**Abstract**

The management of forests “closer to nature” has in recent decades increased in significance in the search for models of sustainable forest management. In this context, studies in existing natural forest reserves play a particular role. Suserup Skov is the best example of a beech dominated, semi-natural deciduous forest in Denmark. Such “field laboratories” can help us to a better understanding of the relationship between natural disturbances and structural and functional dynamics of mixed deciduous forest ecosystems. This work analyses the results of forest dynamics on the basis of studies carried out during 1992-2002 and discusses the findings in relation to their application in sustainable forest management, including applying the concept of “Forest Development Types” (FDT) for developing long-term goals for close-to-nature forest management in Denmark.

**Key words:** disturbance regime, stand dynamics, forest structure, development phases, close-to-nature forest management

**Introduction**

Suserup Skov in central Zealand/Denmark although small is one of the best conserved and well described semi-natural woodlands in the northwest European lowland. Pollen analysis shows that the forest has a continuity of tree cover at least back to 4200 BC (Hanon et al. 2000) thus probably a direct descendent of the primeval forest, which developed after the Weichsel Glaciation 12,000 years ago. Although influenced by humans over the past 6,000 years reflecting the regional land-use history, its 19 ha present one of the most important references for natural forest dynamics in Denmark. Hence, it serves as an excellent reference for perceiving and understanding the relationship between disturbances – natural and man-made – and the structural and functional dynamics of mixed deciduous forest ecosystems. This knowledge is crucial for developing forest management methods and techniques in accordance with close-to-nature or nature-based principles, which at present are looked upon as one of the answers to achieve sustainable forest management, i. e. to achieve a better balance between utilisation of the forest and protection of its (bio)diversity (Gamborg and Larsen 2003).

To establish a common basis for present and future research activities, Heilmann-Clausen et al. (2007) compiled the history and present conditions of Suserup Skov. In 1992, an inventory of the forest structure and mapping of the different developmental phases was conducted (Emborg et al. 1996). The full-scale inventory was repeated in 2002 for comparison with the 1992-inventory (Christensen et al. 2007, Emborg and Heilmann-Clausen 2007). Further, studies of the structural complexity and its effects on understory light intensity were carried out (Emborg 1998, Nielsen and Hahn 2007), thereby the impact of a gale in 1999 on forest structure was monitored and analyzed (Bigler and Wolf 2007). The carbon pools and its partitioning in above and below ground as well as dead wood biomass in relation to the forest cycle were studied (Vestradal and Christensen 2007). Further, detailed studies on nutrients, hydrology and ecophysiology in an instrumented gap (Ritter et al. 2005, Dalsgaard 2007, Einhorn 2007) were combined with analyses of regeneration and growth of dominant tree species (Emborg 2007, Hahn et al. 2007a, b) and biodiversity of fungi, soil nematodes, and the vascular flora (Heilmann-Clausen and Christensen 2003, Bjørnland and Christensen 2005, Thomsen et al. 2005, Hahn and Thomsen 2007). Finally, the results from these extended research activities in Suserup Skov were synthesised and perspectives for forest management were outlined (Hahn et al. 2007a, b). This paper analyses the results in order to “translate” the findings into practical silviculture, thus answering the question “Which lessons can be adopted and which have already been implemented into Danish forestry?”

**Perspectives for sustainable forest management**

**Species composition and competition**

The vegetation history of Suserup Skov (Hannon et al. 2000, Heilmann-Clausen et al. 2007) teaches us several lessons. In general it describes the over-all forest development of the region, but is gives additional, valuable information about the causes for this development. Especially the influence of forest fires based on the periodic occurrence (200 to 300 years intervals) of macroscopic charcoal residues from 4500 BC until 800 DA probably due to small scale disturbances by humans is interesting. It is likely, that infrequent fire disturbances have had an important influence on maintaining the species richness in pre-historic time, and that their absence during the last 1,000 years consequently has promoted the beech dominance. The findings of Hannon et al. (2000) and Heilmann-Clausen et al. (2007) show the potential of larger disturbances including fire as a management tool in order to enhance species richness – even in the deciduous forests.

Another interesting story from Suserup is the recent (in a Holocene time perspective) distinct retreat of oak. The pollen analyses show that oak has been continuously present for the last 6,500 years (Heilmann-Clausen et al. 2007). Today only few very old oaks exist in the forest, and although oak frequently regenerates, no oak trees between 3 and 60 cm dbh are found. The retreat of oak and the increasing dominance of beech started approximately 200 years ago.
as the forest was gazetted thus excluding the life stock (Heilmann-Clausen et al. 2007). It seems obvious, that under the small-scale disturbance regime and with the absence of grazing pressure, oak is not able to compete with beech. Similar conclusions are obtained by Lüpk and Hauskeller-Bullerjahn (1999) for Lower Saxony. Hence, intimate mixtures of beech and oak should be omitted in management practice. The general problem of maintaining pioneer species in climax forest systems is acknowledged in the definition of forest development types dominated by light demanding pioneer species (Larsen and Nielsen 2007).

While oak in the long run seems to be outcompeted, other species are able to co-exist with the dominating beech. The study of growth patterns of beech and ash demonstrates the well recognized difference between the two species where the light demanding ash colonizes gaps in the forest canopy followed by the shade tolerant beech leading to a group micro-succession from ash to beech as an integral part of the forest cycle (Emborg 1998, Figure 1). Detailed studies reveal a more complex picture with "rush" ash and "stop and go" beech trees, which in combination with a rather high shade tolerance of young ash explaining competitive patterns allowing co-existence of early successation species in the climax forest (Emborg 2007). Further, analyses of the 2002-inventory data show that not only ash but also sycamore maple is clearly expanding, indicating that this species is also able to co-exist in the beech-dominated climax forest in a shifting steady state mosaic, where ash and maple will "colonize" the gaps in the innovation phase followed by beech, which will take over during the early biostatic phase (Figure 1) (Emborg and Heilmann-Clausen 2007). Whether the sycamore maple, which is a "newcomer" in Suserup Skov, is able to coexist with beech throughout the full forest cycle is still pending. Further, it is interesting to note that the presence and regeneration of ash and sycamore in Suserup is not restricted to specific moist sites as described by Ellenberg (1996) in the Carpathians but occurs independent of site.

Disturbances and stability
Stability is a significant concern in forest management especially due to a number of catastrophic storm events during the last decades not only in Denmark with 5 devastating storms during the last 50 years but throughout Europe. Further, the expected climatic changes accentuate the importance of enhancing stability in general through forest management.

Within the study period 1992-2002, Suserup Skov has been influenced by two major disturbances, an extreme storm and Dutch elm disease (Bigler and Wolf 2007, Emborg and Heilmann-Clausen 2007). Both disturbances had big impacts on forest structure and species composition. Although, almost 20% of the standing volume were wind-blown during the 1999 storm event no gaps larger than 0.45 ha occurred (Bigler and Wolf 2007). As an ecological system it has proved to be very robust to such external disturbances, since the forest almost instantaneously regenerated maintaining the forest and its processes and functions. This underlines the high resistance (small scale disturbances) and especially resilience (rapid regeneration) of these mixed deciduous forests. These findings should have a direct impact on practical forestry by emphasising the stability of the species and structure rich forests specifically promoted by close-to nature management. Small scale disturbances caused by infrequent storms create gaps and opportunities for regeneration of other species and release of suppressed individuals also described at the Fontainnebleau forest reserve (Wijdeven 2003).

Regeneration and gap scale dynamics
Within which time and size limits can the manager interact with forest structures without exceeding its ability to react/repair, and how can he influence the long-term species composition? The shifting mosaic in Suserup Skov, described by the forest cycle (Figure 1) and the maps of the developmental phases in 1992 and 2002. (Figure 2), gives information about the temporal and spatial scale of forest renewal and regeneration.

The shifting mosaic regeneration pattern shows us a typical group-wise forest renewal where beech is favoured by small scale disturbances. In order to maintain or promote other species such as ash, lime and oak interventions on a larger scale are required (Schütz 1991).

However, forest management is not only a question of scale but also of time. In order to optimize wood production, forestry constantly bypasses the full temporal cycle omitting the late biostatic and especially the degeneration phase. The revised forest cycle (Christensen et al. 2007) gives an interesting picture of the developmental processes in Suserup Skov emphasizing several "short cuts" of the full circle original proposed by Emborg et al. (2000). The effect of a shortcut is that a specific mosaic/patch in the forest shifts from one phase to another but not to the phase clock-wise ahead. Figure 1 shows such "phase-shifts" caused by either crown expansion (horizontal replacement) or under storey take over (vertical replacement) bypassing the innovation stage and omitting the late biostatic and the degeneration phase. Further, both Dutch elm disease and especially the storm of 1999 created abbreviations of the full circle by destruction inducing the innovation phase. Some of these short cuts can directly be adapted into practical forestry especially in relation to developing nature-based, small-scale group-selection silvicultural systems (Larsen 2006).

The specific studies of the nutrient and water cycling in relation to gap dynamics reveal partly well described but also some unexpected results. Ritter and Vetserdal (2006) found leaching rates of about 20 kg N ha⁻¹ year⁻¹, which is an unexpected result in a semi-natural forest ecosystem characterized by small scale disturbances. A possible explanation is the pronounced deposition of N during the last
could be stored in managed forests by conversion from traditional age by changing management methods suggesting that more carbon systems). This emphasizes the great potential for additional C-stor from 240 to 266 Mg ha
parable results (353 Mg ha
Studies of carbon pools of northwest European beech forests under classical managed beech forests on similar soil types (Vejre et al. 2003). In Suserup Skov (382 Mg ha
biodiversity?

Forest management: carbon storage and biodiversity

Rather new aspects of forest management are storage of carbon and biodiversity preservation. Thereby semi-natural, unmanaged forest can serve as reference: How much and in which compartments is carbon stored, and which habitats are important for safeguarding biodiversity?

According to Vesterdal and Christensen (2007) the total C-pool in Suserup Skov (382 Mg ha\(^{-1}\)) is substantially larger than in comparable managed beech forests across age classes (77 Mg C ha\(^{-1}\)). Further, the soil C-pool in Suserup Skov is also high compared to classical managed beech forests on similar soil types (Vejre et al. 2003). Studies of carbon pools of northwest European beech forests under different silvicultural management regimes (Mund 2004) show comparable results (353 Mg ha\(^{-1}\) for the unmanaged forest Hainich and from 240 to 266 Mg ha\(^{-1}\) for different continuous cover management systems). This emphasizes the great potential for additional C-storage by changing management methods suggesting that more carbon could be stored in managed forests by conversion from traditional forest management systems based on shelter wood regeneration with rapid canopy removal to continuous cover forestry (Vesterdal and Christensen 2007), and even more carbon can be stored when leaving the forest unmanaged. It should be stressed, however, that the additional storage of carbon is limited to the transition phase. The sink function will cease when the new level of carbon is reached.

Suserup Skov shows us that forests on fertile soils in Denmark left unmanaged can develop into structurally rich systems with a mixture of different species in a mosaic of different developmental stages. This is contrasting the findings of lower species diversity in northwest Germany beech dominated forest reserves (Meyer et al. 2000), which might be explained by the very high nutrient status and water supply in Suserup compared with the German sites. The rather fine grained variation of shifting habitats provides excellent opportunities for the persistence of different organisms – if you can not survive in time you can escape in space. Mimicking this time-space continuum of forest structures as proposed by many close-to-nature forest management concepts, might thereby contribute to active biodiversity protection.

Classical forestry bypasses the later developmental phases (late biostatic and degradation) in order to harvest the trees at the economically optimal time. This implies the absence or reduction of habitats related to these phases, i.e. especially standing and lying dead wood. Hence, the amount, distribution and continuity of dead wood in Suserup Skov give additional information in terms of managing dead wood for biodiversity preservation in managed forests.

Combined with studies of dead wood in beech forests across Europe, it is clear that the amount of dead wood is in the order of 10-20 times higher in unmanaged forest reserves than in intensively managed production forests (Christensen et al. 2005). Therefore, it is imperative to include dead wood as a management target in forestry and to save wood-inhabiting organisms, a substantial sacrifice of timber trees is necessary. Dead wood – standing and lying – and its distribution in time and space in Suserup as well as in other comparable forest reserves create an important foundation for management of these habitats (Christensen et al. 2005, Jonsson et al. 2005). In the short term, this can be accomplished by leaving harvestable trees in the forest and by protecting a number of trees from felling, so that they can develop into future veteran trees to decay and collapse naturally (Butler et al. 2002). To conserve biodiversity connected to dead wood, it is also important to conserve both standing (snags) and lying (logs) dead wood (Heilmann-Clausen and Christensen 2003). Various insects and lichens have a strong preference for sun-exposed stumps and snags, bird species prefer veteran or standing dead trees for nesting and seeking food, bats preferentially roost in hollow trees, and cavity breeding animals need available snags. Fungi and bryophytes have their highest diversity connected to logs, with fungi having the highest diversity in the intermediate decay stages (Heilmann-Clausen and Christensen 2003), and bryophytes in both medium and late decay stages, combined with a need for constantly high air humidity (Odor and Standovar 2001).

The dispersal rates of different organisms make it difficult to come up with exact recommendations for the spatial distribution of dead wood. But as a general rule to integrate dead wood in sustainable forest management, care should be taken to provide both standing and fallen dead wood and veteran trees, in different decay stages and securing a continuous supply of dead wood. However, the proportion is depending on the decomposition time of the dead wood and thus on species and site (Dröffler and Lüpke 2005). To safeguard dead wood habitats in practical forestry, dead wood could be registered and marked in the same manner as more permanent key habitats. However, Suserup and other forest reserves do not tell us about threshold values of dead wood in managed forests. Here special long-term studies in managed forests have to be conducted.
Developing future scenarios for close-to-nature forest management: lessons learned – and applied

According to the National Forest Programme (2002) Danish state forests should be managed in concurrence with close-to-nature principles (Forest and Nature Agency 2005). This decision to transform “classical” age-class forests (plantation forestry) towards nature-based forest stand structures implied a paradigmatic shift in the management of state owned forests (Larsen 2006).

Nature-based or close-to-nature forestry is based upon the principle of supporting natural processes of the forest ecosystem by facilitating natural regeneration and making use of natural self differentiation (Otto 1994, Schütz 1996). Hence, the complex character of near-natural forest structures and dynamics requires integrative and flexible management frameworks and tools (Larsen and Nielsen 2007).

The concept “Forest Development Type” (FDT) provides one such adequate framework for advancing and describing long-term goals for stand structures and dynamics in stands subjected to nature-based forest management (Perpeet 2000). An FDT describes the direction for forest development on a given locality (climate and soil conditions) in order to accomplish specific long-term aims of functionality (ecological-protective, economical-productive, and social-cultural functions). It is based upon an analysis of the silvicultural possibilities on a given site in combination with the aspirations of future forest functions. It will serve as a guide for future silvicultural activities in order to “channel” the actual forest stand in the desired direction (Larsen and Nielsen 2007).

Such a common understanding and agreement upon the desired development are crucial, since the conversion from age-class to nature-based stand structures is a continuing process. With the LOWE-Programme (Otto 1989) the Forest Development Type-concept has been successfully introduced to facilitate the transition to close-to-nature forest management in the state forests of Lower Saxony.

Hence, the FDT-concept comprises a broader understanding of natural disturbance regimes and succession processes. As such it has great similarities with the forest cycle models that have successfully been used to describe the temporal and spatial dynamics and cyclic preoccupation of a specific forest type in natural forest reserves. Consequently, the lessons from Suserup Skov had a decisive influence on some of the 19 FDT developed as long term goals for close-to-nature forest management in Denmark (Larsen and Nielsen 2007) – especially the FDT 12: Beech with ash and sycamore.

Figure 3 describes the FDT 12, which in its species composition and regeneration dynamics has been derived directly from the species composition and structural dynamics of Suserup Skov:

- **Species composition**: beech: 40-60%, ash and maple: 30-50%, cherry, hornbeam, oak, lime and others: up to 20%.
- **Structure and dynamics**: Species rich well structured forest with beech as the dominating element mixed with ash and cherry, and in south-eastern Denmark additionally with hornbeam and lime. The mixed species occur mainly in groups. The horizontal structures arise between groups of varying size and age. Where the light demanding species such as ash, sycamore and cherry dominate, vertical structures occur with shade trees (beech, hornbeam, elm, and others) periodically in sub-canopy strata. Beech regenerates mainly in groups and smaller stands. Ash and sycamore, as gap specialists, regenerate in gaps later followed by beech. Hornbeam belongs to the sub-canopy stratum and regenerates under shade, whereas the pioneer species (cherry and oak) only regenerate after larger openings and/or in relation to forest edges.
Through the forest development concept, subsequently, several lessons from Suserup Skov have been translated into long term goals for Danish forest management and communicated effectively to the practitioners.

Conclusions

The aim of this article is to show how studies of structures and processes in a Danish forest reserve can and already have inspired forest management in developing management methods, which to a higher degree than conventional age-class management can generate stable forest and balance wood production with biodiversity protection. There are of course many restrictions in interpreting results from a small forest reserve into general management guidelines. To what extent represent the structures and processes studied general aspects of ecosystem development and how much are they influenced by former human influences and by chance? How can understanding from one specific site be extrapolated to larger regions? And further, how can such retrospective analyses be applied in forest management facing the challenge of adapting to climate change, since they basically are looking at past and present structures aiming at understanding causal processes?

Forest management, however, is at present confronted with the task to develop more sustainable management methods. In most of the European countries this implies the application of close-to-nature or near-nature management based on continuous cover principle. In contrast to “classical” age-class management characterized by intensive research over the past 150 years close-to-nature management has a very weak scientific foundation. In this context and in spite of the above mentioned limitations, forest reserve studies play an important scientific platform and inspiration for the application of new management methods. This underlines the importance of sustained research in forest reserves especially in relation to climate change responses and to keep an ongoing dialogue between scientists and forest practitioners.

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