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The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark

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Abstract

Nature-based silviculture is a promising approach to meet the criteria for sustainable forestry. This brings the natural forest into focus as a basic reference for forest management. The present study focuses on the structural dynamics of a near-natural temperate deciduous forest in Denmark as a reference for forestry. The study was conducted in Suserup Skov (55° 22′N, 11° 34′E, 19.2 ha), an ancient woodland with a long history of low human impact. It is a mixed deciduous forest dominated by *Fagus sylvatica* L. and *Fraxinus excelsior* L. with some *Quercus robur* L. and *Ulmus glabra* Huds. The dynamics and structures of Suserup Skov can be described in time and space according to the mosaic-cycle concept.

A specific model of the forest cycle in Suserup Skov was developed, including five sequential phases. The typical duration of each phase was determined: innovation (14 years), aggradation (56 years), early biostatic (96 years), late biostatic (108 years) and degradation (10 years) phases, equalling some 284 years for the full cycle. In principle, the forest cycle takes place at any given patch of the forest, asynchronous from patch to patch, resulting in a shifting mosaic of the constituent phases. The mosaic, mapped in a 10.65-ha plot in 1992, had an average patch size of 839 m^2, ranging from 100 to 12 730 m^2. The patches of the shorter phases (innovation, degradation) were on average considerably smaller than the patches of the longer phases, which can be explained partly by fusion of neighbouring patches. The aggregate areas of each phase were almost directly proportional to their respective duration, suggesting that the shifting mosaic was close to the steady state. The disturbance regime and disturbance history of Suserup Skov is discussed. It is concluded that several disturbances of smaller scale had occurred during the past centuries and that the most influencing recent disturbance has been the long period of human influence by rural, woodland management (pannage, pasture and coppicing) before the enclosure of the forest in 1807. The Suserup Skov example shows that a temperate deciduous forest under a relatively calm disturbance regime can develop into a very fine-grained mosaic, apparently approaching the shifting mosaic steady state within a rather small area. The structural steady state in Suserup Skov occurs, even though the overall species composition is still under successional change. Further, ‘climax microsuccession’ from *Fraxinus* to *Fagus* occurs as an integral part of the forest cycle in Suserup Skov. Cyclic and directional processes are intermingled in Suserup Skov, highlighting the complex relationships between the concepts of

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succession and climax. The paper finally exemplifies how natural forests can be used as a reference for silviculture, nature conservation and landscape planning.

Keywords: Climax microsuccession; *Fagus sylvatica*; *Fraxinus excelsior*; Mosaic cycle; Nature-based silviculture; Shifting mosaic; Steady state

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1. Introduction

It is a matter for debate whether traditional forest management based on clear cutting of even-aged monocultures fulfils the central criteria for sustainability, for example (i) protection of biodiversity; (ii) nutrient cycling; and (iii) securing long-term stability of the forest ecosystem (Franklin, 1988; Franklin, 1995; Larsen, 1995; Christensen and Emborg, 1996). Scientists, foresters and the forestry authorities have, during the last ten years, discussed many aspects of sustainable forestry. *Nature-based forestry* is now widely accepted as a promising approach to meet the criteria for sustainable forest management (Koop, 1989; Boot et al., 1993; Broekmeyer and Vos, 1993; Schlaepfer et al., 1993; Attiwill, 1994; Bradshaw et al., 1994; Franklin, 1995; Christensen and Emborg, 1996; Larsen, 1997). Nature-based forestry aims to achieve reasonable economic targets while minimising modification of forests from their natural condition. Ideally, forestry operations should not result in lasting impact on the biological and biogeochemical components of the system. With the silvicultural approach of mimicking natural forest structures, processes and dynamics, the natural forest ecosystem comes into focus as a basic reference for forest management. The present study focuses on the structural dynamics of a near-natural temperate deciduous forest in Denmark, dominated by *Fagus sylvatica* L. (beech), as a reference for forest management.

A.S. Watt (Watt, 1925; Watt, 1947) developed a conceptual model of *the forest cycle* describing the continuous sequential shift between a series of upgrading and downgrading developmental phases: gap, regeneration, building, mature, ageing, degenerating, gap, etc. The gap triggers regeneration and initiates a new turn of the cycle. Such cyclic gap-dynamics take place at any given patch of the forest, though asynchronous from place to place, resulting in a shifting mosaic of the constituent phases of the forest cycle. The whole system in time and space is referred to in short as the mosaic-cycle (Remmert, 1991), and is widely accepted as a basic description of the natural dynamics of temperate deciduous forest (Mueller-Dombois, 1987; Peet and Christensen, 1987; Oldemann, 1990; Veblen, 1992). The dynamics of pure beech forests in western France (Faille et al., 1984; Koop and Hilgen, 1987; Lemée, 1987; Lemée, 1989) and mixed forests in central Europe (Mayer and Neumann, 1981; Korpel, 1982) have been described by the mosaic-cycle concept. Successional phenomena may occur within the cyclic dynamics of the climax as an integral part of the forest cycle (Watt, 1947). Forcier (1975) introduced the term *climax microsuccession* to describe the cyclic successional replacements between *Betula alleghaniensis*, *Acer saccharum* and *Fagus grandifolia* within the forest cycle in Hubbard Brook, New Hampshire. (Remmert, 1985, 1987, 1991) and Wissel (1991) described successional interaction between *Betula pendula* and *Fagus sylvatica* within the forest cycle in a middle-European climax forest. Bormann and Likens (1979) proposed a model for secondary successions after clear cutting in a northern hardwood ecosystem. They suggested that the initial even-aged condition of the ecosystem after about a 100 years gradually changed into a shifting mosaic of developmental phases due to gap-dynamics. After simulating several hundred years of development the system achieved a dynamic but relatively stable condition; the shifting-mosaic steady state. In steady state, the condition of the system, for example expressed by the total biomass, is characterised by fluctuations and oscillations rather than directional processes at whole-system level (Bormann and Likens, 1979; Glenn-Lewin and Van der Maarel, 1992). The shifting-mosaic steady state can be regarded as a preliminary dynamic end-point to succession, lasting until the next major disturbance occurs. Watt (1947) used the term *phasic equilibrium* to describe the steady state hypothesised to evolve in a constant environment. In phasic equilibrium, the aggregate areas of the phases are directly proportional to the duration of the phases.

Disturbance is undoubtedly a major force moulding the development, structure and function of forests (Pickett and White, 1985; Attiwill, 1994). Wind is the major natural disturbance in most natural temperate broad-leaved deciduous forests, partly because they are not prone to fire (Jones, 1945; White, 1979). This also seems to be the case in the near-natural forest, Suserup Skov, in eastern Denmark.

The aim of the present study is to describe the structural dynamics of Suserup Skov as a reference for nature-based silviculture. The objectives are:

(i) to develop a specific model of the forest cycle in Suserup Skov, based on the general phase model;
(ii) to estimate the duration of each phase of the cycle;
(iii) to map the actual shifting mosaic of Suserup Skov; and, finally,
(iv) to test the hypothesis that Suserup Skov is in the shifting mosaic steady state.

The key result in this context is whether *the duration* of each phase is directly proportional to *the area* occupied by each phase.

2. Materials and methods

2.1. The site

The study was conducted in a 10.65-ha plot of Suserup Skov (19.2 ha), a near-natural temperate deciduous forest in central Zealand (located 55° 22′N, 11° 34′E at the Northern side of the lake Tystrup Sø). The climate is cool-temperate, sub-oceanic (Troll and Paffen, 1963). The annual mean temperature is 8.1°C, and the annual mean precipitation—635 mm, with maximum rain occurring in late summer and fall.

Historical studies of Suserup Skov conclude that the studied plot represents the least human influenced part of the forest (Part A in Emborg et al., 1996). The plot consists of a level-to-undulating plateau on the north (slope 0–10%) and some steeper downward slopes (5–15%) towards a lower plateau on the south. Most of the soils of the studied plot have developed from loamy glacial till (Vejre and Emborg, 1996). The growth conditions are favourable, as is indicated by tree heights of up to 41 m. To the south and east, the plot is surrounded by high forest. On the west, the plot borders on a fairly dense formation of ash trees (10–20 m high) on pasture land. To the north, the plot borders on recently abandoned farmland slowly growing into forest, wet willow shrubs and the gardens of a farm, implying some edge effects.

A combined pollen and macrofossil study from a forest hollow within the plot indicates that the plot has been forest all through Holocene, except for a period of rather open (maybe even savannah-like) forest condition from ca. 600 B.C to ca. 900 A.D. (Hannon et al., in press). After this period of rather open forest, beech established, became dominant and closed the forest together with ash (*Fraxinus Excelsior* L.) and oak (*Quercus robur* L.). The pollen and macrofossil data from Suserup Skov shows that fire has not been a frequent disturbance agent since beech expanded and became dominant at the site ca. 900 A.D. (Hannon et al., in press). During Medieval and Early Modern times, Suserup Skov was profoundly influenced by traditional, rural woodland management, for example pannage (pigs feeding on mast in the forest), pasture, coppicing etc. (Fritzbøger and Emborg, 1996). In 1807, Suserup Skov was fenced as protection against browsing cattle (Fritzbøger and Emborg, 1996). After the enclosure, management interventions were few and of low impact, and since the 1850s Suserup Skov has been managed as a minimal intervention forest even though some harvesting took place (Fritzbøger and Emborg, 1996). Limited compulsory felling occurred during the Second World War, and some cutting of *Ulmus glabra* Huds. (elm) occurred, especially in the period 1930–1940. Since 1961, the forest has been kept as a strict non-intervention forest. In October 1967, a gale struck from the direction of the lake (W–SW). The gale felled some 40 beech trees larger than 30 cm DBH, in the whole forest (19.2 ha), according to aerial photos and field observations (Emborg et al., 1996). This is considered a modest perturbation regarding the strong force of the gale (Jacobsen, 1986) and the storm only felled a few trees in the studied plot. No large-scale disturbances (natural or human conditioned) have perturbed the ecosystem of Suserup Skov since the forest was fenced in 1807.

Four tree species, beech, ash, oak and elm, account for 98% of the total basal area (BA) in the plot. Beech (64% of the BA) and ash (13% of the BA) dominate the plot. A relatively small number of large oak trees

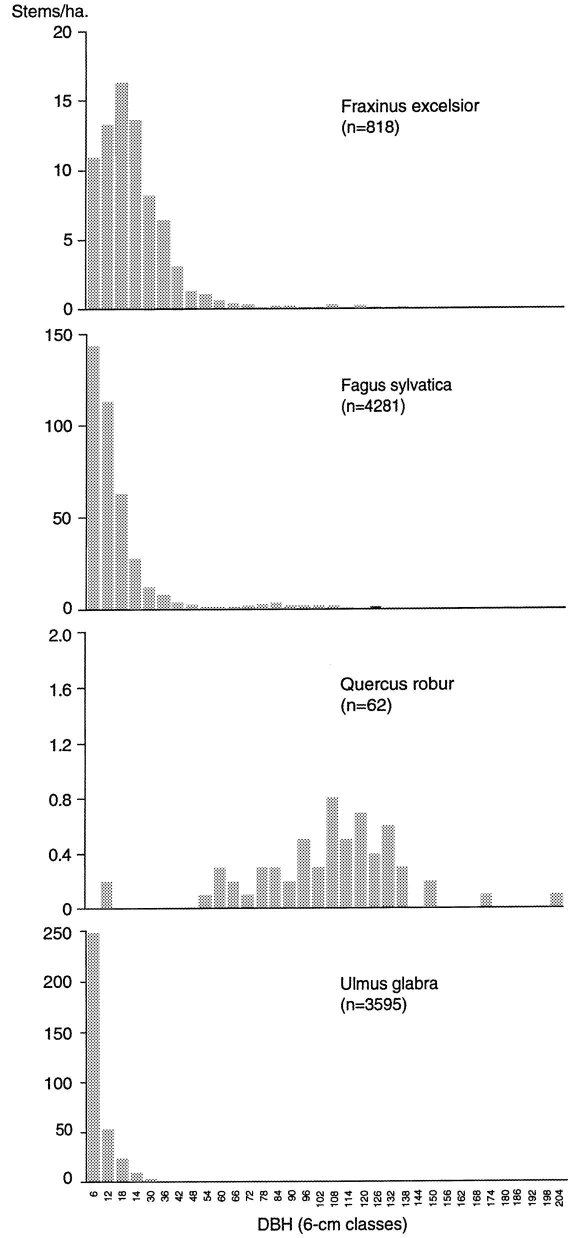

Fig. 1. Size–class distributions, including all trees larger than 3 cm DBH of *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur* and *Ulmus glabra* in the studied plot (10.65 ha).

account for 15% of the BA and a large number of small elm trees in the sub-canopy stratum account for 6% of the BA. The diameter distribution of beech (Fig. 1) is typical for a shade-tolerant 'climax' species, with many small recruits and also a considerable number of full-size canopy trees. The bell-shaped section of the beech diagram (50–150 cm DBH) reflects a major natural regeneration event in the decades following 1807, as the forest became fenced and cattle browsing stopped (Emborg et al., 1996; Fritzbøger and Emborg, 1996). Ash regenerates successfully and has relatively high numbers in the smaller diameter classes, representing potential canopy trees. Ash is only represented by a few trees larger than 80 cm DBH. Oak is represented by a few large individuals, typically between 250 and 500 years old, remaining from past periods of cattle browsing in the forest. Today there is hardly any regeneration of oak and only a few specimens of oak smaller than 60 cm DBH. Elm typically occurs as a sub-canopy species, represented by many small individuals and only a few full-size canopy trees, mainly located in the forest edges.

2.2. A specific model of the forest cycle in Suserup Skov

From the general models of the forest cycle, we have defined a specific model of the forest cycle for Suserup Skov (Fig. 2). The specific model includes five developmental phases termed the innovation, the aggradation, the early biostatic, the late biostatic and the degradation phase, in accordance with Oldemann (1990). Our objective was to develop a model, in which the phases can be defined unequivocally and distinguished from each other in the field by easy measurable criteria. The criteria for distinguishing the five phases from each other (Fig. 2) was defined before the field mapping took place, based on ecological considerations and arguments: 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 taller than 20 cm per m^2 (less for bigger plants, assessment). The beginning of the *aggradation* phase is defined as the moment when the established regeneration have competing vegetation under control, that is when the regeneration has reached a height of 3 m. The early biostatic phase begins when the trees have reached the upper canopy layer, that is have reached a height of 25 m. 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. The *degradation* phase begins when degrad-

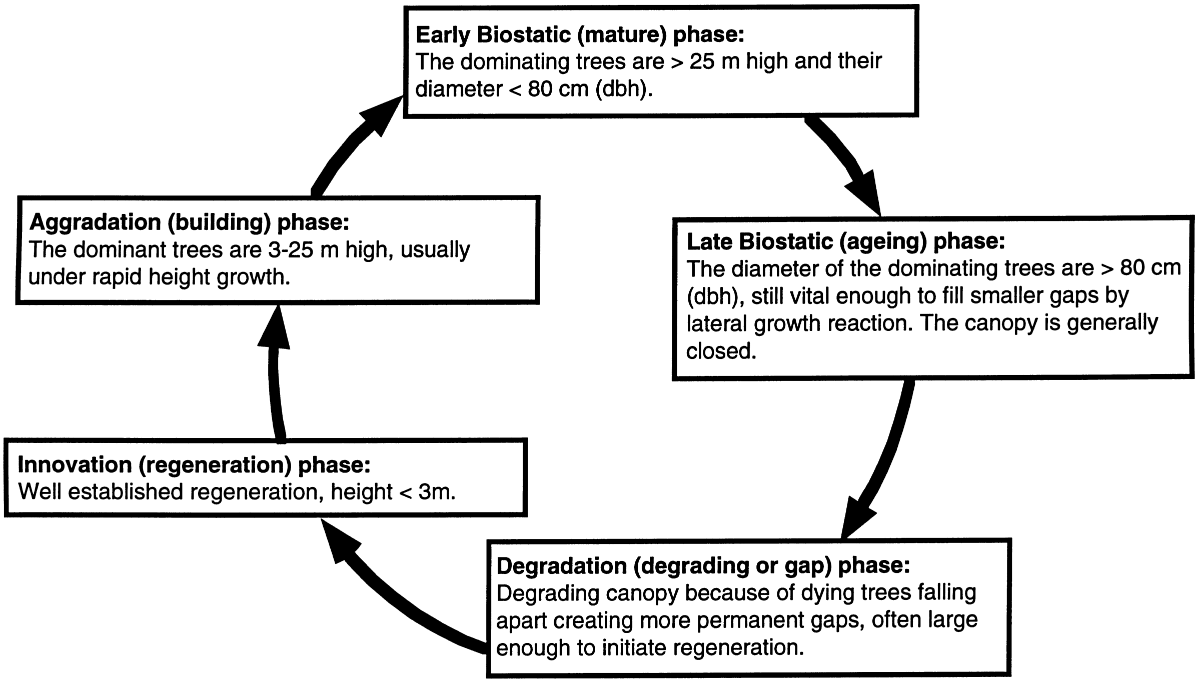

Fig. 2. Model of the forest cycle of Suserup Skov. The phases are defined by measurable criteria, as indicated in the boxes. Usually climax microsuccession from *Fraxinus excelsior* to *Fagus sylvatica* occurs during the innovation, the aggradation and the early biostatic phases.

ing trees causes more permanent gaps in the canopy, large enough to initiate regeneration, that is gaps $>100\ \mathrm{m}^2$, which cannot be filled by lateral growth of the surrounding trees. *All phases* are defined by the uppermost canopy layer of the patch.

With reference to the phase definitions, the ideal course of the forest cycle in Suserup Skov can be described as follows:

> The *innovation* (regeneration) phase begins when regeneration has established in a gap. Ash establishes first due to its pioneer features, spreading lots of wind-dispersed seeds almost every year. Beech establishes within a few years, typically after the first mast year.
>
> The *aggradation* (building) phase begins when the dominant saplings, usually ash, have eliminated herbs and shrubs. The canopy is usually dominated by fast growing ash above a lower stratum of beech throughout the phase.
>
> The *early biostatic* (mature) phase begins when the dominant trees have reached the upper canopy layer. Ash dominates from the beginning, but during the early biostatic phase beech completely takes over the canopy stratum.
>
> The *late biostatic* (ageing) phase begins when the dominant trees become old and vulnerable. 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.
>
> The *degradation* (degrading) phase begins when more permanent gaps occurs in the canopy as a result of breaking branches, dying trees, windthrow, etc. It can be regarded as an interface between the late biostatic and the innovation phase. It may start suddenly as a result of windthrow, 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.

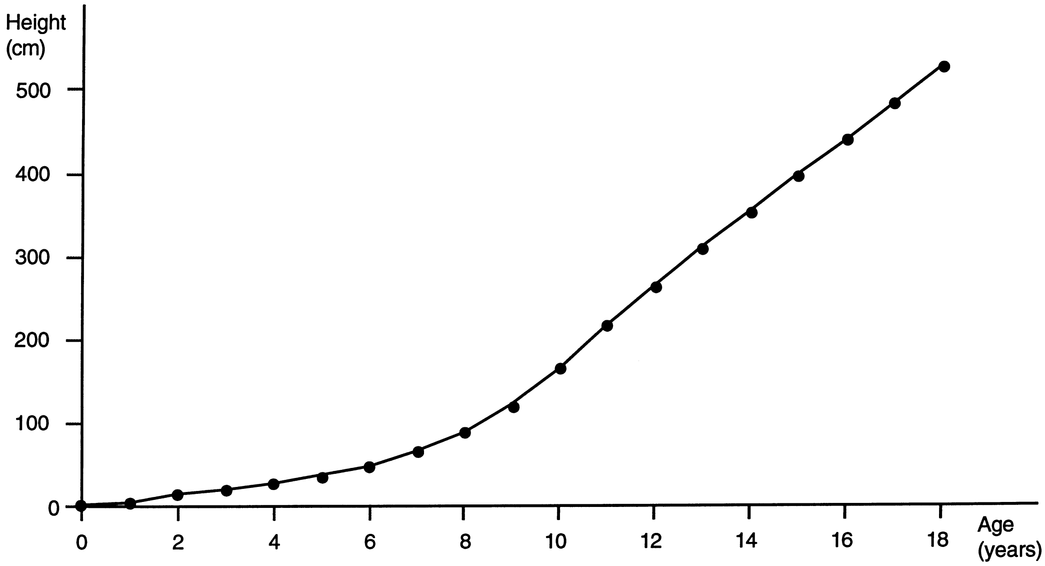

Fig. 3. Growth curve for regeneration of *Fraxinus excelsior* (ash), expressing height (m) as a function of age. The curve is generated on the basis of 627 paired observations of height and annual height growth of ash plants in five different gaps.

2.3. Estimation of the average duration of each phase

Tree-ring analyses, regeneration-growth studies and aerial photos were used to estimate the average duration of each phase. Cores for tree-ring analysis were taken at breast height and tree rings were recorded to nearest 0.1 mm using a microscope and a moveable stage connected to a microcomputer (ADDO Årsringsmätmaskin, Sweden). The average duration of the *innovation* phase was estimated from 626 paired observations of the *plant height* (before the growth season) and the *height-growth* of the proceeding growth season, measured at 84 ash plants in five different gaps. The whole material included annual growth data from the years 1980–1993. From these data, the average annual height growth could be expressed as a function of the plant height. From this *height–annual height growth* curve, we constructed the age–height curve (Fig. 3) by use of the following iterative process (example):

$$h_0 = 0\,\mathrm{cm} => \mathrm{d}h/\mathrm{d}t = 3\,\mathrm{cm} => h_1 = 3\,\mathrm{cm};$$

$$h_1 = 3\,\mathrm{cm} => \mathrm{d}h/\mathrm{d}t = 4\,\mathrm{cm} => h_2 = 7\,\mathrm{cm};$$

$$h_2 = 7\,\mathrm{cm} => \mathrm{d}h/\mathrm{d}t = \ldots \text{ etc.},$$

where h_0 is the height at the beginning of Year 1, h_1 the height at the end of Year 1, h_2 the height at the end of Year 2; and d*h*/d*t* the height-growth in one growth season.

The average age of beech plants at breast height (1.3 m) was estimated by the same procedure, based on 254 paired observations of height and annual height growth of 77 beech plants in five different gaps.

The average duration of the *aggradation phase* was estimated from a sample of 16 dominant or co-dominant (IUFRO-code combinations from 111xxx to 222xxx, Röhrig and Gussone, 1990) ash trees of ≈25 m height (range 23–27 m). The estimated average age of ash at a height of 1.3 m (Fig. 3) was added and the estimated duration of the innovation phase was subtracted.

The average duration of the *early biostatic phase* was estimated by tree-ring analysis on a sample of 10 beeches with a diameter of, or slightly above, 80 cm DBH. The estimated average age of beech plants in a height of 1.3 m (as estimated for ash Fig. 3), and the estimated establishment delay between ash and beech was added, and the duration of the preceding phases subtracted. The establishment delay between ash and beech was estimated to three years, based on literature on mast year frequencies of beech in north-western

Europe (Watt, 1925; Holmsgaard and Olsen, 1960; Burschel et al., 1964). The average duration of the *late biostatic phase* was estimated by counting the tree rings from 80 cm DBH to the bark at a sample of 12 actually degrading beeches. The average duration of the *degradation phase* was subjectively estimated from field studies in combination with aerial photos. Detailed aerial photos from 16 years covering the time period 1945–1991 (1945, 1954, 1959, 1960, 1967, 1969, 1971, 1972, 1978, 1979, 1981, 1982, 1985, 1989, 1990 and 1991) were analysed under magnification and compared. The approximate year of death of 100 trees, larger than 80 cm DBH, was traced. This enabled us to make a rather coarse reconstruction of the degradation patterns in time and space during the period 1945–1993. By subsequent field studies of regeneration and canopy layer fragmentation. the average duration of the degradation was estimated as a qualified guess. The duration of the full cycle was estimated as the sum of the estimated duration of each phase.

2.4. Mapping of the shifting mosaic

The shifting mosaic was mapped in the field in winter 1992/1993 on the basis of field charts (1 : 500) of a stem position map including all trees >29 cm DBH (Emborg et al., 1996). Phases were defined by the uppermost canopy layer of the patch. As an example, regeneration on the forest floor was only defined as an innovation phase patch in case there was a gap above, and trees between 3 and 25 m height were only defined as an aggradation phase patch if they formed the uppermost canopy layer of the patch. The advantage of this mapping method is that there can be no spatial overlap between neighbouring patches. The spatial resolution corresponded to a minimum patch size of 100 m^2. Patches not fitting into any other phase, for example all-sized structure within 100 m^2, were defined as *mixed phase*. A pilot study (Christensen et al., 1993) showed that a spatial resolution of 200 m^2 was too coarse, resulting in a 22% mixed phase. With the high resolution of 100 m^2, and the described set of clear and measurable phase definitions, it was possible to map the phases unequivocally (no patches of mixed phase) by use of a clinometer, a calliper and measuring tapes. Each patch of the mosaic was marked on the field charts, digitised and the area of each patch was computed.

3. Results

3.1. Estimated duration of the phases

The average duration of the innovation phase was estimated to 14 years (Fig. 3, the age at 3 m height), The aggradation phase to 56 years (Table 1), the early biostatic phase to 96 years (Table 2), the late biostatic phase to 108 years (Table 3), and the degradation phase to 10 years. One turn of the whole cycle in Suserup Skov is, accordingly, estimated to last some 284 years on average in Suserup Skov.

The younger phases (innovation, aggradation) seem to be less variable in duration than the older phases (early/late biostatic) according to the sample standard deviations (Tables 1–4). The degradation phase can be very short (e.g. in the case of a windthrown healthy tree) or quite long (e.g. in case of a slowly degrading old tree, dying from age), probably up to some 30 years.

3.2. The shifting mosaic in Suserup Skov

All phases of the forest cycle were represented in the shifting mosaic in the plot, mixed across the area (Fig. 4). A total of 127 patches with an average size of 839 m^2 formed a fine-grained mosaic of the developmental phases of the forest cycle (Fig. 4, Table 4). The patch size varied from 100 to 12 730 m^2. The shape of the larger patches, in particular, was irregular, often small patches appeared as islands in larger patches. The average patch size varied between the phases (ranging from 384 to 1467 m^2), The degradation and the innovation phases having the smallest patches, while the early biostatic phase on average formed the largest patches (Table 4). The minimum patch size recorded was <200 m^2, for all phases. The maximum recorded patch size varied from 670 m^2 in the degradation phase to 12 730 m^2 in the early biostatic phase.

3.3. The mosaic-cycle in time and space

The relative areas of each phase (as mapped in the field) can be compared with the relative duration of

Table 1
Estimation of the average duration of the aggradation phase, the duration of the aggradation phase being estimated as the mean $\text{Age}_{\text{total}}$ minus the duration of the innovation phase ($70 - 14 = 56$ years)

Tree No.	Height (m)	Tree rings_{BH} No.	$\text{Years}_{\text{0-130 cm}}$ (year)	$\text{Age}_{\text{total}}{}^{a}$ (years)
1	23	56	10	66
2	24	50	10	60
3	27	54	10	64
4	26	57	10	67
5	23	61	10	71
6	23	62	10	72
7	27	67	10	77
8	27	56	10	66
9	26	72	10	82
10	24	69	10	79
11	24	59	10	69
12	27	68	10	78
13	23	50	10	60
14	25	53	10	63
15	27	62	10	72
16	26	58	10	68
Mean $\text{Age}_{\text{total}}$		70 years		
Sample standard deviation		7 years		

[a] Ages of a sample of 16 dominant or co-dominant (IUFRO-code combinations from 111xxx–222xxx, Röhrig and Gussone, 1990) ash trees (*Fraxinus excelsior* L.) of ≈25 m height (range 23–27 m).

Table 2
Estimation of the average duration of the early biostatic phase. Ages of a sample of 10 beech trees (*Fagus sylvatica* L.) with DBH = 80 cm (or slightly >80 cm)

Tree No.	DBH (cm)	Tree rings_{BH}, No.	$\text{Years}_{\text{0-130 cm}}$	$\text{Age}_{\text{total}}$ (years)
1	80	154	11	165
2	80	148	11	159
3	80	155	11	166
4	80	142	11	153
5	80	142	11	153
6	86	146[a]	11	157
7	80	192	11	203
8	82	185[a]	11	196
9	86	140[a]	11	151
10	89	144[a]	11	155
Mean $\text{Age}_{\text{total}}$		166 years		
Sample standard deviation		20 years		

[a] These data have been corrected for the tree rings from 80 cm DBH and out to the bark.

[b] The average duration of the early biostatic phase was estimated as the mean $\text{Age}_{\text{total}}$ minus the duration of the innovation and the aggradation phase ($166 - (14 + 56) = 96$ years).

each phase in Table 4. This comparison gives the key result, that the areas occupied by each phase in the forest were close to being directly proportional to the estimated average duration of the phases. The main results of the study are condensed in Fig. 5, showing the mosaic cycle in time and space.

Table 3
Estimation of the average duration of the late biostatic phase; ages of a sample of 12 actually degrading beech trees (*Fagus sylvatica* L.)

Tree No.	DBH (cm)	Tree rings$_{>80\ \mathrm{cm\ DBH}}$ n
1	120	127
2	110	114
3	118	96
4	110	101
5	100	81
6	114	85
7	130	116
8	94	40
9	140	224
10	120	112
11	128	100
12	106	102
Mean	108	
Sample standard deviation	43	

[a] The mean value of tree rings$_{>80\ \mathrm{cm\ DBH}}$ is a direct estimate on the average duration of the late biostatic phase (108 years).

4. Discussion

4.1. The model of the forest cycle

With the phase definitions—developed in this study for Suserup Skov—in hand, it was possible to map the phases of the mosaic cycle unequivocally in the field. We concluded that the main prerequisites for an unequivocal field mapping of the shifting mosaic is

(i) the hierarchical approach of defining phases by the uppermost canopy layer of the patch
(ii) the use of high spatial resolution, in Suserup Skov corresponding to a minimum patch size of 100 m^2, and
(iii) easy measurable criteria for distinguishing the different phases from each other; however, we also experienced that some use of qualified assessment is unavoidable in work like this, for example when determining the beginning and the end of the degradation phase.

The specific Suserup model of the forest cycle (Fig. 2) is based on the following three assumptions:

(i) that recruitment to the canopy takes place in gaps (gap-phase dynamics) rather than as a continuous sub-canopy recruitment;
(ii) that ash establishes before beech in new gaps; and
(iii) that climax microsuccession from ash to beech occurs as an integral part of the forest cycle.

The three assumptions are discussed in the following.

4.1.1. Gap phase dynamics

Field observations show that shortcuts of the full cycle do occur, for example when sub-canopy trees fill gaps (ahead of new regeneration). Sub-canopy beech trees filling gaps after ash trees are, however, included in the model as climax microsuccession in the aggradation and the early biostatic phases. During the late

Table 4
The duration of each phase of the forest cycle, as estimated with reference to the model of the forest cycle, and the actual area covered by each phase of the shifting mosaic, as mapped in the field

Phase	Model duration			Mosaic (as mapped in the forest)				
	(years)	ssd[a]	(%)	summarised area		patches		
				(ha)	(%)	No.	(m^2/patch)	range (m^2)
Innovation	14		5	0.2	2	5	478	100–1530
Aggradation	56	7	20	2.3	22	27	850	140–5550
Early biostatic	96	20	34	4.0	37	27	1467	110–12 730
Late biostatic	108	43	38	3.3	33	52	683	100–5860
Degradation	10		4	0.6	6	16	384	200–670
Total[b]	284		100	10.7	100	127	839	100–12 730

[a] Sample standard deviation.

[b] Totals are calculated using values *before round off* which explains the deviations from the sums of the columns.

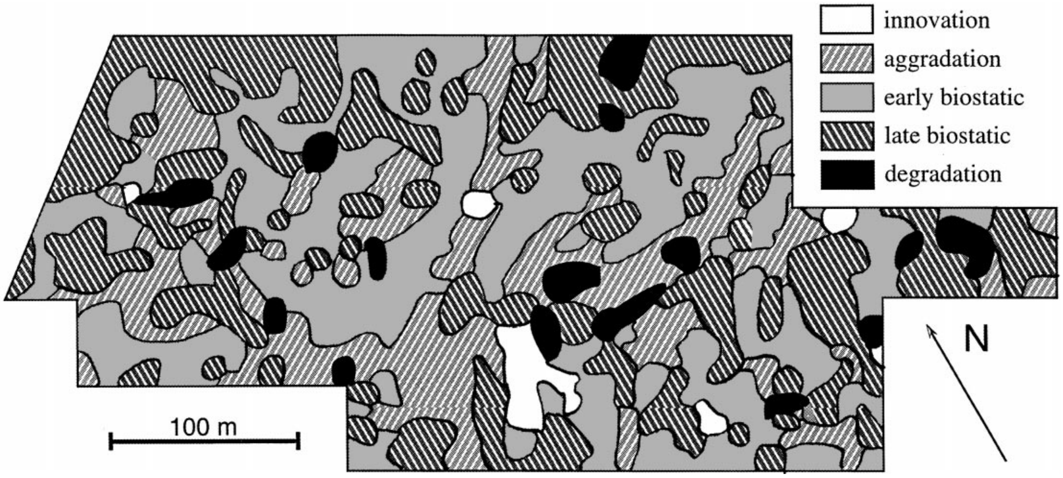

Fig. 4. The shifting mosaic of the studied plot (10.65 ha), mapped in Suserup Skov, 1992.

biostatic phase no considerable understorey is usually allowed to develop under the dark canopy of pure beech (Emborg, 1998), and accordingly new regeneration has to develop in gaps.

If gap formation coincides with a mast year of beech, beech regeneration may be able to oust regeneration of ash, especially in relatively dark places, like gap edges and small gaps. Patches of pure beech in the aggradation phase are present in Suserup Skov. The diameter distribution of elm (Fig. 1) indicates that elm is primarily present in the understorey. Field observations suggest that elm has a preferred habitat in the epicentre and periphery (sensu Oldemann, 1990) of fallen canopy trees. In such gaps, more or less broken elm trees often rapidly gain control over the area by spreading an umbrella of long sprouts with large leaves, efficiently impeding establishment of other tree species. In the long run, however, beech seems to over-top elm in these patches. In a way, elm in these places partly substitutes ash in the forest cycle. The conclusion is that the presence of elm is more or less restricted to the sub-canopy strata and as such elm does not take part in, or interfere much with, the later stages of the forest cycle. The conclusion is supported by periodical inventories (Management Plans of Suserup Skov, 1815–1992) showing only few elm trees >40 cm DBH, but weakened by the fact that some cutting of elm occurred 1930–1960. The future role of elm is interesting, because Dutch elm disease (*Ophiostoma novo ulmi* (Buism.) Nannf.) is now spreading in Suserup (first appearance early summer 1994, personal observation).

The diameter distribution (Fig. 1) indicates that, in the long run, oak is disappearing from the system, as there are no recruits of oak. Oak grows older, shades less, and degrades more slowly than beech. Probably the duration of the late biostatic and the degradation phases are longer at oak-dominated places. The regeneration pattern under degrading oak trees presumably differs from the pattern under beech. The oaks allow more undergrowth to develop. When gaps occur, the degradation phase may turn directly into the aggradation or the early biostatic phase, without the establishment of new regeneration. Considering the limited number of oak trees, the overall influence of oak on the forest cycle is assumed to be limited, and under all circumstances diminishing since oak is retreating from the system (Emborg et al., 1996).

4.1.2. Establishment dynamics

Ash is a gap specialist in the climax forest, with pioneering features, while beech is a typical shade tolerant species (Iversen, 1967; Grubb, 1977; Etherington, 1982; Finegan, 1984; Oldemann, 1990). The seed production of beech is strongly periodical (mast years) with heavy seeds (Burschel et al., 1964; Holmsgaard and Olsen, 1960; Watt, 1925). In contrast to beech, ash produces seed in most years with light wind-dispersed seeds (Watt, 1925; Mitchell, 1974). These differences in the regeneration niches of ash and

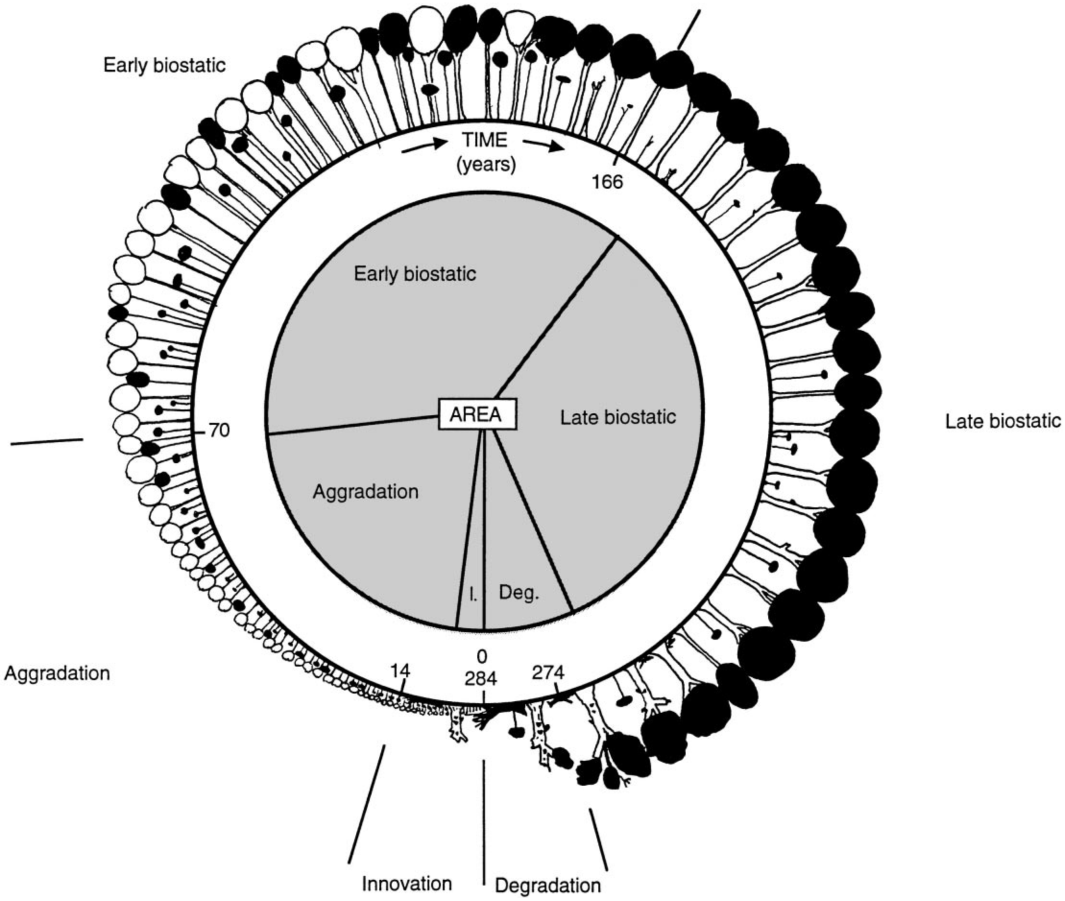

Fig. 5. The mosaic cycle in time and space, Suserup Skov, 1992. The pie in the middle shows the accumulated area of each phase of the shifting mosaic. The outer circle indicates the calculated duration of each phase of the forest cycle, numbers indicate years from start of the cycle. The typical structure of the forest throughout the forest cycle is illustrated. Note the climax microsuccession from *Fraxinus excelsior* (white) to *Fagus sylvatica* (shaded) during the innovation, the aggradation and the early biostatic phases.

beech, result in a high probability of ash establishing prior to beech in gaps. A detailed gap study in Suserup Skov (Emborg, 1998) showed that the ash regeneration plants, on average, were one year older ($p = 0.0003$, $n = 226$) than the beech regeneration plants. Almost all beech plants were established during one (mast) year, 1989, while the ash plants were established over several years. Peet and Christensen (1987) concluded that one year head start of a species in a gap was sufficient to give the species a clear initial advantage, especially under favourable light conditions. Further, ash grows fast in the juvenile stage compared with beech (Møller, 1977). As expected, ash was far ahead of beech after only a few years of growth, in accordance with the suggested model including climax microsuccession. In general, the success of ash vs. beech in gaps is expected to be related to gap size (small gaps in favour of beech).

4.1.3. Climax microsuccession

Climax microsuccession from ash to beech implies that ash trees of a given age on average should be higher than beech trees of the same age, at least during the aggradation and the beginning of the early biostatic phase. Tree-ring data from Suserup Skov has been used to test this assumption (Emborg, 1996). A hundred ash trees and 151 beech trees were measured. The material was sorted into 10-year age classes, and the average sizes of beech and ash were compared by age classes. Ash was considerably higher and thicker than beech in all age-classes, in keeping with the assumed microsuccession from ash to beech. The successional interaction between ash and beech comes to an end during the early biostatic phase when beech takes over canopy control, either due to the shorter life duration of ash or due to the ability of beech to grow through (the light) canopies of ash. Beech typically degenerates at an age of 250 years (Tables 3 and 4), while ash typically degenerates at a much lower age, presumably ca. 130 years in Suserup Skov (Emborg, 1996).

Regarding the three assumptions, the overall conclusion is that it seems reasonable to assume that canopy recruitment usually is a result of gap-phase dynamics in Suserup Skov, that ash as a rule establishes before beech in gaps, and that the forest cycle is governed by beech and ash in a microsuccessional interaction, while elm is subordinated in this regime. Oak has a limited and diminishing influence on the course of the cycle. We consider the forest cycle as a reasonable basic description of the dynamics in Suserup Skov, underlining, however, that this model (like any other model) should be regarded as a simplified abstraction from reality.

4.2. *The shifting mosaic*

The shifting mosaic represents the spatial match to the forest cycle running over time. The forest structure of Suserup Skov is a fine-grained shifting mosaic (Fig. 4), with the smallest patches of the size of a single small canopy tree (100 m^2). The mosaic structure of Suserup Skov is quite similar to the structure described by Mayer and Neumann (1981) for Corkova Uvala, a mountain forest in Croatia dominated by *Fagus sylvatica* and *Abies alba*, except that the Suserup mosaic is more fine-grained.

The patches of the short phases (degradation, innovation) were on average considerably smaller than the patches of the longer lasting phases (Table 4). The same pattern was seen in Corkova Uvala (Neumann, 1978). A possible explanation is that neighbouring patches often fuse together during long phases, because the relative difference between patches diminishes (Oldemann, 1990). Another explanation could be the domino effect, caused by the sudden exposure and/or bark damage of the trees next to a gap (Nicolai, 1986; Wissel, 1992). Exposed, often damaged, trees are susceptible to windthrow, sunscald, fungi or insect attacks. Especially, trees to the north and east of gaps are at risk, which could explain the tendency to a NE–SW oriented structure of the mosaic (Fig. 4). The patch size peaks in the early biostatic phase, succeeded by decreasing size in the late biostatic phase (Table 4). This could be explained by the formation of new gaps due to single tree death during the late biostatic phase, dividing large patches into smaller ones (Oldemann, 1990).

Some edge-effects are to be expected at the northern edge of the plot. Gaps develop slightly differently at forest edges, because of side-light and a more dense understorey. Hence, there might be a tendency towards more continuous canopy-recruitment, rather than gap-phase recruitment, at forest edges than inside the forest. Generally, at north facing edges (in the Northern Hemisphere), the edge-effects are expected to be relatively limited, in this case probably restricted to the outermost 10–15 m.

4.3. *Disturbance and steady state*

Forests are assumed to approach the shifting mosaic steady state after several hundred years of undisturbed growth (Bormann and Likens, 1979). Accordingly, the role of natural and human disturbances in Suserup Skov in the past becomes a key issue for discussion. The key result, that the actual area occupied by each phase in the forest is more or less directly proportional to the duration of each phase, could lead to the conclusion that Suserup Skov has approached the shifting mosaic steady state. Before forwarding this possible conclusion, we focus on the disturbance history of Suserup Skov.

4.3.1. *Human disturbances*

Pollen analyses indicate that Suserup Skov has been continuously wooded since the end of the last glaciation (Hannon et al., in press). The epoch of rather open forest from 600 B.C. to 900 A.D. was presumably a result of anthropogenic disturbance (Hannon et al., in press). In the Middle Ages, the area presently occupied by Suserup Skov again became heavily affected by Man (Fritzbøger and Emborg, 1996). As an integral part of the open field rural landscape, Suserup Skov was subject to pannage, grazing animals and temporary cultivation and selective cutting of trees. Modern woodland management was not initiated before the enclosure of Suserup Skov in 1807, and human impact since that time has remained modest compared to other forests. The general state and development of the stands are described in the management plans. The first management plan for the Sorø Forest District was issued in 1815, according to which: "…the main stock of trees (in Suserup Skov) consists of oak and beech trees ready to be cut, all of them still sound and fit and well growing. Among the beech and oak trees a number of good ash and elm trees grow. The old forest is still so dense that it can be regenerated by means of natural sowing, and regeneration, especially of elm and ash trees already exist" (translated from the Danish). The intentions of the management plan was obviously to utilise the forest resource of Suserup Skov, but as a matter of fact these intentions were never realised, according to the succeeding management plans. The 1833 management plan states that Suserup Skov: "…contained a considerable stock of old forest, even though it is hardly dense anywhere. An extraordinary regeneration, among which lots of ash and elm trees, has sprouted up" (translated from Danish). The beech and oak trees were in general considered to be 'over-ripe'. In the 1885 management plan, the major part of Suserup Skov (the part considered in the present paper) was described as: "… a scattered stand of old, huge and tall beech trees with broad canopies mixed with generally sound oak trees and ash and elm trees in different ages. Partly dense understorey of elm trees mixed with beech and hazel" (translated from Danish). These descriptions indicate a heterogeneous, but not very dense, forest structure in the nineteenth century.

No major, human-caused disturbances seem to have taken place during the nineteenth century, and since the 1850s the forest was administratively preserved (minimal intervention) by the forest district for reasons of recreation (Fritzbøger and Emborg, 1996). In his posthumously published book *De danske Skove*, Vaupell (1863) writes that Suserup Skov was managed by minimal intervention with the result that the natural competition between oak and beech trees progressed unimpeded. But even though the forest was protected, human interventions have occurred. In the period from 1833 to 1910, some harvesting took place, according to old felling records <1.5 m^3/ha/year on average in the period, primarily firewood of oak and beech (Fritzbøger and Emborg, 1996). Some compulsory fellings of old beech trees took place during World War I (1910)–1915: approximately 10 m^3/ha/year, Fritzbøger and Emborg, 1996). The firewood cutting continued at least until 1929. In 1926, a legally binding minimal-intervention preservation was claimed on Suserup Skov. However, some cutting of elm was still going on (as suggested in the preservation claim), presumably especially during the 1930s. During The Second World War, compulsory fellings of some old beech trees took place. According to the former forest guard S.B. Rasmussen, only very old degrading trees were felled. He estimates that harvesting during The Second World War probably was of the same order of magnitude as during World War I, some 10 m^3/year/ha. Since 1960, the forest has been maintained as a strict non-intervention forest reserve (Emborg et al., 1996).

4.3.2. Natural disturbances

Wind is regarded as the major natural disturbance agent in most temperate deciduous forests (Jones, 1945; White, 1979) including Suserup Skov. Sorø Forest District has been ravaged by severe tempests in 1863, 1880, 1894 and 1902, however, the effects are not very conspicuous in the felling records (Fritzbøger and Emborg, 1996). During the twentieth century the southern part of Denmark has been hit by tempests in 1931, 1934, 1941, 1956, 1962 and 1967, of which the last by far was the most severe (Jacobsen, 1986). The gale of 1967 (October) struck Suserup Skov while the leaves were still on the trees and the soil was soaked from several days of heavy rain. This gale led to the largest windthrow in broad-leaved trees ever recorded in Denmark (Jacobsen, 1986). In Suserup Skov, as well, the storm was a dramatic event: a total of ca. 40 beech trees in the diameter range of 30 to 150 cm DBH were felled by the wind (Emborg et al., 1996). The windthrow was concentrated in two patches of the forest, with a size of 0.6–0.9 ha per patch and about 0.7 ha within the studied plot. Most of the fallen trees were of 70–90 cm DBH, considerably below the average diameter, 110–130 cm DBH, of trees that fell during the rest of the period 1945–1994. A possible explanation of this surprising pattern could be that the fallen trees (70–90 cm DBH) had already reached the top of the canopy (i.e. they were vulnerable), but still they were less rooted than the bigger/older trees of the canopy layer. The storm, however, speeded up the gap formation by harvesting some of the ageing, potentially degrading trees, thus contributing to the slight under-representation of the late biostatic phase in the mosaic (Fig. 5, Table 4). The gaps made by the gale are, probably, now contributing to the slight over-representation of the aggradation phase and the under-representation of the innovation phase in the plot (Fig. 5, Table 4). Presumably, the gale's harvest of premature trees implied reduced gap formation in the years following the gale. This illustrates the ability of the system to return to the dynamic equilibrium after a perturbation (resilience). In this way, the effects of the gale were levelled out in the years following the perturbation and the overall effect of the perturbation has been limited.

4.3.3. Conclusions regarding disturbances in Suserup Skov

During the past centuries, Suserup Skov has not been perturbed by major natural or human disturbances in orders of magnitude which were able to 'reset' the whole system (like, for instance, fire can do to boreal forests or hurricanes in temperate forests). But several disturbances of smaller scale occurred, for example tempests, firewood cutting and compulsory fellings during the two world wars. We conclude that the most influencing disturbance has been the long period of human influence by traditional rural woodland management (pannage, pasture, coppicing, etc.) in Medieval and Early Modern times before the enclosure of forest in 1807. This disturbance influenced the whole area, and gave more room for light demanding species, for example *Crataegus* spp., *Malus sylvestris* Miller and *Corylus avellana* L. in the understorey, and oak in the canopy layer (Emborg et al., 1996), impacts that are still visible in the forest today. The development from relatively open forest type to the dense dark forest of today has increased the standing volume in Suserup Skov from some 110 m^3/ha (harvestable trees) in 1815, to some 430 m^3/ha in 1925 and 700 m^3/ha (total standing volume) in 1993 (Fritzbøger and Emborg, 1996). The gale in 1967 represents the largest recent natural disturbance in Suserup Skov, affecting some 10% of the area, but certainly not changing or resetting the whole system.

Regarding the model calculations of Bormann and Likens (1979), it seems reasonable that Suserup Skov has become close to a structural steady state after some 200 years of relatively undisturbed development. Korpel (1982) and Koop (1989) found that areas of 25–40 ha were required to continuously represent the shifting mosaic steady state in beech dominated forests. The fine-grained mosaic found in Suserup Skov partly explains how the only 10.65 ha large plot, in Suserup Skov, can be that close to steady state.

4.4. Succession, climax and steady state

The shifting-mosaic steady state represents a dynamic equilibrium, in which variables like total biomass, phase representation and species composition oscillate around mean values. The smaller an area is, the larger the expected oscillations would be due to random influences. How can large oscillations be accepted within the steady state? It has been argued that there is no need for a climax or a stable end-point to succession within a non-equilibrium theoretical framework (Pickett and White, 1985; Glenn-Lewin and Van der Maarel, 1992). Ecosystems are always structurally and functionally changing because of climatic change, invasion of new species, and disturbances of different scales. Changes occur within the time required for the ecosystem to reach equilibrium (Raup, 1957; White, 1979; Davis, 1981). Our model includes an element of succession, that is directional process within the otherwise cyclic dynamics. Further, the whole system undergoes a long-term successional change regarding species composition. The occurrence of oak is a result of human influence, and now the system is slowly moving back through a slow process of resilience. Cyclic and directional processes are intermingled: The Suserup system has achieved a structural steady state, while the species composition is still changing, that is a cyclic development superimposed on an overall directional trend (succession). Further, the cyclic development includes a directional process, namely the climax microsuccession from ash to beech, within the forest cycle. This example from Suserup Skov illustrates the complex relationship between succession and climax, between directional trends and cycles.

4.5. Implications for forest management

The two most striking features that differentiate the near-natural forest, Suserup Skov, from a traditionally managed forest in Denmark are:

(i) the extreme variation in structure (Fig. 4); and
(ii) the long-lasting phases dominated by old, large trees representing high amounts of decaying wood.

Natural and near-natural forests can be used as references at many scales and levels for silviculture, forest management, nature conservation and landscape planning. Three examples are outlined here:

(i) establishment of forest reserves;
(ii) biodiversity management; and
(iii) forest stability maintenance.

4.6. Establishment of forest reserves

In Europe, many non-intervention forest reserves have been established recently (Broekmeyer and Vos, 1993). Most reserves are, and will be, established in former managed forests, including homogeneous even-aged forest stands. It seems reasonable to assume that the biological value of such future forest reserves can be increased by management interventions in the initial stages of forest reserve establishments. Felling groups of trees could dissolve the homogeneity by establishing mosaic-structures and initiating gap-phase dynamics, while the amounts of dead wood could be increased by leaving felled trees behind at the forest floor. Such management activities can help speed up the development of natural structures, processes and habitats, before the reserves are to be considered completely non-intervention forests.

It may seem contradictory to intervene in the process of establishing non-intervention reserves. It can be argued that the starting point is non-natural in any circumstance, because of the former management activities. The main purpose of establishing forest reserves is, from our point of view, to generate biological values and processes over time, the faster the better. The forest cycle model of Suserup Skov model indicates some possibilities and guidance for the fast transformation of even-aged managed beech forest into habitat-rich non-intervention forest reserves, for example.

4.7. Biodiversity in managed forests

The homogenisation of the managed forests and the use of management practices that hardly contain any structural elements from the right-hand side of the forest cycle (Fig. 5) has led to loss of habitats and, hence, loss of biodiversity (Franklin, 1988; Franklin, 1993; Christensen and Emborg, 1996). One approach to increase the habitat diversity of managed forests could be to develop management systems that mimics the natural patterns and processes related to the mosaic cycle. The specific model of the structural dynamics of Suserup Skov indicates which structures and disturbances to mimic in this particular region. Management practices, mimicking the natural structural development driven by small-scale disturbances, should generally protect the authentic forest-related biodiversity more efficiently than management systems based upon periodically large-scale process disruptions (e.g. clear-cuts or shelterwood regeneration).

4.8. Forest-stability maintenance

One key problem of the traditional even-aged forests are their general susceptibility to, and low resilience after, storms (Jacobsen, 1986; Larsen, 1995). The structural steady state, as found in Suserup Skov, indicates a high long-term resistance and resilience towards disturbances, such as storms. Although windthrow often occurs in natural temperate forests, at the level of single trees or groups of trees, the general forest climate will usually remain more or less intact, indicating relatively small changes in the biogeochemical processes. Mimicking the natural forest structure and disturbance regime by means of group selection harvesting might, therefore, contribute to a higher resistance and resilience in managed stands. These examples illustrate how natural forests can be used as reference for management purposes. Other examples could be outlined: development of silvicultural systems based on *the principle of nature-automation*, that is maximum utilisation of natural patterns and spontaneous natural processes in forestry.

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