

Changes in structural inequality in Norway spruce stands on peatland sites after water-level drawdown

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Abstract: Size structural dynamics of naturally established Norway spruce (*Picea abies* (L.) Karst.) stands growing on peatlands drained for forestry were investigated. The study was based on modelling of diameter at breast height (DBH) distributions of repeatedly measured stands in southern Finland. The Weibull function was used to parameterize the DBH distributions and mixed linear models were constructed to characterize the impacts of different ecological factors on stand dynamics. Initially, the positive skewness of the DBH distributions increased after drainage as a result of increases in stem numbers and a reduction in mean diameters. Simultaneously, the size inequality among trees increased. These changes were due to regeneration and (or) ingrowth and indicated only little competition from the larger trees. Subsequently, the DBH distributions changed from positively skewed to normal and finally to negatively skewed resulting from tree growth and a reduction in the number of small DBH trees. This indicated increased asymmetric intertree competition. Size inequality did not change during this later stage in stand development, suggesting a concurrent component of symmetric competition. Thinnings had little impact on DBH distribution trends. The observed stand dynamics allow the allocation of growth resources to the desired crop component by appropriate silvicultural treatments.

Résumé : La dynamique de peuplements naturels d'épicéa commun (*Picea abies* (L.) Karst.) établis dans des tourbières drainées a été analysée en termes de taille et de structure. L'étude se base sur la modélisation des distributions du diamètre à hauteur de poitrine (DHP) de peuplements mesurés à maintes reprises dans le Sud de la Finlande. La fonction de Weibull a été utilisée pour paramétrer les distributions du DHP et des modèles linéaires mixtes ont été construits de façon à caractériser les impacts de différents facteurs écologiques sur la dynamique des peuplements. À la suite du drainage, l'asymétrie gauche des distributions du DHP augmente dans un premier temps à cause de l'augmentation du nombre de tiges et de la réduction des diamètres moyens, en même temps qu'augmente l'inégalité de la taille entre les arbres. Ces changements sont dus à la régénération ou au recrutement et traduisent le peu de compétition de la part des arbres les plus grands. Les distributions du DHP passent ensuite d'une asymétrie gauche à la normalité puis à une asymétrie droite, à la suite de la croissance des arbres et de la réduction du nombre d'arbres de petit DHP. Ceci indique une compétition asymétrique plus forte entre les arbres. L'inégalité des tailles ne change plus pendant ce dernier stade de développement du peuplement, laissant entrevoir l'existence d'une composante concurrente de compétition symétrique. Les éclaircies avaient peu d'impact sur l'évolution des distributions du DHP. Les résultats de l'observation de la dynamique des peuplements permettent d'envisager une allocation des ressources de croissance vers les composantes les plus désirées de la récolte grâce à des traitements sylvicoles appropriés.

[Traduit par la Rédaction]

Introduction

In boreal peatlands, high water table level generally controls the rate of primary production, in particular tree stand growth (Jeglum 1974). Trees survive only on the most fa-

avourable microsites because of the shortage of aerobic rooting volume and the rising of the mire surface caused by *Sphagnum* growth (e.g., LeBarron 1945). Although tree growth varies according to microsite heterogeneity, it is generally slow (Macdonald and Yin 1999). As a consequence, stands have a heterogeneous size and spatial structure (Heikurainen 1971; Gustavsen and Päivänen 1986; Groot and Horton 1994; Norokorpi et al. 1997; Macdonald and Yin 1999). Minerotrophic mires are sites that have the highest potential to produce timber on peat soils (Gustavsen et al. 1998). In northern Europe, the most productive mesotrophic to eutrophic mires are usually dominated by Norway spruce (*Picea abies* (L.) Karst.) with varying admixtures of pubescent birch (*Betula pubescens* Ehrh.) (Paavilainen and Tiihonen 1984).

Forest drainage has been used to improve tree growth in peatlands in northern Europe and some parts of North America. After water-level drawdown, the aeration of the surface

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peat layer increases (Silins and Rothwell 1999), resulting in changes in growing conditions that are more significant at wetter sites. Smaller, younger trees generally show greater drainage-induced release growth than larger, older trees (Heikurainen and Kuusela 1962; Seppälä 1969, 1976). Stands become denser as open spaces fill up with rapidly growing small trees. The increase in stand density continues for some decades after drainage (Hökkä and Laine 1988) and maintains an uneven-aged and -sized stand structure characterised by a reverse J-shaped diameter distribution. There is evidence, however, that over a longer time period, drainage may cause a decline in tree size inequality because of reduced variability in growth rates among trees (Macdonald and Yin 1999). Consequently, the diameter distributions may become less skewed (Hökkä and Laine 1988).

Drainage-induced release growth of spruce trees is usually evident for about 20 years after water-level drawdown (Seppälä 1976). Thereafter, the radial growth rate depends on the available resources. After the adjustment of growth rates following release, Seppälä (1976) found only little size-dependent variation in radial growth rates. If this were a persistent phenomenon, within-stand differences in the tree diameters would remain relatively constant and changes in the shape of diameter distributions would result only from changes in the population due to ingrowth, cuttings, or mortality. However, competition for resources among trees also influences growth rates of individual trees, their subsequent stand structure, and density-dependent mortality rates (Ford 1975).

An increase in size inequality may result from one-sided (asymmetric) competition, i.e., larger trees have higher relative growth rates than suppressed smaller trees. One-sided competition is assumed to be competition for light (Cannell et al. 1984; Cannell and Grace 1993; Schwinning and Weiner 1998; Wichmann 2001). Stable size ratios or reduction in size inequality with increasing density may result from no competition or two-sided (symmetric) competition, mainly competition for belowground resources (Weiner and Thomas 1986; Brand and Magnussen 1988; Schwinning and Weiner 1998; Wichmann 2001).

Most literature on size structure dynamics in tree populations deals with even-aged stands, either naturally regenerated (Knox et al. 1989) or plantations (Gates 1982; Brand and Magnussen 1988). In even-aged stands on well-drained soils, with the exception of microsite differences, all trees have relatively equal opportunities for development. Thus, size variability results from variation in intrinsic growth rates and asymmetric competition (e.g., Weiner 1990). In the few studies where structural dynamics have been monitored in drained peatland stands, the stands were fairly even aged (Stoll et al. 1994; Macdonald and Yin 1999). Even-aged peatland stands are common in continental climates because establishment occurs after severe fires (Lieffers 1986; Groot and Horton 1994). However, in maritime or semimarine climates, it is common that peatland stands are highly uneven aged in the absence of intense disturbances that would destroy the whole tree population (Hörnberg 1995). The secondary succession dynamics of such stands after water-level drawdown are still largely unexplored, in spite of a wealth of literature dealing with their total productivity (Paavilainen and Päivänen 1995).

The aim of this study was to (i) describe stand-level structural development in Norway spruce dominated peatland forests following water-level drawdown and (ii) analyse factors affecting the structural dynamics to better understand the underlying ecological processes. We used diameter at breast height (DBH, 1.3 m) distribution as the indicator of stand structure and we constructed models to identify the relative impacts of different ecological factors on stand dynamics. We assumed that if the diameter distributions remained positively skewed over time in our sites, this would indicate no competition, or symmetric size-dependent competition among trees. In contrast, strongly asymmetric competition would result in a change from positively to negatively skewed distributions. We expected that intensive competition would result in mortality of trees of all sizes in the case of symmetric competition and of the smallest trees in the case of asymmetric competition.

Materials and methods

The study material consisted of 31 repeatedly measured permanent sample plots in different stands maintained by the Finnish Forest Research Institute and University of Helsinki. The sites included had to meet the following criteria: (i) either herb-rich or *Vaccinium myrtillus* site type according to the classification by Laine (1989), (ii) known year of ditching, (iii) tree stand dominated by Norway spruce (more than 50% of the volume), (iv) tree stand had established naturally (before drainage) and represented the first generation following drainage, (v) no fertilization done, and (vi) data available from at least three successive measurements. Twelve plots represented the herb-rich type characterized by tall ferns, e.g., *Athyrium filix-femina*, and herbs, e.g., *Oxalis acetosella*, and 19 plots represented the *Vaccinium myrtillus* type characterized by *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and mesic herbs, e.g., *Trientalis europaea*. The sites were located in southern Finland in a region between 60°15′–62°04′N and 24°34′–24°50′E. The mean annual temperature sum (accumulated mean daily temperatures >5°C) in the region varies between 1150 and 1400 degree-days. The annual precipitation varies between 600 and 750 mm of which 200–300 mm is snowfall.

The ditching year of the sites varied between 1907 and 1965. The stands had a varying natural admixture of pubescent birch and Scots pine (*Pinus sylvestris* L.). The tree stands had been measured, on average, six times at 5- to 18-year intervals. None of the stands were totally unmanaged. Over the years, mainly suppressed, dying trees had been harvested and tree species composition had been altered by the removal of relatively more birch. We refer to all of these cuttings as “thinnings”, irrespective of their intensity. The average removal was 10% of the stand basal area.

All trees in the sample plots, sized 600–2500 m², had been measured for DBH. The smallest measured DBH was 1 cm. Sample trees, 10–25 depending on stand characteristics, had also been measured for height and diameter at 6 m. Standard stand characteristics, such as stem number per hectare, basal area (m²·ha⁻¹), mean diameter (cm), and mean volume (m³·ha⁻¹), are shown in Table 1.

Table 1. Mean (standard deviation in parentheses) stand characteristics in the material by drainage age-classes.

	Drainage age-class ^a					
	10	20	30	40	50	60
Herb-rich type						
Basal area, m ² ·ha ⁻¹	14.1 (6.7)	23.2 (7.7)	24.6 (8.3)	28.2 (5.9)	32.1 (6.4)	32.7 (5.8)
Mean DBH, cm ^b	7.1 (6.1)	7.8 (4.2)	13.5 (4.9)	20.3 (3.8)	19.6 (5.4)	28.8 (7.9)
Max. DBH, cm	18.8 (7.4)	22.4 (7.4)	25.5 (7.0)	33.2 (3.1)	34.0 (5.4)	42.3 (6.1)
Stand volume, m ³ ·ha ⁻¹	89.6 (58.2)	161.8 (86.3)	184.9 (93.3)	297.6 (80.6)	320.6 (89.7)	428.3 (78.7)
Hardwood proportion, % ^c	40.5 (23.1)	35.4 (18.4)	26.6 (13.3)	22.3 (14.9)	21.1 (13.0)	6.0 (6.7)
Stems·ha ⁻¹	3941.0 (2345.0)	4562.2 (2943.1)	1669.5 (660.8)	1002.1 (395.6)	1000.0 (273.8)	548.3 (246.7)
<i>n</i>	10	16	15	13	11	11
Vaccinium myrtillus type						
Basal area, m ² ·ha ⁻¹	22.2 (10.1)	20.4 (11.5)	18.7 (6.8)	25.5 (6.5)	25.0 (5.1)	32.1 (6.6)
Mean DBH, cm ^b	13.0 (7.2)	8.4 (7.2)	11.0 (9.8)	12.4 (9.5)	12.0 (6.5)	23.1 (7.5)
Max. DBH, cm	21.4 (10.5)	22.1 (10.9)	23.9 (10.0)	27.2 (9.2)	24.8 (6.7)	32.6 (8.1)
Stand volume, m ³ ·ha ⁻¹	183.8 (98.9)	138.3 (106.9)	144.9 (98.1)	206.8 (120.0)	195.2 (67.5)	302.4 (84.8)
Hardwood proportion, % ^c	38.8 (27.5)	32.9 (20.5)	26.0 (12.0)	18.5 (9.7)	16.7 (7.8)	11.5 (10.2)
Stems·ha ⁻¹	2337.4 (1400.0)	5223.8 (3866.0)	4325.6 (4208.1)	3946.9 (3817.1)	2417.9 (1122.3)	1476.2 (885.5)
<i>n</i>	6	12	12	13	12	13

^aClass 10, 1–15 years elapsed since drainage; class 20, 16–25 years elapsed since drainage; class 30, 26–35 years elapsed since drainage, etc.

^bArithmetic.

^cProportion of total stem number.

Fitting the Weibull function to the diameter distributions

The empirical DBH distributions per hectare were calculated for each sample plot and measurement occasion, with 1-cm classes, for spruce and birch. The pines growing on some of the sites were combined with spruce. The DBH distributions were smoothed with the Weibull function, which has proved to be feasible and flexible in smoothing distributions of different shapes (Bailey and Dell 1973). The function produces two or three numerical parameters that describe the characteristics of the empirical distribution. Furthermore, the analytic cumulative distribution function is also known. Therefore, the Weibull function has been widely used to describe the DBH and basal area distributions of stands (Rennolls et al. 1985; Kilkki and Päivinen 1986; Kilkki et al. 1989; Knox et al. 1989; Maltamo et al. 1995; Siipilehto 1999).

We used the two-parameter Weibull function in which the probability density function for random variable x is

$$[1] \quad f(x) = \frac{c}{b} \left(\frac{x}{b}\right)^{c-1} \exp\left[-\left(\frac{x}{b}\right)^c\right], \quad \text{when } x \geq 0$$

$$f(x) = 0, \quad \text{when } x < 0$$

and the corresponding cumulative distribution function is

$$[2] \quad F(x) = 1 - \exp\left[-\left(\frac{x}{b}\right)^c\right], \quad \text{when } x \geq 0$$

$$F(x) = 0, \quad \text{when } x < 0$$

where $f(x)$ is the probability density, and $F(x)$ is the cumulative probability density of the number of trees in DBH class x . The scale parameter b indicates the location of the peak of the diameter distribution (the diameter where 63% of the cumulative DBH distribution is represented). Parameter c de-

scribes the shape of the distribution: $c \leq 1$, the distribution pattern is positively skewed (a reversed J shape); $1 < c < 3.6$, the distribution is dome shaped and positively skewed; $c = 3.6$, the distribution is approximately normal; $c > 3.6$, the distribution is negatively skewed.

We used the two-parameter Weibull function and assumed the minimum DBH to be 0. The parameters were estimated by fitting eq. 2 to the empirical DBH distributions that had been transformed into proportional cumulative diameter distributions. The parameters estimated from the basal area distributions produced overestimates of the stem number of the stand, especially for small-diameter trees. Moreover, parameter c of the DBH distribution described the stand structure more realistically than that of basal area distribution, in which larger trees get relatively more weight than smaller trees. As a result, we present the results from the DBH distributions only. The fitting was done using the MODEL procedure included in the SAS statistical software, which applies the maximum likelihood method (SAS Institute Inc. 1996).

Analysing the variation in stand structure

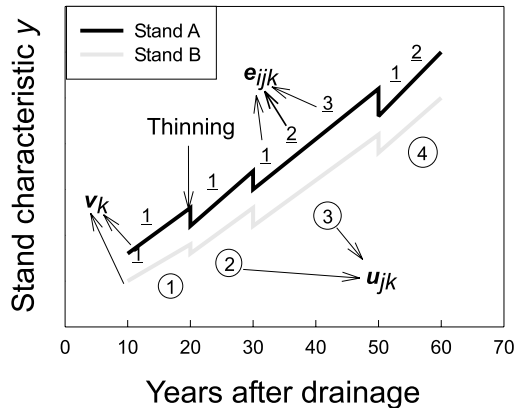
The material consisted of repeatedly measured stands and because of the hierarchical data structure, a mixed model approach was used. We identified three hierarchical levels of variation: (i) between stands, (ii) within stands between interthinning periods (periods between two successive thinnings), and (iii) within periods between the measurement time points (Fig. 1).

The mixed model had the following form:

$$[3] \quad y_{ijk} = \alpha_{ijk} + \beta_1 x_{1ijk} + \beta_2 x_{2ijk} + \dots + \beta_n x_{nijk} + v_k + u_{jk} + e_{ijk}$$

where y_{ijk} is the response variable (Weibull parameter b or c) for the measurement time point i within interthinning period j in stand k . The fixed part consists of intercept α , parame-

Fig. 1. Structure of random variation in the mixed models used for analysis of stand structure. Stand characteristic y denotes any stand characteristic that changes systematically along stand development (in our model, distribution parameter c). The term v_k indicates the random variation of the stand characteristic between stands k (stands A and B in the figure), u_{jk} indicates the variation between interthinning periods j (circled numbers) within stand k , and e_{ijk} accounts for the variation between measurements i (underlined numbers) within interthinning period j within stand k .



ters β_1 – β_n , and stand and site characteristics x_{1ijk} – x_{nijk} (see below for a list). In the random part, v_k is the random effect of stand k , u_{jk} is the random effect of the interthinning period j in stand k , and the random error e_{ijk} accounts for the within-stand variation between measurement time points. The random variables were assumed to be independent and to follow multivariate normal distribution with zero mean and variances σ_v^2 , σ_u^2 , and σ_e^2 .

Linear regression models were constructed by tree species for parameter c . Parameter b was solved analytically by eq. 4 (Kilkki and Päivinen 1986), as parameter c was predicted and the stand median diameter (D_M) was known:

$$[4] \quad b = \frac{D_M}{[-\ln(0.5)]^{1/c}}$$

The stand and site characteristics tested as possible predictors in the models included species-specific basal area (G , $\text{m}^2 \cdot \text{ha}^{-1}$), D_M (cm), maximum stem diameter in the stand (D_{Max}), stem number (N , ha^{-1}), stand volume (V , $\text{m}^3 \cdot \text{ha}^{-1}$), proportion of deciduous trees of total basal area and stem number, years elapsed since drainage, site type (two classes), geographic location of the site (three classes), thickness of the peat layer (cm), distance from the centre of the sample plot to the nearest ditch (m), and width of the drainage strip (m). To account for the effect of thinning intensity on parameter values, the following variables were determined: (i) a thinning dummy variable (if no cuttings had been done or the thinning removal was below 5% of the stand stem number, the value of this variable was 0, otherwise 1), (ii) change in D_M caused by thinning, (iii) change in N caused by thinning, and (iv) an interaction term of the change in D_M and N .

The parameter estimation was done by using MLwiN software (Goldstein et al. 1998), which estimates the fixed and random parameters simultaneously with the restricted iterative generalized least square method. The models were con-

structed by entering the variables into the model one by one. The relations between dependent and independent variables were linearized by appropriate transformations when necessary. The likelihood ratio test was applied to test the significance of each added predictor. The value of $-2 \log$ likelihood was used as an indicator of the overall goodness-of-fit of the models. Systematic error (bias) and relative bias were calculated to evaluate model reliability. The DBH distributions simulated by applying the two predicted parameters (b and c) in eq. 1 were examined visually for appropriate outcomes.

We used the Shannon index to examine the postdrainage development of tree size diversity within the stands. This method has been widely used to compute tree stand diversity characteristics (e.g., Buongiorno et al. 1994; Kuuluvainen et al. 1996). For this study, the Shannon index (H') was defined as

$$[5] \quad H' = \sum_{i=1}^n p_i \ln p_i$$

where p_i is the proportion of trees in diameter class i . The index was determined separately for spruces and birches at each measurement time point and stand.

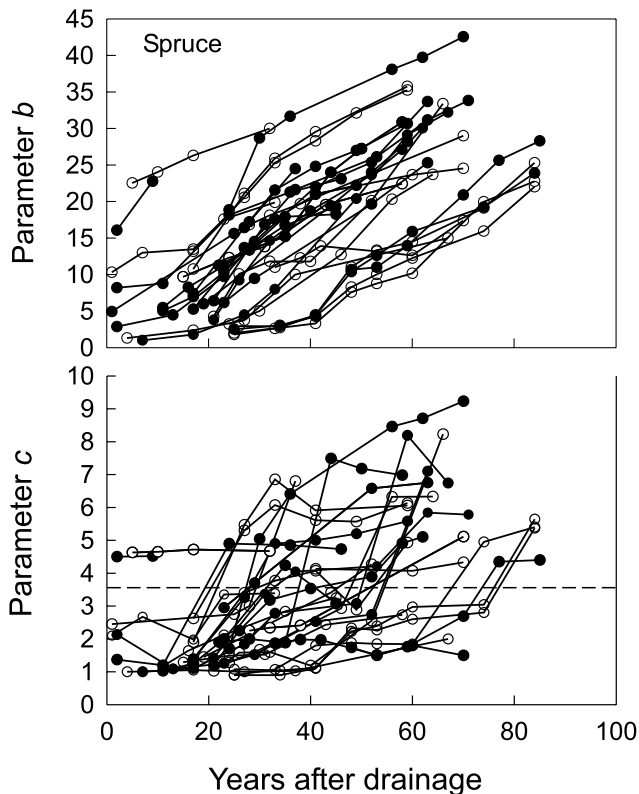
Results

The values of the DBH distribution parameters changed considerably after drainage (Figs. 2 and 3). The pattern of change was rather steady and similar for the two site types, even though the changes were somewhat faster in stands of the herb-rich type (Table 2). Variation in the values of the distribution parameters was large during the whole time period covered (Figs. 2 and 3). During the first two decades following drainage, the peak of the DBH distribution (value of parameter b) changed slightly towards smaller DBH classes. After that, the peak moved steadily towards larger diameter classes, the average increase being $0.33 \text{ cm} \cdot \text{year}^{-1}$ for spruce and $0.32 \text{ cm} \cdot \text{year}^{-1}$ for birch, respectively.

At the earliest stage of postdrainage development, the DBH distributions of spruce and birch were positively skewed (Figs. 2–4; Table 2) and this skewness remained or even increased during the first two decades. Later, a change in the opposite direction was observed and by drainage age 40 years, the average shape of the distribution was close to normal (Figs. 2 and 3; Table 2). For birch, the change continued steadily to negative skewness ($c > 3.6$). For spruce, the distributions remained close to normal for some time. By drainage age 60 years, the DBH distributions of spruce had become negatively skewed as well. The range of the diameters within stands remained very wide or even slightly increased over 60 years after drainage (Fig. 5). The Shannon diversity index (H') estimates showed an initial increase in the size inequality for both spruce and birch, after which the size inequality remained relatively constant (Fig. 6; Table 3).

Over a 20-year period, the mean total stem number increased from the initial $3000 \text{ stems} \cdot \text{ha}^{-1}$ to $4800 \text{ stems} \cdot \text{ha}^{-1}$ and then decreased to $950 \text{ stems} \cdot \text{ha}^{-1}$ by drainage age 60 years (Table 1). Pubescent birch accounted for, on average, 40% of the total stem number during the first two de-

Fig. 2. Standwise change of the peak (Weibull parameter b) and shape (parameter c) of the Norway spruce DBH distributions during time elapsed since drainage. Lines connect consecutive observations within the same stand. Open circles depict stands of herb-rich site type and solid circles depict stands of *Vaccinium myrtillus* site type. The broken line shows the value of parameter c at which the shape of the DBH distribution approximates normal distribution ($c = 3.6$). For means and standard errors by drainage age-class, see Table 2. Note that the scale of parameter b directly corresponds to that of DBH (cm).

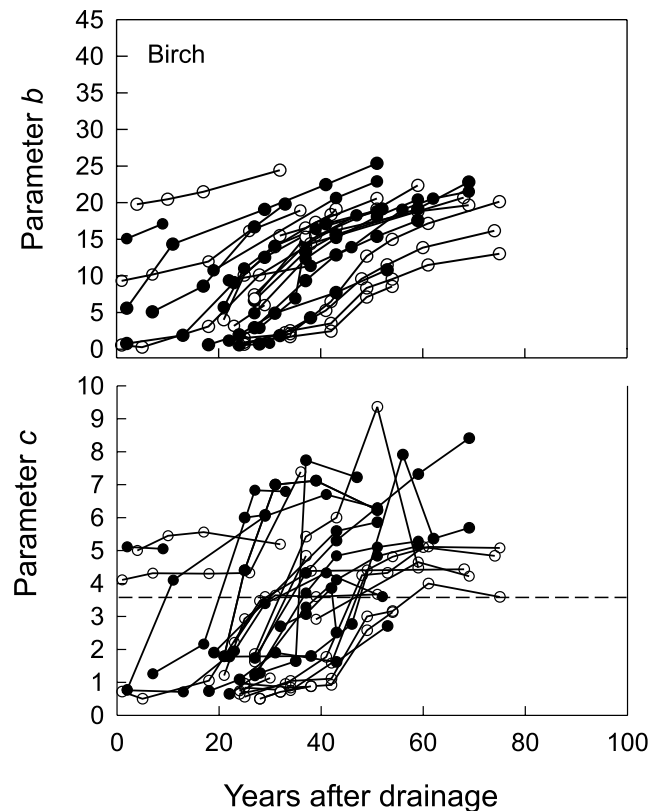


ades after drainage. It decreased gradually to 0–10% in 60-year-old drainage areas.

In the models for the shape of the DBH distribution (parameter c), the ratio of D_M to D_{Max} (which performed better than D_M alone by decreasing the heterogeneity of the residuals) for both spruce and birch was the single most important explanatory variable (Table 4). Further, stem number of spruce and years elapsed since drainage were significant explanatory variables in the model for spruce (Table 4). For birch, the basal area ($m^2 \cdot ha^{-1}$) improved the fit of the model (Table 4). For spruce, random variation between and within stands was significant, but the random effect of the interthinning period was not. However, for birch, random variation among the interthinning periods (u_{jk}) and random residual variation (e_{ijk}) were significant, while between-stand variation (v_k) was not.

Examination of the residuals revealed no systematic error in the predicted parameter c for spruce. The mean relative bias (in relation to the original parameter values) for the estimates was 5.7 and 6.3% for spruce and birch, respectively (Table 4). The relative bias for solved parameter b (eq. 4) was 1.2% for spruce and 13.1% for birch. In stands with a

Fig. 3. Standwise change of the peak (Weibull parameter b) and shape (parameter c) of the pubescent birch DBH distributions during time elapsed since drainage. Lines connect consecutive observations within the same stand. Open circles depict stands of herb-rich site type and solid circles depict stands of *Vaccinium myrtillus* site type. The broken line shows the value of parameter c at which the shape of the DBH distribution approximates normal distribution ($c = 3.6$). For means and standard errors, see Table 2. Note that the scale of parameter b directly corresponds to that of DBH (cm).



small number of diameter classes, the reliabilities of the predicted parameter values were lower. In mature stands (over 60 years elapsed since drainage or birch D_M over 20 cm), it was not possible to predict parameter c accurately for birch if the stem number of birch was low.

Discussion

Our material consisted of repeatedly measured permanent sample plots. At best, we were able to follow the development of the same stands for more than 60 years. Their structure was described by DBH distributions whose characteristics (shape, peak) were modelled. As the initial stocking varied considerably, the study plots were representative of the variation in stands to be found in Norway spruce dominated mires.

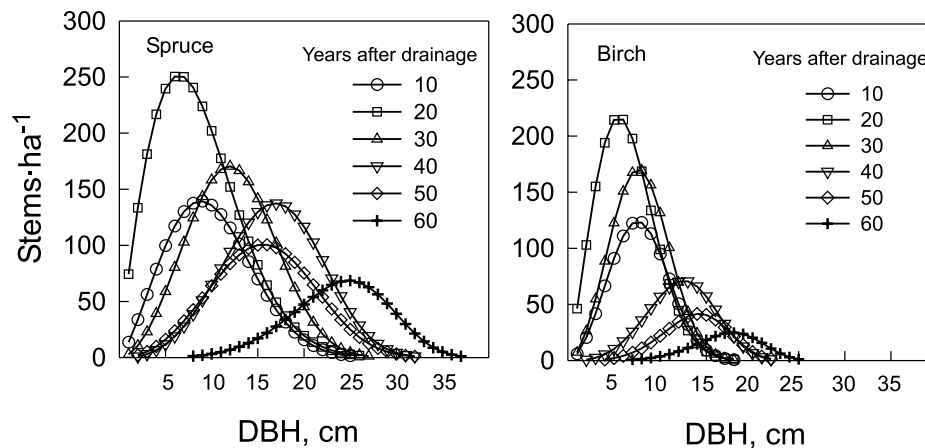
The initial positive skewness of the DBH distributions first increased after drainage mediated by increases in the stem numbers and shifts of the peaks of the DBH distributions towards smaller diameters. Simultaneously, the size inequality among trees increased. These changes were due to a flush of regeneration and (or) ingrowth of saplings reaching

Table 2. Means (standard errors in parentheses) of the estimated Weibull parameters b and c for Norway spruce and pubescent birch DBH distributions on drained spruce mires.

Drainage age-class ^a	Spruce		Birch	
	b	c	b	c
Herb-rich type				
10	7.964 (2.098)	2.046 (0.438)	7.551 (2.423)	2.312 (0.725)
20	9.205 (1.226)	1.901 (0.241)	7.602 (1.424)	2.003 (0.309)
30	15.042 (1.338)	3.116 (0.250)	10.222 (1.735)	3.603 (0.611)
40	22.213 (1.072)	4.539 (0.462)	14.484 (1.060)	4.516 (0.497)
50	21.699 (1.617)	4.001 (0.507)	17.894 (1.545)	4.899 (0.573)
60	30.800 (2.126)	6.380 (0.640)	19.920 (0.732)	6.570 (0.603)
<i>Vaccinium myrtillus</i> type				
10	14.481 (1.997)	2.616 (0.365)	10.095 (3.604)	3.348 (0.888)
20	9.964 (2.221)	1.901 (0.316)	6.441 (2.349)	1.791 (0.540)
30	12.504 (2.309)	2.737 (0.502)	7.195 (1.853)	2.130 (0.485)
40	14.765 (2.726)	2.665 (0.511)	12.705 (1.657)	3.228 (0.454)
50	13.353 (1.954)	2.470 (0.301)	12.200 (1.400)	4.269 (0.582)
60	20.956 (2.395)	4.118 (0.556)	16.730 (1.340)	4.668 (0.231)

^aClass 10, 1–15 years elapsed since drainage; class 20, 16–25 years elapsed since drainage; class 30, 26–35 years elapsed since drainage, etc.

Fig. 4. Mean DBH distributions for Norway spruce and pubescent birch by drainage age-classes. Class 10, 1–15 years elapsed since drainage; class 20, 16–25 years elapsed since drainage; class 30, 26–35 years elapsed since drainage, etc.



the measurement limit (1.3 m in height and 1 cm DBH) resulting from improved growing conditions following the lowering of the water level (Roy et al. 2000). At this stage, the competition from the larger trees was obviously not intensive enough to prevent the establishment and growth of smaller trees. As the stands aged, the distributions changed from positively skewed to normal and finally to clearly negatively skewed. However, during this development, the size inequality did not change. These changes were mediated by shifts of the peaks of DBH distributions towards larger diameters because of tree growth and decreases in stem numbers especially for small-DBH trees. The last-mentioned changes may be caused by either the inherent development dynamics of the stands with advancing drainage succession or the management applied.

Natural stand development in boreal coniferous forests is controlled by both allogenic (climate, site properties, or dis-

turbances such as forest fires, storms, snow, insects, and fungi) and autogenic (competition among plants) factors (Steijlen and Zackrisson 1986; Kuuluvainen 1994; Hörnberg 1995). In our analysis, much of the variation in stand structure due to site properties (site type, peat thickness, ditch spacing) and geographic location was implicitly accounted for by the explanatory variables in the models; stand median diameter explained most of the variation in stand structure, and at a given stage of development, it was firmly correlated with site properties and geographic location (i.e., climate). As neither the site characteristics nor the location affected the relationship between the median diameter and the shape of the DBH distribution, they did not explain structural changes.

Except for drainage and thinnings, our stands had not experienced any major disturbances. The effect of thinning was explicitly accounted for in the fixed part of the model, in

Fig. 5. Ranges of the DBH distributions, i.e., the difference between maximum and minimum DBH class within which 90% (5% of both tails of distributions excluded) of the total stem number of the stand is included.

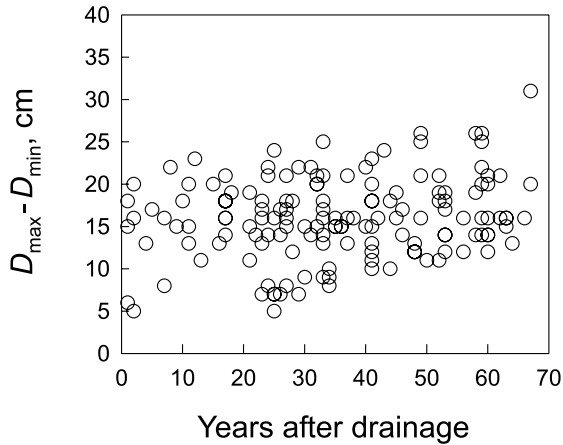


Fig. 6. Standwise change of the Shannon diversity index values for Norway spruce and pubescent birch during time elapsed since drainage. Lines connect consecutive observations within the same stand. Open circles depict stands of herb-rich site type and solid circles stands of *Vaccinium myrtillus* site type. For means and standard errors by drainage age-class, see Table 3.

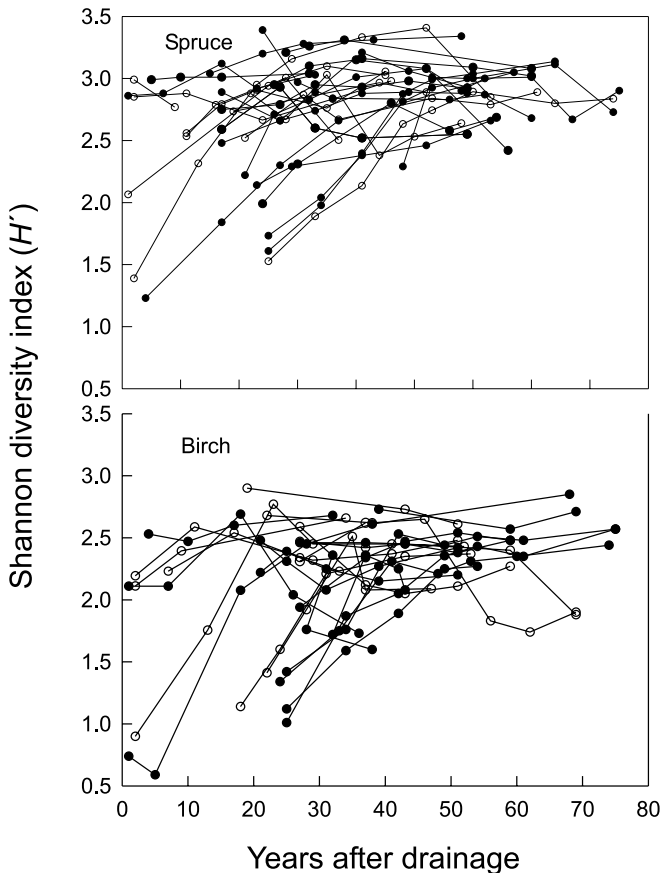


Table 3. Means (standard errors in parentheses) of the Shannon index (H') values for the within-stand diversity of tree sizes for Norway spruce and pubescent birch.

Drainage age-class ^a	H'	
	Spruce	Birch
Herb-rich type		
10	2.520 (0.155)	2.024 (0.211)
20	2.686 (0.130)	2.149 (0.278)
30	2.742 (0.114)	2.291 (0.092)
40	2.874 (0.090)	2.387 (0.068)
50	2.959 (0.100)	2.391 (0.084)
60	2.792 (0.069)	2.003 (0.108)
<i>Vaccinium myrtillus</i> type		
10	2.668 (0.289)	1.758 (0.354)
20	2.460 (0.143)	1.886 (0.179)
30	2.725 (0.082)	1.943 (0.109)
40	2.849 (0.101)	2.252 (0.074)
50	2.842 (0.059)	2.335 (0.039)
60	2.892 (0.069)	2.452 (0.035)

^aClass 10, 1–15 years elapsed since drainage; class 20, 16–25 years elapsed since drainage; class 30, 26–35 years elapsed since drainage, etc.

which the stand attributes had values reflecting the standing trees following thinning. However, neither the interthinning period variance component nor the thinning dummy variable proved significant for spruce. We concluded that thinnings had no effect on the drainage-induced trends in the changes of DBH distributions of spruce; obviously, the thinnings had removed trees of all sizes that would have died as a result of self-thinning. This was also the purpose of the management. For birch, the significant impact of thinning on the shape of the DBH distribution indicated that the management of the stands had altered the stand development: more small-DBH birches had been removed than would have died as a result of self-thinning. The decline in the proportion of birch has also been observed in pristine spruce mires as the stands matured (Norokorpi et al. 1997), but in our stands, management expedited this development.

We compared the density of our stands with the self-thinning limit modelled by Hynynen (1993) and Hynynen et al. (2002) for even-sized upland spruce stands (Fig. 7). The self-thinning limit describes the stand density limit where self-thinning begins. In general, the stem number – quadratic mean diameter relationships in our stands approached those indicating the theoretical self-thinning limit. This suggests that our stands were fully stocked, which supports the conclusion that the thinnings did not reduce total stem numbers more than would have happened as a result of self-thinning if the stands had not been managed.

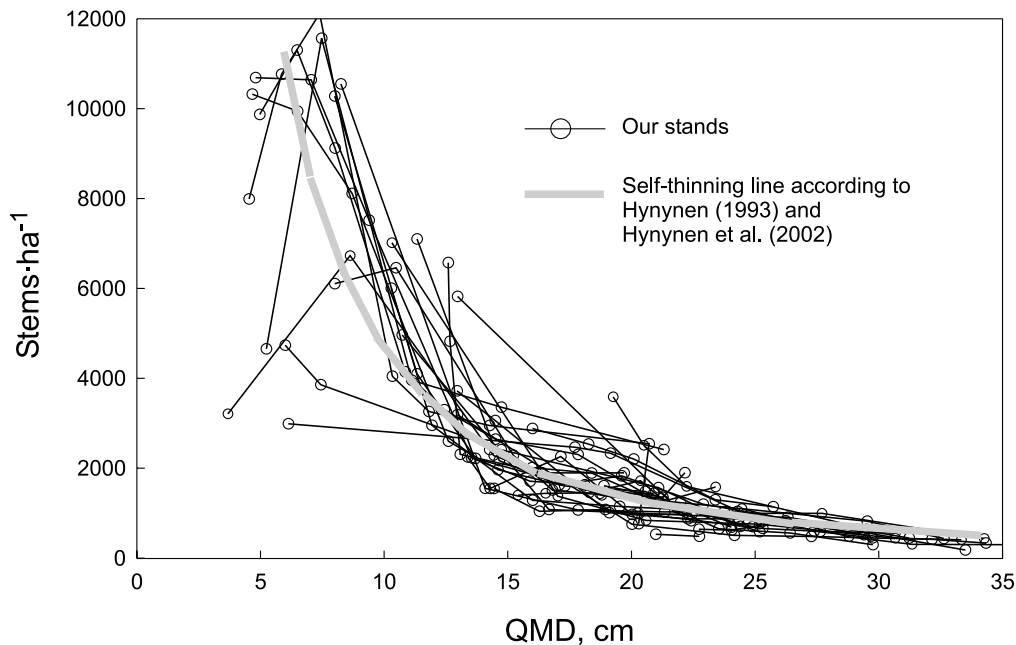
Because thinnings did not largely affect postdrainage changes in stand structure, we postulated that the structural changes in our stands reflect their inherent growth dynamics and the effects of intertree competition. We recognized three processes that partially overlap in time. First, in drained peatland stands, the size and the vigour of a tree at the time of drainage, rather than age, determine its intrinsic post-

Table 4. Models for the shape parameter (Weibull parameter c) of Norway spruce and pubescent birch DBH distributions on drained spruce mires.

Dependent variable	Fixed part variable	Parameter	Random part variable	Parameter
Spruce				
ln(c)	α	-6.7573 (1.3332)		
	$(1/\ln(D_M/D_{Max}))^{0.1}$	8.8299 (0.7278)	$\sigma^2 v_k$	0.0162 (0.0056)
	$\ln(N_s)^{0.5}$	-0.5511 (0.2436)	$\sigma^2 e_{ijk}$	0.0288 (0.0034)
	Year	0.0028 (0.0011)		
	Bias	-0.0842		
	Bias _r	-0.0568		
Birch				
ln(c)	α	-6.6609 (2.6820)		
	D_M/D_{Max}	3.1727 (0.0915)	$\sigma^2 u_{jk}$	0.0343 (0.0082)
	$(G)^{0.01}$	6.0152 (2.6573)	$\sigma^2 e_{ijk}$	0.0178 (0.0049)
	Bias	-0.0490		
	Bias _r	-0.0639		

Note: Standard errors are given in parentheses. α , constant; D_M , stand median diameter (cm) at breast height (1.3 m); N_s , spruce stems·ha⁻¹; year, years after drainage; D_{Max} , maximum tree diameter of the stand; G , stand basal area (m²·ha⁻¹); variance components: $\sigma^2 v_k$, random effect of stand k ; $\sigma^2 u_{jk}$, random effect of interthinning period j in stand k ; $\sigma^2 e_{ijk}$, within-stand variation between measurement time points. Bias_r, relative bias; the biases are presented after making the exponential transformation to the logarithmic models. The variance correction term $(\sigma_v^2 + \sigma_u^2 + \sigma_e^2)/2$ must be added to the logarithmic predictions before making the exponential transformation.

Fig. 7. Standwise change of the relationship between stem number per hectare and quadratic mean diameter (QMD) (mean diameter weighted with basal area). Lines connect consecutive observations within the same stand. The grey line depicts the self-thinning limit for even-aged and -sized Norway spruce stands in upland sites according to Hynynen (1993) and Hynynen et al. (2002).



drainage growth dynamics (Heikurainen and Kuusela 1962; Seppälä 1969, 1976). The drainage-induced radial growth response of larger trees is often slower and weaker than that of smaller ones (Seppälä 1969, 1976), which would enable the development of a more even size distribution after drainage (Macdonald and Yin 1999). Second, regeneration and ingrowth, indicated by increased stem numbers per hectare during the first decades after drainage, had a reverse effect,

increasing the number of trees in the small-diameter classes and thus increasing the positive skewness (toward smaller DBHs) of the distribution. Third, as the density of the stand increased after drainage, the impact of intertree competition on tree growth became more intensive.

High structural diversity was retained in our stands throughout the whole observation period. This high diversity comprised different structural groupings during the course of

the succession after drainage: first by advanced regeneration and growth of small trees and later on by widened DBH range of the trees. Our results were in accordance with those of Hökkä and Laine (1988) because structural inequality increased during the first 20–30 years after drainage. However, our results contradict findings suggesting that the DBH distributions of spruce stands growing on drained peatlands remain positively skewed as the stands mature (Laiho et al. 1997). We assume that this discrepancy is due to the different approaches in analysing the dynamics from cross-sectional or longitudinal data. Cross-sectional data used in all previous studies generally lead to overestimation of the proportion of small trees (Päivänen 1999).

We conclude that during early postdrainage development, competition among trees, if any, was symmetric. The steady change from positively skewed to normal to clearly negatively skewed DBH distributions towards the end of the 60-year postdrainage stand development is evidence of increasing asymmetric intertree competition (Cannell et al. 1984; Cannell and Grace 1993; Schwinning and Weiner 1998). The asymmetric competition was not intensive enough to result in distinct differentiation of separate tree layers, but the range of tree diameters slightly increased. On the other hand, size inequality among trees remained rather constant after an initial slight increase following drainage. This suggests a simultaneous component of symmetric competition (Weiner 1990).

For management guidelines, the early stage of stand development with high stem numbers and symmetric competition provides an opportunity to direct the increased growth potential to the desired crop component by precommercial thinnings. Later on, the impact of intermediate cuttings depends on the mode of competition. In the case of pure asymmetric competition, thinnings will not affect the growth of dominant trees; they may only benefit the manager by capturing self-thinning removal. As a component of symmetric competition seems to remain in these stands, it is likely that thinnings will increase the growth of retained trees, including the dominant trees. Thus, by removing less valuable and suppressed trees, the manager may again allocate the growth resources to the desired crop component to increase its production.

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