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The structure of Suserup Skov, 2002. The first re-measurement of a long-term permanent plot study of forest dynamics started in 1992

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Suserup Skov (19.2 ha) is an old growth temperate forest dominated by beech *Fagus sylvatica*, pedunculate oak *Quercus robur*, ash *Fraxinus excelsior,* wych elm *Ulmus glabra,* and black alder *Alnus glutinosa*, admixed with lime *Tilia platyphyllos* and sycamore maple *Acer pseudoplatanus*.
In 1992, a complete inventory of trees exceeding 3 cm in diameter at breast height (DBH, 1.3 m above forest floor) was carried out, as a starting point to study the long-term dynamics of the forest. In 2002 a first re-inventory was carried out including all trees ≥ 29 cm DBH in the whole forest, while trees with DBH > 3 cm were remeasured in three 1 ha plots. Based on the new inventory changes in the forest structure are analyzed and discussed in relation to ecological stability and forest management. A stem-position map based on the 2002 data was made to present an overview of the changes since 1992 and also as a practical tool for future research. The following conclusions were reached from the analysis of the results of the 1992 and 2002 inventories.
1) Between 1992 and 2002 Suserup Skov has been impacted by two important disturbances: an extreme storm and the Dutch elm disease. As an ecological system, the forest has proved relatively resistant. Although some changes have occurred in the diameter distribution, the forest ecosystem has not been pushed back into an early successional stage and no decline in the standing volume occurred.
2) The forest is still undergoing changes resulting from the cessation of livestock grazing around 1807 and the subsequent gradual cessation of management. Oak is retreating from the stand, while beech is losing some terrain to ash, lime and sycamore maple after a period of extensive dominance. On the wetter ground at the lake-shore, alder is still dominant, but ash is increasing.
3) The ecological disturbance caused by the 1999-storm has interacted with and speeded up the ongoing gradual long-term successional changes predicted in 1992. A fair number of large beech trees were blown over in the storm, whilst trees in smaller diameter classes were less affected and have shown vigorous growth. Especially sycamore maple, lime and (to some degree) ash have increased in importance, being capable of filling many of the gaps created where mature beeches have fallen.

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In a previous paper (Emborg et al. 1996) we established a basis for long-term studies of forest dynamics in Suserup Skov, which is one of the most interesting old growth deciduous forests in north-western Europe. This was done by presenting basic data on forest structures based on field-measurements carried out in 1992. Repeated measurements of basic structural data represent a simple and reliable approach to the study of forest dynamics. The problem with this type of study is, however, that they require a long period of time and a long-term commitment, i.e. they are difficult to sustain. This article represents the second step in a hopefully long chain of recordings in which long-term changes in the stand structure of Suserup Skov will be monitored. Each recording will document the actual state of the forest over time – like a time-series of photos. The first picture is from 1992. This article presents the 2002-picture, documents changes since 1992, and discusses the current development of the forest ecosystem.

The site

Suserup Skov (19.2 ha) is an old growth temperate deciduous forest, situated north of lake Tystrup Sø, on the island of Sjælland (Zealand), Denmark, 55°22′N, 11°34′E. The site has been intensively studied during the last decade and several scientific articles have been published, dealing with the history, ecology and biodiversity of the forest (Fritzbøger and Emborg 1996, Vejre and Emborg 1996, Emborg et al. 2000, Heilmann-Clausen 2001, Heilmann-Clausen and Christensen 2003, Thomsen et al. 2005). It supports mixed stands dominated by beech *Fagus sylvatica*, pedunculate oak *Quercus robur*, ash *Fraxinus excelsior,* wych elm *Ulmus glabra,* and black alder *Alnus glutinosa*, with lime *Tilia platyphyllos* and sycamore maple *Acer pseudoplatanus* otherwise important. The soils are of glacial origin. They vary in composition and include clayey, loamy and sandier deposits as described in detail by Vejre and Emborg (1996). Much of the site supports relatively fertile, mesotrophic soils that are moderately free-draining, but locally in a low central plateau the soils are gleyed due to waterlogging. Conditions for tree growth are generally favorable, as indicated by an upper canopy height of ca 40 m (Emborg et al. 1996).

According to pollen and macrofossil records it seems likely that Suserup Skov has been under more or less continuous tree cover since forest vegetation spread in the landscape after the last ice-age (Hannon et al. 2000). For various reasons the site has never been cleared completely, though it undoubtedly has a long history of human use, acting as a source for wood and other materials and for grazing livestock. The forest was not commercially exploited for timber during the 18–19th centuries, which is exceptional for north-western Europe. In 1854 the owner, Sorø Academy, decided to protect Suserup Skov by not allowing commercial forest management. Although some limited tree cutting and removal of dead wood took place until 1961, the forest has since been kept as a strict non-intervention reserve (Fritzbøger and Emborg 1996). For an overview of the history of the forest see Heilmann-Clausen et al. (2007).

Methods

The site was partitioned into three distinct ecological units when the study was initiated in 1992 (Emborg et al. 1996). These were named part A (10.7 ha), part B (4.9 ha) and part C (3.7 ha). Each represented a distinctive set of environmental conditions and had a different forest history. In the 1992 recording, the forest (part A, B, and C) was divided into 50 × 50 m (0.25 ha) plots. All stems ≥ 3 cm DBH were measured to the nearest 2-cm diameter-class in each plot and the position of trees ≥ 29 cm DBH was recorded. The 2002 recording repeated the 1992 methodology, except for two points: 1) tree heights were not measured in 2002, and 2) trees with DBH ≥ 3 cm were in 2002 recorded only in three 1 ha (100 × 100 m) sample plots (A1, A2, B1) from parts A and B, representing different forest development types: plot A1 was situated on undulating loamy tills and was selected to represent a typical beech/ash dominated stand with some remaining large, old oaks. Plot A2 was situated on flat, fine-grained, mainly lacustrine sediments and was similar to plot A1, except for the presence of lime. Plot B1 was situated on undulating, mainly sandy tills and was selected to represent part of the former wood-pasture area, where mature oaks were prominent amongst younger ashes and expanding sycamore maple.

The fieldwork was carried out during the summer of 2002. The inventory was based on the 50 × 50 m grid established in 1992, which was marked in the field by numbered steel poles. The position and size of all trees ≥ 29 cm DBH (dead or alive, upright or fallen) was recorded. The location of new trees that had recruited since 1992 was determined by sighting and measuring from the grid. The position of surviving trees was checked only where these appeared to be misplaced. The size of trees ≥ 29 cm DBH was measured as a circumference with a measuring tape (and converted to diameter assuming they were circular in cross-section). Smaller trees had the diameter measured with calipers.

Density, basal area and standing volume calculations

The density (of trees ≥ 29 cm DBH) came directly from the total inventory. Basal area (BA) was computed per diameter-class for each species, assuming $BA = (d/2)^2 \times \pi$, where d = DBH. Standing volume was computed per diameter-class for each species, using the equation SV = BA ×

h × f, where BA = basal area, h = tree height, and f = form factor (the ratio of tree volume to the volume of a geometrical solid, here a cylinder, that has the same diameter and height as the tree, Husch et al. 2003). Multiple stems arising from one individual were recorded and treated separately for exact calculation of basal area and standing volume.

Tree heights (h) were calculated per tree species and DBH-class using the d/h-regressions developed by Emborg et al. (1996): $h = H_{dom} \times ((d/(d+k))^3) + 1.3$, where d = DBH; H_{dom}= dominant (maximum) tree height; and k = constant determining the inflection point of the sigmoidal curve. The curve passes the point (0, 1.3), performs an "S" asymptotically approaching the value of H_{dom} for increasing diameters. Species-specific d/h-regressions were computed for beech (n=482) and ash (n=214). The d/h-relation for oak was graphically estimated (n=31), whilst all other species were pooled to compute a common d/h-regression (n=215). For further details see Emborg et al. (1996).

Form factors (f) were taken from the Danish standard forestry yield tables (Madsen 1987). The error caused by using forestry yield tables is unknown, but presumably small since the tables are based on single tree volumes, having entries for both height and diameter. For other species we simply used the yield table for beech because no form factors were available for them.

Annual growth rates (DBH mm yr^{-1}) were calculated per tree species based on trees ≥ 29 cm DBH in 1992 that remained alive in 2002. To provide an annual rate for each tree, overall changes in DBH over 1992–2002 were divided by ten years.

Throughout the paper the term "small trees" is used for trees ≥ 3 and < 29 cm DBH, whilst "large trees" is used for trees ≥ 29 cm DBH.

Climate and disturbances in the period 1992–2002

Certain events during 1992–2002 had an important impact on stand development. Over the decade the temperature was higher than normal. The mean annual temperature was 8.3°C (varying from 6.8°C in 1996 to 9.2°C in 2002), which was 0.6°C above the long-term average (1873–2003, Cappelen 2004). The average annual precipitation was 741 mm, varying from 505 mm (1996) to 905 mm (1999), which was slightly above the long-term average of 674 mm (Cappelen 2004). No exceptional drought periods or extreme winter conditions occurred but there was a major hurricane event. This was the most important climatic event in the period. It struck the southern part of Denmark with severe strength on 3 December 1999, and was the strongest windstorm ever recorded in Denmark (the climatic station at Flakkebjerg, 13 km from Suserup Skov, measured gusts at 45 m s^{-1}). The hurricane was of rather short duration – some eight hours at full strength – but occurred after a period of heavy rain. It caused massive uprooting of trees throughout Denmark and was a major disturbance event in Suserup Skov. For a more comprehensive description of the storm and its immediate consequences for Suserup Skov see Bigler and Wolf (2007).

Another important disturbance agent in Suserup Skov during 1992–2002 was Dutch elm disease. This is a response to infection by the fungus *Ophiostoma ulmi* s.l., which is spread by *Scolytus* beetles and often results in the death of elm trees (Röhrig 1996). It was observed for the first time in the early summer of 1994, at the northern edge of the forest. Since then, it has spread widely, killed a large number of elm trees, and created numerous canopy gaps.

Results

Stem position map

Based on the inventory we produced a 2002 stem position map, which is interesting to compare with the map of 1992. The two maps are shown in Fig. 1 and 2.

Density, basal area and standing volume, large trees

The total number of trees ≥ 29 cm DBH increased in all three parts (A, B, and C) of the forest from 1992 to 2002 (Table 1). This means that the number of trees growing into the group of trees ≥ 29 cm DBH exceeded the number of trees that died or fell over. The basal area and standing volume changed little in parts A and B, whilst part C experienced an increase in basal area and standing volume of almost 20%.

At the tree species level, it is clear that oak decreased in density, basal area and volume in all three parts, both absolutely and relatively (Fig. 3). Beech also showed a relative decline in standing volume in all forest parts (Fig. 3), but at the same time increased in numbers (Table 1), indicating that its decline in importance was mainly due to the loss of large trees in the 1999 hurricane. Ash increased in relative importance in parts A and C, but declined in part B (Fig. 3). This was mainly due to a loss of large ash trees, as the number of ash actually increased in all three parts.

Of the subordinate tree species, alder, lime and sycamore maple increased in relative importance in the forest parts where they occurred (Fig. 3). This was especially evident for sycamore maple in part B and alder in part C. Despite the outbreak of Dutch elm disease, elm did not decrease in relative importance (Fig. 3) or in numbers, basal area or volume (Table 1), apparently because of significant regeneration and growth of surviving trees. Finally, changes in the combined group of low frequent "other species" were relatively limited in all parts of the forest.

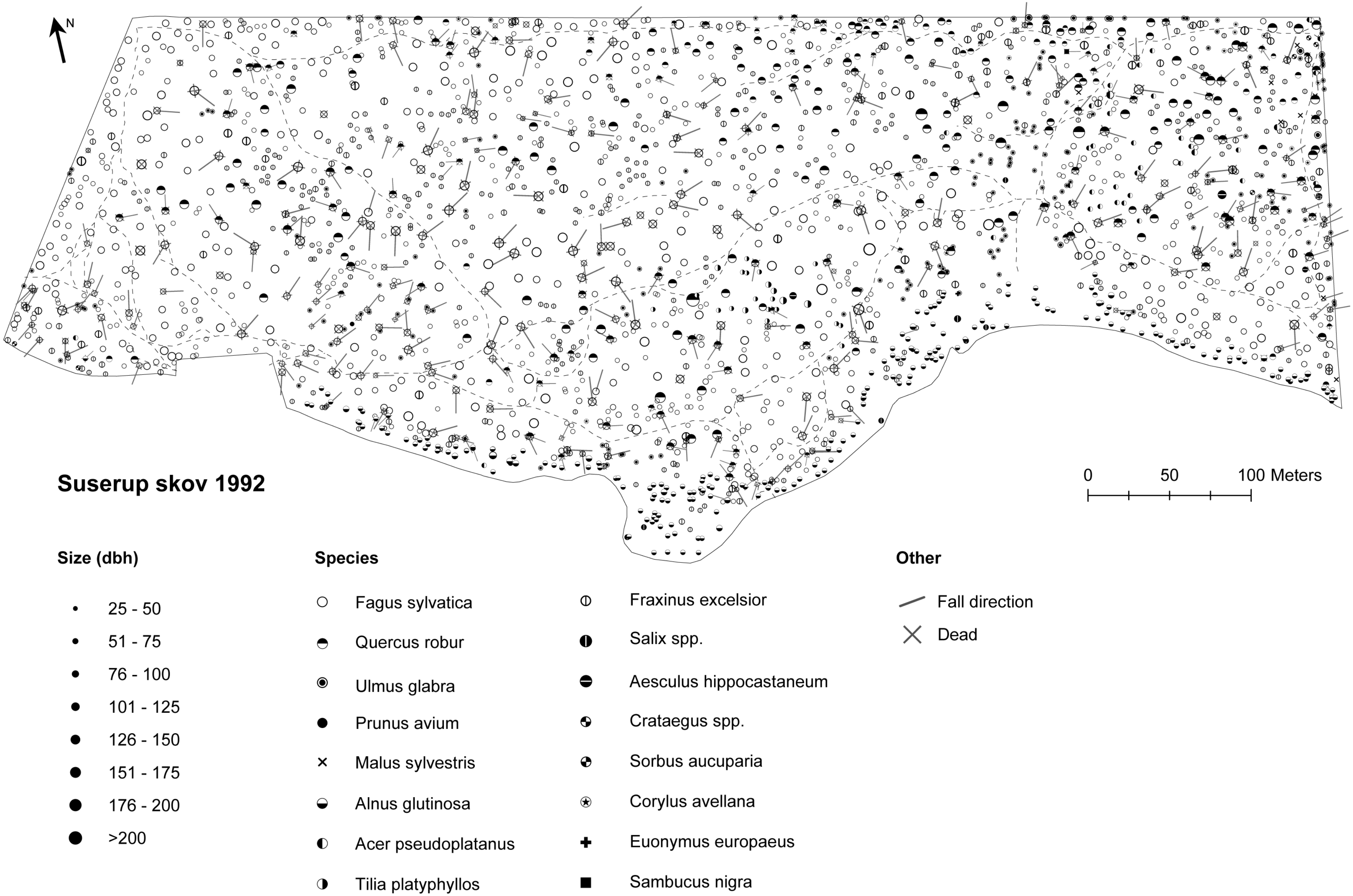

Fig. 1. Stem position map including all trees (trees ≥ 29 cm DBH) recorded in 1992. The dotted lines indicate an existing network of footpaths. Drawn by Morten Christensen, Martin Kyhn and Anders Busse Nielsen. The map is available in electronic form from the authors of the paper or download the figure as file Ecol.Bull.52 from <www.oikos.ekol.lu.se/appendix>.

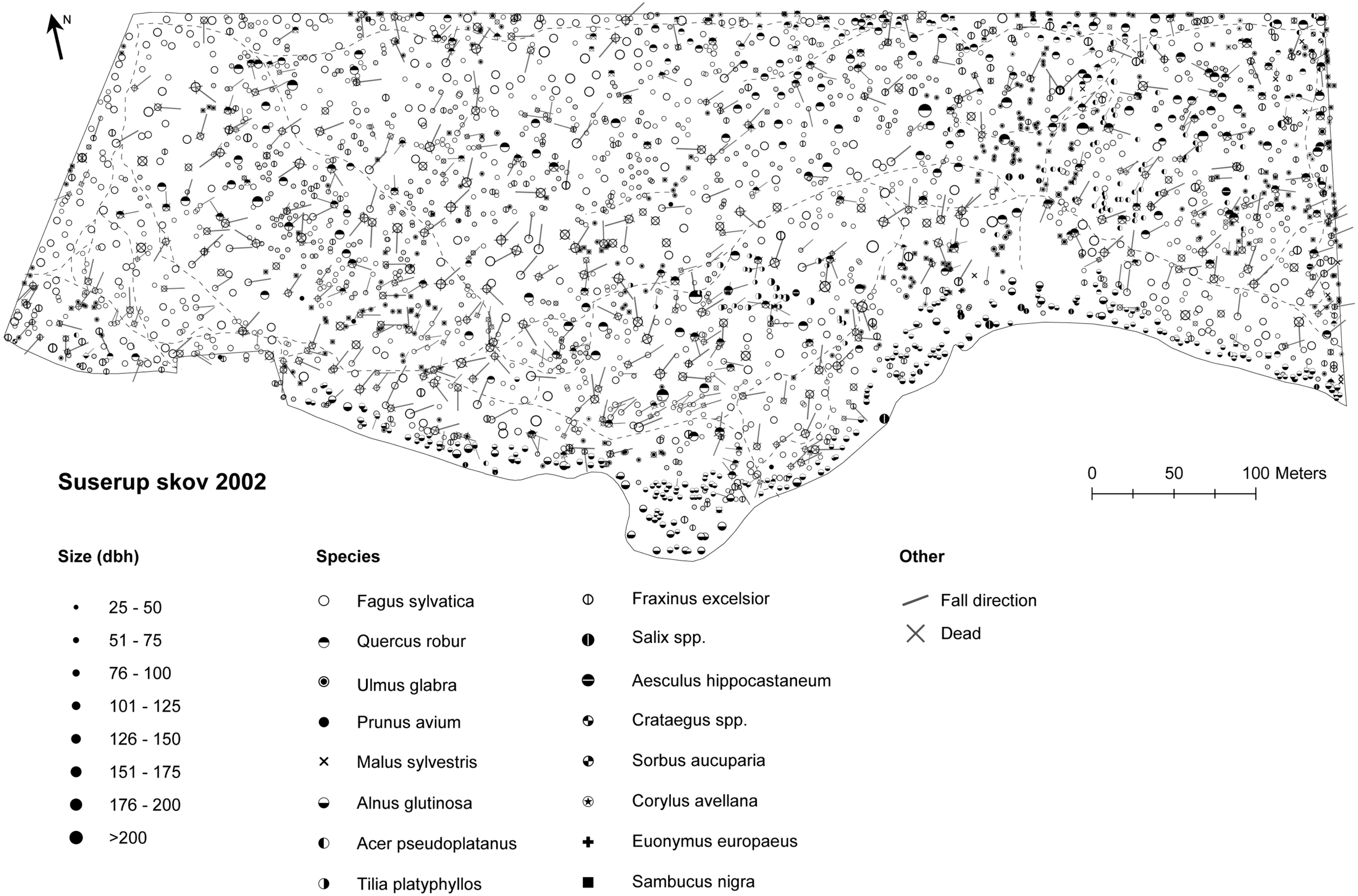

Fig. 2. Stem position map including all trees (trees ≥ 29 cm DBH) recorded in 2002. The dotted lines indicate an existing network of footpaths. Drawn by Morten Christensen, Martin Kyhn and Anders Busse Nielsen. The map is available in electronic form from the authors of the paper or download the figure as file Ecol.Bull.52 from <www.oikos.ekol.lu.se/appendix>.

Table 1. Density, basal area and volume of large trees (≥ 29 cm DBH) in the three forest parts recorded in Suserup Skov in 1992 and 2002.

	No. of trees ha^{-1}		Basal area m^2 ha^{-1}		Volume m^3 ha^{-1}		Proportion of volume (%)	
	1992	2002	1992	2002	1992	2002	1992	2002
Part A (10.7 ha)								
Fagus	46.7	56.9	19.0	18.8	381.7	370.4	68.4	67.2
Fraxinus	18.8	26.7	3.5	4.3	67.1	81.2	12.0	14.7
Quercus	5.5	4.7	5.6	4.8	97.8	84.1	17.5	15.3
Tilia	1.9	2.2	0.4	0.5	5.7	7.3	1.0	1.3
Ulmus	2.3	3.9	0.2	0.4	3.1	4.9	0.6	0.9
Other species	1.1	1.4	0.2	0.2	2.5	3.5	0.4	0.6
Total	76.4	95.9	28.9	29.0	557.8	551.3	100.0	100.0
Part B (4.9 ha)								
Acer	6.7	11.8	0.8	1.5	11.3	20.2	1.8	3.3
Fagus	30.4	35.9	10.6	10.3	209.0	201.6	33.0	32.7
Fraxinus	25.3	28.0	7.4	7.1	150.2	143.3	23.7	23.2
Quercus	18.0	16.3	14.1	13.5	244.3	235.1	38.6	38.1
Ulmus	8.2	10.2	1.0	1.1	14.0	13.7	2.2	2.2
Others species	2.0	1.4	0.3	0.2	4.0	3.2	0.6	0.5
Total	90.6	103.6	34.3	33.7	632.9	617.1	100.0	100.0
Part C (3.7 ha)								
Alnus	75.4	88.1	9.3	12.5	126.3	172.6	26.8	31.2
Fagus	30.0	34.6	10.6	11.1	208.0	216.7	44.1	39.1
Fraxinus	20.0	24.1	4.7	6.2	93.4	123.4	19.8	22.3
Quercus	3.2	2.4	2.0	1.5	34.3	25.5	7.3	4.6
Ulmus	4.1	4.3	0.4	0.5	5.7	6.6	1.2	1.2
Other species	2.4	4.1	0.3	0.6	3.9	8.8	0.8	1.6
Total	135.1	158.1	27.4	32.5	471.6	554.7	100.0	100.0

Mortality, in-growth and growth of large trees

Figure 4 presents an overview of the turnover in standing volume in the three forest parts due to mortality, in-growth and growth of surviving trees. Beech, ash and oak suffered from a loss of volume due to mortality in all parts of the forest. This was especially distinct for beech, which suffered a high loss in all forest parts. Ash mortality was highest in part B, whilst oak loss was relatively even. Alder and elm accounted for a notable amount of the volume lost due to mortality in parts C and B respectively. Beech and ash accounted for most of the in-growth volume in parts A and B, whilst alder, beech and ash accounted for most of the in-growth volume in part C. In part B, elm and sycamore maple contributed significantly to in-growth volume in addition to beech and ash. In contrast, hardly any oaks passed the 29 cm DBH threshold.

For beech, the increase in volume of surviving large trees exceeded the contribution from in-growth in all forest parts. For ash these two values were rather similar in parts A and B, while elm and sycamore maple had much greater in-growth than growth of large trees present in 1992.

Average growth rates of surviving trees were calculated between 1992 and 2002. Average rates for beech, ash, sycamore maple, lime and elm were between 4–5 mm yr^{-1} (Fig. 5). For oak the growth rate (1.9 mm yr^{-1}) was significantly lower than in other species, while alder had a slightly, but not significantly lower (3.2 mm yr^{-1}), growth rate than most other species. A more detailed analysis of average growth rates in ash, beech and oak (results not shown) revealed that the growth rates for beech and ash decreased significantly for trees > 69 and > 89 cm DBH respectively. Oak, unlike beech and ash, showed low growth rates across its size range, no doubt related to overtopping and canopy competition from beech and ash.

Diameter distributions, large trees

The distribution of trees across DBH classes changed from 1992 to 2002 (Fig. 6). In all three forest parts there was a marked increase in the number of trees smaller than ca 70 cm DBH and a less distinct decrease in the number of trees larger than ca 70 cm DBH. This was related to: 1) the loss of large trees in the 1999-storm; and 2) the vigorous recruitment of smaller trees. These changes pushed the diameter-distributions in all three parts towards a steep negative exponential curve, with a tendency to stronger recruitment in the smaller diameter-classes and a general smoothing across the larger diameter-classes (which in 1992 had a slight peak around ca 90–100 cm DBH).

Detailed study including all trees ≥ 3 cm DBH, 1-ha intensive plots

Plot A1 is, with respect to small trees (3–29 cm DBH) representative of the beech-dominated part A (without lime and sycamore maple) with elm and ash as subdominants (Table 2). The proportion of the BA in the plot made

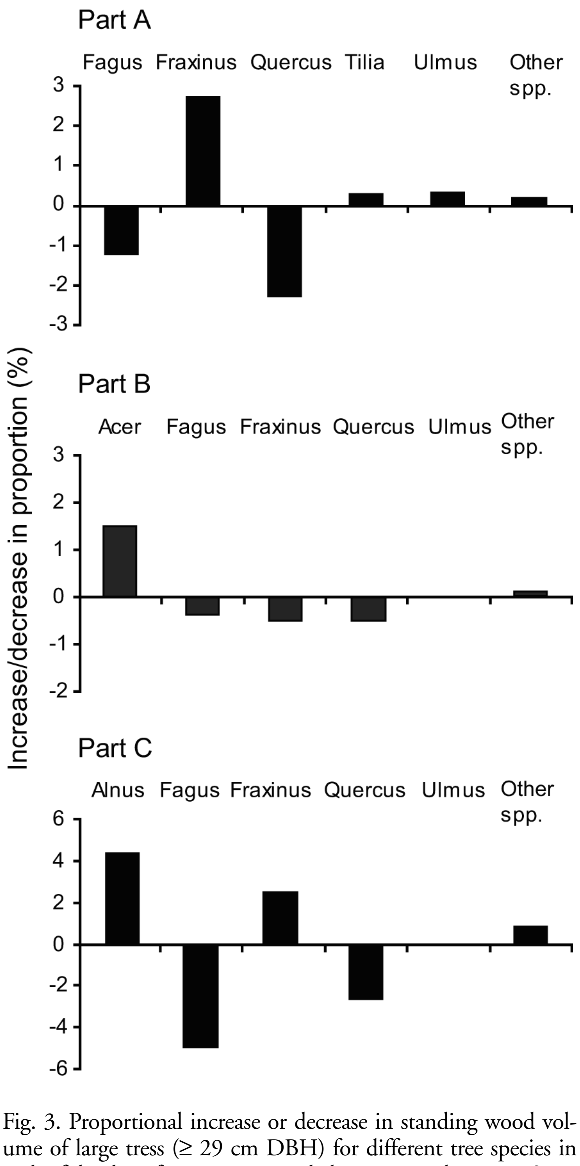

Fig. 3. Proportional increase or decrease in standing wood volume of large tress (≥ 29 cm DBH) for different tree species in each of the three forest parts recorded in 1992 and 2002 in Suserup Skov. The figures illustrate change in the relative contribution of each species to the total wood volume at each date. Note variable scaling of the y axes.

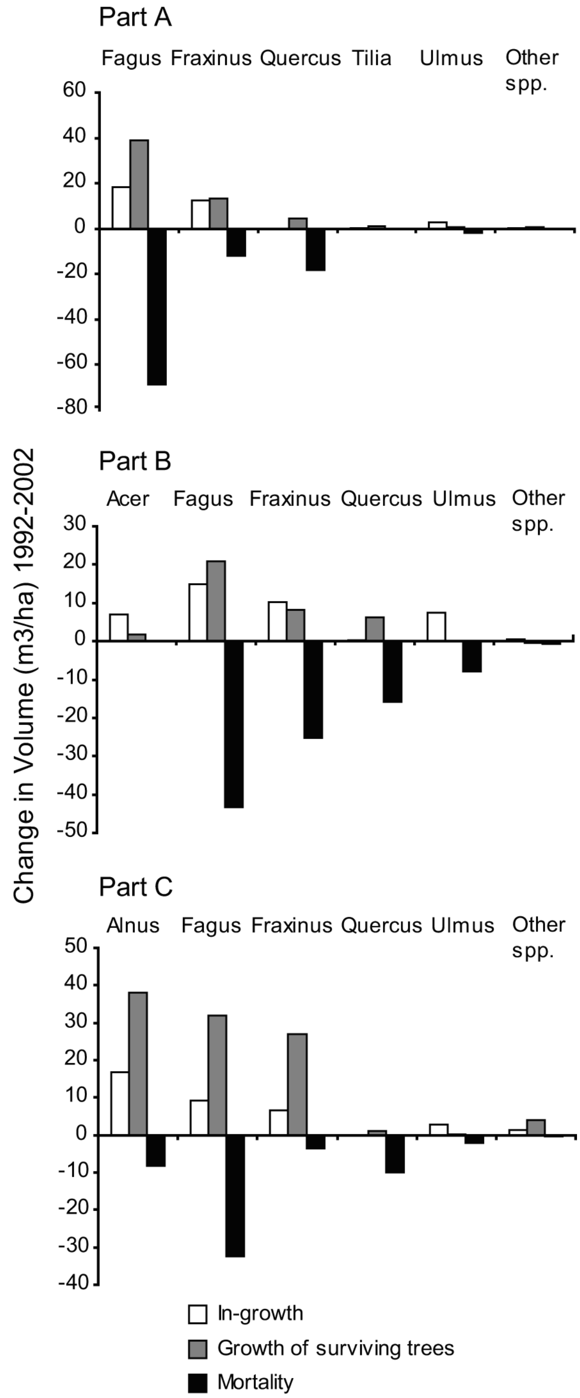

Fig. 4. The contribution to changes in wood volume between 1992 and 2002 in each of the three parts of Suserup Skov, distinguishing between "in-growth", i.e. trees growing into the survey (reaching 29 cm DBH) between 1992 and 2002, "growth of surviving trees" i.e. increase in standing volume of living trees (≥ 29 cm DBH) present in both 1992 and 2002, and "mortality", i.e. trees ≥ 29 cm DBH in 1992, which died between 1992 and 2002. Note variable scaling of y axes.

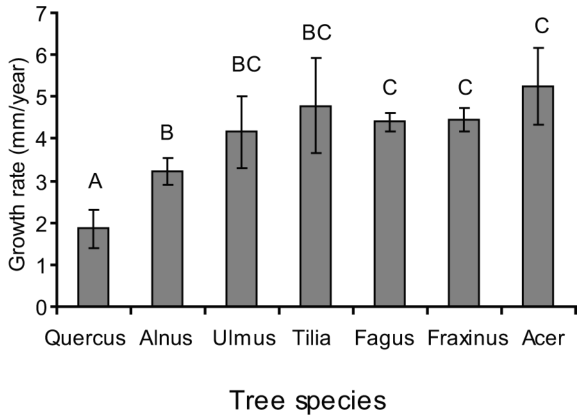

Fig. 5. Average diameter growth rates of the main tree species in Suserup Skov based on repeated DBH measurements of individual trees in 1992 and 2002. Different letters indicate tree species with significantly different average growth rates ($p<0.05$; ANOVA, Tukey test).

up by beech was very similar for small and large trees, while ash was more prominent among the small trees (Fig. 7). Elm was represented almost exclusively by smaller trees, whilst small trees of oak were absent, even though it represented 31% of the BA of large trees (Fig. 7).

The number of small trees in the plot had decreased considerably since 1992 (Table 2). This was because some trees grew over 29 cm DBH in the period and, more importantly, because mortality was high and far exceeded recruitment (Fig. 8). Change in the total basal area was not so pronounced, because the average basal area of remaining small trees relatively increased (Table 2).

Beech retained its importance among the smaller trees in the plot, and showed a distinct increasing trend in relative importance since 1992 (Table 2). Ash decreased in relative importance, because a relatively large number of trees reached 29 cm DBH and mortality was high amongst those that did not. Elm remained relatively stable, as Dutch elm disease only affected the plot slightly. In summary, this plot seems to have been rather stable with ash and beech remaining the main competitors for light and space.

Plot A2, like plot A1, is dominated by beech, but is in a section where lime is prominent and ash scarce. Beech and elm were clearly dominant among the small trees in this plot, while lime and ash were present in smaller quantities. The relative contribution to the BA of small and large trees was similar amongst beech, ash and lime (Fig. 7). As in plot A1, elm was strongly overrepresented by small trees, while oak occurred only as a large tree (Fig. 7).

The number of small trees in the plot increased slightly over the study period, with increases in the number of lime and elm and declines in the number of beech and ash (Table 2). Relatively, the proportion of ash declined dramatically from 13% in 1992 to 4% in 2002. This was due to a high proportion of ash (30%) growing into the group of large trees and only minimal recruitment (Fig. 8). The numbers and BA of lime and elm increased, and both increased their relative proportion of BA among the small trees.

Overall, the plot seems to represent a rather steady development in which oak is losing territory, whilst elm and lime are expanding.

Plot B1 is representative of the oak-rich Part B area of the forest, but has more sycamore maple than the average for part B. Among the small trees, sycamore maple, beech and elm were dominant, with the last species represented by high numbers of mostly small trees (Table 2). It is distinct that beech and ash mostly contributed to the BA of large trees, whilst sycamore maple contributed mostly to the BA of small trees (Fig. 7). Elm and oak, like in the two other plots, show completely opposite patterns. Elm thus was almost absent among the large trees but accounted for 35% of the BA of small trees, whilst oak was present only as large trees, accounting for 44% of the BA of such trees.

The total number of small trees in the plot decreased considerably due to high mortality rate except in sycamore maple. In elm the decrease was mostly due to Dutch elm disease, while competition was important for decline in beech and other species. Also the number of trees reaching 29 cm DBH was rather high, especially for sycamore maple and beech (Fig. 8). Sycamore maple increased its proportion of the basal area (Table 2) from 24 to 30% at the expense of all other tree species except ash. Overall sycamore maple seems to be strongly expanding in the plot, while oak and (to a lesser extent) beech is declining. Ash seems to be maintaining itself, whilst elm is in decline mainly due to the Dutch elm disease.

Discussion

Disturbances and the overall stability of the system

In 1999 Suserup Skov was hit by the strongest storm recorded in Denmark (since 1874). This gives a unique opportunity to evaluate the resistance and response of the ecosystem to this type of ecological disturbance. The storm caused severe wind-throw in many forests and plantations in southern Denmark. The total volume of downed or damaged trees exceeded 3.4 million m^3, equivalent to more than twice the annual cut for the whole country (Fodgaard and Enevoldsen 2001). It was therefore surprising that over the studied 10-yr period in Suserup Skov, we found that the overall standing volume of wood actually showed a slight increase.

This does not, however, mean that the forest was unaffected by the storm. The diameter distribution of trees clearly changed during the 10-yr period: partly as a result of the storm "harvesting" larger trees, and partly because of

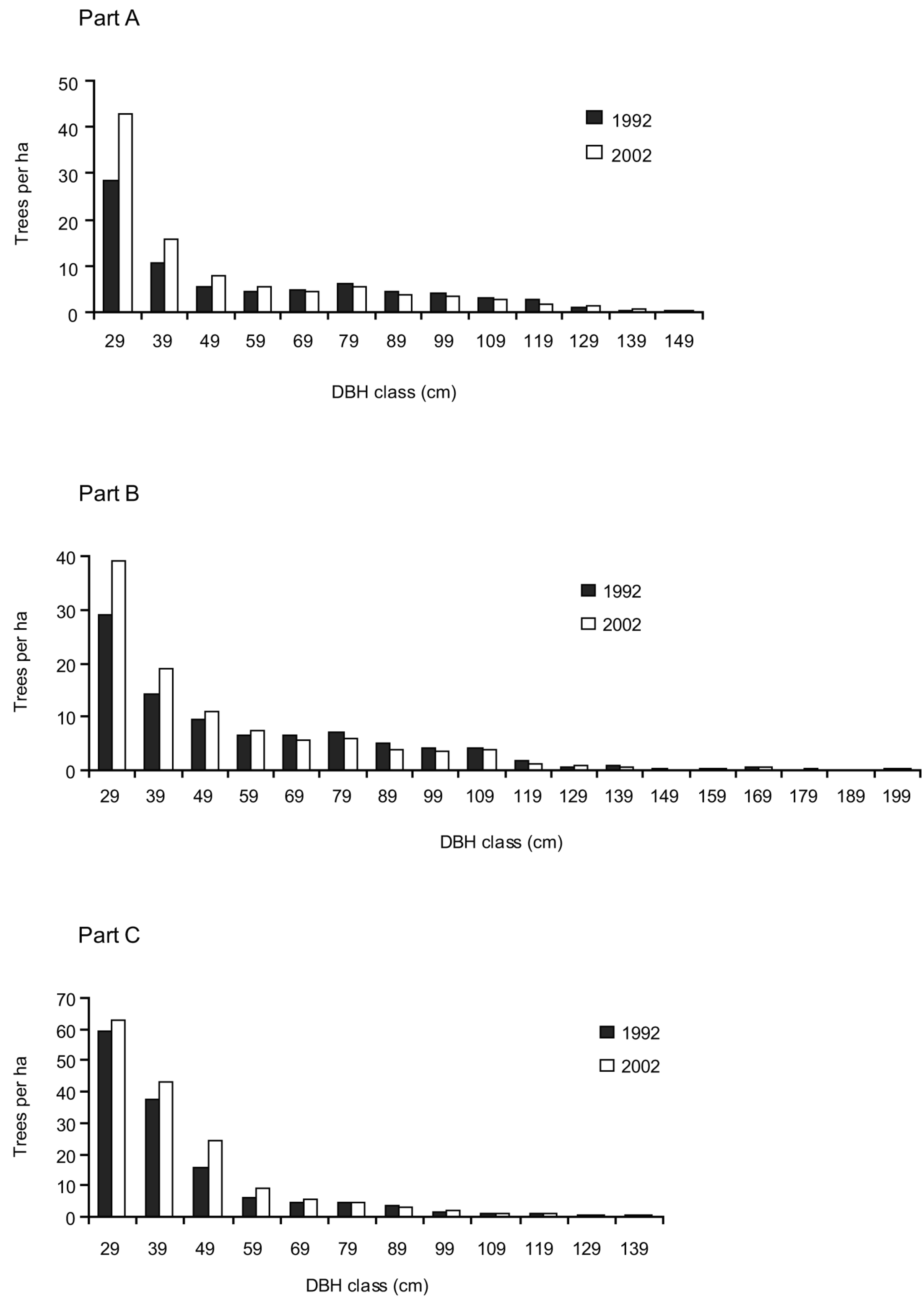

Fig. 6. Diameter class distributions (10 cm intervals) of large trees (≥ 29 cm DBH) in 1992 and 2002 in Suserup Skov. The figure shows the distributions for all trees pooled in each of the three forest parts. For each diameter class the minimum DBH is given. Note the general increase in tree numbers ≤ 69 cm DBH and decrease in tree-numbers > 69 cm DBH in parts A and B.

Table 2. Density, basal area and relative proportions of small trees (≥ 3 cm and < 29 cm DBH) in the three intensive plots recorded in Suserup Skov in 1992 and 2002.

	No. of trees ha^{-1}		Proportion of trees (%)		Basal area m^2 ha^{-1}		Proportion of BA (%)	
	1992	2002	1992	2002	1992	2002	1992	2002
Plot A1								
Fagus	412	368	41	45	5.14	5.87	43	51
Fraxinus	191	118	19	14	3.99	3.18	33	27
Ulmus	362	316	36	38	2.48	2.33	21	20
Other species	32	20	3	2	0.39	0.23	3	2
Total	997	822	100	100	12.00	11.61	100	100
Plot A2								
Fagus	209	180	36	31	3.08	2.91	52	51
Fraxinus	23	17	4	3	0.75	0.24	13	4
Tilia	41	48	7	8	0.57	0.76	10	13
Ulmus	270	310	47	53	1.43	1.75	24	30
Others species	33	27	6	5	0.11	0.08	2	1
Total	576	582	100	100	5.94	5.74	100	100
Plot B1								
Fagus	122	80	13	11	3.03	2.22	27	25
Fraxinus	39	25	4	3	0.76	0.62	7	7
Acer	141	114	15	16	2.71	2.69	24	30
Ulmus	564	471	61	65	4.15	3.06	37	35
Other species	61	34	7	5	0.44	0.26	4	3
Total	927	724	100	100	11.09	8.85	100	100

a strong recruitment of smaller trees. For trees ≥ 29 cm DBH, the diameter distribution developed closer to negative exponential curve, particularly because the 1999 storm removed a lot of large trees that originally formed a "hump" in the size-distribution. It has traditionally been believed that unmanaged, old growth forests characterised by frequent but relatively small disturbances tend to develop negative exponential (reverse-J) distributions at a relatively small scale (Cousens 1974, Oliver and Larson 1990, Peterken 1996), while early successional or severely disturbed forests tend to show normal (bell-shaped) size-distributions (Hough 1932, Veblen 1992, Peterken 1996). On this background, Emborg et al. (1996) concluded that the hump in the size-distribution could be traced back to a major regeneration event in the decades after the forest was fenced against grazing animals in 1807. The approximation of the diameter-distribution in Suserup to the negative exponential function taking place from 1992 to 2002 could accordingly be interpreted as the 1999 storm counterbalancing former cultural impact. Recent reviews (Rubin et al. 2006, Westphal et al. 2006) however, have shown that the diameter-distribution in unmanaged old growth forests often have a systematic deviation from the negative exponential distribution, quite similar to the hump in the 1992 dataset. The resulting, so-called rotated sigmoid diameter distribution appear to be pronounced in virgin beech forests in SE-Europe and seem to reflect a low mortality rate among vigorous canopy trees successfully reaching the canopy, succeeded by increasing mortality among very large, ageing trees (Westphal et al. 2006). Following this concept the change in diameter-distribution from 1992 to 2002 might in fact express a fluctuation away from a "natural" normal diameter-distribution in unmanaged beech forest caused by the heavy storm disturbance.

The other major disturbance agent observed during the study period was Dutch elm disease. This started to spread from about 1994 (Emborg et al. 1996). By 2002 dead elm trees could be seen all over the forest and several new canopy gaps had been created where groups of 10–20 m tall elm had been killed (see Christensen et al. 2007 for more details). Considering the dramatic attack, it is somewhat surprising that this is not reflected more strongly in the results of this study. Nevertheless, among the large trees, a considerable number of elm trees have died and the net diameter-growth of surviving trees is close to zero in all three areas studied (parts A, B and C, Fig. 2). This has, however, been compensated for by plentiful recruitment of smaller elms into the group of large elms, very similar to the response reported by Peterken and Mountford (1998) from an unmanaged elm stand in the UK subjected to the same disease. The more detailed analysis of the number of small elm trees in the three intensive 1-ha study plots showed a remarkable variation in turnover:

there was a net loss in plots A1 and B1, whereas in plot A2 there was a considerable net gain. This seems to reflect differences in the timing and intensity of elm disease attack. It is most likely that the attack will continue and it is too early to evaluate the full consequences of this relatively slow developing disturbance of the system. However, it is probable that it might produce a long rotation of small, slow-growing elm because vigorous trees are most susceptible to the disease (Peterken and Mountford 1998). Elm might therefore be able to maintain itself as an important

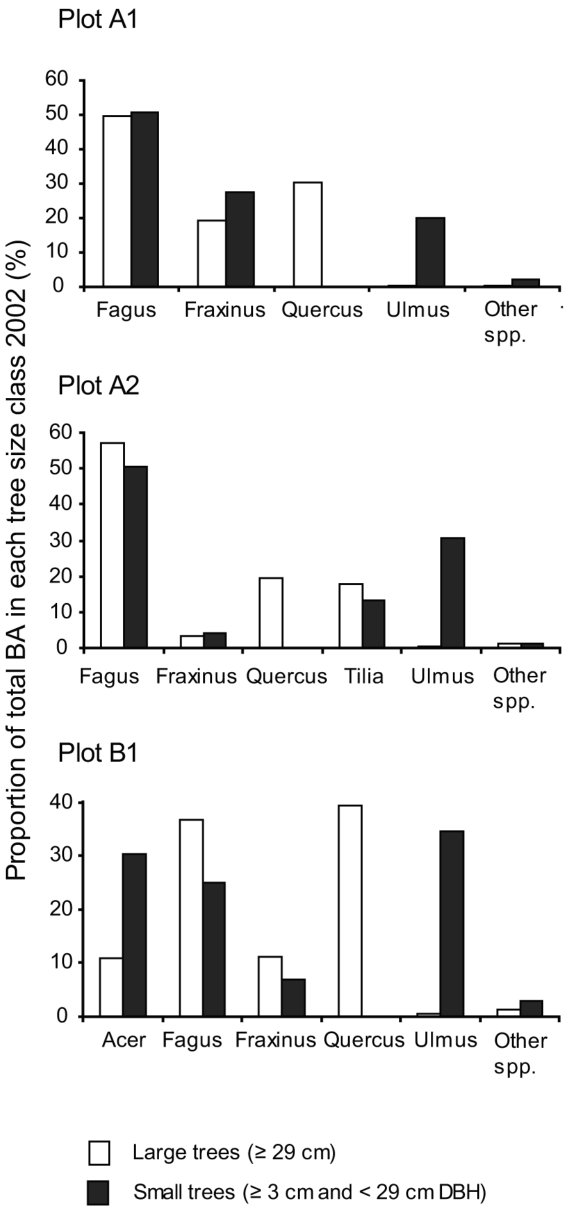

Fig. 7. The proportion of the basal area made up by each tree species in 2002 in the three intensive plots, distinguishing between small and large trees. Note variable scaling of y axes.

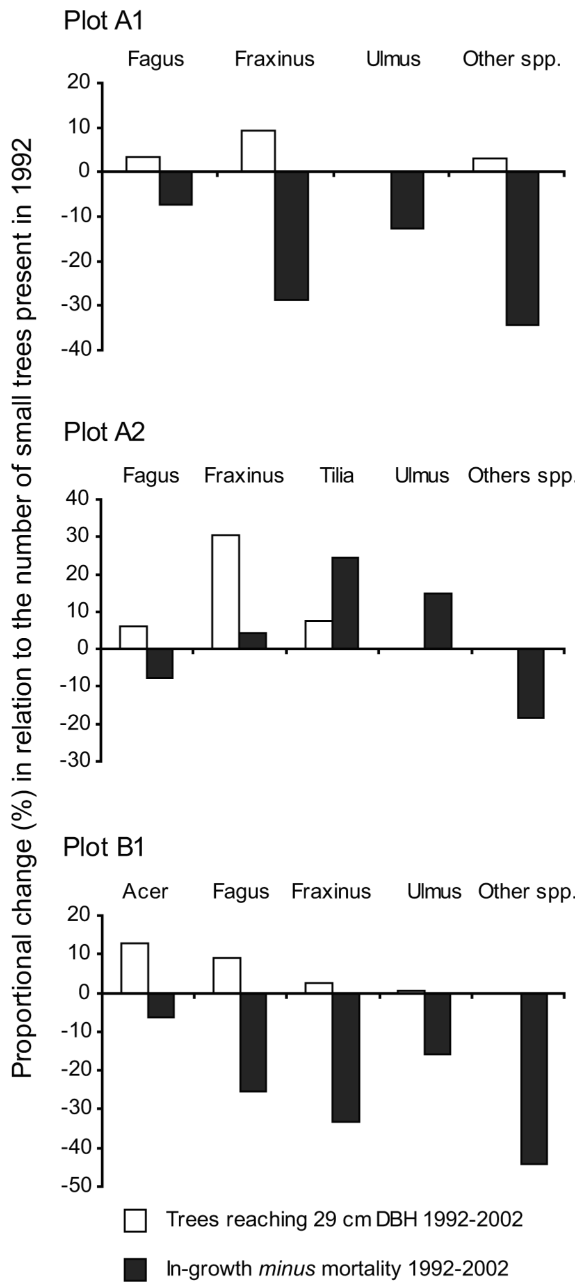

Fig. 8. Change in the number of small trees (≥ 3 and < 29 cm DBH, including all stems on each individual) between 1992 and 2002 in each of the detailed plots in Suserup Skov. White columns show the proportion of trees present in 1992 reaching DBH ≥ 29 cm in 2002, while black columns show the net change resulting from new trees reaching 3 cm DBH ("in-growth") less those that died (i.e. trees present in 1992 and dead by 2002). Negative values shows that mortality exceeded in-growth in the period, while positive values shows that in-growth exceeded mortality.

component of the understorey (Emborg et al. 1996) for many decades even if no trees succeed in reaching the canopy.

Successional trends

Oak is distinctly retreating from Suserup Skov, reflecting a long-term successional trend from open wood-pasturage to the present day forest characterized by shady, closed stands and relatively small-scale gap dynamics. Although livestock grazing stopped in the forest ca 200 yr ago, the effects of this change in ecological conditions are still apparent in the system. Beech was the first species to benefit from the retreat of oak (Heilmann-Clausen et al. 2007), but ash, lime and sycamore maple are now distinctly expanding. The latter species was recently introduced into the forest. The status of lime is more uncertain, for although it is known that it occurred in the forest ca 3000 BC (Hannon et al. 2000), it is possible the existing trees are planted and represent a reintroduction. The results of this first reinvestigation of the forest support the assumption made by Emborg et al. (1996) that lime and sycamore maple are steadily consolidating their position and moderately expanding in Suserup Skov. These two species appear to be capable of conquering some of the domain of the other major tree species in the coming generation. They have successfully established in some of the gaps formed after the 1999-storm or due to Dutch elm disease. Thus, recent disturbances seem to have accelerated a shift in species composition of the forest.

The relative importance of beech has decreased somewhat in the period primarily due to wind-throw in 1999. A considerable number of the beech trees harvested by the storm will probably be succeeded by sycamore maple or lime. In spite of this, we believe that beech will be able to maintain its present dominant position in the coming generation. Beech establishes and competes efficiently following a step-wise "stop and go" recruitment strategy based on persistent shade tolerance (Emborg 2007). Ash appears likely to maintain its position as the most important gap specialist, although lime and sycamore maple seem capable of exploiting some of the space presently held by the species – either by their ability to establish as advanced regeneration (before gap formation, ready to go when released) or due to their higher shade tolerance. It is characteristic that the relative proportion made up by the ash differs considerably among and within the intensive plots, both in space and over time. But because ash is a gap-specialist (Emborg et al. 2000, Emborg 2007), it is not surprising that the occurrence of the species is rather patchy. The species depends on episodic recruitment, especially after the irregular formation of larger gaps. The 1999 storm in this context represent an opportunity for ash to generate new regeneration patches in newly created gaps, thereby consolidating its present position.

While the present disturbance regime, where canopy gaps create semi-open conditions in a patchy and irregular pattern, is benefiting fast growing gap-specialist species, especially ash and sycamore maple, oak appears poorly adapted to establishment in canopy gaps where low grazing levels make way for a very strong competition for light and space (Hofmeister et al. 2004). Further, oak seems to have better competitive abilities under more stressful conditions, as imposed e.g. by high grazing levels or marginal water and nutrient supply (e.g. Diekmann 1996). We therefore believe that the species will disappear from the interior of Suserup Skov, unless dramatic changes occur in the disturbance regime. However, established oaks can be very long-lived and persistent: it looks certain that at least some oak trees will remain as a component of the system for many years to come.

The expansion of alder along the lake-shore (as studied in part C) conflicts partly with the prediction in by Emborg et al. (1996) that a development from alder- to ash-dominance would take place in the former meadows close to the lake. However, it is still too early to evaluate this point in detail as alder is still obviously in a phase of vigorous growth and expansion. Nevertheless, it is noteworthy that ash is expanding in part C. Unfortunately no intensive study plots were placed in part C, and hence no data on small trees was available to give insight in the recruitment patterns among small trees.

The long-term effects of succession processes in Suserup Skov are not possible to predict in detail, but it seems that irregular, relatively large-scale disturbances will result in pulses of rapid change followed by periods of adjustment and steady, continuous development. Our qualified guess is that in places sycamore maple and lime will be sustained together with the old inhabitants, beech and ash, whilst oak will continue to decline and even be eliminated if the prevailing conditions continue.

Conclusions

The analysis of the results from inventories of Suserup Skov in 1992 and 2002 point to the following conclusions: 1) between 1992 and 2002 Suserup Skov has been impacted by two important disturbances: an extreme storm and the Dutch elm disease. As an ecological system, the forest has proved relatively resistant. Although some changes have occurred in the diameter distribution, the forest ecosystem has not been pushed back into an early successional stage and no decline in the standing volume occurred. 2) The forest is still undergoing changes resulting from the cessation of livestock grazing around 1807 and the subsequent gradual cessation of management. Oak is in retreat from the stands, whilst beech is losing some terrain to ash, lime and sycamore maple after a period of extensive dominance. On the wetter ground at the lake-shore, alder is still dominant, but ash is increasing. 3) The ecological disturbance caused by the 1999-storm has interacted with and speeded up the ongoing gradual long-term successional changes predicted in 1992. A fair number of large beech trees were blown over in the storm, whilst trees in smaller diameter classes were less affected and have shown vigorous growth. Especially sycamore maple, lime and (to some degree) ash have increased in importance, being capable of filling many of the gaps created where mature beeches have fallen.

Implications for forest management and nature preservation

In Denmark, like in many other countries, the forestry ideal has for many years been influenced by the concept of even-aged monocultures. In this context Suserup Skov is in many respects far from desirable. With an increasing interest in near-natural forestry natural forest systems are however becoming increasingly interesting study objects, as means to inspire forest management (Larsen 1995, Gamborg and Larsen 2003). Thereby this study gives insight into features and mechanisms of forest ecosystems relevant in a management context. The studied ecosystem is much more structurally complex than most managed forests of the region. The ecological stability (resistance as well as resilience) of the system seems to be part and parcel of these complex structures (Larsen 1995). Even after the "storm of the century", Suserup Skov remained reasonably well covered by trees and in the gaps created trees were able to naturally regenerate or recover. Even though in total > 1400 m^3 of wood were blown over or killed by the storm (Bigler and Wolf 2007), reflecting a large timber volume compared to a managed forest, the standing volume measured a few years before and a few years after the storm were little different. Our study therefore lends support to the view that near-natural forestry, in which the structural complexity of natural forests is mimicked, may not only represent a more resistant silvicultural system in respect to ecological disturbances, but also a more stable productive system, with the potential for higher timber yields in the long run. Apparently, the intimate mixture of tree species and age classes allow different species to fill out different roles and to interact, together forming a coherent, highly productive ecosystem (but see Koricheva et al. (2006) for an alternative view).

Considerations like the above suggest that insight into natural forests structures and dynamics represents a valuable source of inspiration for forest management and nature preservation. The future role of sycamore maple will be an interesting example for managers to learn from; the same is the case for the complex interactions between beech and ash. As a straightforward example we can also draw the conclusion, that oak probably is unsuitable for managed structural heterogeneous, mixed deciduous forests, at least on rich soils, unless competitor species are limited, while oak recruits are carefully fostered during thinning/regeneration episodes. This represents a serious challenge for near-natural forestry. The problem with oak regeneration is also a serious challenge to biodiversity conservation in unmanaged forests. Oak has a long history as an important tree species in the managed lowlands of NW-Europe, and many threatened species are dependent on veteran oaks to survive (Jonsell et al. 1998, Ranius and Jansson 2000, Dahlberg and Stokland 2004). Even Suserup Skov hosts populations of several endangered insects and fungi associated with old oaks, e.g. the oak polypore *Piptoporus quercinus* which is threatened all over Europe and protected by law in the UK (Boddy et al. 2004). There is little doubt that this species is at risk of extinction in the long term – not only in Suserup Skov, but also in other protected unmanaged forests with old oaks dating back to a period with more open forest conditions. Thus, the conservation of old oak-dominated, former wood-pastures represents a true dilemma, as many such areas are dedicated to non-intervention and have relatively low grazing/browsing pressure. Part of the solution could be to rely more on forest grazing in some reserves, either by organized livestock grazing in small reserves or by introducing large stocks of wild or semi-wild grazers in large reserves, while in other reserves the vegetation is left to develop with low or variable grazing pressure. Other solutions could be to provide reserves on soil types where oak has a stronger competitive potential (e.g. poor, sand or wet, gley soils), in case such stands are available and includes species of conservation concern.

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