**Dissertationes Forestales 29**

# Stand structural dynamics on pristine and managed boreal peatlands

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Academic dissertation

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# ABSTRACT

The objectives of this study were to investigate the stand structure and succession dynamics in Scots pine (*Pinus sylvestris* L.) stands on pristine peatlands and in Scots pine and Norway spruce (*Picea abies* (L.) Karst.) dominated stands on drained peatlands. Furthermore, my focus was on characterising how the inherent and environmental factors and the intermediate thinnings modify the stand structure and succession.

For pristine peatlands, the study was based on inventorial stand data, while for drained peatlands, longitudinal data from repeatedly measured stands were utilised. The studied sites covered the most common peatland site types in Finland. They were classified into two categories according to the ecohydrological properties related to microsite variation and nutrient levels within sites. Tree DBH and age distributions in relation to climate and site type were used to study the stand dynamics on pristine sites. On drained sites, the Weibull function was used to parameterise the DBH distributions and mixed linear models were constructed to characterise the impacts of different ecological factors on stand dynamics.

On pristine peatlands, both climate and the ecohydrology of the site proved to be crucial factors determining the stand structure and its dynamics. Irrespective of the vegetation succession, enhanced site productivity and increased stand stocking they significantly affected the stand dynamics also on drained sites. On the most stocked sites on pristine peatlands the inter-tree competition seemed to also be a significant factor modifying stand dynamics. Tree age and size diversity increased with stand age, but levelled out in the long term. After drainage, the stand structural unevenness increased due to the regeneration and/or ingrowth of the trees. This increase was more pronounced on sparsely forested composite sites than on more fully stocked genuine forested sites in Scots pine stands, which further undergo the formation of birch and spruce undergrowth beneath the overstorey as succession proceeds. At 20-30 years after drainage the structural heterogeneity started to decrease, indicating increased inter-tree competition, which increased the mortality of suppressed trees within stand.

Peatland stands are more dynamic than anticipated and are generally not characterized by a balanced, self-perpetuating structure. On pristine sites, various successional pathways are possible, whereas on drained sites the succession has more uniform trend. Typically, stand succession proceeds without any distinct developmental stages on pristine peatlands, whereas on drained peatlands, at least three distinct stages could be identified. Thinnings had only little impact on the stand succession. The new information on stand dynamics may be utilised, e.g. in forest management planning to facilitate the allocation of the growth resources to the desired crop component by appropriate silvicultural treatments, as well as assist in assessing the effects of the climate change on the forested boreal peatlands.

Keywords: mire, forest succession, DBH distribution, *Pinus sylvestris*, *Picea abies,* drainage

# PREFACE

The basic roots of this study were established in the "Suopuu"-project (1999-2001), which was part of the Finnish Forest Cluster Research Programme - Wood-Wisdom financed by the Ministry of Agriculture and Forestry in Finland. During this project, as a young forestry student, I had an excellent opportunity to get myself acquainted with the scientific work and research problems related to the sustainable use of Finnish peatland forest resources that inspired me to begin this work and made the start financially possible. This work has been long and challenging, and it has, on its part, filled the gaps in our knowledge about the forest structure and dynamics on peatlands. The used time has, however, been short in respect to the rotation period of the forest stands growing on the boreal zone.

This study was financed mainly by the Graduate School of Forest Sciences and the Foundation for Research of Natural Resources in Finland. Additional financial support was obtained from the University of Helsinki and the Finnish Cultural Foundation. I am grateful to them for trusting on my project.

The study was primarily carried out in the Department of Forest Ecology at the University of Helsinki, but time periods spent in the Rovaniemi Research Unit in the Finnish Forest Research Institute were also necessary to accomplish the study. I wish to thank the staff of both organisations for their supportive and friendly working environment.

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August, 2006 Sakari Sarkkola

## LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, which are referred to in the text by Roman numerals. Some additional results obtained from the data presented in article II and IV, are also presented.

**I** **Sarkkola, S.,** Hökkä, H. & Penttilä, T. Size and age structures of Scots pine on pristine boreal mires in Finland: implications for stand dynamics (submitted manuscript)

**II** **Sarkkola, S.,** Alenius, V., Hökkä, H., Laiho, R., Päivänen & J., Penttilä, T. 2003. Changes in structural inequality in Norway spruce stands on peatland sites after water-level drawdown. Canadian Journal of Forest Research 33: 222-231.

**III** **Sarkkola, S**., Hökkä, H., Laiho, R., Päivänen, J. & Penttilä, T. 2005. Stand structural dynamics on drained peatlands dominated by Scots pine. Forest Ecology and Management 206: 135-152.

**IV** **Sarkkola, S**., Hökkä, H., & Penttilä, T. 2004. Natural development of stand structure in peatland Scots pine following drainage: results based on long- term monitoring of permanent sample plots. Silva Fennica 38: 405-412.

S. Sarkkola is fully responsible for the summary part of this doctoral thesis. Studies I-IV: S. Sarkkola was the main writer, was responsible for most of the planning and all the data analysis and model constructions.

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## TERMINOLOGY AND ABBREVIATIONS

**Peatland:** Ecosystem (also **Mire**) and substrate, which is formed in cool and humid climatic conditions where part of the dead organic matter accumulates as a slowly decomposing layer i.e. peat on the soil surface. The vegetation consists of mosses and vascular plants adapted to wet conditions with low oxygen availability. Peatland can be formed through the succession of ecosystem from aquatic towards terrestrial systems (terrestrialisation), through the conversion of a mineral soil site to a peatland due to a rise in the water table level (paludification) or through a process whereby the soil surface is occupied by mire vegetation immediately after the retreat of water e.g. sea or glacial ice (primary peat formation).

**(Genuine) forested site types:** Naturally forested, mostly Norway spruce or Scots pine dominated peatland sites. They support a rather dense natural tree stand and relatively uniform hummock vegetation dominated by dwarf-shrubs. These sites are either shallow-peated swamps, “recently” evolved from paludified forest land, or they are thick-peated forested bogs representing a late successional stage of the mire development (Tallis 1983, Laine & Vasander 1996). The trophy level of these sites ranges from **minerotrophic** to **ombrotrophic** sites. Abbreviated as **Group I sites** in this study.

**Sparsely forested composite site types:** These sites are wetter than the forested sites and they have an irregular mosaic-like character of vegetation, with microsites ranging from dry hummocks to wetter lawns. The hummocks are dominated by dwarf-shrub vegetation and the hollows by sedge (*Carex sp.*) or sedge-like (e.g. *Eriophorum vaginatum*) vegetation. In these sites, trees are generally found in hummocks. These sites are mostly **minerotrophic**. Abbreviated as **Group II sites** in this study.

**Drainage of peatlands:** Lowering the water table level in peatlands by man-made management by digging a ditch network on the target peatland area.

**Ecohydrology of peatlands:** Temporal and spatial variation in the amounts and quality of water flowing to a site that controls the establishment, development and function of the peatland ecosystem. For example, the spatial variation in the microsites of the peatland surface is result from the site’s ecohydrological characteristics

**Tree stand**: A tree stand is defined as a relatively uniform group of forest trees that can be clearly differentiated from surrounding stands by its structure, tree species composition and site type. Closely related to the term of “forest compartment” much used in the operational forestry as the management unit. In this study, the tree stand is described either by permanent sample plots having fixed area (drained peatlands) or by the set of three circular sample plots having varying radius (pristine peatlands). Furthermore, a stand can be categorized into substands by tree species or tree’s dimensional variation. In contrast, a landscape-level forest consists of several individual stands.

**First post-drainage tree generation**: A tree stand in a site, where most of the dominant tree individuals have been established before drainage of the pristine peatland or immediately after drainage, when the drainage induced plant succession, in which the mire plants gradually will be replaced by the upland forest plant species, have not yet proceeded. The tree generation ends at the final cutting.

**Stand structure:** It can be defined with various ways (see Chapter 1.2.3.). Basically, the stand structure is the distribution of trees in a stand, which can be described by species, vertical or horizontal spatial patterns, size of trees or tree parts, age, or a combination of these. In this study, the most important describer of stand structure is the tree diameter distribution in the stand measured at breast height (1.3 m) of trees.

**Stand succession** or **stand dynamics:** A gradual temporal change of stand characteristics (e.g. variation in tree size, stem number, stand volume, tree species composition) and structure in a given tree stand. Commonly, the stand succession includes the sequence of **seral/developmental stages**, which replace one another in time. In drained peatlands, the stand succession takes place in pace with the secondary vegetation succession, i.e. a change in the plant species composition induced by water level drawdown.

**Chronosequence:** A cross-sectional sequence of tree stands that are similar with respect to species composition and site quality, but differ from one another primarily, because they are usually situated in different locations and may represent different stages of stand development.

| | | |
|---|---|---|
| DBH | cm | Tree diameter at breast height, 1.3 m |
| DM | cm | Arithmetic tree median diameter |
| DgM | cm | Stand basal area median diameter |
| $D_{Max}$ | cm | 95% of the maximum DBH of stand |
| G | $m^2ha^{-1}$ | Stand basal area |
| N | $ha^{-1}$ | Stand stem number |
| V | $m^3ha^{-1}$ | Stand total stem volume |
| VTD | | Proportional share of timber-sized trees ($d_{1.3}$ > 19cm) of the total stand volume |
| $H_{dom}$ | m | Stand dominant height (the mean height of 100 thickest trees of given stand) |
| $D_{diff}$ | cm | Difference between stand DgM and DM |
| DBH range | cm | Difference between minimum and maximum tree diameter of a given stand |
| AM | years | Arithmetic stand mean age |
| $A_{dom}$ | years | Stand dominant age (the mean age of trees whose diameter exceed the stand basal area median diameter) |
| BirchG% | | Proportional share of deciduous trees (pubescent birch) of the total stand basal area |
| SpruceG% | | Proportional share of Norway spruce of the total stand basal area |
| CutN% | | Proportional cut-removal of stand stem number in the previous thinning treatment |
| Tsum | degree days | Temperature sum: sum of daily average temperatures exceeding +5°C |
| Yeard | years | Years since drainage |
| StripW | m | The width of the strip between ditches |

| | |
|---|---|
| $^{2}_{k}$ | Variance component of the random effect of stand k |
| $^{2}_{jk}$ | Variance component of the random effect of inter-thinning period j in stand k |
| $^{2}_{ijk}$ | Variance component of the within-stand variation between measurement time-points i |
| Kurtosis | Statistical measure of whether the data are peaked or flat relative to a normal distribution. In case of normal distribution, the value of kurtosis is zero |
| Skewness | Statistical measure of symmetry of distribution. In case of normal distribution, the value of skewness is zero |
| Shannon index H’ | A mathematical measure used to describe the diversity of tree diameters and ages within stand |
| Weibull distribution | Statistical probability distribution, which can be formed by the parametric Weibull function |
| Bias | difference between observed and predicted value |
| Biasr | relative bias: the bias in relation to the observed value |

# 1. INTRODUCTION

## 1. 1. Background

Boreal peatland (mire) ecosystems are formed in cool and humid climatic conditions, where the organic matter decomposition is limited and where organic matter accumulates as peat on the soil surface. Mire vegetation consists of mosses and vascular plants adapted to wet conditions where there is low oxygen availability (Ingram 1983). Some peatlands support trees naturally, but due to excessive water in the substrate, the growth of trees in pristine sites is usually low (Jeglum 1974, Gustavsen and Päivänen 1986). In some countries (e.g. Canada) operational scale forestry is carried out on pristine peatlands (Haavisto and Jeglum 1991). In most countries, (e.g. Finland, Sweden, Norway, the Baltic countries, Russia, Belarus, Poland, Scotland and Ireland), however, peatland forestry mainly refers to drained peatlands. Forestry on pristine sites is usually unprofitable (Paavilainen and Päivänen 1995). Drainage significantly increases tree growth and site productivity (Starr 1982).

In Finland, about 29% (about 10 million hectares) of the total land area has originally been covered by mire vegetation communities capable of forming peat. Of this area, about 4.9 million hectares of peatlands and about 1.3 million hectares of waterlogged mineral soil sites have been drained to increase wood production (Tomppo 2005). The first systematic forest drainage operations were done on state owned land in the beginning of 1900s, but the bulk of the drainage operations were carried out during the 1960s and 1970s. Drainage operations peaked in 1969, when about 300 000 hectares of peatlands were drained (Paavilainen and Päivänen 1995). The drainage of pristine peatlands thereafter decreased year by year, and had practically ceased by the beginning of 1990s (Hökkä et al. 2002). Nowadays, the focus of the drainage operations is on the maintenance of the existing ditch networks, such as ditch cleaning and complementary ditching (Joensuu 2002). According to the present forest certification system applied in Finland (FFCS), pristine peatlands are no longer to be reclaimed for forestry (Metsäsertifioinnin…2005).

Scots pine (*Pinus sylvestris* L.) is one of the most common tree species on both drained and pristine peatlands. About 3.4 million hectares, i.e. 67% of the total peatland area drained for forestry, are dominated by Scots pine, mainly growing on poor minerotrophic or ombrotrophic sites (Hökkä et al. 2002). Norway spruce (*Picea abies* (L.) Karst.) typically dominates the productive minerotrophic peatland sites, covering about 0.9 million hectares. The rest of the drained forested peatland area is dominated mainly by pubescent birch (*Betula pubescens* Ehrh.) (Tomppo 2005).

On average, drainage has increased the annual forest growth on peatlands more than twofold, being at present about 21 million $m^3$ $yr^{-1}$. The total growing wood stock on peatlands is estimated to be 480 million $m^3$, of which 81% is growing on drained peatlands (Tomppo 2005). Peatlands have played only a minor role in wood harvesting in respect to their share of the total wood resources, however. There are several reasons for this, including: 1) most of the areas have been drained rather recently and consequently, only a minority of the stand stockings have reached maturity for commercial merchantable thinnings (Hökkä and Laine 1988), 2) the low bearing capacity of the ground for heavy machinery and commonly long transportation distances increase the harvesting costs (Sirén 2004), and 3) knowledge about available wood assortments, wood quality and appropriate silvicultural methods, such as thinning regimes, that are ecologically and economically applicable for peatlands, is lacking. But the allowable cut of peatland wood will increase significantly in the near future. According to recent scenarios based on data from the 8th National Forest Inventory (NFI8), the annual allowable cut on peatlands would increase up to 15-20 M $m^3$ $yr^{-1}$ over the next 20 years (Nuutinen et al. 2000). Thinnings are becoming a common management procedure on drained peatlands, but regeneration cuttings in mature peatland stands are also being increasingly practiced. The amount of mature stands on peatlands has been estimated to be 7% (Hökkä et al. 2002). Particularly, the more nutrient-rich spruce peatland sites have considerable potential for high-quality saw timber production (Rikala 2003).

## 1.2. Tree stand structural dynamics

### *1.2.1. Basic principles of succession*

On any given site, plant communities, including forest and peatland ecosystems, tend to change their structure over time (Odum 1959, Pickett 1976, Niering 1987). This dynamic process is called succession. Succession includes directional changes both in the abiotic and biotic parts of the ecosystem, e.g. changes in the structural complexity, changes in the composition and diversity of plant species, changes in the relationships of the plant individuals and plant species, changes in the system energy flow and element allocation, as well as changes in the availability of growth resources such as light, water and nutrients (Pickett 1976, Barbour et al. 1986, Oliver and Larson 1990). The trend and speed of succession is largely controlled by autogenic factors, e.g., site productivity (availability of necessary growth resources), inter-individual and inter-species competition and the ecology of plant species, and allogenic factors such as climate conditions and management activities (Luken 1990). Disturbances can be of both man-made and natural origin, such as cuttings, fires, flooding, storms etc. (Pickett 1976, Oliver and Larson 1990, Jentsch et al. 2002, Zenner 2004). An important man-made disturbances that dives succession, is drainage on peatlands (Päivänen 1998).

The concept of plant community succession can be divided into primary and secondary succession. In primary succession, a plant community is established on a bare site, which has not earlier been covered by plants, whereas secondary succession originates on a site where an earlier plant community has been disturbed and is being replaced by a new one (Egler 1954). In secondary successions, the characteristics and the species of the previous community may significantly affect the development of the new community. A typical example of primary succession is the peatland or forest establishment and development on a rising coastline (Svensson and Jeglum 2001). The succession that takes place on drained peatland are secondary succession, where the mire vegetation is gradually replaced by forest plant species due to water-level drawdown (Sarasto 1952, Hotanen et al. 1999, Korpela 1999). The transition of vegetation towards drier communities can be called ”hydroseral succession” (e.g. Hughes and Barber 2004). The changes in stand structure considered in this study are thus secondary successional changes.

In literature, the theory of vegetation succession has been described in several ways that emphasize e.g. the function of different processes modifying the development of plant community during succession (Clements 1916), the importance of the variation and availability of the growth resources (Drury and Nisbet 1973), as well as competition (Pickett et al. 1987) as the most important modifying powers of plant community succession. Some scientists also emphasize the effect of the previous plant community on the following one (Connell and Slatyer 1973).

The traditional approach is so-called the floristic succession theory, which is largely based on Clements's (1916) work. In this theory, the plant community, which is established on bare soils, undergoes given specific processes during the succession. The floristic approach has been widely used in forest research, in which succession has been categorized to seral stages based on the given modifying events or processes taking place temporarily within a stand (e.g. Long and Smith 1988, Oliver and Larson 1990, Carey and Curtis 1996, Spies and Franklin 1996, Harper et al. 2005). Generally, the theories of stand succession describe the stand developmental pathway, which has been established on a bare soil and develops further as even-aged and –sized. Thus, the succession theories are often ideal for the even-aged stands (Oliver and Larson 1990). It is also worth noting, that stand succession has been studied earlier mainly on mineral soil sites and the validity of the above mentioned theories has not been tested on peatland sites.

### *1.2.2. Stages of forest succession*

Stand structural development can be depicted using trends in the changes of abundance of different structural components. These trends can then be used to define and describe the stages of stand succession (Harper et al. 2005). Applying the floristic theories, stand succession can be crudely categorized into the following seral stages: 1) disturbance creation, which makes space for new tree generation 2) stand initiation, 3) canopy closure, 4) self-thinning, 5) maturation, and 6) old-growth (climax) stage. The duration of any single stage is dependent on the site's potential, the ecology of the tree species in question and the climate conditions (Oliver and Larson 1990, Franklin et al. 2002).

In (secondary) forest succession, disturbance events create prerequisites for the establishment of new tree generation on a site by decreasing the competition. The rotation period and the severity of the disturbances essentially affect the pathway of stand succession (Frelich and Reich 1998, Cyr et al. 2005). A disturbance can be small-scale, i.e., only tree groups or single trees may be killed by wind or partial fires creating gaps in the stand (Hytteborn et al. 1987). In turn, large-scale disturbances such as severe fires, insect outbreaks and storms encounter the whole ecosystem destroying the whole stand (cf. Bergeron 2000). On the other hand, the stand may also remain alive, but the availability of the growing resources in a site may be changed significantly resulting secondarily in changes in the structure of the plant community and stand development (see Pickett and White 1985). Drainage of peatlands, which can be caused by nature, e.g. climate change (Gorham 1991), or by direct human impact aimed to increase wood productivity, is an example of the latter mentioned disturbance type (Päivänen 1998).

In the initial phase of stand development, a new tree cohort occupies a site and stand density increases (Oliver and Larson 1990, Franklin et al. 2002). During this stage, the inter-tree competition within the cohort, particularly the competition for light, which is assumed to be generally size-asymmetric, is usually low (Brand and Magnussen 1988, Nilsson 1993) and thereby a new stand is often dominated by fast growing, but light-demanding species, e.g., deciduous trees in the boreal zone.

As trees grow, the stand canopy will gradually close resulting in a change in the environmental conditions and the relationships between the trees. The rate of canopy closure depends on the density of the trees and the site productivity (Franklin et al. 2002). After canopy closure the inter-tree competition gradually increases and starts to modify the stand structure. The role and the mode of the competition as a modifier of stand structure and development have been rather widely discussed in the literature. In crowded stands, the size-asymmetric competition mainly for light is generally considered to be the most important autogenic factor controlling the relationships between trees along stand development (Ford 1975, Cannell et al. 1984, Newton and Jolliffe 1998, Wyszomirski et al. 1999, Kohyama et al. 2001, Bauer et al. 2004, Doležal et al. 2004). However, besides solar energy, trees compete also for the below ground resources like nutrients and water, and in some sites, where the availability of these resources have been restricted, such as in nutrient poor peatlands or in areas with harsh climate conditions, this size-symmetric competition may play an important role affecting the stand growth and development (Hökkä et al. 1996, Stoll et al. 1998, Wirth et al. 1999, Doležal et al. 2006).

Increasing size-asymmetric competition results gradually in the formation of tree size hierarchy in a tree stand, which means increasing variability in the tree size and the eventual expression of dominance by the large individuals (Harper 1977). The tree size inequality increases, because the dominant trees have higher relative growth rates than suppressed trees (Ford 1975, Cannell et al. 1984, Wyszomirski et al. 1999), because in comparison with dominant trees their acquisition of the growing resources is more limited and it is not as efficient (Binkley et al. 2002).

As the inter-tree competition intensifies it gradually results in dying of the suppressed trees (density dependent mortality) within the stand, which decreases the stem number and structural inequality (Mohler et al. 1978, Knox et al. 1989). Trees are disposed to die (self-thinning) when “the maintenance cost” of the living cells of conducting sapwood and associated tissues per unit of photosynthesising foliage exceeds the canopy's capacity to sustain them (Waring 1987). By this self-thinning stage, the tree cohort has reached the dominant position in the site and the maximum growth rate of the stem biomass (Franklin et al. 2002). For example, on mineral soil sites in Finland, Scots pine stands reach the maximum stand volume growth at the age of 30-50 years (Vuokila 1960) and Norway spruce stands at the age of 40-50 years depending on the site’s productivity (Kallio 1957). In practical forestry, the first commercial thinnings are timed to be carried out at this stage in order to utilize the trees, which would otherwise die, and to reduce the competition among the remaining trees.

In the maturation stage, tree height growth generally decreases and the trees reach their maximum height and canopy size (Franklin et al. 2002). The density dependent mortality of trees decreases and the proportion of other factors causing mortality, such as diseases (e.g. fungi) and wind damages, increases. Simultaneously, as the available growing space increases within a stand, a new tree generation, which consists of shade-tolerant species, may be established below the dominant trees in the undergrowth cohort, which may gradually extend to the dominant canopy layer. Oliver and Larson (1990) and Carey and Curtis (1996) call this stage also “an understorey re-initiation stage”. In practical forestry, the maturation stage has been used as the end phase of stand rotation when it is economically reasonable or legal to regenerate a stand. For example, in Finnish forest legislation, Norway spruce stands reach the maturity for regeneration at 80-110 years of age and Scots pine stands at 70-130 years of age depending on the site’s fertility and its geographic location (Maa- ja metsätalousministeriön…1997).

In traditional succession theories, on mineral soil sites, the stand succession has been presented to culminate in a stage, where the tree stand reaches a “self-perpetuating state”; it is in equilibrium with the physical habitat, there is usually no net accumulation of organic matter and there is high structural and species diversity (Sirèn 1955, Oliver and Larson 1990, Franklin et al. 2002). Simultaneously, the age related mortality of trees and the amount of dead wood increases, the tree species composition is stabilized, and small-scale disturbances make gaps in the tree stand. Thus they make space for regeneration of new seedlings and generate the stand structural complexity (multicohort and spatially patchy stand structure) (Zackrisson et al. 1995, Kuuluvainen et al. 1998b, Franklin et al. 2002, Hytteborn et al. 1987, Linder et al. 1997, Kuuluvainen et al. 2002, Kneeshaw and Gauthier 2003, Lilja et al. 2006). During this “climax” or “old-growth” stage, surface vegetation in the site also achieves its ”normal” species composition and its ecological niche, which depends on the site’s ecologic-biological characteristics (described in the boreal zone e.g. by Cajander (1909, 1949)). On mineral soil sites in the boreal zone, a Scots pine stand is suggested to reach the old-growth stage at the biological age of about 150 years (Pennanen 2002). On the other hand, it may require even over 300 years to attain certain old-growth structural attributes in boreal coniferous stands (Lilja et al. 2006). This stage may last much longer than the duration of the previous seral stages overall if no catastrophic disturbance takes place (Franklin et al. 2002). However, considering old-growth, it has been suggested to be more realistic to describe it as a stage, which consists of several overlapping seral stages forming a mosaic or patchy pattern within a stand (e.g. Oliver and Larson 1990, Prentince and Leemans 1990, Lilja et al. 2006). Some researchers differentiate this phase from the concept of forest succession into its own type of forest dynamics (e.g. Angelstam and Kuuluvainen 2004). In this stage, the stand is suggested to be in “a quasi-equilibrium state”, which has been maintained by the continuous small-scale gap formation (Kuuluvainen et al. 1998a).

In reality, the development of any single stand is seldom a strict continuum of given seral stages. Multiple pathways of stand development may exist affecting the trends of stand development, as well as the timing and number of the seral stages (Pickett et al. 1987, Kint et al. 2004). However, the mechanistic categorization of the succession helps to conceptualize the stand development and the processes modifying the stand during its development. For example, in Finland, a system of classification of stands according to their developmental stage has been widely used in practical forestry and in the forest inventories as a tool for the proper management needed.

Stand succession can be described in various ways such as by quantifying the temporal changes in the composition of plant species and plant biomass. In order to understand the function of the forest ecosystem, as well as the economic utilization of forest stands, perhaps the most important characteristics are the stand structural features and their changes in space and time (Oliver and Larson 1990). In this study, forest succession will be described as the temporal change of stand structure.

### *1.2.3. Definition of tree stand structure*

Many definitions have been used in describing tree stand structure in research, as well as in practical forestry. In many cases, the term stand structure has been used for characterising a forest in general. However, commonly, tree stand structure is considered as a physical or temporal distribution of trees at within-stand –level (Oliver and Larson 1990). It is an outcome of ecosystem processes (e.g. site productivity, nutrient cycling, and regulation of hydrological cycles) and the ecology and diversity of the species in question (Spies 1998, Franklin et al. 2002). In forest ecosystem research, forest structure has also been characterised on the landscape –level, which consists of structural attributes over a number of single stands (e.g. Kuuluvainen et al. 2002).

Stand structure can be described either directly of indirectly using stand characteristics (tree species composition, stand volume, height, age, stand density) or frequency distributions, like tree size distribution (diameter, height, basal area, volume, biomass, canopy dimensions) and tree age distributions expressed for the whole stand or separately by tree species or trees canopy classes (cf. Svensson and Jeglum 2001, Zasada and Cieszewski 2005, Hotanen et al. 2006). Stand structure can also be described by spatial distributions and patterns, like the vertical or horizontal spacing of the trees (tree size structure) or in time (tree age structure), that can be analyzed with various distance-dependent diversity indices (e.g. Lähde et al. 1999a, Neumann and Starlinger 2001), statistical functions (e.g. Kuuluvainen et al. 1998b, Freeman and Ford 2002) or point process methods (Stoyan and Penttinen 2000). The landscape-level structure can be analysed descriptively (e.g. maps) or by statistical methods e.g. grid-data analysis (Pennanen and Kuuluvainen 2002) and spatial complexity models (cf. Busing and Mailly 2004).

Considering the stand structure, characteristics of tree size variation in a stand expressed as tree diameter distribution have been widely used in forest research. Diameter distribution gives direct, ecologically and economically important information on the tree stand such as the quantity of timber assortments and their variability, the stand density and developmental stage. Furthermore, it enables to predict and simulate the future stand development and the stand target states for management objectives, e.g. decision on thinnings, prediction of stand growth and yield etc. (Harper 1977, Carleton and Maycock 1978, Hyink and Moser 1983, Franklin et al. 2002, Hynynen et al. 2002). Furthermore, the tree diameter distribution is a good surrogate to characterize the potential biological diversity within a stand (Buongiorno et al. 1994). It is also a simple and easily measurable structural characteristic of a stand (Päivinen 1980). Due to the reasons mentioned, the characteristics of tree diameter distributions have been used for describing the stand size structure also in this study.

### *1.2.4. Evenly- vs. unevenly- structured stand: dynamics and management*

Tree stand age and size structure can be roughly classified into two categories according to the variation in tree size and age within a stand: unevenly (irregularly) structured and evenly (regularly) structured stands or also uneven-aged and uneven-sized vs. even-aged and even-sized stands (e.g. Assmann 1970, Lähde et al. 1999b). Tree age structure has often been used as a synonym of tree size structure, because tree age usually correlates with tree size (Clark et al. 2003). However, in many cases the relationship between tree age and size has proved to be weak, e.g. in old-growth stands (Kuuluvainen et al. 2002), in extreme growing conditions such as on timber lines (Knowles and Grant 1983) and on pristine peatlands (Ågren and Zackrisson 1990). Also on drained peatlands, the correlation between tree age and size has been proved to be weak; tree age does not necessarily have significant influence on the release in tree growth following drainage (Hökkä and Ojansuu 2004). Thus, the age structure of stands on drained peatlands has not been considered relevant in this study.

As a typical characteristic of an uneven-sized structure, the shape of the stand DBH distribution resembles reverse J i.e., the distribution is positively skewed so that the smallest trees are the most frequent in a stand (Oliver and Larson 1990) (Fig. 1). At stand level, it has been suggested that the uneven structure is due to the more or less constant mortality rate over the tree age and size classes, and constant regeneration of seedlings, in general (Ågren and Zackrisson 1990, Rouvinen et al. 2002, Ranius et al. 2003). In uneven-sized stands, there also usually is a large inequality of tree dimensions, as well as two or more canopy stories (multicohort-structure) (Sirèn 1955, Lundqvist 1993, Lähde et al. 1999b). A stand is judged to be storied if two or more clear peaks can be distinguished in the DBH distribution or there is a distinct empty interval between diameter class groups in the stand (Laiho et al. 1999). Respectively, in even-sized stands the shape of the DBH distribution is bell-shaped, i.e. it approaches the statistical normal distribution or it can even be negatively skewed, where only small horizontal and vertical variation exists in the stand (Assmann 1970, Oliver and Larson 1990) (Fig. 1). As a classical example, Ilvessalo (1920a, 1920b, 1937) studied the development of fully stocked natural pure Scots pine, Norway spruce and silver birch tree stands and demonstrated their DBH distributions to follow the shape of the normal distribution ("naturlich normalische bestände"). Further, Lönnroth (1925) classified the trees within single stands to numerous canopy classes, in which the shape of the DBH distributions were suggested to follow normality.

In practice, there is no clear limit whether a given stand is unevenly or evenly structured, but it is more or less abstract concept. Some scientists have, however, tried to make mathematical definition for the criteria of these structures. For example, Daniel et al. (1979) presupposed a stand to be even-aged if there is at the most 20% variation in tree ages of the stand's biological rotation age and more or less normal DBH distribution. Lähde et al. (1991) and Norokorpi et al. (1994) presented that in the even-sized stands, the diameter variation covers at most 15 cm (three DBH classes of 5 cm). However, any appropriate ecological interpretations have not been presented for these definitions.

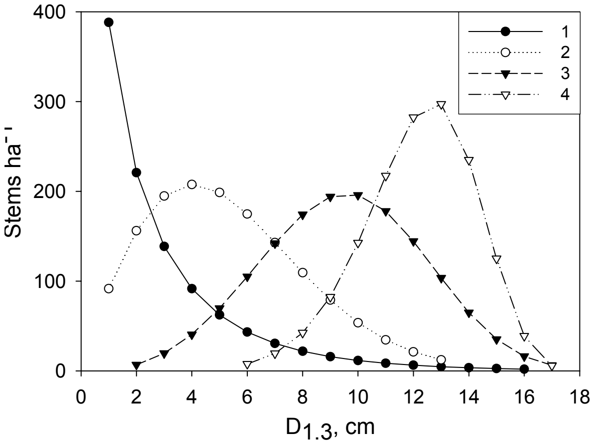

**Figure 1.** Different schematic types of DBH distribution (stand structures). 1. Reverse J-shape (uneven-sized structure; also all-sized or irregular structure), 2. Positively skewed distribution (intermediate between uneven-sized and even sized structure), 3. Normal or bell-shaped distribution (even-sized or regular structure), 4. Negatively skewed distribution (even-sized structure). Redrawn from Rennolls et al. (1985).

In the last decades, the interest in stand structural characteristics has increased significantly as human impacts on forest ecosystems and biological diversity have been assessed. Also new "close-to-nature" or "nature-oriented" methods for forest management and silviculture have been developed in order to improve the ecological sustainability of forestry, to protect the diversity of biotopes and to smooth over the conflicts between different forms of forest use (Schütz 1999, Lähde et al. 2001). The traditional forestry, particularly in Northern Europe, has been based on the frame of even-aged management, i.e., on the regimes of successive thinnings from below and final cuttings. In this approach, the stand is grown as even-aged and –sized in order to maximize the timber production and the economic income obtained mainly from the final cuttings (Buongiorno 2001, Nabuurs et al. 2001). More nature-oriented silviculture is based on the intention to create and maintain the stand structure of virgin (or old-growth) stands, which have e.g. wide, continuous reverse J-shaped DBH distribution, large horizontal and vertical tree size inequality and spatially patchy multicohort tree arrangement (Gove et al. 1995, Lähde et al. 1999b, Schütz 1999, Lähde et al. 2001, Schutz 2001, Sterba 2004, Lilja et al. 2005). As management method, selection or partial cuttings, where single trees or small tree groups are removed aiming at natural regeneration of the formed gaps, have been suggested (Groot 2002, Lähde et al. 2002, Saksa 2004). Simultaneously, the natural tree mortality is permitted and the stand rotation is lengthened (Nabuurs et al. 2001). This nature oriented management is suggested to be most suitable for stands consisting of shade-tolerant tree species such as Norway spruce (Lähde et al. 2002), but it has even been suggested to suite the management of Scots pine stands (Lähde et al. 1994, Lähde et al. 1999b).

One basic problem related to developing these kinds of new silvicultural methods or assessing the “naturalness” of the present methods is the poor knowledge about the natural stand-level structural dynamics of different tree species on different site types. How to generate a self-perpetuating, balanced situation in which the stand succession takes place as a gradual exchange of individuals within the tree population? This may cause large challenges in many sites. On its part, the observations on the extreme heterogeneity of natural forests are based on landscape-level inventories and resiling the traditional concepts of stand compartments and developmental stages (e.g. Lähde et al. 1999b).

The landscape-level structural characteristics do not however necessarily appear at stand-level. For example, the stand regeneration conditions may vary spatially considerably even within a stand depending on soil texture, soil moisture, vegetation competition and the thickness of the raw-humus layer (Vaartaja 1954). Consequently, the structural characteristics may vary considerably and even a certain unmanaged forest area may consists of a variety of patchy stands having a different seral stage (Jentsch et al. 2002). At the stand level, the size structure of trees may be rather homogenous even in old natural stands (e.g. Ilvessalo 1920a, Szwagrzyk and Szewczyk 2001). Similarly, some uneven-sized stands can be relatively even-aged and all uneven-aged stands do not represent a self-perpetuating balanced situation (Groot and Horton 1994).

The focal framework in studying stand dynamics is based on the theories of forest succession and the concepts of the stand structure. The creation of sustainable forest management methods is also tightly linked to these concepts. When considering stand structure and management, and due to the lack of knowledge available, an essential target is the forests growing on organic soil sites, which deviate largely from the forest ecosystems of mineral soil sites. The differences in the site properties reflect to e.g. in the tree growth and the stand structural characteristics.

## 1.3. Peatlands and tree growth

### *1.3.1. Tree stands on pristine peatlands*

In pristine boreal peatlands, the most important difference to mineral soil sites is the high water table level that controls tree growth (Jeglum 1974, McDonald and Yin 1999) and seedling survival (Ohlson and Zackrisson 1992, Hörnberg et al. 1997). This is due to the shortage of aerobic rooting volume. Thus, the trees survive only on the most favourable microsites i.e. hummocks (LeBarron 1945, Ohlson et al. 2001). Consequently, the tree stands are often low-stocked, they show only low wood productivity and the stand succession is generally slow. Characteristically, the mire vegetation consists of the plant species adapted to wet conditions, and the thickness of the peat layer, as well as the slow mineralization conditions may restrict the supply of the available nutrients (Verhoeven et al. 1990).

The stands growing on pristine boreal peatlands have been demonstrated to be highly unevenly structured: there is large vertical and horizontal variation in tree dimensions, and the shape of their age- and size-distribution typically resembles a reverse J, proved to be typical both in Scots pine and Norway spruce peatlands in northern Europe (Heikurainen 1971, Gustavsen and Päivänen 1986, Finer et al. 1988, Ågren and Zackrisson 1990, Hörnberg et al. 1995, Norokorpi et al. 1997, Uuttera et al. 1997, Ohlson et al. 2001, Korpela 2004). Furthermore, the stands are often spatially clumped. Since the pristine peatland stands share many structural features also typical to old-growth mineral soil stands (Linder et al. 1997, Kuuluvainen et al. 2002), they have even been considered to be more or less stable “climax” or “old-growth” stands, i.e., they are at the final stage of the stand succession (Heikurainen 1971).

The abiotic factors like varying moisture conditions (particularly the hummock-lawn spatial pattern) generally control the variation in the seed germination, seedling survivability and tree growth rates more than biotic factors (Hörnberg et al. 1997, McDonald and Yin 1999). Furthermore, genetic differences in tree growth rates may play a role as well, like that shown for black spruce (*Picea mariana* (P. Mill.) BSP) dominated peatlands (Lieffers 1986). Although it has also been suggested that there are hardly any differences e.g. in the provenances between Scots pine stands on peatlands and mineral soil sites (Lukkala 1952, Päivänen 1988). Due to the moisture in the substrate, forest fires on peatland sites are rare (Hörnberg et al. 1998, Hellberg et al. 2004), but not unknown (Tolonen 1983). However, abrupt flooding may result in systematic tree mortality on peatlands (Rouvinen et al. 2002) with subsequent variation in tree growth and spatial arrangement, which further maintains low stocking and open canopy structure. Furthermore, the rising of the peatland surface due to the typically slow decomposition rate of organic matter (Malmer and Wallén 2004) and general variations in the water table level control tree establishment as the growing *Sphagnum* tends to bog down the seedlings (Saarinen 1933, Ohlson et al. 2001). These factors also set constraints on the maximum tree age (Tallis 1983). Because of these conditions, heterogeneous stand structures may prevail in peatlands. However, even-aged peatland stands have been reported to be more common under continental climates e.g. on Canadian black spruce peatlands where they regenerate after severe fires taking place in dry summer times (e.g. Lieffers 1986, Groot and Horton 1994, Lavoie et al. 2005). Groot and Horton (1994) observed that the site’s hydrology and vegetation interactions may be important in regulating the stand dynamics on black spruce dominated peatlands. The water content in the surface peat seems to cause differences in stand stocking on peatland sites. It is thus probable that the stand structures and their dynamics are also dissimilar on sites with different hydrological regimes.

Site properties influence stand development, because nutrients and moisture are the constraints for tree growth locally. In Finland, the classification of peatland sites is based on the features and the compositions of the vegetation communities, which are expected to reflect the site’s ecological characteristics and fertility (see Cajander 1913, Cajander 1949, Eurola et al. 1984). Cajander (1913) proposed 35 different site types, which can be presented in a two-dimensional space where the dimensions are related to the site wetness and trophic status (Ruuhijärvi 1983, Laine and Vasander 1996). These site types have been later much used in operational-scale forestry as indicators of productivity of drained peatland sites (Heikurainen 1959). Huikari (1952) developed a comparable floristic classification system, where the characteristics of a site on pristine peatland are supposed to be connected to the site nutrient status. In his system, the peatland sites have been grouped into six site quality classes, which can be supplemented using additional explanation of the special features of the site. Vegetation based classification system for peatlands has also been developed e.g. in Canada (Harris et al. 1996).

In general, the sites supporting tree growth are classified into two categories on the basis of the main tree species and the given species groups of surface vegetation, whose occurrence reflects the site's nutrient conditions and the composition of the surface vegetation (Cajander 1913). These categories are spruce peatlands (*korpi*), which are typically characterized by the mesic herbs as key plant species in the field layer and the dominance of Norway spruce, and pine peatlands (*räme*), where dwarf shrubs are key species in the vegetation of the field layer and Scots pine generally is the dominating tree species. Spruce peatlands typically occupy more nutrient rich and intermediate minerotrophic sites, whereas pine peatlands occur in poor minerotrophic and ombrotrophic sites (Keltikangas et al. 1986).

Pubescent birch is the most abundant admixtural (sometimes also dominant) tree species on the spruce peatlands and in the most nutrient rich pine peatlands (Heikurainen 1959, Keltikangas et al. 1986, Norokorpi et al. 1997). and its amount even tends to increase after drainage (Keltikangas and Seppälä 1977). On spruce peatlands, its proportion of the total stand stocking significantly increases from southern to northern Finland, but on pine peatlands the situation is opposite, however (Heikurainen 1959, Keltikangas et al. 1986). In northern Finland the stand stocking on a pristine peatland site is on average 60% of that in southern Finland (Tomppo 2005). On average, the coverage of the birch admixture within stands is generally larger on peatlands than in the forests on comparable mineral soil sites (Hotanen et al. 2006).

Because the site hydrology strongly determines the pattern or even the existence of trees on the site, the "*korpi*" and "*räme*" sites are usually grouped into two site type groups according to the stand properties and the site's hydrology: "genuine" forested (fully stocked) peatland site types and sparsely forested composite peatland site types (Ruuhijärvi 1983, Laine and Vasander 1996). The genuine forested peatlands represent the dryer peatland sites in the hydrological gradient. They support a rather dense natural tree stand and relatively uniform ground vegetation dominated by dwarf-shrubs. Typically these sites are either shallow-peated swamps, "recently" evolved from paludified forest land, or they are thick-peated forested bogs representing a late successional stage of the mire development (Tallis 1983, Laine & Vasander 1996). The sparsely forested composite sites are wetter and they have an irregular mosaic-like character of vegetation, with microsites ranging from dry hummocks to wetter hollows. Especially on these sites, the irregularities in the microsite character contribute to the establishment of trees, because the hummocks support better growth and survival of seedlings than do the hollows, which mostly remain treeless (LeBarron 1945, Ohlson & Zackrisson 1992). The uneven distribution of favourable regeneration locations on peatland sites is thus the primary reason for the uneven clumped spatial arrangement of trees.

Besides the site's hydrology, the climatic conditions (temperature sum and climate fluctuation) are also suggested to be important primary factors affecting the tree growth and seedling regeneration and consequently, the structure and its development on pristine peatlands (Ågren et al. 1983, Hökkä and Ojansuu 2004). Furthermore, the stand stocking is proved to be the most important secondary factor that affects the amount of the total stand yield (Gustavsen and Päivänen 1986). However, in contrast to mineral soil sites, as well as drained peatland sites, the site’s nutrient regime has been shown to significantly affect the tree growth rate only on the most nutrient-rich pristine peatland sites (Heikurainen 1971, Gustavsen and Päivänen 1986). Site properties and geographical location may cause the stand dynamics to vary, because of the variability in primary growth factors. Consequently, it is evident that the factors related to the site’s ecohydrological characteristics may be important affecting also the stand structure and succession dynamics.

### *1.3.2. Effect of drainage on forested peatland ecosystem*

Drainage, i.e. the water-level drawdown caused by the natural processes or more commonly, man-made drainage (ditching), increases the aeration of the surface peat layer. The wetter the peatland site before drainage, the greater the improvements in growing conditions of trees following drainage. On forested peatlands, drainage releases the trees' growing potential and decreases the mortality of seedlings resulting, in general, in increasing stand productivity as the post-drainage succession proceeds (Tanttu 1915, Seppälä 1969, 1976, Hånell 1988, Gustavsen et al. 1998, Laiho and Laine 1997, Hökkä and Penttilä 1999, McDonald and Yin 1999). The increase in growth and yield is higher the more nutrient rich the site is, the higher the temperature sum and the larger the original stand stocking (Heikurainen and Seppälä 1973, Keltikangas et al. 1986, Gustavsen et al. 1998). A similar increasing trend is also observed in the canopy coverage and tree species number after drainage (Hotanen et al. 2006). In Scots pine stands, it usually takes 5-10, and in Norway spruce stands 10-20 years for the radial growth of trees to reach its maximum (Seppälä 1969, 1976). After this period of release in growth, the growth level is close to that of stands growing on the mineral soil sites having comparable fertility (Seppälä 1969). Smaller and younger trees generally show greater drainage-induced response in the radial growth than larger and older trees (e.g., Heikurainen and Kuusela 1962).

A special feature, which typically characterizes the stand succession in most of the drained peatland sites, is the occurrence of trees established already before drainage. Furthermore, some spatial effect on the stand growth is caused by the spatial changes in the hydrology and nutrient conditions within strips (Westman and Laiho 2003). The radial growth is often significantly faster in the vicinity of a ditch than at a greater distance from it (Tanttu 1915, Lukkala 1929, Jutras et al. 2002). The wider the strip the lower the stand yield in general (Seppälä 1972).

As a tree ages, its growth gradually decreases (Assmann 1970). This phenomenon has been reported to be slower on drained peatland sites than on the comparative mineral soil sites at least in the first post-drainage tree generation (Buss 1964, Seppälä 1969). Regarding e.g. the climatic impact on the tree growth the situation may however be reverse: the mean annual tree growth has been observed to decrease faster on peatlands than on upland sites in pace with decreasing temperature sum (Heikurainen and Seppälä 1973).

In pace with improved growing conditions, the stands may become denser as open spaces fill up with fast growing small trees. This is assumed to occur as a result of the changed competitive conditions and improved seedling survivability caused by drainage (Hökkä and Laine 1988). The increase in the number of trees per hectare continues for some decades after drainage (Hånell 1984, Hökkä and Laine 1988). Thereby, the uneven-aged and -sized structure of the stands is at least preserved or in some cases even enhanced, after drainage (Hökkä and Laine 1988, Hotanen et al. 2006). On the other hand, in some of the first reported observations concerning the post-drainage stand development, it was suggested that the stand structure is gradually tending to develop to resemble the ”regularly-structured” stands growing on comparable mineral soil sites (Multamäki 1923). Also, in some later studies where structural dynamics have been monitored in drained peatland stands, the stands dominated by Scots pine (Stoll et al. 1994), black spruce (McDonald and Yin 1999) or bog pine (*Pinus uncinata* Ramond var. *rotundata* (Link) Antoine) (Frelechoux et al. 2000) have been proven to be fairly evenly structured.

The secondary succession induced by drainage has also significant effects on the surface vegetation communities of a peatland site. Trees and the surface vegetation are in strong interaction with each other. The original mire plant community on drained peatlands suffers from the decreased soil moisture and increasing shading (i.e. increased competition) of the growing stand, forest herbs and dwarf shrubs and thus, its coverage gradually decreases along the post-drainage ground vegetation succession (Sarasto 1952, Laine et al 1995, Korpela 1999). The speed of this change depends mainly on the site's fertility and moisture, and the tree stand of the original peatland type (Laine et al. 1995, Korpela and Reinikainen 1996, Korpela 1999). On spruce peatlands, the original mire plants (e.g. *Sphagnum* and *Carex* species) are gradually replaced by mesic forest herb and moss (e.g. *Hylocomium splendens*) species, which already dominate the surrounding upland forest sites (Cajander 1913, Sarasto 1952, Korpela 1999). On pine peatlands, particularly the cover of dwarf shrubs (e.g. *Ledum palustre*) and drier heath forest mosses (e.g. *Dicranum spp., Pleurozium schreberi*) increase remarkably (Laine et al. 1995). These changes in vegetation diminish the site’s receptivity for tree regeneration and it may have an impact on the tree stand structure when "the ingrowth" decreases (Kaunisto and Päivänen 1985). At the same time, the inter-tree competition increases further the tree mortality.

In present Finnish site type classification (see Laine 1989), the drained forested peatlands have been classified into seven drained peatland forest site types. Determination of these site types is based on the specific post drainage plant community and whether a given site had initially been genuine forested or sparsely forested composite site type. The differences in the hydrology of the original peatland sites before drainage are shown to affect the stand growth for a long time after drainage (Hökkä and Ojansuu 2003). Evidently, these site properties may further affect the stand succession following drainage.

## 1.4. The scope and the objectives of the study

Although much research attention has been paid lately to the stand succession dynamics and to the development of alternative silvicultural methods, most of the research has concentrated on forest ecosystems on the mineral soil sites. On a global scale, the economic or ecological significance of forested peatlands is marginal. However, in the boreal zone, such as in Finland, peatlands and peatland forests are very important feature in the landscape and their significance on the biodiversity and local economy is considerable. Drained peatlands form a remarkable raw wood resource.

In drained forested peatland sites, tree stand growth and yield and their responses to various management procedures, particularly at tree-level, are known fairly well (ref. Paavilainen and Päivänen 1995, Miina 1994, Miina and Pukkala 1995, Miina 1996, Hökkä et al. 1997, Gustavsen et al. 1998, Jutras et al. 2003). Also on pristine sites, the tree growth and yield have been studied to some extent (e.g. Heikurainen 1971, Gustavsen and Päivänen 1986, Korpela 2004). However, the tree stand structure and its inherent long-term succession dynamics both on pristine and drained peatland sites are still largely unexplored. For example, for natural Scots pine stands, no specific studies have been done concerning stand succession on peatlands, partly because the stands have been implicitly assumed to be in a balanced uneven-aged stage due to the observed irregular size- and age structures.

Natural forests are ranked high by the nature conservationists, because they provide niches for endangered forest species and sustain biological diversity (Kneeshaw and Gauthier, 2003), as well as they provide other non-economical values (Landres et al. 1999). Understanding the natural dynamics of boreal forested peatland ecosystems is necessary, for example, in order to sustain their biological diversity and function under varying human impacts and climate change. Similarly, reference information is needed to assess and quantify the effects of forest management on stand development, as well as to assess the ecological sustainability of the silvicultural treatments in relation to natural dynamics. Tree stand treatment in connection with active restoration of managed peatlands lacks basic information on natural stand dynamics, which could be applied to rehabilitate the function of the peatland ecosystems and the dynamics of the natural stands as quickly as possible.

For drained peatlands, an understanding of the stand structure and its dynamics would be necessary for the sustainable utilization of the wood resources. This knowledge is needed e.g. when planning feasible silvicultural guidelines and cutting regimes, especially considering the number and timing of thinnings, and predicting more accurately the distribution of the wood assortments and outturn of the future cuttings. According to the scenarios of the future allowable cut, thinnings should become a common management procedure on drained peatland sites (Nuutinen et al. 2000). However, the thinnings are currently done without sufficient knowledge about the structure of these stands and the impacts of management on them. Knowledge about the stand structure and its development may also help to assess the long-term effects of management on the peatland ecosystem. Furthermore, knowledge about the stand dynamics on pristine peatlands and the secondary succession following drainage may help to understand and estimate the effects of predicted climate change on peatland ecosystems. Climate change scenarios predict higher temperatures and reduced growing season precipitation in the boreal zone, which will likely result in a drawdown of the water table levels (Gitay et al. 2001), and further, enhanced forest succession in peatlands (Laiho et al. 2003).

The aims of this study are:

1. to determine tree age and size structures and their succession dynamics on unmanaged Scots pine stands on pristine peatlands (Study **I**),

2. to describe the effect of drainage on tree size structure and its long-term development in stands dominated by Norway spruce (Study **II**) and Scots pine (Study **III**),

3. to find out the effects of the ecological factors (site, stand and climate) and tree stand management (thinnings) on stand structural dynamics on drained peatlands (Studies **II** and **III**),

4. to describe the tree mortality dynamics of unmanaged peatland stands dominated by Scots pine on drained peatland sites (Study **IV**).

Forest succession can be studied either by monitoring regularly a set of permanent sample plots, or collecting cross-sectional data from stands of different ages and arranging them in a chronosequence to establish a view of the temporal dynamics. Since the former method is extremely time consuming in slow-growing boreal tree stands, the latter has been commonly applied, and also used in previous studies on pristine peatlands (Heikurainen 1971, Gustavsen and Päivänen 1986, Ågren and Zackrisson 1990), as well as on drained peatlands (e.g. Hånell 1984, Hökkä and Laine 1988, Korpela 2004). In this study I use inventorial cross-sectional stand data of pristine peatlands, because of the slow stand growth and development on those sites. No sufficiently long longitudinal data sets, which could be necessary in order to properly describe the stand dynamics, are available. For drained peatlands I use however repeatedly measured longitudinal stand data, which is more effective in order to clarify the succession dynamics of fast growing tree stands than ordinary cross-sectional data.

I hypothesise that on pristine peatlands, the natural Scots pine stands are basically uneven in age and size as suggested in previous studies, but that site ecohydrology and climate (geographical location) are primary factors influencing stand structure and may cause different succession dynamics in different conditions. I also assume that a chronosequence based on stand dominant age could be used to characterize the ongoing stand succession and possibly identify the stand structures being in self-perpetuating state in different climatic regions.

Further, I hypothesise that after drainage, the stand development increases significantly in speed as suggested in earlier studies. I assume that the highest tree-size inequality is found soon after drainage due to the released growth of the initial trees, enhanced regeneration (regeneration of the gaps within stand) and better survival of saplings. I postulate that this is the first stage in the post-drainage stand succession both in Norway spruce and Scots pine dominated peatlands (“release stage” of succession, Fig. 2). Later, increased inter-tree competition modifies the stand structure resulting in more even-sized structures due to increased mortality of suppressed, smaller trees (“normalisation stage”). However, I expect to find different species-specific temporal trends in stand density and later structural development among site types, because of differences in the conditions for, e.g., regeneration (Kaunisto and Päivänen 1985). Furthermore, I hypothesise that the changes in growing conditions and stand density (severing inter-tree competition) appear also as changes in the tree mortality dynamics in a stand, and that the thinning cuttings speed up the temporal change of stand structure if the mostly suppressed trees are removed.

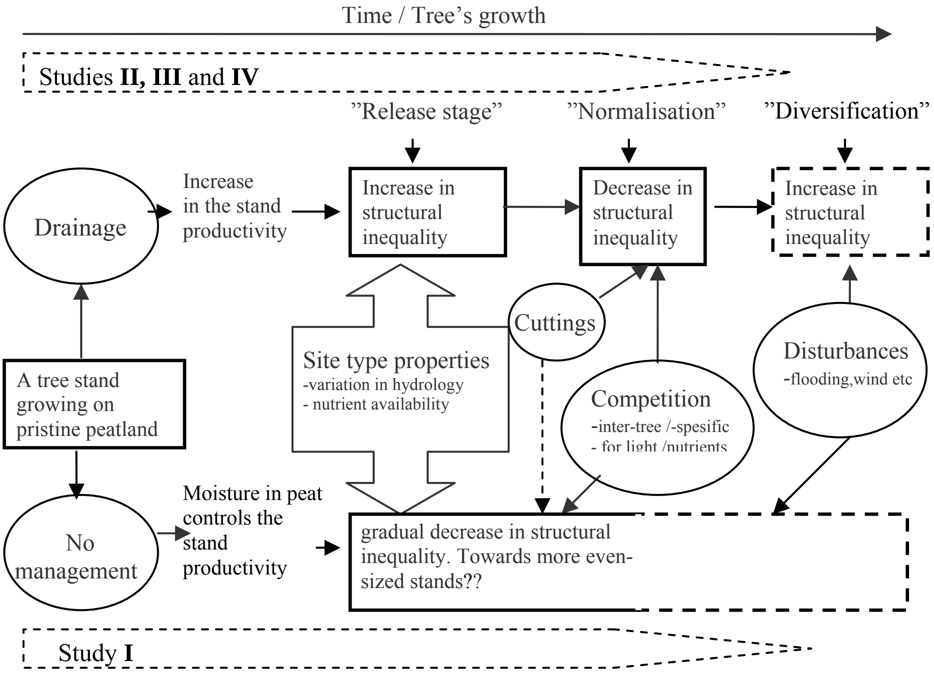

**Figure 2.** The hypothesised stages of stand structural development (succession) and the most important primary and secondary factors assumed affecting stand dynamics on pristine and drained peatlands. The "temporal cover" of the stand dynamics of the materials used in the Studies **I, II, III** and **IV** has been presented by dashed lined box-arrows

# 2. MATERIAL

## 2.1. Study sites on pristine peatlands

### *2.1.1. Sample plots*

Stand structural characteristics on pristine peatlands were studied (study **I**) by using the stand data, which was selected from a set of permanent sample plots on forested peatland sites (SINKA) set up during 1984-88 in northern Finland, and 2001-2003 in southern Finland for tree growth research objectives by the Finnish Forest Research Institute (Metla) (Penttilä and Honkanen 1986). They comprise a sub-sample of 7th Finnish National Forest Inventory (NFI) sample plots. Each SINKA sample plot (varying from 380 $m^2$ to 3050$m^2$ in size) was composed of a cluster of three circular sample plots located 40 m apart but within the same forest compartment considered to be reasonably inherently homogeneous with respect to site type and stand structure.

Altogether 70 pristine sites (stands) were included in the SINKA dataset. From this dataset, sites meeting the following criteria were selected: i) the sites supported naturally established Scots pine; admixtures of pubescent birch or Norway spruce were permitted; ii) stocking was at least 2 $m^2$ of basal area per hectare and at least 300 trees per hectare; iii) there was no evidence of recent (20 years) cuttings as judged by visual examination in the field. Some of the stands may have been slightly managed during their history, although evidence of this was not detected. The stands had not even experienced any large disturbances. Altogether 52 stands (20 stands in southern Finland and 32 stands in northern Finland) meeting these criteria were chosen for the analysis (Fig. 3).

The sites were classified into the two major site type groups: “genuine" forested sites (Group I sites) and sparsely forested composite sites (Group II). For more detailed classification of the study sites into site types, see Table 1 in study **I.**

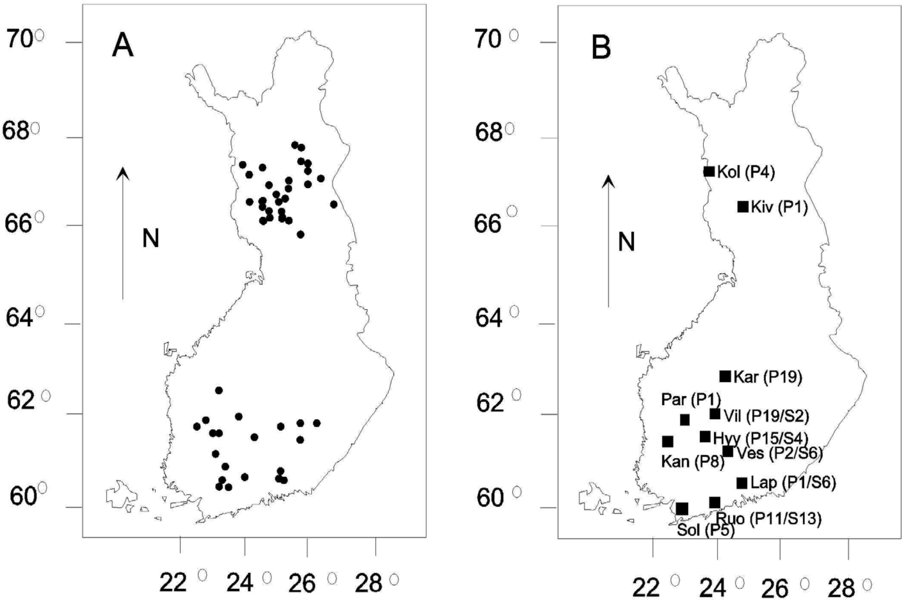

**Figure 3. A**: Location of the inventory stand data (SINKA) of pristine peatlands (Study **I**); **B**: Location of the study areas of repeatedly measured sample plot data on drained peatlands (the letters express the abbreviation of the municipality: Kol=Kolari; Kiv=Kivalo; Kar=Karstula; Par=Parkano; Vil= Vilppula; Hyy=Hyytiälä; Kan=Kankaanpää; Ves=Vesijako; Lap=Lapinjärvi; Ruo=Ruotsinkylä; Sol= Solböle). The number of Norway spruce (letter S) dominated (Study **II**) and the number of Scots pine (letter P) dominated sample plots (Studies **III** and **IV**) presented by study areas.

### *2.1.2. Stand measurements*

On a given site, the site’s elevation above the sea level, site type and peat thickness were recorded. All live trees over 4.5 cm in diameter at 1.3 m above ground level (DBH) were inventoried on each sample plot with 0.1 cm accuracy. Tree height (m), diameter at 6m (cm) and age (years) were measured from the sample trees within a smaller sub-plot on each plot (Study **I**, Fig. 1). Thus, the distributions of tree age and size were defined based on different size of tree groups. The area of the sample plots was adjusted according to the stand density so that the number of sample trees was approximately equal in all stands (100 trees from the three plots altogether). The area of the sub plots was one third of the area of the sample plot. For measuring tree age at breast height, all coniferous sample trees (DBH > 4.5 cm) were cored to the pith at breast height. Tree age was determined in the laboratory by using a bi-ocular microscope. In the following, tree or stand ages refer to age at breast height. Age data of 1468 trees were recorded and 1422 trees were accepted for this study.

The basic stand characteristics (such as stand basal area (G, $m^2$ $ha^{-1}$), stand volume (V, $m^3$ $ha^{-1}$), stand stem number (N, $ha^{-1}$) and basal area median diameter (DgM, cm) by tree species were calculated using the KPL program (Heinonen 1994). Both arithmetic mean age (AM) and dominant age ($A_{dom}$) were used to characterise the stand age. The dominant age was defined as the mean age of trees with a diameter larger than the basal area median diameter of the given stand (see Hökkä and Ojansuu 2004).

## 2.2. Study sites on drained peatlands

### *2.2.1. Sample plots*

The study material on drained peatlands consisted of 31 Norway spruce dominated (Study **II**) and 88 Scots pine dominated (Study **III** and Study **IV**) repeatedly measured permanent sample plots (300-2500 $m^2$ in size) in different stands. The stands have been maintained by Metla (98 plots) and University of Helsinki (21 plots). The Metla's data belongs to a wide and geographically representative network of permanent sample plots established on drained peatlands in the 1920-1930's in Metla's research forests throughout Finland. Originally, the aim of the sample plots was to monitor the effects of drainage and compare the growth and yield of thinned and unmanaged stands (Lukkala 1929). The rest of the used data (21 plots) came from the vicinity of the Hyytiälä Forestry Field Station of the University of Helsinki where a set of permanent sample plots (about 70 plots) had been established originally for educational purposes aimed to monitor the post-drainage stand growth and yield, as well as to demonstrate the effects of the silvicultural operations on the stand development (Ekola and Päivänen 1991).

For studies **II** and **III**, the sample plots (in the following referred as stands) were located in southern Finland within a region between 60°15'-63°00'N and 22°25'-26°40'E. For study **IV**, the material consisted of 10 sample stands, which were located in southern Finland (5 plots) and in northern Finland (5 plots) within a region delimited by 60°01'-67°10'N and 23°07'-26°40'E. Note that the southern stands in study **IV** are also included in the material of the study **III**.

Stands had to meet the following criteria: i) established naturally before drainage, thus representing the first tree generation following drainage, ii) dominated by Norway spruce (Study **II**) or Scots pine (Study **III** and **IV**) (more than 50% of volume at least at the time of the last stand measurement), iii) the year of drainage known, and iv) data from at least three successive stand measurements available. Furthermore, the Scots pine stands, which had not been managed by cuttings, and where the dead trees had been measured, were separately selected (study **IV**).

The following site types of drained peatlands were represented in the study material (Table 1) (classification according to Laine 1989):

Spruce peatlands (Study **II**)

- Herb-rich site type (HrT I, 11 plots) characterised by tall ferns, e.g. *Athyrium filix-femina*, and herbs, e.g. *Oxalis acetosella*, and

- *Vaccinium myrtillus* type (MT I, 5 plots and MT II, 15 plots), characterised by *V. myrtillus*, *V. vitis-idaea*, and mesic herbs, e.g. *Trientalis europaea.*

Pine peatlands (Study **III** and **IV**)

- *Vaccinium myrtillus* (MT II, 14 plots) site type characterized by *V. myrtillus* L., *V. vitis-idaea* L. and herbs of mesic sites, e.g. *Trientalis europaea* L.
- *Vaccinium vitis-idaea* (VT I, 9 plots and VT II, 31 plots) site types characterized by *V. vitis-idaea* and *V. myrtillus*
- Dwarf-shrub site type (DsT I, 29 plots) characterized by mire dwarf-shrubs, e.g. *Ledum palustre* L., *Vaccinium uliginosum* L. and *Betula nana* L.

In study **IV**, the site types MT II, VT II and DsT I types were only represented (Table 1). In spruce peatlands all the site types were minerotrophic, whereas in pine peatlands the site types formed a nutrient gradient from minerotrophy (meso-oligotrophy and oligotrophy) to ombrotrophy.

The Roman numeral given in conjunction with the acronyms (Table 1) indicates the original (pre-drainage) site type groups, i.e. "genuine" forested type sites (Group I) and sparsely forested composite type sites (Group II). The differences in the pre-drainage hydrology of the sites are also reflected in their nutrient regimes (Westman and Laiho 2003). Differences between Group I and Group II sites in terms of Scots pine post-drainage height development have been fundamentally demonstrated by Hökkä and Ojansuu (2004).

**Table 1.** The material of the Studies **II, III** and **IV** as composed of thinned (managed) and unthinned (unmanaged) stands and the number of measurements of the dominant canopy layer, by site type and site group (presented by Roman numeral): I = Genuine forested peatland sites; II = Sparsely forested composite peatland sites.

| | **Thinned** | | **Unthinned** | |
|---|---|---|---|---|
| | Number of | | Number of | |
| **Site type** | stands | meas. | stands | meas. |
| Study **II**, spruce peatlands | | | | |
| *Herb-rich* (HrT I) | 12 | 87 | - | - |
| *Vaccinium myrtillus* (MT I) | 12 | 47 | - | - |
| *Vaccinium myrtillus* (MT II) | 7 | 42 | - | - |
| **Sum** | **31** | **176** | - | - |
| Study **III,** pine peatlands | | | | |
| *Vaccinium myrtillus* (MT II) | 11 | 55 | - | - |
| *Vaccinium vitis-idaea* (VT I) | 7 | 39 | 3 | 14 |
| *Vaccinium vitis-idaea* (VT II) | 26 | 149 | 6 | 39 |
| *Dwarf-shrub* (DsT I) | 21 | 119 | 9 | 41 |
| **Sum** | **65** | **362** | **18** | **94** |
| Study **IV,** pine peatlands | | | | |
| *Vaccinium myrtillus* (MT II) | - | - | 5 | 25 |
| *Vaccinium vitis-idaea* (VT II) | - | - | 3 | 29 |
| *Dwarf-shrub* (DsT I) | - | - | 2 | 8 |
| **Sum** | - | - | **10** | **62** |

Initial ditching of the sites was conducted between years 1907 and 1965. Ditch spacing varied from 35 to 150 m. The drainage condition had been maintained at an adequate level for tree growth during the entire monitoring period on every site. On average, each stand had been measured six times, the interval between measurements varying from 3 to 25 years. Depending on the stand, the length of the monitoring period varied between 15 and 70 years (on average 40 years). Apart from having been drained and most of them thinned, the stands had not experienced any major disturbances.

The spruce stands had a varying natural admixture of pubescent birch and Scots pine. In most of the Scots pine stands located on minerotrophic sites, there appeared Norway spruce and pubescent birch mixed with pine. None of the spruce stands were totally unmanaged, whereas for Scots pine, 18 stands were unmanaged, and 65 stands had been managed by applying light silvicultural cuttings. Over the years, mainly suppressed, dying trees had been harvested. Originally, these thinnings were done to obtain maximum stand vitality and productivity to meet the initial research objectives. Commercial thinnings had also been carried out by thinning trees from below. In the following, all of these cuttings are referred as “thinnings”. For Norway spruce stands, the average removal in an individual thinning operation had been 10% of the total stand basal area (Study **II**), and for Scots pine stands, ca 14%, respectively (Study **III**).

### *2.2.2. Stand measurements*

On a given site, the site's elevation above sea level, site type and peat thickness were recorded. All (live) trees growing on the sample plots were measured for diameter at DBH, the smallest one being 1 cm. In addition, in Study **IV**, the dead trees larger than 4 cm DBH were measured. Sample trees, 10-25 trees in each stand depending on stand characteristics had been measured for their height and diameter at 6 m. Concerning measurements of stands made more than 20 years ago the information on stand characteristics was based on the records of manual calculations. The later calculations have been done by computer based KPL-program. The tree measurements of the sample plots in Hyytiälä were updated for this study. Some standard stand characteristics, classified by post-drainage 10-year classes, are displayed in Study **II**: Table 1, in Study **III:** Table 2 and in Study **IV:** Table 1.

## 3. METHODS

### 3.1. DBH distributions as a characteristics of tree size structure

The stand DBH distribution per hectare was used as a primary characteristic of tree size structure. *For pristine pine peatlands* (Study **I**), stand-wise DBH distribution per hectare with 5 cm DBH classes were formed for the whole tree stand. If several tree species occurred within the stand, the distributions were formed separately for pine, spruce and birch. The tree species were separated due to their different ecological characteristics (e.g. shade tolerance of tree species). Because pine formed the dominant stand and the occurrence of spruce and birch on these sites seemed to be more or less random having only low stem frequencies, the distributions of pine were only used in further analysis.

*For drained peatlands*, the DBH distributions were formed separately for spruce and birch (Study **II**), and for the dominant canopy layer of pine and birch (Study **III** and **IV**). If the stand was storied, the DBH distribution was formed separately for each storey. Furthermore, in Study **IV**, the DBH distributions were formed for the dead trees. In spruce stands (Study **II**), the pines growing on some of the sites were combined with spruce. In pine stands (Study **III**), the birches in the dominant canopy layer were combined with pine, as well as with any single large spruces occurring in the stand. The understorey was separated on the basis of the shape of DBH distribution and tree species (see Study **III:** Fig. 2). The understorey usually consisted of spruce and/or birch in pine stands and spruce in spruce stands. The data of the understoreys were utilised only in Study **III**.

### 3.2. Statistical and analytical methods describing the stand structure and analysing the structural variation

### *3.2.1. Fitting Weibull function to the diameter distributions (Studies **II, III** and **IV**)*

In order to model an empirical distribution, the natural random variation should be removed. This can be made by using some theoretical distribution such as statistical probability distributions to smooth the trivial variability (Päivinen 1980). In this study, all the DBH distributions were smoothed and parameterized with the parametric Weibull function. This method was chosen, because it has proved to be feasible and flexible in smoothing distributions of different shapes and the parameters are informative in describing the characteristics of DBH distributions. Furthermore, they are rather simple to model by regression approach. Thus, Weibull has been widely used also earlier to describe the DBH or basal area distribution of tree stands (Bailey and Dell 1973, Rennolls et al. 1985, Knox et al.1989, Maltamo et al. 1995, Siipilehto 1999).

The Weibull-method, as well as other parametric methods, is most applicable for regular and unimodal distributions, because their ability to describe multi-modal and highly irregular distributions is not necessarily adequate (Droessler ja Burk 1989, Maltamo et al. 2000). In these cases, so-called “non-parametric” or “distribution-free” methods can produce better estimates of the distributions (see e.g. Droessler ja Burk 1989, Uuttera and Maltamo 1995, Maltamo ja Kangas 1998, Maltamo et al. 2000, Zhang et al. 2001). Also, significant differences in the biases of the estimates of different parametric methods have been found (e.g. Hafley and Schreuder 1977, Siipilehto 1999). In these materials, no such a problem was noticed, which could have fully prevented the use of parametric method in describing the stand DBH distributions on peatlands. The risks in the smoothing of the distributions related to the multimodality in the distributions were decreased by estimating the distributions separately for tree species and tree storeys (Studies **II**, **III** and **IV**).

One advantage of the Weibull function is the small number of its parameters needed for describing a distribution. The Weibull function produces two or three numerical parameters that describe the characteristics of the empirical distribution. Because of larger flexibility and for modelling reasons, the two-parameter Weibull function was used. The earlier studies support the use of the two-parameter Weibull function for the estimation of the DBH distributions. The use of fixed minimum value (in this case zero) is more applicable than without fixing (e.g. the three-parameter Weibull, where the minimum diameter is varying freely from stand to stand): first, due to the simplified parameter estimation and parameter prediction (e.g. Hafley and Schreuder 1977), and, second, due to the usually smaller variation in the estimated parameters (see e.g. Knoebel and Burkhardt 1991). These characteristics may result in the better performance of the parameters as the describer of the DBH distribution, larger correlation of the parameters with the variation in stand characteristics and better predicting models (Siipilehto 1999).

For the DBH distributions, the Weibull probability density function has the following form:

$$[1] \qquad f(dbh_i) = \frac{c}{b}\left(\frac{dbh_i}{b}\right)^{c-1} \exp\left[-\left(\frac{dbh_i}{b}\right)^{c}\right], \text{ when } dbh_i >= 0$$

$f(dbh_i) = 0$, when $dbh_i < 0$,

and the corresponding cumulative distribution function is:

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

$F(dbh_i) = 0$, when $dbh_i < 0$,

where $f(dbh_i)$ is the probability density and $F(dbh_i)$ is the cumulative probability density of the number of trees in DBH class $i$, and $b$ and $c$ are the parameters. The scale parameter $b$ indicates the peak of the distribution and the parameter $c$ describes the shape of the distribution as presented in Studies **II** and **III**.

The Weibull function was fitted to the diameter distribution data using the maximum likelihood (ML) method. The MODEL procedure included in SAS statistical software was used in fitting (SAS 1999). The ability of the Weibull function to fit the empirical DBH distributions was checked by comparing the smoothed DBH distributions with empirical ones. On drained peatlands, the fitting managed fairly well for the living dominant trees (see Material and Methods in Studies **II, III** and **IV**), as well as for the dying tree stand (Study **IV**). For understorey stands, the fitting was less successful, however (Study **III)**.

### *3.2.2. Other methods and analyses for describing the stand structure*

On pristine peatlands, skewness and kurtosis were applied for describing the DBH distributions of tree stands (Study **I)**. Furthermore, as a measure of the modality of DBH distributions, the difference between stand DgM and DM ($D_{diff}$) were calculated for each stand. As an additional measure to characterise the DBH distributions, the range of the DBH distributions were calculated in stands both in pristine and drained sites (Studies **I, II** and **III**).

For Study **I,** stand age structure was examined in order to clarify the within and between stand heterogeneity in age. It was examined by calculating the mean age of sample trees and plotted by 5 cm DBH classes for each stand. Furthermore, the age frequency distributions (20 year classes) of sample trees were formed for each stand.

Shannon index (see e.g. Buongiorno et al. 1994) was used to examine the diversity of tree size within the stands both in pristine and drained sites (Studies **I, II** and **III**). This method was further used to examine the diversity of tree ages in pristine sites (Study **I**). For this study, the Shannon index for stand DBH and age distributions was defined as:

$$[3] \qquad H' = \sum_{i/j=1}^{n} pt_{i/j} \ln pt_{i/j} \,,$$

where $p_i$ is the proportion of trees in diameter class $i$ (Studies **I, II, III**) or in age class $j$ (Study **I**).

Shannon indexes and correlation analyses were done using SAS 8.2 statistical software (SAS 1999), and for other statistical analyses, SYSTAT 9.0 for Windows was used (SPSS 1999).

## 3.3. Examining the factors affecting stand structure

In Study **I**, the effect of primary factors on the stand structure, the differences within the site types (Group I and II sites) and the climate areas (southern Finland and northern Finland) on the stand characteristics and stand structural properties (characteristics of DBH and tree age distributions) were tested by the covariance model (ANCOVA). Stand dominant age ($A_{dom}$) was used as a covariate in order to remove the effect of age on the stand characteristics when testing the site and area effects. For the analysis, the stand characteristics G, $D_gM$, N and the age of trees in the smallest DBH class were also chosen, because they were assumed to manifest the factors affecting the stand structure such as inter-tree competition

For Studies **II** and **III**, the stand DBH distributions were analysed by applying the parameter prediction method (PPM), *a priori* estimated regression models for prediction of the DBH distribution of the target stand (e.g. Schreuder et al 1979). The regression equations were constructed to the estimated Weibull shape parameter (parameter *c*). Because of the hierarchical data structure, a mixed model approach was used in the model construction (Searle 1987). For Studies **II** and **III**, three hierarchical levels of variation were identified: i) between stands, ii) within stands between inter-thinning periods (periods between two successive thinnings) and iii) within inter-thinning periods between the measurement time-points.

The mixed model had the following form:

$$[4] \qquad y_{ijk} = {}_{ijk} + \beta_1 x_{1ijk} + \beta_2 x_{2ijk} + \ldots + \beta_n x_{nijk} + v_k + u_{jk} + {}_{ijk,}$$

where $y_{ijkl}$ is the response variable (i.e. Weibull parameter *c*) for the measurement time-point *k* within the inter-thinning period *j* in stand *i*. The fixed part of the model consisted of the intercept , the parameters $\beta_1$-$\beta_n$, and stand and site characteristics $x_{1ijk}$- $x_{nijk}$. In the random part, $v_k$ is the random effect of stand *k*, $u_{jk}$ is the random effect of the inter-thinning period *j* in stand *k*, and the random error $\varepsilon_{ijkl}$ accounts for within-stand variation between measurement time-points. The random variables were assumed to be independent and to follow multivariate normal distribution, with the mean 0 and constant variances and covariances at each level. Separate models were constructed for the spruce and birch on drained spruce peatland (Study **II**) and for the dominant canopy layer, as well as the understorey spruce and the understorey birch on drained pine peatlands (Study **III**).

The scale parameter (parameter *b*) was solved analytically using the predicted shape parameter and the median diameter ($D_M$) derived from the measurement data (for estimation, see Kilkki and Päivinen 1986) as presented in studies **II** and **III**. This was done,

because, separate models would produce more biased parameter predictions and thus they may increase the bias in the predicted DBH diameter distributions. Furthermore, the parameter *b* directly corresponds to the stand median diameter, and the more profound analysis of this parameter would not provide significantly new findings of the stand dynamics in contrast to the shape of DBH distribution, which is a more informative indicator of the stand structure.

The stand and site characteristics tested in the fixed part included total basal area of the dominant canopy layer (G, $m^2$ $ha^{-1}$), stand median diameter ($D_M$, cm), 95% of the stand maximum diameter ($D_{Max}$), stand stem number (N, $ha^{-1}$), stand volume (V, $m^3$ $ha^{-1}$), proportion of deciduous trees (mainly birch) of the total basal area and stem number (in Study **III**), the stem number of trees in sawlog dimensions ($d_{1.3} \geq 19$ cm) and their proportion of the total stand volume, years elapsed since drainage, geographical location of the site (four categories), temperature sum (degree days), thickness of peat layer (cm), distance from the centre of the sample plot to the nearest drainage ditch (m) and width of the drainage strip (m). In Study **III**, different site effects were tested by using dummy variables referring to either individual site types or site groups (Group I and Group II sites). Furthermore, to account for the effect of thinning intensity on the DBH distributions several discrete and dummy variables describing the cuttings were determined.

The fixed and random parameters were estimated simultaneously with the iterative generalized least-square (IGLS) method using MLwiN software (Goldstein et al. 1998, Rasbash et al. 2001). The models were constructed by entering the variables into the model one by one. Transformations were made to linearise the relationship between dependent and independent variables and to homogenize the variance if necessary. The likelihood ratio test was applied to test the significance of each added predictor. The value of –2*log-likelihood was used to compare models of increasing complexity. The final models were estimated with the restricted iterative generalized least-square (RIGLS) method recommended for small samples. This is a method producing unbiased restricted maximum likelihood (REML) estimates for the parameters. For the alternative models, residual plots were produced to check any trends in the residuals against different independent variables. To evaluate the model reliability and accuracy, systematic error (Bias) and relative systematic error ($\text{Bias}_r$) were calculated as follows:

$$[5] \qquad \text{Bias} = \sum_{i=1}^{n} (y_i - \hat{y}_i)/n$$

$$[6] \qquad \text{Bias}_r = \sum_{i=1}^{n} ((y_i - \hat{y}_i)/y_i)/n,$$

where n is the number of observations, $y_i$ the observed value of parameter $c$ and $\hat{y}_i$ the predicted value of parameter $c$.

To visually examine the ability of the models to produce appropriate DBH distributions, simulations were made by applying the two predicted parameters ($b$, $c$) in the Weibull density function and by giving varying values to the explanatory variables. Furthermore, the measured stand basal area and the measured stand stem number, as well as the estimates for the stem number and third and fourth powers of the cumulative frequencies of DBH's ($\sum d^3$ and $\sum d^4$) obtained from the predicted distributions were compared with the measured ones. The advantage of $\sum d^3$ and $\sum d^4$ is that they do not require the height information (which was not completely available in this data) while they can still provide reasonable estimates of the accuracy in the 'volume' and in the 'value' of the growing stock, respectively (see Kilkki and Päivinen 1986, Maltamo et al. 1995)

### 3.4. Analysing stand succession dynamics

The temporal stand dynamics on pristine peatlands (Study **I**) was examined by comparing the stand-wise graphs of mean tree ages by DBH classes, and describing the age-related changes in stand characteristics, stand age and size structures as a function of $A_{dom}$ in a chronosequence. $A_{dom}$ was used in describing the stand age, because it may provide more information about the tree cohort, which includes most of the living biomass. In order to compare and quantify the within stand heterogeneity of tree size, the standard deviation of trees DBH and height were analysed as a function of dominant stand age.

The Shannon index of tree ages and tree diameters were arranged according to increasing $A_{dom}$ and the relationship was compared by the site type groups (Group I and

II) and climate areas (southern and northern Finland). Correlation analysis (Spearman) was used to examine the effect of stand age on the stand characteristics and structure. Furthermore, the correlations between $A_{dom}$ and G, $D_gM$ and the number of trees in tree size-classes (DBH classified by 5 cm classes) by site type groups and climate areas were calculated to analyse the age-related changes (dynamics) in a stand.

On drained peatlands (Studies **II**, **III** and **IV**), the analysis of stand dynamics was based on the long-term monitoring of the stands, where the temporal changes in the smoothed DBH distributions, in the development of stand characteristics and in the tree size diversity were visually examined. For analysing the mortality dynamics in unmanaged stands on drained peatlands (Study **IV**), the temporal changes in the mortality DBH distributions (smoothed distributions) and the average size of dead trees in pine stands were examined.

# 4. RESULTS

## 4.1. Stand structure and its variation on pristine peatlands (Study I)

### *4.1.1 Characteristics of tree age and size structure*

On pristine peatlands, the average stand size structures differed significantly between the major site type groups (genuine forested sites and sparsely forested composite peatland sites) and climate areas (northern and southern Finland). Based on the shape of the DBH distribution, two structural patterns were observed: genuine forested sites (Group I) in southern Finland showed more bell-shaped and flatter DBH distributions, indicating more even-sized structures than in northern Finland, where uneven-sized structures with positively skewed, reverse J-shaped DBH distributions were found in both site type groups; they were, however, more pronounced in composite sites (Group II) (Fig. 4, Study **I**: Table 2). The stands on Group I sites in the north and on Group II sites in the south showed an intermediate structural pattern, where both skewed and almost flat DBH distributions were represented (Fig. 4). The range of DBH, which varied between 15-20 cm, did not differ significantly between site types and climate areas, however (Study **I**: Table 2).

On average, the stands were significantly more stocked on Group I sites in the south compared to those on southern Group II sites, and further, more stocked compared to the stands on northern sites (Study **I**: Table 2). In composite peatlands, the proportion of deciduous trees, mostly pubescent birch, of the total stand basal area was significantly largest on Group II sites in the south (Study **I**: Table 2). In a single stand, pubescent birch could share as much as 40% of the total stand basal area on those sites. In contrast, a significant proportion of Norway spruce occurred mostly on genuine forested sites in the north (Study **I**: Table 2). Both of these tree species occurred mainly among the smallest trees in stands.

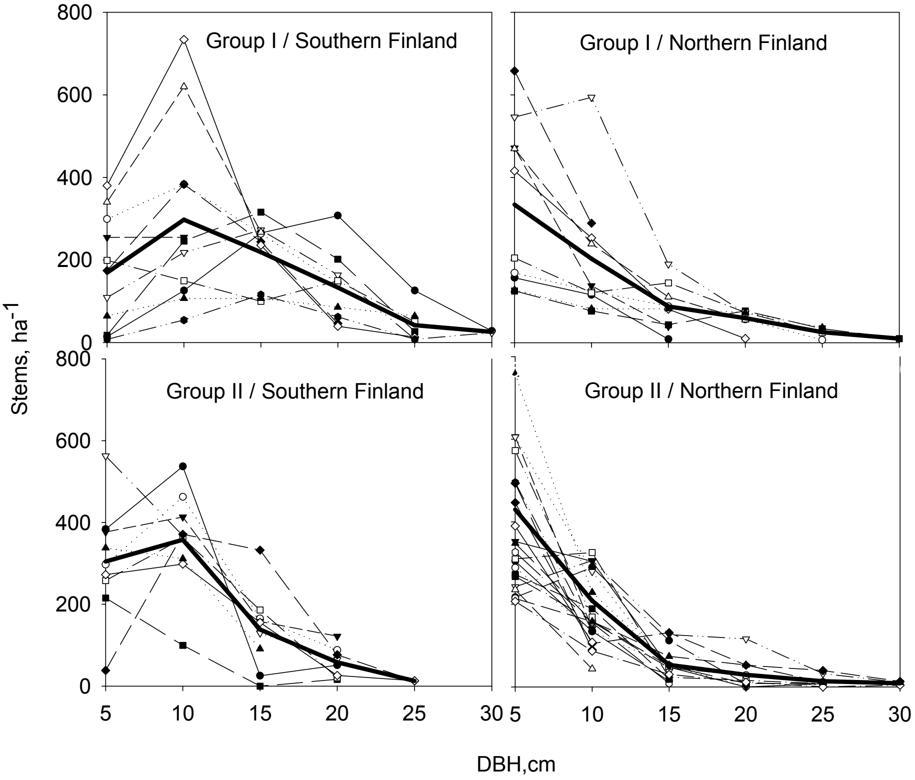

**Figure 4.** The DBH distributions of the sample stands by site type groups (Group I and II) and climate areas (southern and northern Finland) on pristine peatlands. The average values over stands are depicted by thick black lines.

Likewise the pattern of tree size structure, the pattern of tree age structure also differed between sites and regions (Fig. 5). On Group I site in the south, the age distributions were mostly flat or multimodal, with some plainly even-aged stands (Fig. 5). On average, the stands were more uneven in age on Group II sites in the south and on both sites in the north.

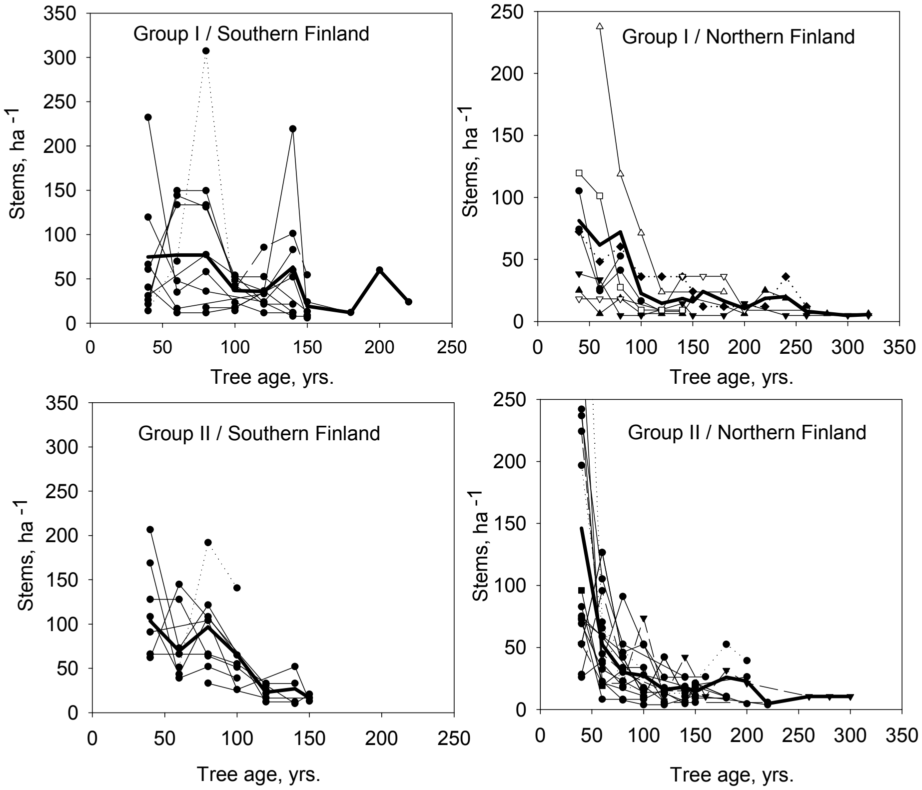

**Figure 5.** The tree age distributions presented by 20 year tree age classes of sample stands by site type groups (Group I and II) and climate areas (southern and northern Finland) on pristine peatlands. The average values over stands are depicted by thick black lines.

In general, tree size should increase as tree age increases. This was found to be true in these data also, except for Group I sites in the south, where trees of different size appeared to be of almost the same age (Study **I**: Fig. 4). Even in the 5 cm size class, the mean age of trees varied from 30 to140 years among stands, while in other groups the variability was much lower. In both groups in the north, the variance of mean age increased as a function of a size class, while no such trend was observed in the south (Study **I**: Fig. 4).

### *4.1.2. Temporal dynamics of stand structure in pristine peatlands*

The diversity of age and size structure in terms of the Shannon index showed differences between site type groups and climate areas (Fig. 6). The diversity of tree DBH increased considerably (1.3 – 1.5 fold) in the $A_{dom}$ chronosequence in the north but there was no relationship in the south (Fig. 6). As for DBH, the largest change in the diversity of tree age as a function of $A_{dom}$ occurred in the north, where the age structure of the stands on Group I sites experienced a change from homogenous to clearly heterogeneous (Fig. 6).

In Group II sites, the relationship was nonlinear with decreasing age diversity after 150 years of age. In the south, there was a slightly increasing non-significant trend in age diversity with $A_{dom}$ in both sites.

Similarly, the range, kurtosis and skewness of the DBH distributions, as well as the modality of DBH distributions ($D_{diff}$) showed positive correlations with $A_{dom}$, which were most significant in the northern sites (Study **I:** Table 3). Mean tree size (DgM) correlated more than age with stand characteristics in both the regions, but more significant correlations were also found more in the north than in the south (Study **I**: Table 3).

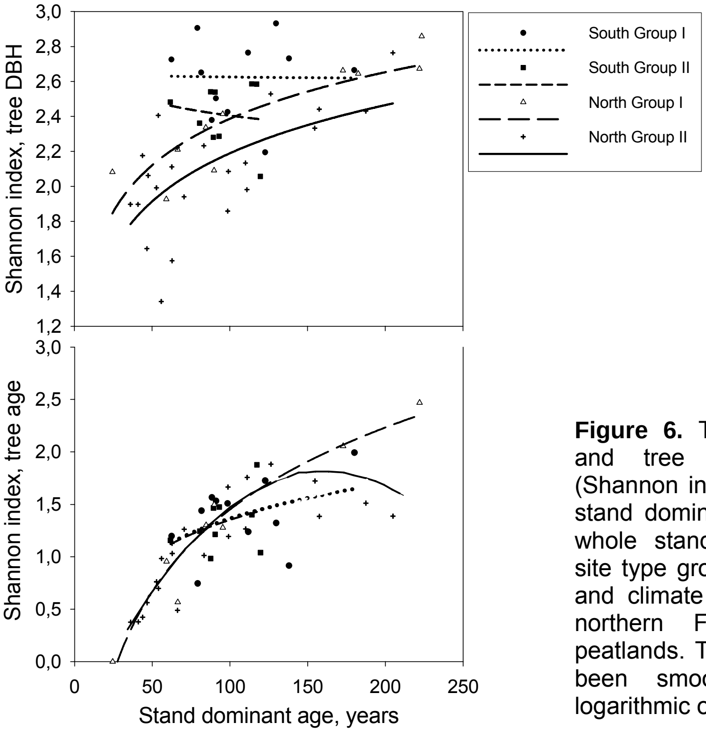

**Figure 6.** The diversity of DBH and tree age within stands (Shannon index) in relation to the stand dominant age ($A_{dom}$) in the whole stand data presented by site type groups (Groups I and II) and climate areas (southern and northern Finland) on pristine peatlands. The observations have been smoothed by fitting a logarithmic or polynomial curve

As the $A_{dom}$ increased in Group I sites in the south, the positive skewness of the DBH distributions, as well as the stand stem number, decreased (Study **I**: Table 3). Simultaneously, on other sites, the positive skewness and the range of DBH distributions even increased. Furthemore, the number of smallest pine trees (in the DBH class of 6 cm) decreased in each site type group and climate areas (Study **I**: Table 4). In spite of larger range in stand ages, clearly smaller temporal changes occurred in stand DBH distributions in the north than in the south (Fig. 7).

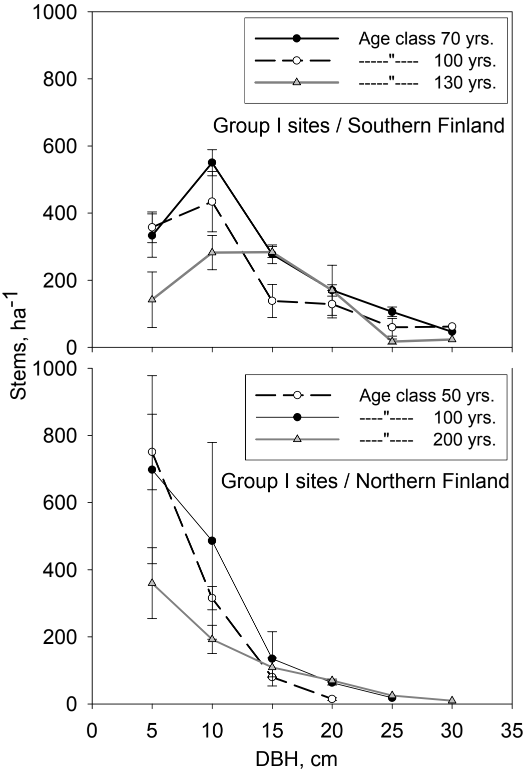

**Figure 7**. The average DBH distributions of Scots pine on pristine peatlands by three stand age classes on genuine forested sites (Group I) in southern Finland and on composite forested sites (Group II) in northern Finland as examples of temporal dynamics of stand structure.

## 4.2. Drainage induced changes in stand structure (Studies II, III)

After drainage, the characteristics of the DBH distributions changed considerably both in spruce dominated stands, as well as in pine dominated stands. The pattern of this change was similar independent on the dominant tree species or site's fertility. At the initial stage of post-drainage development, the DBH distributions of the dominant canopy layer were positively skewed in most cases (Study **II**: Fig. 2 and Fig. 3, Study **III**: Fig. 3, Table 4 and Table 5). Drainage resulted in a secondary succession, which was shown at first as increase in the structural heterogeneity of the stands. The average stand stem number increased, depending on the site type and stand management, from two to threefold during the first 20 years after drainage. However, after 20 years, the increase in the positive skewness, indicated by decreasing values of Weibull parameter *c,* ended, and the DBH distributions started to gradually approach a bell-shaped distribution in southern Finland. In northern Finland, the culmination of the stand stem number took place about 10 years later, but otherwise the trend was very similar to that in southern Finland (Study **IV**: Fig. 2A). On average, the stands reached a stage, where the DBH distribution of the dominant canopy layer was bell-shaped and close to symmetric, when 40-50 had elapsed since drainage. This development was faster in spruce stands than in pine stands. Later on, the DBH distributions even continued to develop towards negative skewness as well ($c > 3.6$).

Expressed by Shannon index, the diversity of tree DBH estimates showed an initial increase in the size inequality for the dominant canopy layer in the spruce dominated stand, after which the size inequality remained rather constant (Fig. 8).

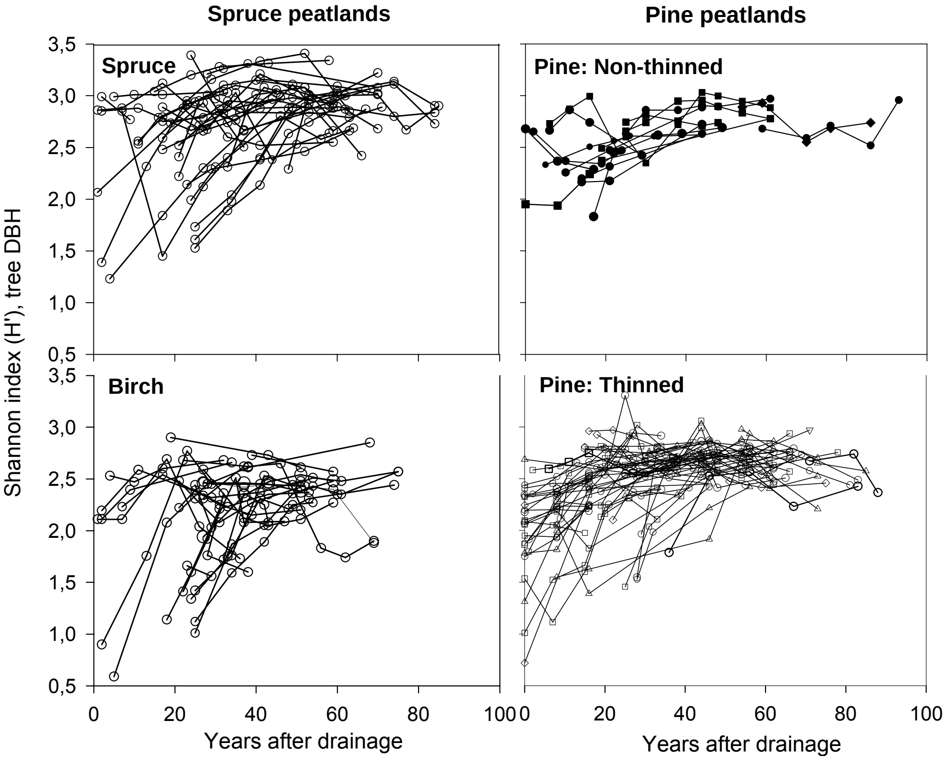

**Figure 8.** Standwise change of the Shannon diversity index values for spruce peatlands (managed spruce and birch stands) and pine peatlands (pine stand managed and non-managed) according to the time elapsed since drainage. Lines connect consecutive observations in each individual stand. Any understorey has been ignored in the values.

In spruce stands, the range of the tree DBHs remained very wide or even slightly increased during 60 years after drainage (Figure 9.). In pine stands, the range of the tree DBH was slightly widened during the first 20 years since drainage. Thereafter, the range remained wide and rather unchanged for decades (Figure 9.). In many stands of both species, the range was more than 20 cm throughout the monitoring period, which was at its longest 70 years.

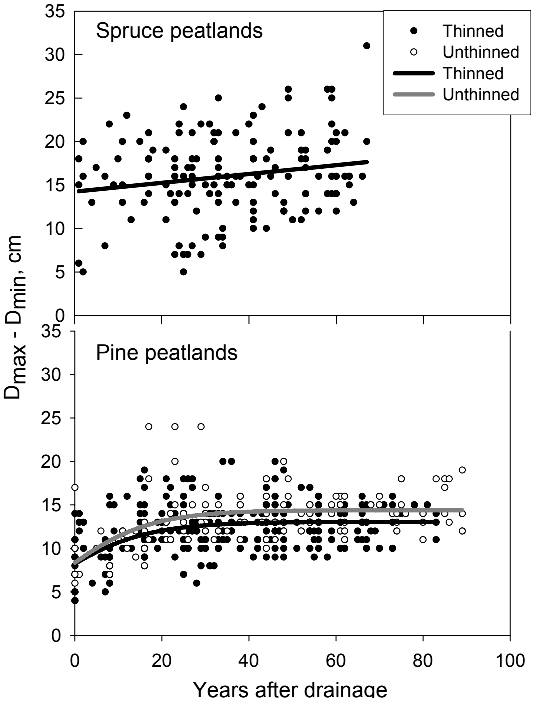

**Figure 9.** Range of DBH in stands on spruce peatlands and pine peatlands according to the time elapsed since drainage in data comprising all measurements. Each point depicts the difference between maximum and minimum DBH classes within which 90% of the total stem number of the stand is included (5% of both tails of the distribution is excluded). The observations have been smoothed by fitting a sigmoid curve by applying the least-squares method. Any understorey has been ignored in the values.

For spruce stands, the pattern of change in the DBH distributions was rather steady and similar for the two site types (HrT I and MT –site types), even though the changes were somewhat faster in the herb-rich type (Study **II**: Table 2). For pine stands (the dominant canopy layer), the differences between site types (Group I and II) were significant, however (See previous chapter 1.3.1). During the first 20 years after drainage, the shape of the DBH distribution changed only slightly on Group I sites, whereas on Group II sites, the positive skewness in the shape of the DBH distribution clearly increased (Study **III**: Fig. 3). Later, the decrease in the positive skewness of the DBH distributions was however faster on Group II sites (see Fig. 13). The inter-stand variation in the shapes of the DBH distribution was large during the whole time period both in spruce and pine stands (Study **II**: Fig. 2 and Fig. 3, Study **III**: Fig. 3 and Fig. 4).

The proportion of pubescent birch of the total stand stocking varied much, particularly between the site types and according to the time elapsed since drainage. For example, in the most fertile sites (MT II –type) of the spruce and pine peatlands, the birch proportion might be over 50% of the total stem number during the first two decades after drainage. On the other hand, the poorer the site and the longer the time elapsed since drainage, the lower the birch proportion seemed to be. The lowest initial birch proportion of the total stand stocking was found in pine stands on DsT I site type (4%). Depending on the site type, the proportion of birch decreased 0.1-28% when 70 years had elapsed since drainage (Study **II**: Table 1, and Study **III**: Table 2.).

For pine stands, very uneven-sized spruce / birch understorey with varying density was commonly found on Group II sites and in the VT I- site type. The quantity and size distribution of understorey spruce changed only little during the 60-year post-drainage period (Fig. 10), whereas the density of birch decreased slowly as the stocking of the dominant canopy layer increased. In old drainage areas (more than 40 years elapsed since drainage), spruce was more abundant than birch in the understorey.

For spruce peatlands, 42% of the stands had distinct layer of suppressed understorey trees, at least in some occasions during the stand monitoring periods. However, the occurrence seemed to be more or less random and mostly not as abundant as on pine peatlands. The understories consisted mainly of spruce and they occurred most frequently on Group I sites.

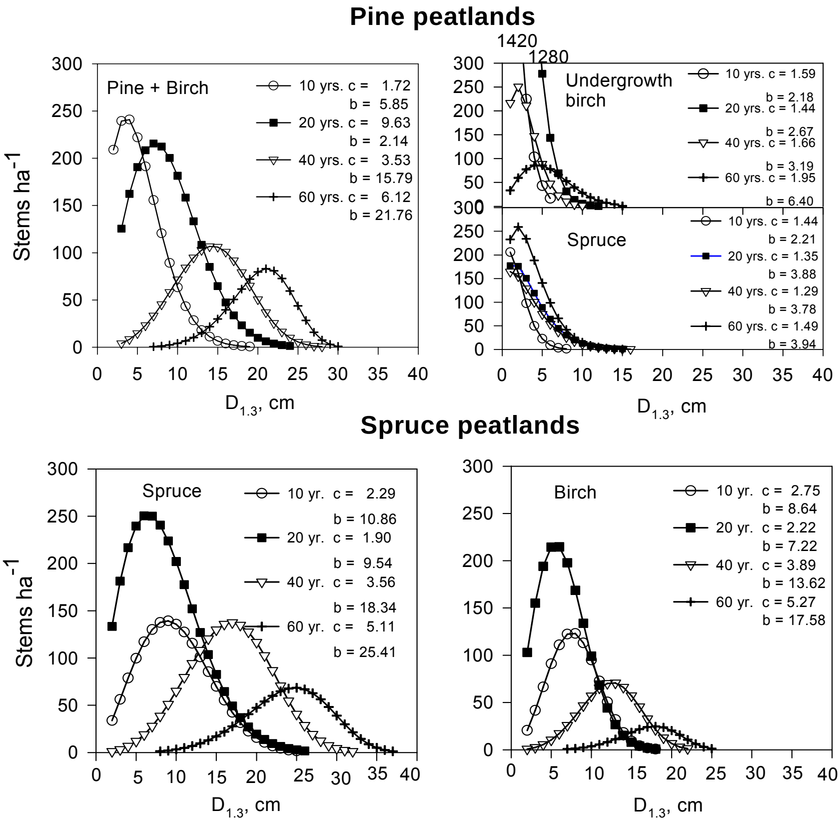

**Figure 10.** Mean DBH distributions of spruce and birch in drained spruce peatlands and pine peatlands (the dominant canopy layer of Scots pine and birch, and understorey spruce and birch) presented by drainage age classes. The Weibull parameters of each DBH distribution have been presented in the legends as examples.

### 4.3. Tree mortality in natural pine stands on drained peatlands (Study **IV**)

In the unmanaged pine stands on drained peatlands, the annual mortality rate in number of trees increased steadily during the first 50 years following drainage, but then decreased towards the oldest drainage ages (Fig. 11). In terms of basal area, the absolute annual mortality rate did, however, increase steadily. In the beginning, the mean diameter of the dead trees was equal to that of live trees, but later the mortality rate of trees with a diameter smaller than the mean of the live trees increased (Fig. 11). The proportion of dead trees was highest in DBH classes below 10 cm, and mortality increased as time elapsed since drainage (Study **IV**: Fig. 3). The shapes of the DBH distributions of the dead trees closely resembled those of live trees in all drainage age classes, but the peaks of the dead tree distributions, however, remained more persistently in smaller DBH classes than in those of the live tree distributions (Study **IV**: Fig 1).

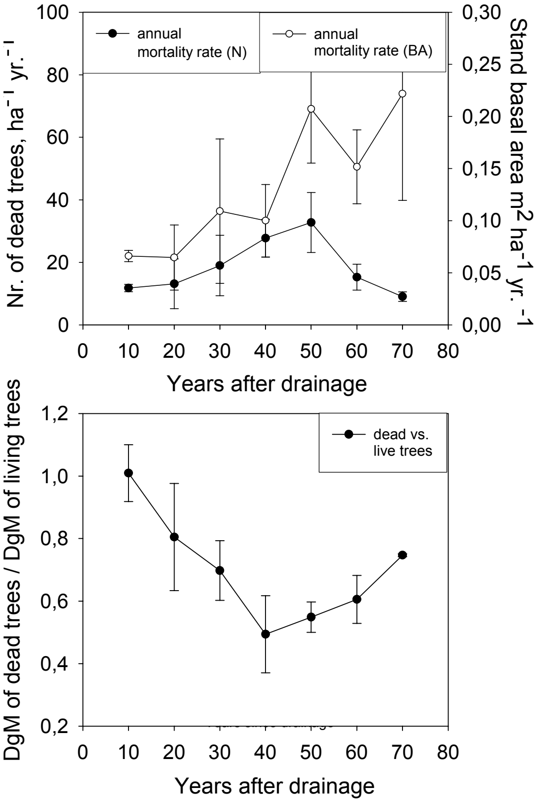

**Figure 11.** The average annual tree mortality rate of stand stem number (No.) and stand basal area (BA) (upper graph) and the relationship between the median diameter of stand basal area (DgM) of dead and live trees for the data combined by drainage age class. Error bars depict standard error of mean.

### 4.4. Effect of stand management on the post-drainage stand development (Study **II** and **III**)

Compared to the pine peatlands, the direct “pure” effect of cuttings on stand structure could not be studied in the spruce peatlands (Study **II**), because no fully unmanaged stands were included in the material. However, because the spruce stands were managed using a large variety of thinning intensities, it was possible to analyse the effect of thinning intensity on the stand development by model approach. According to the results the cuttings had no direct significant effect on the shape of the DBH distribution of the spruce and mixed birch stands on spruce peatlands.

In unthinned Scots pine dominated sites, the shape of the DBH distributions of the dominant canopy layers approached bell-shaped distribution when 50-60 years had elapsed since drainage, whereas in thinned stands the DBH distributions reached normality by the time 40 years had elapsed since drainage (Study **III**: Fig 3 and Table 4). The large range of DBH indicated that the DBH distributions of the unthinned stands became flatter and had larger variation of DBH than that of the thinned stands (Study **III**: Table 5). The proportion of trees fulfilling saw timber dimensions of the total volume was significantly larger in spruce stands than in pine stands during the whole post-drainage period monitored. In pine stands, the thinnings did not significantly affect the total volume compared to unthinned stands (Note: the post-thinning stand growth is included in the values), but the volume of saw timber wood was significantly larger in successively thinned stands (Fig. 12). Once a stand reached its maturity at about 60 years following drainage the proportion of saw timber trees out of the total stand volume was 70-90% in spruce stands and 40-65% in pine stands. Respectively, there grew about 400 timber trees per hectare in spruce stands and 320 timber trees in managed pine stands. In unthinned Scots pine stands the number of timber trees was about 250 after 60 years since drainage. These numbers are significantly larger than those reported earlier by e.g. Hökkä and Laine (1988). The characteristics of the understorey tree stand were unaffected by the thinnings.

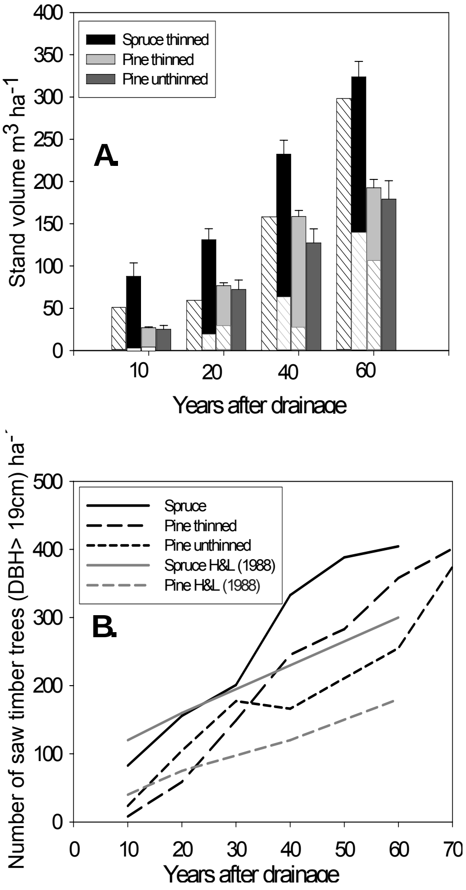

**Figure 12**. **A:** The average stand total volume and the volume of trees fulfilling saw timber dimensions (lineated bars) by drainage age classes in spruce and pine peatlands. For pine stands, the volumes of unthinned and successively thinned stands are presented separately. **B:** The moving average of stem numbers of saw timber trees across drainage age classes in spruce stands (solid black line) and in pine stands (dashed black lines). The comparative average stem numbers of saw timber trees in spruce stands (grey solid line) and in pine stands (dotted line) after drainage according to Hökkä and Laine (1988), are presented.

## 4.5. Factors affecting the stand structure on drained peatlands

### *4.5.1. Models for predicting the DBH-distributions*

In the models for the shape of the DBH distribution (parameter *c*) in spruce peatlands (Study **II**), as well as in pine peatlands (Study **III**), the ratio of $D_M$ and $D_{Max}$ was the single most important explanatory variable (Table 2). It performed better than $D_M$ alone by decreasing the heterogeneity of the residuals.

In spruce peatlands, stem number of spruce and years elapsed since drainage were significant explanatory variables in the model for spruce (Table 2). For birch, the basal area of birch ($m^2ha^{-1}$) improved the fit of the model (Table 2). For spruce, random variation between and within stands was significant, but random variation among the inter-thinning periods was not. For birch, the random effect of the inter-thinning periods ( $_{jk}$) and random residual effect ($e_{ijk}$) were significant, while the stand effect ( $_{k}$) was not. No significant site type effect was observed.

In pine peatlands, individual site types did not differ significantly from each other in the models for pine stands. Nevertheless, the site type groups (Group I and II sites) differed from each other as indicated by statistically significant different parameter values of the $D_M$ / $D_{Max}$ ratio for the site type groups and by a dummy variable for site II (Table 2). The model for understorey spruce could be constructed reliably only for the Group II sites, because of the very few spruces on Group I sites.

In the model for pine, the stem number, the proportion of large trees ($d_{1.3}$ > 19 cm) of the total stand volume (VTD), and the ratio between stem number and basal area (N/G) were significant variables on all of the sites. Furthermore, for Group II sites only the proportion of birch (BirchG%), the proportion of the thinning removal of the total stem number (CutN%), and the site type group dummy were significant explanatory variables (Table 2). Thinning intensity had been greater on Group II sites and the thinning removal had concentrated more on the smaller trees than on Group I sites, which was seen as a significant dummy variable in the model.

For the model for understorey birch, the temperature sum (Tsum) was statistically significant and for the model for understorey spruce, the temperature sum and the width of the drainage strip (StripW) were statistically significant (Table 2).

For pine, all components defined in equation (4) were statistically significant in the random part, whereas for the model for understorey birch and spruce, only the measurement level variance ($\sigma^2_e$) was significant. More complex variance structures at stand level were also tested for models of pine and spruce, but found to be statistically insignificant.

**Table 2.** Models for parameter c of the DBH distributions in spruce peatlands (spruce and birch) and in pine peatlands (pine+birch of the dominant canopy layer and understorey spruce and birch). Standard errors (sem) are given in parentheses.   = Constant; $D_M$ = Stand median diameter at breast height (1.3 m, cm); $D_{Max}$ = 95 % of the maximum DBH of stand; N = stem number of the tree stand of the model concerned, $ha^{-1}$; G = basal area of tree stand of the model concerned; VTD = proportional share of timber-sized trees ($d_{1.3}$ > 19 cm) of the total stand volume; BirchG% = proportional share of deciduous trees of the total stand basal area; CutN% = proportional cut-removal of stand stem number in the previous thinning treatment; Group I, II = site groups; Tsum = temperature sum; yeard= years since drainage; StripW = the perpendicular distance between adjacent ditches; Variance components: $^2_k$ = random effect of stand k, $^2_{jk}$= random effect of inter-thinning period j in stand k, $^2_{ijk}$ = within-stand variation between measurement time-points; $Bias_r$ = relative bias. The biases are presented after exponential transformation of the logarithmic models.

| | Spruce peatlands | | Pine peatlands | | |
|---|---|---|---|---|---|
| Dependent variable | **Spruce**<br>(Ln(c)) | **Birch**<br>(Ln(c)) | **Pine + Birch**<br>(Ln(c+2)) | **UG-Spruce**<br>(Ln(c)) | **UG-Birch**<br>(Ln(c)) |
| Variable | | | Parameters (sem) | | |
| **Fixed part** | | | | | |
| | -6.7573 (1.333) | -6.6609 (2.682) | -0.9746 (0.388) | -8.3821 (0.878) | -4.9079 (1.051) |
| $(1/-\ln(D_M / D_{Max}))^{0.1}$ | 8.8299 (0.728) | | | 7.3830 (0.817) | 7.8571 (0.625) |
| $D_M / D_{Max}$ | | 3.1727 (0.091) | | | |
| $\ln(N_s)^{0.5}$ | -0.5511 (0.244) | | | | |
| $\ln(N)^{0.6}$ | | | -0.1444 (0.052) | | |
| $(G)^{0.01}$ | | 6.0152 (2.657) | | | |
| ln(N/G) | | | -0.3243 (0.057) | | |
| $\ln(N/G)^2$ | | | 0.0273 (0.005) | | |
| $(1+VTD\%)^{0.5}$ | | | 0.0099 (0.003) | | |
| Group I: $(1/-\ln(D_M / D_{Max}))^{0.1}$ | | | 3.7214 (0.245) | | |
| Group II: $(1/-\ln(D_M / D_{Max}))^{0.1}$ | | | 2.9509 (0.242) | | |
| Group II: $(\ln(1+BirchG\%))^4$ | | | -0.0003 (0.0001) | | |
| Group II: CutN% | | | 0.0012 (0.0004) | | |
| Group II: Site(0/1) | | | 0.8044 (0.238) | | |
| yeard | 0.0028 (0.001) | | | | |
| Tsum | | | | 0.0013 (0.0003) | -0.0019 (0.001) |
| StripW | | | | | -0.0042 (0.001) |
| **Random part** | | | | | |
| $^2_k$ | 0.0162 (0.006) | | 0.0045 (0.001) | 0.0030 (0.003) | 0.0182 (0.013) |
| $^2_{jk}$ | | 0.0343 (0.008) | 0.0051 (0.001) | | |
| $^2_{ijk}$ | 0.0288 (0.003) | 0.0178 (0.005) | 0.0059 (0.001) | 0.0260 (0.005) | 0.1021 (0.016) |
| Bias | -0.0842 | -0.0490 | -0.0509 | -0.0042 | -0.0117 |
| $Bias_r$ | -0.0568 | -0.0639 | -0.0605 | -0.0253 | -0.0960 |

### *4.5.2. Model evaluations*

Examination of the residuals revealed no systematic error in the predicted parameter *c* for the modelled stand parts both on the drained spruce and pine peatlands. In spruce peatlands, the average relative bias (overestimation) for the parameter *c* estimates was 5.7%, and 6.3% for spruce and birch (Table 2.). Respectively, in pine peatlands, the model overestimated the shape parameter on average by 6.0%. For understorey birch and spruce, the overestimations were 9.6% and 2.5%, respectively (Table 2).

In stands with a small number of diameter classes the reliabilities of the predicted parameter values were lower. For example, in mature stands on spruce peatlands (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.

In spruce peatlands, the relative bias for solved parameter *b* (solved analytically) was 1.2% for spruce and 13.1% for birch. In pine peatlands, the relative overestimation for parameter *b* for the combined model was +3.3%, and +16.5% and +1.4% for understorey birch and spruce, respectively.

Simulations applied to test the models' ability to produce appropriate distributions and predict stand yield performed well in stands both on spruce peatlands (spruce and birch for all sites combined) and pine peatlands (pine by site type groups). The simulated DBH distributions are presented in Fig. 13, and the biases of the model on stand stem number, stand basal area, and the variables describing stand volume ($\sum d^3$) and stand value ($\sum d^4$) are presented in Table 3. The largest biases occurred in the predicted estimates of the model for birch in spruce peatlands; particularly in the variables describing the stand volume ($\sum d^3$) and stand value ($\sum d^4$) (biases 13% and 18%). Based on the residual examination, the model predicted the amount of birch stems below 5 cm at DBH to be too low. For pine model, the largest relative biases observed in regard to stem number, basal area, volume and value were on the recently drained sites (< 20 years since drainage).

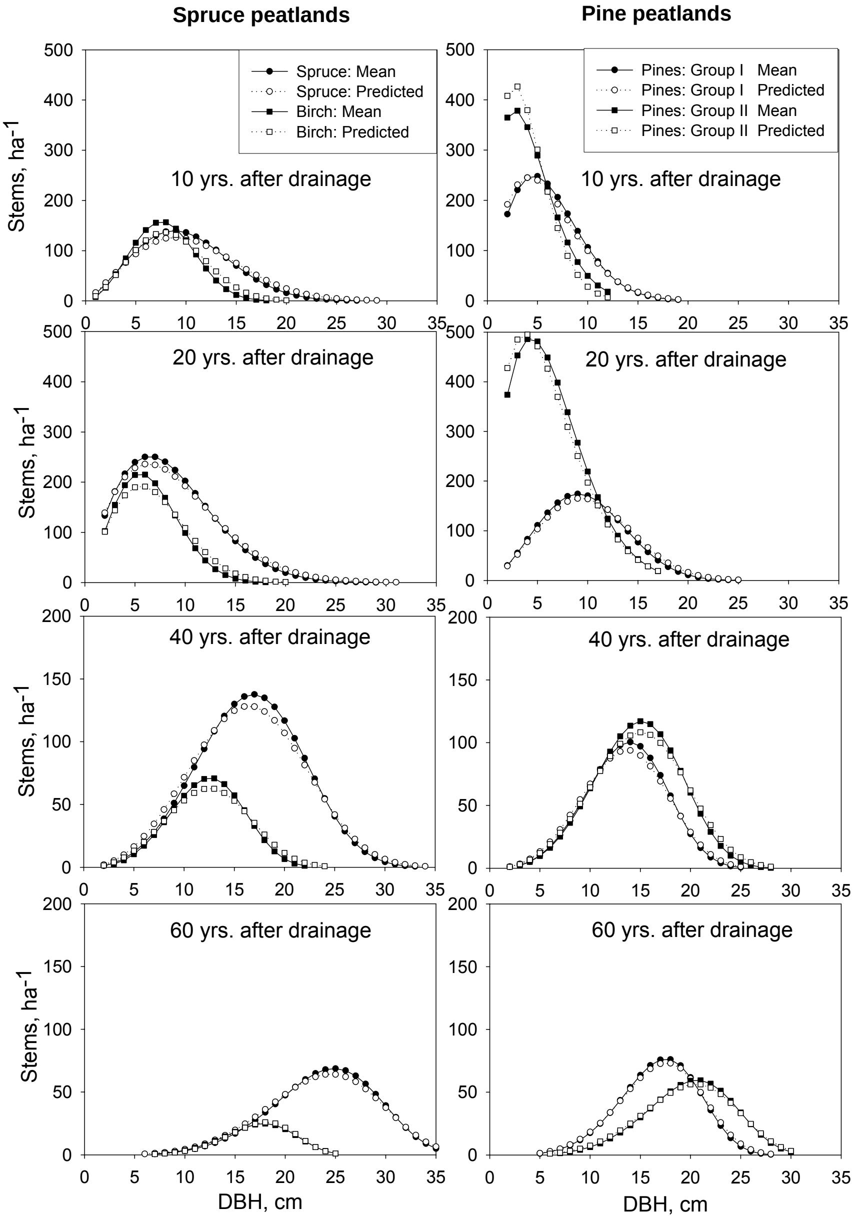

**Fig. 13.** Average smoothed DBH distributions (filled symbols) and predicted DBH distributions in Spruce dominated sites (spruce and birch) and in Pine dominated peatland sites (the dominant canopy layer) obtained by using the model of parameter c (open symbols), by drainage age class (10, 20, 40 and 60 years elapsed since drainage). For spruce peatlands the DBH distributions are presented for all sites combined and for pine peatlands within site type groups: Group I sites = genuine forested peatland sites; Group II = sparsely forested composite peatland sites.

**Table 3**. Average biases of the predictions of the stand DBH distribution models for spruce and pine peatlands in relation to stand basal area, stand stem number, stand volume ($\sum d^3$) and stand value ($\sum d^4$). The predictions have been compared to the estimates of the smoothed DBH distributions.

| **Model** | **validation variable** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Stems | | G | | $\sum d^3$ | | $\sum d^4$ | |
| | Bias | $Bias_r$ | Bias | $Bias_r$ | Bias | $Bias_r$ | Bias | $Bias_r$ |
| **Spruce peatlands** | | | | | | | | |
| Spruce<br>all sites | +10.6 | 0.011 | +0.19 | 0.011 | +10070 | 0.016 | -1310846 | 0.020 |
| Birch<br>all sites | -41.8 | 0.038 | +0.21 | 0.038 | -60751 | 0.127 | -1497482 | 0.179 |
| **Pine peatlands** | | | | | | | | |
| Pine<br>Group I sites | +31.5 | 0.012 | +0.14 | 0.009 | +45263 | 0.043 | +996688 | 0.053 |
| Group II sites | +11.9 | 0.008 | +0.01 | 0.002 | -13613 | 0.011 | -823810 | 0.032 |

# 5. DISCUSSION

## 5.1. Material validity and methodological aspects

Two types of stand datasets were used to investigate the stand structure and its temporal dynamics on peatland sites: 1) the inventory data ("the pristine data") consisting of circular sample plots based on systematically stratified sample of sites (Study **I**), and 2) the longitudinal data ("the drainage data") consisting of repeatedly measured permanent sample plots (Studies **II, III** and **IV**). Considering the investigation of the stand development, the given differences between these data types may be significant for describing the temporal changes in stand structure. Inventory data is relatively cost-effective and fast to collect compared to the long-term time series. Thus, it has been commonly applied for studying temporal stand dynamics by arranging the stand data into different age chronosequences (cross-sectional data).

The characteristics among stands of a given stand age may, however, vary considerably even within the same site type. Consequently, when a chronosequence is constructed based on stand age (or drainage age) only, the stands may actually represent widely varying stages of stand development. Thus chronosequences do not necessarily always describe the temporal changes of the stand structure correctly. For example, they may easily result in the over-estimation of the stand stem number, particularly the number of small trees when stands representing different developmental stages have been included in the averages (Päivänen 1999). Instead, repeatedly measured stand data is evidently superior in demonstrating the dynamics of a long-lived population, because no differences exist in the initial site and stand characteristics between the observations within a stand; of course provided that the tree population remains as the approximately same during the monitoring period. Furthermore, the development history of each stand sequence is known. Thus, the ideal method would have been to use a longitudinal data overall in order to study the stand dynamics, that was however not possible in this study. On the other hand, in pristine peatlands, the stand development typically is very slow and thus, the investigation of stand succession would require very long time-series. However, on drained peatlands, the temporal changes in stands are generally faster. Thus, in drained peatlands, it is more appropriate to use even a short longitudinal data, like in this study, to investigate the stand dynamics, whereas in pristine peatlands, a chronosequence, which has large temporal range, would be more appropriate. In this study, the pristine data covered stand ages between about 50 to 225 years in pristine peatlands, whereas in the drainage data, at its best, it was possible to follow the development of individual stands for 75 years.

It is essential for the accuracy and precision of empirical data to adequately represent in the target population and to be free of significant systematic errors in the measurements. In inventorial studies, the minimum statistical requirement is that the data is a randomized or systematic sample covering well the variation within the population. The desirable accuracy of the data then determines how large the sample size should be. In this study, both the data sets used are not based on the extensive randomized sampling of the all Finnish peatland sites. It is true that, e.g., the stem distribution curves of single stands based on temporary sample plots may give biased view if extended to describe the situation for large forest areas. On the other hand, the object of this study was not to get unbiased areal information on the characteristics of peatland stands, but to find out regularities in the inherent patterns and processes taking place within stands. Thus, the stands sampled in the datasets should be considered as replicates within treatments (geographical location, site type, cuttings etc.) when studying the characteristics of the phenomenon. By utilising sample plots having a firm area (circular plot or permanent forest sample plot) instead of e.g. angle-count sampling, which has been earlier widely used as a stand inventory method, it is possible to describe the stand structure more reliably. This is possible, because in the angle-count sampling, the largest trees are weighed more in the sampling and cause bias in the estimates of the smallest trees, particularly trees below DBH of 10 cm (Maltamo and Uuttera 1998).

The representativeness of the drainage data was improved by substantial variation in site and stand characteristics included in the data. The dataset covered considerable variation with respect to initial stocking, stand age, site fertility, management and climatic variation. Furthermore, the most usual peatland site types supporting tree growth naturally in the northern European boreal zone, which have also been the most common targets of drainage, were included in both of the data sets. For the purpose of monitoring the stand structural dynamics, both of the used data were the best available.

In this study, the properties of the DBH distributions, together with other stand characteristics, were the main targets in describing the stand structure and its temporal dynamics (that were studied by standard analytical and statistical methods). Even though, the Weibull -method has certain problems that appear particularly in estimating the distributions of the heterogeneous stands (e,g. Maltamo et al. 2000), the possible sources of errors related to the technical estimation, as well as the ecological "reality" of the estimates could be controlled fairly well (see Study **III**). Besides the shape of the DBH distribution, the range and the flatterness of the distribution, as well as tree size/age diversity and the stand characteristics describing the stand stocking completed and clarified the ecological interpretations on the stand structural variation and dynamics. On the other hand, the conclusions on the factors modifying stand dynamics had to be partly based on the indirect interpretations in this study. These concern particularly the effects of ecohydrology and the inter-tree competition on the stand structure that would otherwise require treewise spatial analysis and growth studies. Furthermore, the tree populations should remain the same when changes in DBH distributions are associated to changes in inter-tree competition. In this study, the conclusions on the hydrology and inter-tree competition were based on the synthesis of the earlier findings on the peatland ecology and stand dynamics (See chapters 1.2 and 1.3). Even though, the single trees were not individualised and the long-term unchangeability of the tree populations could not be fully ensured in this material, by means of the successive measurements –separated to tree species and tree storeys– it could be proved that the temporal changes in stand stem numbers were consequences of either cuttings, natural mortality or "ingrowth" of trees, however. Furthermore, their effects were possible to separate from each other fairly well in the interpretations of the results.

## 5.2. Stand structure and dynamics on pristine peatlands

It is known that climate conditions and site properties affect tree growth on pristine peatlands (Gustavsen and Päivänen 1986). Significant differences also appeared in the characteristics of stand structure between climate areas and between site type groups that were composed on the basis of geographical location and hydrological regime (Study **I**): in the south, the stand structure is largely fairly even-aged and –sized, and the structural variation increases from genuine forested sites (Group I) to sparsely forested composite sites (Group II), and further from south to north. The most unevenly structured stands, as well as the smallest inter-stand variation can be found on Group II sites in the north. These findings are also in accordance with the DBH distributions of pine, which at the time of drainage were on average close to bell-shaped form in southern and central Finland (Study **III**), and the distributions had clearly reverse J-shaped pattern in northern Finland (Study **IV**).

Based on the shape of the DBH distribution, most stands on southern sites were fairly even-sized and thus differed greatly from those on northern sites. In the south, the tree size diversity was also relatively high and the range of DBH exceeded 15 cm, which has been suggested as a maximum for pure even-sized stands, however (e.g. Lähde et al. 1991). Moreover, the distributions were significantly flatter (*negative kurtosis*) in the south (Study **I**: Table 2). A wide range of DBH, as well as multimodal DBH distributions are regarded as a typical feature of natural Scots pine stands on mineral soil sites (Kuuluvainen et al. 2002, Rouvinen and Kuuluvainen 2005). However, in this material, very few stands clearly had two or more peaks in DBH distributions. In bell-shaped distributions, the peak was located mainly within DBH classes of 10 cm and 15 cm, which indicate the low productivity and weak dependence of it on the site fertility on pristine peatlands.

Particularly in the south, many of the standwise DBH distributions differed significantly from those presented as typical for pristine peatland sites in earlier studies (e.g. Heikurainen 1971, Ågren and Zackrisson 1990, Norokorpi et al. 1997). On the other hand, the average DBH distributions of the two site type groups were much closer to each other, and they were more skewed than those observed in the single stand-wise distributions (Fig. 4). This discrepancy is probably mainly due to the “averaging” effect, which combines stands of the same site type but having different structural characteristics, and thus cleans too much the structural variation. This may easily result in biased conclusions on the actual stand structural characteristics and stand dynamics. Similar results can be easily obtained when considering forest structure on the landscape-level, where a variety of different stands representing different developmental stages and sites may be included in the average values of the forest structure. Consequently, it can be concluded that the larger the inventoried forest area, the greater the probability to get a descending DBH distribution as a result.

The studied structural attributes suggested that stands at higher $A_{dom}$ had larger structural inequality in northern than in southern conditions. In the south, the tree size structure developed in a more even-sized direction with increasing $A_{dom}$, particularly on Group I sites. The random inter-stand variation was so high that it obscured most of the temporal variation, however (Fig. 5). Furthermore, the range of tree age was narrower in the south than in the north. These may be reasons for the weak or non-significant correlation between the stand ages and other stand characteristics in southern sites. On the other hand, it was evident that large inter-tree tree size variation in relation to tree age existed even in relatively young stands on southern Group I sites (stand age <100 years). This structural feature was shown as small differences in mean age between DBH classes, and as a relatively high age of small trees. The high tree size variation in relation to the tree age and the weak dependence of tree size diversity on $A_{dom}$ (Fig. 6) indicates further that the stand age structure, particularly on southern sites, is not as good an indicator of stand size structure as on e.g. mineral soil sites (vs. Clark et al. 2003). Because, the variance of mean age increased as a function of a size class more distinctively in the north than in the south, it indicates that more variable patterns of stand development can be found in the north than in the south. Obviously, the spatial variation in the tree growth conditions determines the tree size structural variation within the stand more than age.

Based on the analysis of tree size and age diversity, which were described with Shannon index, the diversities did not depend on stand age in the south, i.e., there was no structural process taking place although the dominant stand age was increasing. When the distributions of single stands or age-classwise averages were however visually compared, the most distinct changes in the shape of DBH took place in the south, particularly on Group I sites (Fig. 7). The comparative discrepancies between the temporal change of DBH distributions and tree size diversity were also found in drained spruce (Study **II**) and pine peatlands (Study **III**). It is thus obvious that the Shannon index cannot reflect all the structural changes that are relevant in stand succession dynamics.

It is typical in the final successional old-growth stage of the boreal coniferous forests that the stand vegetation is self-perpetuating and in equilibrium with the physical habitat, no net accumulation of organic matter appears and the tree stands have a patchy spatial pattern and high structural complexity (Sirén 1955, Franklin et al. 2002, Frelich and Reich 2003, Lilja et al. 2006). In these stands, the structure is characterized by large old living and dead trees with young tree cohorts appearing in the secondary gaps, considerable amounts of coarse wood debris, snags and stumps; self-thinning plays only a minor role in tree mortality (Siitonen et al. 2000, Kuuluvainen et al. 2002, Ranius et al. 2003, Zenner 2004). In pristine peatlands, the stands have given features, which may indicate the old-growth stage, such as stable tree size-age distributions and high horizontal structural variation of tree age and size (Study **I**). Nevertheless, the temporal changes observed in stand structure and stand characteristics, such as increase in tree size heterogeneity and stand stocking, indicate that in an individual stand, its growth and mortality are not necessarily in balance in pristine peatlands (see e.g. Goodburn and

Lorimer 1999). Particularly, in the southern genuine forested sites, the observed differences in the trends of the structural variation between the climate areas, with simultaneously decreasing abundance of small trees, indicate stronger forces modifying stand structure than in northern conditions.

## 5.3. Post-drainage stand succession on spruce and pine dominated peatlands

After drainage, the stand structural succession becomes significantly faster and more dynamic than in pristine peatlands and it goes through several distinct developmental stages as hypothesised. During the first two decades after drainage, the marked unevenness in tree size structure increased both in spruce dominated (Study **II**) and pine dominated stands (Study **III** and **IV**) 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 resulting from improved growing conditions following the lowering of the water level (Kaunisto and Päivänen 1985, Roy et al. 2000), and were to be expected from observations in other studies (Hånell 1984, Hökkä and Laine 1988). The smallest trees generally respond most vigorously to drainage (Heikurainen and Kuusela 1962, Seppälä 1969) and are evidently able to fill the initial openings in the stand. This initial stage, as hypothesised the so called “release stage” (Fig. 14), lasted only a rather short time after drainage. This stage is consistent with “the regeneration stage” described in the succession theories of coniferous stands on upland sites (ref. Franklin et al. 2002). At this stage, the competition from the larger trees was obviously not intensive enough to prevent the establishment and growth of smaller trees. Because the stem number increased mostly in Group II sites, it indicates gaps in the canopy caused by the initial microsite variation within a site. The new seedlings were mainly spruce in spruce dominated stands, and pine and pubescent birch in pine dominated stands. In pace with increase in the stand stem number, the biomass of mire shrub species, such as *Betula nana*, *Ledum palustre* and *Vaccinium uliginosum* proliferates as well during the first decades following drainage when enough light is available for their growth (Laiho et al. 2003).

As the stands aged, the structural unevenness, however, decreased and developed towards a more homogeneous stand structure. This “normalisation stage” (Fig. 14) was the result of the change from positively skewed to bell-shaped DBH distributions within spruce and pine stands (Studies **II, III**), as well as the increased mortality of smaller trees over time as observed in non-thinned pine stands (Study **IV**). Some features of high structural diversity (Fig. 8) were, however, retained in the stands throughout the whole monitoring period. This diversity was comprised of different structural patterns during the course of the succession after drainage: first by advanced regeneration and growth of small trees, later on by widened DBH range, as well as the large dimension diversity of the trees. These results were in accordance with those of e.g. Hökkä and Laine (1988), because structural inequality has been reported to increase during the first 20-30 years after drainage. On the other hand, similar later stand development, in which the structural inequality decreases, has also been reported in a bog pine (*Pinus uncinata* var. *rotundata*) stand on a peatland following drainage of an adjacent cut-over peat extraction area (Freléchoux et al. 2000). Furthermore, McDonald and Yin (1999) have reported a decrease in the size variability of trees in mixed black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch) stands following drainage. However, the results contradict with some earlier studies, where DBH distributions of peatland stands remained positively skewed (Hånell 1984, Hökkä and Laine 1988, Laiho et al. 1997, Korpela 2004), or the tree size variation of the stands and the proportion of the deciduous tree species of the stand stocking evenly increased after drainage (Hotanen et al. 2006), even when the stands matured. This apparent discrepancy may partly originate from the different methodological approaches. However, the approach of this study, based on truly longitudinal data, may better reflect the general trends in post-drainage temporal dynamics.

In some stands, the inequality of stand structure increased again once "normalised" after 60-70 years since drainage. This seems to be a result of the increase in the number of small trees within the stand. This, together with the decrease in the number of large trees, indicates small-scale tree mortality in most of the spruce stands (Study **II**), as well as in the well-stocked unthinned pine stands (Study **III**). This can be suggested as the initiation of "the diversification stage" as postulated, which in the long term would further result in the old-growth stand structures if the stand is not regenerated. In upland sites, these gap-dynamics is proved to particularly characterise the late succession of pristine old *Picea* –dominated stands resulting in the gradual heterogeneisation of stand structure (Qinghong and Hytteborn 1991, Kuuluvainen et al. 1998a,b, Pham et al. 2004). In drained peatlands, the process of the structural heterogenisation is probably fastest in spruce stands, because they are susceptible to wind damages due to the very shallow root system of spruce and the weak bearing capacity of the substrate. On the other hand, the gradual increase in the age-related mortality among the oldest large trees in pine stand in the long run (Study **IV**) may speed up the structural heterogeneisation in stands, where most of the dominant trees have been born before drainage. In this study, the monitoring period of 70 years elapsed since drainage was, however, too short in order to detect all the stages of stand succession on drained peatlands.

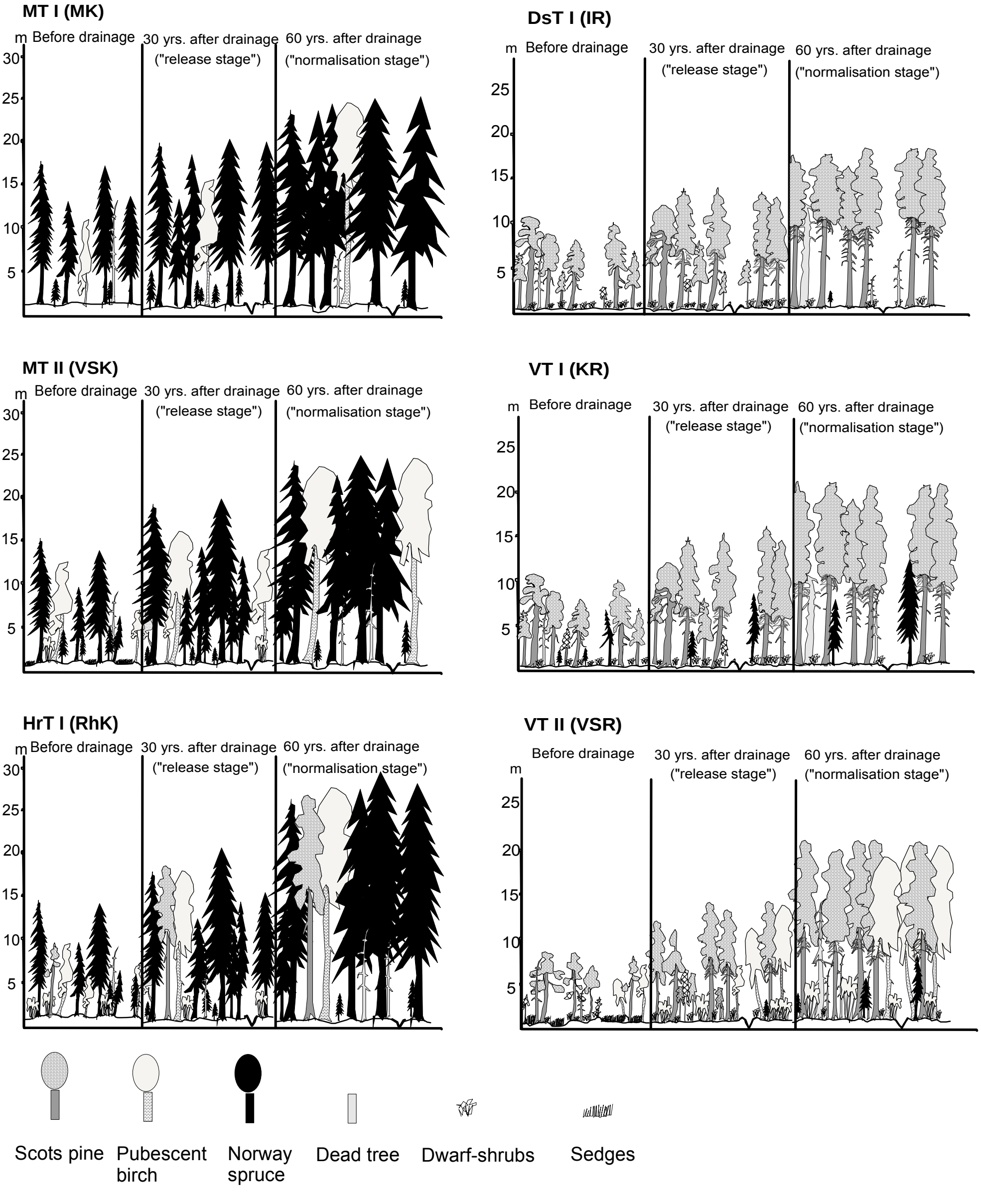

**Figure 14.** Stages of post-drainage secondary succession in Norway spruce and Scots pine dominated stands by site type groups (I=genuine forested sites, and II=sparsely forested composite sites) in spruce and pine peatlands presented as schematic illustration. HrT=Herb-rich sites; MT=*Vaccinium myrtillus* sites; VT=*Vaccinium vitis-idaea* sites; DsT=Dwarf-shrub sites. An example mire site type within site type groups has been presented in parentheses (nomenclature of single mire site types according to Laine and Vasander 2005).

## 5.4. Factors found to affect stand dynamics on pristine and drained sites

### *5.4.1 Primary factors*

When studying the tree stand dynamics on peatland sites, an important question is how the observed structural changes are linked to the present common theories constructed to model and conceptualize the forest succession (see chapter 1.2). In general, factors such as site ecohydrological properties (soil texture, water and nutrient regimes) and climate conditions create basic prerequisites for stand succession controlling the tree establishment, tree species composition and tree growth. *In pristine pine peatlands* (Study **I**), the clear differences in the structural patterns between site types reflect unequally distributed spatial variation in growing conditions (water and nutrients) within the site (Westman 1981). Of course, conclusions on the site effect on stand structural dynamics are indirect only, because any spatial examinations were not possible to do in this study. In contrast to sparsely forested sites (Group II), in genuine forested sites (Group I), there is less spatial variation in moisture conditions and, consequently, probably also in nutrient concentrations, which are a primary factor affecting the conditions of tree regeneration on peatlands (seed establishment and survivability) (Kaunisto and Päivänen 1985, Ohlson and Zackrisson 1992), as well as stand growth and productivity (Hökkä and Ojansuu 2004). For example, the reversed J-shaped distributions in pristine peatlands are probably due to the patchy spatial stand structure induced by the inherent site properties, not the stand gap dynamics typical to old-growth stands on mineral soil sites (Rouvinen et al. 2002, Kneeshaw and Gauthier 2003). The characteristics of the site type groups have also proved to have long-lasting effects on stand development following water-level drawdown (Study **III**).

After drainage, the lawns and hollows covered by a layer of *Sphagnum* provide excellent moist microhabitats for seed germination (Sarasto and Seppälä 1964, Ohlson and Zackrisson 1992, Frelechoux et al. 2000). Furthermore, the decrease in the growth of peat thickness, as well as the gaps in the initial canopy provide opportunities for new seedlings to be established on a site. This may explain the rapid increase in the number of small trees on Group II sites, the corresponding increase in positive skewness of the DBH distribution of the pine stands (Hökkä and Laine 1988), and further, the increase in the range of the tree DBH (Hotanen et al. 2006).

*In drained spruce peatlands* the non-significant differences in the stand structure between site types may be due to too little data. Furthermore, the fertility gradient is narrower than in pine peatlands, where more significant differences exist (see Hotanen et al. 2006). However, the species-related ecology of spruce may also be logical explanation: Norway spruce is a shade tolerant tree and thus the performance of spruce seedlings is not as dependent on the amount of available light as pine or birch (Assmann 1970). On the other hand, it is worth noting that in the models (Study **II** and **III,** Table 2), much of the variation in stand structure due to the primary factors (site properties i.e. site type, peat thickness, ditch spacing) and geographic location were, however, implicitly accounted for by the explanatory variables. Thus, the site effects are not significant, particularly if the inter-site differences in stand characteristics are small and the within-site ones are large. For example, in the model for spruce, 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. On the other hand, it has also been observed that in northern mature Norway spruce stands, tree size determines the growth and survival of individual trees more than stand density or spatial variation (Doležal et al. 2006). Thus, the possible microsite variations on the peat surface within sites do not necessarily reflect differences in the stand structure between site type groups in this material.

*In drained pine peatlands*, the differences in the site's productivity reflected in the stand structural dynamics (Study **III**). Most of the Group I sites were of dwarf shrub type (DsT I), which is poorer in soil nutrients than the poorest Group II site. The better nutrient status on the Group II sites affects stand structure in three ways: Firstly, the development of the dominant canopy layer may be quicker. Thus, the stands may reach the bell-shaped DBH distribution phase during the same time period after drainage as those on Group I sites, despite the initially greater, and even at first further pronounced, heterogeneity. Secondly, the abundance of birch, which requires more nutrients than pine (Finér 1989), may be greater in the dominant canopy layer. Thirdly, an understorey of birch and spruce may be established particularly on Group II sites. The proportion of the spruce mixture in the dominant storey remained small in every stand (Study **III**), which is probably a result of the fact that except for the most fertile sites, the pine peatlands are too poor for spruce to compete equally for the site's growing resources with pine (Paavilainen and Päivänen 1995).

The effect of climate on the stand succession was as expected: the stand structural development became slower moving from southern Finland to northern Finland both on drained and pristine peatlands (Studies **I, IV**). This is related to the strong relationship between the tree growth and temperature sum shown to be an important factor on tree growth on drained peatland sites (Heikurainen and Seppälä 1973, Hökkä et al. 1997). Gustavsen and Päivänen (1986) found a trend between stand growth and temperature sum even in pristine peatlands. Climate conditions also affect the annual seed production of trees, and particularly in the harsh northern conditions, they affect stand regeneration as well (Zackrisson et al. 1995). Most of the peaks found in the age distribution of the northern pristine pine stands can be explained by the variation in the climate periods favourable for seed production (Study **I**). The observed significance of the geographical location on the stand structure and development (Study **I**) might indicate that climate would be at least as strong a factor affecting the stand dynamics as the high water table level itself. This would, however, need more research.

### *5.4.2. Secondary factors*

The temporal changes observed in stand structures both on pristine and drained sites may be largely due to the changes (deterioration) in tree regeneration conditions in the site. This would provide external secondary disturbances directly affecting the trees' mortality (e.g. flooding or rise of the peat thickness in pristine peatlands) or indirectly (e.g. drainage) affecting it by increasing the competition for vegetation through changes in the site's hydrology, tree growth and plant species composition (Kaunisto and Päivänen 1985, Korpela 1999). In this study, the role of the secondary disturbances in the stand succession was not considered, because sites suffering from floodings or large wind damages were not included in the material.

On mineral soil sites, the inter-tree and inter-specific competition for light (size-asymmetric competition) is shown to be an important factor modifying the stand structure, particularly after the tree canopy closure (Ford 1975, Bauer et al. 2004, Doležal et al. 2006). Also in peatlands, the bell-shaped, slightly flat DBH distributions and the subsequent speeding up of tree-size differentiation indicate the eventual expression of dominance by a few large individuals. This may indicate the existence of asymmetric competition affecting the stand structure (Ford 1975, Cannell et al. 1984, Wyszomirski et al. 1999, Binkley et al. 2002, Doležal et al. 2006). However, in harsh northern conditions or very poor sites, also in drained peatlands, tree growth and the closure of tree canopies are generally a slow process (see Hotanen et al. 2006). Thus, the strengthening of competition is also slow and the heterogeneous stand structure with reverse J-shaped DBH distribution may prevail within the stand. This may be the reason for the better correlation between pine age and size in the north than in more favourable southern conditions in pristine peatlands. Because of more available light, regeneration is also active in old stands. The lack of inter-tree competition can also indirectly obscure the effects of other factors controlling the stand dynamics. It seems that in the southern conditions, the site type determines the pattern of stand development, while in the north, several kinds of patterns are likely to be developed irrespective of the site type (Study **I**).

In earlier studies it has also been shown that in pine stands on drained sites, the probability for tree mortality increases (Jutras et al. 2003) and individual tree growth decreases (Hökkä et al. 1997) as stand stocking (basal area) increases. The decreased growth has been explained to be related to intensifying inter-tree competition (Penner et al. 1995, Hökkä et al. 1997). Also in the drained sites of this study, the competition seemed to cause density-dependent mortality, which was realised as increasing mortality of small trees and as a decreasing trend in the proportion of deciduous trees as stand stocking increased. Nevertheless, the gradual increase of the mean size of dying trees after 40 years from drainage may partly be due to the age-related mortality of the largest trees, as a matter of fact they were old already at the time of drainage. In spite of this, most of the largest trees maintained their initially more competitive positions until the end of the monitoring period. The results are consistent with those of Ruha et al. (1997), who observed that in naturally regenerated Scots pine sapling stands on mineral soil sites, the height positions are established during the first 5-10 years of stand development and are virtually invariant after reaching their height of 1.5-2 m.

Despite the rapid post-drainage increase in the stand stocking and changes in the dominant tree storey, particularly on pine dominated Group II sites, the persistently heterogeneous structure of the understorey was somewhat surprising, especially as the understorey was not only formed by shade tolerant spruce but also by pubescent birch. Pubescent birch demands more light than spruce, even though it needs less light than silver birch or Scots pine (Kujala 1946). Hotanen et al. (2006) also reported a post-drainage increase in the abundance of undergrowth trees particularly on mesotrophic pine peatlands, of which most of them are represented by the Group II type sites. Obviously, the competition from the dominant trees was too weak to prevent regeneration, even under mature stands, but strong enough to keep the understorey suppressed (see also Hånell 1984, Laiho et al. 1997). In later phases of development most of the new seedlings on these sites were spruce (Study **III**). This contradicts with the results of Hotanen et al. (2006), who reported a post-drainage decrease in the proportion of the undergrowth pubescent birch occurring only on the spruce peatlands, but however, is consistent with the findings that the abundance of undergrowth spruce increases along post-drainage succession both in spruce and pine peatlands (Lukkala 1946, Saarinen 1989, Hotanen et al. 2006). The abundance of spruce, even in the late successional stages, is consistent with the assumption of increasing inter-tree competition for light as stands mature. In principle, the initiation of advanced understorey is also in accordance with the theories of natural stand succession developed for upland forests (e.g. Oliver and Larson 1990, cf. Franklin et al. 2002). The post-drainage increase in the occupancy of spruce is probably related to the compaction and accelerated rate of decomposition of the surface peat, mostly occurring in the shallow-peated and nitrogen rich minerotrophic pine peatlands (Minkkinen and Laine 1998). The mineralisation of elements may enhance the growing conditions changing more favourable for spruce.

Even though the intensified light competition seems to be an important factor modifying the stand structure in stocked peatlands, it does not explain all the features appearing in the DBH distributions along stand development. For example, stable size ratios or increase in size inequality with increasing density may indicate low inter-tree competition, but also the existence of two-sided (size-symmetric) competition within stand, mainly competition for belowground resources such as nutrients (Weiner and Thomas 1986, Brand and Magnussen 1988, Schwinning and Weiner 1998, Wichmann 2001, Doležal et al. 2006). Hökkä et al. (1996) showed that the inter-tree competition for nutrients may be a significant factor in Scots pine stands on drained peatlands. On mineral soil sites, size-symmetric competition is also suggested to significantly affect the performance of Norway spruce stands in harsh northern conditions as stands mature, and the competition is further suggested to be promoted by the decreasing nutrient availability combined with the accumulation of slowly decomposing needle litter and the shallow root system of spruce (Doležal et al. 2006).

*In pristine peatlands*, low inter-tree competition may be the reason for the better correlation between tree age and size in the north than in more favourable southern conditions. Because of more available light, regeneration is also active in old stands and variation in ecohydrological conditions and regeneration history of stands may result in large variation in the stand developmental pathways even within the same site type group and climate area. Another explanation for decreased regeneration in southern Finland may be the detrimental impact of trees on *Sphagnum* performance on a site (Ohlson et al. 2001): the increase in pine size (and stand density) will reduce *Sphagnum* growth and coverage, and consequently decrease the tree regeneration conditions. In contrast, *on drained peatlands*, the coverage of *Sphagnum* gradually decreases after drainage due to the competition of trees for light, more competitive forest species and accumulation of a slowly decomposing layer of woody debris (Korpela 1999, Laiho et al. 2003). These phenomena decrease further the favourable microsites for regeneration. Thus, the effect of the tree stand on the other plant species reflects as feedback on its own development. Intensified competition of trees after canopy closure reflects also a rapid decrease in the nutrient uptake and biomasses of mire shrubs and graminoids at least in the drained pine peatlands (Laiho et al. 2003, 2006).

### 5.5. Effect of stand management on stand structure

The stands monitored on pristine peatlands had not struck any discernible management operations. However, on drained sites it was possible to analyse the effect of management. Since no completely unthinned stands were included in the material of spruce stands, the effect of thinning could be analysed only by the model approach. For pine stands, the direct comparisons of the structural characteristics between unthinned and thinned stands were feasible.

In *drained spruce peatlands*, based on the non-significance of the inter-thinning period variance component and the thinning dummy variable, it can be concluded, -contrary to the hypotheses of this study - that thinnings had no effect on the drainage-induced trends in the changes of DBH distributions of Norway spruce (Study **II**). Obviously, those trees, which otherwise would have died due to self-thinning, had been removed in the thinnings. For birch, the significant impact of thinning on the shape of the DBH distribution indicated that the management had speeded up the stand development for birch, when more birches than the natural removal had been removed in thinnings. This is also consistent with the common thinning regime, which favours conifers in thinnings on peatland sites (e.g. Uuttera et al. 1997). The temporal decline in the proportion of birch has also been observed in unmanaged pristine spruce peatlands as the stands mature (Norokorpi et al. 1997).

Also in *drained pine peatlands*, most of the early light thinnings had only minor influence on stand structure (Study **III**). However, later, the DBH distributions in thinned pine stands reached bell-shaped distribution about 20 years earlier and were less flat than in unthinned stands. On upland sites, thinnings from below have also been reported to decrease the heterogeneity and the multimodality of pine stands (Maltamo et al. 2000). This development may be due to the larger removal of the suppressed trees in the thinnings compared to the natural self-thinning and due to the higher growth rate of the retained trees as a result of decreased inter-tree competition (see e.g. Pukkala et al. 1998). The results are in accordance with earlier studies carried out on peatlands, where thinnings in Scots pine stands have resulted in an immediate decrease in the stand structural unevenness (Kojola et al. 2004), and even later speeding up this structural development (Sarkkola et al. 2004).

Thinnings seemed to have only minor effect on the stand stocking of the pine stand, which is due to the low thinning intensities. This may also be evident result if only the most stocked stands have been thinned. On mineral soil sites, the successive thinnings decrease the total stand stocking permanently both in Scots pine (Nyyssönen 1954, Maltamo et al. 2000, Mäkinen et al. 2006) and Norway spruce dominated stands (Vuokila 1956, Mäkinen et al. 2006). On the other hand, thinnings have been proven to increase the production of saw timber trees, which is due to the increase in the growth of the co-dominant and medium-sized trees (Nyyssönen 1954, Pukkala et al. 1998, Peltola et al. 2002, Mäkinen and Isomäki 2004a,b, Mäkinen et al. 2006), which benefit from the improved light conditions. However, on drained peatland sites, also the growth of the dominant trees seem to react positively on thinnings (see Penttilä et al. 2000, Sarkkola 2004). This may be a consequence of the decreased size-symmetric competition within stand (Penttilä et al. 2000). On the other hand, Kojola et al. (2004) reported only a small increasing effect of thinnings on the saw timber production in pine dominated stands. This was suggested to be due to the structural heterogeneity of the trees retained within stand.

The average proportions of saw timber trees out of the total stand volumes on drained peatlands were relatively high in this study. However, the wood quality was not taken into consideration, and thus, the real proportion of the trees fulfilling saw wood qualifications is smaller. Rikala (2003) proved – partly based on the same stands used in this study- that in spruce stands, most of the harvested saw logs fulfilled the criteria for high quality saw wood, but in pine stands, particularly dry branches and form defects decreased the quality of the saw logs.

In this study, the significantly larger proportion and amount of trees fulfilling saw timber dimensions in thinned than in unthinned stands indicate that by carrying out even light repeated thinnings, it may be possible to increase the timber production significantly in drained peatlands. According to preliminary econometric calculations the most profitable management system in pine stands on drained peatlands seems to be based on intermediate thinnings, which will be carried out as relatively strong and repeated only 1-2 times during the rotation (Penttilä et al. 2003). In spruce stands, the site's productivity would, however, enable several thinnings during the rotation, and the similar principles employed in operational forestry on mineral soil sites can be used in the selection of the removable trees in the thinnings (Repola et al. 2006). However, more research is needed in order to find out “the optimal” thinning regimes for different sites and management regimes on peatlands.

Thinnings did not seem to affect the stem number and structure of the birch and spruce understorey in many pine stands. This is probably due to the large variation in the understorey abundance in unthinned stands, which may have masked thinning effects. After cutting, birch easily regenerates via stump sprouts (Kauppi et al. 1988) under improved light conditions. Thus, thinnings may have even increased the stem number of understorey birch in these sites.

### 5.6. Models for predicting the DBH distributions in drained peatlands

In many earlier studies, models predicting diameter distributions have applied explanatory variables that are generally available in forest inventory data such as median diameter of stand basal area ($D_{gM}$) and stand basal area (G, $m^2$ $ha^{-1}$) (e.g. Kilkki and Päivinen 1986, Kilkki et al. 1989, Hökkä et al. 1991, Maltamo 1997). This type of distribution model applies best to even-sized, advanced and mature stands, while in stands with more structural variation, they may fail in predicting the stand structure (Siipilehto 1999). On the other hand, the modelling of basal area distributions instead of empirical DBH distributions, enable more accurate predictions for the most valuable parts of the stands such as saw timber trees. For example, the models presented in this study predicted stand volume and value weaker than the total stand stem number (Table 3). This would indicate biased predictions in the stems and basal area of the largest trees. This bias seemed to be larger the lower the stand stem number (the largest bias i.e. the underestimation in the volume and value of the admixtural birch in spruce stands), which results from the big random variation in the DBH distributions due to the low stem frequencies within DBH classes. The bias is further emphasized when the distributions are smoothed. More recent studies have shown that the performance of the models may be improved by applying additional stand information such as stem number or additional diameter characteristics (Siipilehto 1999, Kangas and Maltamo 2000, Maltamo et al. 2000).

The superior performance of $D_M$ / $D_{Max}$ in all models (Study **II** and **III**) as compared with other single diameter variable simply indicates that including two diameter variables in the model better describe the form of the stand structure. For pine stands, the importance of large trees is further emphasized by the significance of the proportion of large trees ($d_{1.3} > 19$ cm) of the total stand volume (VTD) in the model. Variation in the size of sample plots can be expected to affect the stand $D_{Max}$ in a way that would cause bias in models when $D_{Max}$ is included as a single explanatory variable. Although some variation in the sample plot size was present in the material, no impact of the sample plot size on the model residuals was found. In the present studies, the best predictions of stand structure were obtained by applying models that included stem number and two diameters as the explanatory variables describing the DBH distribution.

Although the models presented here were primarily meant for analysing the structural development of peatland stands following drainage, they have also resulted in reliable and reasonably unbiased predictions of DBH distribution in a large variety of stand structures. However, their possible practical applicability requires further testing and inspection. Because most of the explanatory variables used in the models are difficult to collect in forest surveys, it would be necessary to develop the models more simple in order to utilize them in the operational applications. The lack of heavily thinned stands in this material may restrict the use of the models in intensively managed pine stands. As regards understorey models, unquantifiable variation remains, because the data available did not completely cover different growing conditions of understorey trees.

# 6. CONCLUDING REMARKS

The results of this study showed that peatland stands are more dynamic than had been considered earlier. It can be concluded that:

> Unmanaged stands on pristine peatlands are not in a balanced, self-perpetuating state, but rather there exist various successional pathways. Distinct developmental stages were not possible to detect in the stands, but rather there is a continuum. The speed and pathway of stand succession are controlled by several abiotic and biotic factors. Climate and ecohydrology are crucial factors determining stand structure and its dynamics. Because of the environmental conditions particular to pristine peatlands (moisture of the substrate and peat formation), some structural features of "old-growth" stands may develop rather quickly after stand establishment, e.g. descending DBH distributions, high diversity in tree size and age.
>
> After drainage, succession speeds up and its mode changes drastically. The peatland ecosystem starts transforming to a forest ecosystem both with respect to ground vegetation composition and to stand dynamics. Two or three distinct developmental stages can be recognised. During the post-drainage stand succession, irrespective of the intensity of management, the irregular stand structure remains only during the first decades when growing space is available for new trees. Drained peatland stand with a highly uneven-sized structure would be associated with low site fertility or harsh climatic conditions or in more productive sites, considerably low stand densities, which favour the survival of smaller trees.
>
> In recently drained sites, small-scale variation of microsites in the level of the soil surface and the dynamics of vegetation create the prerequisites for seedling establishment and development. The pre-drainage ecohydrological conditions significantly affect the development of stand structure of Scots pine stands during the first post-drainage tree generation, particularly in areas where there are less climatic constraints on tree growth. From both the ecological and forestry point of view, it is recommended that ecohydrological conditions, expressed as site type (genuine forested sites and sparsely forested composite type sites), are taken into consideration in classifying the drained pine peatland sites, particularly in southern and central Finland.
>
> The initial spatial variation in microsite conditions in Scots pine stands on sparsely forested composite sites effects stand development by firstly resulting in a flush of new seedlings and growth of saplings, which increases the structural inequality. In the later phase of stand succession, an undergrowth of spruce and pubescent birch with varying density develops. In genuine forested sites, the effect of drainage largely appears as an increase in the growth and yield of the stand, which is mainly established before drainage.

In well-stocked stands, inherent processes such as inter-tree competition plays an important role in modifying the stand structure, through affecting tree growth, increasing tree mortality, and decreasing regeneration. In such stands, the inter-tree competition is probably mainly size-asymmetric, and otherwise it is size-symmetric or it do not occur at all. In sparse stands, factors other than inter-tree competition play a more important role and mortality is more random. The mortality dynamics of trees, including the amount and size of dead trees and their significance on biodiversity, remains unexplored.

The dynamics of density-dependent tree mortality in drained peatland stands differs from that on mineral soil sites, at least during the first post-drainage tree generation. The dynamics of self-thinning should be studied in more detail. Self-thinning models are widely used in forest planning as a part of forest simulators controlling the stand maximum density. In Finland, these models are based on more-or-less evenly structured stands growing on mineral soils. Applying these models to peatland stands may result in unrealistic estimates of living stand volume.

The early stage of stand development towards high stem numbers and size-symmetric competition provides an opportunity to direct the increased growth potential to the desired crop component in pre- and first commercial thinnings. Later on, the impact of intermediate cuttings depends more on the mode of the competition. In the case of size-asymmetric competition, after canopy closure, thinnings will largely not affect the growth of the dominant trees; but the manager may benefit by harvesting those trees that would otherwise have died. In the case of size-symmetric competition (or both modes of the competition occurring simultaneously), it is likely that thinnings will increase the growth of the retained trees, including the dominant ones. Thus, by removing the less valuable and suppressed trees, it may be possible to improve the wood quality in stands and increase the saw timber production for example.

Abundant undergrowth of small trees may impede wood harvesting in pine stands on sparsely forested composite sites. On the other hand, it may be possible to utilise the secondary spruce undergrowth to regenerate spruce peatlands, at least, on more fertile pine peatlands (i.e. drained sites classified as MT II sites). This aspect requires more study, however.

On drained sites, if large-scale disturbances such as regeneration cuttings or wind fall do not occur, the structure of the stand will probably come to resemble that of “old-growth” forests on mineral soil sites in the long run. This development is fastest in spruce peatlands. On stocked sites, water uptake by the stand is usually capable to sustain adequate site drainage, even if the drainage ditch network has deteriorated (Laine 1984). In sparse low-productive stands, as is the case with most pine peatlands, deterioration of the ditches leads to a decrease in tree growth, and the ecosystem may gradually change back to a functional peatland ecosystem (Heikurainen 1980). A similar effect can be generated through active restoration, promoted nowadays to increase landscape-level biodiversity (Vasander et al. 2003). If drainage of the site is maintained, it is probable that, after tree stand regeneration, the stand structure and dynamics will deviate significantly from those of the first tree generation. Pre-drainage conditions no longer have significant impact on the site properties, and very old trees do not exist in the stand any more. More research on the stand structure and dynamics is needed in order to predict the future yields of these stands correctly, for example. There may also be a need for further development of the present site classification systems for drained peatlands.

Water table level drawdown in boreal pristine peatlands may occur also as a result of climate change. The annual temperature sum and the length of growing seasons would increase (Gorham 1991). This can be expected to result in the initiation of forest succession similar to man-made drainage (Laiho et al. 2003). Based on this study, it can be concluded that climate change would result in a decrease in stand structural diversity on pristine peatlands. It is hard to say, however, what this would mean for the biodiversity on an ecosystem scale. The deterioration of a functional peatland ecosystem is always a threat to the diversity of boreal mire plant communities. But when considered as a forest ecosystem, a drained peatland may also develop a "positive" biodiversity effects (see Hotanen et al. 2006). From the forestry point of view, if tree growth and yield increase (e.g. Talkkari 1998), then climate change may not necessarily be considered a threat as such.

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