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The Structure of Suserup Skov, a Near-Natural Temperate Deciduous Forest in Denmark

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Suserup Skov (19.2 ha) is a near-natural temperate deciduous forest dominated by *Fagus sylvatica L.*, *Fraxinus excelsior L.*, *Quercus robur L.* and *Ulmus glabra Huds.*. The aim of this study was to present and analyze basic data, producing a scientific basis for further analysis of the site. A total inventory including all trees ≥ 3 cm dbh showed an average density of 959 stems/ha, an average basal area of 41.1 m^2/ha and an average standing volume of 722 m^3/ha. Based on these data a stem-position map including a 50 m x 50 m grid was made. The forest was divided into three parts. Part A, dominated by *Fagus*, characterized by minimal human impact during the last 200 years. Part B, grazed until 1792, now dominated by *Quercus* and *Fagus*. Part C, a strip along a lake side, in wet places dominated by *Alnus glutinosa (L.) Gaertner*. The diameter-distributions of part A, B and C all resemble negative exponential functions for trees 3-60 cm dbh, typical for natural temperate forests characterized by relatively frequent but small disturbances. A major regeneration event after the forest was fenced in 1807 is still reflected in the diameter-distributions. *Fagus sylvatica* is profiled as a shade-tolerant 'climax' species, *Ulmus glabra* as a shade-tolerant understorey species, *Fraxinus excelsior* as a gap-specialist and *Quercus robur* as a light-demanding species slowly being ousted. *Tilia platyphyllos Scop.* and *Acer pseudoplatanus L.* have successfully established expanding colonies in Suserup Skov. Several successional processes occur within this relatively mature system, confirming the modern view of vegetation change, and emphasizing disturbances and continuous change as the norm.

Keywords: basal area, climax forest, diameter distribution, disturbance, *Fagus sylvatica, Fraxinus excelsior, Quercus robur,* standing volume, succession, *Ulmus glabra.*

Symbols used: (BA) basal area, (dbh) diameter at breast height, (SV) standing volume, (std) standard deviation.

Introduction

Sustainable forest management is a major challenge facing modern forestry. Research should support the new management approaches e.g. management mimicking natural forest dynamics (Koop 1989; Kimmins 1991; Brown & Whitmore 1992; Boot et al. 1993; Broekmeyer & Vos 1993; Schlaepfer et al.

1993; Attiwill 1994; Bradshaw et al. 1994). The structure and dynamics of natural forest ecosystems are key issues in this context.

Time represents a special problem when studying forest dynamics, because of the slow development of forest ecosystems. Scientists have tried to overcome the problem of time in different ways, e.g. by small-scale pollen analyses (Iversen 1969; Bradshaw 1988; Andersen 1989), archive studies (Peterken & Tubbs 1965; Peterken 1976; Whitney 1987), modelling (Botkin 1981; Shugart et al. 1981; Prentice 1986), tree ring analysis (Peterken & Tubbs 1965; Canham 1990), photo interpretation and 'space for time' substitutions (Mueller-Dombois & Ellenberg 1974; Peterken 1993). Such attempts to eliminate the time problem are often the only realistic approaches. In fact most of our present knowledge about forest dynamics is based on research using indirect measures of time. Such studies will, however, never be as reliable as genuine long-term studies of permanent plots (e.g. Stephens & Waggoner 1980; Scheiner & Teeri 1981; Peterken & Jones 1987). Several authors have recently stressed the need for more long-term studies in permanent plots (e.g. Koop 1989; Glenn-Lewin & van der Maarel 1992; Peterken 1993; Peterken 1996).

The aim of our work was to produce and analyze a set of basic data on the vegetation structures of Suserup Skov, by this forming a basis for future research, including long-term permanent plot studies on this site.

Materials and methods

The site

Suserup Skov (19.2 ha, 55°22'N, 11°34'E) is a near-natural temperate deciduous forest at the northern side of the lake, Tystrup Sø in eastern Denmark. The climate is cool-temperate, sub-oceanic with an annual mean temperature of 8.1°C and an annual mean precipitation of 635 mm with maximum occurring in July to December.

To the north, Suserup Skov borders on recently abandoned farmland, slowly growing into forest, wet willow scrub and the gardens of a farm. To the west the forest borders on pasture land with fairly dense tree cover of variable height (10-20 m). To the east, the forest borders on a field and abandoned farmland with 10-20 m tall trees. Within a few decades most of Suserup Skov will be surrounded by forest.

The physiographic setting of Suserup Skov is an undulating elevated plateau to the North and some 10-15% downward slopes towards a lower terrace along the lake side. Most soils in the higher elevated parts of the forest have developed from glacial till, consisting of a calcareous mixture of clay, sand, and silt, with boulders. The low terrace is pedologically different consisting of lacustrine soils, developed through a slow land reclamation process along the lake side caused by accumulation of organic material. Pockets of clay-rich lake sediments and glacio-lacustrine clay, sand and silt have also been observed (Vejre & Emborg, 1996).

The growth conditions are generally favorable as indicated by a typical maximum tree height of about 40 meters. The dominant tree species are *Fagus sylvatica L.* (beech), *Fraxinus excelsior L.* (ash) , *Quercus robur L.* (oak) and *Ulmus glabra Huds.* (elm). The herb flora is generally dominated by perennial species like *Anemone spp.*, *Mercurialis perennis L.* and *Corydalis bulbosa (L.)*

DC. Along the side of the lake there are several springs and hollows, forming small bogs and swampy patches dominated by *Alnus glutinosa (L.) Gaertner* (alder) and ash. A total of 41 woody species have been recorded in Suserup Skov (Christensen et al. 1993).

The forest was administratively protected in 1854, and protected by law in 1926 (Bang 1926). Vaupell (1863) described Suserup Skov as a wild-looking forest in which it was possible to study the result of the free interaction among tree species, especially beech and oak (Fritzbøger & Emborg, 1996). However, human intervention has occurred in the forest during the past century, e.g. compulsory selective felling of old beech trees during The Second World War and some cutting of elm, as suggested in the preservation claim (Bang 1926), especially during the 1930s. Since 1960 the forest has been kept as a strict non-intervention forest reserve. Human impact has varied over time for different parts of the forest, and clearly the ecological conditions along the side of the lake are quite different from those of the rest of the forest. For this reason the forest was stratified into three parts.

Methods

All field work was carried out during 1992. The forest inventory was made using a 50m x 50m grid. Unfortunately it was not possible to introduce a high resolution grid (e.g. 10m x 10m) within the economic limits of the project. The positions and diameters of all trees ≥ 29 cm dbh, dead or alive, upright or fallen, were recorded by sighting and measuring from the grid. For each 50m x 50m square of the grid the diameter of all stems >3.0 cm dbh (n=18451) was recorded to the nearest cm noted in 2-cm diameter classes. Diameters ≥29 cm dbh were measured with measuring tape and trees <29 cm dbh were measured with a steel caliper. Multiple stems arising from the same root system, were recorded as separate individuals for exact calculation of basal area (BA). From the number of stems in each diameter class the BA was computed for each species. Tree heights were measured with a clinometer to the nearest 0.2 m on a random sample of trees (n=942), representing the most common species in the forest. Tree ring cores were taken at breast height from a total number of 60 trees of oak, ash and alder for age determination. Tree rings were recorded to nearest 0.1 mm using a microscope and a moveable stage connected to a microcomputer (ADDO Årsringsmätmaskin, Sweden).

Results and discussion

Stem-position map

The differences between parts A, B, and C are exemplified in Figs. 1 and 2, showing the explicit distribution patterns of oak, alder and *Crataègus spp.*. The forest was stratified into three parts (Fig. 1): Part A, characterized by minimal human intervention at least during the last 200 years. Part B, which has been affected by heavy grazing until 1792, followed by human seeding of oak around 1820. Part C, forming a strip along the lake side, is characterized by wet soils, which is clearly reflected in the tree species and floral composition. Several criteria were used to define the boundaries between the three parts. Ideally, the boundaries should reflect history, geology and hydrology, be easily

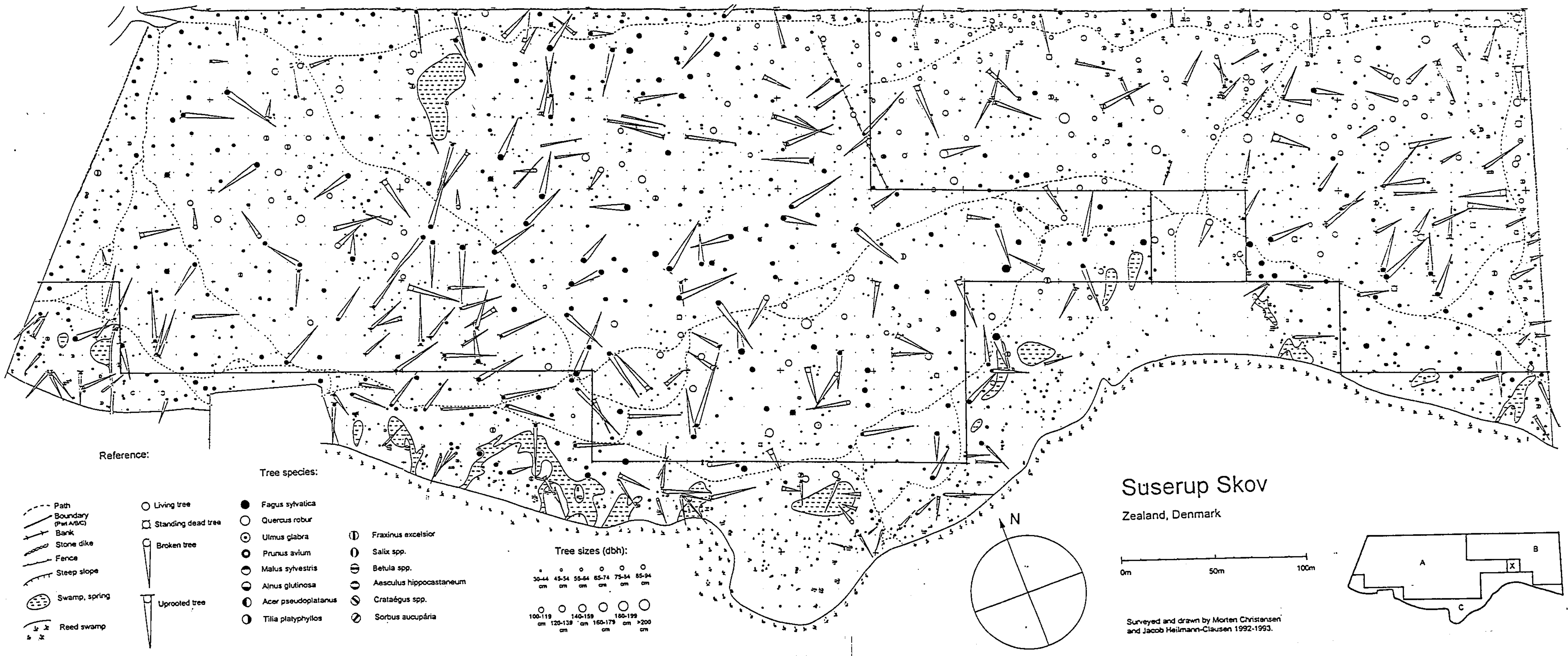
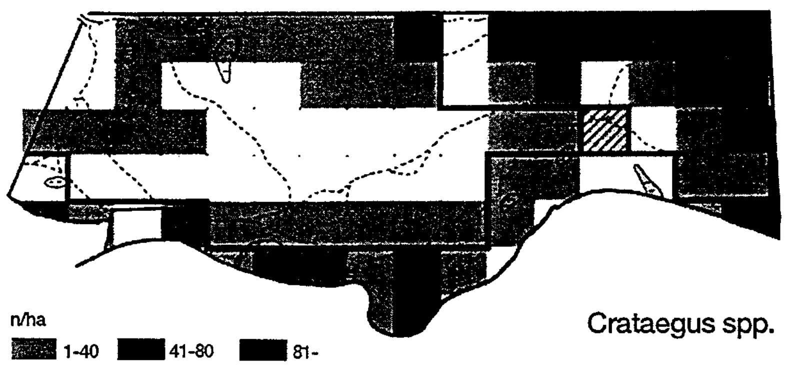


Fig. 1. *Stem position map of Suserup Skov (19.24 ha). The cornerpoints of the grid (+) and the borderlines between parts A, B and C are marked. Part X is the site of a burned house.*

Fig. 1. Continued.



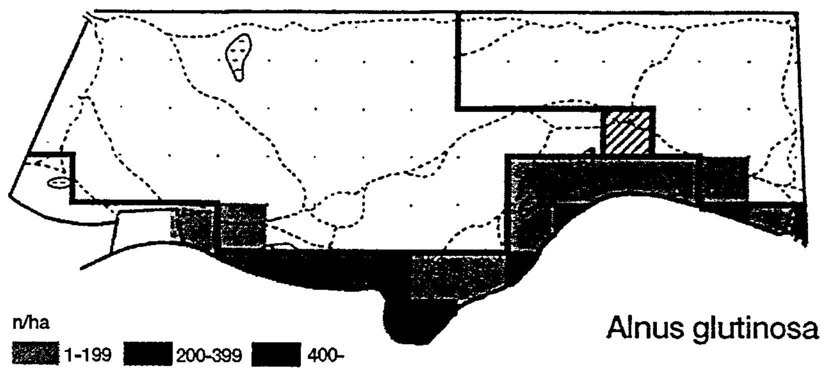


Fig. 2. *The spatial distribution of Crataegus spp. and Alnus glutinosa in Suserup Skov. Numbers are given in stems/ha. The site of a burned house is hatched.*

Fig. 2. Continued.

detectable in the field and follow the grid. A north-south-oriented bank was chosen as a good landmark to separate part A from part B. Part B was delimited from part C as closely as possible to the borders of the area marked 'oak' on the management chart of Sarauw (1834). Part C was defined as the wet areas along the lake side, including swamps and former meadows grazed until the beginning of this century. With our research plans in mind, we delimited part A to be as 'pure' as possible, by excluding all former meadows and swampy patches along the lake side from part A. As a consequence part C became rather heterogeneous, in fact about half the area of part C consists of relatively dry, elevated soils. The forest edges were included in the respective parts. The site of a small house which burned in 1978 (part X, 0,25 ha, Fig. 1), was not included in either part A, B, or C.

General description of parts A, B and C

Part A (10.7 ha) is dominated by beech. Most trees have long and relatively straight boles (Fig. 3), except a number of very old oak trees indicating a former period of a more open forest type. Tree ring counts (n=9) showed that the age of the oak trees ranged from about 250 to 500 years. In the 1834 management plan part A was described as beech forest admixed with oak, ash and elm (Sarauw 1834). Vigorous regeneration in many places, especially of ash and elm, was further mentioned though the forest was still considered as old, with a considerable stock of old trees.

Part B (4.9 ha) is now dominated by oak, of which many have wide crowns and short boles (Fig. 4). There are considerable numbers of *Crataégus spp.*, *Malus sylvestris Miller* and *Corylus avellána L.* pointing to a history of grazing and more open conditions. The forest was fenced in 1807 (Fritzbøger & Emborg, 1996) at which time part B was dominated by oak (Ulrich 1815). The 1815 plan suggested seeding acorn in some small glades. The seeding probably occurred around 1820 according to the 1834 plan (Sarauw 1834). Evidence of this was supported by tree ring dating of two oaks from this area, measured to have an age of 160-162 years 'at breast height'.

Part C (3.7 ha) is now dominated by alder along the side of the lake and by beech in the more elevated parts. On old maps two areas along the side of the lake were indicated as meadows. Grazing continued here until about 1925 (Bang, 1926). Afterwards, alder probably invaded the abandoned meadows by natural seeding from older specimens. Cores were taken from 22 randomly chosen, non-coppiced alder trees at the former meadows. They were on average 66 yr (std=8.4) indicating a relatively even-aged group of trees established shortly after 1925. In places it is still possible to distinguish the borders of the former meadows in the vegetation structure, e.g. old beeches stretching low branches out above the former meadows. Stems from some older, previously coppiced individuals (n=6) were on average 108 yr (std=22.3) indicating that the last coppice of alder in Suserup Skov took place around 1880.

Diameter distributions

Diameter distributions including all trees > 3.0 cm dbh for parts A, B and C were computed. Meyer (1933) described the diameter distributions of selection forest in Switzerland by use of negative exponential functions:

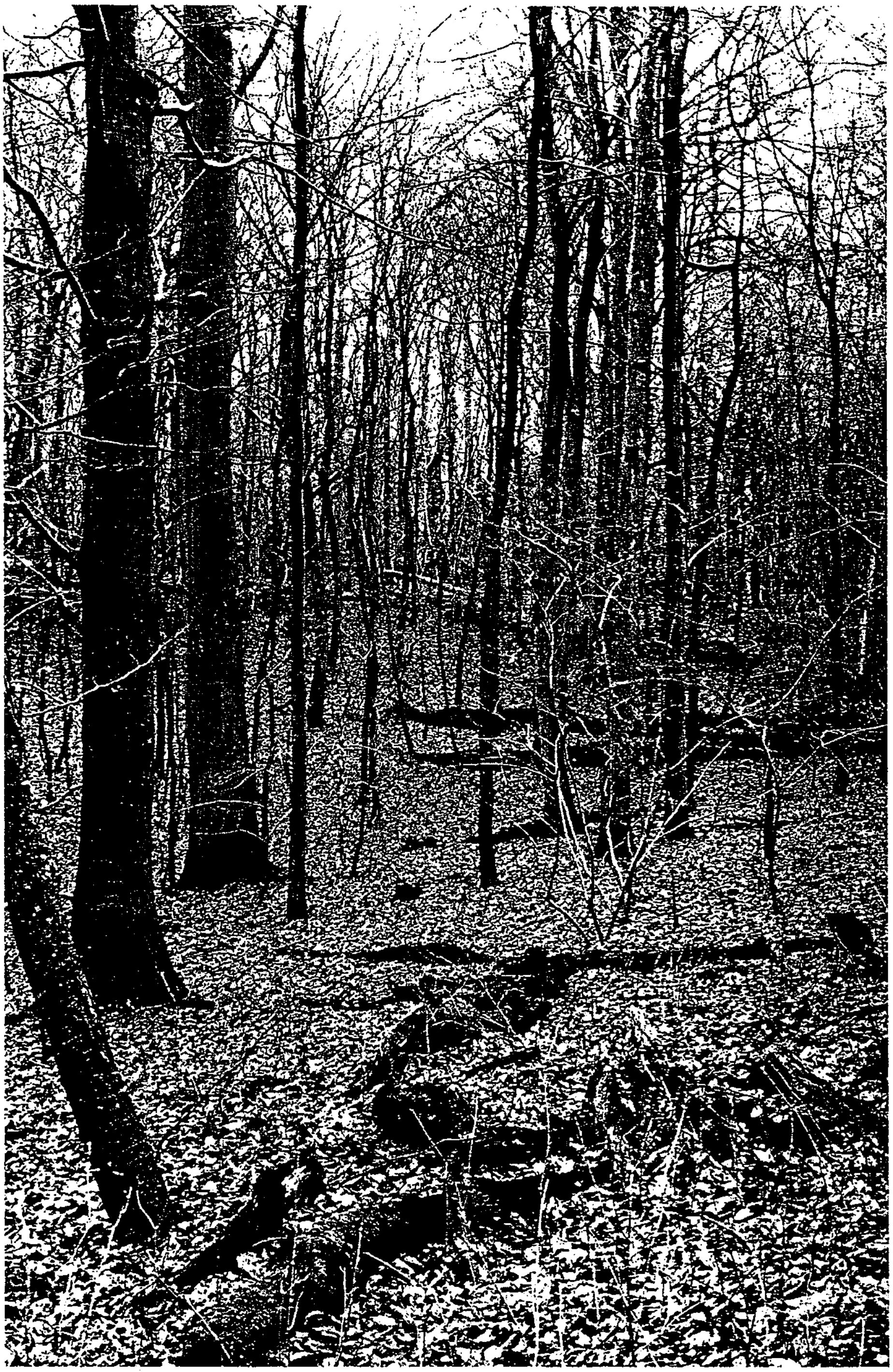


Fig. 3. *Photo from part A. Fagus sylvatica and Fraxinus excelsior dominates the canopy layer, Ulmus glabra is present in the scrub layer. In the foreground regeneration of Fraxinus excelsior. (Photo: Flemming Rune).*

Fig. 4. *Photo from part B. The canopy layer is dominated by Quercus robur, of which many have wide crowns and short boles. The sub-canopy stratum is generally well developed. (Photo: Flemming Rune).*

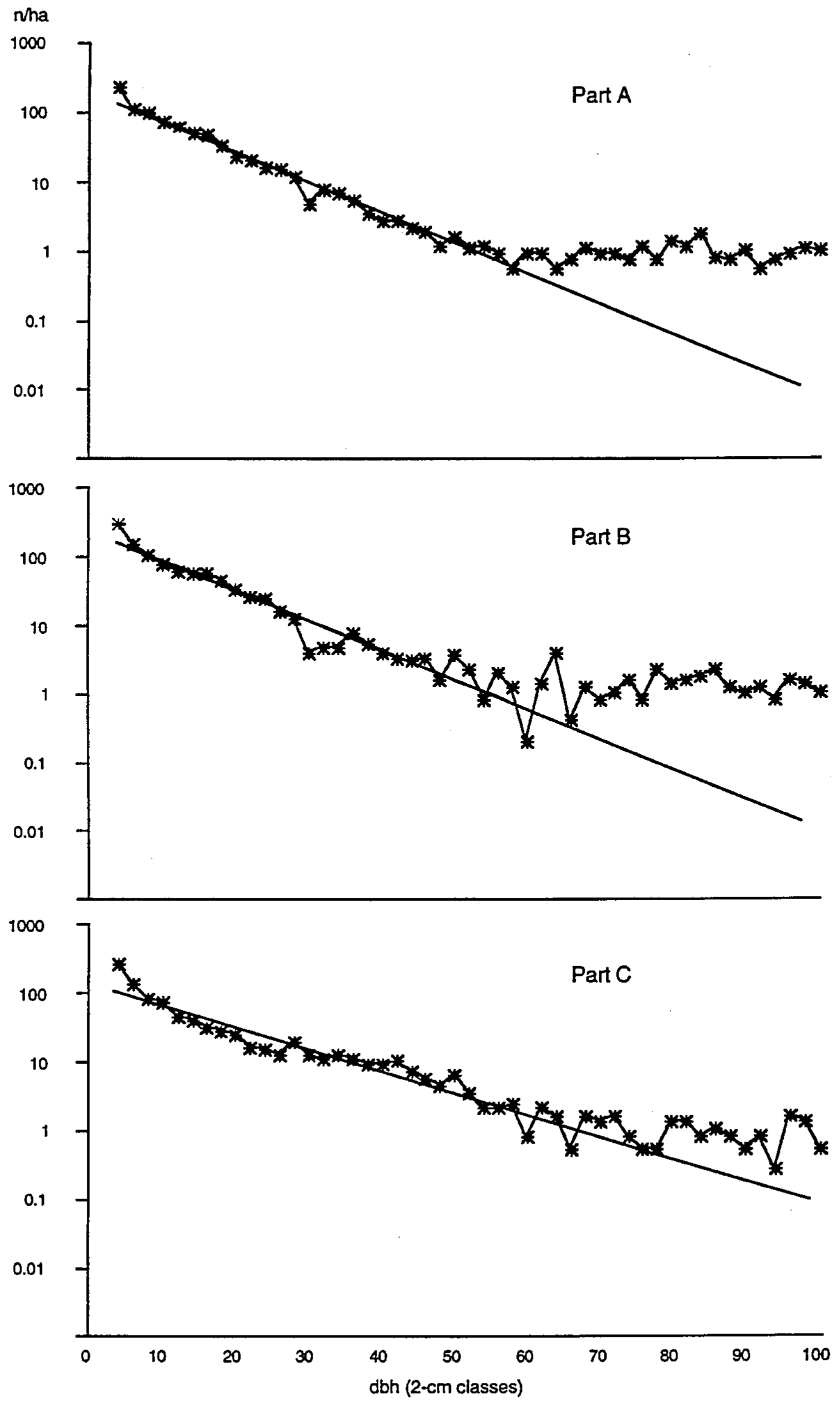


Fig. 5. *Diameter class distributions including all trees from 3-100 cm dbh in parts A (10.7 ha), B (4.9 ha), and C (3.7 ha). The straight lines indicate the best fitted (3-60 cm dbh, least squares method) negative exponential functions.*

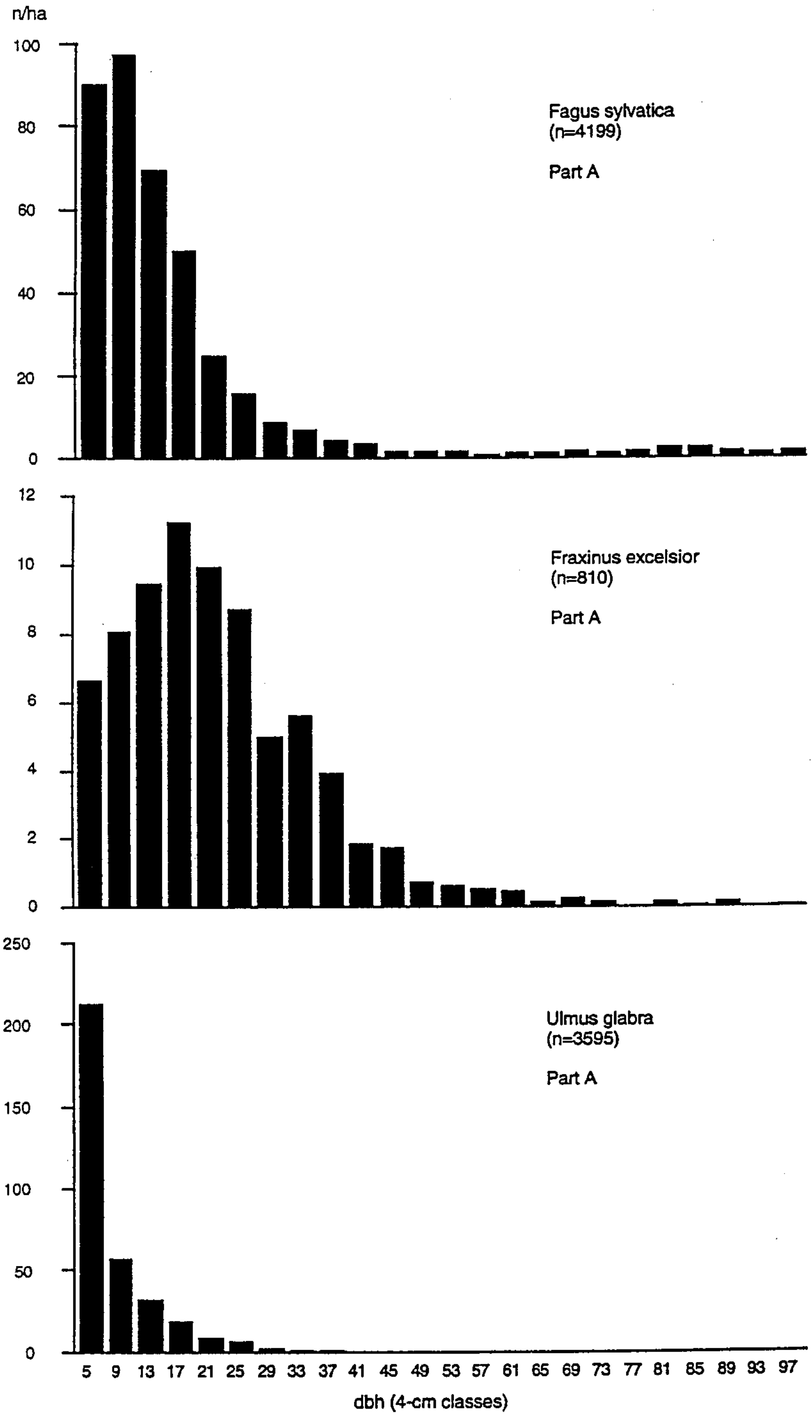


Fig. 6. *The diameter class distributions of Fagus sylvatica, Fraxinus excelsior and Ulmus glabra for part A. Note differing scales on the y-axis.*

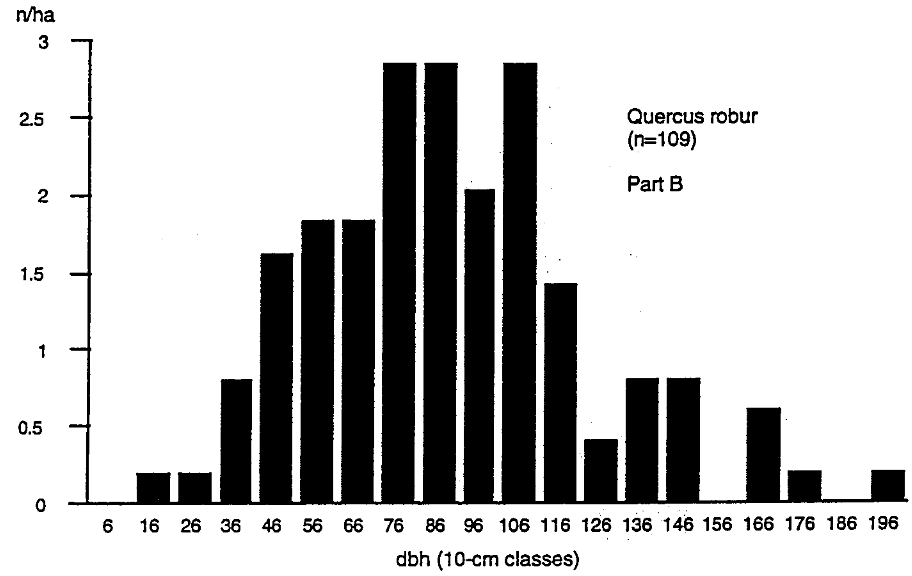


Fig. 7. *The diameter class distributions of Quercus robur for part B.*

$$n = k*e^{(-c*d)}$$

where c and k are positive constants; d = mid-point of diameter class; n = trees/ha in the diameter class. The negative exponential function describes a diameter distribution in dynamic equilibrium, characterized by constantly high recruitment to the smallest diameter class and a constant mortality rate in the larger diameter classes (Harper 1977; Veblen 1992; Silvertown & Doust 1993).

Negative exponential functions have been successfully applied to describe the diameter distribution of 'old growth' or 'climax' forests (Meyer & Stevenson 1943; Schmelz & Lindsey 1965; Leibundgut 1972; Lemée 1989).

The diameter class distributions of parts A, B and C including all species are shown as semi-logarithmic graphs in Fig. 5. The distributions of parts A, B and C basically follow the same overall pattern: The number of trees decrease with increasing diameters for trees <60 cm dbh closely following a straight line plotted on a semi-log scale, the numbers of trees are almost constant in the diameter classes 60-120 cm dbh, and for the diameter classes > 120 cm dbh the numbers decrease with size. Beech and oak account for most of the larger trees, both represented by more or less bell-shaped sections in the diameter classes around 80-90 cm dbh (Figs. 6 and 7). The largest trees were about 200 cm in dbh.

The bell-shaped section of the beech diagram reflects a major natural regeneration event in the decades following 1807, at the time when the forest was fenced. This regeneration event was described in the management plans of 1815 and 1834 (Ulrich 1815; Sarauw 1834). An alternative explanation for the high numbers in the larger diameter-classes found in Suserup (for beech Fig. 6

and in general Fig. 5) is that the mortality rate actually decreases with age/size (Hett & Loucks 1976; Veblen 1992), as competition abates among trees reaching their maximum size. The break of the curves (Fig. 5 A, B and C) around 60 cm dbh could reflect the changeover from 3-dimentional (two horizontal, one vertical) competition to 2-dimentional (no vertical) competition as the trees reach their maximum height.

The diameter classes < 60 cm dbh are particularly interesting, because they represent the recruitment stage in which the trees compete to obtain a permanent position in the upper canopy layer. It seems biologically reasonable to assume a constant mortality rate independent of size/age during the recruitment stage (from sapling to canopy size). Therefore the best fitted (least squares) negative exponential functions for parts A, B, C and the whole forest pooled were computed, taking account only of trees of 3-60 cm dbh (first 'n' was ln-transformed, and then 'c' and 'k' were estimated by linear regression):

Part A	$\ln(n) = 5.29 - 0.0998\ d$	($R^2 = 0.98$)
Part B	$\ln(n) = 5.47 - 0.0995\ d$	($R^2 = 0.93$)
Part C	$\ln(n) = 4.95 - 0.0737\ d$	($R^2 = 0.92$)
Total	$\ln(n) = 5.25 - 0.0913\ d$	($R^2 = 0.98$)

The model corresponded well to the data, explaining 98% of the total variation in ln(n) between diameter classes in part A, 93% in part B, and 92% in part C. The actual stem numbers in the smallest diameter-classes were higher than calculated from the model in all three parts (Fig. 5). This could be a result of a decreasing mortality rate for trees with increasing diameters in the smallest diameter classes (Hett & Loucks 1976; Veblen 1992), but part of it reflects that every stem was recorded as an individual in the present study; accordingly, typically multistemmed species like *Ulmus glabra*, *Sambucus nigra L.* and *Salix spp.* were 'over-represented' especially in the smallest diameter classes. The curve of part B shows a pronounced dip around 30 cm dbh, which cannot immediately be explained. The systematic (S-formed) deviations from the straight line of part C (Fig. 5) reflect an even-aged bulk of alder (also reflected in Fig. 8 as a peak around 30-45 cm dbh), originating from the invasion of alder into the abandoned meadows along the lake side. The high numbers of ash in the smallest diameter classes, and the moderate number of small alder trees in part C indicate a possible succession from alder to ash taking place in the former meadows (Fig. 8). Primary succession from alder to ash, in Sweden has been described by Tapper (1993).

Disturbance

Old growth or 'climax' forest characterized by frequent but relatively small disturbances tend to develop diameter distributions showing a characteristic negative exponential decline of numbers against size (Cousens 1974; Mayer & Neumann 1981; Lemée 1989; Oliver & Larson 1990; Peterken 1996). By contrast, the diameter distribution of an even-aged stand usually resembles a normal distribution (Hough 1932; Schmelz & Lindsey 1965; Veblen 1992; Peterken 1996). Accordingly, diameter distribution data can be used as a measure of successional stage and disturbance history (Schmelz & Lindsey 1965). Major disturbances tend to synchronize regeneration, thus moving the diameter distribution away from the exponential function and towards a normal distri-

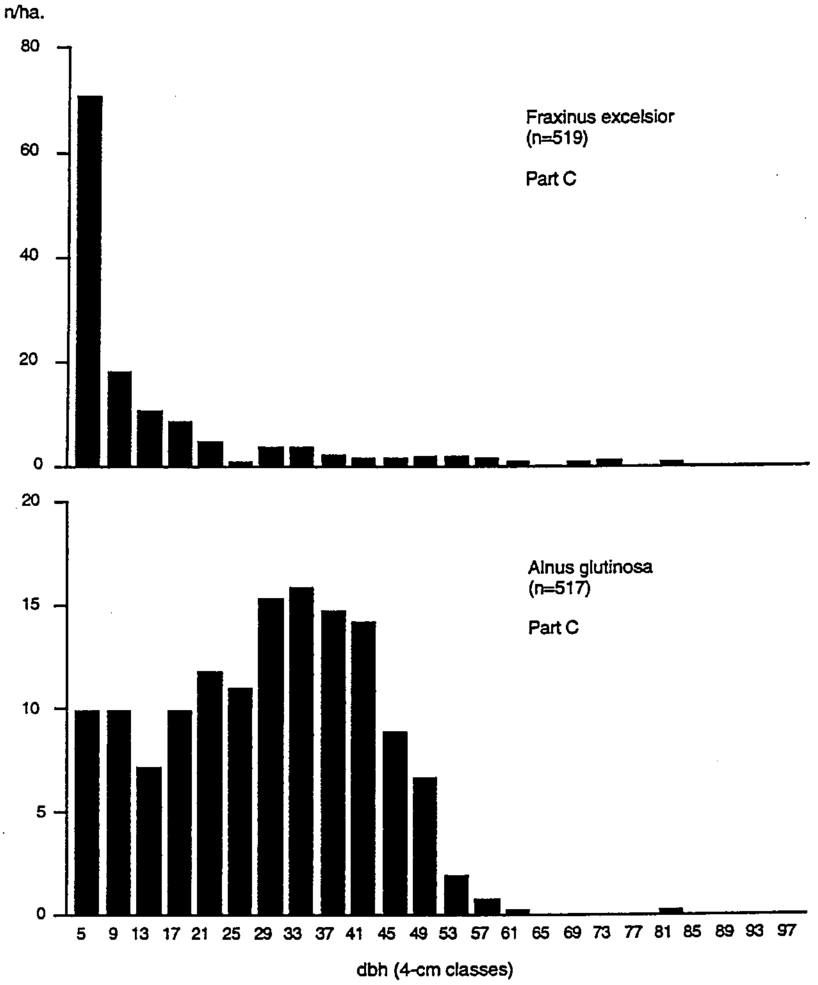


Fig. 8. *The diameter class distributions of Fraxinus excelsior and Alnus glutinosa for part C. Note differing scales on the y-axis.*

bution. Schmeltz & Lindsey (1965) concluded that the coefficient of determination (R^2) was the clearest index of the degree of past disturbances.

The size distributions of parts A, B and C could all roughly be described by negative exponential functions, considering only trees of 3-60 cm dbh. The coefficients of determination suggest that parts B (R^2=0.93) and C (R^2=0.92) were more disturbed than part A (R^2=0.98). This result is in agreement with the historical evidence. The result can, however, partly be explained by the fact that A represents a larger area than parts B and C. From the facts that R^2 for the whole forest is equal to R^2 for part A, and that part C shows a systematic deviation (S-shaped curve) from the model, it can be concluded that the result is not just a question of sample size. Both part A, B and C are characterized by a stable recruitment of smaller trees into the larger diameter classes, as typical of old growth forest stands. It is interesting that the storm in October 1967

(Jacobsen 1986) was not clearly reflected in the diameter distributions (Figs. 5-8), even though the storm was a dramatic event in Suserup Skov. A total of about 40 beech trees in the diameter range of 30-150 cm dbh were blown down, about half of them between 70-90 cm dbh (according to analysis of aerial photos and field observations), indicating that the storm primarily harvested in the 'over-represented' diameter classes. In fact, the storm counter-balanced the effects of a disturbance in the past, the fencing of the forest 200 years ago which triggered a regeneration wave of now old trees. It is remarkable that the storm is not even reflected as a peak in the smaller/intermediate diameter classes, which also points to the relative insensitivity of this analytical technique. The stock of old oak trees was not seriously affected by the storm, but it is not clear to what extend the oaks actually stabilized the forest against the storm.

Density, basal area and standing volume

The basal area (BA) was computed per 2 cm diameter class for each species. Diameter-height-regressions was used for the calculation of the standing volume (SV). Several regression models have been suggested to describe the relation between height and diameter (e.g. Shugart et al. 1981, Leemans & Prentice 1987, Lemée 1987, Urban & Shugart 1992). The regression suggested by Prodan (1965) describing the d/h-relation in selection forest resulted in the best fit to the Suserup data. Prodans regression (Prodan 1965, p. 253) can be reduced, as shown by Holten-Andersen (1985), to a more convenient equation:

$$h = H_{dom} * ((d/(d+k))^3) + 1.3$$

where h = tree height; d = dbh; H_{dom}= dominant (maximum) tree height and k = constant determining the inflection point of the sigmoidal curve. The curve passes through the point (0,1.3), performs an 'S' asymptotically approaching the value of H_{dom} for increasing diameters. The sigmoidal shape of the d/h-curve seems more reasonable than e.g. a second degree polynomial, which shows decreasing heights for increasing diameters above a certain limit (e.g. Shugart et al. 1981). Further, the curve describes the typical height growth rhythm, slow-fast-slow, of trees passing through juvenile, dynamic and senescent life stages (Oldemann 1990). Species-specific d/h-regressions were computed for beech (n=482) and ash (n=214) (Fig. 9). The d/h-relation for oak was graphically estimated (n=31), while all 'other species' were pooled to compute a common d/h-regression (n=215).

The standing volume (total volume above ground) was computed per diameter class for each species:

$$SV=BA*h*f.$$

The BA was taken from our calculations per diameter class, heights (h) were calculated on the basis of the d/h-regressions and the form factor (f) was derived from the Danish standard volume functions (Madsen 1987). The error caused by using standard volume functions (based on even-aged production forest stands) is unknown, though presumably small since the functions are based on single tree volumes, having entries for both height and diameter. For 'other species' the volume function for beech was used, representing a resonable approximation.

The basal area (m^2/ha), density (n/ha) and standing volume (m^3/ha) of the

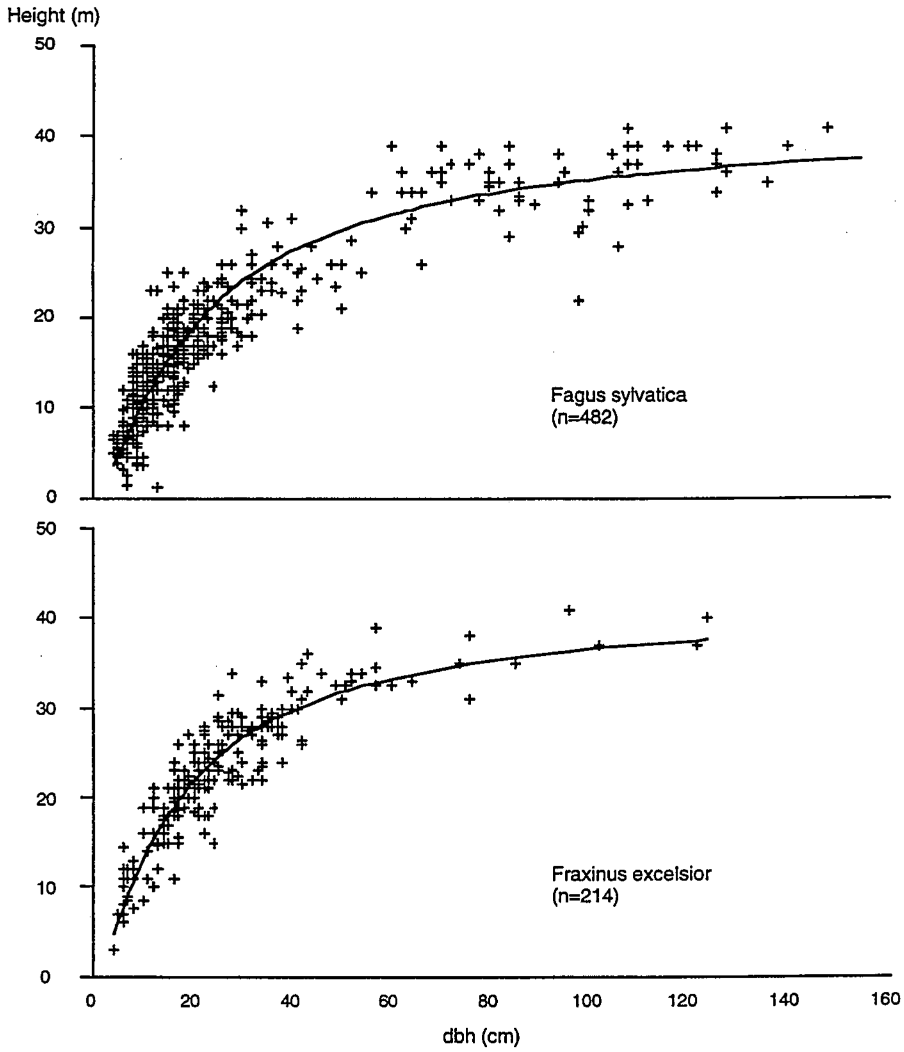


Fig. 9. *Diameter/height regressions for Fagus sylvatica,* $h = 41 * (d/(d+6.46))^3 + 1.3$ *and Fraxinus excelsior,* $h = 41 * (d/(d+5.16))^3 + 1.3$.

most important species are presented in Table 1. Regarding BA, beech dominates part A, while oak/beech dominate part B and beech/alder dominate part C. Elm has the highest overall density but plays only a minor role in terms of BA.

Part A was completely dominated by only four species: beech, ash, oak, and elm accounting for 98% of the BA. *Tilia platyphyllos Scop.* (lime) accounted for most of the residual 2% of the BA. 'Other species' accounted for 6% of the BA in part B, mostly *Acer pseudoplatanus L.* (sycamore). *Crataégus spp.*, *Corylus avellána* and *Sambucus nigra* were present in part B with high density. In part C 'Other species' accounted for 5% of the BA, representing 28% of

Table 1. *Density and basal area for parts A (10.7 ha), B (4.9 ha) and C (3.7 ha) in Suserup Skov. Alle trees ≥ 3 cm dbh have been measured.*

	Part					
	A		B		C	
Basal area (m²/ha)		(%)		(%)		(%)
Fagus sylvatica	24.7	(64.2)	14.6	(30.5)	14.4	(38.2)
Fraxinus excelsior	4.9	(12.7)	8.8	(18.4)	6.3	(16.7)
Quercus robur	5.6	(14.6)	16.0	(33.4)	2.0	(5.3)
Ulmus glabra	2.4	(6.2)	5.4	(11.3)	2.5	(6.6)
Alnus glutinosa	0.2	(0.5)	0.1	(0.2)	10.7	(28.4)
Other species	0.7	(1.8)	3.0	(6.3)	1.8	(4.8)
Total	38.5	(100.0)	47.9	(100.1)	37.7	(100.0)
Density (stems/ha)						
Fagus sylvatica	402	(45.6)	185	(17.1)	165	(17.5)
Fraxinus excelsior	77	(8.7)	74	(6.8)	140	(14.8)
Quercus robur	6	(0.7)	22	(2.0)	4	(0.4)
Ulmus glabra	338	(38.4)	598	(55.1)	235	(24.9)
Alnus glutinosa	2	(0.2)	1	(0.1)	139	(14.7)
Other species	56	(6.4)	205	(18.9)	261	(27.7)
Total	880	(100.0)	1085	(100.0)	944	(100.0)

Table 2. *Density, basal area and standing volume at different lower diameter (dbh) culling levels for parts A (10.7 ha), B (4.9 ha) and C (3.7 ha) in Suserup Skov.*

	Part		
	A	B	C
Density (stems/ha)			
> 3 cm	880	1085	944
> 7 cm	533	622	534
>13 cm	298	370	328
>20 cm	153	192	215
Basal Area (m²/ha)			
> 3 cm	38.5	47.9	37.7
> 7 cm	37.9	47.0	36.8
>13 cm	36.1	45.1	35.3
>20 cm	33.1	41.4	32.9
Standing Volume (m³/ha)			
> 3 cm	696	837	613
> 7 cm	693	834	610
>13 cm	680	821	599
>20 cm	649	782	574

the stems, mostly smaller individuals of *Salix spp.*, *Sambucus nigra* and *Crataégus spp.*.

The relation between relative BA and the relative density (Table 1) varies among the species, some species, e.g. oak, are represented by a few large stems while others, e.g. elm, are represented by many small stems.

Part B has a very high BA (47.9 m^2/ha) and SV (837 m^3/ha), Table 2, also compared with other European semi-natural temperate forests (Röhrig 1991). The high BA and SV can be explained by a relative large number of thick old oak trees (Fig. 7), under which a rather large stock of other species has developed. The situation resembles the biomass peak occurring during the transition phase in the secondary succession simulated by Bormann & Likens (1979).

Not all surveys of natural forests use the same lower diameter cut-off values. To facilitate comparison, and in order to evaluate the sensitivity of the results, the density, BA and SV were computed using different lower diameter culling levels (Table 2).

The ecological roles of beech, oak, ash and elm

The diameter distribution of beech (Fig. 6) is typical for a shade-tolerant 'climax' species, many small recruits but also a considerable number of full-size canopy trees.

Hardly any recruits of oak exist in Suserup skov (Fig. 7), oak is clearly fading out, even though the old oaks will persist in the ecosystem for centuries. Scattered oak plants have been observed in gaps, but usually they are ousted by fast growing ash and the heavy shade from beech. The retreat of oak is probably linked to the structural change from relatively open forest to more closed forest during the last two centuries. However, oak might persist at low frequency due to occasional successful regeneration in larger gaps.

The diameter distribution of ash (Fig. 6) has a peak around 17 cm dbh. A sample of ash trees of 15-19 cm dbh were tree ring dated to an average age of 52 years (n=21, std=13 yr). Accordingly, the peak does not reflect the windthrow in 1967. It could, however, reflect compulsory felling during The Second World War and the cutting of elm during the 1930s. The diameter distribution of ash is characteristic of a gap specialist, reflecting the irregular occurrence of gaps through time. The steep d/h-regression curve of ash, compared with beech (Fig. 9), documents that ash has a pronounced height growth and a moderate diameter growth in youth. This growth pattern illustrates the recruitment strategy of ash, a gap specialist able to exploit gaps, ahead of competing tree species.

Elm is represented in large numbers in the smallest diameter classes and in small numbers in the bigger classes (Fig. 6), typical of a shade tolerant understorey specialist. This is rather surprising as elm in fact can grow to be very large. The cutting of elm in Suserup Skov, especially during the 1930s, partly explains the absence of large elms. But it stands to reason that the result actually reflects the role of elm as an understorey species in Suserup Skov. The management plans (1815-1970) document that there was never any representation of larger elm trees in considerable numbers during the past two centuries. In 1815, only 10 elm trees with an average standing volume of 1.2 m^3 were recorded (Ulrich 1815), and in 1885, 41 elm trees of an average volume of 1.5 m^3 were recorded (Lillienskiold 1885). Today the few large elm trees are concentrated in the edge of the forest. Apparently elm has a special regeneration niche in the epicenter and periphery of fallen trees, due to its strong ability to recover from physical damage. Dutch elm disease *(Ophiostoma ulmi (Buism.) Nannf.)* is now spreading throughout Denmark. The first attack, in Suserup Skov, was observed in early summer 1994, at the northern edge of the forest. Attacks of elm disease often lead to the death of most elm trees in the forest

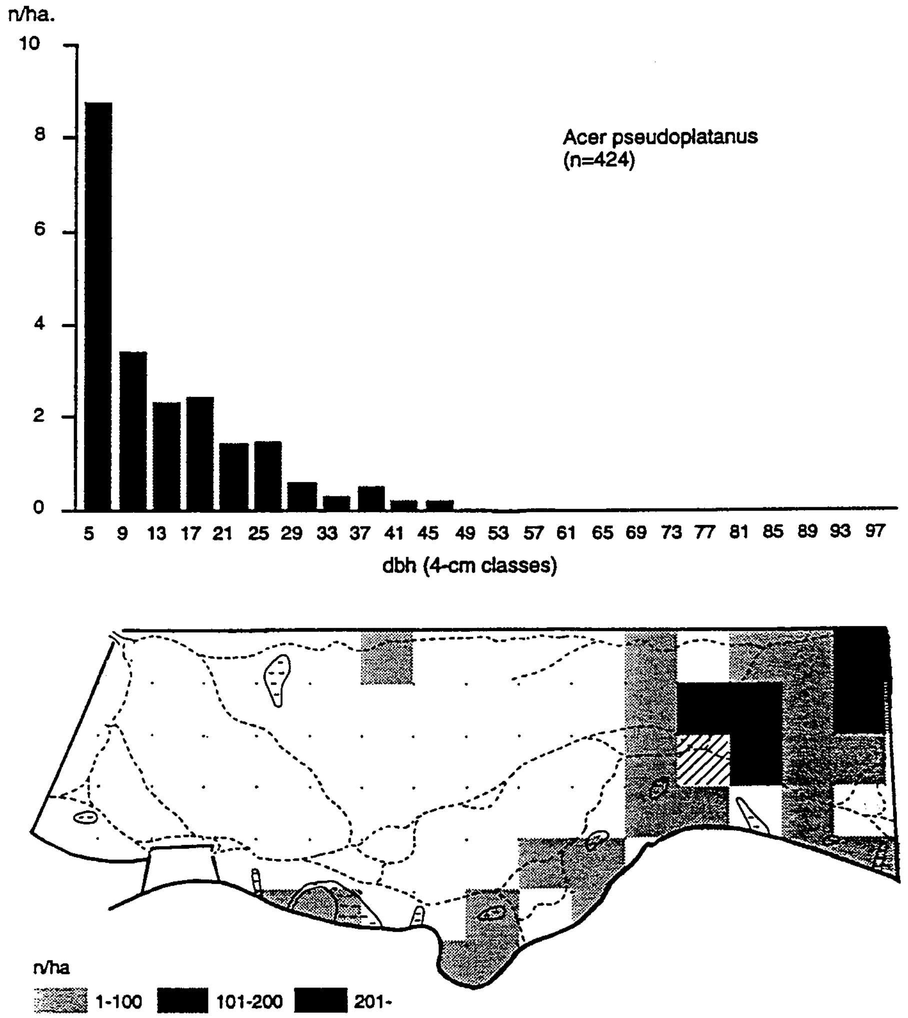
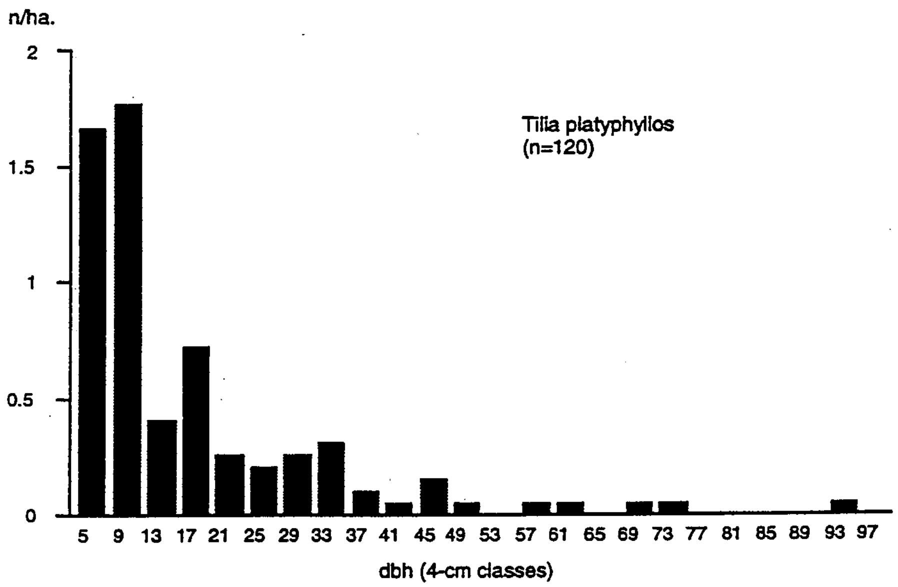
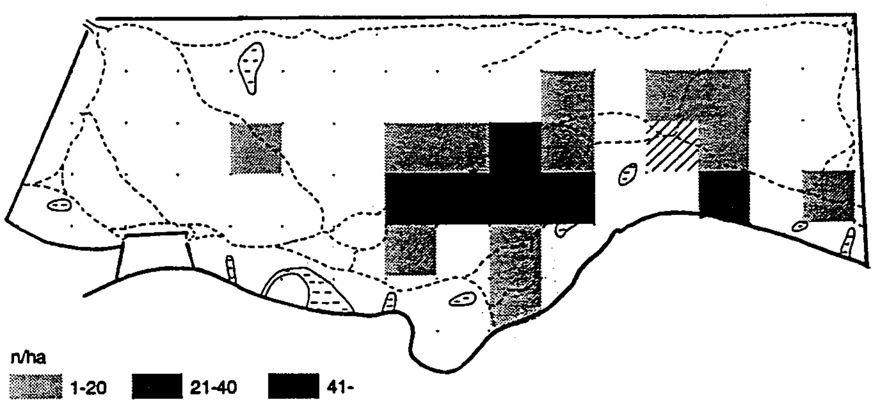


Fig. 10. *Diameter class distribution and spatial distribution of Acer pseudoplatanus and Tilia platyphyllos in Suserup Skov.*

within a few years (Peterken & Jones 1987; Dal & Fabricius 1993). This may happen in Suserup as well.

Lime has been spreading successfully from a few old specimens, probably introduced by humans, on the low elevated plateau located centrally in the forest (Fig. 10). Seedlings and saplings have become established in several places, mostly within a radius of about 100 meters from the old lime trees. Sycamore has spread from two centers in part B. Seedlings and saplings are now present in many places (Fig. 10). Most likely, lime and sycamore will continue to expand in Suserup Skov. According to field observations, sycamore invades at the expense of both ash and beech, as also reported from England (Watt 1925; Peterken & Jones 1987), while lime seems to invade mostly at the





expense of beech. It does not seem likely that lime and sycamore will oust other species; they rather affect the frequency of species gently pushing the whole system towards a new dynamic equilibrium. Temperate deciduous forests in eastern USA (Oosting 1942; Barnes 1991) and East Asia (Ching 1991) contain many more tree species than comparable forests in Europe. Presumably there will be enough room for a few additional species in Suserup Skov.

Conclusions

1) The results form a basis for future research in Suserup Skov. The authors can be contacted for maps and other basic data.
2) The overall diameter distributions (3-60 cm dbh) especially in part A, but

also in parts B and C, resembled negative exponential functions, typical of climax forest with a relatively calm disturbance regime. Trees > 60 cm dbh were 'over-represented', reflecting a decreasing 'mortality rate' with increasing tree sizes, a major regeneration event of beech triggered by the fencing of the forest in 1807, and the accumulation of old oak trees caused by grazing periods in the past.
3) The species-specific diameter distributions reflected the ecological role of each species. Beech, a typical shade-tolerant 'climax' species, elm a shade tolerant understorey species, ash a gap specialist and oak a long-lived, light-demanding species in slow retreat in a changing system.
4) Compulsory felling during the Second World War and cutting of elm during the 1930s, evidently favored regeneration of ash.
5) Several successional phenomena can be observed in the forest. Oak is fading out in favour of ash and beech in part B, while succession from alder to ash occurs in the abandoned meadows along the lake side (part C).
6) Lime and sycamore have successfully established small colonies in the eastern and central parts of Suserup Skov, from where they seem to expand slowly but steadily to other parts of the forest.
7) The overall structure, as reflected by the diameter distributions, is not far from the characteristic dynamic equilibrium of a 'climax' forest in steady state, while the species composition is under continuous change. The fact that several successional processes are taking place within this relatively mature system conforms the modern view of vegetation change, emphasizing the importance of repeated, relatively frequent disturbances and the continuous change in vegetation as the norm.

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References

Andersen, S.T. 1989: Natural and cultural landscapes since the ice age. Journal of Danish Archaeology, 8:188-199.

Attiwill, P.M. 1994: The disturbance of forest ecosystems: the ecological basis for conservative forest management. Forest Ecology and Management, 63:247-300.

Bang, N. 1926: Letter from the Ministry of Education, Nina Bang. Brev Nr. 223, København 2. Januar 1926, Undervisningsministeriet, Journal Nr. 1688/25, 1 p.

Barnes, B.V. 1991: Deciduous Forests of North America.-*In*:Röhrig, E. & Ulrich, B. (eds.): Temperate Deciduous Forests. Ecosystems of the World 7. Elsevier, Amsterdam, London, New York, Tokyo. pp. 219-344.

Boot, D., Boulter, D., Neave, D., Rotherham, T. & Welsh, D. 1993: Natural forest landscape management in Canada. Setting a global standard for implementing sustainable development. Forest Resource Management Edition, Forestry Canada, Ottawa, 16 pp.
Bormann, F.H. & Likens, G.E. 1979: Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist, 67:660-669.
Botkin, D. B. 1981: Causality and succession pp. 36-55 *In*:West, Shugart & Botkin: Forest succession, concepts and application. Springer-Verlag, New York, Heidelberg, Berlin.
Bradshaw, R.H.W. 1988: Spatially-precise studies of forest dynamics. pp. 725-752 *In*:Huntley, B. & Webb III, T. (ed.): Vegetation history, Kluwer Academic Publishers, Dordrecht, Boston, London.
Bradshaw, R., Gemmel, P & Bjørkmann, L. 1994: Development of nature-based silvicultural models in Southern Sweden: The scientific background. For. & Landsc. Res. 1:95-110.
Broekmeyer, M.E.A. & Vos, W. 1993: Forest reserves in Europe: a review pp. 9-28 *in* Broekmeyer, M.E.A., Vos, W. & Koop, H. (eds.): European Forest Reserves, Proceedings of the European Forest Reserves Workshop, 6-8 May 1992, Wageningen Netherlands.
Brown, N.D. & Whitmore, T.C. 1992: Do dipterocarp seedlings really partition tropical rain forest gaps? Philosophical Transactions: Biological Sciences, 335:369-378.
Canham, C.D. 1990: Suppression and release during canopy recruitment in Fagus grandifolia. Bulletin of the Torrey Botanical Club, 117(1):1-7.
Ching, K.K. 1991: Temperate Desiduous forests of East Asia. *In*:Röhrig, E. & Ulrich, B.: Temperate Deciduous Forests. Ecosystems of the World 7. Elsevier, Amsterdam, London, New York, Tokyo. pp. 539-555.
Christensen, M., Heilmann-Clausen & Emborg, J. 1993: Suserup Skov 1992, opmåling og strukturanalyse af en dansk naturskov. Skov- og Naturstyrelsen, København, 80 pp. (In Danish, summary in English).
Cousens, J. 1974: An introduction to woodland ecology. Oliver & Boyd, Edinburgh.
Dal T. & Fabricius, P. 1993: Vorsø V - Registrering af vedvegetationen i skovene og udvalgte prøveflader på Vorsø 1992. Skov- og Naturstyrelsen, Miljøministeriet, Denmark. 76 pp. (In Danish, summary in English).
Fritzbøger, B. & Emborg, J. 1996.: Landscape history of the deciduous forest Suserup Skov, Denmark, before 1925. For. & Landsc. Res., 1996: 1: 291-309.
Glenn-Lewin, D.C. & van der Maarel, E. 1992: Patterns and processes of vegetation dynamics. pp. 11-59 in Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T.: Plant succession, theory and prediction, Chapmann & Hall.
Harper, J. L. 1977: Population biology of plants. Academic Press, London, New York, San Fransisco. 857 pp.
Hett, J.M. & Loucks, O.L. 1976: Age structure models of balsam fir and eastern hemlock. Journal of Ecology, 64: 1029-1044.
Holten-Andersen, P. 1985: Extensivering af distriktstaxation ved udnyttelse af tidligere planinformation. Den Kgl. Veterinær- og Landbohøjskole, Sektion for Skovbrug, Ph.D. thesis.
Hough, A.F. 1932: Some diameter distributions of forest stands of northwestern Pennsylvania. Journal of Forestry, 30:933-943.
Iversen, J. 1969: Retrogressive development of a forest ecosystem demonstrated by pollen diagrams from fossil mor. Oikos Suppl. 12:35-49.
Jacobsen, B. 1986.: Abiotiske skader i danske skove i tiden 1890-1984. Det Forstlige Forsøgsvæsen i Danmark, Beretninger bd. 40:213-224. (In Danish, summary in English).
Kimmins, J.P. 1991: Sustainable forestry: Can we use and sustain our forests? Forest Industry Lecture Series, no. 27, Faculty of Agriculture & Forestry, University of Alberta, Canada.
Koop, H. 1989: Forest dynamics. SILVI-STAR: A comprehensive monitoring system. Springer, Berlin, Heidelberg, New York, London, Paris, Tokyo, Hong Kong. 229 pp.
Leemans, R. & Prentice, I.C. 1987: Description and simulation of tree-layer composition and size distributions in af primaeval Picea-Pinus forest. Vegetatio 69:147-156.
Leibundgut, H. 1972: Struktur eines Emmentaler Plenterwaldes. Forstwissenschaftliches Centralblatt, 91:222-237.

Lemée, G. 1987: Dynamique de fermeture par régénération et évolution morphométrique du hêtre dans les vides d'une forêt non exploitée (Réserves biologiques de la forêt de Fontainebleau). Bulletin d'Écologie, 18(1):1-11.

Lemée, G. 1989: Structure et dynamique de la hëtaie de réserves biologiques de la forêt de Fontainebleau: un cas de complexe climacique de forêt feuillue monospécifique tempéré. Acta OEcologica/OEcologia generalis, 10(2):155-174.

Lillienskiold 1885: Driftsplan for Sorø Akademis 1. Skovdistrikt 1885-95. Sorø Akademi.

Madsen, S.F. 1987: Vedmassefunktioner ved forskellige aflægningsgrænser og nøjagtighedskrav for nogle vigtige danske skovtræarter. Det Forstlige Forsøgsvæsen i Danmark, beretning nr. 350, bd. XLI, h.2, pp. 47-242. (In Danish, summary in English).

Mayer, H. & Neumann, M. 1981: Struktureller und entwicklungsdynamischer Vergleich der Fichten-Tannen-Büchen-Urwalder Rothwald/Niederöstereich und Corkova Uvala/Kroation. Forstwiss. Centralblatt, 100:111-132.

Meyer, H.A. 1933: Ein mathematisch-statistische Untersuching über den Aufbau des Plenterwaldes, I-III. Schweizerische Zeitschrift für Forstwesen, pp. 33-46, 88-103,124-131.

Meyer, H.A. & Stevenson, D.D. 1943: The structure and growth of virgin beech-birch-maple-hemlock forests in northern Pennsylvania. Journal of Agricultural Research, 67(12):465-484.

Mueller-Dombois, D. & Ellenberg, H. 1974: Aims and methods of vegetation ecology. John Wiley & Sons, New York, Toronto, London, Sidney. 547 pp.

Oldemann, R.A.A. 1990: Forests: Elements of silvology. Springer-Verlag Berlin, Heidelberg, New York, London. 624 pp.

Oliver, C.D. & Larson, B.C. 1990: Forest stand dynamics. McCraw-Hill, Inc. New York, Hamburg, London, Tokyo. 467 pp.

Oosting, H.J. 1942: An ecological analysis of the plant communities of Piedmont, North Carolina. The American Midland Naturalist, 28(1):1-126.

Peterken, G.F. 1976: Long-term changes in the woodlands of Rockingham Forest and other areas. Journal of Ecology, 64:123-146.

Peterken, G.F. 1993: Long-term studies in forest nature reserves. pp. 35-48. In: Broekmeyer, M.E.A., Vos, W. & Koop, H. (eds.): European Forest Reserves, Proceedings of the European Forest Reserves Workshop, 6-8 May 1992, Wageningen, The Netherlands.

Peterken, G.F. 1996: Natural woodland, ecology and conservation in northern temperate regions. Cambridge University Press. 522 pp.

Peterken, G.F. & Jones, E.W. 1987: Forty years of change in Lady Park Wood: the old-growth stands. Journal of Ecology, 75:477-512.

Peterken, G.F. & Tubbs, C.R. 1965: Woodland regeneration in The New Forest, Hampshire, since 1650. Journal of Applied Ecology, 2:159-170.

Prentice, I. C. 1986: The design of a forest succession model. pp. 253-256 in Fanta, J. (ed.): Forest dynamics research in Western and Central Europe. Proceedings, IUFRO, September 1985, Wageningen, The Netherlands. Pudoc, Wageningen.

Prodan, M. 1965: Holzmesslehre. J.D. Sauerländer, Frankfurt am Main. 644 pp.

Röhrig, E. 1991: Vegetation structure and forest succession. In Röhrig, E. & Ulrich, B.: Temperate deciduous forests. Ecosystems of the World 7, pp. 35-49. Elsevier, Amsterdam, London, New York, Tokyo.

Sarauw. 1834: Driftsplan for Sorø Akademies 1. Skovdistrikt. Sorø Akademis Skovdistrikt.

Scheiner, S.M. & Teeri, J.A. 1981: A 53-year record of forest succession following fire in northern Lower Michigan. The Michigan Botanist, 20:3-14.

Schlaepfer, R., Innes, J., Stewart, R. & Langevin, F. 1993: Workshhop on environmental criteria/indicators for the sustainable development of boreal and temperate forests. Seminar of CSCE experts on sustainable development of boreal and temperate forests, Montreal, Canada, september 1993, report, 11 pp.

Schmelz, D.V. & Lindsey, A.A. 1965: Size-class structure of old-growth forests in Indiana. Forest Science, 11(3):258-264.

Shugart, H.H., West, D.C. & Emanuel, W.R. 1981: Patterns and dynamics of forests: An application of simulation models. pp. 74-94 in West, D.C, Shugart, H.H. and Botkin, D.B. (eds.): Forest succession, concepts and application. Springer-Verlag, New York, Heidelberg, Berlin.

Silvertown, J.W. & Doust J.L. 1993: Introduction to plant population biology. Blackwell Scientific Publications, London, Edinburgh, Boston, Paris, 210 pp.

Stephens, G.R. & Waggoner, P.E. 1980: A half century of natural transitions in mixed hardwood forests. The Connecticut Agricultural Experiment Station, New Haven, Bulletin 783. 43 pp.

Tapper, P.G. 1993: The replacement of Alnus glutinosa by Fraxinus excelsior during succession related to regenerative differences. Ecography, 16:212-218.

Ulrich 1815: Driftsplan for Sorø Akademies 1. skovdistrikt. Sorø Akademis Skovdistrikt.

Urban D.L. & Shugart. H.H. 1992: Individual-based models of forest succession. pp. 249-292. – *In*:Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T.:Plant Succession, theory and prediction. Chapmann & Hall.

Vaupell, C. 1863: De Danske Skove. P.G. Philipsens Forlag.

Veblen, T.T. 1992: Regeneration dynamics. Pp. 152-187.-*In:* Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T.: Plant succession, theory and prediction, Chapmann & Hall.

Vejre, H. & Emborg, J. 1996: Interactions between vegetation and soil in a near-natural temperate deciduous forest. For. & Landsc. Res. 1996, 1: 335-347.

Watt, A.S. 1925: On the ecology of british beechwoods with special reference to their regeneration. Part II, sections II and III: The development and structure of beech communities on the Sussex Downs (continued). Journal of Ecology, 13:27-73.

Whitney, G.G. 1987: An ecological history of the Great Lakes forest of Michigan. Journal of Ecology, 75:667-684.

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