Ann. Zool. Fennici 31:53–60
Helsinki 31 January 1994

ISSN 0003-455X

Species richness of boreal understorey forest vegetation in relation to site type and successional factors

Tiina Tonteri

Tonteri, T., Department of Forest Ecology, The Finnish Forest Research Institute, P.O. Box 18, FIN-01301 Vantaa, Finland

Received 30 August 1993, accepted 21 October 1993

Relationship of species richness to the most important environmental gradients explaining understorey vegetation variation in the boreal forests of Finland was described by means of generalized additive models (GAM). Site quality was the most important factor in explaining the number of species. Also species richness pattern related to successional factors was dependent on site type. Herb-rich sites were more species-rich than mesic or xeric sites. In the southern and middle boreal zones, species richness increased until stands were 10–30 years old, and decreased thereafter, except on southern boreal herb-rich sites, where it continued increasing until stands reached an age of 80–100 years. Species richness was only weakly related to total crown coverage of trees and shrubs. The variation of species richness along the environmental gradients was small in the northern boreal zone.

1. Introduction

Species richness is often regarded as the most important component of alpha diversity. In a plant community, it is a product of many factors, like environmental variation and history of a site, environmental tolerance and dispersal ability of different species, interactions within a community, and ecological and spatial scales of variation. It is not possible to study influences of all these factors simultaneously, but summarizing patterns of species richness in relation to most important factors structuring plant communities can still reveal the basic patterns of variation.

It is known of forest vegetation that the number of species is positively correlated with nutrient quantities, or with the site index H_{100} commonly used in forestry (e.g. Ilvessalo 1922, Kuusipalo 1984, Nieppola 1993). It has also often been reported to be high at the pioneer stage and decrease as succession proceeds (e.g. Ilvessalo 1922, Shafi & Yarranton 1973a, Horn 1974, Malmer et al. 1978, Lindholm & Vasander 1987, Zobel 1989). But, in most studies a linear approach is used, and conclusions are drawn from few cases. This paper will describe the species richness pattern of understorey forest vegetation in relation to site quality, stand age and crown coverage of trees and shrubs by means of nonparametric nonlinear regression. A large material allows comparison between subzones of the boreal zone, but because the study is based on a data set from an extensive survey, the examination will be limited into one spatial scale.

2. Material

The original material consists of understorey vegetation descriptions of forests on mineral soils, collected during the Eighth National Forest Inventory of Finland in 1985–1986. The systematically sampled study area covers the whole country. Sites on rock outcrops, mountain tops and fells, as well as a few sites with peculiar vegetation were excluded from the material. Each sample comprised three vegetation quadrats of 2 m^2, which were randomly chosen from three to six systematically placed quadrats of each sample plot. See Tonteri et al. (1990) for methodological details and information about the general patterns of vegetation variation.

Because the number of species is known to decrease in a regional scale towards the north (for vascular plants, see Lahti et al. 1988), and the latitude has strong covariation with the principal vegetation variation (Tonteri et al. 1990), the material was divided into three biogeographic subzones according to the Atlas of Finland (1988, original zonation by Kalela 1961). The combination of southern boreal and hemiboreal zones, which will be called the southern boreal zone here, included 718 samples. The middle boreal zone included 432 samples, and the northern boreal zone included 253 samples.

The following environmental variables were used in modelling:

1) `site`: Site type gradient, which is the only canonical axis of a canonical correspondence analysis (ter Braak 1986) of understorey vegetation, where the ordered Cajander forest site type classes (see e.g. Cajander 1926; Lehto & Leikola 1987) were used as the only constraining variable. The following site type classes were used:
   Herb-rich forests (including FT, GDT, GFiT, GOFiT, GOMaT, HeOT, OMaT)
   Herb-rich heath forests (GMT, GOMT, OMT, PyT)
   Mesic heath forests (DeMT, HMT, LMT, MT, VMT)
   Sub-xeric heath forests (EMT, EVT, UEMT, VT)
   Xeric heath forests (CT, ECT, MCClT, UVET)
   Barren heath forests (ClT)
2) `cove`: Visually estimated percentage cover of tree crowns and shrubs on a circular sample plot of 300 m^2, obtained by summing separate estimates for each species and each canopy layer.
3) `age`: Stand age in years, obtained from a tree ring count of one sample tree representing the dominant canopy layer.

3. Statistical modelling

In studies of species richness patterns in ecological space, there is no reason to make any *a priori* assumptions of the shape of the relation. For instance, it is often mentioned that number of species first increases in the beginning of succession and after a while decreases, but it is difficult to detect the correct shape of the relation to time in regression analysis. A better approach is to let the data determine the pattern profile. Therefore, these relationships were modelled with generalized additive models (GAM) (Hastie & Tibshirani 1986, 1990), which is a non-parametric smooth maximum likelihood extension of generalized linear models (GLM) (McCullagh & Nelder 1989). GAMs have already recently been applied to ecological data (Yee & Mitchell 1991).

A generalized additive model relates the response variable Y with mean $\mu = E(Y|X_1,X_2...X_p)$ to independent variables $X_1, X_2... X_p$ by

$$g(\mu) = \alpha + f_1(X_1) + f_2(X_2)... + f_p(X_p)$$

where f_j is an unspecified function which is obtained from non-parametric smoothing, α is an intercept and g is a specified link fuction (Hastie & Tibshirani 1990). Deviances of nested models can be compared like those of generalized linear models. It is also possible to fit interactions of type $f_{12}(X_1,X_2)$. However, in applications it is often more convenient to write the models in a modelling language, using names of the variables instead of $f_j(X_j)$. This will be done also here (see e.g. Table 1).

Weighted running line smoothing (Nelder 1989) was used in GLIM (Payne 1986), with normal error and identity link. Naturally, normality of the data and residuals was checked both before and after the modelling procedure. This check was performed with Q-Q-plots (see e.g. Aitkin et al. 1989). The span width was optimized with generalized cross-validation to minimize bias and variance of estimates simultaneously (Hastie & Tibshirani 1990). The relative span width was 0.25 for the southern boreal zone, 0.20 for the middle boreal zone, and 0.30 for the northern boreal zone. In practice, these widths mean rather strong smoothing.

The best model of the main effects was chosen with stepwise forward selection, but, as recommended by Hastie & Tibshirani (1990), at each step testing if any of the variables in the model could be dropped out. Comparisons of the nested models were done with F-tests. Note that F-tests are informal in GAM, but can be used for screening models (Hastie & Tibshirani 1990). Fortunately, they have the advantage of scaling of deviances in the F-ratio. Thus there is no need for additional adaptation of the model to overdispersion, even if there exists no natural scale for the dependent variable, like in the case of species richness.

Since interaction terms include main effects in additive models, and in conventional stepwise modelling it is not possible to distinguish influ-

Table 1. Analysis of deviance tables, F-ratios and P-values of main effect models for the species richness data. Each subzone of the boreal zone was analysed separately. Abbreviations of independent variables: `site` = site type variable; `cove` = crown coverage of trees and shrubs; `age` = stand age.

	Deviance	ΔDev	df^{err}	Δdf^{err}	F	P
Southern boreal zone:						
`null`	26784		710.0			
`site`	21229	5555	705.7	4.3	42.94	0.000
`cove`	26582	202	705.8	4.2	1.28	0.277
`age`	25911	873	705.5	4.5	5.28	0.000
`site+cove`	21085	144	701.5	4.2	1.14	0.337
`site+age`	20612	617	701.2	4.5	4.66	0.001
`site+age+cove`	20473	139	697.0	4.2	1.13	0.343
Middle boreal zone						
`null`	12073		431.0			
`site`	11077	996	425.5	5.5	6.96	0.000
`cove`	11872	201	425.8	5.2	1.39	0.226
`age`	9841	2232	425.9	5.1	18.94	0.000
`age+site`	8839	1002	420.4	5.5	8.66	0.000
`age+cove`	9636	205	420.6	5.3	1.69	0.132
`age+site+cove`	8520	319	415.1	5.3	2.93	0.011
Northern boreal zone:						
`null`	5400		252.0			
`site`	4624	776	248.9	3.1	13.47	0.000
`cove`	5381	19	248.2	3.8	0.23	0.914
`age`	5071	329	248.3	3.7	4.35	0.003
`site+cove`	4574	50	245.1	3.8	0.71	0.582
`site+age`	4423	201	245.3	3.6	3.10	0.020
`site+age+cove`	4250	173	241.5	3.8	2.59	0.040

ences of interaction terms from those of main effects, Hastie & Tibshirani (1990) recommend examining residuals for interactions and iterating a new term into the model once an interaction has been identified. When a main effect model was fitted, raw residuals were extracted and used as a new dependent variable for one pairwise interaction effect at a time. Models with more than one interaction term led into concurvity, or, only one of the almost equally strong interactions was selected into the model. In cases of three significant interactions, I solved this problem by using three different final interaction models for interpretation, keeping one of the explanatory variables at a time as a covariate, which is not displayed in the figures. These models were:

1) `site + cove + age + site*cove`
2) `site + cove + age + site*age`
3) `site + cove + age + cove*age`

More complex interactions are difficult to model and interpret in GAMs (Hastie & Tibshirani 1990).

Gradient edges with only few observations were excluded from the figures.

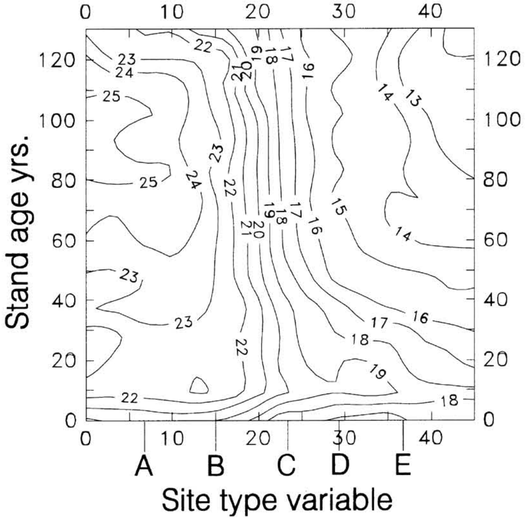

Fig. 1. Expected species richness in relation to site type and stand age in the southern boreal zone. Centroids of following types are marked along the site type axis: A = herb-rich forests; B = herb-rich heath forests; C = mesic heath forests; D = sub-xeric heath forests; E = xeric heath forests. The generalized additive model used was: `site + age + site*age`.

4. Results

4.1. Southern boreal zone

Species richness had a significant relation to the site type variable and stand age (Table 1). When the interaction `site*age` was fitted to residuals, the deviance dropped by 807 and df^{err} by 4.7, resulting to a F-ratio of 6.04, which is significant ($P = 0.000$). So, `site + age + site*age` was accepted as the final model.

In general, the number of species was higher on herb-rich sites than on xeric ones in stands of the same age (Fig. 1). However, the species richness pattern related to stand age depended on site type. On herb-rich sites, the number of species was lowest in young stands, and grew until the stand was about 100 yrs. old. On the contrary, on mesic to xeric sites, the species richness increased rapidly in the beginning of the succession, reaching its maximum when the stand was about 10–20 years old. After this it decreased slowly. On xeric sites the decrease was fastest. This means that differences in expected species richness between the site types were smallest when the stand was about 15 yrs. old (range 17–22 species), and largest when the stand was about 100 yrs. old (range 12–26 species).

4.2. Middle boreal zone

All the main effects were included into the model during the forward selection procedure (Table 1). But, it should be noted that crown coverage alone was not significant. This situation could be due to two reasons. First, when samples are unevenly distributed in the space of environmental variables, the (possibly strong) response of species richness to the other two variables can confuse the interpretation of the pattern related to crown coverage, if these two are not included in the model. Second, concurvity, which is a GAM counterpart of multicollinearity, can arise due to strongly intercorrelated independent variables or strongly influential outlier observations. However, the independent variables were only weakly correlated, and there were no large outlying residuals in the second step model `site + age`. Further examination also revealed that the variable `cove` had a significant, although weak, relationship to residuals of this model. Therefore, I decided to accept crown coverage into the model.

When interaction terms were fitted to residuals of the full main effects model, the `site*cove` interaction dropped the deviance by 1613 and df^{err} by 5.7 ($F = 16.77$, $P = 0.000$); the interaction `site*age` caused the deviance drop by 1598 and df^{err} by 5.7 ($F = 16.58$, $P = 0.000$); and the interaction `cove*age` dropped the deviance by 1773 and df^{err} by 5.8 ($F = 18.54$, $P = 0.000$). I decided to use three alternative models for interpretation, as explained above.

The species richness pattern was much the same in the site type variable – stand age plane as that of the southern boreal zone, though a two-dimensional plot is not so clearly interpretable as there is an additional dimension in the model (Fig. 2). In herb-rich forests the number of species increased slowly, and started to decrease when stand was about 60–80 years old. In herb-rich heath forests to xeric heath forests the behaviour of species richness was similar to that in the southern boreal zone.

The response of species richness to crown coverage of trees and shrubs was weak and not very clear (Fig. 2). But it seems that the number of species was lowest in very high coverages. It also was low in old stands with very high coverages.

4.3. Northern boreal zone

All main effects were included into the model during the stepwise procedure (Table 1). The variable `cove` behaved in the same way as in the middle boreal zone during the modelling. Also an examination of the model led to the same conclusion: there was no reason to exclude crown coverage of trees and shrubs from the model.

All interactions explained the residuals of the main effects model significantly. `Site*cove` dropped the deviance by 366 and df^{err} by 4.1 ($F = 5.46$, $P = 0.000$); `site*age` decreased the deviance by 468 and df^{err} by 4.0 ($F = 7.35$, $P = 0.000$); and `cove*age` dropped the deviance by 442 and df^{err} by 3.9 ($F = 7.07$, $P = 0.000$). So, three alternative models were used here as well.

The rich end of the site type gradient was now excluded from the interpretations, because there were only few samples at this end. In contrast to the patterns of other biogeographic zones, stands on mesic sites had fewer species than stands of the same age on sub-xeric and xeric sites (Fig. 2). The number of species was slightly higher in young stands than in older ones, but the difference between young and old stands was not so pronounced as in other biogeographic zones.

It seems that species richness was highest in relatively young stands with moderate crown coverage, and lowest in old stands with low crown coverage. On sub-xeric and xeric sites the number of species was highest when crown coverage was about 40–60%. No clear pattern could be found on mesic sites.

5. Discussion

5.1. Species richness, site and succession

The results revealed that changes in species richness during the course of succession depended on site type, most clearly in southern and middle boreal zones. The drier the site, the faster the number of species decreased after the colonization phase of young stands. In the middle boreal zone this took place slightly later than in the southern boreal zone. But, it was surprising that on herb-rich sites of the southern boreal zone species richness reached its maximum as late as in 100-year-old stands, when some workers (e.g. Ilvessalo 1922, Lindholm & Vasander 1987, but see an opposite case described by Vanha-Majamaa & Lähde 1991) have reported that species richness is highest in young stands, and decreases later on. Horn (1974, see also Shafi & Yarranton 1973a, Brown & Southwood 1987) stated that the decrease of species richness during succession is a 'universal truth'. However, this can be a question of scale. On one hand, in 10–20-year-old forests the total field layer coverage was largest on herb-rich sites and often dominated by a few rapidly expanding species. On the other hand, ground layer was very sparse in these places, and thus it could not contain many spe-

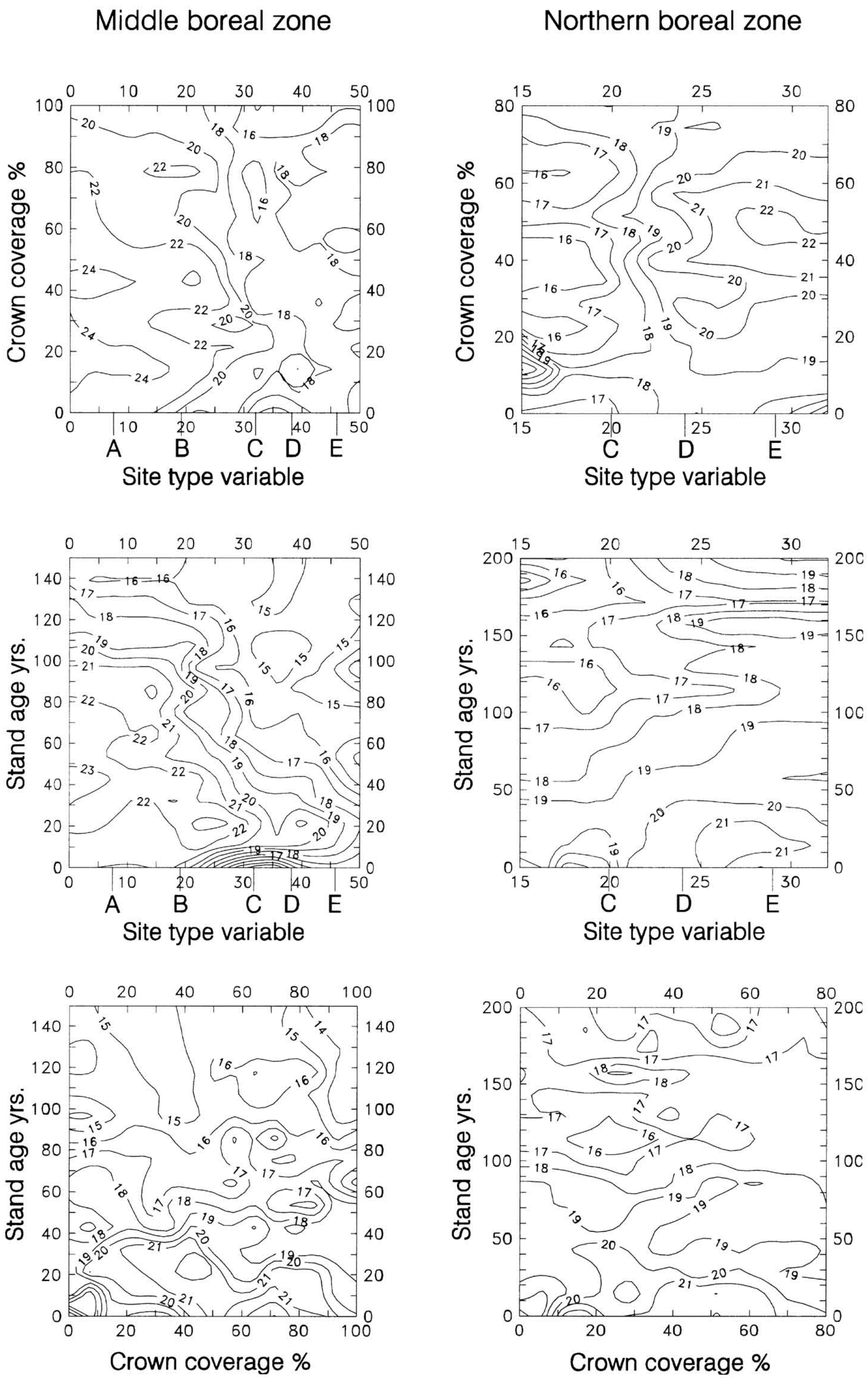

Fig. 2. Expected species richness in relation to site type, crown coverage of trees and shrubs, and stand age in middle and northern boreal zones. Centroids of site types as in Fig. 1. The generalized additive models used were: `site + cove + age + site*cove` (top), `site + cove + age + site*age` (center) and `site + cove + age + cove*age` (bottom).

cies. So, the successional species richness pattern observed on herb-rich sites can be mainly explained by decrease of field layer dominants, and by development of ground layer.

Among others, Zobel (1989) and Nieppola (1992) see pioneer species in clear-cut areas as a temporary addition to the 'normal' forest flora. It is true that many of the species of mature stands are present already in young stands, because almost all successions in the forests of Finland are caused by clearcutting, which does not completely destroy the understorey vegetation. But, on the other hand, some pioneer species can persist long in the vegetation, if the light conditions are favourable. It should also be noted that large changes in species richness at certain stages of the succession does not necessarily mean large compositional turnover, since compositional turnover means change in species abundancies, which may be uncorrelated with species presences and absences.

In the northern boreal zone, the number of species was relatively high in old stands on subxeric and xeric sites compared to those of other zones. The coverage of ground layer was low in these samples, but there were many lichen species. Xeric and barren sites of northern Finland are heavily grazed by reindeer. This continuous disturbance reduces the dominance of some species and changes the diversity pattern (Helle & Aspi 1983). Also species richness of mesic sites was in general high. It is typical of northern boreal vegetation that peatland species occur on mineral soils, and thus increase the number of species.

5.2. Spatial heterogeneity and scale of alpha diversity

Spatial heterogeneity of vegetation is one of the properties of the diversity pattern of a community. For instance, it has been suggested frequently that succession proceeds patchily (Greig-Smith 1952, Whittaker 1953, Reiners et al. 1971, Shafi & Yarranton 1973b). Spatial heterogeneity of vegetation may be caused by small-scale environmental variation (Smith & James 1978, Palmer & Dixon 1990). In addition to local variation of soil, tree stand is an important factor causing environmental heterogeneity in forests: the canopy creates a mosaic of well-lit and poorly lit patches (Smith et al. 1989), and trees decrease availability of water and nutrients locally (Kuuluvainen & Pukkala 1989, Kuuluvainen et al. 1993). Spatial variation of vegetation may also be a product of within-community interactions. If the environment is assumed to be constant, this diversity component is sometimes called pattern diversity (Pielou 1966, Zobel et al. 1993).

The scale of spatial heterogeneity may change during succession, and it is often reported to increase in various kinds of plant communities (Greig-Smith 1952, Whittaker 1953, Margalef 1958, Pielou 1966, Shafi & Yarranton 1973b). In boreal forests of Northern Europe this could mainly be caused by growth of clonal plants like *Vaccinium myrtillus* L., *V. vitis-idaea* L. and *Calluna vulgaris* (L.) Hull, and that of rapidly expanding mosses and lichens, e.g. *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G. and *Cladina* (Nyl.) Nyl. *spp.* For instance, Bråkenhielm & Persson (1980) reported the late succession in Swedish lichen-rich pine stands to mostly be expansion of *Calluna* clones.

In this study, the species richness pattern is described only in one spatial scale, which, however, is often used in Nordic vegetation studies. One should be careful with generalizing the results to smaller or larger scales of communities, because species dominance relationships are variable, and the relevant scale of spatial variation can be different for individual site types, successional situations and stands subject to various treatments of forest management.

Acknowledgements. The study was financed by the Academy of Finland and the Finnish Cultural Foundation. Valuable comments on the manuscript were given by Jussi Kuusipalo, Esko Valkeila and an anonymous referee.

References

Aitkin, M., Anderson, D., Francis, B. & Hinde, J. 1989: Statistical modelling in GLIM. — Oxford University Press, Oxford.

Atlas of Finland, folio 141–143; Biogeography, nature conservation. — National Board of Survey, Geographical Society of Finland, Helsinki 1988.

ter Braak, C. J. F. 1986: Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. — Ecology 67:1167–1179.

Bråkenhielm, S. & Persson, H. 1980: Vegetation dynamics in developing Scots pine stands in Central Sweden. — Ecol. Bull. (Stockholm) 32:139–152.

Brown, V. K. & Southwood, T. R. E. 1987: Secondary succession: patterns and strategies. — In: Gray, A. J., Crawley, M. J. & Edwards, P. J. (eds.), Colonization, succession and stability: 315–337. Blackwell, Oxford.

Cajander, A. K. 1926: The theory of forest types. — Acta Forest. Fennica 29(3):1–108.

Greig-Smith, P. 1952: Ecological observations on degraded and secondary forest in Trinidad, British West Indies. II. Structure of the communities. — J. Ecol. 40:316–330.

Hastie, T. & Tibshirani, R. 1986: Generalized additive models. — Statistical Sci. 1:297–318.

— 1990: Generalized additive models. — Chapman & Hall, London.

Helle, T. & Aspi, J. 1983: Effects of winter grazing by reindeer on vegetation. — Oikos 40:337–343.

Horn, H. S. 1974: The ecology of secondary succession. — Ann. Rev. Ecol. Syst. 5:25–37.

Ilvessalo, Y. 1922: Vegetationsstatistische Untersuchungen über die Waldtypen. — Acta Forest. Fennica 20:1–73.

Kalela, A. 1961: Waldvegetationszonen und ihre klimatischen Paralleltypen. — Arch. Soc. Vanamo 16 (Suppl.):65–83.

Kuuluvainen, T., Hokkanen, T. J., Järvinen, E. & Pukkala, T. 1993: Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of a vegetation-soil system. — Can. J. Forest. Res. (in press).

Kuuluvainen, T. & Pukkala, T. 1989: Effect of Scots pine seed trees on the density of ground vegetation and tree seedlings. — Silva Fennica 23:159–167.

Kuusipalo, J. 1984: Diversity pattern of the forest understorey vegetation in relation to some site characteristics. — Silva Fennica 18:121–131.

Lahti, T., Kurtto, A. & Väisänen, R. A. 1988: Floristic composition and regional species richness of vascular plants in Finland. — Ann. Bot. Fennici 25:281–291.

Lehto, J. & Leikola, M. 1987: Käytännön metsätyypit. [Forest site types in practice]. (In Finnish) — Kirjayhtymä, Helsinki.

Lindholm, T. & Vasander, H. 1987: Vegetation and stand development of mesic forest after prescribed burning. — Silva Fennica 21:259–278.

Malmer, N., Lindgren, L. & Persson, S. 1978: Vegetational succession in a South Swedish deciduous wood. — Vegetatio 36:17–29.

Margalef, D. R. 1958: Information theory in ecology. — Gen. Syst. Yearb. 3:36–71.

McCullagh, P. & Nelder, J. A. 1989: Generalized linear models. 2 ed. — Chapman and Hall, London.

Nelder, J. A. 1989: Generalized additive models and GLMs. — GLIM Newsletter No. 18. Numerical Algorithms Group, Royal Statistical Society.

Nieppola, J. 1992: Long-term vegetation changes in stands of Pinus sylvestris in southern Finland. — J. Veget. Sci. 3:475–484.

— 1993: Understorey plants as indicators of site productivity in Pinus sylvestris L. stands. — Scand. J. Forest. Res. 8:49–65.

Palmer, M. W. & Dixon, P. M. 1990: Small-scale environmental heterogeneity and the analysis of species distributions along gradients. — J. Veget. Sci. 1:57–65.

Payne, C. D. (ed.) 1986: The GLIM system release 3.77 manual. — Numerical Algorithms Group, Royal Statistical Society, Oxford.

Pielou, E. C. 1966: Species-diversity and pattern-diversity in the study of ecological succession. — J. Theor. Biol. 10:370–383.

Reiners, W. A., Worley, I. A. & Lawrence, D. B. 1971: Plant diversity in a chronosequence at Glacier Bay, Alaska. — Ecology 52:55–69.

Shafi, M. I. & Yarranton, G. A. 1973a: Diversity, floristic richness, and species evenness during a secondary (postfire) succession. — Ecology 54:897–902.

— 1973b: Vegetational heterogeneity during a secondary (postfire) succession. — Can. J. Bot. 51:73–90.

Smith, D. W. & James, T. D. 1978: Characteristics of prescribed burns and resultant short-term environmental changes in Populus tremuloides woodland in southern Ohio. — Can. J. Bot. 56:1782–1791.

Smith, W. K., Knapp, A. K. & Reiners, W. A. 1989: Penumbral effects on sunlight penetration in plant communities. — Ecology 70:1603–1609.

Tonteri, T., Mikkola, K. & Lahti, T. 1990: Compositional gradients in the forest vegetation of Finland. — J. Veget. Sci. 1:691–698.

Vanha-Majamaa, I. & Lähde, E. 1991: Vegetation changes in a burned area planted by Pinus sylvestris in Northern Finland. — Ann. Bot. Fennici 28:161–170.

Whittaker, R. H. 1973: A consideration of the climax theory: the climax as a population and pattern. — Ecol. Monogr. 23:41–78.

Yee, T. W. & Mitchell, N. D. 1991: Generalized additive models in plant ecology. — J. Veget. Sci. 2:587–602.

Zobel, K., Zobel, M. & Peet, R. K. 1993: Change in pattern diversity during secondary succession in Estonian forests. — J. Veget. Sci. 4:489–498.

Zobel, M. 1989: Secondary forest succession in Järvselja, southeastern Estonia: changes in field layer vegetation. — Ann. Bot. Fennici 26:171–182.