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The forest cycle of Suserup Skov – revisited and revised

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We quantified changes in forest structure in Suserup Skov based on two detailed inventories of forest development phases carried out in 1992 and 2002. The inventories were based on a forest cycle model for Suserup Skov, which included five sequential development phases (innovation, aggradation, early biostatic, late biostatic, and degradation). Due to a multitude of different development processes nearly half of the total area changed phase during the 10 yr, which was more than three times the expected. To a large extent, the observed changes between developmental phases followed the basic forest cycle. However, many deviations did occur, of which the most important can be summarised as: 1) the majority of the area in the innovation phase in 2002 originated from phases other than degradation. This was caused by storm damage resulting in aggregate tree fall and the massive spread of Dutch elm disease resulting in sudden die back of patches dominated by elm trees; 2) the majority of the area in the early biostatic phase in 2002 originated from phases other than the aggradation phase, due to crown expansion of trees in the early biostatic phase surrounding canopy gaps; and 3) the majority of the area in the aggradation phase in 2002 was recruited from other phases than the innovation phase, because of a well developed understorey that gradually replaced areas with a degraded canopy. These processes are discussed and presented in a revised model of the overall structural dynamics in Suserup Skov and discussed as a reference for nature-based forest management of deciduous, temperate forests.

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Since the introduction of the forest cycle concept (Watt 1947), researchers have described forest cycles in different ways and at different spatial resolution of units – from a coarse-grained landscape scale mosaic (Bormann and Likens 1979) to stand-scale structural mosaics studied within a few hectares of near-natural forest (Emborg et al. 2000) and managed forests (Grassi et al. 2002). In fact, Watt (1947) developed the concepts of the time-space mosaic (including the upgrading-downgrading cycle of change) from studies of both extremely fine-scale and large-scale ecosystems.

All authors describe forest cycles as a number of continuous sequential shifts between a series of upgrading and degrading developmental phases. When related to both time and space the forest cycle is referred to as the mosaic-cycle (Remmert 1991), and is now widely accepted as a basic description of the natural dynamics of temperate, deciduous forests (Oldeman 1990). Here patches of trees pass through the forest cycle asynchronously from patch to patch, resulting in a shifting mosaic of developmental phases.

A basic forest cycle model for Suserup Skov, Denmark was developed from an inventory in 1992 (Emborg et al.

2000). Suserup Skov is a near-natural, temperate, deciduous forest dominated by beech *Fagus sylvatica* in mixture with ash *Fraxinus excelsior*, elm *Ulmus glabra*, and oak *Quercus robur*. The forest cycle describes the overall structural dynamics as a fine-grained mosaic structure maintained mainly by gap-dynamics where the smallest structural patches are of the size of a single small canopy tree (100 m^2) (Table 1, Fig. 1). The fine-grained mosaic makes Suserup a relevant reference for further development of the "Plenter" system, small-cluster and coexisting group sys-

Table 1. Definition and duration of the five developmental phases in Suserup Skov according to Emborg et al. (2000). The phases are defined explicitly using ecological considerations and arguments and distinguished from each other by easily measurable criteria.

The innovation phase	Definition: the beginning of the innovation phase is defined as the moment when regeneration is well established in a gap, that is more than ca five vital plants > 20 cm m^{-2} (less for larger plants). Comment: often ash establishes first due to its pioneer features, with many wind-dispersed seeds almost every year. Beech establishes within a few years, typically after the first mast year. In addition to the tree vegetation, herbs, grasses, bushes and smaller trees find their place in the open and light conditions. Average duration: based on tree-coring and tree height measurements the average duration of the innovation phase is estimated to 14 yr.
The aggradation phase	Definition: the beginning of the aggradation phase is defined as the moment when the established regeneration has the competing herbal vegetation under control, which is when the regeneration has reached a height of 3 m. Comment: the first part of the phase is often dominated by fast growing ash, but often with scattered small trees like elm, wild cherry and elder. Beech often dominates the lower stratum throughout the phase. Average duration: based on tree-coring and tree height measurements the average duration of the aggradation phase is estimated to 56 yr.
The early biostatic phase	Definition: the early biostatic phase begins when the trees have reached the upper canopy layer, that is has reached a height of 25 m. Comment: most often ash dominates from the beginning, but during the early biostatic phase beech completely takes over the canopy stratum. Average duration: based on tree-coring and tree height measurements the average duration of the early biostatic is estimated to 96 yr.
The late biostatic phase	Definition: the late biostatic phase begins when the trees becomes old, have wounds and scars, and tend to become more vulnerable to biotic and abiotic damages, that is when the trees have reached a DBH of 80 cm. Comment: usually beech completely dominates the upper canopy stratum throughout this phase, while scattered undergrowth of elm and beech may occur. Towards the end of the phase the old beeches begin to degenerate, dropping even large branches creating small often short-lasting gaps in the canopy. Average duration: based on tree-coring and tree height measurements the average duration of the late biostatic phase is estimated to 108 yr.
The degradation phase	Definition: the degradation phase begins when degrading trees cause more permanent gaps in the canopy, large enough to initiate regeneration, that is gaps >100 m^2, which cannot be filled by lateral in-growth of the surrounding trees. Comment: the phase can be regarded as an interface between the late biostatic and the innovation phase. It may start suddenly as a result of wind-throw, or it may develop gradually as old trees lose vitality and eventually die. Well-established regeneration in a gap defines the end of the degradation phase and the start of a new turn of the forest cycle. Average duration: based on tree-coring and tree height measurements the average duration of the degradation phase is estimated to 10 yr.

One turn of the basic forest cycle in Suserup Skov is, accordingly, estimated to 284 yr on average.

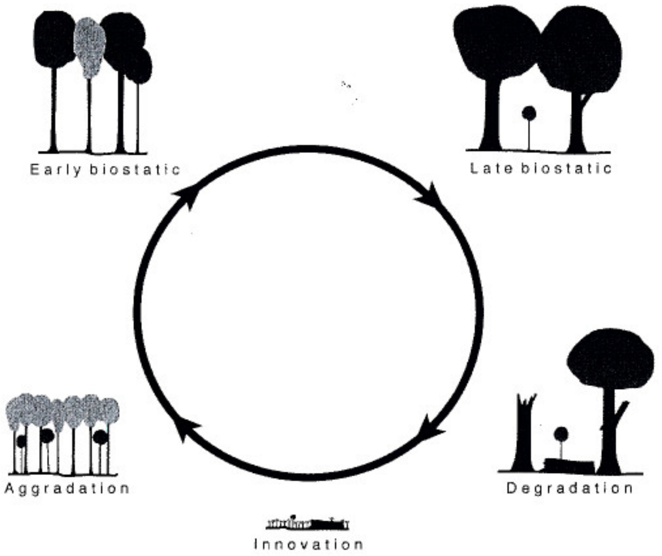

Fig. 1. Model of the basic forest cycle, including five developmental phases termed the innovation, the aggradation, the early biostatic, the late biostatic and the degradation phase, in accordance with Oldeman (1990). The definitions of the phases are described in Table 1.

tems which are highly topical as tools for nature-based management of deciduous forests in many NW European countries. These silvicultural systems are widely applied in nature-based forest managed to create irregular and diverse stand structures in conifer and mixed stands in central and eastern Europe (Schütz 2002). In contrast, experiences with them in management of deciduous forests are limited.

Forest cycle models – like the one developed for Suserup Skov – have in many cases supported the understanding of the basic dynamics in natural forests from tree generation to tree generation (Standovár and Kenderes 2003). However, several authors have argued that their simplification can lead to misinterpretation because of the exclusion of complexity of developmental processes (Franklin et al. 2002, Standovár and Kenderes 2003). Muth and Bazzaz (2002) describe the importance of crown expansion at gap edges for the forest dynamics and Pontailler et al. (1997) and McCarthy et al. (2001) describe the complexity of regeneration and the process of understorey trees gradually taking over the canopy layer.

Similar processes have been observed in Suserup Skov. Bigler and Wolf (2007) studied the impact of the 1999 hurricane in Suserup Skov, and documented how the wind created numerous really small gaps (10–100 m^2). A dendro-ecological study Emborg (2007) documented how beech in Suserup Skov can utilise such small temporary canopy gaps to approach the canopy, step by step, as part of a "stop and go" strategy. Finally, in a detailed study of the forest structure Nielsen and Hahn (2007) document well-developed understorey and concludes, that the light patterns and dynamics on the forest floor are extremely complex and to a large extent determined by understorey characteristics and the canopy dynamics in the surroundings of any particular patch. These studies all point to a rich and detailed variation in the processes, which appears to have substantial impact on Suserup Skov. However, our understanding of their impact on the overall structural dynamics in terms of changes between developmental phases in Suserup Skov remains fragmented.

A re-inventory in 2002 made it possible to quantify the different development processes in terms of changes between developmental phases on the base of 10 yr of observation since the first inventory in 1992. This allowed for a critical evaluation and refinement of the basic forest cycle. Correspondingly, the objectives of this paper are to 1) quantify changes in development phases from 1992 to 2002 with reference to the basic forest cycle model; 2) evaluate and further develop the basic forest cycle model; and 3) discuss the implications of the results in the context of nature-based forest management.

Methods and materials

Study site

Suserup Skov is a 19.2 ha forest reserve located in the central part of Zealand (Sjælland) in eastern Denmark. The forest is a near-natural, temperate, deciduous forest dominated by beech in mixture with ash, elm, and oak. The soil is glacial sediments where both clay, loamy and sandy till occur (Vejre and Emborg 1996). The study was carried out in "part A" of Suserup Skov (10.60 ha, see Emborg et al. 1996), for which pollen analysis suggests a history of forest cover during the last 6000 yr (Hannon et al. 2000). Management has been minimal since 1854 and since 1961 Suserup Skov has been a strict non-intervention reserve (Emborg and Fritzbøger 1996, Heilmann-Clausen et al. 2007).

Climate and disturbances from 1992 to 2002

Climatically, the 10-yr period from 1992 to 2002 was not substantially different from previous decades. Average annual temperatures were 8.3°C, which is slightly higher than the average from 1874 to 2003 of 7.6°C, and varied from 6.8°C (1996) to 9.2°C (2002). The average annual precipitation was 741 mm and varied from 505 mm (1996) to 905 mm (1999), compared to an average of 674 mm from 1874 to 2003 (Cappelen 2004). No exceptional droughts or extremely cold winters occurred in the period. On 3 December 1999 the southern part of Denmark was hit by a severe storm (mid-latitude cyclone). The storm was accompained by heavy rain after a long period with low precipitation, causing many trees in Suserup Skov to uproot. Scattered single trees were damaged throughout the forest, while some areas experienced heavier damage, resulting in a range of small to intermediate sized gaps (for a detailed description of the storm and analyses of the impact on Suserup Skov, see Bigler and Wolf 2007). Another important disturbance event in the 10-yr period was the arrival and subsequent spread of Dutch elm disease caused by *Ophiostoma ulmi* sensu lato beginning in 1995. Elm mortality continued until 2002, and created gaps of varying size where patches of elm formed the uppermost canopy layer.

Mapping of the developmental phases

The development phases were mapped in winter 1992/1993 and autumn 2002. The mapping was done on the basis of "stem-position maps" (1:500) including all trees >29 cm DBH (Emborg et al. 1996, Emborg and Heilmann-Clausen 2007). The canopy defined the phase of a given patch in the forest; i.e. regeneration on the forest floor was only defined as an innovation phase patch when there was a gap above, and trees between 3 and 25 m height were only defined as a patch of aggradation phase if they formed the canopy layer of that patch (Emborg et al. 2000). This way spatial overlap between neighbouring patches was avoided. The spatial resolution corresponded to a minimum patch size of 100 m². Clinometers, callipers, and measure lines were used to ensure a strict mapping of patches according to the phase definitions (Table 1). Each patch of the mosaic was marked on field charts.

Data analysis

All development phases in the 1992 and 2002 inventories were digitized with AutoCad and incorporated into ArcGIS. Spatial Analyst and Geo Processing tools in ArcGIS were used for exact (1 m²) calculation of changes in the areas of development phases between 1992 and 2002. However, the presentation of the results has been rounded off to a precision of 100 m², to provide a framework for analysing and discussing the observed changes. We performed the following two sets of calculations for the expected changes, presuming a hypothetical dynamic phasic equilibrium (Watt 1947), also called the shifting-mosaic steady state (Bormann and Likens 1979) in which the aggregate area of a phase is directly proportional to the duration of that phase:

1. The expected aggregate area of each of the five phases was calculated, using the equation:

$$E_a = (i/I) \times A \tag{1}$$

where, E_a is the expected area, i is the duration of the phase, I is the duration of the full forest cycle (284 yr), and A the area of the whole plot (10.60 ha).

2. The expected turn over of phases during the 10-yr period was calculated using the equation:

$$E_t = (Y/i) \times E_{1992} \tag{2}$$

where E_t is the expected turn over, Y is the studied period (10 yr), i is the duration of the phase and E_{1992} is the aggregate area of the phase in 1992.

Results

Shifting mosaic and aggregate area of the phases

The maps of the shifting mosaics from 1992 and 2002 are shown in Fig. 2. Despite the recent disturbances caused by the severe 1999 storm and the attack of Dutch elm disease, the aggregate area of the individual phases remained surprisingly stable and close to the expected aggregate areas (Fig. 3). Moreover, the average patch size of each phase hardly changed (Table 2). The number of patches in the innovation phase, however, increased considerably, leading to an increment in the aggregate area of the innovation phase from 0.24 ha in 1992 to 0.80 ha in 2002, which was a larger increment than expected (according to eq. 1) (Fig. 3). Also, the aggregate area of the continuing upgrading phases of aggradation and early biostatic was larger than expected. In contrast, the area of the degrading phases of late biostatic and degradation was less than expected, which was a direct effect of the 1999 storm (Fig. 3).

Turn over in phases 1992–2002

A closer look into the dynamics of the individual patches from 1992 to 2002 uncovered additional information about several important processes during the 10-yr period. For all phases, except degradation, the observed turn over in the 10-yr period was larger than expected. In total, 4.96 ha changed phase during the period corresponding to 47% of the total plot (10.60 ha), which was nearly three fold the expected turn over (Table 3).

The high turn over in phases observed over the 10-yr period was caused by a multitude of development series which are illustrated in Fig. 4. To a large extent these mechanisms followed the basic model of the forest cycle (Emborg et al. 2000). The most important series can be summarised as follows: 1) a major part (0.12 ha of 0.24 ha) of the innovation phase in 1992 changed into the aggradation phase in 2002. 2) A major part (0.97 ha of 2.29 ha) of the aggradation phase in 1992 changed into the early biostatic phase in 2002. 3) A major part (0.16 ha of 0.28 ha) of the degradation phase in 2002 originated from areas of the late biostatic phase in 1992.

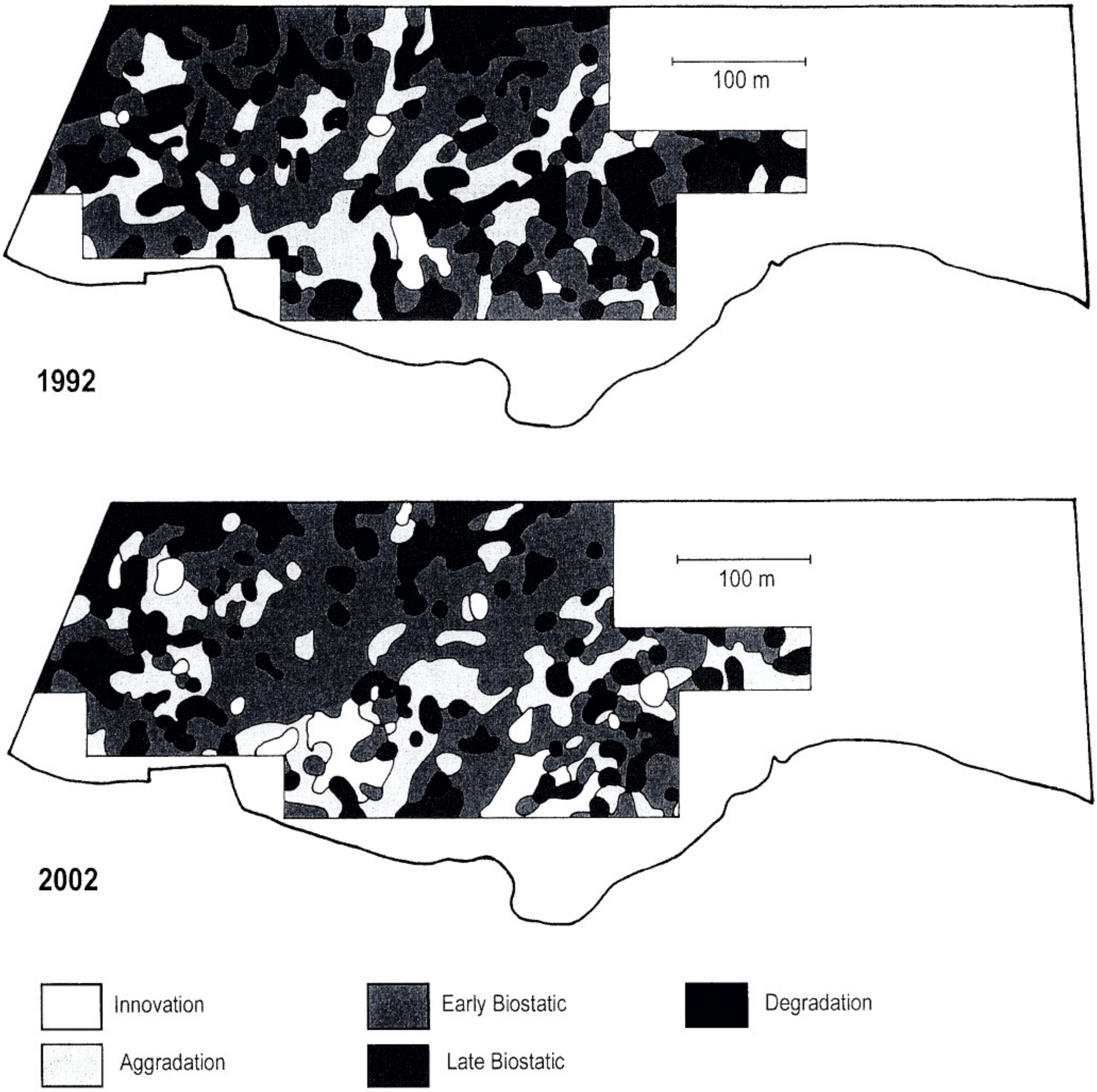

Fig. 2. Maps of the developmental phases in 1992 and 2002.

However, deviations from the basic forest cycle (Fig. 1) occurred in all the developmental phases from 1992 to 2002, of which the most important can be summarised as follows: 1) the majority of the area that changed into the innovation phase originated from phases (0.74 ha) other than the degradation phase (0.05 ha). 2) Nearly half of the area (0.84 ha) that changed into the early biostatic phase originated from phases other than the aggradation phase (0.97 ha). 3) The majority of the area that changed into the aggradation phase originated from phases (1.35 ha) other than the innovation phase (0.12 ha).

Discussion

Our results indicate that the development of the forest structure from 1992 to 2002 does not follow the basic forest cycle model strictly from patch to patch over time. Many different processes and changes between developmental phases that deviate from the basic model occurred, which may also serve to counterbalance each other – as illustrated by the arrows pointing back and forth between phases in Fig. 4. These deviations from the basic forest cycle model resulted from either: 1) the 1999 storm and the

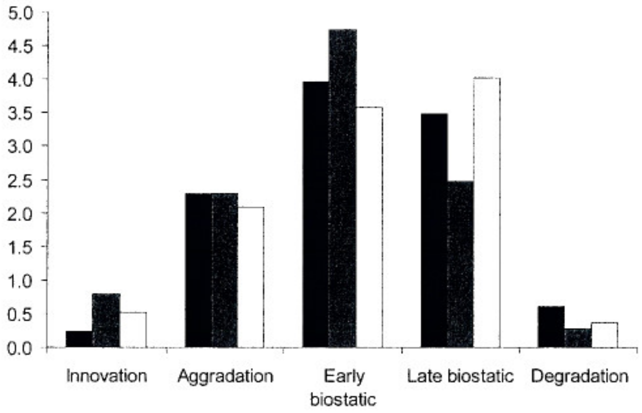

Fig. 3. Aggregate area of the different phases observed in 1992 (black) and 2002 (grey) and expected aggregate area of the phases in 2002 (E_a) (white) according to eq. 1.

arrival of Dutch elm disease in 1995, 2) crown expansion of canopy trees in the early biostatic phase, or 3) a well developed understorey that gradually replaced the canopy. In the following each of these processes is discussed with reference to the basic forest cycle.

1) Creation of the innovation phase

The aggregate area of the innovation phase increased considerably from 0.24 ha (2%) in 1992 to 0.8 ha in 2002 (8%). This is directly related to the 1999 storm and the spread of Dutch elm disease. The proportion of gaps in 2002, however, corresponds to reports from other wind disturbed NW European beech dominated forest reserves, e.g. the Fontainebleau reserve (9–11%) in France (Koop and Hilgen 1987).

In the 10-yr period the 1999 storm was the most important initiator of gaps > 100 m². The extremely strong winds during the storm (Bigler and Wolf 2007) caused direct mortality and damage to both healthy canopy trees as well as senescent ones. These processes explain why approximately half the area in the innovation phase in 2002 originated from patches that were in the early biostatic or late biostatic in 1992 (Fig. 4). Bigler and Wolf (2007) found that the 1999 hurricane also created a large number of gaps (> 20% of the area of part A), of which many were small gaps (10–100 m²). The present study was too coarse-grained (only patches > 100 m² were monitored) to capture the effect of the small gaps on the overall forest dynamics. Crown expansion (see below) probably explains a substantial part of the decrease in gap area after the storm; 20% in 1999 (according to Bigler and Wolf 2007) vs 8% in 2002 (according to the present study). However, it seems clear from other studies (Emborg 2007, Nielsen and Hahn 2007) that small, temporary canopy openings have substantial influence on the development, growth and vitality of sub-canopy trees. Even very small canopy gaps are reported to initiate substantial growth responses in understorey trees (Canham 1985, 1990).

The spread of Dutch elm disease was the second major factor that initiated patches of the innovation phase in the 10-yr period. Dutch elm disease spread rapidly in Suserup Skov after its arrival in 1995, causing mortality of nearly all elms > 10 cm DBH by 2002. Many of the dead trees formed patches in the aggradation (and early biostatic phase). Most often, such areas changed into the innovation phase, which explains why nearly half of the area (0.35 ha) in the innovation phase in 2002 originated from patches of the aggradation phase in 1992 (Fig. 4). Similar mortality patterns of elm in unmanaged forests have also been observed in Austria (Mayer and Reimoser 1978), UK (Peterken and Mountford 1998) and Germany (Huppe and Röhrig 1996). The attack of Dutch elm disease and its impacts can be regarded as a peculiar example of the rich variety of disturbances that are involved in shaping the dynamics of temperate deciduous forests.

2) Crown expansion

In forest ecosystems, light is a critical resource (Emborg 1998, Grassi et al. 2002), which is particularly patchy in nature (Nielsen and Hahn 2007), so that trees actively dis-

Table 2. Aggregate area, number of patches and average patch size observed in 1992 and 2002 according to the five developmental phases.

	1992			2002		
Phase	Aggregate area (ha)	Number of patches	Average size (m²)	Aggregate area (ha)	Number of patches	Average size (m²)
Innovation	0.24	5	476	0.80	15	533
Aggradation	2.29	27	848	2.28	21	1088
Early biostatic	3.97	27	1469	0.75	32	1484
Late biostatic	3.49	52	671	2.48	49	506
Degradation	0.61	16	384	0.28	14	203
Total	10.60	127	834	10.60	131	809

Table 3. Expected and observed turn-over of phases from 1992 to 2002.

Phase	Duration[1] yr	Area (ha) 1992	Expected turnover (E_t)[2] ha	%	Observed turnover[3] ha	%
Innovation	14	0.24	0.17	71	0.23	96
Aggradation	56	2.29	0.41	18	1.48	65
Early biostatic	96	3.97	0.40	10	1.03	26
Late biostatic	108	3.49	0.31	9	1.63	47
Degradation	10	0.61	0.61	100	0.59	97
Total	284	10.60	1.89	17	4.96	47

[1] Duration of phases is according to Emborg et al. (2000). See also Table 1.
[2] According to eq. 2.
[3] According to Fig. 4.

place their crowns towards high-light patches, such as canopy gaps (Muth and Bazzaz 2002).

In Suserup Skov, we observed that patches surrounded by the early biostatic phase were most vulnerable to crown expansion processes. Frequently, small patches of e.g. innovation, aggradation and degradation simply closed and larger patches decreased considerably in size due to crown expansion of surrounding canopy trees in the early biostatic phase. Such canopy expansions explain why one quarter of the area in the degradation phase (0.15 ha of 0.61 ha) and innovation phase (0.07 ha of 0.24 ha) changed into the early biostatic phase in 2002 (Fig. 4). There was also a 0.62 ha change from the late biostatic phase in 1992 to the early biostatic phase in 2002 (Fig. 4). This is likely the result of trees in the early biostatic phase that expanded their crowns into gaps created by the 1999-storm related damage and mortality of trees in the late biostatic phase. Similar processes of beech tree crown expansion into canopy gaps have been reported from unmanaged temperate beech forests in central Europe (Koop and Hilgen 1987, Knapp and Jeschke 1991, Tabuka and Meyer 1999) and experimental studies on canopy displacement at forest gap edges in North American mixed hardwoods with *Fagus grandifolia* (Muth and Bazzaz 2002).

The fact that arrows points to the early biostatic phase from about all other phases, could be taken as an indication of the "expansive vitality" of this phase and the derived ability to expand borders at the expense of other phases. Far fewer arrows points to the late biostatic phase which might indicate the abating ability of older trees to expand their canopy.

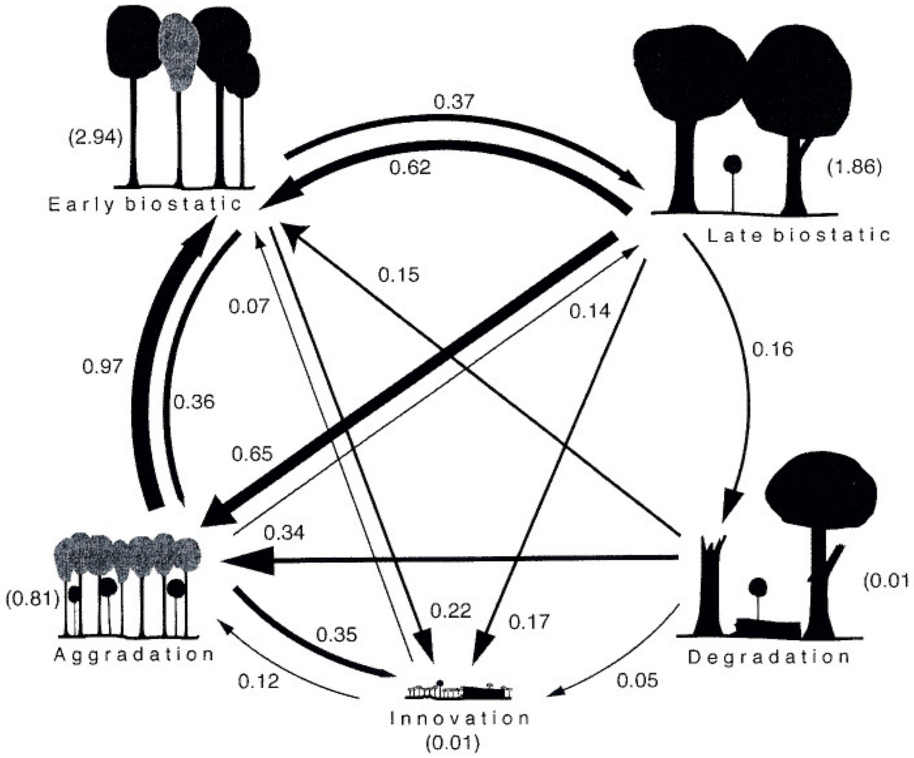

Fig. 4. Refined forest cycle model illustrating area of changes and non-changes (in ha) 1992–2002. The numbers written next to the illustrations of the phases are areas which not changed. The thickness of the arrows indicate the importance of different processes.

It is not surprising that vital trees in the early biostatic phase expand their crowns toward canopy openings, thereby causing a turn-over in phases. What is surprising is the amount of shifts in phases that, according to our interpretation, can only be explained by this process. Consequently, lateral crown expansion does not only have implications for individual trees – it is also an important process for the overall structural dynamics because it initiates substantial turn-over in terms of phases. However, processes related to lateral crown expansion are seldom revealed as players in the overall structural dynamics of natural forests because of a coarser scale in the mapping of developmental phases. From this perspective further research into crown expansion dynamics and speed of different tree species in relation to development phases and processes could improve our understanding of the overall structural dynamics in deciduous natural forests.

3) Understorey trees taking over the canopy

Understorey characteristics are often overlooked in studies of the structural dynamics in unmanaged forests (McCarthy et al. 2001, Franklin et al. 2002) and beech is often described as a heavy shading species which does not allow the understorey to develop (Knapp and Jeschke 1991, Jenssen and Hofmann 1996). However, our results document well-developed understorey in Suserup Skov and indicate that the release of understorey trees following canopy breakdown is a main driving process, enabling most patches to bypass the innovation phase. When interpreting our results, the majority of overstorey-understorey transitions appear to be from beech to beech in wind-throw patches with understorey trees (often referred to as advanced regeneration).

The change from the early biostatic to the aggradation phase is a direct result of wind-throw in patches with a well-developed understorey. Since beech trees account for more than half of the total number of trees in the early biostatic phase damaged in the 1999-storm (Bigler and Wolf 2007) much of the understorey developed as advanced regeneration beneath a beech canopy. Similarly, the change from the late biostatic to aggradation phase is also a result of wind-throw. Moreover, since few ash grow to a DBH > 80 cm in Suserup Skov (Emborg et al. 2000), and because very few oaks were damaged in the 1999 storm (Bigler and Wolf 2007), trees that developed beneath a beech canopy appears to account for the majority of this change as well. This interpretation is supported by Emborg (2007) who shows that beech in Suserup Skov is able to hold a position in the understorey for many years in the deep shade of canopy beech trees, and still remain the capacity to respond to release.

Well developed understorey in wind-thrown patches explains why more than half of the area (1.35 of 2.28 ha) in the aggradation phase in 2002 was either in the early biostatic phase (0.36 ha), late biostatic phase (0.65 ha), or degradation phase (0.34 ha) in 1992 (Fig. 4). Finally, well developed understorey explains why nearly all the degradation phase areas bypassed the innovation phase and developed directly into the aggradation phase during the 10-yr period (Fig. 4). The character of such well-developed understorey in Suserup Skov has been exemplified on profile diagrams by Nielsen and Hahn (2007).

Concluding remarks

The quantification of different developmental processes in Suserup Skov using a small minimum patch size (100 m^2) exemplifies the "unpredictable" nature of forest with natural dynamics. Many and complex developmental processes and an intensive dynamic were identified. The irony is that the discovered processes apparently to a large extent counterbalance each other with the result of only small changes in the aggregate area of the different developmental phases over the 10-yr observation period. This could be used as an argument for applying a more coarse-grained scale, which is the traditional approach taken in many well-known examples of forest cycles like e.g. Leibundgut (1959) and Zukrigl et al. (1963). However, the high spatial resolution applied in the two here presented inventories of Suserup Skov (1992 and 2002) enables an interesting dive under the surface (Fig. 4) and the identification and quantification of many important processes which were only ascribed a secondary role in the hitherto understanding of the overall structural dynamics in forest (Fig. 1).

During the 10-yr observation period, the turn over in phases as well as the number of processes deviating from the basic forest cycle model was surprisingly high. The effects of the 1999-storm and the arrival of Dutch elm disease in 1995 explain some of these deviations. However, the majority of deviations seem to occur because the basic forest cycle model does not incorporate the process of lateral crown expansion or the process of canopy replacement by understorey trees.

The process related to well developed understorey manifests in patches by-passing the degrading part of the forest cycle and also the innovation phase. As such understorey characteristics played an unexpected large role in the overall structural dynamics in Suserup Skov. From this perspective further research into these dynamics would appear to be a valuable supplement to the current focus on regeneration processes related to gap-dynamics in nature-based management of beech dominated forests in Europe.

Also lateral crown expansion by canopy trees surrounding gaps or patches with up-growth played a larger role in the spatial and temporal structure and dynamics than expected. Especially trees in the early biostatic phase closed small patches and reduced larger ones dramatically by lateral crown expansion. Consequently, the results indicate that improved understanding of the processes related to lateral crown expansion of individual trees and borderline dynamics between patches of trees is crucial for the further development of the "Plenter" system, small-cluster and coexisting group systems that all aims at fine grained mosaic structures and structural dynamics with parallels to those observed in Suserup Skov. These selective/group systems are highly topical in the ongoing adaptation to more nature-based management of deciduous temperate forests in many NW European countries.

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