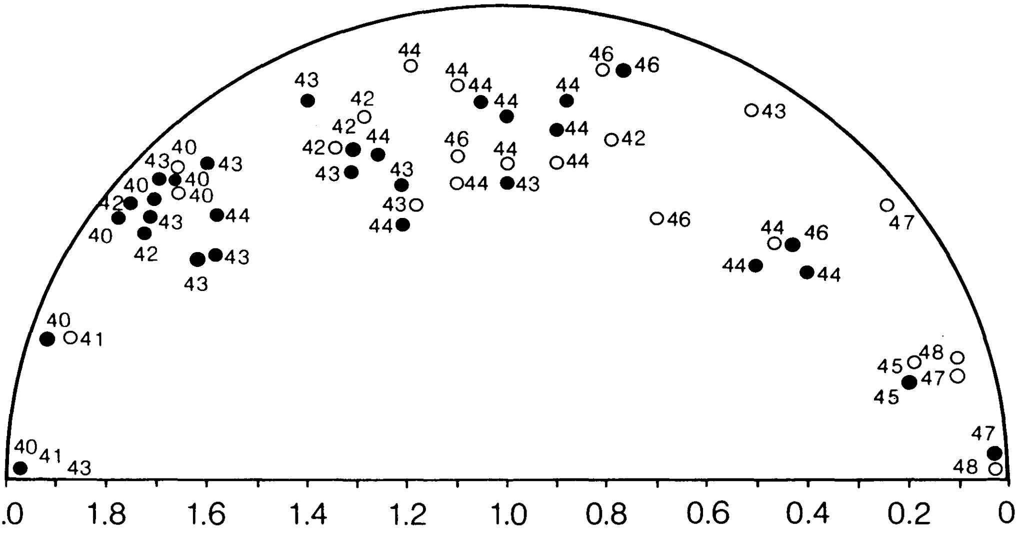


Fig. 15. Well's distance diagram for the Kinselmeer population of *Symphytum officinale*. The Euclidean distance to the reference points was calculated for each plant; cytotype 2n = 40 = 2.0; cytotype 2n = 48 = 0.0. Open dots: white-flowered plants; solid dots: purple-flowered plants. Numbers refer to chromosome numbers.

backcrossing. This means that introgression towards the cytotype 2n = 40 is more frequent in the moist bank zone and towards the cytotype 2n = 48 more frequent in the dry dike zone. Since about 70 % of the individuals of this population grow in the bank zone, the overall result of hybridization is introgression towards the cytotype 2n = 40.

Instead of a completely hybridized habitat (Anderson 1949) there seems to be an adaptive continuum. A comparison of the distribution of the cytotypes of the bank zone and of the dike zone (Figs 10, 12) suggests two adaptive peaks, but the intermediate meadow sub-population made it clear that the term adaptive continuum is more appropriate. Plants sharing most of the genes with the 2n = 40 cytotype are fittest in the bank zone, those with many genes in common with the 2n = 48 cytotype are fittest in the dike zone.

This hypothesis was tested by making artificial hybrids and by analysis of cytology and 10 morphological characters of both artificially produced and natural hybrids of lake Kinselmeer.

A hybrid index (Anderson 1949) and a distance diagram (Wells 1980) were constructed. Both methods revealed that the morphological and cytological variation were closely correlated (Figs 14, 15).

The Wells diagram represents a new graphical technique for testing of morphological intermediacy in studies of suspected hybridization. It has advantages over Anderson's method because it is not based on a simple sum, but on Euclidean distance from each hybrid to parental reference points: reference point for 2n = 40 is 2.0, for 2n = 48 is 0.0. These reference points were based on plants from pure populations of the 2n = 40 and 2n = 48 cytotypes, in which no hybridization occurred (Fig. 15). Since white-flowered plants with 40 chromosomes are completely absent from pure 2n = 40 populations, these plants may be regarded as end-products of introgressive hybridization. The genes for white

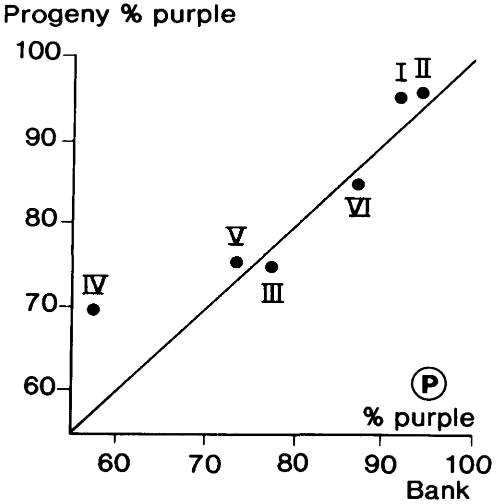


Fig. 16. Relationship between flower colour of parents and progeny derived from open pollination in *Symphytum officinale*, collected in 6 subzones (I-VI) of the moist bank zone of Lake Kinselmeer.

flower colour were absorbed by the 2n = 40 cytotype from the 2n = 48 cytotype via a number of successive steps, which were tested and resynthesized experimentally.

Mericarps collected in the field were grown in the experimental garden. If the proportion of purple-flowered plants was high in the field (as in the bank zone), the offspring showed a high percentage of purple-flowered individuals too (Fig. 16). The flower colour marker demonstrates that most interbreeding takes place between neighbouring individuals. The chromosome number variation provides additional evidence for the relationship between distance and the amount of gene flow. The average chromosome number of 20 plants per 100 m interval along the moist bank zone and the corresponding intervals along the dry dike zone was determined. Often the difference in the average chromosome number turned out to be largest when the distance between these zones is largest (Fig. 17). This again demonstrates that gene-flow is restricted by distance (Levin & Kerster 1971, 1974, Grant 1977).

The frequency of cytotypes among established plants in the different ecological zones was compared during the years 1971, 1984 and 1985. In 1985 attention was also given to the distribution of cytotypes among a representative sample of seedlings, grown from mericarps collected in nature. In all 390 established plants were compared during this period (75 in 1971, 315 in 1984/1985). The average chromosome number of the bank zone plants increased very slightly from 1971 to 1984, undoubtedly as a consequence of gene flow from the plants growing on the dike and in the meadow. The plants from the dike had on average a decreased chromosome number as a consequence of the gene flow from bank zone plants. The percentage of the purple-flowered plants in the bank zone was only slightly lower among the offspring than in the established population, showing that the influence from the zones with more white-flowered plants was not large.

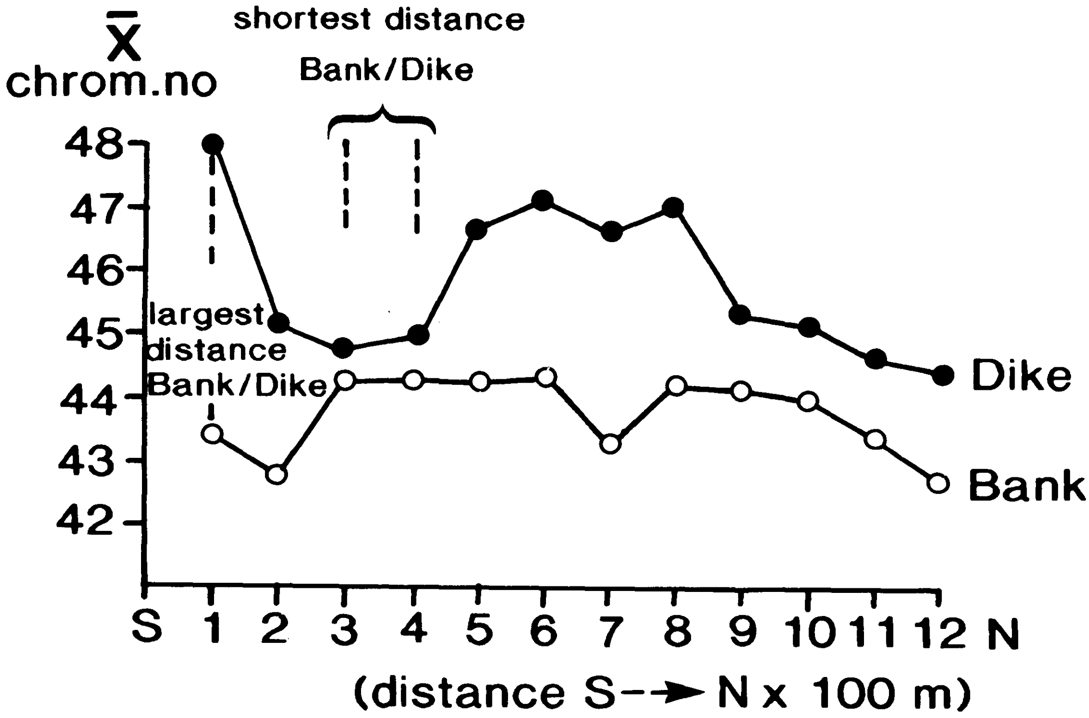


Fig. 17. Difference in the average chromosome number of 20 plants of *S. officinale* per 100 meter interval along the moist bank zone and the dry dike zone of Lake Kinselmeer. S - South; N - North; total length of transect: 1200 m.

Conclusion

These studies showed that experimentally based ecological and genetic studies in a large polymorphic plant population over several years may provide adequate information about the relationships between pattern and process. The processes underlying the patterns should be studied experimentally.

Biosystematics combines the study of pattern and process and is therefore of vital importance for the investigations of plant evolution. The role of botanical gardens for making contributions to our knowledge of population variation and evolution continues to be invaluable.

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MORPHOLOGICAL, CYTOTAXONOMIC AND EVOLUTIONARY STUDIES IN *ANTHOXANTHUM ODORATUM* L. S. LAT. - A CRITICAL REVIEW

Inga Hedberg

Hedberg, I. 1990. Morphological, cytotaxonomic and evolutionary studies in *Anthoxanthum odoratum* L. s. lat. - a critical review. - Sommerfeltia 11: 97-107. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

The occurrence of diploids and tetraploids in *Anthoxanthum odoratum* L. s. lat., and the existence of two different karyotypes at each ploidy level, have resulted in a number of cytotaxonomic studies in this group. Whereas the cytodemes are easily recognized cytologically they have so far proved impossible to separate safely on morphological grounds. Some of the earlier investigations were based on insufficient material and therefore led to premature or faulty conclusions. This situation may cause complications in future studies on *A. odoratum* s. lat. Since the conditions in the group are of general interest also from an evolutionary point of view, earlier studies on morphology, distribution, ecology and karyotypes are summarized and critically reviewed. The taxonomic handling of the cytodemes is discussed and the need for further hybridization work underlinded.

La présence des diploides et tetraploides d'*Anthoxanthum odoratum* L. s. lat. et de deux caryotypes différents à chaque niveau de ploidie a resulté dans un nombre d'études cytotaxonomiques de ce groupe. Tandis que les cytodèmes sont cytologiquement facilement distinguées il a jusqu'ici été impossible de les séparer morphologiquement, avec certitude. Puisqu'un nombre d'autres études sont basées sur des matériaux insuffisants, elles sont menées à des conclusions prématures ou fausses. Cette situation pourrait causer des complications pour des études d'*Anthoxanthum odoratum* à l'avenir. Puisque les conditions dans ce groupe ont aussi un interêt général du point de vue évolutionaire, des études antérieures en morphologie, distribution, écologie et caryologie sont résumées et critiquement revues. Le traitement taxonomique propre des cytodèmes est discuté, et la nécessité de faire encore d'hybridisation est souligné.

Keywords: *Anthoxanthum*, cytodemes, karyotypes.

Inga Hedberg, Department of Systematic Botany, Uppsala University, Box 541, S-751 21 Uppsala, Sweden.

INTRODUCTION

The cytological conditions within the perennial Linnean species *Anthoxanthum odoratum* have been the object of a number of investigations, especially in recent years. The tetraploid number (2n = 20) was first published from central Europe by Katterman (1931) and Avdulov (1931) independently, and the diploid number (2n = 10) first reported by Östergren (1942) from Swedish Lapland. Further investigations revealed that tetraploids are widespread in Europe whereas diploids are restricted to boreal (subarctic) regions.

The difficulties in finding reliable morphological differences between diploids and tetraploids were stressed by Östergren (1942) and elucidated by me in studying extensive material from Scandinavia and the Alps (Hedberg 1967, 1969). However, other scientists, using more limited material from restricted areas have maintained that it is possible to judge the ploidy level from morphological inspection (cf., e.g., Tutin 1950, Rozmus 1958, Teppner 1969, 1970, Felber & Girard 1986).

Improvements in cytological techniques in the early 1960s have made it possible to study chromosome morphology in greater detail. Application of these new techniques has led to the discovery of karyotypic differentiation both at diploid and at tetraploid levels in *A. odoratum* s. lat.

Such studies were reported by K. Jones (1964) who was the first to describe marked differences in karyotypes between tetraploids and the boreal diploid. Apart from two annuals he also included in his study an "unnamed diploid species" from Crete; "probably perennial, which is very much like *odoratum* in appearance and distinct from *alpinum*".

The occurrence of two karyotypes *within* the tetraploid was first reported by me in material from Switzerland (Hedberg 1970). Whereas the bulk of the material showed the same karyotype as my material from Scandinavia and the material investigated by K. Jones (1964) - and suggested by him to be of allopolyploid origin - five specimens from one population had a typical autotetraploid karyotype based on the boreal diploid. Later in the same year, Teppner (1970) reported similar autotetraploids from one population in France (Massif Central) and ascribed the karyotype mentioned by Jones (1964) in Mediterranean material to "diploid *Anthoxanthum odoratum* L.".

A number of spontaneous triploids have been found by me in Scandinavia (Hedberg 1967) and one triploid specimen was also found in the Alps (Hedberg 1969). A further triploid was reported by Felber (1986). Some of my Scandinavian triploids were found in pure diploid populations in areas where tetraploids do not occur. Others were found in mixed populations, as was also the Swiss triploid mentioned.

Comparative studies of morphological variation, distribution and ecology of the four cytodemes, together with spontaneous and artificial triploids, provide unique opportunities to trace the genesis of the tetraploid. For such purposes detailed and correct information is, however, very important. Reliable conclusions can only be achieved through thorough investigations of extensive, representative and properly documented material. Unfortunately this requirement has been disregarded in several investigations, not least in recent ones like those of Teppner (1969, 1970) and Felber (1986, 1988). In view of my own results, based on investigations carried out during many years, I have therefore found it necessary to discuss their results and conclusions.

For many years the nomenclatural treatment of both diploids and tetraploids has been highly unsatisfactory. The discovery of different karyotypes within each ploidy level has certainly not facilitated this treatment. Hence I found it desirable to give here a summary of names used by various authors.

MATERIAL AND METHODS

Material of *Anthoxanthum odoratum* L. s. lat. has been collected from different parts of Europe (Hedberg 1967, 1969, 1986). Whenever possible I have collected at least four (sometimes up to 33) specimens from each population. The specimens were kept in cultivation in pots in the Botanic Garden of Uppsala University. Herbarium material from each specimen was also secured in the field. Additional living material was put at my disposal by a few colleagues.

For routine chromosome counts in extensive material from Scandinavia and the Alps (Hedberg 1967, 1969) root tip sections were used. Detailed studies of chromosome morphology were performed in squash preparations, prepared according to a slight modification of the method elaborated by Östergren & Heneen (1962, cf. Hedberg 1970) and included material from Scandinavia, Austria, Switzerland, USSR and Greece (Hedberg 1970, 1986).

Crossing experiments have been - and are currently being - carried out between all four cytodemes.

Voucher specimens are kept at the Department of Systematic Botany, Uppsala University.

RESULTS

Morphology

Investigation of extensive material of *Anthoxanthum odoratum* s. lat. (Hedberg 1967, 1969) confirmed the difficulties in distinguishing between the boreal-alpine diploid and the widespread tetraploid on morphological grounds. In Scandinavia they could in most cases be separated by using a combination of characters: in tetraploids hairiness in at least some parts of the plants and lack of scabridulae on fertile lemmata, in diploids lack of hairiness and presence of scabridulae (Hedberg 1967). Such a possibility does not exist in material from the Alps, however, where hairiness occurred in about half the number of diploids investigated and scabridulae on fertile lemmata were found in almost one-fourth of the tetraploids (Hedberg 1969), cf. Tab. 1.

After the discovery of two different karyotypes in the material from the Alps (Hedberg 1970), the possibility of correlating the above characters to karyotype was investigated (cf. Tab. 1). In spite of the sparse material available it was obvious that the cytodemes could not be separated on morphological criteria since the same character combinations were found in both.

Of considerable interest in this connection is that the first discovery of the restricted (auto)tetraploid was *not* made because of deviating morphology but through crossing experiments. When, in such experiments, I obtained from one single crossing (tetraploid x diploid) a considerable number of triploid offspring plants, compared to the sparse hybrid output (two or three specimens at most) I had obtained in earlier attempts, karyotype studies were started in the tetraploid material, which revealed its autoploid constitution.

The two diploid cytodemes are morphologically rather well separated in that almost all specimens from Scandinavia and the Alps have scabrid lemmata whereas those of the Rhodean (Mediterranean) specimens are glabrous (Hedberg 1986). Furthermore, most of the

Tab. 1. Relationships between cytological and morphological characteristics in *Anthoxanthum odoratum* L. s.lat. from the Alps. Morphological characters: h - hairiness in the plant, s - scabridulae on fertile lemmata. A hyphen indicates lack of character in question. Tetraploid karyotypes: I - the widespread, II - the restricted.

Material	Morphological character combination			
	hs	h-	-s	--
total diploids	27	0	30	0
total tetraploids	10	42	3	4
tetraploid I	0	10	2	0
tetraploid II	3	1	1	0

latter show a degree of hairiness which is seldom found in the boreal diploid. The Rhodean diploid obviously shows the character combination typical for most of the widespread tetraploids and cannot, in fact, be separated from them on morphological grounds.

Taxonomy

Ever since Östergren (1942) discovered that the Linnean species *Anthoxanthum odoratum* comprised also diploids in addition to the earlier known tetraploids, the taxonomic and nomenclatural handling of material belonging to different ploidy levels/cytodemes has been rather careless.

Whereas Östergren himself refrained from giving taxonomic rank to the diploid (Östergren 1942), Löve & Löve (1948) did not hesitate to describe it as a new species, *A. alpinum* A. & D. Löve, basing their description mainly on Östergren's observations. Two years later Tutin (1950) pointed out that diploid material from Japan, morphologically very similar to or indistinguishable from the European diploid (*A. alpinum* A. & D. Löve), had been known since 1926 under the name *A. nipponicum* Honda.

Later, B. Jones & Melderis (1964) reduced the European diploid to a subspecies, *A. odoratum* ssp. *alpinum* (A. & D. Löve) Jones & Melderis, since they found it very difficult to separate it from the tetraploid.

A survey of names used for *Anthoxanthum odoratum* L. s. lat. is given in Tab. 2.

Karyotypes

In his detailed studies on chromosome morphology in *Anthoxanthum*, K. Jones (1964) reported conspicuous differences between tetraploid *A. odoratum* (material from the British Isles) and the boreal diploid, especially in the morphology of their SAT-chromosomes. From his microphotographs (K. Jones 1964) it is also obvious that in its SAT-chromosomes the "unnamed diploid species" from Crete differs from the boreal diploid but is more or less identical with the widespread tetraploid.

The different karyotypes occurring in *A. odoratum* s. lat. are illustrated by idiograms in Figs 1-4 (cf. also microphotographs in Hedberg 1970, 1986: Fig. 1). For any discussion

Tab. 2. Survey of names used for material of different ploidy level and cytodemes in *Anthoxanthum odoratum* L. s.lat.

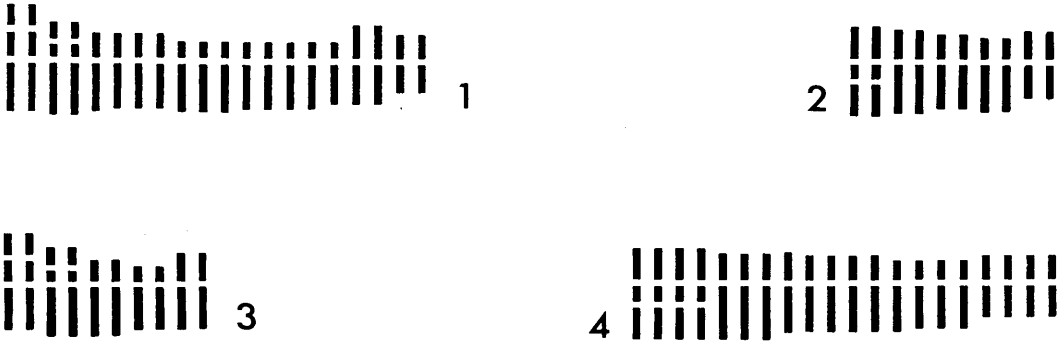
Author	Widespread tetraploid	Restricted Swiss-French tetraploid	Boreal-alpine diploid	Mediterranean diploid
Östergren (1942)	odoratum		odoratum	
Löve & Löve (1948)	odoratum		alpinum	
Tutin (1950)	odoratum		alpinum = nipponicum?	
Hadač & Hašková (1956)	odoratum var. alpinum			
Rozmus (1958, 1960)	odoratum		alpinum*	
Bøcher (1961)	odoratum		odoratum ssp. alpinum	
B.M.G. Jones (1963)	alpinum**			
B.M.G. Jones & Melderis (1964)	odoratum		odoratum ssp. alpinum	
K. Jones (1964)	odoratum		alpinum	unnamed species
Tateoka (1966)	odoratum		?nipponicum	
Hedberg (1967, 1969)	tetraploid odoratum		diploid odoratum	
Löve & Löve (1968)	odoratum		nipponicum	
Hedberg (1970)	tetraploid odoratum (K_I)	tetraploid odoratum (K_{II})	diploid odoratum	
Teppner (1970)	tetraploid odoratum	tetraploid alpinum	diploid alpinum	diploid odoratum
Hedberg (1986)	tetraploid odoratum (K_I)	tetraploid odoratum (K_{II})	diploid odoratum	diploid odoratum
Felber (1986, 1988)	tetraploid odoratum	tetraploid alpinum	diploid alpinum	diploid odoratum
Tateoka (1987)	odoratum ssp. odoratum		odoratum ssp. alpinum	

* Position uncertain since Rozmus on morphological grounds identified his diploid material as "*A. alpinum* Löve & Löve" but described and depicted the SAT schromosomes of the widespread tetraploid, which he reported to occur also in the diploids.

** Name obviously based on absence of hairiness in the material - B.H.G. Jones in doubt as to the specific status of *A. alpinum* A. & D. Löve.

on - or comparison of - chromosome morphology it is very important to be aware of various pitfalls: differences in contraction of chromosomes may occur even between cells in the same preparation, secondary constrictions do not always show up, etc. Consequently, too much attention should not be given to minor differences in arm ratios or total length of chromosomes, nor to small differences in the position of secondary constrictions. A detailed discussion of these phenomena is given by Hedberg (1970).

Given these limitations, the following statements can be made: (1) The striking similarity in karyotypes between the boreal-alpine diploid (Fig. 2) and the restricted tetraploid in Switzerland and France (Fig. 4) leaves no doubt about the autoploid origin of



Figs 1-4. Idiograms of the four caryotypes occurring in *Anthoxanthum odoratum* L. s. lat. Fig. 1. The widespread tetraploid. Fig. 2. The boreal diploid. Fig. 3. The Mediterranean diploid. Fig. 4. The restricted tetraploid. Cf. also microphotographs in Hedberg (1970, 1986).

the latter. (2) The SAT chromosomes of the Mediterranean diploid (Fig. 3) occur also in the widespread tetraploid (Fig. 1). Also the submedians are matched but the small medians in this tetraploid do not occur in the diploid.

Distribution and ecology

The distribution of *Anthoxanthum odoratum* L. s. lat. based on a large number of literature references was mapped by Hultén & Fries (1986), cf. Fig. 5. Whereas little is known about the occurrence and distribution of the different cytodemes outside Europe, a considerable amount of information is available for European material. The results of my own investigations so far are summarized in Fig. 6.

To the information gathered by me, mainly from Scandinavia and the Alps (Hedberg 1967, 1969) and Rhodes (Hedberg 1986), should be added data from further studies in Switzerland (Felber 1986), and Austria and Southern Europe (Teppner 1969, 1970). It must, however, be pointed out that the distribution in Austria (Teppner 1969) is based largely on material in which the chromosome number is not known, which considerably reduces the value of the map.

According to a recent report (Felber 1988) the boreal diploid also occurs in France but only in the most easterly part.

To the isolated finds of the restricted (auto)tetraploid in Switzerland (Hedberg 1970) and in France (Teppner 1970), Felber adds a considerable number of localities in western Switzerland and in the Massif Central (France). The widespread tetraploid is reported from various places in France and seems to be the only cytodeme occurring in the Pyrenees.

The extent to which the two tetraploid cytodemes have overlapping distribution is not known. They do occur in the same populations (Hedberg 1970, Felber 1986) and hybridization is indicated by the finds of a few specimens with intermediate karyotypes (Hedberg, unpubl., Felber 1986).

The Mediterranean diploid, "diploid *A. odoratum*", was reported from Italy, Yugoslavia (and Greece) by Teppner (1970).

As to altitudinal distribution, the boreal-alpine diploid is a regular constitutent in early

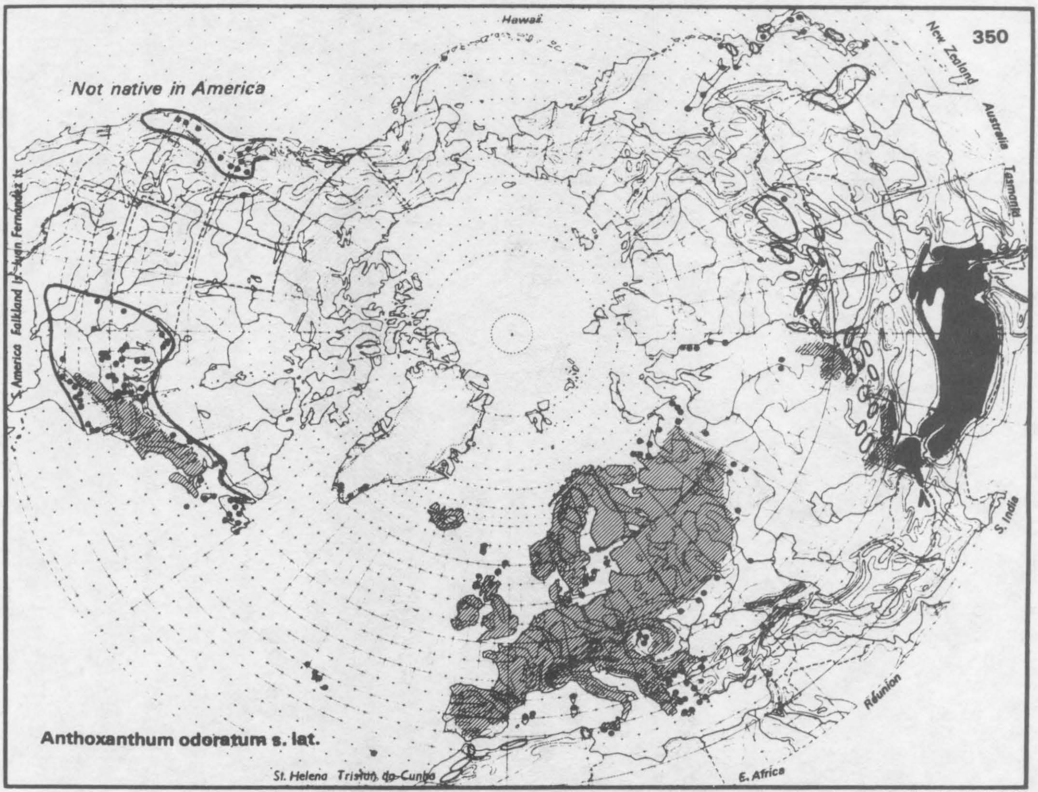


Fig. 5. Distribution of *Anthoxanthum odoratum* L. s. lat. (from Hultén & Fries 1986).

snow-bed communities of alpine and subalpine environments, whereas tetraploids occur mainly at lower levels. According to my investigations there is, however, no sharp borderline between diploids and tetraploids - they meet and form mixed populations both in Scandinavia (Hedberg 1967) and in the Alps (Hedberg 1969). In some of those populations triploids, obviously of hybrid origin, are found (Hedberg 1970, Felber & Girard 1986).

There is also a certain difference in ecological requirements but also in this respect there is according to my experiences a considerable overlap (Hedberg 1967, 1969).

The Mediterranean diploid seems to occur mainly at high altidudes in mountains within its distribution area.

Crossing experiments

I performed a number of crossing experiments in 1964-1968 (Hedberg 1970). The many attempts to get hybrids between tetraploids and the boreal diploid in most cases failed almost completely. At that time, however, the existence of two tetraploid karyotypes was not known and the experiments probably included almost exclusively the widespread

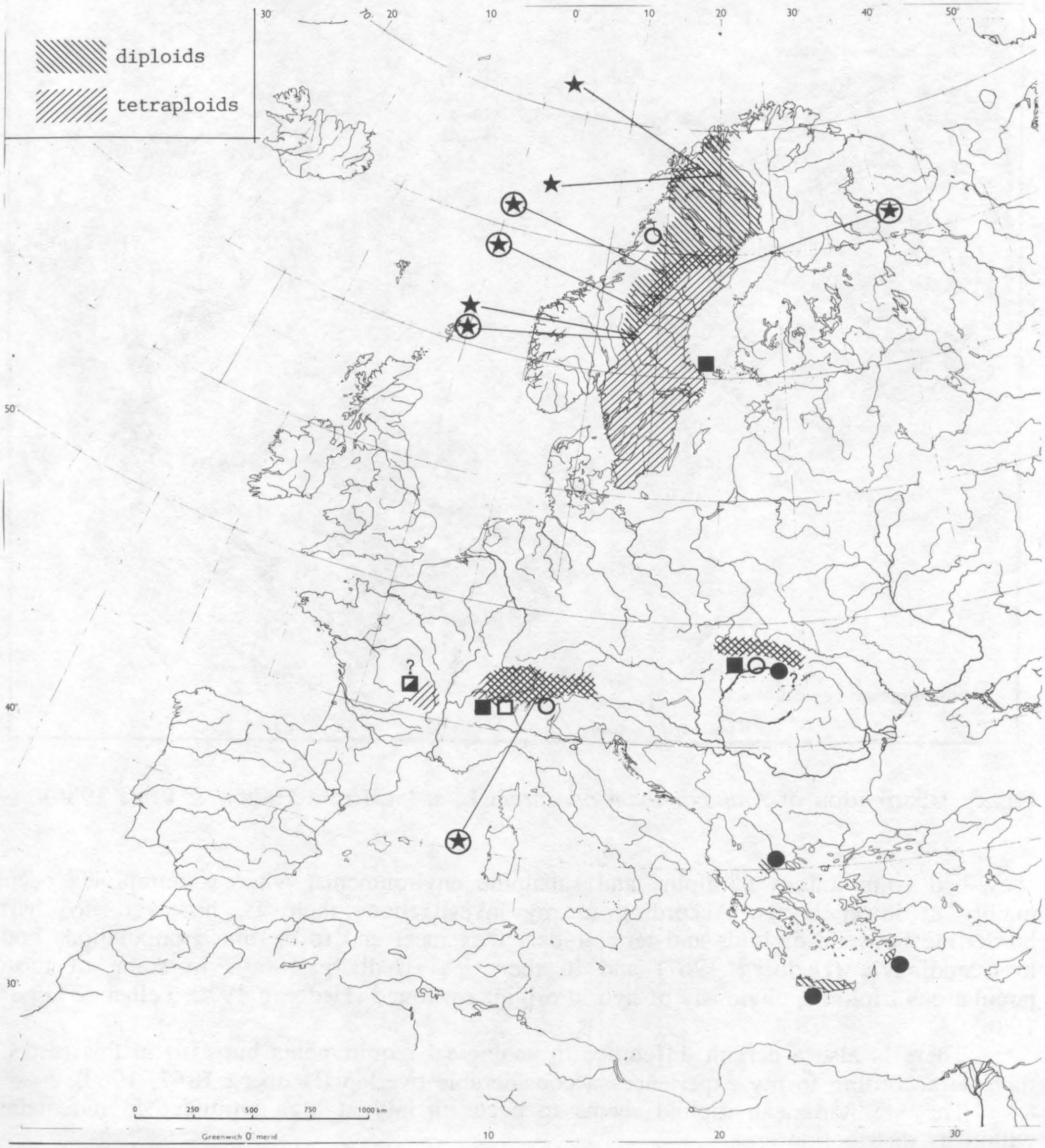


Fig. 6. Distribution of diploid and tetraploid cytodemes of *Anthoxanthum odoratum* L. s. lat., based almost entirely on the author's own observations. Open circles - boreal-alpine diploid, filled circles - Mediterranean diploid, open squares - restricted diploid, filled square - widespread tetraploid. Arrows indicate triploids in pure diploid populations (indicated by stars) and in mixed populations (star in circle). A question mark indicates uncertain karyotype.

tetraploid. From one crossing, however, a considerable number (28) of triploid offspring plants were obtained. The mother plant in this experiment turned out to have the karyotype of the restricted tetraploid. Lack of resources unfortunately made it impossible to follow up the experiments with fertility studies, etc. in the triploids.

In recent years I have also carried out crossing experiments between the diploid cytodemes as well as between the widespread tetraploid and the Mediterranean diploid. A number of triploids have been obtained from the last mentioned crossings, some of them very vigorous, and the results are being processed (Hedberg, unpubl.).

DISCUSSION

Based on his investigations of *Anthoxanthum odoratum*, Felber (1986) draws fairly far-reaching conclusions about the origin, distribution and ecology of the cytodemes. Whereas some of his statements may seem acceptable, it must nevertheless be pointed out that his material is far from sufficient for safe conclusions. To establish with any reasonable degree of certainty the distribution and ecology of the cytodemes one requires a fairly high number of population samples, each comprising a certain number of specimens selected to cover as far as possible both cytological and morphological variation.

This need is well illustrated by my own collections from Scandinavia. In population samples of normally four specimens I attempted to secure diploids as well as tetraploids. After cytological examination the existence of both could sometimes be proved even in samples in which only two specimens survived, whereas in other cases samples of four up to eight specimens gave only one chromosome number also in areas where, with a very high probability, both occur (Hedberg 1967: Tab. 13 and Fig. 1). Similar results were obtained in my Austrian and Swiss material (Hedberg 1969: Tab. 1). One or two specimens from each locality taken at random obviously cannot provide a satisfactory sampling for conclusions on distribution and ecology of the cytodemes. Unfortunately only comparatively few samples investigated by Felber (1986) comprise more than one or two specimens: out of 88 samples from Switzerland no less than 38 comprise only one specimen and 28 comprise two. This is probably the reason why no mixed samples are reported amongst those investigated by Felber (1986) whereas in my material from the Alps eight samples comprised both diploids and tetraploids, one of them also a triploid plant (Hedberg 1969).

Also from France the specimens in each sample are generally very few (Felber 1988).

For valid conclusions on the ecological requirements and the altitudinal distribution of diploids and tetraploids in the Alps and other mountainous areas, transects from each area are needed, since only by comparison of material growing along the same slope can reliable conclusions be drawn on differences in those respects. Unfortunately, no such transects have been studied by Felber (1986, 1988), whose investigations comprise a large number of population samples but practically in no case more than one sample from each slope.

Investigations of transects from one slope (Chasseral, Berne, Switzerland) are reported by Felber & Girard (1986). Studies on chromosome number and morphology were, however, only made in material from a small sample area of 15 x 4 m in the "contact zone" and from plants between 160 and 235 m along one transect. The number of specimens investigated caryologically is not stated. The sorting of specimens along the other three profile lines (Felber & Girard 1986: Fig. 1) into "alpinum" and "odoratum" is evidently based only on presence or absence of scabridulae on fertile lemmata. As shown above, this feature varies within tetraploids and consequently this approach to identification is not only unreliable but also leads to circular reasoning when the variation is interpreted as proving introgression.

CONCLUSIONS

For a number of reasons the four cytodemes within *Anthoxanthum odoratum* L. s. lat. would seem to offer ideal possibilities for cytological investigations: the chromosome numbers are low, the chromosomes are fairly large, the SAT chromosomes are readily recognizable and material is easily available in various parts of Europe. Together with the occurrence of triploids they also provide very suitable material for studies on the genesis of polyploids.

From other points of view, however, the occurrence of different cytodemes causes considerable difficulties. As shown above, they cannot be reliably separated on morphological grounds, which means that for any safe conclusion on distribution and ecology to be drawn, material is needed in which both chromosome number and karyotype are known. Some of the previously published information on distribution of the cytotypes is therefore unreliable. Much more material has to be investigated before it is possible to establish with any reasonable degree of certainty the geographical and altitudinal distribution of the cytodemes.

In the same way, the taxonomic handling is far from easy. For the purpose of general classification they must, because of the difficulties accounted for above, be brought to the same taxon, *Anthoxanthum odoratum* L.

A number of hypotheses on the origin of the widespread tetraploid cytodeme that have been put forward by various authors (e.g. Böcher 1961, Borrill 1962, K. Jones 1964, Hedberg 1970, 1986, Felber 1986) must be tested through further hybridization work.

At present the hypothesis advanced by me: doubling after hybridization between the two diploid cytodemes (Hedberg 1986) seems highly probable. However, results of current crossing experiments (Hedberg, unpubl.) also point to the possibility of an autoploid origin (cf. also Felber 1986).

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PROBLEMS IN *CAREX JEMTLANDICA* AND *C. BERGROTHII* (CYPERACEAE) IN SWEDEN

M. Hedrén

Hedrén, M. 1990. Problems in *Carex jemtlandica* and *C. bergrothii* (Cyperaceae) in Sweden. - Sommerfeltia 11: 109-115. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

The evolution of the Fennoscandian endemic species *Carex jemtlandica* and *C. bergrothii* in the *Carex flava* group (Cyperaceae) is discussed. Preliminary results indicate that both species, as presently circumscribed, are polyphyletic and contain elements of hybrid origin.

Keywords: *Carex bergrothii, Carex flava* group, *Carex jemtlandica*, Fennoscandia.

M. Hedrén, Department of Systematic Botany, Uppsala University, Box 541, S-751 21 Uppsala, Sweden.

INTRODUCTION

The *Carex flava* group has since long caught the interest of Scandinavian botanists, resulting in detailed treatments in floras and in many separate papers (Andersson 1850, Callmé 1887, Palmgren 1918, 1937, 1943, 1946, 1958, 1959, Lindman 1926, Wiinstedt 1936, 1947, Skårman 1940, Palmgren & Hylander 1966). Many more or less endemic taxa have been described from Fennoscandia, but it is difficult to assess their distinctness from the publications, and the status of some taxa has been questioned (Schmid 1983). This was the reason for their exclusion in Borgen's (1987) enumeration of endemic Scandinavian vascular plant taxa.

In other parts of Europe, a more biosystematic approach has been taken in order to analyse the variation within the *C. flava* group. Major contributions are those of Davies (1953a, 1953b, 1953c, 1953d, 1955, 1956) for the British Isles and Schmid (1980, 1981, 1982, 1983, 1984) for Switzerland. Particularly important studies are those of Davies (1955) and Schmid (1980, 1982) on cytology and hybridization. They also point out the potential rôle of introgression between taxa within the group. Other important papers have been published by Havlíčková (1982) on the variability of morphological characters and Vonk (1979) on floral biology.

It is time now to examine the Fennoscandian endemic taxa in the light of these discoveries. This contribution deals with two taxa, *C. jemtlandica* Palmgr. and *C. bergrothii* Palmgr., and is mainly concerned with the situation in Sweden. The paper is meant as a starting point for possible further studies in the group, and thus more hypotheses than results will be presented. It is based on literature studies, the author's own field studies, and to some extent examination of herbarium material and the author's own material collected in the field.

It should be pointed out that the results are preliminary. A large number of specimens have been collected from every population studied by the author, but so far only a minor part of this material has been examined in detail. *Carex jemtlandica* has been studied at ten localities altogether, one on Gotland, four in Dalarna, two in Jämtland, and three in Kuusamo, Finland. *Carex bergrothii* has also been studied at ten localities, five on Gotland, one in Östergötland, two in Uppland, one in Jämtland, and one in Kuusamo, Finland. First, a presentation of each species will be given.

RESULTS AND DISCUSSION

Carex jemtlandica

Carex jemtlandica is apparently most closely related to *C. lepidocarpa* Tausch. It differs in being larger, having taller vegetative shoots, larger bracts to the female spikes which are large and egg-shaped, and the larger utricles with a straighter beak. In many respects it also approaches *C. flava* L., but the ligules are short, as in *C. lepidocarpa*, and the hybrids with *C. flava* are almost completely sterile (i.e., female sterility, no mature fruits are produced). Schmid (1983) regarded it as conspecific with *C. flava*. This conclusion, however, was based on a collection from Switzerland that was apparently misidentified by Palmgren. (A collection from W Jämtland, very similar to what is considered as *C. flava* var. *alpina*, has also been identified as *C. jemtlandica* by Palmgren.) Hybrids between *C. jemtlandica* and *C. lepidocarpa* are not known.

Carex jemtlandica largely replaces *C. lepidocarpa* in Dalarna and northwards, although some material identified as *C. lepidocarpa* has been collected in Härjedalen and Jämtland. *Carex jemtlandica* has also been reported from provinces further to the south, where *C. lepidocarpa* is more common (Palmgren 1959, Weimarck 1963). Such material from Gotland has been given varietal rank, *C. jemtlandica* var. *gotlandiae* Palmgr. Areas where material of the two species has been seen in the field by the present author are indicated in Fig. 1.

Carex bergrothii

Carex bergrothii is similar to *C. oederi* Retz., but is taller and stouter and has larger and more strongly inflated utricles with a more distinct beak.

The species has scattered occurrences in areas with extremely rich fens in Sweden (Fig. 2). It is also known from Norway, Finland, and Estonia. In Sweden it is common on Gotland, but is rare on the Swedish mainland north to Jämtland. *C. oederi* is widespread in the whole area. The two species often grow together, but at least on Gotland, they seem to remain more or less distinct from each other, although material of intermediate appearance seems to be fertile.

Morphological distinctness

The *Carex flava* group comprises several variable and very similar taxa among which the two endemic taxa treated here are particularly difficult to distinguish. There is no single

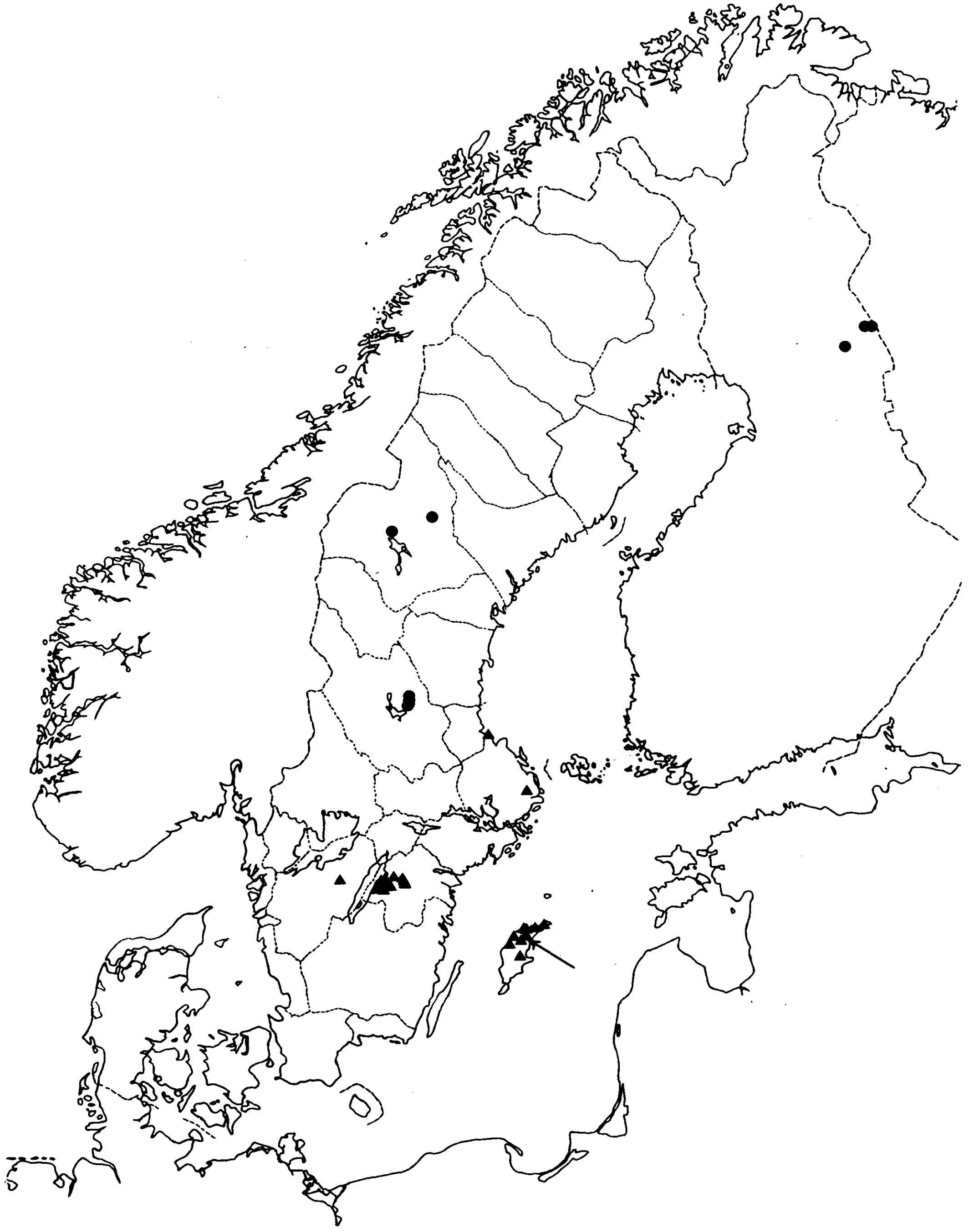

Fig. 1. Sites of *Carex jemtlandica* (dots), *C. jemtlandica* var. *gotlandiae* (arrow) and *C. lepidocarpa* (triangles) as known from the author's observations in the field.

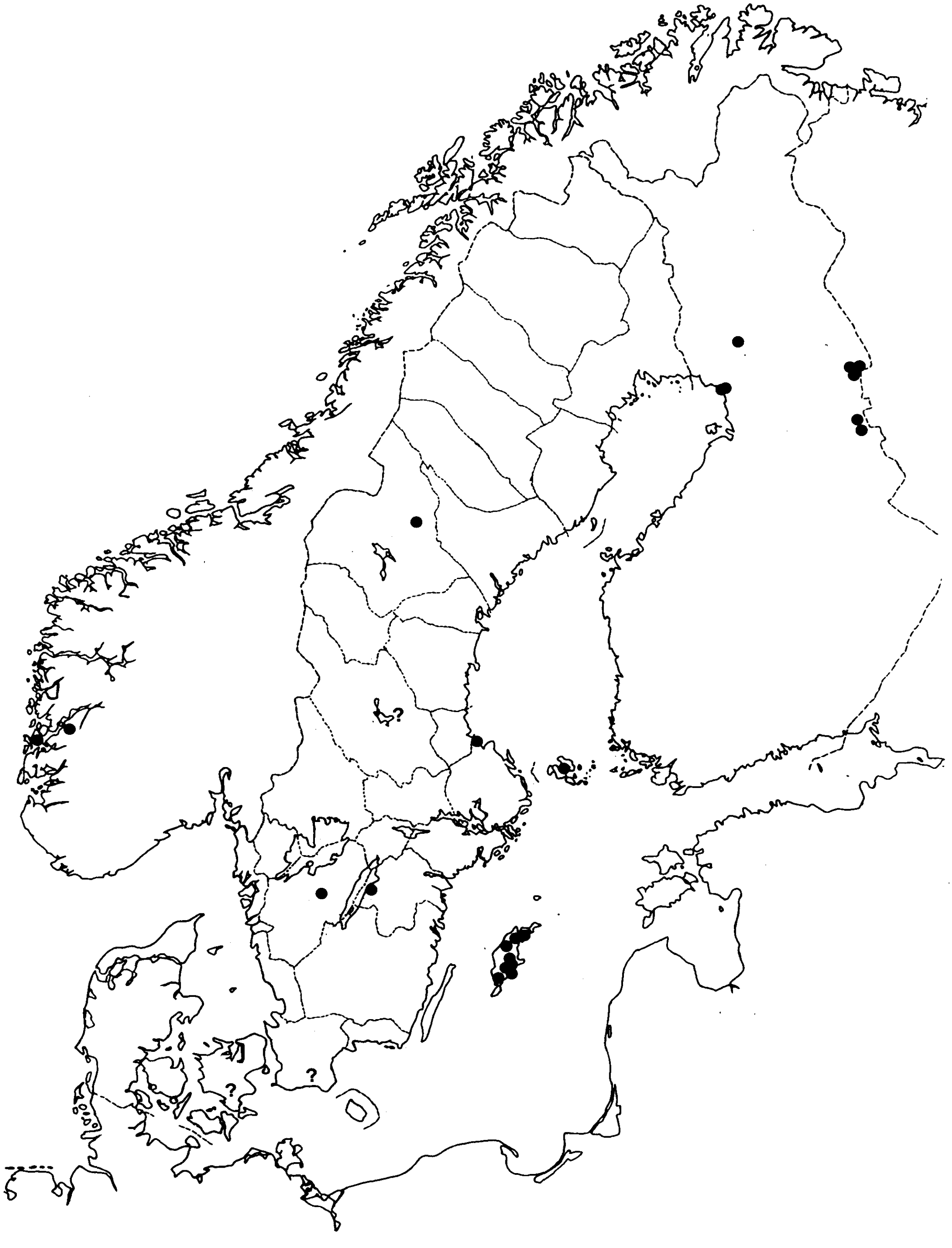

Fig. 2. Distribution of *Carex bergrothii*. Data from Hultén (1971) supplemented with the author's own observations in the field.

character distinguishing any of the endemic taxa; one has to consider a combination of characters. This contrasts with the way in which these species are keyed out in most field floras covering Fennoscandia.

Furthermore, many of the distinguishing characters concern size of different organs. However, local populations can be variable and factors such as water supply and light seem to have great influence on size characters. Thus it is possible that shape of organs, e.g. expressed as ratios, and combinations of characters are better suited to discriminate between taxa.

From the foregoing, the separation of the endemic taxa may seem questionable. However, there seem to be discontinuities or at least relative discontinuities in the morphological variation that distinguishes the endemic taxa from the more widespread species.

Where *C. bergrothii* grows together with *C. oederi*, it is usually possible to classify most individuals to either of the two. The situation is similar on Gotland where *C. jemtlandica* var. *gotlandiae* grows together with *C. lepidocarpa*.

A better knowledge of the morphological distinctness of the endemic taxa requires detailed morphometric studies based on large material. To reduce the effect of phenotypic plasticity, material should also be grown in a garden for comparison, and/or transplantation experiments should be performed. When data are analysed, statistical methods should be employed to compare the variation within taxa with the variation between taxa in order to find the characters that are best suited to discriminate between the widespread and the endemic taxa.

Hypotheses on origin

At present both *Carex jemtlandica* and *C. bergrothii* have highly disjunct distributions, leading to interesting questions regarding their origin. One hypothesis is that each of the endemic species originated on one single occasion and spread to its present localities, or that the endemics represent species with formerly more continuous distributions which are now fragmented due to shortage of suitable habitats. An alternative hypothesis is that what are now considered as endemic taxa originated several times as a result of similar selection pressures or due to genetic drift in small populations.

In *Carex jemtlandica*, the populations in Dalarna, Jämtland and Kuusamo in Finland are remarkably similar to each other. Thus these northern populations are probably closely related to each other despite the great disjunctions. *C. jemtlandica* var. *gotlandiae* seems to differ from the northern populations and has probably originated separately (see below). The populations of *C. bergrothii* on Gotland are similar to each other and are probably closely related, but differ somewhat from those in Östergötland and Uppland. The population seen in Jämtland also differs from the rest (see below).

Since the endemic species are largely defined on the basis of morphological evidence, data from morphometric studies are of limited value for testing hypotheses of polyphyletic origin. An analysis of the isoenzyme variation within and between populations would be more useful. Within the *Carex flava* group there is variation in isoenzymes both within and between populations (Hedrén, unpubl.). A second possibility would be to study DNA restriction site variation.

Palmgren seems to have believed that the different species in the *Carex flava* group were reproductively isolated from each other, since the hybrids rarely developed mature fruits. However, Hultén (1971) seems to have regarded *C. bergrothii* as a possible introgression product between *C. lepidocarpa* and *C. oederi*. Schmid (1980) demonstrates that introgression is possible within the group: despite the inability of the F1 between *C. flava* and *C. oederi* to produce fertile fruits, some of its pollen appeared to be fertile and back-crosses with the parents were produced.

A hypothesis of origin by hybridization and introgression seems to fit some situations found in nature. The population of *C. jemtlandica* var. *gotlandiae* studied at Othem on Gotland is very similar to sterile hybrids between *C. oederi* and *C. lepidocarpa* found at other localities on Gotland. Most plants at Othem produce mature fruits, but some are at least partially sterile. *Carex lepidocarpa* and *C. oederi* both occur at the Othem locality.

A particularly intriguing population is found near Gisselås in Jämtland. The variation is such that a large hybrid swarm can be suspected. Many individuals are more or less sterile. Probable parents present are *C. flava* (common), *C. jemtlandica* (rare), and *C. oederi* (very common). Plants closely resembling *C. bergrothii* are also present, but they are not morphologically distinct from the hybrid individuals. Thus, the plants resembling *C. bergrothii* at this locality may have originated locally through hybridization. On Gotland *C. bergrothii* sometimes grows together with *C. oederi* and *C. lepidocarpa*, but the three taxa remain quite distinct. In this case a hybrid origin of *C. bergrothii* seems less obvious, but it is possible that through selection on a hybrid swarm, a derived, stabilized and relatively distinct taxon has developed.

The hypothesis of a hybrid origin can be tested with a variety of methods using morphological data (see, e.g., Adams 1982). Furthermore, data from isoenzyme analysis or DNA restriction site mapping can also be employed for this purpose.

Age of the endemic taxa

Palmgren (1937) explained the disjunct present distribution of *Carex jemtlandica* by assuming the species was an old taxon that suvived the last glaciation at several refugia close to the ice. This hypothesis would fit a monophyletic origin of the species. Alternatively, *C. jemtlandica* may have been widespread just after the retreat of the ice. The continuous leaching of soil minerals and the high intensity of competition from a closed plant cover may explain the restriction of *C. jemtlandica* to the most favourable sites. This hypothesis does not contradict a monophyletic origin of the species. A postglacial origin of *C. jemtlandica* is thus possible, as has been discussed also for other endemic plant taxa by Hultgård (1987). Similar arguments may be applied to *C. bergrothii.*

If the hypothesis of a polyphyletic origin is accepted, the endemic taxa may be of quite recent origin. The endemic taxa are not sufficiently morphologically different from the most similar widespread taxa to render a postglacial origin improbable. A derived population may develop within a few generations from hybrid origin.

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POLYPLOIDY AND DIFFERENTIATION IN N EUROPEAN POPULATIONS OF *PRIMULA* SUBGENUS *ALEURITIA*

U.-M. Hultgård

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A first report of an ongoing biosystematic study of *Primula* taxa of the subgenus *Aleuritia* (Duby) Wendelbo in N Europe is presented. An extensive investigation of chromosome numbers in *P. farinosa* populations from Sweden has been performed in response to previous reports on polyploidy in the species, but only the diploid number was found. In contrast a number of counts from *P. stricta* populations revealed apparent genetic instability. Chromosome numbers of N and C European *Primula* subg. *Aleuritia* populations investigated by the author are published. Variation patterns of heterostyly and homostyly are described. Pollen morphology has been studied and the results so far obtained are presented. Some taxonomic and evolutionary problems are indicated.

Keywords: Cytology, Evolution, Morphology, N Europe, *Primula*, *Primula* subg. *Aleuritia*, Taxonomy.

Ulla-Maj Hultgård, Department of Systematic Botany, Uppsala University, Box 541, S-751 21 Uppsala, Sweden.

INTRODUCTION

The subgenus *Aleuritia* (Duby) Wendelbo of the genus *Primula* is represented by five main taxa in northern Europe: *P. farinosa* L., *P. scotica* Hook., *P. scandinavica* Bruun, *P. stricta* Hornem., *P. nutans* Georgi and until recently also *P. egaliksensis*; the last taxon was known from one locality in N Iceland but is now reported to be extinct (J. Pálsson, pers. comm.). Their distribution is shown in Fig. 1.

P. farinosa has a wide, but disjunct distribution in Eurasia; the European centres are in the Alps and the Baltic region; the Asian in southern Siberia and in Kamtchatka. Its frequency in the lowlands of N Europe has decreased during the 20th century because of destruction of many habitats. The present distribution of *P. farinosa* in N Europe is discontinuous (Fig. 1). In Scandinavia *P. farinosa* occurs from north central Sweden southwards to E Denmark and the island of Bornholm. In Finland the species is restricted to the Åland Islands and the adjoining SW Finnish archipelago. It is found neither in Norway nor on Iceland. The endemic *P. scotica* is confined to a limited coastal area of N Scotland and the Orkney islands. The number of colonies has diminished considerably during the 20th century. *P. scandinavica* occurs with scattered localities throughout the mountains of Norway and Sweden and is considered endemic to Scandinavia. *P. stricta* has

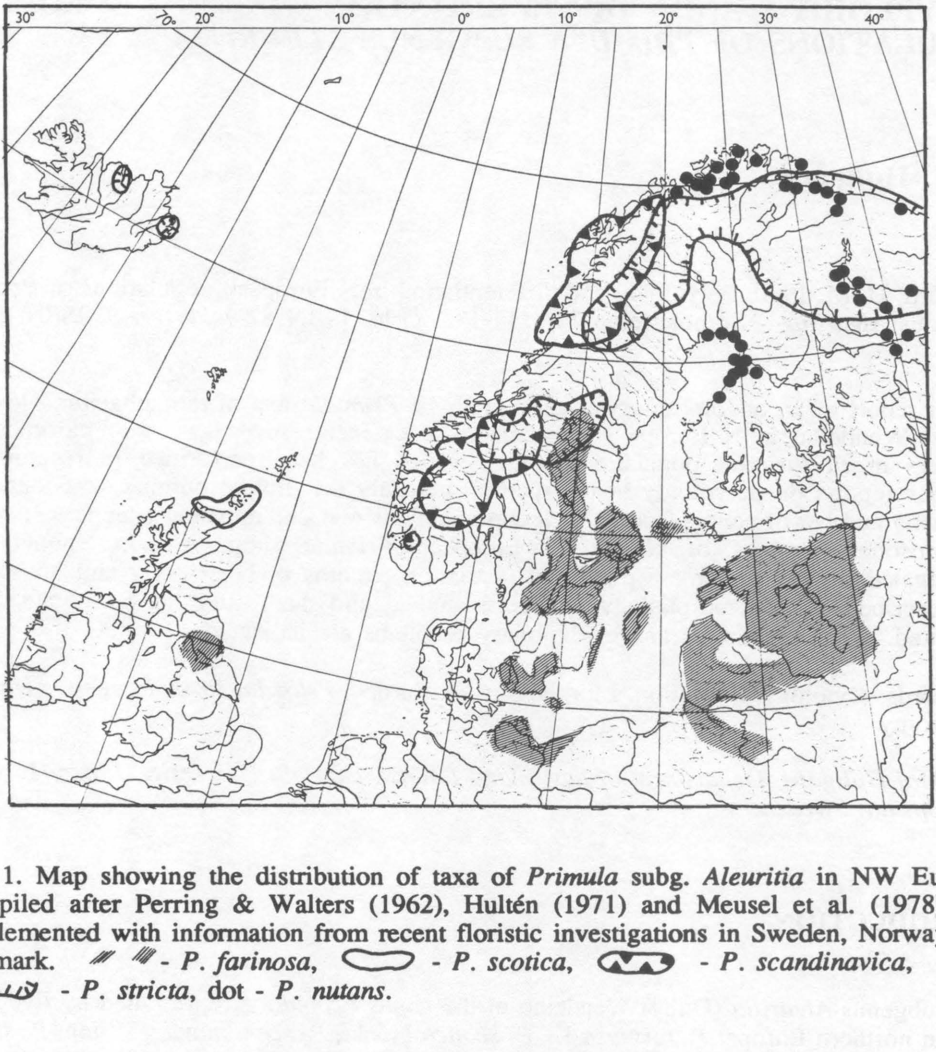

Fig. 1. Map showing the distribution of taxa of *Primula* subg. *Aleuritia* in NW Europe. Compiled after Perring & Walters (1962), Hultén (1971) and Meusel et al. (1978) and supplemented with information from recent floristic investigations in Sweden, Norway and Denmark. ▨ ▨ - *P. farinosa*, ⬭ - *P. scotica*, ▲ - *P. scandinavica*, ⊥ - *P. stricta*, dot - *P. nutans*.

a distribution similar to *P. scandinavica* but occurs also in NE Fennoscandia, on Iceland and in northernmost Russia. It is also widely distributed in arctic North America. *P. nutans* is a northeastern species mostly bound to shore meadows at the Bothnian Gulf and the Polar Sea of arctic Europe.

Scandinavian distributions of *P. scandinavica* and *P. stricta* partly overlap but *P. farinosa* is separated from all other taxa except for a small area in north central Sweden where it meets *P. stricta*. One of my localities from this area included a mixed population (Hultgård 8819).

The delimitation of the five taxa with the rank of species is generally accepted (Valentine & Kress 1972, Lid 1985). However, certain specimens from northernmost Scandinavia have been described as *P. stricta* var. *obesior* Norm. and have been interpreted as intermediates between *P. stricta* and *P. scandinavica* (cf. Nilsson 1986).

The status of the *Primula* subg. *Aleuritia* populations found in the arctic and subarctic regions of NE Europe has been disputed. Specimens from the islands Vaygatch and Novaya Zemlya have been interpreted differently by different authors: as *P. farinosa* (Feilden 1898, Knaben 1982), as *P. scandinavica* (Bruun 1938, Wendelbo 1959), and as *P. stricta* (Fedorov 1952).

Although the delimitation of the species in NW Europe seems rather clearcut, the morphological and genetic variation within and among local populations is incompletely known. Furthermore the origin and spread of the polyploid taxa as well as their evolutionary relationships raise interesting problems which need to be investigated more closely.

The present paper is a first report from an ongoing biosystematic study of North

Tab. 1. N European populations of *Primula farinosa*, *P. scotica*, *P. scandinavica* and *P. nutans* examined cytologically. Voucher specimens are deposited in UPS. n_i - number of individuals examined. n_b - number of individuals with accessory (B-) chromosomes. * - population samples grown from seeds.

Species	Locality	n_i	2n	n_b	Voucher
P. farinosa	S: Öl: Torslunda, Igelmossen	5	18 + 0-1 B	1	Hultgård 8830
	S: Gtl: Fleringe, Hoburgsmyr	13	18 + 0-1 B	7	Hultgård 8829
	S: Gtl: Kräklingbo, Nygårdsmyr	2	18 + 0-2 B	1	Hultgård 8601
	S: Gtl: Kräklingbo, Torsburgen	2	18		Hultgård 8602
	S: Gtl: Lojsta, Rammträsk	1	18		Hultgård 8603
	S: Ög: Skänninge, Örbacken	1	18		Hultgård 8434
	S: Ög: Ödeshög, Sjöstorp	1	18		Hultgård 8910
	S: Ög: Rogslösa, Borghamn	2	18		Hultgård 8911
	S: Srm: Tunaberg, Nyäng	1	18		Hultgård 8413
	S: Upl: Forsmark, Johannisfors	3	18		Hultgård 8809
	S: Upl: Östhammar, Ornöviken	4	18 + 0-1 B	1	Hultgård 8810
	S: Upl: Östhammar, Lösholmen	6	18		Hultgård 8811
	S: Upl: Östhammar, Stenalma	1	18		Hultgård 8812
	S: Upl: Hjälsta, Dumdals dike	1	18		Hultgård 8901
	S: Dlr: Orsa, Lindänget	17	18 + 0-5 B	10	Hultgård 8814
	S: Dlr: Boda, Gulleråsen	2	18		Hultgård 8826
	S: Hls: Los, Långtjärnsbäcken	6	18 + 0-6 B	4	Hultgård 8815
	S: Hrj; Linsell, Orten	9	18		Hultgård 8816
	S: Jmt: Sunne, Bleksjön	27	18 + 0-4 B	10	Hultgård 8817
			27		
	S: Jmt: Ås, Tysjöarna	16	18 + 0-7 B	13	Hultgård 8819
	S: Jmt: Sunne, Svedjesjön	8	18 + 0-2 B	7	Hultgård 8823
	GB: Cumbria: Hale Moss*	2	18		Hultgård 8837
P. scotica	GB: Scotland: Caithness*	1	54		Hultgård 8854
P. scandinavica	N: Hdm: Alvdal*	2	c. 70,71		Hultgård 8836
	N: Rog: Hjelmeland: Stråpastøl	1	72		Hultgård 8908
	N: Hrd: Kvam: Karaldenut	1	72		Hultgård 8915
	N: SoFj: Aurland: Ramnanosa	12	c.70 - c.75		Hultgård 8825
	N: STr: Oppdal	3	72, c.74		Hultgård 8824
P. *nutans*	N: Fnm: Lakselv	2	22		Hultgård 8828
	N: Fnm: Alta	1	22		Hultgård 8903

Tab. 2. C European populations of *Primula* subg. *Aleuritia* examined cytologically. Voucher specimens are deposited in UPS. n_i - number of individuals examined. n_b - number of individuals with accessory (B-) chromosomes. * - population samples grown from seeds.

Species	Locality	n_i	2n	n_b	Voucher
P. farinosa	I: Piem: Sauze d'Oulx, P. Rocca, 1990 m	6	18		Hultgård 8701
	I: Piem: Sauze d'Oulx, L. Pilone, 2200 m	2	18 + 1 B	2	Hultgård 8702
	I: Piem: Sauze d'Oulx, L. Nero, 2300 m	3	18 + 0-1 B	2	Hultgård 8703
	I: Alto Adige: Seiser Alm, 1950 m	3	18, 27		Hultgård 8801
	I: Alto Adige: Seiser Alm, 1875 m	2	18		Hultgård 8802
	I: Alto Adige: Seis, Gstatsch, 1500 m	1	18		Hultgård 8803
	I: Alto Adige: St. Michael, 1400 m	2	18		Hultgård 8804
	A: Salzburg*	2	18 + 0-2 B	1	Hultgård 8838
P. halleri	I: Trentino: Sellapass, 2035 m	2	36		Hultgård 8807

European taxa of *Primula* subg. *Aleuritia*. I have focused my interest upon *P. farinosa*, *P. scotica*, *P. scandinavica* and *P. stricta* with some reference to *P. nutans*. The purpose of this paper is to report the results of an initial survey of chromosome numbers and some morphological features that may be of significance for understanding processes of evolution and differentiation in *Primula* subg. *Aleuritia* populations. My intention is also to point out and discuss problems connected with the origin and migration history of these populations.

MATERIAL AND METHODS

Material from the following herbaria was studied: BG, E, O, S, and UPS. Population samples of living plants selected at random were collected from the sites mentioned in Tabs 1-3. Some plants were kept in cultivation in the Botanical Garden at the University of Uppsala. Chromosome numbers were determinated on the cultivated material, at the metaphase of mitosis in somatic cells from root tips, fixed in chromacetic formalin (Navashin-Karpechenko, modified according to Münzing 1933). Counts were generally made in two root tips from each individual.

Pollen grains, taken from my own collections and the herbarium material, were studied in the light microscope (LM) and the scanning electron microscope (SEM, JEOL JSM-35 operating at 15 kV). In describing the exine the terminology of Praglowsky & Punt (1973) is followed.

Floral characters (heterostyly and homostyly) were examined on herbarium material and my own collections in a Wild M 5 binocular with camera lucida attachment which was used for the drawings. In order to get exact measures without causing damage to the flowers, the method with transmitted light described by Pettersson (1986) was used. The method for measurement of floral characters is shown in Fig. 4.

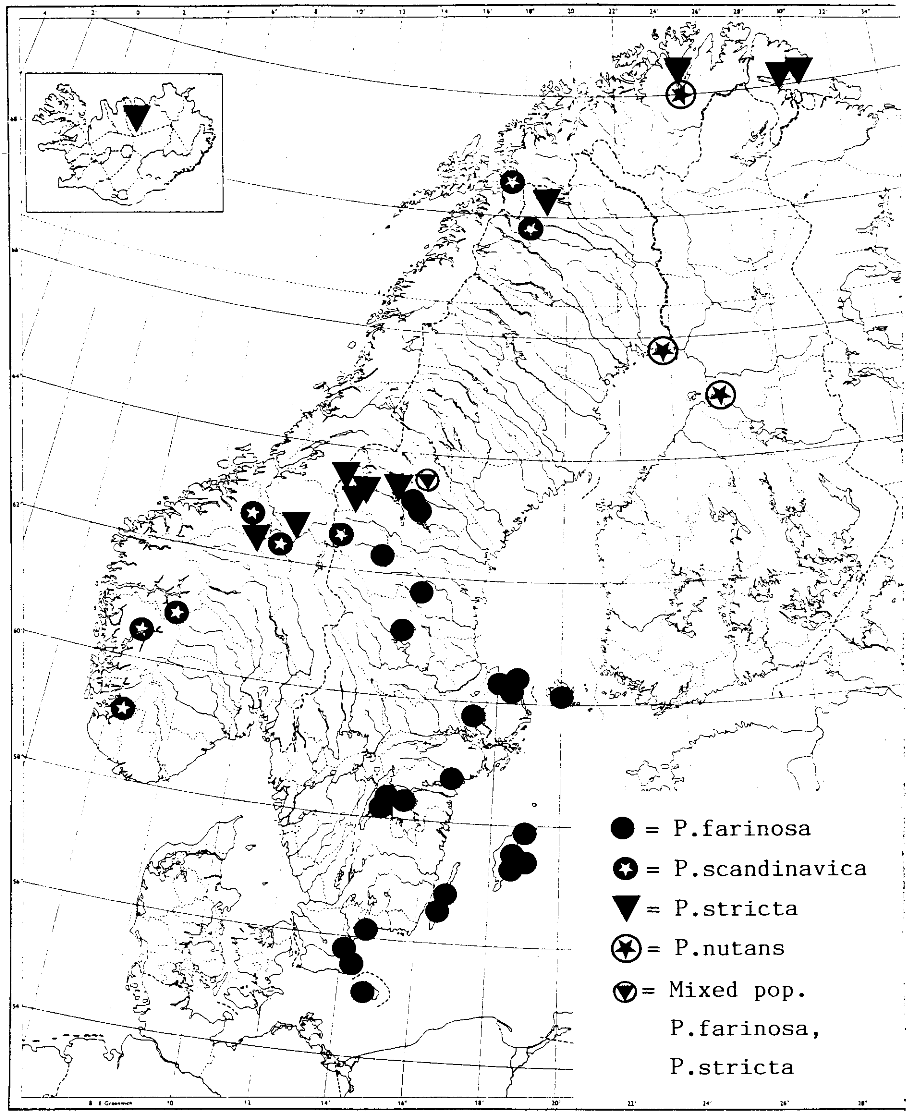

Fig. 2. Sites with *Primula* subg. *Aleuritia* populations in Scandinavia from which chromosome numbers are known. Based on records in Tabs 1-3 and Bruun (1932), Sorsa (1963), Mäkinen & Mäkinen (1964), Larsen (1965), Laane (1967) and Lövkvist (unpubl.).

RESULTS AND DISCUSSION

Cytology

The NW European taxa of the subg. *Aleuritia* are represented by two diploids *P. farinosa* (2n = 18) and *P. nutans* (2n = 22) and three polyploids: *P. scotica*, a hexaploid with 2n = 54, *P. scandinavica*, an octoploid with 2n = 72, and *P. stricta* a high polyploid, as it seems, with an unstable number of chromosomes (Tabs 1, 3). In addition, a tetraploid *P. farinosa* (haploid number n = 18) has been reported by Davies (1953) from Gotland. Sites with taxa of Scandinavian *Primula* subg. *Aleuritia* populations from which chromosome numbers have been reported are shown in Fig. 2.

The chromosome numbers previously recorded for the Scandinavian taxa of subg. *Aleuritia* were based on very restricted material. Bruun, who made the first chromosome counts of most taxa within the genus, cited only two specimens from one local population of *P. farinosa*, for *P. scandinavica* two specimens from two different populations in Sweden and 8 specimens fixed together from one population in Norway and for *P. stricta* four specimens from two local populations (Bruun 1932: 55-56). The report of Davies (1953) on tetraploid *P. farinosa* from Gotland has no indications of the number of counts and individuals examined. No voucher specimen is known to me. Davies' report has been given much attention by subsequent authors (Ritchie 1955: 45, Dovaston 1956: 289, Löve & Löve 1961: 278, Kress 1963: 228, Valentine & Kress 1972: 17, Knaben 1982: 233, Richards 1986: 252, Sarkar 1988: 123), as the question of polyploidy in European *P. farinosa* has general significance.

The results of my own cytological investigations of European populations of *Primula* subg. *Aleuritia* are shown in Tab. 1. With the exception of one triploid, all my counts of *P. farinosa* from Sweden revealed the diploid level (Tab. 1). The triploid individual was found in Jämtland (voucher Hultgård 8817: 5). Since the tetraploid cytotype has not turned up so far, it must have a very limited range (if present at all). A large number of

Tab. 3. N European populations of *Primula stricta* examined cytologically. Voucher specimens are deposited in UPS. n_i - number of individuals examined. * - population samples grown from seeds. 2nm - mean chromosome number in population.

Locality	n_i	2n	2nm	Voucher
S: Jmt: Rödön. Vikekärret	16	c.91 - c.120	108	Hultgård 8818
S: Jmt: Ås, Tysjöarna	29	c.104 - c.127	111	Hultgård 8819
S: Jmt: Åre, Gevsjön	10	c.122 - c.129	126	Hultgård 8820
S: Jmt: Åre, Handölsbrottet	5	c.101 - c.120	111	Hultgård 8821
S: Jmt: Åre, Enaforsholm	10	c.104 - c.130	117	Hultgård 8822
N: Hdm: Alvdal	2	c.111 - c.115	113	Hultgård 8834
N: STr: Oppdal, Kongsvold	1	c.112		Hultgård 8835
N: Fnm: Svartnes	3	c.104 - c.108	107	Hultgård 8841
Is: Akureyri, Kjarni	8	c.87 - c.129	118	Hultgård 8839
Is: Akureyri, Hort. bot.*	1	c.129		Hultgård 8840

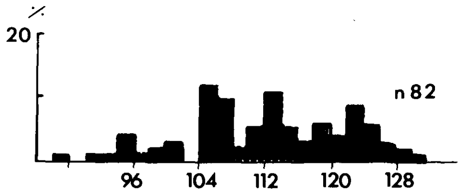

Fig. 3. Variation in chromosome numbers in Scandinavian *P. stricta* as shown by the material in Tab. 3. n - number of individuals.

specimens from the disjunct occurrence of *P. farinosa* in N England proved to be diploid as reported by Dovaston (1956). My investigation of eight different *P. farinosa* populations from the Alps has yielded the diploid number only (Tab. 2). The diploid number has also been reported for material from C and SW Europe by other authors: Kress (1963) from Bavarian Alps and Kress (1969) from central Pyrenees, Wraber (in Löve 1972) from Slovenia, and Yordanov & Peev (1970) from Bulgaria.

Thus, the available evidence does not support the conclusion of an established polyploidy in European *P. farinosa*. However, in a limited area of southern Siberia both the diploid and the tetraploid numbers have been reported (Krogulevich 1978). No information of the material examined is, however, given by Krogulevich.

The chromosomal complement of *P. farinosa* is normally composed by 18 chromosomes. In my material from Sweden both satellited and accessory chromosomes (B-chromosomes) have been observed. Accessory chromosomes are observed in nearly half of the Swedish populations examined (Tab. 1). They vary in number from one to seven; most often they are one to two. Regional differences in this respect can be seen. *P. farinosa* populations from southern Sweden generally have a low frequency of accessory chromosomes and their number is usually not higher than one or two. By contrast north central Swedish populations show a clear dominance of chromosomal sets *with* accessories, mostly in larger number than one or two. So far I have not found accessory chromosomes in the polyploid taxa. Absence of accessory chromosomes appears to be a general feature of polyploids (Stebbins 1971:69).

The five populations of *Primula scandinavica* examined showed numbers at the octoploid level, mostly 2n = 72 (Tab. 1).

The somatic number given by Bruun (1932) and Löve & Ritchie (1966) for *Primula stricta* is 2n = 126, indicating a 14-ploid, if we assume the basic number n = 9. Sokolavskaya & Strelkova (1960) report the number 2n = 136. My investigation of 82 individuals from ten different populations in NW Europe (altogether 150 counts), revealed a striking inconsistency in chromosome numbers. Although the exact number of chromosomes in high polyploid plants is notoriously difficult to determine, the chromosome numbers of *P. stricta* are nonetheless clearly seen to vary from c. 87 up to c. 130 (Fig. 3). Laane (1967), examining plants from E Finnmark, observed numbers not lower than 95 but scarcely as high as 126. The available evidence thus indicates an apparent genetic instability in the NW European *P. stricta* populations. The cytology of the taxa of *Primula* subg. *Aleuritia* raises several interesting questions, some of which will need a more detailed investigation than has yet been performed.

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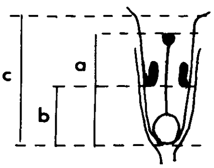

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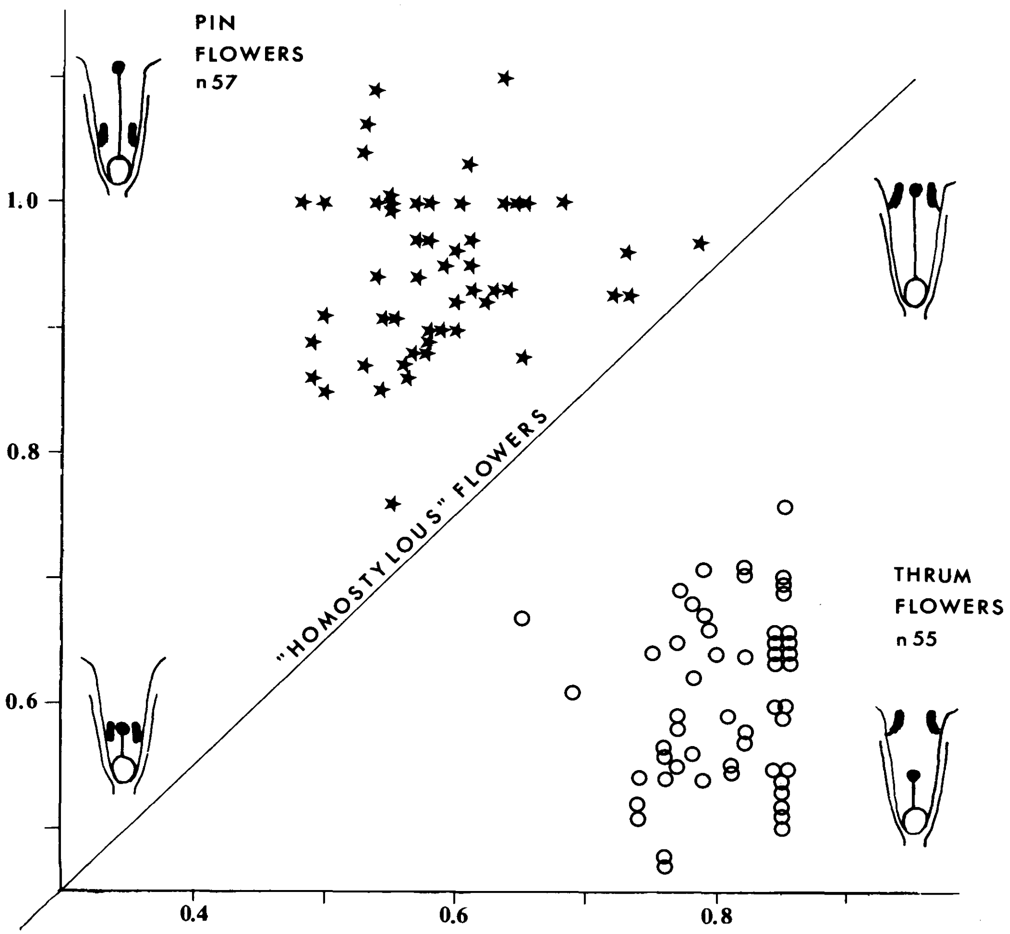


Figs 4-5. Variation in heterostyly in Swedish populations of *P. farinosa*. Fig. 4. Measurements a-c used for Fig. 5. Fig. 5. Variation in heterostyly. Horizontal axis represents the ratio of position of anthers to length of corolla tube (b/c). Vertical axis represents the ratio of position of stigma to length of corolla tube (a/c). n - number of individuals.

Morphology

The variation between and within populations of the *Primula* subg. *Aleuritia* taxa has been thoroughly investigated for a large number of morphological characters. Results concerning some features of floral structure and pollen morphology are given in the present paper. The remaining results will be presented in a forthcoming paper (Hultgård, in prep.).

Floral dimorphism

Heterostyly in *Primula* includes several aspects of which the position of stigma and anthers will be considered here. The variation in these characters is traditionally categorized as pin and thrum flowers (longistylous and brevistylous). The variation in the position of the stigma and the anthers in 112 *P. farinosa* individuals, selected at random from different geographical areas in Sweden, is illustrated in Fig. 5. In my material, a typical pin flower has the stigma at the mouth of the corolla tube and the anthers fixed somewhat above the middle of the tube. In a typical thrum flower the stigma reaches a little above the middle of the corolla tube and the anthers are fixed near the mouth of the tube. However, according to my observations on the Scandinavian material, intermediate forms are frequent. Pin and thrum flowers were found, as would be expected, in about equal numbers.

"Homostylous" flowers (close to the diagonal in Fig. 5) are also found. These are infrequent, but in one population sample from Gotland the number was exceptionally high; out of 18 individuals 7 had stigma and anthers at the same level just below mouth of corolla tube.

Most polyploid taxa in the genus *Primula* are known to be homostylous and autogamous. On the assumption that heterostyly is basic and old in the genus *Primula* (cf. Stebbins 1971, Charlesworth & Charlesworth 1979a), the polyploid taxa constitute secondarily homostyled populations. In taxa with homostyly as basic breeding system two main forms are found: short homostyles and long homostyles. The great majority of secondarily homostyled *Primula* taxa are known to be long homostyles (Ernst 1953). The results obtained by Dowrick (1956) and Charlesworth & Charlesworth (1979b) from studying models for the breakdown of heterostyly clearly showed the superiority of long homostyles over short ones, when both were introduced in heterostyled populations. Charlesworth & Charlesworth (1979b: 511) suggested that the "only circumstance in which short homostyles can spread is when, due to stochastic fluctuations, a short homostyle manages to establish itself before long homostyles can spread".

In natural populations in NW Europe different types of long homostyles may be distinguished. No pure short homostyles have been observed. Forms with the position of stigma clearly above or below the anthers were occasionally found within all three homostylous taxa. The form typical of each of the three homostyled taxa is illustrated in Fig. 6 and the pattern of variation in anther position, length of corolla tube, and ratio anther position/tube length is shown by histograms (Fig. 6). In *P. scotica* the position of anthers and stigma is close to the mouth of the corolla tube. In *P. scandinavica* and *P. stricta* the anthers are mostly fixed about 2 mm below the corolla mouth (mean value for *P. stricta* 2.1 mm and for *P. scandinavica* 2.4 mm). Since tube length in *P. stricta* is shorter (mean value 7.3 mm and for *P. scandinavica* 9.4 mm), the position of anthers will be about almost 1/3 below the corolla mouth. Thus *P. stricta* flowers are usually intermediate between long and short homostyles. In addition to a slightly different position of stigma and anthers the size of anthers was found to be smaller in *P. stricta*.

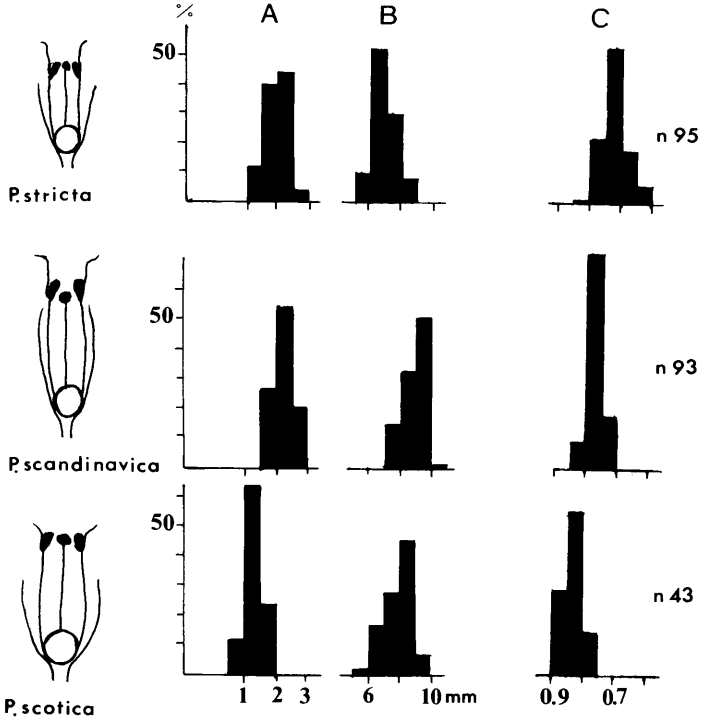


Fig. 6. Different types of homostyly and their patterns of variation as shown by NW European populations of *P. scotica*, *P. scandinavica* and *P. stricta*. Column A - anther position in mm from corolla mouth. Column B - length of corolla-tube. Column C - ratio anther position to length of corolla-tube. n - number of individuals.

Pollen

As indicated by Spanowsky (1962), features of pollen morphology in the genus ***Primula*** may have both taxonomic and phylogenetic importance. Within the genus he found three basic types of pollen, termed (a) *auricula*-type, (b) *farinosa*-type and (c) *veris*-type. Among the taxa of ***Primula*** subg. ***Aleuritia*** investigated by Spanowsky only ***P. farinosa*** is represented in NW Europe. Punt et al. (1974) examined pollen from ***P. farinosa, P. scotica*** and ***P. stricta*** in NW Europe stating that the "***P. scotica*** type is distinctly related both to the ***P. farinosa*** type and to the ***P. stricta*** type". The descriptions given by Spanowsky (1962) and Punt et al. (1974) with respect to pollen morphology in ***Primula*** subg. ***Aleuritia*** have been supplemented and partly corrected during my own investigation. A forthcoming study on pollen morphology in taxa of ***Primula*** subg. ***Aleuritia*** will also include N American and Asian material (Hultgård, in prep.). The results so far obtained on the European material can be summarized as follows.

The polyploid taxa have consistently larger pollen. There is an increase in pollen size from ***P. farinosa, P. scotica, P. scandinavica*** up to ***P. stricta***; the least significant differences are between ***P. scotica*** and ***P. scandinavica*** (Fig. 7). All four taxa mentioned

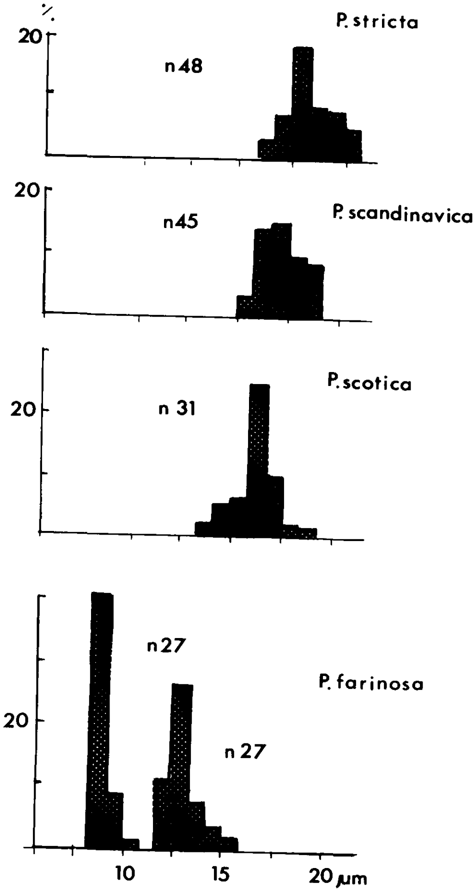


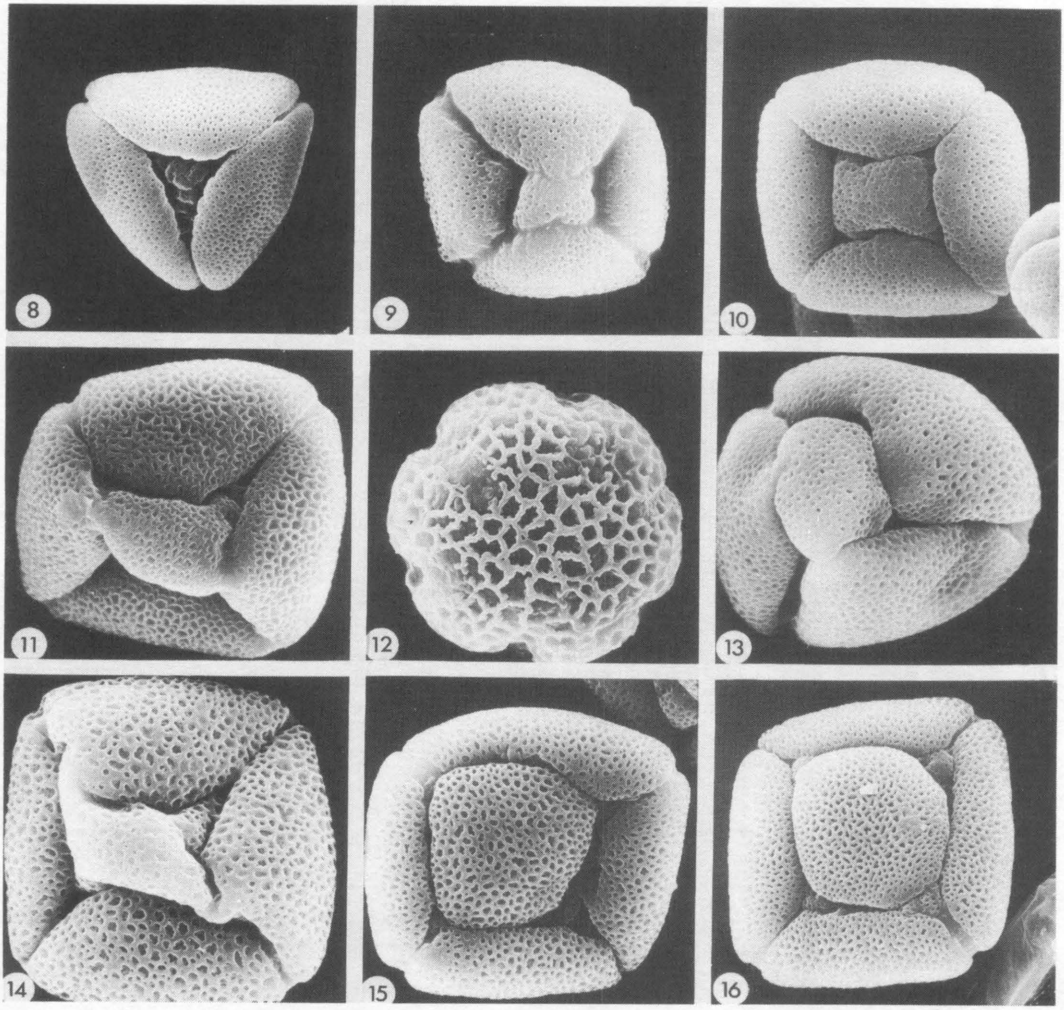
Fig. 7. Variation in pollen size as shown by NW European populations of *P. farinosa* (left column - pin flowers, right column - thrum flowers), *P. scotica*, *P. scandinavica* and *P. stricta*. n - number of individuals.

have parasyncolpate grains with perforations and lumina varying in size and shape. *P. farinosa* pollen grains are tri- or tetracolpate with a dominance of tricolpate grains in most but not all individuals. The exine is a tectum perforatum (Fig. 8).

In accordance with the heterostyly, *P. farinosa* has dimorphic pollen (Fig. 7). Shortstyled thrum flowers produce larger pollen grains and longstyled pin flowers smaller ones. Pollen production is more abundant in the pin flowers. Moreover, the longistylous plants have grains with smaller and less numerous perforations than brevistylous plants.

P. scotica and *P. scandinavica* have tetra- or pentacolpate grains. The proportions were found to be similar within both taxa: c. 70 % tetracolpate and c. 30 % pentacolpate grains. The same basic surface pattern as in *P. farinosa*, a tectum perforatum, is found in pollen from *P. scotica* and *P. scandinavica* (Figs 9-10).

Pollen grains of *P. stricta* in my material normally have 4 or 5 colpi, occasionally 3 or 6 (as contrasted with the statement "usually with 6 colpi" according to Punt et al.



Figs 8-16. Scanning electron micrphotographs of pollen of *Primula* subg. *Aleuritia*. Fig. 8. *P. farinosa* (Hultgård 8834). Fig. 9. *P. scotica* (Bruun UPS fix. 303). Fig. 10. *P. scandinavica* (Hultgård 8825). Fig. 11. *P. stricta* (Hultgård 8839). Fig. 12. *P. nutans* (Hultgård 8828). Fig. 13. *P. halleri* (Hultgård 8807). Fig. 14. *P. stricta* (Hultgård 8818). Fig. 15. *P. stricta* (Hultgård 8820). Fig. 16. *P. stricta* (Bruun UPS fix. 308). Rule - 10 μm.

1974)). The *P. stricta* grains have microreticulate ornamentation and more variable surface structure (Figs 11, 14-16) than pollen of *P. farinosa, P. scotica* and *P. scandinavica*.

Compared with the other taxa of *Primula* subg. *Aleuritia* in NW Europe *P. nutans* presents a different type of pollen (Fig. 12), belonging to the *veris*-type in the terminology of Spanowsky (1962). The grains are not syncolpate and have a fairly large apocolpium.

The surface pattern is clearly reticulate. Pollen of *P. nutans* appear to belong to the same type of pollen as that found in the N American *P. egaliksensis.*

Pollen grains from the *P. halleri* population listed in Tab. 2 were 3- or 4-colpate. It should be noted that their surface pattern no doubt belongs to the same type as in *P. farinosa, P. scotica* and *P. scandinavica* (Fig. 13). According to Spanowsky (1962: 166), pollen of *P. halleri* is of the *auricula*-type with transitions to the "*farinosa*-type" in structure of the colpi.

General discussion

Bruun (1932) arranged the NW European taxa of *Primula* subg. *Aleuritia* in a polyploid series beginning with the hexaploid *P. scotica,* followed by *P. scandinavica,* and ending with the high polyploid *P. stricta.* With reference to the cytological evidence Bruun considered them as being derived from the diploid *P. farinosa.*

The close relationship between *P. farinosa, P. scotica* and *P. scandinavica* is supported by similarities in pollen ornamentation, though the process of differentiation cannot be reconstructed in detail.

P. stricta, on the other hand, may have a more independent position. The surface pattern of its pollen is different from the pollen pattern shared by *P. farinosa, P. scotica* and *P. scandinavica.*

Furthermore, *P. stricta* lacks some morphological characters common to the taxa in the *P. farinosa* group, for example the dense farina on leaves and stems. Finally it shows a different distribution and is usually interpreted as belonging to the west arctic element in the Scandinavian flora (e.g. Hultén 1971, Nordal 1985).

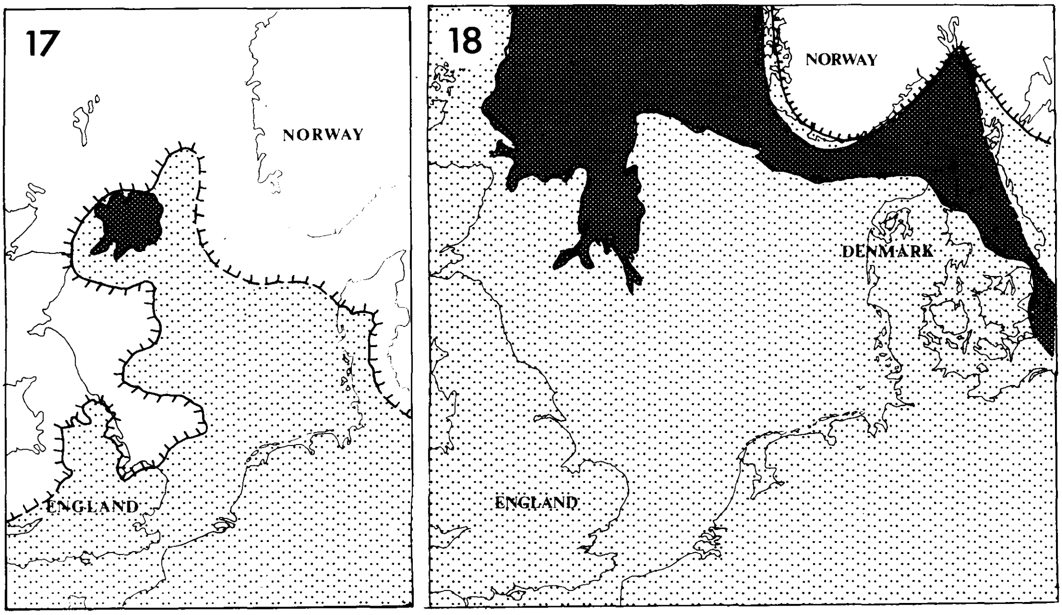
The wide variation in size and shape of lumina and muri in the pollen surface pattern as well as the genetic instability of the Scandinavian *P. stricta* populations may be interpreted as evidence of a certain amount of hybridization with other taxa. *P. stricta* specimens collected in arctic Russia (Kanin, Kolgujev, Vaygatch) and Novaya Zemlya have pollen which in shape and exine structure fall entirely within the range of variation encountered in Scandinavian populations. *P. stricta* may be a northwestern or northern immigrant having survived or evolved during the last Glaciation in ice-free areas of the Arctic. After the retreat of the ice sheet it may have spread to Iceland and Scandinavia in the late glacial and early Holocene period.

The progenitors of the present *P. farinosa* populations in N Europe certainly arrived from the south and southeast in late glacial and Preboreal times. Pollen finds of *P. farinosa* dated 9000 B.P. have been reported from S Finland (Tolonen & Ruuhijärvi 1976).

The origin and migrational history of *P. scotica* and *P. scandinavica* at present seem to be more difficult to understand.

The genesis of *P. scandinavica* has briefly been discussed by Knaben (1982). She suggests that this octoploid taxon arose on shallow ice-free banks in the North Atlantic perhaps during the period of Pleistocene glaciations, either from the hybrid between the diploid *P. farinosa* and the hexaploid *P. scotica* (9 + 27 = 36) followed by a duplication of the chromosome set, or directly from a tetraploid *P. farinosa.* According to Knaben, the first combination is more likely to have occurred since *P. scandinavica* is morphologically close to *P. scotica.*

The presence of more widespread tetraploid *P. farinosa* populations in Europe has not been confirmed, and an alternative should be considered. Together with diploid *P. farinosa* the tetraploid *P. halleri* might have been involved in the genesis of the *P. scotica* and *P. scandinavica* polyploids. *P. scotica* is a relict taxon which once had wider distributional



Figs 17-18. The North Sea basin in late Middle and Late Weichselian periods. Redrawn after Jansen et al. (1979) and Jelgersma (1979) and supplemented with information from Godwin (1975), Andersen (1979) and Berglund (1979). Fig. 17. Maximum extension of ice sheet at about 18 000 B.P. Fig. 18. Hypothetical shoreline at 12 000 B.P. ⊥⊥⊥ - ice-sheet. ● - sea. ∷∷ - dry land.

range (Ritchie 1955, Dovaston 1956). A fossil seed indicates its presence in southern England during full glacial time (Godwin 1975, Dovaston 1956). *P. halleri* occurs today in C Europe but may have been present farther to the northwest in the Pleistocene period. In this respect it should be noted that another fossil seed found in the same place as that of *P. scotica* bears close resemblance to *P. halleri* (Dovaston 1956). Despite its distinctive, elongate corolla tube, *P. halleri* is closely related to *P. farinosa, P. scotica* and *P. scandinavica* as is evident from other characters (cf. Wright Smith & Fletcher 1943) such as pollen structure and chromosome morphology. During the Weichselian glaciation when most of the N European flora survived farther south, good opportunities were created for contact and hybridization with elements of the C European and alpine floras.

The distributional pattern of *P. scandinavica* has been taken as evidence for survival of the last glaciation on ice-free refugia along the western coast of Norway (Bruun 1938, Dahl 1946, Wendelbo 1959, cf. also Knaben 1982). However, other explanations are also possible. Palynological evidence indicates the presence of *P. scandinavica* in deglaciated parts of southwestern Norway already during the late glacial at 13 000 B.P. (Paus 1988), not far from its present distributional limit in the coastal mountains in the province of Rogaland (Ryvarden & Kaland 1968; cf. Fig. 1). This strongly suggests a migration of *P. scandinavica* populations into Scandinavia from the south and southwest over the North Sea continent (cf. also Paus 1988). A similar migrational route may apply to populations of *Artemisia norvegica* (Ryvarden & Kaland 1968, Paus 1988), *Parnassia palustris* (Hultgård

1987), and *Papaver radicatum* (Paus 1988) as well. The North Sea continent occupied vast territories of the present North Sea (cf. Fig. 18).

The importance of the North Sea continent as a reserve from which elements of the late glacial flora could migrate into Scandinavia is underlined by geological and climatic evidence (for general surveys see Lundqvist 1974, Jansen et al. 1979, Jelgersma 1979, Anundsen 1985). Large parts of the northern and central North Sea remained unglaciated land through much of the Weichselian period (cf. Figs 17-18 and Jansen et al. 1979) and could serve as a large refugial territory for an arctic and subarctic flora which during the late glacial and Preboreal periods followed the retreating ice sheets into S Norway and Scotland (cf. Fig. 18). For most plants, the short distance separating the Norwegian coast from the North Sea continent is not likely to have constituted a serious barrier to dispersal.

P. scandinavica is favoured by open or disturbed ground and appears to be a poor competitor. It is also dependent on a base-rich substrate. These ecological preferences suggest that the species may have been more abundant in the late glacial and Preboreal periods when such environmental conditions were prevailing (cf. Iversen 1958, Elven 1980). In Boreal and Atlantic periods the species may have suffered a considerable retreat and its present distribution may be of a relict character, as with other late glacial species which closely followed the receding ice margins, e.g. *Draba cacuminum* (Elven & Aarhus 1984).

Bruun (1932) and Richards (1986) have pointed to the correlation between polyploidy, latitude and homostyly in the section *Aleuritia*: the heterostylous diploids have the most southern distribution range, the homostylous polyploids, in order of ploidy level, occupy more northern latitudes with the high polyploid *P. stricta* as the northernmost taxon. Polyploidy in itself hardly leads to homostyly. The breakdown of heterostyly is rather caused by inefficient insect pollination (Ernst 1953, Charlesworth & Charlesworth 1979b). Paucity of pollen vectors during extreme conditions as in the periglacial during the Pleistocene, at higher altitudes and in arctic regions, may account for the development and maintenance of autogamy and homostyly in the polyploid *Primula* taxa of N Europe. In this connection it should be pointed out that many Scandinavian mountain plants are in fact known to be autogamous (Warming 1886, Lindman 1887).

It may be postulated that homostyled *P. scotica* and *P. scandinavica* populations as well as heterostyled *P. farinosa* populations were growing on the North Sea continent. The heterostylous populations depended on the presence of both pin and thrum flowers and the presence of pollinators for their survival. Thus, homostyled individuals are particularly suited to successful long distance dispersal since one autogamous plant could start a new population (cf. Baker 1955). During the late glacial migrations across the North Sea into the broken topography of the mountainous regions of Scandinavia, homostyled populations would be at an advantage. The absence of the heterostylous *P. farinosa* from Norway should be noted.

The genesis and migrations of the polyploid *Primula* taxa of N Europe must also be considered in the light of the striking parallelism afforded by the related taxa of *Primula* subg. *Aleuritia* taxa from eastern N America (Tab. 4). *P. farinosa* and *P. mistassinica* seem to be closely related diploids, since many populations of the variable *P. mistassinica* complex are virtually impossible to distinguish from the Eurasian *P. farinosa* (cf. Vogelmann 1960: 37). The pollen morphology of *P. mistassinica* is very similar to *P. farinosa*. *P. mistassinica* occurs in southern Canada from Yukon in the west to Newfoundland in the east. *P. farinosa* has a correspondingly broad, although somewhat disjunct distribution in Europe. *P. laurentiana* and *P. scandinavica* display close similarities in many respects. They share the ploidy level, the pollen is closely similar and the leaves of both species are strongly farinose beneath. Both taxa share a pronounced preference for calcareous soil and the habitats are similar: slopes, screes and cliffs, and they have more

Tab. 4. *Primula* subg. *Aleuritia* taxa of NW Europe and eastern N America arranged in order of increasing ploidy levels.

Level	NW Europe		Eastern N America	
	Taxon	2n	Taxon	2n
2x	P. farinosa P. nutans	18 22	P. mistassinica	18
4x	-		P. egaliksensis	36, c.40
6x	P. scotica	54	P. laurentiana	54
8x	P. scandinavica	72	P. laurentiana	72
10-14x	P. stricta	c.90 - c.130	P. stricta	126

limited distribution ranges, *P. laurentiana* in easternmost Canada and adjacent parts of the USA, *P. scandinavica* in the western parts of central and northern Scandinavia. Pentaploid individuals of *P. laurentiana* are known (Vogelmann 1960), corresponding to *P. scotica* in ploidy level. *P. stricta* which occurs in both areas, has been interpreted as a west arctic element in the Scandinavian flora (Hultén 1971, Nordal 1985: 186).

In N Europe there is a gap in the polyploid series of the *Aleuritia* taxa at the tetraploid level. In N America a tetraploid species is found in the widespread *P. egaliksensis* which has a more northern main distribution than the diploid *P. mistassinica. P. egaliksensis* is placed within subsection *Sibirica* by Wright Smith & Fletcher (1943) who state that it has sometimes been confused with *P. sibirica* and *P. stricta.* Only two reports on chromosome numbers have so far been published, one giving 2n = 36 (Jørgensen et al. 1958; material from Greenland) and the other 2n = c. 40 (Hedberg 1967; material from Canada). It is, therefore, doubtful whether *P. egaliksensis* belongs to the polyploid series starting with *P. mistassinica.* From pollen morphology *P. egaliksensis* appears to be closely related to *P. nutans* (cf. Fig. 12) and the chromosome report of Hedberg (1967) might indicate a basic number x = 11.

The parallelism between the *Primula* subg. *Aleuritia* taxa of eastern N America and those of N Europe raise some questions: Is the existence of corresponding polyploids the result of independent evolution from vicariant diploids (*P. mistassinica* and *P. farinosa*) or is there a historical connection, in particular between *P. laurentiana* and the *P. scotica/ P. scandinavica* group? How does this parallelism relate to the general migration routes for the arctic-alpine *Primula* species suggested by Stebbins (1984), a northward migration in Eurasia but a southward migration in N America (since temperate diploids are "few or lacking in the New World")? Closer comparative investigation of the N American and Eurasian taxa is needed before any hypothesis in response to these questions can be brought forward.

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EVOLUTIONARY TRENDS AMONG PLANTS IN THE BALTIC LAND UPLIFT AREA

B. Jonsell

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The Baltic area combines in a unique way a number of abiotic factors of great importance to its vegetation: brackish water, non-tidal water level shifts, isostatic land uplift in largely flat coastal areas. Owing to varying geological conditions and the existence of extensive archipelagos the habitat diversity is very great. A permanent, natural pioneer situation prevails, supposed to be evolutionarily dynamic. This is thought to be reflected by for Nordic conditions a considerable number of endemic taxa recognized among Baltic plants, few, however, on the species level. At most 12,000 years have been available for evolution within the area. The differentiation observed in some Baltic coastal plants is discussed in relation to life-forms, reproductive systems, habitat diversity and immigration routes.

Keywords: Baltic land uplift area, Ecology, Endemism, Evolution.

Bengt Jonsell, Bergius Foundation, Royal Swedish Academy of Sciences, Box 50017, S-104 05 Stockholm, Sweden.

INTRODUCTION: HISTORY OF THE BALTIC COASTLAND

In the Baltic area, with about 12,000 years available for plant life along some parts of its shores after the last glaciation, a number of historical and recent abiotic factors combine to form unique environmental conditions. During this period the Baltic has undergone a few shifts between freshwater and saline stages, and only about 3,000 years ago conditions very similar to the present ones were established. The Baltic stage immediately preceding the present one, the Littorina Sea, was considerably more saline and warmer. We do not know anything about the littoral flora of that time but it may be presumed to have been similar perhaps to the south coasts of the North Sea today. An important share of north-eastern flora elements may have been present owing to the connections with the White Sea area. Although the geographical structure and temporal coherence of such a connection has been debated and reconsidered in later years (Hyvärinen & Eronen 1979), the recurring distributional patterns indicate for a number of littoral and aquatic Baltic plants an immigration via a north-eastern route (cf. below on *Deschampsia bottnica*).

The isostatic land uplift of most of the Baltic coasts (Fig. 1) is high, above 60 cm in a century (Fig. 1, Åse 1982) in areas where the country is largely very flat, which means that coast displacement, i.e. the gain of new land over time, has been and is considerable. However, not even this process has progressed unidirectionally, but

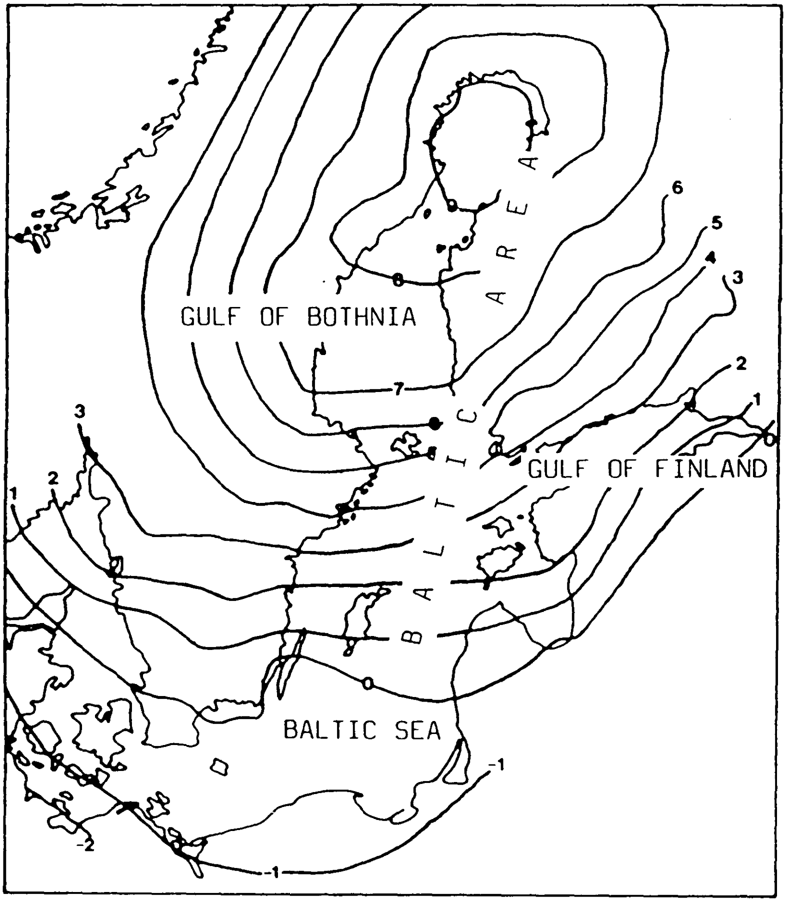
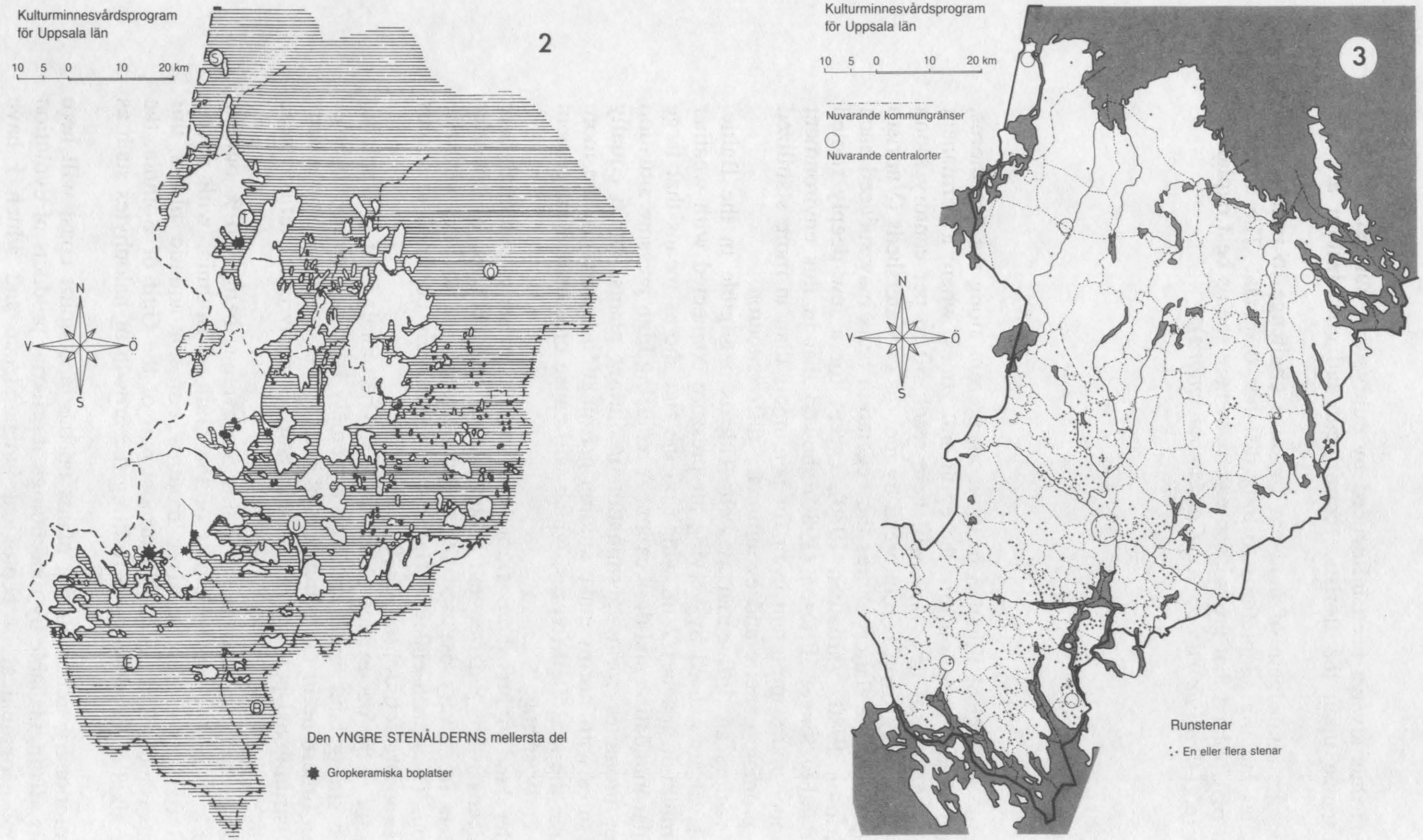


Fig 1. Isopleths of the present-day land uplift in the Baltic area in mm/year. The values are relative, i.e. not corrected for the eustatic rise in sea-level (ca 1 mm/year). From Ericson & Wallentinus (1979).

transgressions connected with the shifts of stages in the Baltic and the eustatic changes of ocean level, at present counteracting land uplift by ca 10 cm per century, have meant standstills and reversions.

When the present brackish and cool conditions of the Baltic were established the region was already largely in the neolithic period, the early phase of agriculture. This means that the present coastlands of the NW Baltic Sea and the Gulf of Bothnia were influenced by human cultivation from their first emergence out of the sea, e.g. the whole province of Uppland, the cradle of the realm of the Suions (Figs 2-3, Bygd att vårda 1984). This would mean constant maintenance of meadows and open woodland along much of the perpetually moving coast, which successively turned into more or less extensively utilized forests inland. The bays and sounds isolated from the sea finally became meadows and mires, which may have been mowed from the start. Smaller areas were converted to



Figs 2-3. Two maps of Uppsala county, E Central Sweden (land is white, sea dark). Fig. 2. Middle neolithic age, ca 4,500 - 4,000 B.P., with coastline ca 40 m above the present level; the stars are known neolithic settlements; the U in a ring the location of present day Uppsala. Fig. 3. Present conditions; parish borders are included; the central ring is Uppsala; the dots are runestones (from ca 1000 B.P.). From Bygd att vårda (1984).

farmland. The coastland has thus always been influenced by cultivation, but details about the impact of this circumstance upon the floristic recruitment and colonization are not known.

It seems obvious that the quick gain of land has meant a challenge to immigration for a number of plant species lacking adaptations to long distance dispersal. The absence of some species from most of Uppland that are widespread elsewhere seems best explained by incomplete distribution (e.g. *Trollius europaeus*, *Cardamine amara*).

ECOLOGICAL FEATURES

In these coastlands a dynamic ecological situation is above all present along the flat shores, from the lower hydrolittoral to the transition into the epilittoral zones, where a permanent pioneer situation prevails. The gain of new land will here reach 50 m per century along a transect or even more where land growth is reinforced by mouths of watersheds (Vuoristo & Rousi 1976, Ericson 1980). On the flattest shores the vegetation belts may succeed each other within a decade (Ericson 1980, Vartiainen 1980), except for a few deeply rooted species that endure considerably longer. Ericson (1980) showed that in this environment reproduction by seeds is much more important even for perennials than in more stabilized ecosystems, which would promote genetic and evolutionary differentiation.

A number of other factors are influential as well. Tide is negligible in the Baltic. Large shifts in the water level are caused by varying air pressure connected with weather conditions. The vertical amplitude reaches 2 m, which on the flat shores means that large areas are subjected to regular inundation and desiccation. A recurring high pressure situation in spring to early summer promotes spring germination in littoral plants, while equally regular autumnal low pressures with storms make autumn germination hazardous, the more so since at that high latitude the sea often freezes, which will cause erosional derangement throughout the winter till early spring.

The diversity of the land uplift shore flora and its evolutionary potentials are enhanced by the dissected coast-line and frequent occurrence of archipelagos, which offer a great variation of habitats from very exposed shores facing open sea to bays virtually protected from wave action. Thus each endemic Baltic taxon is largely confined to shores with a certain degree of exposure (cf. Jonsell 1988: Tab. 1).

Another variable factor is the occurrence of basic soils. The moraines of N Uppland, in the southern part of the strong land uplift area, are extremely base-rich owing to large deposits of cambro-silurian limestone in the south part of the Gulf of Bothnia. Northwards acid conditions prevail. Distributional patterns of coastal plants in many cases reflect these differences.

Salinity decreases from south to north in the Baltic, on average being 0.6 % outside Uppland and less than 0.1 % in the northern part of the Gulf of Bothnia, with strong seasonal fluctuations and deviations outside river mouths. For non-aquatic plants this gradient seems of less importance. Even in the innermost part of the Gulf of Bothnia, the shore meadows may have alkaline depressions permitting the growth of halophytes such as *Salicornia*.

A discussion of evolutionary trends among plants on the land uplift coast will here focus on the visible (that is, distinguishable by morphological criteria) products of evolution which have attained some geographical or ecological independence and which I have previously designed as microendemics (Jonsell 1988). Only a few will be mentioned here as examples. Most known cases were enumerated by Jonsell (1988: Tab. 2). There is almost a total lack of knowledge about chromosomal and allozymic differentiation.

EVOLUTIONARY TRENDS AMONG PLANTS

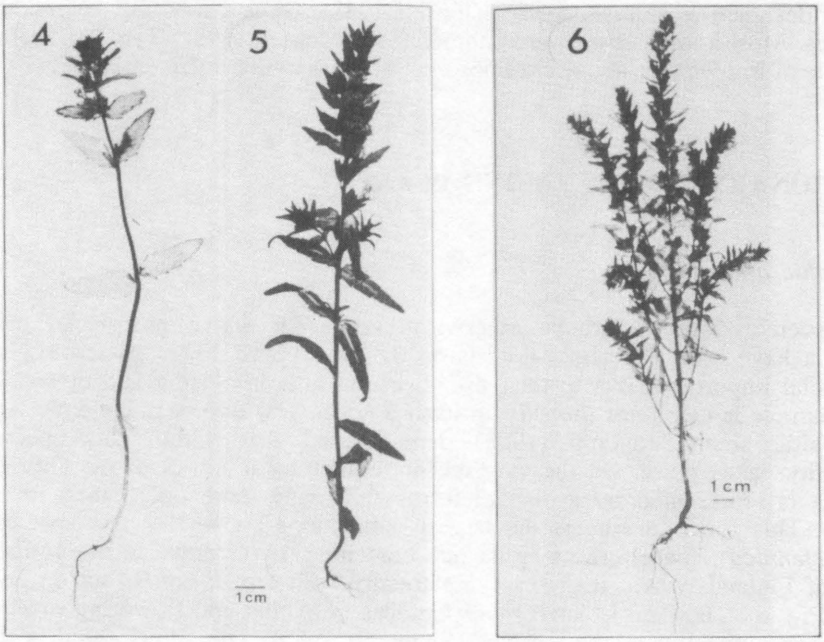
Heterotrophic annuals

Not unexpectedly species groups otherwise known for active postglacial evolution in Scandinavia have been efficient colonists on the land uplift shores. Heterotrophic annuals are of special importance due to their establishment also in closing and closed vegetation. A good example is *Odontites litoralis*, in itself a north-west European endemic concentrated in the Baltic area. Snogerup (1983) demonstrated that within this species further differentiation takes place. On the very recent southernmost shores of the Gulf of Bothnia *O. litoralis* is represented by a distinct form with many more nodes than in other areas (Figs 4-6). This form constitutes the largest populations known for this species. Another form (ssp. *fennica*), characterized by its rich branching, is restricted to the northern side of the Gulf of Finland, where it grows sympatrically with ssp. *litoralis*, but on another type of shore (Fig. 6). They are isolated by differences in habitat and flowering time, reinforced by the strong autogamy of this species (Snogerup 1983). The Rhinanthoideae offer more examples, within *Euphrasia*, *Rhinanthus*, and possibly *Pedicularis*.

The heterotrophics also include *Gentianella*, a genus in which quick differentiation into ecotypes adapted to land use is well documented (cf. Karlsson 1974). In addition forms adapted to particular natural conditions have evolved. One of the most distinct in the Nordic flora is the so-called *G. uliginosa* of Baltic land uplift shores, which belongs to *G. amarella* s.lat. It is peculiar in its spring germination followed by very slow development, which makes it the last plant to start anthesis on these shores, usually not before mid-August. Effective, regular seed production, which is vital for such a plant, is probably dependent on the mild autumnal climate actually on the shores, much more rarely affected by early frosts than places only short distances inland. It grows in moderately exposed shore meadows and is basiphilous, which in addition to its need for a fairly long growth period confines it to the southernmost parts of the land uplift area. It seems to be maintained by ecological and seasonal isolation. Statements that *G. uliginosa* differs as to ploidy level from *G. amarella* s.str. seem, however, to be incorrect for the Baltic shore population (T. Lennartsson, unpubl.). The N German plant originally described as *G. uliginosa* most probably belongs to a taxon different from the one discussed here.

Outbreeding perennials

Among perennials *Dactylorhiza incarnata*, a richly differentiated and probably actively evolving species provides one example. Within a small area on the southern, calcareous coast of the Gulf of Bothnia the species is represented by different forms in three habitats close to but clearly demarcated from each other: slightly exposed sea-meadows, forest fens, and open calcareous fens. All three habitats have a patchy distribution in the area and each locality is small, rarely more than 100 m across. The nearest locality, of any kind, is usually within 1 km, and the non-shore localities not more than ca 5 m above sea level.



Figs 4-6. Habit of three forms of *Odontites litoralis*. Fig. 4. Ssp. *litoralis* from SE Sweden (Blekinge, V. Skällön, B. Snogerup 158, LD). Fig. 5. Ssp. *litoralis* from the south coast of the Gulf of Bothnia (Uppland, Hållnäs, B. Jonsell 5216, LD, UPS). Fig. 6. Ssp. *fennica* from NE Gulf of Finland (Karelia australis, Siikasaari, B. Snogerup 71, LD). From Snogerup (1983).

This means that none of the present fens left the sea shore stage earlier than ca. 1,000 years ago, and for a much shorter period the present ecological conditions have prevailed. The sea-shore form, in some respects approaching ssp. *cruenta*, is endemic to the southern Gulf of Bothnia, while the others have counterparts elsewhere. In spite of quick succession of habitats and the prevailing outcrossing, the differentiation is maintained. The populations of the calcareous fens are, however, intermediate and more variable, which may reflect genetic influence from the population present at the earlier sea shore stage (Jonsell 1982).

Among a number of other perennial herbs with obvious differentiation related to the land uplift shores is the obligate outbreeder *Galium palustre* s. str., the diploid taxon (cf. Apelgren 1987). On brackish marshes along much of the Swedish east coast a form easily distinguishable from populations in the adjacent inland grows abundantly. The brackish form may be found up to about 5 m above sea level, but then only in man-made habitats. These occurrences may be interpreted as relictual in line with a number of other taxa, but dispersal from sea shores to suitable localities off the coast may of course occur; the distance from sea rarely exceeds 10 km (Apelgren & Lernstål 1990).

A nice case of the intensity with which selectional forces are able to operate in a rising Baltic archipelago was put forward by Vilkki (in Rousi et al. 1986) for *Allium schoenoprasum*. In spite of being an outbreeder and producing abundant seeds and bulbils, populations along a 100 km gradient across the S Finnish archipelago from the outermost,

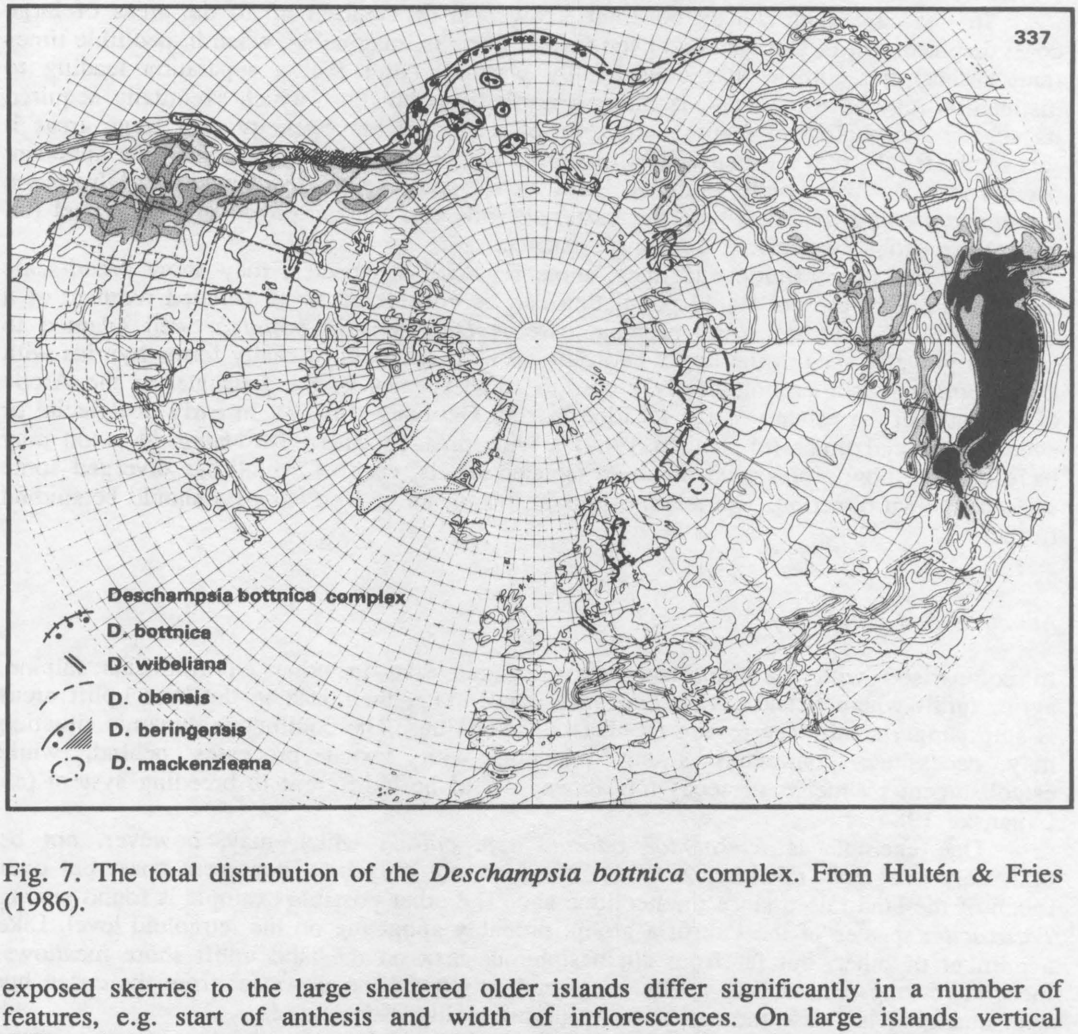


Fig. 7. The total distribution of the *Deschampsia bottnica* complex. From Hultén & Fries (1986).

exposed skerries to the large sheltered older islands differ significantly in a number of features, e.g. start of anthesis and width of inflorescences. On large islands vertical differentiation seems to take place, with the shore populations there agreeing more with those of the outer, youngest skerries. The three last mentioned examples indicate prevention of gene flow between distant terrestrial habitats but effective dispersal across the brackish water.

While the examples cited seem to reflect differentiation within a widespread species in which isolation along ecological lines has built up, other cases may rather be explained from previous distribution patterns. I will give two examples.

Along the south coasts of the Gulf of Bothnia a form of *Mentha aquatica*, most often called var. *litoralis*, grows abundantly on little exposed shores. It differs from the main Swedish population of *M. aquatica* in being glabrous except at the nodes and in some other features. *M. aquatica* has its northern limit about 200 km S of the rich occurrences of var. *litoralis* and grows in base-rich fens and shores of lakes and streams. Between the two areas, along the coast of the Baltic Sea, small scattered populations occur, which are not distinct var. *litoralis* and often have hybrid influence from *M. arvensis*.

In this case a previously coherent S Swedish distribution up to the areas of large coast displacement in Uppland and even further north is imaginable, when in neolithic times (and earlier) the climate was considerably warmer. After that a separation leading to disjunction may have occurred, isolating a northerly population, which eventually acquired its special morphological features. In spite of its clonal homogeneity over large areas it sets seeds. It falls into a group of late flowering southern species with isolated but abundant occurrences on the South Bothnian land uplift coast (e.g. *Brachypodium sylvaticum*, *Eupatorium cannabinum*), where the base-rich soils and the prolonged growth period (cf. above) are probably decisive for their existence.

The "stronger" Baltic endemics, some regarded as species, may show broad-scale disjunctions. The present Baltic population can be considered as an isolated remnant of a once more coherent taxon. A possible case is *Deschampsia bottnica*, well adapted to exposed gravelly sites in the upper hydrolittoral belt. Although it easily forms hybrids with *D. cespitosa* it is morphologically closer to some species in the Beringia, at the Arctic Ocean, and in the estuary of the R. Elbe in NW Germany (Fig. 7). In early postglacial or even interglacial times (cf. Hultén 1964) a widespread northern *Deschampsia* taxon may have existed, now represented by these isolated relicts, each of which has diverged some way in its own direction. The relationships in this group of *Deschampsia* should be studied further.

Apomixis and polyploidy

In comparison with the importance of apogamic taxa in other environments (alpine, agricultural) where Scandinavian endemics concentrate, their role in the land uplift areas is surprisingly small. The reason for that is not obvious. The continuous dynamic situation may necessitate continuous strong selection with sexual processes behind, while establishment by means of seeds (cf. above) would be indifferent to breeding system (cf. Urbanska 1984).

One example is *Hierochloë odorata* ssp. *baltica* which may, however, not be obligately apogamic (Weimarck 1971). It occurs not only on the present coast but over much of the land raised since the neolithic age. The other possible example is found among *Taraxacum* species of the Palustria group, probably apogamic on the tetraploid level. Like a number of other, but far from all, basiphilous taxa on the land uplift shore meadows, these have long remained as relicts on grazed or mowed meadows far from the coast, but with changing land use these sites have almost totally disappeared.

An interesting case connected with altitudinal levels in the land uplift area is the distribution of cytotypes within *Parnassia palustris* (Hultgård 1987). On the east Swedish mainland the diploid cytotype does not descend below ca 20 m a.s.l., i.e. to land appearing after ca 4,000 years B.P. Below that level, and particularly on the coast, only the tetraploid cytotype occurs. The latter might at about that time have invaded the sea-shores of those days from the north, or it may be autochtonous in the dynamic area, a result of successful autoploidization.

Final remarks

The land uplift situation is not only influential on the structure of plant populations at the actual coast-line. The conditions for relictual populations, mainly dependent on human activities, were briefly noted above. Quite natural situations occur as well. In the calcareous areas south of the Gulf of Bothnia the richest fens are found at 5 - 7 m a.s.l., i.e. places which left the sea-shore stage about 1,000 years ago. This amount of time seems to be needed for their optimal development; with increasing age and elevation leaching and other deteriorating processes set in (Ingmar & Moreborg 1976). Some species are confined to these very base-rich fens and have to migrate with coast displacement to survive in their rather narrow zone. One of them is *Dactylorhiza traunsteineri*, the variation of which is now compared with populations in less dynamic places.

The Baltic has lately been put into focus as an area of high significance in evolutionary studies, in particular as concerns marine organisms as seaweeds (Russel & Thomas 1988). The examples pointed out here show that the land uplift shores especially, but also the recently formed inland, offer a number of cases worthy of analyses against the background they have in common, the limited postglacial period for their differentation.

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CYTOLOGY AND REPRODUCTION IN ARCTIC *COCHLEARIA*

I. Nordal & M.M. Laane

Nordal, I. & Laane, M.M. 1990. Cytology and reproduction in Arctic Cochlearia. - Sommerfeltia 11: 147-158. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

Plants from N Norway (Finnmark), Svalbard and Iceland are compared. Finnmark houses 4 ecotypes, all with 2n = 24, which are referred to three different subspecies of *C. officinalis* L. All are self-incompatible. Svalbard houses 2 ecotypes ("beach" and "bird cliff"), all with 2n = 14. They are fully self-compatible. The flowers of the Svalbard material, which will be referred to *C. groenlandica* L., are significantly smaller than in the Finnmark material. Iceland houses two ecotypes: "beach cliff" and "alpine". "Beach cliff" is cytologically heterogeneous: 2n = 12 in a part of the south coast, and 2n = 14 elsewhere. "Alpine" has 2n = 14. The Icelandic populations tested are, with few exceptions, autogamous. They are referred to *C. groenlandica*.

Keywords: Arctic, *Cochlearia*, Cytology, Ecology, Reproduction, Taxonomy.

Inger Nordal, Botanical Garden and Museum, University of Oslo, Trondheimsveien 23B, N-0562, Oslo 5, Norway.

Morten M. Laane, Biological Institute, Dept. of Botany, University of Oslo, P.O. Box 1045, N-0316 Oslo 3, Norway.

INTRODUCTION

The title of this symposium is "Evolution in higher plants: Patterns and processes". We will in this study present some preliminary results on the variation *patterns* in cytology, morphology, and reproduction in Arctic representatives of the genus *Cochlearia*. We will touch on the *processes* by including some hypotheses on evolution based on the observed patterns.

The genus *Cochlearia* is widely distributed from the temperate to the Arctic/Alpine regions of the northern hemisphere with one centre of variation in Europe and another in the Himalayan region. The section *Cochlearia* is circumpolar, but centred in Europe. It consists of 5 to 10 species, depending on the species concept. The section displays a large amount of cytological variation with the following haploid numbers represented: n = 6, 7, 12, 13, 18, 21, 24.

This study is part of a joint project at the University of Oslo aimed at a better understanding of the evolutionary and ecological relationships in this complex section (cf. Nordal et al. 1986, Nordal 1988, Eriksen & Nordal 1989). In a recent paper (Nordal & Stabbetorp 1990) it is concluded that the ecotypic differentiation in N Scandinavia should be classified into 3 subspecies. It is shown that all of them have n = 12, and that they are self-incompatible. We will here, in addition to presenting corresponding data from the neighbouring Arctic islands, also compare the two data sets and thus hopefully be able to answer the question of how to delimit the high Arctic *C. groenlandica* L. from the N European *C. officinalis* L.

For the cytological comparisons we have based our discussion on our own new results, complemented with information from Matsuura & Sutô (1935), Böcher (1938), Böcher & Larsen (1950), Holmen (1952), Saunte (1955), Lövkvist (1963), Gill (1965, 1971, 1973), Mosquin & Hayley (1966), Rollins (1966), Löve & Solbrig (1965), Hedberg (1966), Löve & Ritchie (1966), Laane (1967), Zhukova (1967), Johnson & Packer (1968), Engelskjøn & Schweitzer (1970), Löve (1975), Löve & Löve (1975), Fearn (1977), Berkutenko & Gurzenkov (1978), Gill et al. (1978), Elkington (1984), Vogt (1985), Nordal et al. (1986), and Pegtel (pers. comm.).

The comparative morphology is largely based on data obtained by growing the plants under similar controlled conditions. When N Scandinavian material is referred to, the data are taken from populations presented in Tab. 1 in Nordal & Stabbetorp (1990). We have been reluctant to include morphological data from other sources, as we know that *Cochlearia* plants are easily modified when exposed to different environments.

MATERIALS AND METHODS

Cultivation

We have included living material from Iceland and Svalbard; the populations studied are listed in Tab. 1. Seeds were collected in the field and sown in standard soils in the phytotrone of the University of Oslo: 16 hours day at 18 °C and 8 hours night at 8 °C. The first year's leaf rosettes were allowed to develop for 6 months before the plants were moved to simulated winter conditions: darkness at slightly above 0 °C. After 3 months the

Tab. 1. Populations of *Cochlearia groenlandica* L. included in the analysis. n - haploid chromosome number.

Locality	Site	Seed coll.	Voucher	n
Iceland: Skaftafellssysla: Ingolfshöfdi	beach cliff	I. Nordal	IN 1804	6
Iceland: Hnuta, S of Djupivogur	beach cliff	I. Nordal	IN 1805	6
Iceland: Hnefill N of Eiriksstadir	Arctic tundra	I. Nordal	IN 1806	7
Iceland: Blönduos	beach cliff	I. Nordal	IN 1808	7
Svalbard: Isfjorden, Grumantbyen	bird cliff	H.P. Leinaas	IN 1383	7
Svalbard: Sassenfjorden, Gipsvika	Arctic tundra	C. Brochmann	IN 1385	7
Svalbard: Nordenskjöldland, Reindalspasset	Arctic tundra	R. Elven	IN 1390	7
Svalbard: Sassen, Fjordnibba	bird cliff	R. Elven	IN 1391	7

plants were brought back to the original conditions, and flowering buds appeared after a few days.

Cytology

The flower buds were fixed in acetic-ethanol (1 part glacial acetic acid and 3 parts absolute ethanol) for about 30 minutes at room temperature. After fixation the fluid was replaced by 70% ethanol, and the specimens were kept at -20 °C awaiting further preparation. The anthers were dissected out from the buds (five plants per population) in a drop of 45% acetic acid on a slide. A drop of aceto-orcein was added, and the slide was heated gently until the anthers burst, and the pollen mother cells swelled. After squashing, the chromosomes were drawn with the aid of a camera lucida. The preparations were made permanent in Euparal (see Laane (1970: 82-87) for details).

Morphology

After 6 months of growth the following characters were scored on 5 leaves per rosette: (1) the length from the point of petiole attachment to leaf apex, (2) the largest leaf width, and (3) the "leaf angle" defined as the angle between the tangents of the leaf margins at the point of petiole attachment.

Reproduction

Two branches of the inflorescences of all the plants were bagged to prevent foreign pollen from entering. One of the branches was left to itself without any manipulation, 10 flowers on the other were actively hand-pollinated with their own pollen. The seed set was recorded.

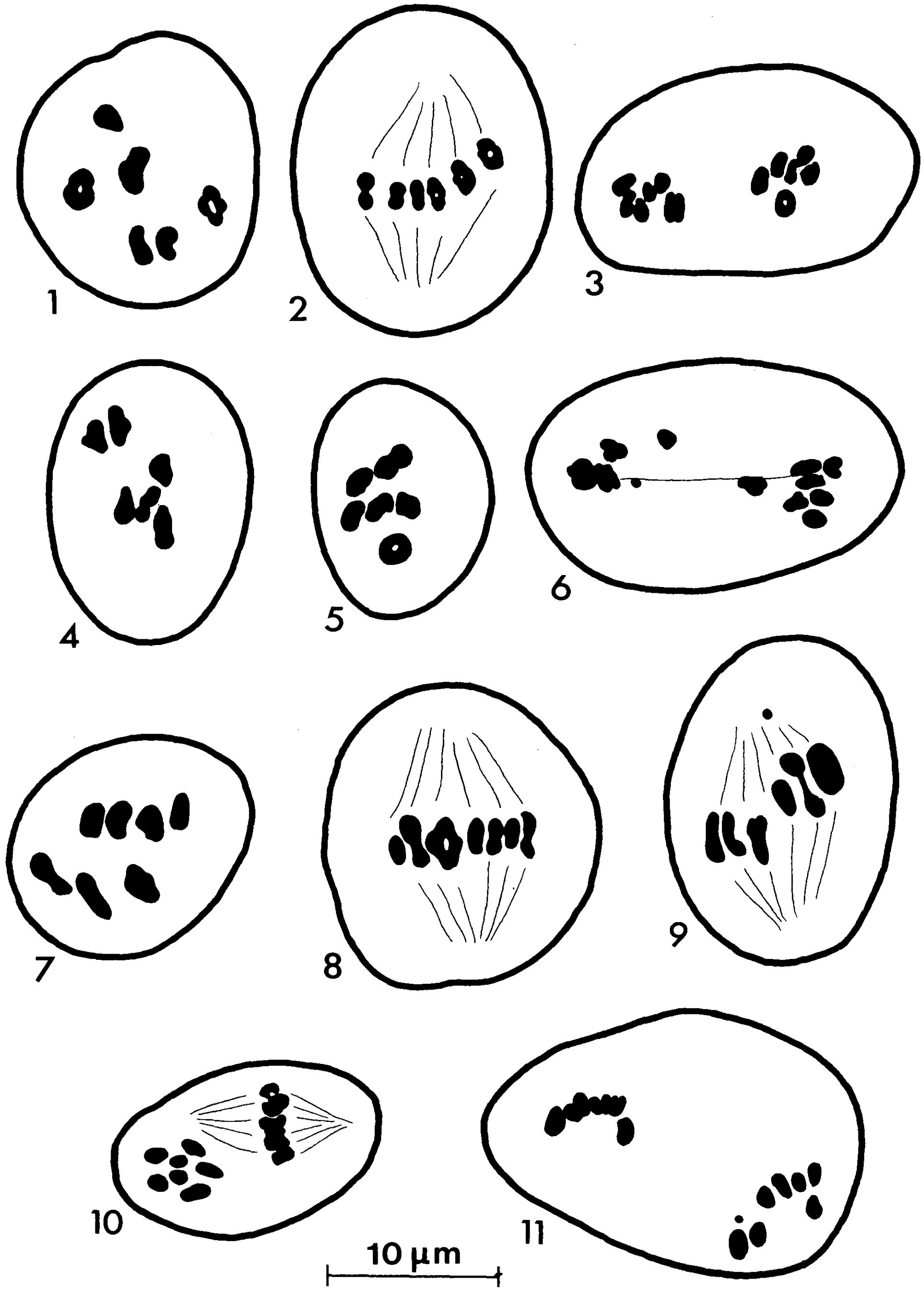
RESULTS

Cytology

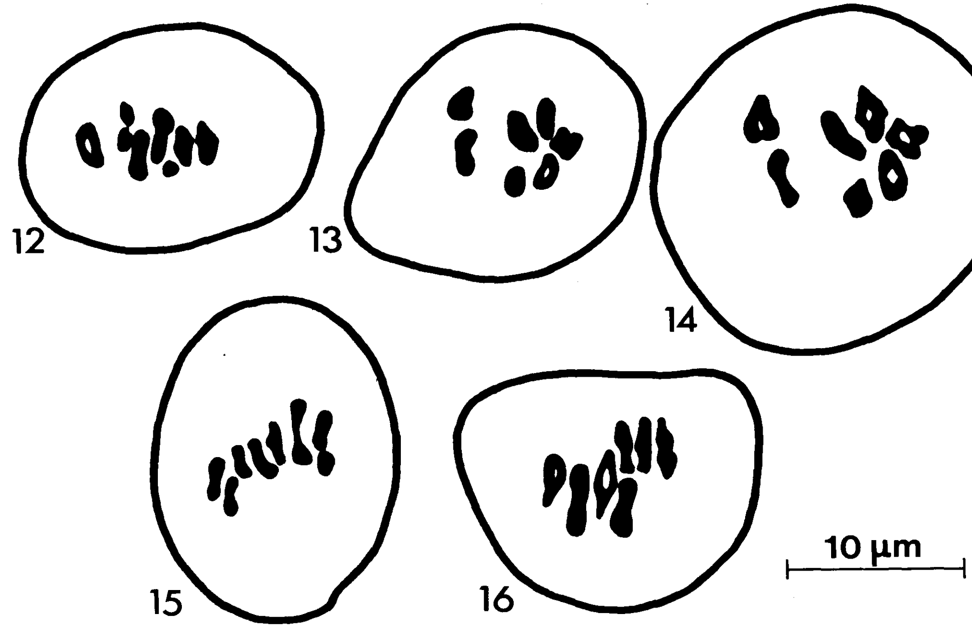
The chromosome numbers are presented in Tab. 1. The two examined beach cliff populations from the south coast of Iceland (IN 1804, 1805) both had n = 6. Both showed regular pairing into 6 bivalents (in about 95 % of the cells). Most of the bivalents formed rings with terminal chiasmata (Figs 1-6). In about 5 % of the cells two lagging chromosomes were seen. Quadrivalents were not observed, neither were B-chromosomes. In IN 1805, 0.5 % of the cells showed a paracentric inversion bridge in A I (Fig. 6).

The Arctic tundra population (IN 1806) and the north coast beach cliff population (IN 1808) both had n = 7 (Figs 7-11), sometimes with one small accessory chromosome present. Again M I showed regular formation of bivalents, quadrivalents were not found. Most bivalents formed two chiasmata, some only one.

The five Svalbard populations examined spanned a range in ecological conditions from rather nutrient-poor Arctic tundra to bird cliffs rich in nutrients. All showed n = 7



Figs 1-11. Meiotic divisions in pollen mother cells in *Cochlearia groenlandica* from Iceland. Population numbers according to Tab. 1. Figs 1-3. IN 1804, n = 6. Figs 4-6. IN 1805, n = 6. Figs 7-9. IN 1806, n = 7. Figs 10-11. IN 1808, n = 7.



Figs 12-16. Meiotic divisions in pollen mother cells in *Cochlearia groenlandica* from Svalbard. Population numbers according to Tab. 1. Figs 12-14. IN 1383, n = 7. Figs 15-16. IN 1391, n = 7.

(Tab. 1, Figs 12-16). Again the bivalent formation was regular, and quadrivalents were never observed. Most bivalents showed two chiasmata, some only one. The bivalents separated synchronously, except for about 5 % of the cells. One accessory chromosome was found in IN 1383, none in the others. In IN 1383 1-2 paracentric inversion bridges were observed in A I cells.

The total distribution of the three cytotypes found in N Scandinavia, including the Arctic islands, is shown in Fig. 3.

Morphology

The Icelandic material was distinctly differentiated morphologically. In the natural habitats there was a considerable difference between the small, prostrate, alpine plants with small lanceolate rosette leaves, and the luxuriant beach cliff plants with large, cordate leaves. The difference in plant size was less pronounced in the cultivation experiment. The differences in leaf shape and size were, however, retained (cf. Fig. 18). The morphological differentiation did not follow the observed cytological polymorphism. There was no difference between the n = 6 and n = 7 beach cliff plants, and the n = 7 cytotype was divided into two different morphological forms.

The genetical differentiation of the Svalbard populations was parallel to the Icelandic ones, but apparently more clinal than on Iceland. When the Svalbard material was added

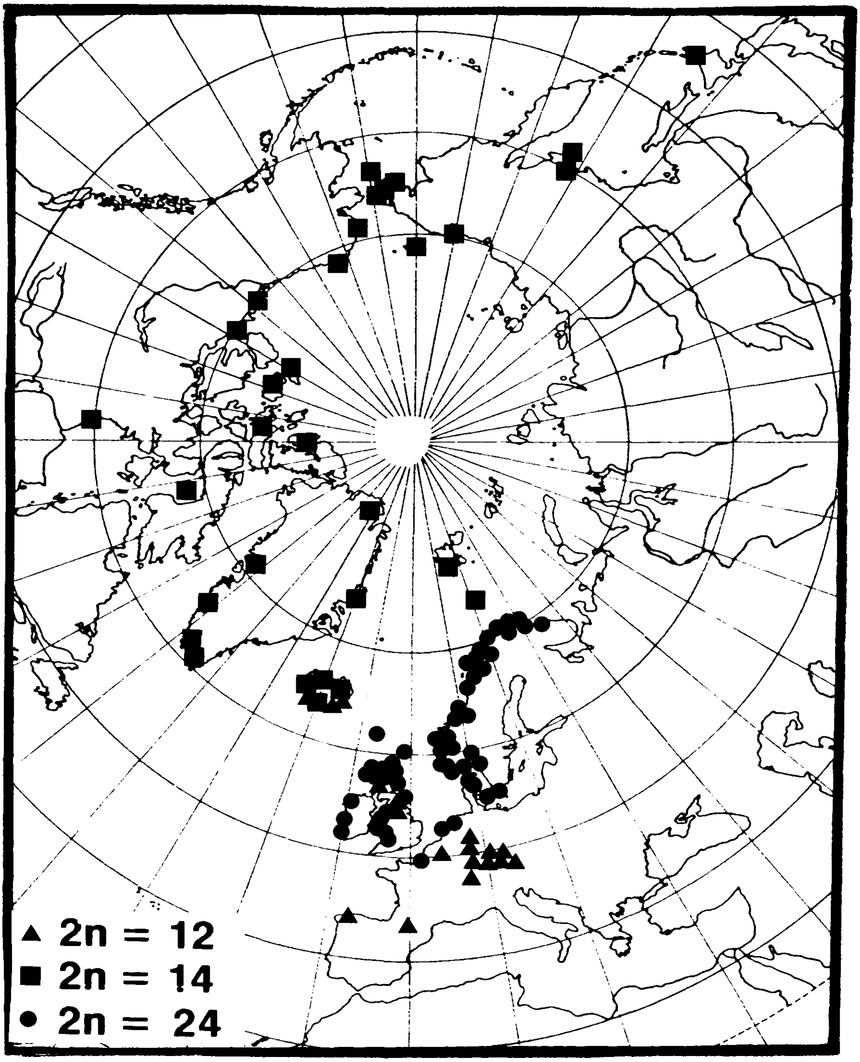


Fig. 17. Global distribution of the three cytotypes 2n = 12, 2n = 14 and 2n = 24 in the sect. *Cochlearia*.

to Fig. 18, the Icelandic discontinuities were "swamped".

There were no differences in leaf characters separating the N Scandinavian populations from those of the Arctic islands. Observations of flower and fruit morphology in the studied populations are at the moment only available from field data. Experience from N Scandinavian material of *C. officinalis* has shown features of the flowers and the fruits to be less liable to phenotypical modification than the leaf characters. In this study we have used the information on flowers and fruits for comparison with populations from

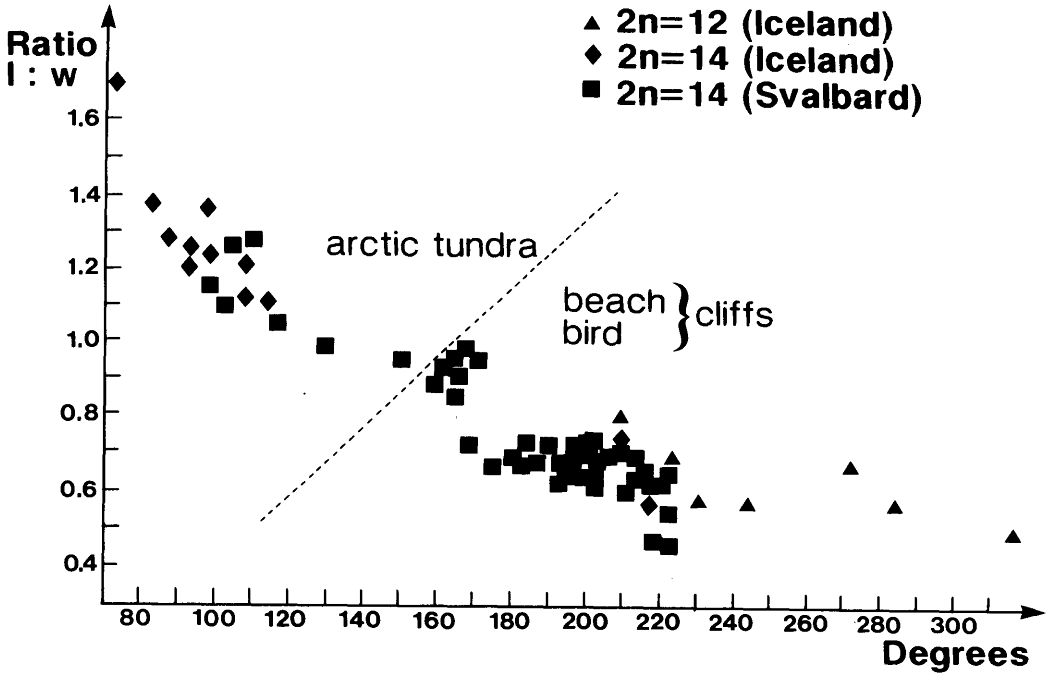


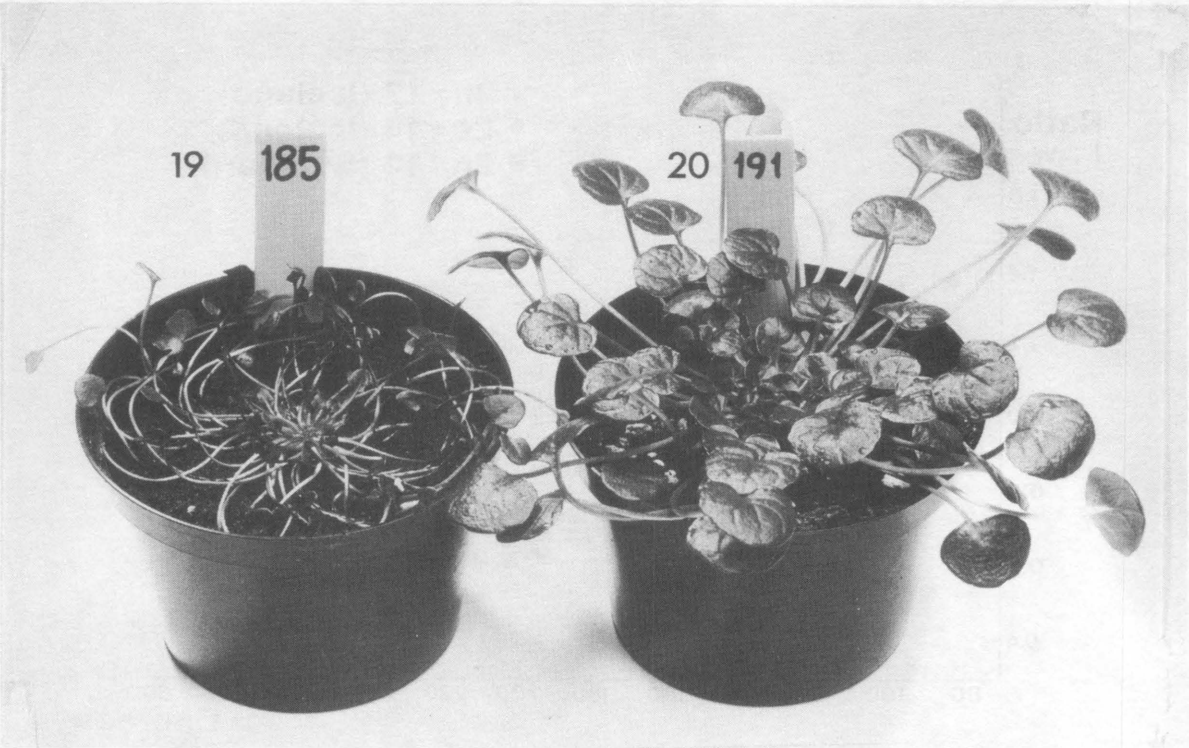
Fig. 18. Scatter plot showing the relation between leaf angle and the length : width ratio of the rosette leaves. The leaf angle is defined as the angle between the tangents of the leaf margins at the point of petiole attachment. The Iceland populations show discontinuous ecotypic variation whereas the Svalbard populations show clinal variation filling in the discontinuity on Iceland.

the Scandinavian mainland and the neighbouring Arctic islands. The two characters giving the best differentiation were petal length and seed size (Figs 21-24). The differences were highly significant, but there was a clear overlap between taxa.

A pilot project for comparison of pollen sizes was undertaken. No significant differences between the cytotypes 2n = 12, 2n = 14, and 2n = 24 were found.

Reproduction

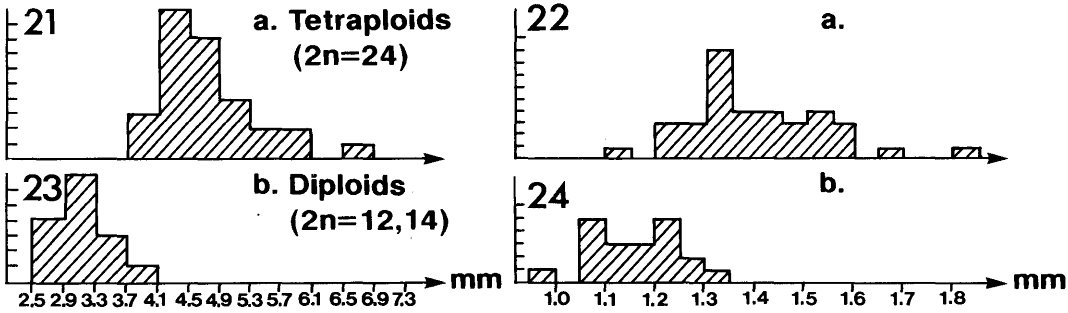
The results from the pollination experiments are given in Tab. 2: the Svalbard populations were all completely autogamous. The seed set was the same whether plants were left to themselves or actively self-pollinated. The Icelandic populations were all self-compatible, but in two of the beach cliff populations (IN 1805, 1808) the seed set was much better when the flowers were actively self-pollinated. The alpine population (IN 1806) behaved as the Svalbard plants. Not surprisingly, there seemed to be a correlaton between flower scent and the need for an active pollinator. All the N Scandinavian populations examined (cf. Nordal & Stabbetorp 1990: Tab. 1) did, as mentioned, turn out to be self-incompatible. Their flowers were also heavily scented.



Figs 19-20. Representatives of the extreme forms of *Cochlearia groenlandica* from Svalbard. Fig 19. IN 1385 from Arctic tundra. Fig. 20. IN 1391 from bird cliff. Both are grown under equal conditions in a phytotrone chamber for 3 months.

Tab. 2. Populations of *Cochlearia groenlandica* L. included in the analysis of reproduction. Population numbers as in Tab. 1.

Country	Voucher	No. of individuals	Percentage of fertile fruits without active selfing	Percentage of fertile fruits with active selfing	Scent
Iceland	IN 1804	3	100	100	-
Iceland	IN 1805	5	28	100	+
Iceland	IN 1806	5	100	100	(+)
Iceland	IN 1807	2	17	100	+
Svalbard	IN 1383	1	100	100	-
Svalbard	IN 1385	2	100	100	-
Svalbard	IN 1390	4	100	100	-
Svalbard	IN 1391	5	100	100	-



Figs 21-24. Histograms showing the variation in petal length (Figs 21-22) and seed length (Figs 23-24) of *Cochlearia officinalis* (2n = 24; Figs 21, 23) from N Scandinavia and *C. groenlandica* (2n = 12, 14; Figs 22, 24) from Iceland and Svalbard.

DISCUSSION

Taxonomy

It has been shown that the Arctic diploids are different from the more southern tetraploids in flower size and seed size. In addition the reproduction systems are different, mainly autogamy in the Arctic diploids and obligate outcrossing in the N Scandinavian tetraploids.

These differences might justify taxonomic delimitation at the level of species. *Cochlearia officinalis* L. will be the correct name for the tetraploid, whereas *C. groenlandica* L. is the oldest name for the Arctic diploids. In his protologue of *C. groenlandica* Linnaeus (1753) included plants from Norway, Iceland and Greenland. There is no type material available, and *C. groenlandica* should be neotypified by material from Iceland or Greenland to maintain the name for the Arctic diploid taxon. This will be done in a later paper. The Norwegian material referred to by Linnaeus (1753) belongs to *C. officinalis* L. ssp. *integrifolia* (Hartm.) Nordal & Stabbetorp.

The distinct ecotypic differentiation in Iceland might deserve subspecific recognition. Because of the intermediate status of the Svalbard plants we have, however, decided not to give the Arctic tundra and the beach cliff ecotypes formal taxonomic rank. The beach cliff ecotype consists of two cytotypes (n = 6, 7), which we are unable to separate by any morphological or biological characteristics. Thus no formal taxonomy will be proposed. The very close relationship between the n = 6 and n = 7 cytotypes in Iceland completely undermines the genus *Cochleariopsis* Löve & Löve (x = 7) differing from *Cochlearia* L. (x = 6) only by the basic chromosome number.

Cytology

The tetraploid (2n = 24) and the diploid (2n = 14) show complete geographical vicariance on a global scale (Fig. 17), whereas the diploid (2n = 12) slightly overlaps with 2n = 14 in Iceland and 2n = 24 in Britain. Gill (1971) wrote: "The count of 2n = 12 from Iceland is of interest, as all previous reports from the area have been 2n = 14, and the specimens have been referable to *C. groenlandica.* Unfortunately all the specimens of this 2n = 12 population died ... and cannot therefore be referred to any particular taxon." His cytological results are thus confirmed by our study. Since the two different diploids in Iceland have turned out to be morphologically indistinguisable, they will both have to be referred to *C. groenlandica.* The delimitation from the C to W European *C. pyrenaica* DC. (2n = 12) needs further study.

Evolutionary considerations

The detailed cytological analyses of Gill (1971, 1973) have nicely shown that the 2n = 12 cytotype is the primitive type, from which the 2n = 14 cytotype has evolved by primary tetrasomy, and the 2n = 24 cytotype by autotetraploidy. The distribution of the 2n = 12 *Cochlearia* spp. (like *C. pyrenaica*) clearly indicates that this taxon survived the Weichsel maximum south of the N European glacier. This original diploid has subsequently only to a slight extent managed to penetrate into the formerly glaciated areas.

The section *Cochlearia* had an advantage at the start of the ice retreat: the basal leaves are green in winter and even exhibit photosynthesis under snow cover. The plants are thus preadapted for living in periglacial areas.

The distribution of the 2n = 24 *Cochlearia* today is typical of one much affected by the glaciation (cf. Fig. 17). It is reasonable to believe that the autotetraploidization took place during, or at the end of, the last glaciation. The polyploidization created a potential for large genetic variation at a number of loci. The great number of new habitats made available by the retreating ice would have produced a selective regime in which increased variation would be of considerable advantage (cf. also Gill 1973). For *Cochlearia officinalis* (2n = 24) this implies that the ecotypical differentiation (recognized at the subspecific level by Nordal & Stabbetorp 1990) probably took place during postglacial times.

Also the tetrasomy will create potential for greater variation, at least in the genes located at the duplicated chromosome pair. Whether self-compatibility or incompatibility is the primitive condition in the section *Cochlearia,* we do not know. It is, however, clear that the 2n = 14 cytotype with its potential for autogamy and independence of external pollinators is better adapted to Arctic conditions than is the self-incompatible 2n = 24 cytotype. The 2n = 14 cytotype has accordingly obtained a circumpolar, high Arctic distribution.

Where and when the evolution of tetrasomy took place cannot be determined. Like the autotetraploid it has its origin in the 2n = 12 cytotype, and it is reasonable to believe that the event took place somewhere in W Europe. If the development of tetrasomy is an evolutionarily unique event, it has probably occurred within the beach cliff ecotype, as seen in Iceland today. When the tetrasomal diploids penetrated further into the Arctic areas, the more prostrate and small-leaved forms (cf. Figs 19-20) evolved. The wider distribution of the 2n = 14 *Cochlearia* spp. compared to those with 2n = 24 might indicate that tetrasomy evolved before tetraploidy. The close morphological connection between the two cytotypes (2n = 12, 14) within the beach cliff ecotype shows that the event after all might not be very ancient.

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MORPHOLOGICAL, PHENOLOGICAL AND BIOCHEMICAL DIFFERENTIATION IN RELATION TO GENE FLOW IN A POPULATION OF *SAXIFRAGA HIRCULUS*

J. M. Olesen & E. Warncke

Olesen, J.M. & Warncke, E. 1990. Morphological, phenological and biochemical differentiation in relation to gene flow in a population of Saxifraga hirculus. - Sommerfeltia 11: 159-173. Oslo. ISBN 82-7420-009-8. ISSN 0800-6865.

The number, size and position of genets in a Danish population of *Saxifraga hirculus* L. were estimated by 4 different approaches. The history of the population is discussed.

The spatial distribution of flowers was very clumped. Three to seven local peaks of flower abundance were found. Petal size varied both within and between populations. The study population consisted of about 11 subunits differing in petal size. Anthesis varied within the population and about 7 phenological subunits were found. Shoot tips were screened for enzymes. Based on variation in GPI-isoenzymes, 5-6 subunits were segregated. In a comparison of the different estimates, 10-17 genets or groups of even-aged genets could be distinguished. The most appropriate method in this species seems to be the study of variation in petal size. Intrapopulational spread of genes by seeds and runners is estimated to be of relatively minor importance compared to pollen-mediated dispersal. Seeds of *S. hirculus* are hypothesized to be or have been dispersed over long distances by large extant or extinct herbivores. Their disturbance of the vegetation is suspected of creating seedling recruitment sites for *S. hirculus*.

The study population may thus consist of a declining number of old genets left without most of their interacting large mammals.

Keywords: Denmark, Distribution, Gene flow, Isoenzymes, Morphology, Phenology, *Saxifraga hirculus*.

Jens Mogens Olesen & Esbern Warncke, Botanical Institute, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark. * - Present address: Department of Ecology and Genetics, University of Aarhus, Ny Munkegade, Building 550, DK-8000 Aarhus C, Denmark.*

INTRODUCTION

Over the past three decades, intrapopulational variation, differentiation and neighbourhood size have received tremendous attention (Schaal 1975, Schaal & Levin 1978). Studies of such variation may involve morphological and biochemical comparisons between different parts of populations. The amount of variation may be a reliable measure of the danger of extinction in rare species (e.g. Prentice 1984).

This paper is a comparative phenological, morphological and electrophoretic study of the number, extent and position of clones or genets (sensu Kays & Harper 1974) in a population of *Saxifraga hirculus* L. in Denmark.

Saxifraga hirculus is a long-lived herbaceous perennial with predominantly clonal growth. Sexual reproduction apparently occurs only after disturbance (Ohlson 1986, 1989a, 1989b, Olesen & Warncke, unpubl.). The species is Arctic-Alpine with a wide circumpolar distribution (Hultén 1971, Hultén & Fries 1986). It occurs in several types of habitats (Ohlson 1987). Within its distributional area *S. hirculus* displays great variation in many traits, e.g. size of petals (Engler & Irmscher 1916). In C and W Europe it is extremely rare, occurring only in small isolated populations. Swedish populations have been studied by Ohlson (1986, 1987, 1988, 1989a, 1989b), and Danish populations by Olesen & Warncke (1987, 1989a, 1989b, 1989c). In Denmark the species is confined to a few spring areas rich in electrolytes. These areas are spatio-temporally highly stable (Warncke 1980). The species is regarded as a postglacial relict (Warming 1895).

MATERIALS

Study sites

Studies were conducted at Rosborg Sø, a bog and helorheocrene spring area surrounded by heathland, situated in an extensive military area, Finderup Øvelsesterræn, Viborg, Denmark (56°25' N, 9°13' E). Field work was carried out June-November 1984 and September-November 1985. No knowledge of the history of this population is available. The general biology of Danish spring areas is described in detail by Warncke (1980) and of Rosborg Sø in particular by Olesen (1988) and Olesen & Warncke (1989a, 1989b, 1989c).

Two small adjacent springs (a southern and a northern one), 900 m^2 each in size, contained *S. hirculus*. The northern one (c. 30 x 30 m) possessed the majority of the flowering shoots, and was treated in this study.

The spring contained several, simultaneously flowering, entomophilous species; e.g., *Cirsium palustre* (L.) Scop., *Epilobium palustre* L., *Euphrasia officinalis* L. coll., *Galium uliginosum* L., *Geum rivale* L., *Lotus uliginosus* Schkuhr, *Lychnis flos-cuculi* L., *Ranunculus acris* L., and *Valeriana sambucifolia* Mikan fil.

In addition, observations were made and petals collected from: (1) the neighbouring southern spring area, July 1984, 0.1 km away from the study population: 28 petals; (2) Vinkel, Denmark (56°26' N, 9°29' E), August 1985, 17 km E of Rosborg Sø: 23 petals; and (3) Col du Marchairuz, Switzerland (46°33' N, 6°44' E), alt. 1400 m, July 1988-1989, about 1000 km S of Rosborg Sø: 53 petals collected. The Swiss population may well be one of the most south-westerly populations of the species in Europe.

The Rosborg population and its flower visitors

During the flowering season, the populational area of flowering shoots of *S. hirculus* reaches a maximum of 134 m^2, the population having an overall density of flowers/m^2 of 11.4 (Olesen & Warncke 1989c).

The flower is mainly visited by *Eurimyia lineata* (Diptera, Syrphidae); to a lesser extent by another syrphid *Neoascia tenur*, a moth *Zygaena trifolii* (Lepidoptera, Zygaenidae), and by a fungus gnat *Asindulum nigrum* (Diptera, Mycetophilidae) (Olesen & Warncke 1989a).

The distribution of interfloral flight distances of the flower visitors is leptokurtic and the mean flight distance is 85 ± 283 cm (± indicates standard deviation of observations). 10 % of the flights are between flower patches and across the entire population, i.e. they are 2 to c. 20 m long. If these flights are excluded from the analysis, the mean flight length is only 28 ± 28 cm. These within-flower patch flights become shorter with increasing flower density. The visitors do not have a nearest-neighbour foraging pattern. The distribution of flight directions is uniform. Seed dispersal distances have a very leptokurtic distribution and a mean dispersal distance of 13 ± 1.1 cm (Olesen & Warncke 1989c).

If each flower is interpreted as an ecological unit, the ecological neighbourhood area is 64.9 m^2 allowing for leptokurtosis. Thus the population consists of less than 3 (134/64.9) neighbourhoods. The population is therefore suspected of being highly homogeneous genetically. The mean flight distance (flights > 2 m excluded) is correlated with the neighbourhood area (Olesen & Warncke 1989c).

Zygaena trifolii is of no quantitative importance to the pollination of *S. hirculus* (Olesen & Warncke 1989a, 1989b), but due to its large proportion of long flights it has a great impact on the size of the neighbourhood area. Thus the evolutionary impact of *Z. trifolii* on the population structure of *S. hirculus* may be very important (Olesen & Warncke 1989c).

In Switzerland, preliminary studies indicate that *S. hirculus* is visited and probably pollinated by different species of Muscidae and Syrphidae (Olesen, unpubl.).

Flowering phenology and flower morphology

The area of the population at Rosborg Sø was divided into squares of 1 m^2 each. At each daily census during the flowering period, all new open flowers were tagged and mapped. A petal was collected from each of more than 400 top flowers. Petals from 50 side flowers were tagged too. The petals were preserved under tape. Their width and length were measured.

Laboratory techniques

Runners, all at the same developmental stage, were collected all over the area of the population at Rosborg Sø and their position mapped. The samples of runners were returned directly to the laboratory in a chilled container for horizontal starch gel electrophoresis. The outermost 3 cm of each runner with its young leaves was used. Different buffer systems were tested. A 0.06 M Tris malate PVP buffer, pH 8.1, turned out to give the best results. The following enzymes were analysed: esterase, glucosephosphate isomerase (GPI), 6-phosphogluconate dehydrogenase (PGD), shikimate dehydrogenase (SKD), and phosphoglucomutase. Of these systems, only GPI, PGD and SKD were sufficiently polymorphic, and only GPI yielded good bands and was used here. GPI is normally a dimeric enzyme in plants (Gottlieb 1981, Lack & Kay 1988). The staining procedures are described by Frydenberg & Simonsen (1973).

The germinability and rate of germination were tested on seeds collected from Rosborg Sø in 1983. Variables were temperature, germination substrate and light intensity.

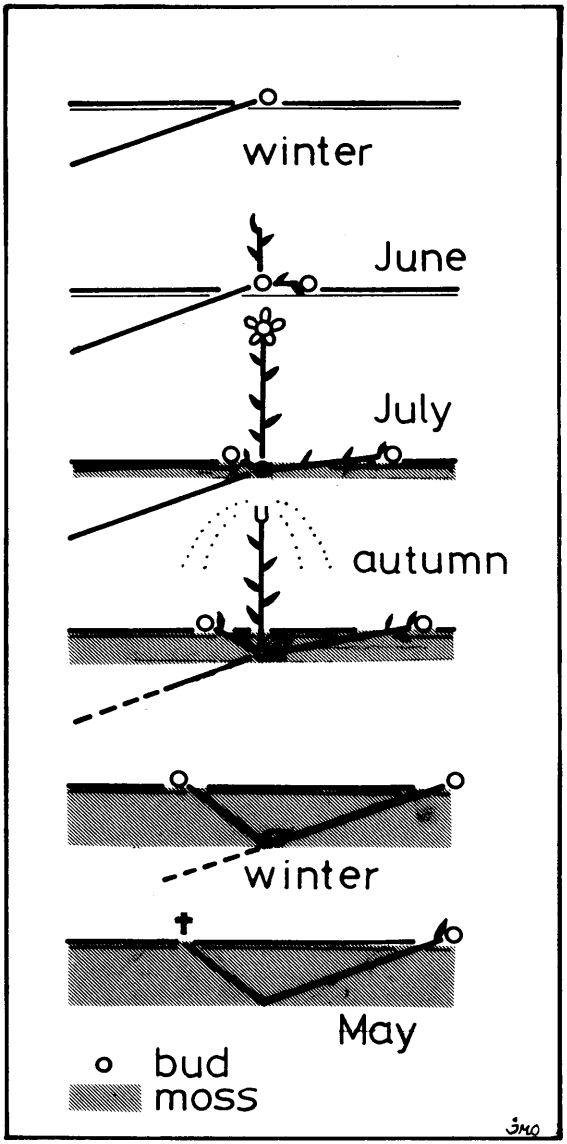

Fig. 1. The life of a ramet of *S. hirculus*.

RESULTS

The vegetative natural history of S. hirculus

In the summer of 1984, a ramet of *S. hirculus* was observed to consist of an inclined rhizome 48 ± 26 mm long (N = 50, range 2-141 mm; June 30) with its apex slightly below

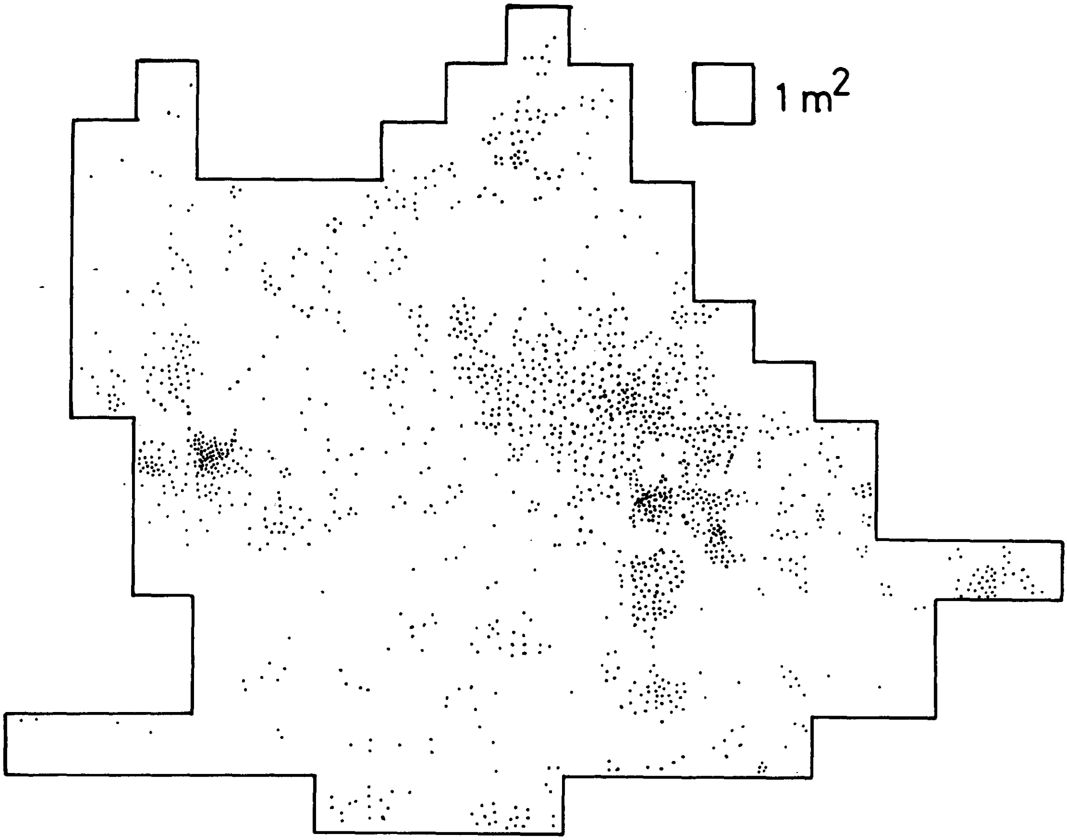

Fig. 2. Map showing the distribution of the flower population of *S. hirculus*. Each dot represents one flower.

the surface of the moss layer and with 1.5 ± 0.8 (N = 48, range 0-4; June 30) and later 1.3 ± 0.9 (N = 27, range 1-5; September 30) new runners spreading out opportunistically (Fig. 1). After three to twelve months, the runners either died or "became rhizomes" due to moss growth. Some of the new rhizomes remained in contact with the older ones. From May on, new runners might grow out from the apex of the rhizome; from June an aerial reproductive shoot becoming 10-30 cm high might arise. The ramets grew in patches and might reach a density of 5.500 per m^2.

During May-June 1984, a runner produced a leaf every 5th day and grew 0.5 mm per day. On June 30, a runner was 27 ± 21 mm long (N = 64, range 2-79 mm) with 6.3 ± 3.3 leaves (N = 64), i.e., 2.3 leaves per cm. On September 30, the runner was 96 ± 40 mm long (N = 45, range 54-215 mm) with 11.5 ± 4.8 leaves (N = 48), i.e., 1.2 leaves per cm. In that period the increase in length had been 0.8 mm per day and one leaf had appeared every 18th day. The decrease in leaf production during summer might be related to an allocative shift of energy to reproductive shoots and an increased competition from mosses. Growth of mosses and decrease in light intensity during autumn caused longer internodes

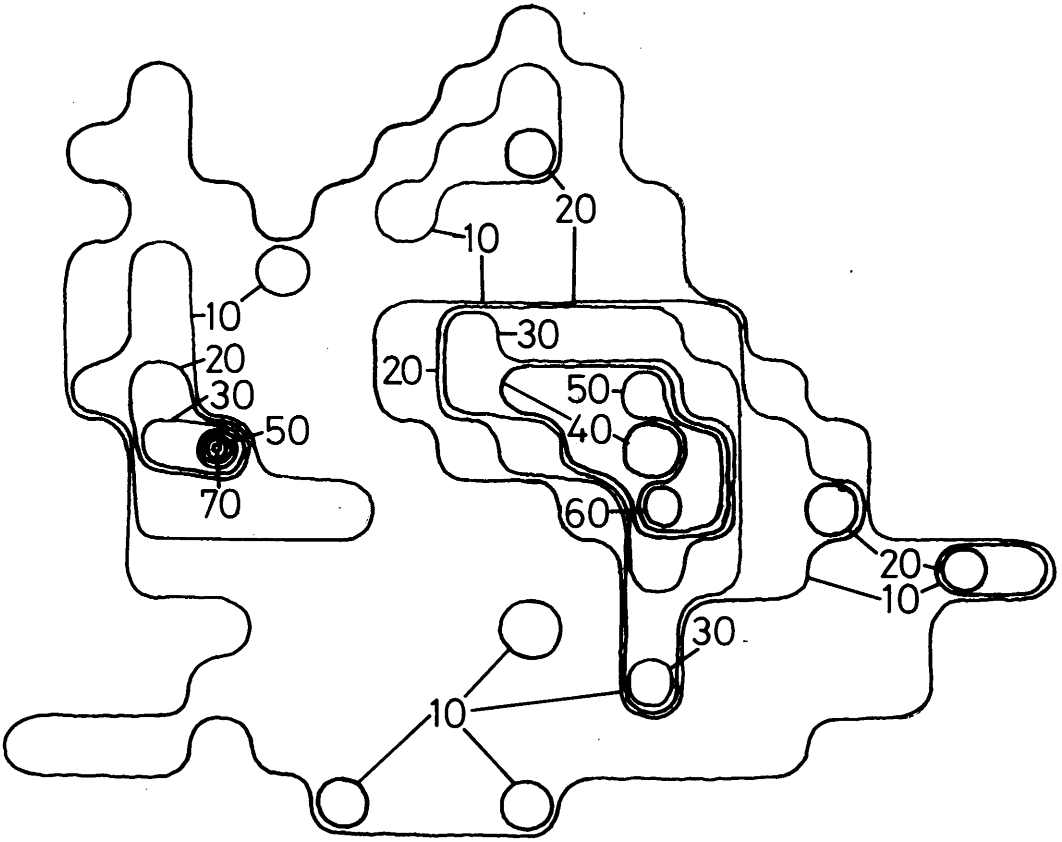

Fig. 3. Number, extent and position of local peaks of flower abundance in the population of *S. hirculus*. Numbers at isolines are no. of flowers/m^2. Flower abundance peaks below 10 are not included.

and more light green leaves. On June 30 and September 30, 12 % and 46 % of the leaf area, respectively, had been consumed by herbivores, especially slugs.

Leaves on aerial shoots were more xeromorphic than leaves on runners. During November-May, the runners lost their leaves and only the apical buds remained green. Aerial shoots were always sexual. Small hibernated rhizomes/runners might only produce small and few new runners. Only rhizomes above a certain biomass seemed able to reproduce sexually. A few of the runners were observed to ramify from a node in September-October, thus producing two hibernating meristems.

Seed germination

The ability and rate of germination of the seeds of *S. hirculus* were tested under different laboratory conditions. Germination was favoured by high temperature. At 11°C unstratified

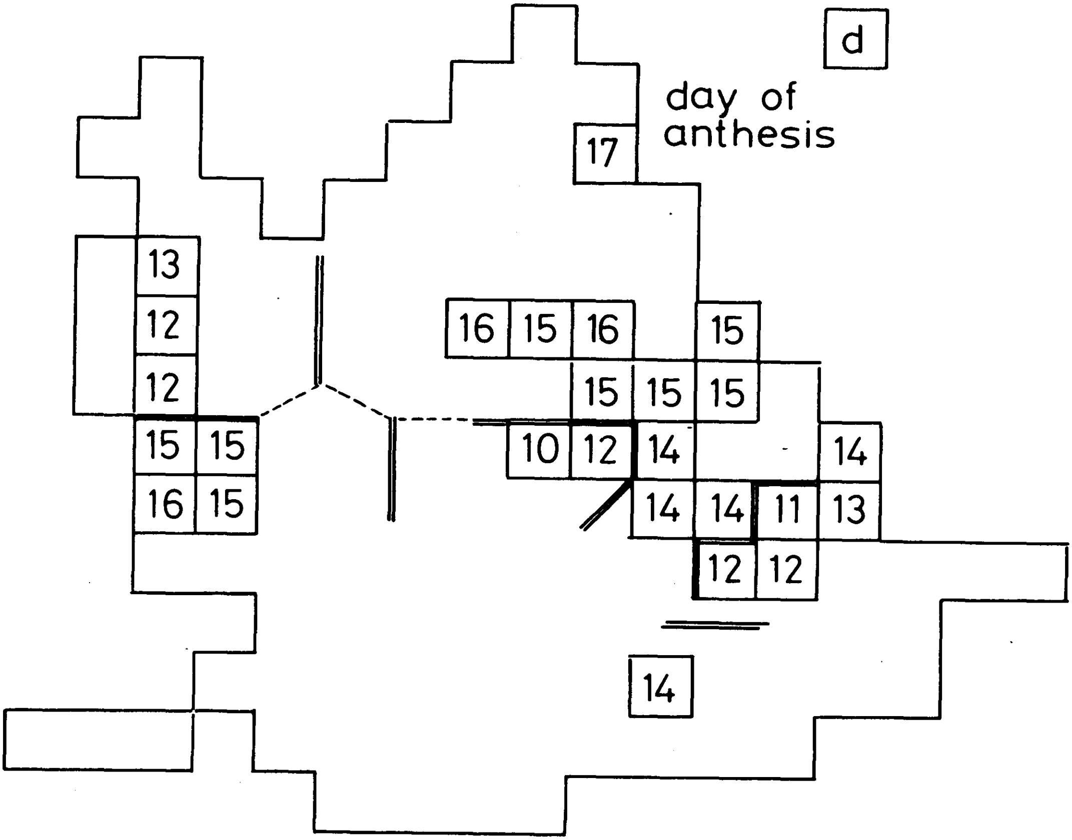

Fig. 4. Variation in anthesis in the population of *S. hirculus*. d = date of initiation of anthesis minus 8. The population commenced flowering on July 9. Double lines indicate statistically significant differences at the 5 % level.

seeds had a germination of 44 % and a t_{50} (No. of days until 50 % germination was reached) of 32 days. At 22°C unstratified seeds had a germination of 59 % and a t_{50} of 16 days. Increased stratification period increased germination. At 22°C seeds stratified for 22 days had a germination of 63 % and t_{50} was 12 days. If stratified for 78 days, 95 % of the seeds germinated, the t_{50} being 9 days. Seeds sown on water-saturated spring area sand, filter paper or spring area peat did not show any differences in germination. Germination was favoured by high light intensity. At 11°C and sown on water-saturated spring area sand 3 %, 49 %, 58 % and 72 % of the seeds respectively germinated at 0, 12, 31 and 78 $\mu E/m^2s$ light intensity.

Intrapopulational variation in flower abundance

The position of all open flowers in the population of *S. hirculus* is shown in Fig. 2. In Olesen & Warncke (1989c) it is demonstrated that the flower abundance is 11.4 flowers/m^2

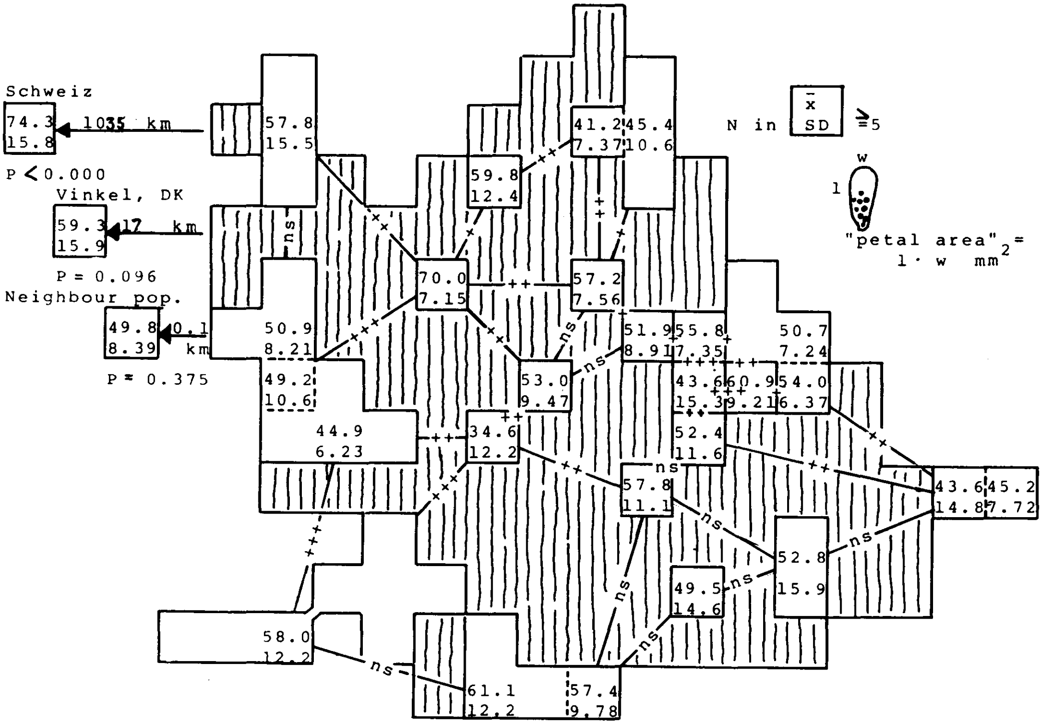

Fig. 5. Variation in petal size in the population of *S. hirculus*. X ± SD = petal length * petal width ± SD. Level of statistical significance inserted, +: <0.05, ++: <0.01, and +++: <0.001. Comparisons are made with the Swiss population and with other Danish populations (Vinkel and a neighbouring one at Rosborg Sø). N/m^2 ≥ 5.

and that the spatial distribution of flowers is very clumped (P < 0.001).

The position, number and extent of local peaks of flower abundance are given in Fig. 3. The number of peaks is estimated to be (2-)3-7.

Intrapopulational variation in flowering phenology

The variation in time for the onset of anthesis for different parts of the population is given in Fig. 4. The figures in squares represent average day of anthesis since flowering began in the population (minus 8). Double lines indicate statistically significant differences at the 95 % level (t-test). The population consisted of about seven phenological subunits. Their extent and position are suggested (Fig. 4).

Inter- and intrapopulational variation in petal size

Statistically significant differences in petal size existed both between and within populations.

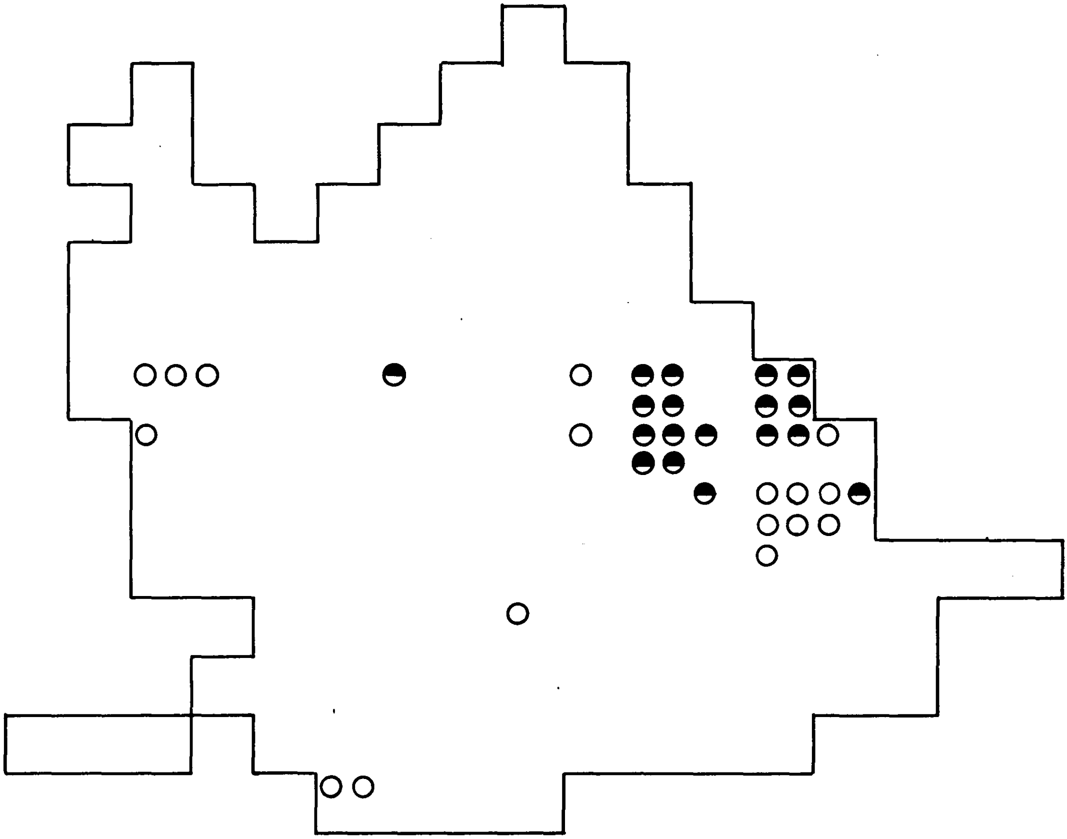

Fig. 6. Distribution of samples homozygous (O) and heterozygous ( ) for genes expressing the GPI-enzyme system in the population of *S. hirculus*.

Average petal size was 52.7 mm^2 at Rosborg Sø, 59.3 mm^2 at Vinkel, and 74.3 mm^2 in Switzerland. The variation was highly significant between countries ($P < 0.01$), non-significant between Danish localities ($P = 0.09$) and between neighbouring populations ($P = 0.38$), highly significant between main and side flowers on the same plant ($P < 0.01$), and non-significant between petals within the same flower ($P = 0.98$). The variation between different patches of the study population is shown in Fig. 5. The population consisted of about 11 subunits differing significantly in flower size. The extent and position of these are suggested in Fig. 5.

Intrapopulational variation in isoenzyme banding

After screening for variation only GPI showed a distinct and reproducible pattern. The other two variable enzyme systems showed less clear banding patterns. Further isoenzyme analysis was therefore carried out for GPI alone. From the variation in GPI-isoenzyme banding pattern 5-6 patches could be segregated. The approximate extent and position of these are indicated in Fig. 6.

DISCUSSION

European S. hirculus *areas*

In broad features the spring areas and fens containing *S. hirculus* show large similarities in Sweden (Ohlson 1989a), Rosborg Sø and in Col du Marchairuz in Switzerland. Flowering seems to start about a fortnight earlier in the spring area studied by Ohlson (1989b) than in the populations at Rosborg Sø and in Switzerland.

The vegetative histories of Swedish and Danish *S. hirculus* are similar in most respects. For instance, the height of the flowering shoot of *S. hirculus* seems to be about the same (Ohlson 1986). The number of runners per flowering shoot is, however, lower in Rosborg Sø than in Swedish spring areas (Ohlson 1986).

Estimate of the number of genets in the population of S. hirculus

The runners of *S. hirculus* move opportunistically. Their orientation is without doubt determined by the level of available resources. We may, however, assume here that every direction is chosen with the same probability. Thus the highest abundance of ramets is assumed to be found where seedlings originally established the clones. No correlation between abundance of ramets and flowers was looked for, but local peaks of flower abundance are assumed to indicate a genet or an even-aged group of genets. Maximum flower abundance in Rosborg Sø is 73/m^2 (Olesen & Warncke 1989c). In Swedish studies, *S. hirculus* may reach a density of > 200 flowering shoots/m^2 four to seven m from the spring (Ohlson 1986).

Patches of flowering shoots with synchronous anthesis and similar petal size also belong to ramets which are regarded as closely genetically related. Flower size probably has a high degree of heritability. Ohlson (1987) has demonstrated that roots of *S. hirculus* show the largest, and flowers the smallest, variation. Differentiation in morphological characters has been found in Swedish transplant studies between plants originating from habitats within a distance of 30 m (Ohlson 1987).

Different genotypes for isoenzymes are also interpreted as evidence for the existence of different genets, although one genet may possess more than one genotype due to somatic mutations during a long clonal life. This was, however, not observed.

If the results from our four approaches to estimating the number of genets in the population are compared we only find small differences. Thus the number, extent and position show great similarities and the overlap in delimitation lines between neighbouring genets/groups of even-aged genets is striking. Ten to seventeen genets/groups of even-aged genets may be distinguished (Fig. 7).

The most appropriate method in the case of *S. hirculus* seems to be to study variation in petal size. The large difference in petal size between Danish and Swiss populations may be caused by differences in chromosome numbers (Hedberg 1967).

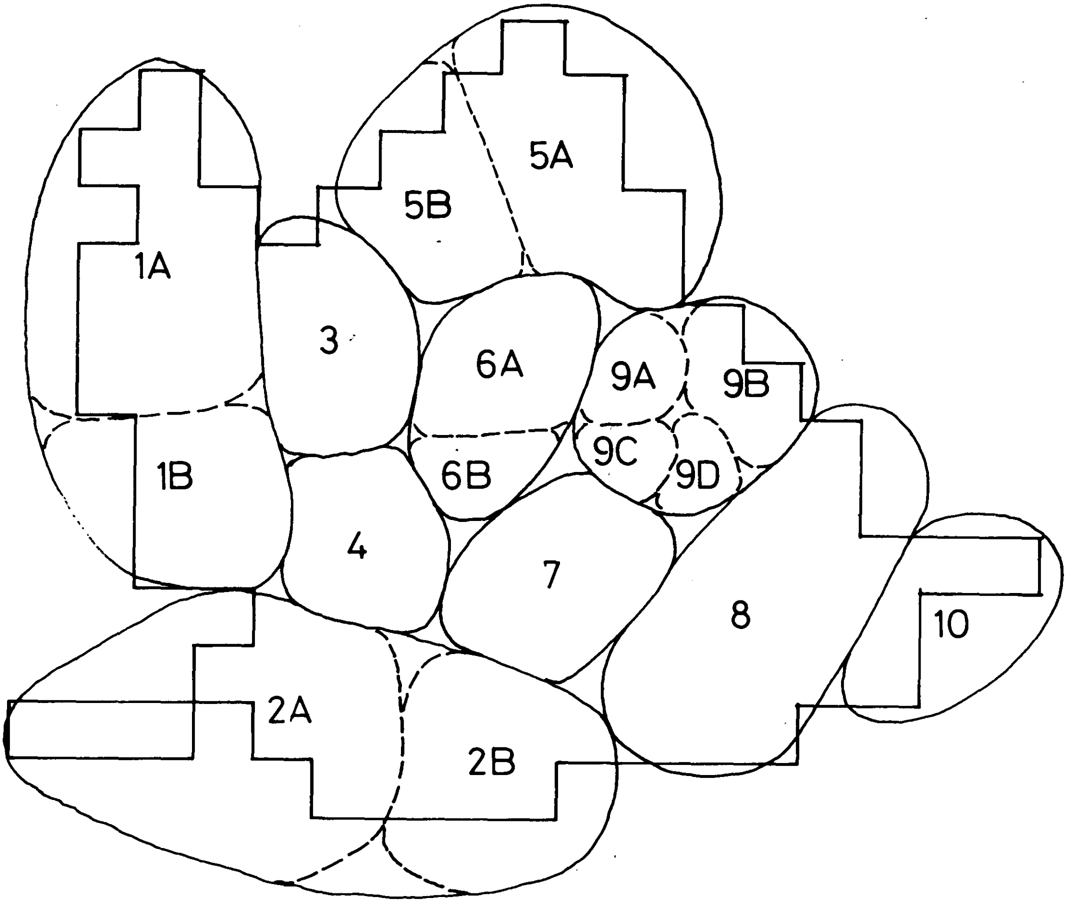

Fig. 7. Number, extent and position of genets/groups of even-aged genets in the population of *S. hirculus* based on data in Figs 3-6. Dotted lines indicate genet borders documented by only one of the four approaches.

The spread of genes by runners in S. hirculus

In populations of plant species with clonal growth, genes are transported not only by pollen and seeds but often to a much greater extent by vegetative organs such as rhizomes or runners. This applies to *S. hirculus* as well. No seedlings have ever been observed in undisturbed vegetation (Ohlson 1986, 1989a, 1989b). The reasons may be the special light requirements for germination, and interference between seedlings and established plant individuals of the same or other species. It is then tempting to incorporate the variance of the length of the runners into the usual formula for neighbourhood area ($NA = 4\pi(0.5*\sigma^2_{pollen} + \sigma^2_{seed} + n\sigma^2_{veg.})$ (Olesen & Warncke 1989c). The neighbourhood area of *S. hirculus* is, however, not influenced to any extent by variance in the length of the runners ($NA = 4\pi(0.5*8.00 + 0.000128 + 0.0016n)$; where n is the number of generations of

Tab. 1. Size and variation in the dispersal of different gene dispersal units in a population of *Saxifraga hirculus*. Data on interfloral pollinator flight distances and seed dispersal from Olesen & Warncke (1989c: Tab. 3).

Dispersal unit	Average distance	S.D. (m)	Variance (m^2)
pollen	0.85	2.83	8.00
seed	0.13	0.0113	0.000128
runner	0.096	0.040	0.0016

runners between two sexual events; Tab. 1).

About 15 subpopulational units were found in the population of *S. hirculus*. The average area of each is then 8.9 m^2. How many years will it take runners originating from one centrally situated seedling to reach the periphery of this area? Year 0, a seed is dispersed to a maximum of 0.98 m away from its father (Tab. 1). Year 1, the seed is supposed to germinate. Year 2, the tip of the runners produced may reach a maximum distance from the original pollen source of (0.98 + 0.096 =) 1.08 m. If year n is the year the clone has expanded to the periphery of the subpopulational area, then:

$$n = [(8.9/\pi)^{1/2}-0.98]/0.096 + 1 = 8.3 \text{ years.}$$

However, since runner production per bud is only 1.3, many runners die during winter, and as the orientation of the runners is random, it may take many more years to expand to the average area of a populational subunit. If the subunit originates from a group of seedlings the spread of runners will be faster.

The relationship between large herbivores and the structure of the population of S. hirculus

The flower abundance peaks and the morphological, phenological and biochemical subunits observed may either be interpreted as genets or as groups of genets. If they are equal to single genets they should display a high degree of homogeneity since the whole population consists of less than 2.1 ecological neighbourhood areas (Olesen & Warncke 1989c). They do, however, display variation in the characters studied. Thus the small number of genets may be old ones without sexual reproduction originating from larger populations. The alternative hypothesis is that the observed subunits each represent groups of genets. If a small area within a population of *S. hirculus* is disturbed, e.g. by red deer (unpubl. obs.), a cohort of new seedlings may appear (Ohlson 1989a). Most of these are probably recruited from neighbouring plants and are thus closely related genetically. Thus we envisage that the population may in this way be a mosaic of "half-sib"-groups (i.e., with one parent in common). This disturbance-colonization hypothesis seems to fit in well with certain observations and speculations. We imagine a scenario where large northern hemisphere mammals, e.g. deer and buffalo, extant or extinct, move around from one wet ecosystem to another during the summer and autumn. These animals are known to wallow in cool vegetation, causing great disturbance. 1/3 of all infructescences was destroyed in Rosborg

Sø in the autumn 1984 by red deer (unpubl. obs.). At the same time, the animals graze. Janzen (1984) suggests that many temperate herbs with tiny seeds have their seeds dispersed by large herbivores. They eat the foliage and with it the seeds. If the importance of these animals to the life of wetland herbs, e.g. *S. hirculus*, is confirmed, we have explained both the dispersal of seeds between spring areas/mires and how the seedlings get established.

Thus we conclude that the different approaches to estimating number of genets or groups of genets in *S. hirculus* largely agree, and postulate that the disappearance over recent millennia of large northern hemisphere mammals has diminished both the disturbance and the recruitment rates of *S. hirculus*. The few genets observed at Rosborg Sø are probably old ones, belonging to an older and larger population in which the recruitment rate of new seedlings has failed to keep up with the mortality rate of old clones.

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POPULATION BIOLOGY OF THREATENED VASCULAR PLANTS IN FINLAND

P. Uotila, T. Lahti, E. Kemppainen & A. Kurtto

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According to the Finnish Red Data Book there are 83 disappeared, endangered or vulnerable vascular plant taxa in Finland. A database of biological characteristics of these and several other rare species has been made. Population biology of four species, viz. *Agrimonia pilosa* Ledeb., *Androsace septentrionalis* L., *Carlina vulgaris* L. and *Crepis praemorsa* (L.) F. W. Walther, has been studied during 1987-1989. Preliminary results are presented here for *Androsace septentrionalis* and *Carlina vulgaris*. The necessity of studies on population biology for use in practical conservation and management acts is emphasized. Difficulties in these studies are also briefly discussed.

Keywords: *Androsace*, *Carlina*, Conservation, Finland, Population biology, Threatened plants.

Pertti Uotila, Tapani Lahti, Eija Kemppainen & Arto Kurtto, Botanical Museum, University of Helsinki, Unioninkatu 44, SF-00170 Helsinki, Finland.

INTRODUCTION

Threatened plant species in Finland: a survey of investigations

A committee for the preservation of threatened animal and plant species in Finland was active from March 1983 to Sept. 1985. Its report was published in 1986 (Rassi et al. 1986; the English version: Rassi & Väisänen 1987). The importance of basic biological data, especially on the population biology of the threatened plants, as a basis for management decisions, is emphasized in the final report of the Committee. The lack of such information was also noted - in fact there is hardly any botanical tradition in the study of the population biology of plants in Finland, except for some single studies by, for example, Kujala (1926), Linkola (1935), Perttula (1949) and Oinonen (1967a, 1967b, 1967c).

We started a three-year project, financed by the Academy of Finland, to collect data on the biological characteristics of the threatened vascular plants of Finland in 1987, following a short pilot project in 1986 (Lahti et al. 1990). The principal aim of this study is to build a database of a number of biological, ecological and biogeographical characteristics of the vascular plant taxa which are regarded as disappeared, endangered or vulnerable in Finland. Furthermore, the population biology and life-cycle of certain species

Tab. 1. Taxa included in the study. E - Endangered, V - Vulnerable, M - In need of monitoring, CE - included in the list by Council of Europe (1983), (S) - Protection and management plan under preparation. Number of references indicate the number of literature references found concerning biology of the species. Nomenclature is according to Hämet-Ahti et al. (1986).

Taxa included	category	No. of present localities	No. of references
Agrimonia pilosa (S)	E	7	0
Aira praecox	V	3	2
Alisma wahlenbergii	M (CE)	many	0
Androsace septentrionalis (S)	E	12	11
Armeria maritima (S)	V	21	8
Artemisia campestris ssp. bottnica	V	8	0
Asarum europaeum	V	5	4
Asperula tinctoria	V	3	1
Asplenium adulterinum	V	7	1
Botrychium lanceolatum	(CE)	many	2
B. matricariifolium	M (CE)	many	1
B. multifidum	(CE)	many	2
B. simplex	E	2	3
B. virginianum	V	12	3
Bromus benekenii	E	2	1
Cardamine flexuosa	E	4	3
Carex remota	E	4	1
Carlina vulgaris ssp. longifolia (S)	E	12	10
C. vulgaris ssp. vulgaris (S)	V	4	
Cephalanthera rubra	E	?	0
Crepis praemorsa (S)	E	4	2
Cynoglossum officinale	V	9	3
Elatine alsinastrum	V	7	3
Epilobium lamyi	V	11	1
E. obscurum (S)	E	7	2
Epipactis palustris (S)	V	14	0
Erica tetralix	E	1	6
Festuca gigantea	E	1	6
Galium saxatile	E	2	1
Gypsophila fastigiata	M	many	1
Hypericum montanum (S)	E	3	3
Kobresia simpliciuscula (S)	V	1	0
Melica ciliata (S)	E	1	2
Ononis arvensis	E	6	0
Ophrys insectifera	E	11	1
Pimpinella major (S)	E	1	0
Polygonum oxyspermum	E	3	2

Tab. 1 (continued).

Taxa included	category	No. of present localities	No. of references
Potentilla neumanniana (S)	E	17	3
P. subarenaria (S)	M	17	1
Salsola kali	V	5	1
Scleranthus perennis	V	4	7
Sium latifolium	E	3	1
Vicia cassubica	V	2	1
V. lathyroides	V	7	0
Viola uliginosa (S)	E	8	4
Total 45 species		(over 350)	104

will be studied in depth in order to elucidate critical phases in their life history. These phases can then be taken into account in the planning of specific conservation and management procedures for the actual species.

A separate project was started in 1987 to collect data for the preparation of protection and management plans for the endangered and vulnerable vascular plants in Finland. It is financed by the Ministry of Environment. In 1989, a similar project was established for the Åland Islands with the financial aid from the Province of Åland. Both projects work in close collaboration with our research project on the biological characteristics of threatened plants.

The taxa studied

The total number of disappeared, endangered and vulnerable vascular plant taxa in Finland is 83 (Rassi & Väisänen 1987). A database will be made for these species from literature, and from herbarium and field studies.

About half of these taxa were selected for more detailed study (Tab. 1). Many of them are grassland species known to have declined during the last few decades. Of these taxa, as many Finnish populations as possible will be studied and monitored during our project. Furthermore, some of the taxa have been studied by research groups at other Finnish universities. The field studies include detailed mapping of local populations, at the level of individuals whenever possible, in order to detect changes in the population size and structure.

Four species were selected for particularly intensive studies, viz. *Agrimonia pilosa* Ledeb., *Androsace septentrionalis* L., *Carlina vulgaris* L. and *Crepis praemorsa* (L.) F. W. Walther. We have studied the local populations of these species every year since 1987, at least two or three and up to 5-10 times per season, in order to obtain data on phenology, proportion of flowering individuals, seed production, presence and survival of seedlings etc. Some ecological parameters (e.g. soil properties) have also been studied and vegetation de-

Tab. 2. Number of flowering plants and seed production of *Androsace septentrionalis* at nine localities in Finland. Seed production has been calculated by multiplying the mean numbers of fertile plants per m^2 by the number of capsule per plant and by the number of seeds per capsule.

Locality	Flowering plants			Seed production			
				seeds/plant		seeds/m^2	
	1987	1988	1989	1987	1988	1987	1988
Åland 1	500	c.100	?	400	?	5500	?
Åland 2	700	150	?	100	?	600	?
Lammi	52	60	41	150	50	600	50
Lahti	25	10	49	200	?	300	?
Heinola 1	164	32	31	400	?	650	?
Heinola 2	125	63	123	100	200	500	350
Heinola 3	c.100000	c.40000	c.150000	200	800	c.100000	c.100000
Heinola 4B	300	550	c.15000	50	1500	7000	44000
Kuopio	?	2	285	?	?	?	?

scriptions have been done. Some experimental work has been, or will be done, such as germination tests of seeds and growth under controlled conditions in the botanical garden (e.g., growing of plants under variable shading). Because the aim of the project is to get information relevant to protection and management of the populations, management experiments were also made.

Some results for two of the intensively studied species are presented below.

RESULTS AND DISCUSSION

Androsace septentrionalis

Androsace septentrionalis (Primulaceae) is one among a dozen annuals regarded as threatened in Finland. It is widely distributed in the northern hemisphere from C and N Europe to North America. In Finland it is considered an archaeophyte, having 12 established localities and a great number of more or less casual finds and formerly possibly established but now disappeared stands (Fig. 1). Morphological variation between the populations indicates that they may have different migration histories. The localities are concentrated in three areas: Åland, and Lammi and Heinola in South Häme. The localities in Åland are dry grasslands, whereas the others are mainly old road and railway banks and warm and dry esker slopes near settlements.

As expected for an annual species, variation between years in shoot number, size, flowering and fruiting was considerable (Tab. 2; also see Symonides 1979). However, dense populations invariably remained denser than sparse ones during the three years. Stands on

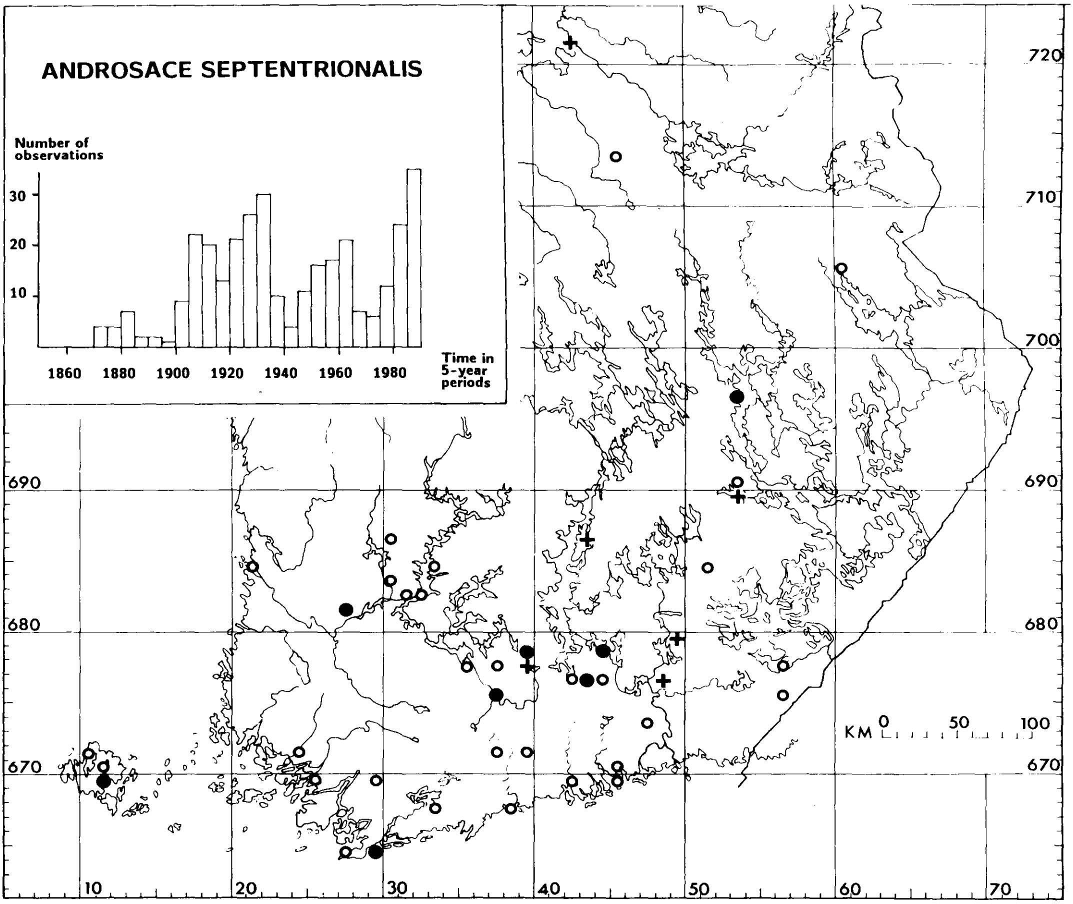

Fig. 1. Observations of *Androsace septentrionalis* in Finland. Dots - existing established populations, circles - casual finds, crosses - disappeared established populations. Insert diagram shows chronological distribution of observations in five year periods.

steep S-facing slopes were denser and plants were taller than in level sites. Size of the plant and number of seeds were positively correlated (cf. Nasir 1985). In dense populations the life-cycle was shorter. This may be a result of more suitable habitats, but perhaps also of stronger intraspecific competition (cf. Symonides 1978).

Seeds of *A. septentrionalis* are released in late summer. Due to poor dispersal, only a small proportion of seeds was dispersed out of the population range. Evidently a high number remain dormant in the soil, thus forming a considerable seed bank. During the dry spring of 1988 all plants on one patch died without setting seed. However, in the following spring the number of emergent plants in this patch was no less than in the surrounding areas. In a sowing experiment, only 2-4 % of the seeds sown in bare soil in May 1988, before the dry season, germinated in 1989.

In the wild seeds of *A. septentrionalis* germinated immediately after the snow had

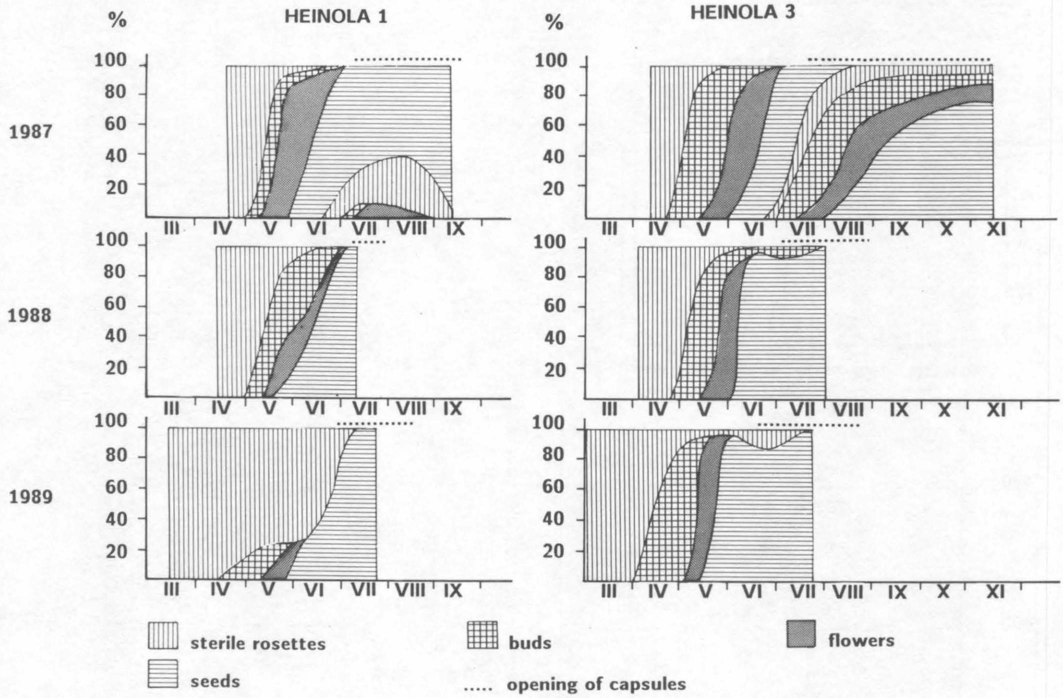

Fig. 2. Phenology of *Androsace septentrionalis* at two localities in Heinola, South Häme, in 1987-1989.

melted (Fig. 2). Under favourable conditions seeds germinated throughout the whole growing season. However, most of the new rosettes died during the winter. In the moist and cool growing season of 1987 the spring germination took place at the beginning of May. In 1988 this occurred about two weeks earlier and in the exceptionally warm spring of 1989 the seeds germinated during a rather long period from the early March to the beginning of May. However, each year flowering started at about the same time, at the end of May (cf. also Symonides 1978). Selfing seemed to be the dominating mode of pollination; in a mixed population with *Arabidopsis suecica* the pollinators frequently visited *Arabidopsis* but avoided *Androsace*.

In 1987 there was an additional germination period at the beginning of June (Fig. 2). Several plants produced a secondary umbel of flowers above the primary umbel, or were in some other way monstrose. Numbers of flowers and seeds per capsule were lower in the secondary umbels than in the primary ones. Secondary umbels were detected neither in 1986 nor in 1988.

In the autumn about 1000 seeds were needed to produce 20 seedlings in the following spring. Some of the seedlings came from seeds of the seed bank. About 60% of the seedlings died (cf. also Symonides 1979). In favourable circumstances almost all plants which started flowering also set seed. However, during dry summers, as in 1989, and in dry habitats, 10-30% of flowering plants withered without setting seed. In all, 1000 seeds seemed to give rise to 4-5 individuals producing new seeds.

In Finland the seed yield of *A. septentrionalis* is usually 100-400 per plant, in Poland ca. 1000-1300 (Symonides 1979), which corresponds to the yield of the densest population in Finland.

If *Androsace septentrionalis* manages to become established at a site it survives for some time if site conditions are not drastically altered (cf. Clemedson 1986). Because of the seed bank, the species can reappear at an overgrown site after the disturbance of the vegetation and surface layers of the soil. In addition to habitat requirements and competition, the crucial point for the species may be seed dispersal, which seems fairly inefficient. The boundaries of the populations have remained almost unaltered during the study period, except for a few centimetres of downward expansion on esker slopes.

Carlina vulgaris

Carlina vulgaris (Asteraceae) is a monocarpic species, flowering once after a one-to-several years long vegetative period as a rosette. It has a wide distribution area from France and Great Britain to the Caucasus and W Siberia. *Carlina vulgaris* is a taxonomically intricate species, and is usually divided into two or three infraspecific taxa. In Finland it occurs in two separate areas, one on the Åland Archipelago, another in the eastern Lake District (Fig. 3). Traditionally, these populations have been included in different subspecies, the population of Åland in ssp. *vulgaris* and the E Finnish populations in ssp. *longifolia* Nyman. However, in the culture experiments considerable morphological differences have been observed between the E Finnish populations. The taxonomy of *Carlina vulgaris* in Finland needs further study.

Both subspecies have declined in Finland during the last few decades. Ssp. *vulgaris* is considered vulnerable and ssp. *longifolia* endangered in the Red Data Book of Finland. However, recent observations suggest that the southwestern populations are even more threatened than the eastern ones. Only four extant localities are known for ssp. *vulgaris*, 12 for ssp. *longifolia*. The main causes for the decline have been the cessation of pasturing, and as a result of this, accelerated closure of previously semi-open grasslands.

The Finnish localities of ssp. *longifolia* are field margins, roadsides in previously pastured forests and areas affected by slash-and-burn cultivation. In many cases populations grow in fairly open pine forests with a field layer dominated by grasses and *Pteridium aquilinum*, but in some cases also in more shaded woods. In general, Finnish populations of *Carlina vulgaris* ssp. *longifolia* cover only a few hundred m^2 (200-2400 m^2), the largest being almost two hectares. The distribution of plants within sites is patchy. The number of flowering plants varied from four to ca. 1000 in 1987, being 10-20 % of the total number of individuals. In 1987 flowering plants were more abundant than in 1988. The high number of sterile plants as compared to fertile ones implies that *Carlina vulgaris* survives several years as a rosette before flowering (cf. Watt 1981, Grubb et al. 1982). Of the 31 rosettes marked in 1987, nine flowered and then died. Of the remaining 22 plants only three flowered in 1988, while the rest (19) were still rosettes. All fertile plants died during the winter after flowering.

In the wild, flowering begins at the end of July and continues till September. In early, dry summers fruits dehisce from capitula in August - September and in rainy and cool summers in late October or they can postripen in the capitula and be dispersed in the winter or spring.

Ssp. *longifolia* is taller than ssp. *vulgaris*, but the shoots do not exceed 40-50 cm. Heavy fruits do not usually disperse far from the mother plant (cf. Sheldon & Burrows 1973). Most populations have not expanded in recent years, probably because the

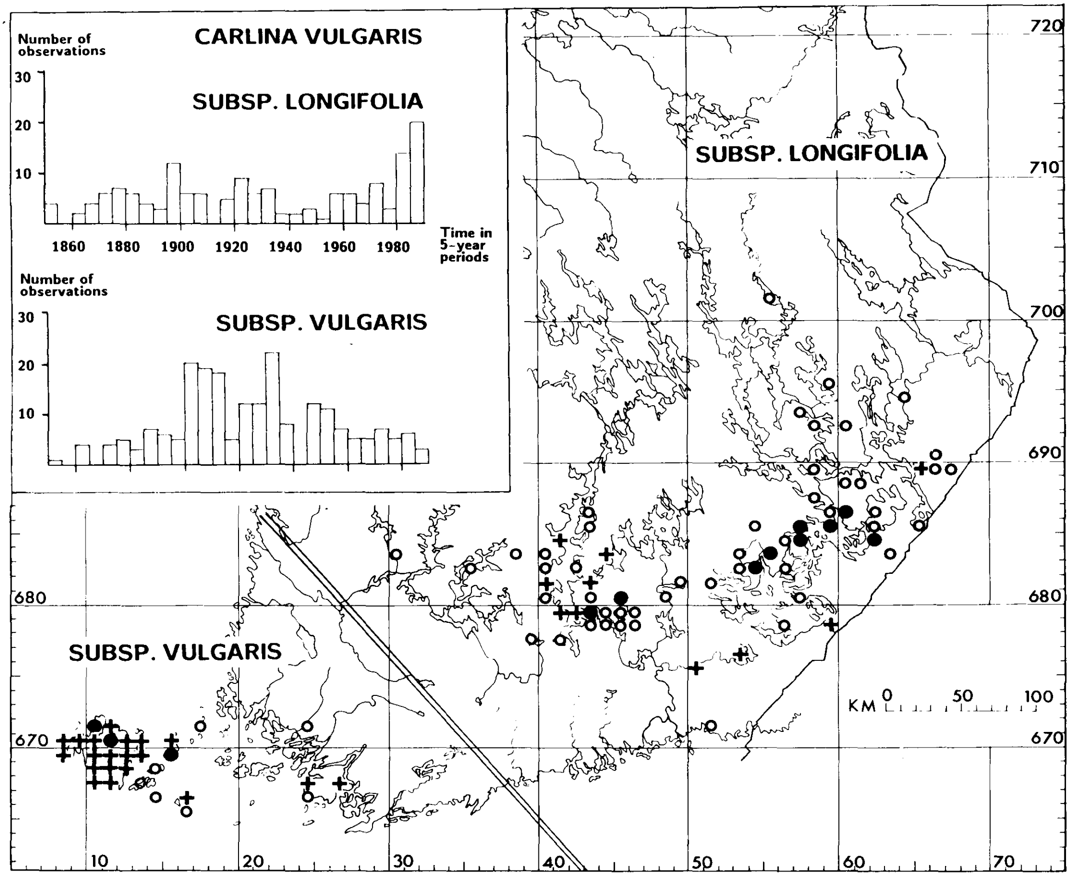

Fig. 3. Observations of *Carlina vulgaris* in Finland. For explanations, see Fig. 1.

surrounding vegetation has grown denser and taller after the cessation of pasturing. However, in two localities the populations have clearly expanded. In one of these, in Savonlinna at Pääskylahti, where many individuals grow on a road bank, diaspores are easily spread by air currents caused by passing vehicles.

On the average, there are ca. 300 flowers in a capitulum. The mean number of achenes in a capitulum was 155 in 1987 and 187 in 1988. These results agree well with the average number of 154 given by Salisbury (1942). According to Greig-Smith and Sagar (1981) the number of achenes per capitulum varies from several up to 300. In Finland one individual produces 300-500 fruits. However, less than half of the fruits are fully developed in plants growing in the shade, whereas in the sun 80-95 % of the fruits are fully developed. In the Netherlands and Great Britain it has been shown that a large proportion of achenes is rapidly destroyed by herbivores and parasites, and *Carlina* has no or only a very small seed bank in the soil (Greig-Smith & Sagar 1981, Schenkeveld & Verkaar 1984). Germination, on the other hand, is high. In our germination experiments fully developed fruits germinated well in all cases (70-98 %), except in total darkness. This is consistent with previous results. According to Grime et al. (1981) achenes of *Carlina vulgaris* do not germinate in the dark, and according to King (1975) they are sensitive to a low R/FR quotient. Mortality was higher and development of seedlings worse in the dark, in accordance with the observations of Verkaar & Schenkeveld (1984). If seedlings manage to survive the first weeks, their probability of establishment is high.

The *Carlina* taxa occur in Finland at their northern distributional limit. Consequently, they need a relatively long growing season to flower and to produce viable seeds. Vegetation closure after cessation of pasturing is fatal, because of decreasing flowering and fruit fertility, restricted dispersal of fruits, and poor survival of seedlings. Late flowering and changes in the composition of the whole flora may result from the lack of pollinators (especially bumble-bees). The lack of a seed bank increases the risk caused by exceptional weather conditions. This is, however, somewhat alleviated by the perenniality of *Carlina*.

GENERAL CONCLUSIONS

Conservation of threatened animals and plants is becoming an increasingly important task, both nationally and internationally. Rational management of small populations of rare species can only be based on comprehensive knowledge of the biology of the target species. The current information on the biology of the threatened vascular plants in Finland is too fragmentary for making rational decisions on management, in the attempt to protect these plants. This can be seen from Tab. 1, where the last column shows the number of literature references found concerning the biology of our target species (floras etc. are excluded). So far our study of the population biology of some threatened vascular plant species in Finland has shown that the collection of relevant data is a time-consuming task. Each species has its own pecularities, which must be built into the research plans.

The study has now progressed for two, or for some populations, three years. The years have been climatically very different (Tab. 3). A period of two or three years is certainly too short a time for any far-reaching conclusions.

Widén (1988) discussed limiting factors in the study of population biology of threatened species. Basic population biology should be studied with more common species,

Tab. 3. Mean temperatures and mean precipitation for the year and for the growing season (May - August) in three localities in Finland: Mariehamn (grid 27° E: 668:10), Lahti (676:42) and Kuopio (697:53).

Year	Temperature (°C)						Precipitation (mm)					
	Mariehamn		Lahti		Kuopio		Mariehamn		Lahti		Kuopio	
	I-XII	V-VIII	I-XII	V-VIII	I-XII	V-VIII	I-XII	V-VIII	I-XII	V-VIII	I-XII	V-VIII
1985	3.3	12.8	3.5	13.4	2.7	13.2	43.0	39.5	57.6	80.5	54.8	62.7
1986	5.6	13.3	4.5	14.5	3.9	14.2	46.7	50.6	58.0	70.1	48.4	59.3
1987	5.0	11.0	3.9	12.1	2.8	11.9	46.2	61.8	52.2	76.9	58.6	93.6
1988	6.5	14.2	5.3	15.8	4.1	15.1	49.3	53.3	59.4	53.0	53.6	71.8
1989	7.4	13.5	6.7	14.8	6.0	14.9	51.9	63.0	54.5	68.4	46.6	52.6

or in areas where our threatened taxa are common enough to allow experiments. The characteristics and status of our marginal populations should then be compared with these results. Most of the difficulties in our study derive from the fact that in many cases we are forced to work with very few and small populations in which all kinds of damage should be avoided. However, population biology of threatened plants may also have general significance because it adds information on the behaviour of small marginal populations, often isolated from the main area at least hundreds of years ago.

Although we are far from the final goal and our knowledge is still very fragmentary, some working hypotheses concerning the population dynamics of several threatened species begin to emerge. The next step is, and will be, the formulation of recommendations for management of the populations of these species. If the hypotheses are correct, populations should increase. Whatever happens, it will add to our knowledge. In this way management of local populations of threatened species, often considered a kind of "applied science", can be seen as a part of experimental research according to the highest standards of "pure science". For that purpose, proper documentation of all management measures at the localities and monitoring of their effects is of great importance.

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