



# sommerfeltia supplement

6

R.H. Økland

**Boreal coniferous forest vegetation in  
the Solhomfjell area, S Norway:  
structure, dynamics and change, with particular reference  
to effects of long distance airborne pollution.**

**1995**



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Final report from the project "Effects of long distance airborne pollutants on the vegetation of boreal coniferous forests" (455.032/87, 455.032/91, and 101583/720) to The Norwegian Research Council, TVLF programme.

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Seventeen original papers that are parts of, or spin-offs from, the TVLF project "Effects of long distance airborne pollution", are summarized. All papers include data from the Solhomfjell reference area, a S Norwegian old-growth boreal coniferous forest with high deposition of long distance airborne pollution relative to other parts of Norway. Vegetation and environmental structure, population and vegetation dynamics, and vegetation change, was integrated by extensive use of the same sample sets. The nested sampling included 100 extended macro sample plots (64 m<sup>2</sup>) for tree species and 200 meso sample plots for the understory (1 m<sup>2</sup>; with 33 environmental variables measured and presence/absence of all species recorded in 16 subplots). Species abundances were recorded in 50 meso plots all years 1988-93, while all 200 plots were analyzed in 1988 and 1993. Other sampling designs were used for three special studies in the Solhomfjell area. Population biology of *Hylocomium splendens* was studied in six of NIJOS' ten areas for vegetational and environmental monitoring of Norwegian boreal spruce forests, as well as in the Solhomfjell area.

Gradient relationships of vegetation at the 1 m<sup>2</sup> scale in the Solhomfjell area are summarized by DCA ordination. Three coenoclines are identified: (1) a broad-scale gradient from xeric, lichen-dominated pine forest via subxeric pine forest dominated by ericaceous species and poor, *Vaccinium myrtillus*-dominated spruce forest to richer, herb-rich spruce forest, (2) a fine-scale gradient in degree of paludification (e.g., dominance by *Sphagnum* spp.), most strongly visible in the bottom layer, and (3) a micro-scale gradient from dominance by small hepatics and mosses to dominance by larger mosses of the forest floor. Associated complex-gradients were identified or hypothesized by use of measured environmental variables: (1) danger of soil moisture deficiency and soil nutrient content, (2) median soil moisture, and (3) several aspects of microtopography. Several kinds of independent evidence indicates that physiological tolerance is more important than interspecific competition in the understory. Temporal variation in soil moisture and soil pH is studied, with reference to the main gradients. Persistence of cryptogams as well as vascular plant species was species-specific and size-dependent, with little variation between years. The rate of vegetation dynamics varied predictably along the main coenocline, in relation to site productivity and environmental harshness. The magnitudes of one-year change in species abundances and vegetation were used to evaluate the significance of change in the five-year period. Significant humus acidification occurred in the five-year period, most strongly in richer spruce forest where several vascular plant species declined and vegetation changed in direction of poor spruce forest. N fertilization may explain the increase of *Deschampsia flexuosa* in spruce forest. Significant enrichment of pine forest humus is demonstrated. Norway spruce and Scots pine showed inconsistent patterns of variation in relative crown density. Stem number and stand volume in permanent plots increased for all tree species.

Modular growth, branching patterns, and hence demography of the clonal moss *Hylocomium splendens*, was strongly size-dependent. Branching increased and risk of termination decreased with increasing segment size. Strong apical dominance was found. A combination of positive density-dependence of mean segment size, and regulation of segment numbers at very high densities was demonstrated. Mean segment size was strongly related to length of the photosynthetically active period. Increase of most bryophytes in the Solhomfjell area 1988-93 was primarily due to several mild, rainy winters during the period.

Advantages of an integrated approach to monitoring of boreal forests (including trees, understory and environment; the population, species and vegetation levels of organization; several spatial and temporal scales; and univariate as well as multivariate statistical methods) are emphasized. Data from other regions and longer time periods are needed to assess the extent of vegetation response to environmental change.

**Keywords:** Acidification, Coniferous forest, DCA, Dynamics, Environmental change, Gradient, *Hylocomium splendens*, Scale, Vegetation.

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## LIST OF PAPERS

The following seventeen original papers (thirteen published or submitted for publication, data analysis completed for the remaining four) are parts of the TVLF project "Effects of long distance airborne pollution", or spin-offs from this project (\*). Papers that include data from other studies (and study areas other than the Solhomfjell area, Gjerstad) are indicated by \*\*. The papers will be referred to by roman numerals, e.g., [VI, XVI]. Papers [V, VI] are based upon the Cand. scient. Thesis of Opheim (1994); paper [VII] upon the Cand. scient. Thesis of Goth & Røeggen (1994).

- I\*\* Økland, R.H., Økland, T. & Eilertsen, O. 1990. On the relationship between sample plot size and beta diversity in boreal coniferous forests. - *Vegetatio* 87: 187-192.
- II Økland, R.H. & Eilertsen, O. 1993. Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. *Sommerfeltia* 16: 1-254.
- III Økland, R.H. & Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. - *J. Veg. Sci.* 5: 117-126.
- IV Økland, R.H. 1994. Patterns of bryophyte associations at different scales in a Norwegian boreal spruce forest. - *J. Veg. Sci.* 5: 127-138.
- V\* Opheim, A. & Økland, R.H. Seasonal variation of moisture in humus along a topographic gradient in a Norwegian boreal coniferous forest. - Manuscript in prep.
- VI\* Opheim, A. & Økland, R.H. Seasonal variation of pH in humus along a topographic gradient in a Norwegian boreal coniferous forest. - Manuscript in prep.
- VII\* Talgo, B.M., Røeggen, O. & Økland, R.H. Micro-scale vegetation-environment relationships in a boreal spruce forest site in the Solhomfjell area, Gjerstad, S Norway. - *Sommerfeltia*, subm.
- VIII\*\*\* Økland, R.H. 1995. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests: demography. - *J. Ecol.* 83: in press.
- IX\*\*\* Økland, R.H. & Økland, T. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. II. Effects of density. - *J. Ecol.*, subm.
- X\* Økland, R.H. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. III. Population dynamics in the Solhomfjell area during a 5-year period. - Manuscript in prep.
- XI Økland, R.H. 1995. Bryophyte and lichen persistence patterns in a Norwegian boreal coniferous forest. - *Lindbergia* 19: 50-62.



- XII Økland, R.H. 1995. Persistence of vascular plants in a Norwegian boreal coniferous forest. - *Ecography* 18: 3-14.
- XIII Økland, R.H. 1995. Species abundance variation in the boreal coniferous forest floor at Solhomfjell, S Norway, 1988-93. - *Nord. J. Bot.* 15: in press.
- XIV Økland, R.H. Year-to-year vegetation dynamics in a Norwegian boreal coniferous forest during a 6-year period. - *J. Veg. Sci.*, *subm.*
- XV Økland, R.H. & Eilertsen, O. Changes in the vegetation of a Norwegian boreal coniferous forest, 1988-93. - *J. Veg. Sci.*, *subm.*
- XVI\*\* Strand, G.-H., Økland, R.H. & Økland, T. Regional variation of change in crown density in coniferous forests: a comparative study of three investigations in southern Norway. - *Scand. J. For. Res.*, *subm.*
- XVII Økland, R.H. Tree population dynamics in a Norwegian boreal coniferous forest, 1988-93. - *Manuscript in prep.*

## INTRODUCTION

### INTRODUCTION

During the 20th century, European forest soils have experienced acidification and cation leaching, apparently due to the effects of long distance airborne pollutants [see II, XIII, XV]. Simultaneous nitrogen enrichment may lead to nutrient unbalance (e.g., Tamm 1991). Since "new forest damages" were first reported from C Europe (see reviews by, e.g., Schütt & Cowling 1985), large efforts have been made to determine extent and causes of forest decline, in Norway as well as in other countries (see Aamlid et al. 1990, Venn et al. 1993). Although causal interpretation of forest vitality measurements is often problematic (e.g., Solberg 1993, Thomsen & Nellemann 1993, Nellemann & Frogner 1994), coniferous trees in SE Norway now seemingly suffer from long-term vitality reductions (Venn et al. 1993, Solberg 1994).

The ground vegetation is likely to be more sensitive than trees to environmental change [see II] because the number of species is high and because many vegetative and generative strategies are represented (see Eriksson 1989, [XI, XII]). Fundamentally different mechanisms of water and nutrient uptake are found in vascular plants and cryptogams (from soil, and mostly directly from the atmosphere, respectively). Thus the two groups are likely to react to different sets of environmental factors and hence, complement each other as biological indicators.

Several recent studies from C Europe and S Sweden have reported increase of acid-tolerating and/or nitrophilous species [see II]. No consistent trends have, however, been reported from N Europe (Norway, N Sweden, Finland) where deposition rates are lower (see Lähde & Nioppola 1987, Dahl 1988, Bjørnstad 1991, Rosén et al. 1992). This may be due to: too low a number of studies still carried out, regionally different patterns of vegetation change, or limitations set by the quality and extent of available data. In the almost complete absence of long time-series of vegetation analyses in permanent plots (see Sunding 1985, [II, XIV]), vegetation change has been approached by reanalysis of previously analysed plots, relocated with the greatest possible precision, or by pseudoreplicated designs (Hurlbert 1984) such as synchronous comparison of areas along deposition gradients [see XV]. Statistical tests and multivariate techniques (see Minchin 1987, ter Braak 1987, R. Økland 1990, Palmer 1993) have so far rarely been used in these studies, because of low number of relocated plots.

Interpretation of vegetation change requires good basic knowledge of the system studied (T. Økland 1990, [III]). Nordic approaches to boreal forest vegetation have mostly been descriptive in scope, with emphasis on classification (cf. R. Økland & Bendiksen 1985, [II]). The existence of one major coenocline in boreal forests; from lichen-rich pine forest to mesic spruce forest, has often been hypothesized [see II for references]. High local importance of other coenoclines has been demonstrated by recent studies applying multivariate techniques to unbiased sample sets (e.g., T. Økland 1990, 1993, Rydgren 1993). A regionally valid gradient reference frame (R. Økland & Bendiksen 1985) that systematizes our present knowledge is urgently needed.

Development of a vegetation model is a major task of contemporary vegetation science (see Austin 1990, Keddy 1992, van der Maarel & Sykes 1993, Austin & Gaywood 1994). Several explanations have been forwarded for species turnover along the major coenocline,

e.g.; (1) resource competition for light versus N (Kuusipalo 1985, Tilman 1988), and (2) centrifugal organization along productivity gradients (Keddy & MacLellan 1990), but others may also be relevant, e.g., (3) species distributions determined by physiological tolerance (cf. Austin 1990). Interspecific competition is attributed high importance in (1) and (2); environmental stress, climatic fluctuations and fine-scale disturbance in (3). Detailed data on the gradient relationships of vegetation may have relevance to evaluation of vegetation models (R. Økland 1992).

Two separate, but methodologically co-ordinated programmes for integrated monitoring of understory vegetation, tree growth and vitality, and soil properties in Norwegian boreal old-growth forests, were started in 1988: (1) NIJOS' vegetational and environmental monitoring of Norwegian boreal spruce forests dominated by *Vaccinium myrtillus*, using ten reference areas in south and central Norway (see T. Økland 1989, 1990, 1993), and (2) the TVLF project "Effects of long distance airborne pollution", in the Solhomfjell reference area, S Norway [see II]. To mitigate several gaps in our knowledge, with high relevance to interpretation of data on vegetation change, basic research was incorporated into the monitoring programmes. Such gaps include (1) species responses to major complex-gradients [T. Økland 1990, 1993, in prep., II, III], (2) interactions between layers [see II, IV], (3) the importance of competition (between and within species; see [II, IV, VII, VIII, IX, XI, XIII, XIV]), (4) fine-scale vegetation-environment relationships [see T. Økland 1990, II, III, IV, VII, VIII], (5) the natural, year to year, vegetation dynamics [see XI, XII, XIII, XIV], (6) population biology and life history of the dominant bryophyte and lichen species [see VIII, IX, X, XI], and (7) environmental variation on fine temporal scales (see Skyllberg 1991, Falkengren-Grerup 1994, [V, VI]).

## AIMS

This paper reports results and conclusions from basic as well as applied research in the Solhomfjell reference area, 1988-94. A study of the population biology of the moss *Hylocomium splendens*, jointly using data from the Solhomfjell area and six of NIJOS' ten monitoring areas [see VIII] is also reported. Data from outside the Solhomfjell area are also included in [I, XVI]. The major, specific aims are: (1) to identify the major gradients in vegetation (coenoclines) in a boreal coniferous forest and to relate them to environmental complex-gradients, (2) to quantify the dynamics of boreal forest vegetation on fine spatial and temporal scales, and (3) to test for long-term change in Norwegian coniferous forests - in plant populations, species abundances, species composition, and tree vitality - and discuss relationships between these changes and environmental and/or climatic change. Effects of deposited long distance airborne pollutants are particularly addressed.

## THE SOLHOMFJELL REFERENCE AREA

### THE INVESTIGATION AREA

The Solhomfjell area in Gjerstad, S Norway, ca. 2 km<sup>2</sup>, 58°58' N, 8°58' E, altitude 350-480 m.a.s.l., established as a reference area for monitoring of boreal forests in 1988, was used for all studies reported in this paper. Data from other areas are included in [I, VIII, IX, X, XVI]. The Solhomfjell area is geologically homogeneous; the bedrock belongs to the central-southern Norwegian Precambrian (Ofte Dahl 1980), and is low-weathering. The bedrock is mostly not covered with morainic deposits, thus most of the soils have been formed *in situ*.

The climate is suboceanic, with an estimated annual temperature *normal* 1961-90 of 4.2 °C and an annual mean precipitation (1961-90 *normal*) of ca. 1300 mm (see paper [II] for details). Except for 1988 and 1991, with permanent snow cover and winter temperatures close to normals, all winters 1988-93 were exceptionally mild (see paper [XIII] for details). The early summers were mostly drier than normal. A particularly strong (early) summer drought occurred in 1992 when low rainfall coincided with periods of high temperatures. Rainfall in the growing season was below the normal in all years except 1988, while winter precipitation was close to, or higher than, the normal. All years were warmer than normal.

Annual amounts of acidifying compounds deposited by precipitation (1992 and 1993 averages) were 7.9 kg N ha<sup>-1</sup> yr<sup>-1</sup> (4.3 kg NO<sub>3</sub>-N and 3.6 kg NH<sub>4</sub>-N) and 6.4 kg SO<sub>4</sub>-S ha<sup>-1</sup> yr<sup>-1</sup>; the annual mean rainwater pH was 4.4 (Tørseth & Røyset 1993, Tørseth & Røstad 1994). The deposition of long distance airborne pollutants is high relative to other parts of Norway (Statens Forurensningstilsyn 1992).

The area is situated in the southern (and middle) boreal zone (in the terminology of Ahti et al. 1968). Forests dominated by Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) alternate with mires as the dominant ecosystem.

The forests have not been commercially exploited, and no traces of logging occur. Trees with fire scars have been observed sporadically, but only outside the sampled transects. It is likely that the development of vegetation has been continuous for a long time, perhaps several hundred years. Tree ages up to 200 years for Norway spruce and 350 years for Scots pine have been recorded. The area is protected as a National Nature Reserve.

### THE SAMPLING DESIGN

A nested sampling design was designed for integrated vegetation monitoring in the Solhomfjell area (and used for all studies except [V, VI, VII]).

Eight transects of different lengths were subjectively selected to cover the variation in boreal forest vegetation in the Solhomfjell area. Every tenth meter along a transect was a potential site for the lower left corner of a macro sample plot, 16 m<sup>2</sup>. Positions were rejected if they included (1) mires, tarns or elements of ecosystems other than forest, (2) more than 50% naked rock, (3) cliffs higher than 1 m, or (4) boulder stones with diameter larger than

1 m. From the accepted positions, macro sample plots were drawn at random except for the following restrictions: (1) plot number per transect was to be proportional with transect length, and (2) total plot number was to be 100. Extended macro plots, 64 m<sup>2</sup>, obtained by including a 2 m zone around each macro plot, were used for studies of tree layer dynamics. Each macro sample plot was divided into 16 macro subplots, of which two (along opposite margins of the macro plot, in fixed positions) were taken as meso sample plots (1 m<sup>2</sup>). Meso plots with (1) more than 25% naked rock, (2) micro-scale cliffs higher than 0.25 m, (3) boulder stones with diameter larger than 0.25 m, or (4) stems of living trees higher than 2 m, were rejected and replaced by a neighbouring plot, selected from a fixed priority list. Each meso sample plot was divided into 16 meso subplots (hereafter referred to as subplots; 0.0625 m<sup>2</sup> each), of which two in fixed positions were taken as micro sample plots and divided into 16 subplots. Further details of sampling are provided in paper [II].

## SUMMARY OF PAPERS

### PAPER I

Nested sample plots from studies of three Norwegian coniferous forest areas [Høylandet, N Trøndelag, C Norway (J. Holten et al., unpubl.); Rausjømarka, Akershus, SE Norway (T. Økland 1990); and the Solhomfjell area] were used (16 and 1 m<sup>2</sup> in Høylandet, otherwise 1 and 1/16 m<sup>2</sup>). For each sample plot size, species quantities were recorded as frequency in subplots. All data sets were subjected to DCA ordination, using the same choice of options. The total abundance recorded for each species, and hence species tolerances which are positively correlated with abundance (Austin 1987), decreased with plot size. This explains why beta diversity, measured as the length of the first DCA axis (calculated by implicitly averaging species tolerances; Hill 1979) was inversely related to sample plot size. Eigenvalues of the axes increased when the plot size was reduced, due to weakening of structure in the data matrices when fine-grained patterns of vegetation are emphasized.

### PAPER II

A gradient reference frame for understory vegetation in the Solhomfjell area was established by identification of major coenoclines and complex-gradients. The main data set included analysis in 1988 of 200 meso sample plots (1 m<sup>2</sup>) with 171 species, provided with measurements of 33 environmental variables. The set of 400 micro sample plots (1/16 m<sup>2</sup>) with 144 species was also used. Species abundance was recorded as frequency in 16 subplots.

DCA and LNMDS ordinations of meso sample plots were largely identical, with two coenocline axes that could be interpreted ecologically. The first axis (DCA 1) was significantly correlated with 20 environmental variables at the  $P < 0.0001$  level; most strongly with topographic position. pH and Total N (both decreasing along DCA 1) and loss on ignition (increasing) were strongly correlated with DCA 1 in the spruce forest (Subset A;  $DCA\ 1 < 3.25$  S.D. units); soil depth, loss on ignition and micro-scale unevenness (all decreasing along DCA 1), topographic position, and Total N (increasing) in the pine forest (Subset B). The ordering of sample plots along DCA 1 was almost perfectly recovered along first axes in separate DCA ordinations of vascular plants (Subset C: 65 species) and cryptogams (Subset D: 106 species), and in the micro plot ordination. This indicates existence of a main coenocline that influences species of all plant groups, and that is a result of two complex-gradients (both related to topography): (1) a topography-soil depth complex-gradient in the pine forest [coenocline from xeric (lichen-rich) pine forest (forest type B2 in subsequent papers;  $DCA\ 1 > 4.50$  S.D. units) via subxeric (*Calluna*- and *Vaccinium*-rich) pine forest (type B1,  $3.25 < DCA\ 1 \leq 4.50$  S.D. units) to submesic *Vaccinium myrtillus*-dominated spruce forests (forest type A2 in subsequent papers,  $2.00 < DCA\ 1 \leq 3.25$  S.D. units)], and (2) a complex-gradient in soil nutrient status in the spruce forest [running from poor spruce forest to richer spruce forest (type A1,  $DCA\ 1 \leq 2.00$  S.D. units)].

DCA 2 was significantly correlated with 10 environmental variables at the  $P < 0.0001$  level; most strongly with canopy cover and soil depth (increasing along the axis), and median soil moisture, extractable Al and inclination (decreasing). Patterns of correlated variables did not differ much between spruce and pine forests. The only other strongly correlated ordination axis was the second axis of the cryptogam ordination. DCA 2 was thus interpreted as a fine-scale paludification gradient that mainly influences the bottom layer, also reflecting the variation from between trees (high soil moisture) to underneath trees. The correlations of DCA 2 with soil depth and inclination indicated that soligenous (rather than topogenous) fine-scale paludification dominates in the Solhomfjell, due to a superhumid climate.

Mechanisms behind gradient responses are discussed. The *soil moisture deficiency hypothesis*; that the limits of vascular plants and bryophytes towards xeric sites are set by physiological tolerance to desiccation (survival of extremely dry periods), is consistent with the absence of variation in soil pH or cation content in pine forest humus. The *increase* in Total N towards the xeric end of the main coenocline may be interpreted as oversaturation and N accumulation due to deposition of airborne  $\text{NO}_3^-$  or  $\text{NH}_4^+$ . Limits of cryptogamic species towards more mesic sites (and towards paludified sites) may be set by competitive ability (growth rates) in accordance with the competitive hierarchy theory, although other mechanisms may also be involved. The most important factor for differentiation of vascular plants along the nutrient gradient in spruce forest is considered to be N availability, while bryophytes probably respond to a complex of factors, including structural properties of the humus layer.

Structuring processes are discussed with reference to the observed patterns. The lack of a closed bottom layer in almost all sample plots is considered a strong indication that fine-scale disturbance and density-independent mortality (physiological tolerance) are more important than interspecific competition.

### PAPER III

Paper [III] presents an alternative treatment of data from paper [II], using the 200 meso plots (also divided into forest type and layer subsets [II; see above] and the 400 micro plots (1988 analyses) from the Solhomfjell area. The 33 environmental explanatory variables measured at each meso plot were classified to four groups (E1: topographic, E2: topographically dependent environmental, E3: soil chemical, and E4: biological and strongly biologically dependent). Nine spatial explanatory variables were derived from geographical co-ordinates as combinations of  $x$  and  $y$  of order up to three. The variation in species-sample plot matrices was partitioned onto different sets of explanatory variables by use of (partial) canonical correspondence analysis, according to the method outlined by Borcard et al. (1992).

Ca. 35 % of the variation in species abundances was explained by the 42 explanatory variables, of which ca. twice as much by significant environmental as by spatial variables. Ca. 45% of the variation explained by environmental variables was due to topography. This supports the hypothesis of macro-scale topographic control of boreal forest vegetation (Kuusipalo 1985, Sepponen 1985, [II]). Topographic variables were most important in pine forest, soil chemical variables in spruce forest [cf. II]. At finer scales (reduced plot size), less variation could be explained by explanatory variables, due to the weakening of vegetation-

environment relationships ([I], Palmer & Dixon 1990, Reed et al. 1993).

The lower fraction of variation in abundance explained for cryptogams than for vascular plants, may be due to: (1) higher relevance of the explanatory variables to vascular plants because they take up water and nutrients from soil while uptake is directly from the air in the ectohydric (Buch 1947) cryptogams which dominate boreal forests, (2) the larger size of vascular plants, integrating the environment over broader scales (Svensson & Callaghan 1988, Palmer & Dixon 1990), (3) higher disorderliness (Fowler 1990) in the bottom layer, due to smaller plant size (lower plant unit area; van der Maarel 1988), perhaps resulting from higher susceptibility to fine-scale disturbance.

Some methodological aspects of CCA with variation partitioning are discussed: improvements, necessary precautions, and advantages over alternative methods.

#### PAPER IV

Patterns of associations between the 36 most frequent bryophyte species and their relationships with trends in  $\alpha$  and  $\beta$  diversity were studied, using 85 meso sample plots (1988 analyses; data from [II]) from poor and slightly rich spruce forest (strongly paludified plots omitted) in the Solhomfjell area. Seven data sets at five spatial scales (from 1 m<sup>2</sup> to 1/256 m<sup>2</sup>) were derived by use of meso and micro subplots. The range and dispersion of  $\alpha$  diversity values (species number per sample plot) in the data sets were significantly higher than in comparable model data sets. This indicated variation from favourable to unfavourable conditions for bryophytes at all scales, probably in relation to cover of the upper layers (the canopy closure gradient, cf. paper II]). The number of positive associations was significantly higher than predicted from a random distribution, for all sample plot sizes except the smallest. This excess of positive associations was due to the presence of (1)  $\alpha$  diversity trends, as demonstrated by a stochastic simulation study, and (2)  $\beta$  diversity (variation along environmental gradients). Facilitation - positive density-dependence caused by more favourable moisture conditions within dense stands [suggested by, e.g., Hobbs & Pritchard (1987), Scandrett & Gimingham (1989), and During (1990)] - is discussed as a possible third cause of excess positive associations. A micro-scale coenocline from dominance of large forest floor mosses to small hepatics was added to the two more broad-scale coenoclines identified in paper [II]

The number of significant negative associations was generally low, and deviated neither from theoretical values assuming random distribution of species, nor from predicted values accounting for  $\alpha$  diversity trends. The low proportion of negative associations, even in the presence of  $\beta$  diversity trends, suggests that interspecific competition is not important in this vegetation. Several alternatives to competition are discussed; (1) static mechanisms for avoidance of competition, (2) mobility, and (3) high importance of density-independent mortality, in particular due to fine-scale disturbance.



## PAPER V

Seasonal variation in volumetric moisture content of the upper 5 cm of the humus layer was investigated in 1992 in 30 sample plots (1 m<sup>2</sup>) from the Solhomfjell area, not included in the main sampling scheme but selected to span the coenocline from xeric pine forest to poor submesic spruce forest (cf. paper [II]). Plot positions along this coenocline (DCA 1 of paper [II]) were found by passive ordination.

Seasonal variation in soil moisture was related to temperature and, even more important, rainfall. Soil moisture contents in a dry and a wet period [within one year (30 plots), and between years (June 1992, under extreme drought, and October 1988, with moisture close to the median; measurements in the 200 meso plots of [II])] were weakly correlated. This supported the hypothesis of paper [II], that there are considerable variation between sites in the cumulative distribution of soil moisture.

Due to nonlinear variation in organic content (highest in subxeric forest) and bulk density of the humus (highest in xeric sites) along DCA 1, the duration of humus moisture (at any level) *increased* in pine forest towards xeric sites, contrary to predictions [in II] from the soil moisture deficiency hypothesis. Soil depth did, however, decrease along DCA 1. This suggested a re-formulation of the hypothesis in terms of total moisture available to plants during dry periods, also taking water stored in deeper soil layers into account.

The median and upper percentiles of moisture duration curves were significantly different between paludified and non-paludified sites. Soil moisture content was negatively correlated with DCA 2 at all sampling occasions except during early summer drought. This confirms the hypothesis [paper II] that DCA 2 depends on median (normal) soil moisture.

## PAPER VI

Seasonal variation in pH<sub>H2O</sub> was studied in the Solhomfjell area, by collecting humus samples from the 30 sample plots of paper [V] at 12 occasions between May and October 1992. pH amplitudes were 0.20-0.75 for single plots, 0.23 for the average. pH was low in spring, generally higher in summer (except for 31 July, when the lowest average was found), and stable at intermediate levels during September and October. Differences from more mesic forests (e.g., dominated by spruce; Hesselman 1937, Skyllberg 1991) were: (1) no correlation between average pH and humus moisture (also see Sirén 1955), and (2) deviant seasonal trends, except for the low early summer pH which has been attributed to cation uptake by plants and microorganisms (Skylberg 1991). The results may indicate lower influence of biological processes on humus pH in pine than in spruce forests.

pH was significantly correlated ( $P < 0.0001$ ) between 38 out of 66 pairs of occasions. Coenocline position (DCA 1 score) and pH were positively correlated (pH increasing towards xeric pine forest) at 11 sampling occasions although significant at  $P < 0.05$  at two occasions only. This gives additional support to the hypothesis [cf. paper II] that in pine forest the main coenocline is not caused by variation in nutrient availability.

## PAPER VII

A gently sloping macro plot of  $14 \times 8$  m in spruce forest in the Solhomfjell area was intensively investigated. This macro plot was divided into 112 contiguous meso plots ( $1 \text{ m}^2$ ) with 1792 micro plots ( $1/16 \text{ m}^2$ ). A detailed map of the macro plot was obtained by levelling points 8.3 cm equidistant and mapping tree crowns, stones, logs etc. Seventeen environmental explanatory variables were recorded at the meso scale, 13 at the micro scale. Three complex-gradients were identified, associated with (1) soil moisture, (2) (micro-)topographic variables, and (3) canopy cover. These were partly inter-correlated. Cover in micro plots was recorded for all species (23 vascular plants, 73 cryptogams) and displayed on maps. Species distributions largely reflected the three complex-gradients.

Sets of meso and micro sample plots were ordinated separately by DCA, as well as passively placed along the interpreted DCA axes of paper [II]. Two coenoclines were present at both scales: (1) from level, *Sphagnum*-dominated plots with high median soil moisture to more strongly sloping and more uneven sites with high importance of hepatics, lichens and smaller mosses, and (2) a coenocline related to canopy closure, partly correlated with (1). The results indicate high local importance of fine-scale paludification, in accordance with paper [II], but also open for local divergence of the canopy cover and median soil moisture gradients. Coenocline (1) corresponds to the cryptogamic coenocline in [IV], associated with plant size. It may be related to disturbance (frequency of impacts) as well as environmental stress.

Semivariations and fractal dimensions were calculated for environmental and biotic variables, and ordination axes. The (average) level of spatial structuring, and spatial dependence as function of distance, both varied among variables and axes. Vegetation was spatially structured to a slightly lower extent than the most strongly spatially structured environmental variables (soil depth and canopy closure).

The fraction of variation in species abundances that could be explained by environmental variables (using the CCA method of paper [III]), were 34% at the meso scale and 14% at the micro scale, while 33% and 17%, respectively, were explained by spatial variables. Correlations between environmental variables and ordination axes (and between pairs of environmental variables) were lower at finer scales. This supports the hypothesis of reduced environmental structuring of vegetation towards finer scales (notably below  $1 \text{ m}^2$ ; cf. [I,III], Reed et al. 1993), probably due to increasing importance of fine-scale disturbance and random processes towards very fine scales.

## PAPER VIII

*Hylocomium splendens*, a perennial clonal moss, is particularly well suited for demographic studies. It is one of the most abundant mosses throughout the circumboreal forest zone, it has annual periodicity in the emergence of new modules (segments), and its ecophysiology has been studied in detail (e.g., Busby et al. 1978, Callaghan et al. 1978, Skre et al. 1983, Sonesson et al. 1992). New growing points usually emerge in spring and develop into mature segments their second summer. Population increase is brought about by ramification

(branching) of the youngest segment or by regeneration from older parts of the shoot system (bud initiation after one or several years of delayed development).

A technique for nondestructive re-identification of segments in permanent vegetation plots is devised. Seven areas were used for this study; six of NIJOS's ten monitoring areas for vegetational and ecological monitoring of boreal spruce forests in south and central Norway (T. Økland 1990, 1993, in prep.), and the Solhomfjell area. A total of 119 permanent sample plots in spruce forest were used. All growing points and mature segments were censused every autumn since 1990, after the current year's mature segment had reached full size. The dry weight of each mature segment (in  $\log_2 DW \cdot 10^{-4}$  g units) was estimated from morphological measurements performed *in situ*. This study is based upon precise demographic information on 9,206 growing points and 7,602 mature segments, obtained during censuses in 1990, 1991 and 1992.

Each mature segment has a potential for production of new growing points that is strongly size-dependent; ca. 40% of the variation in a segment's size could be explained by the size of its mother segment. Size relationships within segment chains indicated that integration is largely restricted to adjacent segments. The number of offspring growing points (by ramification as well as regeneration) was positively size-dependent, while termination risk was negatively size-dependent. Mature segments produced by regeneration were smaller, while segments produced by ramification were larger than the average segment. Strong apical dominance was demonstrated. Annual recruitment 1989-92, averaged over populations, areas and years, was 32.3%; 23.3% by regeneration, 7.5% by ramification, and 1.5% by accidentally introduced shoots. Annual mortality was 19.7%; 6.8% by loss, 1.9% by grazing, and 11.0% by termination for other reasons.

Demographic data for growing points and mature segments were analyzed separately by stage-structured transition matrix models. The total population increased every year, the average intrinsic rate of increase,  $\lambda$ , equalled 1.10-1.11. Vital rates, and hence fitness, were strongly size-dependent. Thus the contributions of ramification (mainly of large segments) and regeneration (mainly giving rise to small offspring segments) to increase in  $\lambda$  were equal despite regeneration was three times more frequent than regeneration. Ramification is important for maintenance of size and risk-spreading among ramets under favourable conditions, while high ability to regenerate from older segments facilitates resilience to, and recovery after, disturbance.

If not interrupted by regeneration after damage or severe disturbance, mean *Hylocomium splendens* segment size is expected to increase gradually to a limit set by the local environment (higher in favourable sites). *Hylocomium splendens* has high flexibility as to life strategy: competitor traits (large segments, high importance of ramification) dominate in favourable habitats with long continuity, stress-tolerator traits (small segments, low importance of ramification) in unfavourable habitats with long continuity, and ruderal traits (small segments, high importance of regeneration) in habitats with high frequency of fine-scale disturbance.

*Hylocomium splendens* is closely similar to clonal forest vascular plants in major demographic traits, such as size-dependence of fitness and branching patterns.

## PAPER IX

This study was based upon demographic information on 14,776 *Hylocomium splendens* growing points from 119 populations (1990-94 censuses of the same sample plots as in [VIII]; see [VIII] for details). Population mean segment size was positively correlated with bryophyte cover (a measure of density); twice as large at 100% cover as at 1% cover. This is probably due to improved moisture conditions in dense stands, notably the prolonged periods with positive net photosynthesis (cf. paper [IV]).

The regeneration frequency declined with increasing density, most strongly when effects of size were corrected for, probably due to light-induced reduction of bud initiation in dense stands. The size-corrected mortality (termination and loss) was not related to density, but burial in the moss carpet (affecting 2.0% of all growing points, *ca.* 10% of all mortality), increased strongly with density and at high densities affected *ca.* 5% of all growing points. Regulation of *Hylocomium splendens* populations at high densities may therefore occur by a combination of reduced branching (ramification and regeneration) and increased burial in the bryophyte carpet. However, this mechanism is apparently rarely invoked; disturbance and environmental variation at scales down to the size of individual *Hylocomium splendens* segments seemingly keep *Hylocomium* populations at lower densities for most of the time.

## PAPER X

The demography of *Hylocomium splendens* in spruce forest in the Solhomfjell area is followed for five one-year periods (see paper [VIII] for details). The relative number of growing points increased 40% from 1989 to 1994; it was unchanged 1989-90 and increased the other one-year periods (6%, 18%, 12%, 1%, respectively). The average size of mature segments (in  $\log_2 DW \cdot 10^{-4}$  g units, see [VIII]) in consecutive one-year periods were 4.61 (segment mature in 1990), 4.47, 4.80, 4.95, and 4.47. Branching rates were dependent on absolute size and relative growth rates [VIII], thus the population increased primarily in years with strong increase in size. Ramification and regeneration after one year's delayed development occurred with constant frequency, while the frequencies of termination and regeneration from older parts and detached fragments varied considerably.

Size declines were observed in 1991 and 1994, for segments that experienced short first autumn growing seasons (1990, 1993) and long winters with stable snow cover until May, that passed directly into dry early summers. The other winters were mild and rainy, without a permanent snow cover. This suggests that growth and population development of *Hylocomium splendens* is primarily determined by the length of the period available for growth. In water-limited ectohydric bryophytes, growth occurs when tissue water content (and temperature) is above a certain threshold (cf. Stålfelt 1937, Busby & Whitfield 1978, Sonesson et al. 1992).

## PAPER XI

Persistence, a species' tendency to remain in its original position and not to colonize new sites, is studied for 36 bryophyte species in spruce forest and 20 species (including 7 lichens) in pine forest in the Solhomfjell area. Data sets include presence/absence in 199 meso plots with 3184 subplots analyzed in 1988 and 1993 [cf. II], and a subset with 50 meso plots (every fourth meso plot) and 800 subplots, analyzed for six consecutive years. Persistence was calculated for different temporal (1-5 years) and spatial (1/16 and 1 m<sup>2</sup>) scales. Persistence patterns in spruce and pine forests were closely similar. Two main components of variation in persistence were demonstrated by PCA analyses: (1) the absolute level of persistence which was strongly associated with size and ran from small bryophytes (mostly hepatics) to large mosses, hepatics, *Sphagnum* and lichens, and (2) variation related to spatial scale. No variation in persistence could be attributed to the main coenoclines (DCA axes 1 and 2 of paper [II]), but the ranking of species according to absolute persistence corresponded to the micro-scale coenocline of papers [IV,VII]. Persistence is discussed in relation to real and apparent disappearances and colonizations. Strong size-dependence of persistence is suggested a typical property of cryptogams, on the levels of species as well as individual shoots.

## PAPER XII

Persistence [cf. paper XI] and other species characteristics [seedling frequency and mobility rate (compiled from literature), mean cover and abundance in the study area] is studied for the most abundant forest vascular plants (25 species in spruce forest and 7 in pine forest) in the Solhomfjell area, using the same data sets as in [XI]. Dominance in the boreal forest floor is mostly by clonal species. Species with optima in poor spruce forest were slightly more mobile and achieved higher cover and abundance than species with optima in richer spruce forest.

Persistence patterns in spruce and pine forests were similar, but persistence decreased towards the xeric pine forests. One main component of variation in persistence was demonstrated by PCA analyses: the absolute level of persistence, which is related to seedling recruitment vs clonal growth, and within clonal species to ramet longevity, abundance, mobility, growth pattern and mode of surviving the unfavourable season. Minor components of variation in persistence were related to spatial scale and temporal scale. Persistence characteristics were species-specific with little variation between years. Several species characteristics could account for variation in persistence, indicating continuous variation in a multidimensional life history characteristics space.

## PAPER XIII

Changes in the occurrence (presence) and abundance (frequency in 16 subplots) of vascular plants, bryophytes and lichens in the Solhomfjell area 1988-93 are studied, using the same

data sets as in paper [XI]. Nonparametric tests were performed all for combinations of species, data type (occurrence or abundance), forest type (spruce or pine), and time period (one-year or five-year). Results are interpreted using data on species persistence [papers XI, XII], and by comparison with European long-term and experimental studies.

No vascular plants showed long-term trends in pine forest. The abundance changes observed for several cryptogams were probably due to short-term (between-year) climatic fluctuations, notably drought. Decrease was noted for liverworts with optima along the main coenocline (DCA 1 of paper [II]) in, or close to, the spruce forest (*Barbilophozia floerkei*, *Calypogeia* spp. and *Ptilidium ciliare*), *Sphagnum capillifolium*, *S. quinquefarium*, and the moss *Racomitrium lanuginosum* with a western distribution, while increase was noted for species favoured by gap creation after drought (notably lichens, e.g., *Cladonia coccifera* agg., *C. squamosa* and *C. chlorophaea* agg., and *Dicranum scoparium*).

Five-year changes that probably represent long-term trends were found in spruce forest: (1) increase of *Deschampsia flexuosa*, (2) decrease of nine vascular plant species with preference for richer sites [very strong for *Oxalis acetosella* (in 1993 absent from 90 of the 231 subplots in which it occurred in 1988, while only 19 new occurrences were noted), strong also for *Calamagrostis purpurea* and *Gymnocarpium dryopteris*], and (3) increase of bryophyte species (very strong for *Dicranum majus*, *Hylocomium splendens*, *Plagiothecium laetum* agg., *Polytrichum formosum*, and *Rhytidiadelphus loreus*, strong for *Dicranum fuscescens* agg., *D. scoparium*, *Barbilophozia floerkei*, *Chiloscyphus profundus*, *Lophozia obtusa* and *Ptilidium ciliare*), notably species with optimum in poor spruce forest.

Fertilization by airborne N may explain the expansion of *D. flexuosa*. Most of the declining vascular plants are among mesotrophic species hypothesized to be particularly vulnerable to long-term soil acidification (Falkengren-Grerup 1986, 1987, Wittig & Werner 1986, Dahl 1988, Wittig 1988), but divergent trends have been reported in other studies.

The increase of bryophytes was characterized by (1) independence of taxonomic group, size, life strategy and growth form, (2) synchronous one-year trends; increase of many species 1988-89, 1989-90 and 1991-92 and decline of many species 1990-91, and (3) similar responses of congeners, e.g., in the genera *Dicranum* (3 species), *Plagiothecium* (3 species), *Barbilophozia* (4 species) and *Rhytidiadelphus* (2 species). This adds to previous evidence [IV, XI] for low importance of inter- (and intra-) specific competition between bryophytes in the boreal forest floor. The synchronous one-year changes and the lack of correspondence with trends in other long-term studies suggest that the bryophyte increase is caused by factors that operate on fine time-scales. Close correspondence with demographic variation in *Hylocomium splendens* [cf. X] and climatic data (p. 9) indicate that the decisive factor is the length of the period available for growth.

#### PAPER XIV

Year-to-year vegetation changes 1988-93 in the Solhomfjell area was studied in 50 meso sample plots (cf. paper [XI]). The number of species per plot differed between vascular plants and cryptogams, and between forest types. One analysis included 78-87% of the six-year total number of vascular plants and 65-80% of cryptogams. This difference reflected among-group differences in persistence, among others related to differences in plant unit area. The number

of vascular plant species in pine forest decreased during dry years. The number of bryophyte species increased in spruce forest, as reported for abundance in paper [XIII].

The dissimilarity of repeated analyses increased with time, indicating considerable stochasticity at the 1 m<sup>2</sup> scale. The dissimilarity between consecutive analyses of a plot (rate of vegetation dynamics), differed between forest types in a temporally invariant way: maximum in richer spruce forest, minimum in subxeric pine forest, intermediate values in the poor spruce and the xeric pine forest. This pattern can be ascribed to gradients in productivity, soil stability and intensity of disturbance. Higher dynamics of more species-rich vegetation indicates positive correlation between  $\alpha$  and  $\beta$  diversity along temporal as well as spatial gradients.

Significant overall vegetation change was demonstrated for most one-year periods and forest types, using CCA with binary time as the only constraining variable and Monte Carlo tests. Analyses from 1989-92 were passively fit into the DCA ordination of 200 sample plots, analyzed in 1988 and 1993. Directed vegetation change (in this ordination) was not related to forest type or one-year period, but a significant type  $\times$  period interaction indicated that forest types were differently impacted by climatic fluctuations.

## PAPER XV

Five-year changes in understory vegetation and properties of the humus layer (8 variables) in the Solhomfjell area are studied, using 400 analyses [200 meso plots  $\times$  2 times (1988 and 1993)]. Soil acidification was strongest in richer spruce forest where pH decreased by *ca.* 0.3 units, exchangeable Al and Mn doubled and Ca decreased. Accumulation of total-N was observed in poor spruce forest and pine forest. Significant overall vegetation change (tested by CCA with binary time as constraining variable, as in paper [XIV]) occurred in most forest types. This change was not explained by change in humus properties.

The interpretation of DCA ordination axes in paper [II] (200 meso plots) also applied to the DCA ordination of 400 analyses. Directed change (along DCA axes) occurred in all forest types, but significant five-year trends were inferred (by comparing variances for five-year change with variances for change during one-year periods [paper XIV]) for spruce forest only. The mean displacement of plots from richer spruce forest (vegetation, vascular plants, and cryptogams) was 0.1 S.D. units in direction of the poor spruce forest. Vascular plant change and change of cryptogams were not correlated and thus probably due to different causes. A long-term and broad-scale response of vascular plants to soil acidification was supported by comparison with other studies. Bryophyte change (both in richer spruce forest along DCA 1, and in poor spruce forest along DCA 2) as observed could be predicted from the increase in abundance (cf. papers [XIII,XIV]) and species optimum positions [II].

The study demonstrates that ordination and constrained ordination methods are complementary approaches to vegetation change and that interpretation of long-term vegetation change benefits from knowledge of short-term vegetation dynamics and environmental change.

## PAPER XVI

Changes in relative crown density of Norway spruce and Scots pine from 1988 to 1993 are studied in three data sets from SE Norway: (1) The two-county data set; 80 sample plots (250 m<sup>2</sup>, with 237 Norway spruce and 280 Scots pine trees) from Telemark and Aust-Agder counties, included in NIOS' 9×9 km regular grid for the national representative inventory (Rørå et al. 1988). (2) The 10 macro plots (50 m<sup>2</sup>, with 64 Norway spruce trees) in Grytdalen, Telemark, an area used for vegetational and ecological monitoring of boreal spruce forests in Norway (T. Økland 1990, 1993, in prep.). (3) The 100 extended macro plots (64 m<sup>2</sup>, with 116 Norway spruce and 68 Scots pine trees) in the Solhomfjell area. Data sets (2) and (3) included old-growth forest stands, while stands of all ages were included in (1).

Crown density increased from 1988 to 1993 for spruce in the two-county data set (2.0%,  $P = 0.02$ ) and for pine in the Solhomfjell area (4.1%,  $P = 0.0001$ ), but declined for spruce in Grytdalen (7.2%,  $P < 0.0001$ ) and the Solhomfjell area (4.4%,  $P = 0.0002$ ). The largest reduction in crown density in Grytdalen occurred in nutrient-rich sites with favourable aspect. No relationship was found between change in crown density and main coenoclines or complex-gradients in the Solhomfjell area.

The semi-variance of change in crown density in the two-county data set increased with increasing distance between plots; a range (distance below which change in crown vigour is spatially structured) of ca. 18 km was indicated. No spatial structure of change in crown density was observed for spruce in Grytdalen and pine in Solhomfjell, while some spatial structuring with a range of ca. 20 m was indicated for spruce in Solhomfjell. Possible reasons for divergent trends in the two-county data set and the intensively studied areas include: differences in management practice, stand age, sampling technique used (representativity and observer errors), and regional differences (climatic, or due to variation in the impact of long-distance airborne pollution).

## PAPER XVII

Tree population dynamics 1988-93 is studied in the Solhomfjell area, using the 100 extended macro sample plots (64 m<sup>2</sup>). The number of trees (> 2 m) increased by 0-10% for *Betula* spp., *Picea abies*, *Pinus sylvestris*, and *Populus tremula*, while *Sorbus aucuparia* increased by 40%. The annual mortality of spruce and pine trees was below 0.5%. The volume of standing trees increased with 2.18% per year for spruce and 2.14% for pine. Tree volume per unit area (stand volume) and average volume per tree decreased along DCA 1 ( $P < 0.01$ ), i.e., with decreasing soil nutrient content in spruce forest and with increasing danger of desiccation in pine forest, cf. paper [II]. For individual trees, volume increment was negatively correlated with initial volume ( $P \leq 0.0001$ ). Stand volume increment decreased along DCA 1 ( $P < 0.02$ ) when differences in stand volume were corrected for. Humus layer acidification in the five-year period was weakly related to stand density ( $P = 0.02$  for  $pH_{H_2O}$ ,  $P > 0.1$  for  $pH_{CaCl_2}$  and Ca); on average  $pH_{H_2O}$  was reduced by 0.09 pH units more in the densest than in open stands.

Size-structured transition matrix models were applied to demographic data for spruce and pine. The number of spruce seedlings and saplings (< 2 m; estimated from occurrences



in 1/16 m<sup>2</sup> subplots) was lower in 1993 than in 1988, in spruce as well as in pine forest. For pine, a decrease in pine forest was balanced by an increase in spruce forest [XIII]. The estimated population growth rates 1988-93 were  $\lambda = 0.9991$  for spruce and  $\lambda = 1.0315$  for pine ( $\lambda = 1.0415$  and  $\lambda = 1.0355$ , respectively, if constant numbers of plants < 2 m were assumed).

Possible reasons for the increase in number and volume of trees in old-growth forest in the Solhomfjell area in the study period include: (1) temperatures above the average in the whole period, (2) N fertilization, and (3) natural stand development.

## DISCUSSION AND GENERAL CONCLUSIONS

### VEGETATION STRUCTURE

#### *Main coenoclines in the Solhomfjell area*

Presence of three main coenoclines is demonstrated for the Solhomfjell area by ordination of vegetation, using sample plots of 1 m<sup>2</sup> or smaller: (1) a main, broad-scale gradient from xeric, lichen-dominated pine forest via subxeric pine forest and poor, *Vaccinium myrtillus*-dominated spruce forest to richer, herb-rich spruce forest [II, III], (2) a fine-scale gradient mainly affecting cryptogamic species composition, and reflecting the degree of paludification (e.g., dominance by *Sphagnum* spp. [II, VII]), and (3) a micro-scale gradient from dominance by small hepatics and mosses to dominance by larger forest floor species [IV, VII]. By use of measured environmental variables on scales ranging from 64 to 1/16 m<sup>2</sup>, the underlying complex-gradients have been identified. Coenocline (1) is related to broad-scale topography, but the decisive factors differ between pine and spruce forest [II, III]. Nutrient availability, suggested by several authors to account for the variation along coenocline (1) from poor spruce to xeric pine forest [cf. II] is ruled out by the results of [II, III, VI] that no nutrient decrease occurs along this coenocline. The soil moisture deficiency hypothesis, that variation in pine forest is set by probability and duration of soil moisture deficiency, was forwarded in [II] as an alternative. In paper [V] it is demonstrated that volumetric humus moisture does not explain variation along this coenocline. Nonlinear variation in soil texture and organic content occurs along the coenocline. An amended version of the soil moisture deficiency hypothesis, that the decisive factor is total moisture availability to plants, also dependent on soil depth, is therefore proposed. A complex-gradient in nutrient availability accounts for variation along coenocline (1) in spruce forest. Variation in median soil moisture, shown in [V] not to be correlated with soil moisture content in periods of extreme drought, explains the variation along coenocline (2) [II, III, V]. Median soil moisture and canopy cover are negatively correlated on broader scales (e.g., in the Solhomfjell area, [II]), but on finer scales they may uncouple and form two complex-gradients [VII]. Coenocline (3) is related to micro-scale variation in topography [VII].

Detailed vegetation ecological studies from other regions are needed before valid generalizations can be made about the gradient structure of boreal forest vegetation.

#### *Relevance to vegetation models: vascular plants*

Low importance of competition relative to physiological tolerance (vegetation model (3), cf. pp. 9) along the main coenocline, the only important coenocline for vascular plants in the Solhomfjell area [II], is indicated by: (1) lack of a closed field layer (occasional exceptions occur in the subxeric pine forest) [II], (2) no increase in nutrient concentrations from xeric pine forest to poor submesic spruce forest [II, VI, XV], (3) occurrence of most species with optima in poor spruce forest also in richer spruce forest [II], (4) ability to explain most species limits along the main coenocline by physiological tolerance [II], (5) dominance by clonal

species with low inter-ramet competition [cf. XII], (6) considerable life strategy variation, also among clonal species [XII], and (7) considerable fine-scale spatial and temporal mobility [XII, XIV]. Points (6) and (7) indicate that coexistence may occur without differentiation along fine-scale gradients, in accordance with the carousel model (van der Maarel & Sykes 1993, cf. [XII]).

*Relevance to vegetation models: cryptogams*

Low importance of competition among cryptogams is indicated by: (1) frequent occurrence of species mixtures in the forest floor, even at very fine scales (Arnborg 1943, T. Økland 1990, [II, IV, VII]), (2) high frequency of bare patches on the forest floor [II], (3) low proportion of negative interspecific associations, even between bryophytes in spruce forest [IV], (4) large surplus of positive associations between congeners [IV], (5) higher average *Hylocomium splendens* size when the bottom layer is closed ([IX]; also see During 1990), (6) low danger of burial of *Hylocomium splendens* in the moss carpet at normal densities [VIII, IX], (7) considerable among-species variation in morphology, growth form, mobility, temporal and spatial persistence, and hence in life strategy [XI, XIV], (8) diffuse growth form makes bryophytes poor effect competitors (i.e.: they have low ability to suppress growth of co-occurring species, cf. Goldberg & Landa 1991) [IV, VIII], (9) high stress-tolerance (to periodic drought, low radiation, etc., cf. Proctor 1982) makes bryophytes good response competitors (i.e.: tolerant to presence of other species) [IV, VIII], (10) synchronous one-year change for bryophytes in spruce forest in the Solhomfjell area 1988-93 [XIII], and (11) the increase of most species, even congeners, in spruce forest 1988-93 [XIII].

The limits of cryptogamic species (along the main coenocline) towards more mesic sites and towards sites with higher median soil moisture (and lower radiation stress) may also be set by lower inherent growth rates [II], in accordance with the competitive hierarchy theory (model (2) on pp. 7-8). This is supported by increasing rates of dynamics along presumed productivity gradients (from subxeric pine forest to richer spruce forest, and from low to higher median soil moisture in pine forest) [cf. XIV], but questioned by several of the points above (notably (2), (7)-(11)). Other possible causes of species limits towards mesic sites are: (1) unfavourable soil/litter conditions (e.g., the loose, unstable litter often present in subxeric pine forest; cf. [V]), and (2) low physiological tolerance to the reduced radiation under a denser field layer in subxeric pine forest and spruce forest; both of which related to occurrence of the deciduous species, *Vaccinium myrtillus*. Low growth rates may operate as a second control mechanism, excluding species from more mesic sites. An analogous control mechanism that is rarely invoked, is the regulation by shoot density in *Hylocomium splendens* populations.

Three explanations (models) may apply to coenocline (3): (1) the competitive hierarchy, indicated by co-ordinated variation in size [XI], persistence [XI], life strategy [VIII, XI], lifetime expectancy and mortality rates [VIII], and rate of dynamics [cf. IV, VII, VIII], (2) stress (physiological tolerance); larger species may be excluded by locally low throughfall precipitation, low radiation and high inclination in the micro-sites, and because of low ability to colonize bare, inorganic soil such as in strong slopes (During et al. 1988, Jonsson & Esseen in Jonsson 1993), also see papers [IV, VII, XI], and (3) micro-scale disturbance; because size increases slowly in clonal bryophyte populations, large size thus reflects long continuity [VIII] and successions towards dominance by large species will be reversed by micro-scale disturbance (e.g., Jonsson & Esseen 1990). (1)-(3) may all be important, and variation in their relative importance is expected to occur locally, regionally, and over time.

### *The competition concept*

The apparent conflict between vegetation models partly results from (1) different usage of terms such as competition (cf. Goldberg 1990, Grace 1990), (2) focus on the whole forest ecosystem including trees or focus on the understory or single layers, and (3) different emphasis on processes that all occur. In particular, the competition concept merits particular consideration. In my opinion, *plant competition* should only be used for neighbour interactions by which two species influence each other's performance (cf. Goldberg 1990). Mutual influence between neighbours mostly occurs within one layer between species with comparable mechanisms of water and nutrient uptake, etc. (a guild; cf. Root 1967). In this terminology, reduced radiation to the spruce forest understory is an example of stress ("external constraints which limit the rate of dry matter production ..."; Grime 1979: 21) rather than competitive action by trees. Species are then excluded from spruce forest by low physiological tolerance to shaded sites rather than by low ability to compete for light. This study gives several examples of main gradients (in vegetation and environmental factors) that are accompanied by variation in productivity, and with species limits set primarily by physiological tolerance (pp. 22-23).

This study emphasizes specific explanations applying to different coenoclines and layers rather than existence of one or a few general assembly rules. A high number of detailed vegetation ecological studies will be needed to decide whether the search for general assembly rules for vegetation will be in vain.

Studies performed in the Solhomfjell area thus suggest existence of three major coenoclines in boreal forest vegetation, that physiological tolerance is of great importance for the distribution of understory species along these coenoclines, that fine-scale disturbance may be important locally at a fine scale, and that the role of interspecific competition has generally been strongly overestimated. The generality of these hypotheses should be tested with data from other parts of the boreal coniferous forest region.

## DYNAMICS OF PLANT POPULATIONS AND VEGETATION

High fine-scale dynamics of the boreal forest understory is demonstrated at the species level. At the population level (within a species), dynamics is size-dependent in *Hylocomium splendens* [VIII, IX] and probably in other species as well. Persistence (a measure of dynamics at the species level) is a species-specific property (with small within-species variation from year to year) [XI, XII], probably reflecting growth rates, environmental stress in preferred sites and disturbance intensity in the species' realized habitat niche. Temporal stability of the relative importance of different plant groups along the main coenocline [XIV] makes differences between forest types in rate of vegetation dynamics temporally invariant [XIV].

In the Solhomfjell area, directed vegetation change (along main coenoclines) appeared to be damped in the spruce forest, while no such damping occurred in pine forest during a five-year period [XV]. This accords with stronger influence of climatic fluctuations on variation in species abundances from year to year in the pine forest [XIII], and is also in accordance with the hypothesis that species abundances in pine forest is ultimately controlled by extreme climatic conditions [e.g., II].

## HAS LONG DISTANCE AIRBORNE POLLUTION CAUSED VEGETATION CHANGE?

The pH reduction in humus in the Solhomfjell area from 1988 to 1993, by *ca.* 0.3 units in richer spruce forest [XV], exceeds the estimates obtained for maximum pH variation within one year (0.23 pH units with a lower number of samples, cf. [VI]) and maximum contribution from natural tree stand development (*ca.* 0.02 pH units, cf. [XVII]). The increase of exchangeable Al and decrease of Ca in richer sites [XV] support the conclusion that soil acidification due to external causes has taken place. The increase of N in pine forest humus from 1988 to 1993 gives strong support to the hypotheses [cf. II] that N is not restricting growth in pine forest and that pine forests in the Solhomfjell area are N-saturated.

Significant change was observed in several tree layer descriptors from 1988 to 1993: (1) the volume of Scots pine and Norway spruce increased [XVII], (2) the number of deciduous trees (> 2 m), notably *Sorbus aucuparia*, increased [XVI, XVII], (3) relative crown density of spruce decreased [XVI], and (4) relative crown density of pine increased [XVI]. The Solhomfjell area is situated in a region with high frequency of defoliated crowns (Nellemann & Frogner 1994). Changes similar to (3) and (4) are reported for old-growth forests in Agder and Telemark by Solberg (1994), while the contrasting results in paper [XVI] for a representative data set was attributed, at least in part, to differences in stand age.

A correlation between with crown defoliation and radial increment has been demonstrated for Norway spruce (Nellemann 1992, Söderberg 1993). Radial increment is strongly correlated with length of the annual leader shoot (Nellemann 1992), thus reduced crown vitality should be followed by reduced volume growth (Venn et al. 1993). Significant spruce volume increase in a period with reduced crown vigour appears a paradox. Increased annual volume increment has, however, been observed for spruce in SE Norway in this period also by Tomter (1993). Minimal increase in N as observed in the spruce forest in Solhomfjell may indicate that negative effects of acidification (leading to crown defoliation) have been more than compensated by addition of N (cf. Venn et al. 1993), the main factor limiting growth [see II]. The favourable climatic conditions in the study period, with high temperatures, no serious frost damage, insect pests, storm fellings etc. may also have contributed to growth increase and low mortality, just as observed in bryophytes.

Five-year change is inferred by: (1) comparison of (i) occurrence and abundance of single species [XIII] and (ii) vegetation [XV] with corresponding one-year changes [XIII, XIV], and (2) due consideration of rates of vegetation dynamics [XIV], species persistence patterns [XI, XII] and climatic fluctuations. Significant five-year vegetation change, likely to be part of a long-term trend, did not occur in pine forest. The decrease in abundance of several moderately demanding vascular plant species in richer spruce forest [XIII], and the change of richer spruce forest vegetation in direction of poor spruce forest [XV], accord with the response to soil acidification expected from theoretical reasoning, and demonstrated in other studies. There are indications from the Solhomfjell studies that vegetation responds to the gradual acidification in a slow and time-delayed manner, at spatial and temporal scales larger than 1 m<sup>2</sup> and 5 years [XV]. The slightly increasing abundance of *Deschampsia flexuosa* in spruce forest is the only observation which accords with expected responses to N fertilization [XIII, XV]. The increase of bryophyte abundances and the directed bryophyte vegetation change in spruce forest are both caused by particularly favourable climatic conditions for growth [X, XIII, XV].

Extended time periods and high-quality data from other regions are needed to evaluate the regional and temporal validity of explanations here proposed.

## INTEGRATED APPROACHES TO MONITORING

The ability to answer basic questions relating to structure, function and natural vegetation dynamics (aims 1 and 2) and the ability to find complex vertical relations (tree - understory - soil interactions, cf. T. Økland 1990) and time - scale interactions (Wiens 1989, cf. also [XIV]), were strongly improved by the integrated approach. In-depth insight into structure and function of the monitored system proved indispensable both for identification of changes and for understanding causes of change. Aspects of integrated approaches, demonstrated to have particular importance for monitoring, are [cf. XV]: (1) that relevant environmental information is recorded at each sample plot (T. Økland 1990), (2) that the main coenoclines, the complex-gradients that cause them, and variation in rates of vegetation dynamics along them, must be quantified, and (3) that all plant groups should be included in the study. Point (3) may be particularly important when interspecific competition, as in the Solhomfjell area and perhaps in other coniferous forest areas, is of low importance. Then plants respond to the environment in accordance with their physiological constraints: moisture-limited ectohydric bryophytes respond to climatic factors (and climatic change), vascular plants restricted by nutrient availability and soil acidity respond to soil acidification and perhaps to N fertilization. The multivariate monitoring system offered by the understory vegetation is likely to be much more sensitive to environmental change than the tree layer, and should be included in all future programmes for terrestrial monitoring.

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## REFERENCES

- Aamlid, D., Venn, K. & Stuanes, A.O. 1990. Forest decline in Norway: monitoring results, international links and hypotheses. - *Norw. J. agric. Sci. Suppl.* 4: 1-27.
- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. - *Ann. bot. fenn.* 5: 169-211.
- Arnborg, T. 1943. Granberget: En växtbiologisk undersökning av ett sydlappländsk granskogsområde med särskild hänsyn till skogstyper och föryngring. - *Norrl. Handbibl.* 14: 1-282.
- Austin, M.P. 1987. Models for the analysis of species' response to environmental gradients. - *Vegetatio* 69: 35-45.
- 1990. Community theory and competition in vegetation. - In: Grace, J.B. & Tilman, D. (eds), *Perspectives on plant competition*, Academic Press, San Diego, CA, pp. 215-235.
  - & Gaywood, M.J. 1994. Current problems of environmental gradients and species response curves in relation to community theory. - *J. Veg. Sci.* 5: 473-482.
- Bjørnstad, O.N. 1991. Changes in forest soils and vegetation in Søgne, southern Norway, during a 20 year period. - *Holarct. Ecol.* 14: 234-244.
- Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. - *Ecology* 73: 1045-1055.
- Braak, C.J.F. ter 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. - *Vegetatio* 69: 69-77.
- Buch, H. 1947. Über die Wasser- und Mineralstoffversorgung der Moose I, II. - *Soc. scient. fenn. Commentes biol.* 9: 16: 1-44 + 20: 1-49.
- Busby, J.R., Bliss, L.C. & Hamilton, C.D. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomentypnum nitens* and *Hylocomium splendens*. - *Ecol. Monogr.* 48: 95-110.
- Busby, J.R. & Whitfield, D.W.A. 1978. Water potential, water content. and net assimilation of some boreal forest mosses. - *Can. J. Bot.* 56: 1551-1558.
- Callaghan, T.V., Collins, N.J. & Callaghan, C.H. 1978. Photosynthesis, growth, and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. - *Oikos* 31: 73-88.
- Dahl, E. 1988. Acidification of soils in the Rondane mountains, South Norway, due to acid precipitation. - *Økoforsk Rapp.* 1988: 1: 1-53.
- During, H.J. 1990. Clonal growth patterns among bryophytes. - In: van Groenendael, J. & de Kroon, H. (eds), *Clonal growth in plants: regulation and function*, SPB Acad. Publ., The Hague, pp. 153-176.
- , Brugues, M., Cros, R.M. & Lloret, R. 1988. The diaspore bank of bryophytes and ferns in the soil in some contrasting habitats around Barcelona, Spain. - *Lindbergia* 13: 137-149.
- Eriksson, O. 1989. Seedling dynamics and life histories in clonal plants. - *Oikos* 55: 231-238.
- Falkengren-Grerup, U. 1986. Soil acidification and vegetation changes i deciduous forest in southern Sweden. - *Oecologia (Berlin)* 70: 339-347.
- 1987. Long-term changes in pH of forest soils in southern Sweden. - *Environm. Pollution* 43: 79-90.
  - 1994. Importance of soil solution chemistry to field performance of *Galium odoratum* and *Stellaria nemorum*. - *J. appl. Ecol.* 31: 182-192.



- Fowler, N.L. 1990. Disorderliness in plant communities: comparisons, causes and consequences. - In: Grace, J.B. & Tilman, D. (eds), *Perspectives on plant competition*, Academic Press, San Diego, pp. 291-306.
- Goldberg, D.E. 1990. Components of resource competition in plant communities. - In: Grace, J.B. & Tilman, D. (eds), *Perspectives on plant competition*, Academic Press, San Diego, pp. 27-49.
- & Landa, K. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. - *J. Ecol.* 79: 1013-1030.
- Goth, B.M.T. & Røeggen, O. 1994. Micro-scale vegetation-environment relationships in a boreal spruce forest site in the Solhomfjell area, Gjerstad, S Norway. - Cand. scient. Thesis, Univ. Oslo, Oslo, unpubl.
- Grace, J.B. 1990. On the relationship between plant traits and competitive ability. - In: Grace, J.B. & Tilman, D. (eds), *Perspectives on plant competition*, Academic Press, San Diego, CA, pp. 51-65.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. - Wiley, Chichester.
- Hesselman, H. 1937. Om humustäckets beroende av beståndets ålder och sammansättning i den nordiska granskogen av blåbärsrik *Vaccinium*-typ och dess innverkan på skogen förnygring och tillväxt. - *Meddn St. SkogsförsAnst.* 30: 529-716.
- Hill, M.O. 1979. DECORANA - A Fortran program for detrended correspondence analysis and reciprocal averaging. - Cornell Univ., Ithaca, New York.
- Hobbs, V.J. & Pritchard, N.M. 1987. Population dynamics of the moss *Polytrichum piliferum* in north-east Scotland. - *J. Ecol.* 75: 177-192.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. - *Ecol. Monogr.* 54: 187-211.
- Jonsson, B.G. 1993a. Treefall disturbance, succession, and diversity in boreal forest floor vegetation. - Fil. dr Thesis, Department of Ecological Botany, University of Umeå, Umeå, Sweden.
- & Esseen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. - *J. Ecol.* 78: 924-936.
- Keddy, P.A. 1992. Assembly and response rules: two goals for predictive ecology. - *J. Veg. Sci.* 3: 157-164.
- & MacLellan, P. 1990. Centrifugal organisation in forests. - *Oikos* 59: 75-84.
- Kuusipalo, J. 1985. An ecological study of upland forest site classification in southern Finland. - *Acta for. fenn.* 192: 1-77.
- Lähde, E. & Nieppola, J. 1987. Vegetation changes in old stands of *Pinus sylvestris* L. in southern Finland. - *Scand. J. For. Res.* 2: 369-377.
- Lahti, T. & Väisänen, R.A. 1987. Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. - *Vegetatio* 68: 145-156.
- Maarel, E. van der 1988. Species diversity in plant communities in relation to structure and dynamics. - In: During, H.J., Werger, M.J.A. & Willems, J.H. (eds), *Diversity and pattern in plant communities*, SPB Acad. Publ., The Hague, pp. 1-14.
- & Sykes, M. 1993. Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. - *J. Veg. Sci.* 4: 179-188.
- Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. - *Vegetatio* 69: 89-107.
- Nellemann, C. 1992. Vitalitetsregistreringer på faste intensive overvåkingsflater 1986-91. - *Rapp. Skogforsk.* 1992: 20: 1-13.

- & Frogner, T. 1994. Spatial patterns of spruce defoliation: relation to acid deposition, critical loads, and natural growth conditions in Norway. - *Ambio* 23: 255-259.
- Økland, R.H. 1990. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. - *Sommerfeltia Suppl.* 1: 1-233.
- 1992. Studies in SE Fennoscandian mires: relevance to ecological theory. - *J. Veg. Sci.* 3: 279-284.
- & Bendiksen, E. 1985. The vegetation of the forest-alpine transition in the Grunningsdalen area, Telemark, SE Norway. - *Sommerfeltia* 2: 1-224.
- Økland, T. 1989. Program "Overvåking av skogens sunnhetstilstand": Vegetasjonsøkologisk overvåking av boreal barskog i Norge. I. Rausjømarka i Akershus. - Norsk Inst. for Jord- og Skogkartlegging, Ås.
- 1990. Vegetational and ecological monitoring of boreal forests in Norway. I. Rausjømarka in Akershus county, SE Norway. - *Sommerfeltia* 10: 1-52.
- 1993. Vegetasjonsøkologisk overvåking av barskog i Gutulia nasjonalpark. - Norsk Inst. Jord- Skogkartlegging Rapp. 1993: 6: 1-76.
- Oftedahl, C. 1980. Geology of Norway. - *Norg. geol. Unders.* 356: 3-114.
- Opheim, A. 1994. Variasjon på fin skala i tid og rom i fuktighet og pH i humuslaget i boreal barskog i Gjerstad, Aust-Agder. - Cand. scient. Thesis, Univ. Oslo, Oslo, unpubl.
- Palmer, M.W. 1993. Putting things in even bertter order: the advantages of canonical correspondence analysis. - *Ecology* 74: 2215-2230.
- & Dixon, P.M. 1990. Small-scale environmental heterogeneity and the analysis of species distributions along gradients. - *J. Veg. Sci.* 1: 57-65.
- Proctor, M.C.F. 1982. Physiological ecology: water relations, light and temperature responses, carbon balance. - In: Smith, A.J.E. (ed.), *Bryophyte ecology*, Chapman & Hall, London, pp. 333-381.
- Reed, R.A., Peet, R.K., Palmer, M.W. & White, P.S. 1993. Scale dependence of vegetation-environment correlations: a case study of a North Carolina piedmont woodland. - *J. Veg. Sci.* 4: 329-340.
- Rørå, A., Kvamme, H., Larsson, J.Y., Nyborg, Å. & Økland, T. 1988. Rapport 1988. Program "Overvåking av skogens sunnhetstilstand". - Norsk Inst. Jord- Skogkartlegging, Ås.
- Rosén, K., Gundersen, P., Tegnhammar, L., Johansson, M. & Frogner, T. 1992. Nitrogen enrichment of Nordic forest ecosystems. - *Ambio* 21: 364-368.
- Rydgren, K. 1993. Herb-rich spruce forests in W Nordland, N Norway: an ecological and methodological study. - *Nord. J. Bot.* 13: 667-690.
- Scandrett, E. & Gimingham, C.H. 1989. Experimental investigation of bryophyte interactions on a dry heathland. - *J. Ecol.* 77: 838-852.
- Schütt, P. & Cowling, E.B. 1985. Waldsterben, a general decline of forests in Central Europe: Symptoms, development and possible causes. - *Pl. Dis.* 69: 548-558.
- Sepponen, P. 1985. The ecological classification of sorted soils of varying genesis in northern Finland. - *Communtnes Inst. for. fenn.* 129: 1-77.
- Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. - *Acta for. fenn.* 62: 1-408.
- Skre, O., Oechel, W.C. & Miller, P.M. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. - *Can. J. For. Res.* 13: 860-868.
- Skyllberg, U. 1991. Seasonal variation of pH<sub>H2O</sub> and pH<sub>CaCl2</sub> in centimeter-layers of mor humus in a *Picea abies* (L.) Karst. stand. - *Scand. J. For. Res.* 6: 3-18.

- Söderberg, U. 1993. The relation between defoliation and increment. - Akt. Skogforsk. 1993: 2: 32-34.
- Solberg, S. 1993. Gulning av bar hos gran, og betydningen av tørk. - Rapp. Skogforsk. 1993: 9: 1-13.
- 1994. Fylkesvise lokale overvåkingsflater. Vitalitetsendringer og kontroll 1994. - Rapp. Skogforsk. 1994: 20: 1-26.
- Sonesson, M., Gehrke, C. & Tjus, M. 1992. CO<sub>2</sub> environment, microclimate and photosynthetic characteristics of the moss *Hylocomium splendens* in a subarctic habitat. - *Oecologia* 92: 23-29.
- Stålfelt, M.G. 1937. Die Bedeutung der Vegetation im Wasserhaushalt des Bodens. - Svenska Skogsvårdsfören. Tidskr. 35: 161-195.
- Statens Forurensningstilsyn, 1992. Overvåking av langtransportert forurenset luft og nedbør. - St. Progm. Forurensningsovervåking Rapp. 506: 1-360.
- Sunding, P. 1985. Faste analyseruter og vegetasjonsforandringer - hva er gjort i SØ-Norge? - K. norske Vidensk. Selsk. Mus. Rapp. bot. Ser. 1985: 2: 74-78.
- Svensson, B.M. & Callaghan, T.V. 1988. Small-scale vegetation pattern related to the growth of *Lycopodium annotinum* and variations in its micro-environment. - *Vegetatio* 76: 167-177.
- Tamm, C.O. 1991. Nitrogen in terrestrial ecosystems. Questions of productivity, vegetational changes, and ecosystem stability. - *Ecol. Stud.* 81: 1-116.
- Thomsen, M.G. & Nellemann, C. 1993. Assessment of bias in monitoring of forest decline. - Akt. Skogforsk. 1993: 2: 37-41.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. - Princeton Monogr., Princeton, NJ.
- Tørseth, K. & Røstad, A. 1994. Program for terrestrisk naturovervåking. Overvåking av nedbørkjemi i tilknytning til feltforskningsområdene, 1993. - Norsk Inst. Luftforsk. Oppdragsrapp. 1994: 25: 1-71.
- & Røyset, O. 1994. Program for terrestrisk naturovervåking. Overvåking av nedbørkjemi i Ualand, Solhomfjell, Møsvatn, Åmotsdalen og Børgefjell, 1992. - Norsk Inst. Luftforsk. Oppdragsrapp. 1993: 13: 1-62.
- Tomter, S. (ed.) 1993. Skog 93. Statistikk over skogforhold og -ressurser i Norge. - Norsk Inst. Jord- Skogkartlegging, Ås.
- Tonteri, T., Hotanen, J.-P. & Kuusipalo, J. 1990. The Finnish forest site type approach: ordination and classification studies of mesic forest sites in southern Finland. - *Vegetatio* 87: 85-98.
- Venn, K., Aamlid, D., Sletnes, A.I. & Joranger, E. 1993. Skogskadesituasjonen i Norge. Status 1992. - Rapp. Skogforsk. 1993: 18: 1-46.
- Wiens, J.A. 1989. Spatial scaling in ecology. - *Funct. Ecol.* 3: 385-398.
- Wittig, R. 1988. Retrospective studies of changes in central European forests by means of repeating phytosociological surveys. - In: Salbitano, F. (ed.), Human influence on forest ecosystems development in Europe, Forest Ecosystem Research Network of the European Science Foundation & Consoglio Nazionale delle Recherche, Pigatora Editrice, Bologna, pp. 139-147.
- & Werner, W. 1986. Beiträge zur Belastungssituation des Flattergras-Buchenwaldes der Westfälischen Bucht - eine Zwischenbilanz. - *Düsseldorfer geobot. Kolloq.* 3: 33-70.



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