

Near-Natural Forests in Southern Sweden

**Silvicultural and palaeoecological aspects
on nature-based silviculture**

Gisela Björse

*Southern Swedish Forest Research Centre
Alnarp*

**Doctoral thesis
Swedish University of Agricultural Sciences
Alnarp 2000**

Acta Universitatis Agriculturae Sueciae

Silvestria 134

ISSN 1401-6230

ISBN 91-576-5868-4

© 2000 Gisela Björse, Alnarp

Abstract

Björse, G. 2000. *Near-Natural Forests in Southern Sweden. Palaeoecological and silvicultural aspects on nature-based silviculture.*
ISSN 1401-6230, ISBN 91-576-5868-4.

Timber production and protection of biodiversity are two main issues in south Swedish forestry. This thesis explores the possibilities of combining the two issues in a nature-based silviculture. Different branches of science, palaeoecology, silviculture and forest vegetation ecology, were combined to give a multidisciplinary approach to the subject.

Mimicking the historical forest composition and processes in the silvicultural measures for the benefit of both biodiversity protection and timber production was identified as one possible way of developing a nature-based silviculture. The long period of human influence on the landscape in southern Sweden has effectively removed all the remnants of natural forest that could have been used as references in the mimicking procedure. Consequently, historical references were searched. A method to describe former forest conditions was developed using palaeoecological data and methods. It was found that the historical deciduous dominance was pronounced. Over 2000 years southern Sweden has been transformed from a deciduous to a coniferous landscape. Human activities were indicated as a major driving force in this change. Several detected historical forest types were possible as references for the mimicking approach, but forest types common in the past and rare today were suggested for maximal efficiency in obtaining high biodiversity. Mixed nemoral deciduous forests were pointed out as a historically widespread forest type with very little resemblance in the present landscape. The small fragments left are important for present biodiversity and from many other aspects. Development of a nature-based silvicultural system for the management of mixed nemoral forest stands based on the theory of mimicking was begun. A silvicultural experiment was established in a near-natural, mixed nemoral forest stand in southern Sweden and the early effects of the silvicultural treatments tested were evaluated with regard to floristic diversity. The early findings indicate that advance growth may be an effective source for regeneration of the forest type. Soil scarification is not recommended when regenerating mixed nemoral deciduous forest stands as the destruction of advance saplings was not compensated by new establishment, and because a tendency towards alteration of the ground flora typical of nemoral forest to a pioneer plant community was traced. Sparse shelterwood cutting is suggested as an appropriate way of combining biodiversity consideration and timber production in mixed nemoral deciduous forest stands. Finally, a framework of an approach to obtain a nature-based silvicultural system was developed, based on the presented results and other information.

Keywords: Nemoral forest, boreo-nemoral forest, deciduous forest, mixed forest, forest history, vegetation dynamics, nature conservation, biodiversity, floristic diversity, mimic, multiple use, shelterwood, soil scarification.

Author's address: Gisela Björse, Southern Swedish Forest Research Centre, SLU, P.O. Box 49, S-230 53 Alnarp, Sweden.



Contents

Introduction, 7

Nature conservation and forestry, 7

Study area: southern Sweden, 7

Abiotic factors, 9

Biotic factors, 9

Cultural factors, 11

Silvicultural factors, 11

Combining nature conservation and forestry in southern Sweden, 12

Objectives of the thesis, 13

Background to and definitions of terms used in the thesis, 13

Summary of the papers, 15

Paper I, 16

Paper II, 16

Paper III, 18

Paper IV, 19

Paper V, 19

Discussion, 20

The constitution of southern Swedish historical forests, 20

Driving forces for the changes of forest composition, 21

Forest types of interest for nature-based silviculture in S. Sweden, 22

Silvicultural aspects on the management of near-natural nemoral forest, 23

The treatments, 23

Advance growth, 24

Soil scarification, 24

Expansion of mixed near-natural nemoral deciduous forests, 25

Effects of silvicultural activities on floristic diversity, 26

Methodological aspects, 26

The palaeoecological method, 26

The silvicultural method, 27

Implications for nature-based silviculture in southern Sweden, 28

Further research, 29

Concluding remarks, 30

Sammanfattning, 30

Acknowledgements, 32

References, 33

Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

- I. Björse, G., Bradshaw, R. H. W. and Michelson, D. B. 1996. Calibration of regional pollen data to construct maps of former forest types in southern Sweden. *Journal of Paleolimnology*, 16: 67-78.
- II. Björse, G. and Bradshaw, R., 1998. 2000 years of forest dynamics in southern Sweden: suggestions for forest management. *Forest Ecology and Management*, 104: 15-26.
- III. Björse, G. Effects of shelterwood density, soil scarification and fencing on natural regeneration within a mixed near-natural nemoral forest stand in southern Sweden. Manuscript.
- IV. Björse, G. Effects of silvicultural treatments on the field layer vegetation and floristic diversity within a mixed, near-natural nemoral forest stand in southern Sweden. Manuscript.
- V. Bradshaw, R. H. W. and Björse, G. Regeneration of deciduous native tree mixtures with consideration to biodiversity in forest stands used for timber production. Manuscript.

Paper I and II is reproduced with kind permission from the publishers.

Introduction

Forestry and the forest industry have been major activities in Sweden for a long time. In recent years, nature conservation has become a major issue, stimulated by pressure from public opinion, environmental organisations (Löf 1993) and international treaties (UN 1992, Loiskekoski and Halko 1994). This has been reflected in political decisions, for example the Swedish Forestry Act (SOU 1992, anon. 1999 a) where the protection of biodiversity is now ranked equal to timber production. The government has made efforts to attain the double objectives, but we still lack a solid scientific base for the most appropriate and efficient way to obtain a desired combination of biodiversity protection and timber production. This lack of knowledge is most apparent in southern Sweden. Few scientific studies have been focused on the issue in the south, although in many ways the problems are more complex than in the northern, boreal regions.

This thesis intends to contribute to the discussion around the combination of timber production and the concern for biodiversity within southern Swedish forestry. Different branches of science: palaeoecology, silviculture and forest vegetation ecology were combined to give a multidisciplinary approach to a fairly unexplored subject. The thesis has an exploratory approach. The intention was to cover many aspects of the issue in order to come up with ideas and results, some of which may form the basis of more detailed studies.

Nature conservation and forestry

The importance of considering biodiversity in forest management can be divided into moral/responsibility and functional aspects. Moral aspects include obligations to species, biotopes and ecosystems that we have caused to become locally, regionally or globally extinct, or threatened (Aronsson 1999), and also cultural-historical ambitions to protect features of former forest- and landscape management systems that are no longer economically viable (Emanuelsson and Bergendorff 1986). Former human activities have created a cultural heritage of biodiversity that is valuable as a base for cultural traditions. Functional aspects deal with the future possibilities of long term utilisation of the forest resource. High biodiversity ecosystems are thought to be stable while low biodiversity ecosystems may be vulnerable under changing conditions (Larsen 1995, Tilman and Dowing 1994). Biodiversity is generally assumed to be lower in a forest heavily utilised for timber production than in the virgin forest (Seymour and Hunter 1999). Traditional forestry is primarily focused on timber production in monocultural stands and was developed during a short time horizon in geological and climatological terms. The adaptability to the steadily ongoing long-term climatic and geological changes has not been considered. This has led to the development of management systems that in part are characterised by reduced stability and low flexibility in terms of future change in human demands and environment (Larsen 1996). Storm, pests, snow damage and insect attacks are

feared to be massive in species-poor systems (Heybroek 1980, Seitschek 1989, Watt 1992), where resistance and resilience are often low (Larsen 1995). These threats are often less pronounced in diverse forests (Schmidt 1978, Huss 1987).

Ranking biodiversity considerations equal to economic production implies a practical and theoretical challenge. It can be approached in at least three principal ways. 1) By intense plantation forestry with maximal volume production in certain areas and full protection of the nature in permanent reserves in other areas (Hunter and Calhoun 1996, Vollbrecht 1996). Liljelund et al. (1992) state that 15% of the productive forest land in Sweden must be set aside in reserves if no general concern for nature is taken in the silvicultural operations. This approach is practiced in, for example, New Zealand, Brazil and Australia. 2) By protecting identified endangered species or isolated habitats, while running a traditional forestry on the main part of the landscape. This approach has been applied during recent decades when selecting areas for nature reserves and for special concern in association with silviculture in sensitive habitats (Gibbons 1992, Hansson and Larsson 1997). 3) By mimicking the structure, tree species composition and dynamics of the natural forest of a region in the silvicultural operations. This approach has been suggested by many authors in recent years (Hunter et al. 1988, Franklin 1992, Angelstam et al. 1993, 1995a and b, Attiwill 1994 a and b, Bradshaw et al. 1994, Roberts and Gilliam 1995, Otto 1995, Angelstam 1996, Angelstam and Pettersson 1997, Bergeron and Harvey 1997, Fries et al. 1997 and 1998, Larsen and Johnson 1998, Ohlsson and Tryterud 1999, Seymour and Hunter 1999). The approach aims to maximise caution for biodiversity given that some silvicultural activities have to take place. By adjusting the severity, spatial pattern and return interval of the silvicultural harvests to the natural regional disturbance regimes, thereby letting the mixture and composition of the remaining stand resemble the state of the virgin forest, a near-natural physical environment can be created as an "arena" for the biological activity. The ecosystem function, including adaptation to ongoing, natural long-term changes, can in such way be maintained despite human utilisation. Hunter et al. (1988) discuss this approach as a possibility to save a large number of species from extinction though the majority of them have not even been described. The natural forest of the region is not one single state, but includes a range of possible ecosystems (Sprugel 1991), also dependent on regional and temporal scale, so the optimal state to mimic varies and overlaps within different scales. In theory, historical manmade features vital for biodiversity are also possible to mimic. The economic outcome of the forestry may be reduced, but not excluded. The described approach of mimicking the natural forest in practical forestry coincides with the concept of nature-based silviculture (Bradshaw et al. 1994).

I wish to emphasise that these three approaches are not mutually exclusive, but rather can complement each other to achieve the optimal benefit for the management of biodiversity and timber production (Hunter et al. 1988).

Study area: southern Sweden

Abiotic factors

This study was made in southern Sweden, a rather flat landscape with altitudes varying between 0 and 350 m a.s.l. on Precambrian granites and gneisses (Lundquist 1994). The southernmost part and the islands of Öland and Gotland have large areas of sedimentary calcareous bedrocks (Lundquist 1994). Quaternary deposits form rather deep soils of mainly varying moraines with podsoil or brown earth (Troedsson and Nykvist 1973). The climate is fairly maritime due to the Gulf Stream, with mean annual temperatures ranging from 5.0° C to 8.0° C (Eriksson 1982), and a growing season of ca.180-220 days (Tuhkanen 1980), with large areas subjected to spring and autumn frosts (Ångström 1974). Prevailing wind direction is from the west (from SW to NW) (Persson 1975), and the mean annual precipitation ranges from ca. 1100 mm in the west coastal areas to 400 mm on the east coast of Swedish and the islands of Öland and Gotland (Eriksson 1983). The precipitation mainly occurs as rain with a maximum in late summer. The mean annual duration of snow cover varies from 30 days in the south to 140 days at the northern border of the boreo-nemoral zone, with great yearly fluctuations (Ångström 1974).

Biotic factors

The major part of Sweden belongs to the boreal vegetation zone. (Sjörs 1965, Ahti et al. 1968) The southernmost part of Sweden, however, like central Europe, is part of the nemoral zone, (Fig. 1). This zone has analogues in the temperate zone in eastern North America (Röhrig 1991). The transition zone between the nemoral and boreal vegetation zones is called the boreo-nemoral or the hemi-boreal vegetation zone (Sjörs 1965, Ahti et al. 1968). This zone also embraces the south-eastern parts of Norway, the southernmost parts of Finland, the Baltic states and extends into Russia. In the north it is limited by limes Norrlandicus and, in the south, the south-western limit of the natural distribution range of Norway spruce. However, due to extensive planting of spruce south of its natural distribution range, it is no longer possible to accurately reconstruct this border (Sjörs 1965). The boreo-nemoral forests are characterised by the dominance of conifer species, spruce (*Picea abies*) and pine (*Pinus sylvestris*), with a significant representation of deciduous forest. Almost all native nemoral deciduous tree species are present (see p. 14). However, hornbeam (*Carpinus betulus*) is restricted to the vicinity of the nemoral border in the south, and beech (*Fagus sylvatica*) is only represented as scattered stands or individuals. Their representation significantly decreases northwards (Hultén 1950). The presence of nemoral deciduous tree species vary within the vegetation zone depending on climatic and/or edaphic conditions (Diekmann 1994), and as a result of human activities over thousands of years (Berglund 1969, Behre 1988, Lindbladh and Bradshaw 1998, Lindbladh et al. 2000).

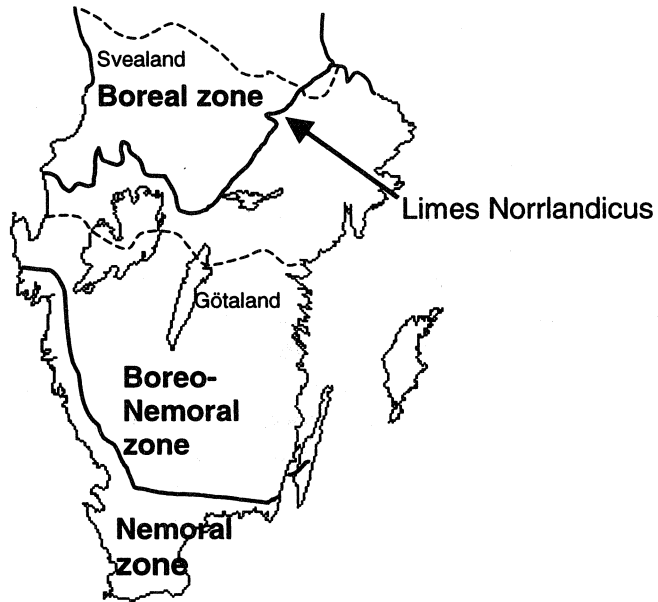


Fig. 1. Southern Sweden with vegetation zones (straight lines), and the provinces of Svealand and Götaland.

Southern Swedish forests are valuable for biodiversity. Several studies show a higher abundance of threatened species than in the north (Berg et al. 1994 and 1995, Berg and Tjernberg 1996, Gustafsson 1994). The small-scale mosaic of biotopes and habitats brings about a rich flora and fauna. The nemoral deciduous forests are particularly important to biodiversity, despite their very small area (Berg et al. 1994 and 1995). Only ca. 0.5 % of the Swedish forested area is nemoral deciduous forest and most of it is in the form of intensively managed production stands (Stener 1998). Stands with a mixture of several nemoral tree species, a large amount of dead wood, large old trees and long tree continuity are most valuable for biological complexity including rare and threatened species (Nilsson 1997, Samuelsson et al. 1994, Fritz and Larsson 1997). This has been stressed in official conservation work, which has focused on nemoral deciduous forest habitats in the nemoral and boreo-nemoral zones (Norén et al. 1995).

The nemoral deciduous forests were characterised in their natural state by small-scale disturbance regimes resulting in small gaps from single trees or small groups of trees (Falinski 1986, Röhrig 1991, Runkle 1985). Wind throws (Falinski 1978 and 1986), grazing and browsing (Bradshaw and Mitchell 1999), rooting from wild boar (Altrell 1995, Welander 2000), and flooding (Schnitzler, 1995, Ellenberg 1988, Naiman et al. 1988) are supposed to be major natural disturbance factors in the nemoral forests. This constitutes a major difference to the boreal forest, which is characterised by the large-scale disturbance by fire (Zackrisson 1977, Engelmark 1984, Bergeron 1991). Human activities should also be regarded as a disturbance factor in the nemoral and boreo-nemoral zones.

Human agricultural activities throughout history increased the biodiversity in southern Sweden by consciously or unconsciously introducing species (Bradshaw 1995, Webb 1985). Several features important for biodiversity are linked to former management regimes, such as the meadow system, pollarding and cattle forest grazing (Emanuelsson and Bergendorff 1986, Slotte and Göransson 1996).

Cultural factors

The south Swedish landscape has been influenced by human activities over several thousands of years (Berglund 1969 and 1991, Lindblad 1998). The earliest evidence of farming in southern Scandinavia has been dated by pollen analyses to around 3500-3000 B.C. (Berglund 1969). The pressure from human utilisation has gradually increased over time. Today there are no remnants of a "natural" or virgin forest left in southern Sweden. There are virtually no international references concerning the nemoral zone, due to an even more intensive land use in the central European countries (Rackham 1980, Thirgood 1989, Pott 1988). This has resulted in an even more vague picture of the ecological features of natural forests in central Europe. In the same way as the Swedes seek boreal analogues in Russia for scientific understanding (Angelstam et al. 1995 a and b), southern Sweden may contribute to the understanding of the nemoral virgin forest of central Europe.

Today, forestry is a major economic activity in southern Sweden, as well as in the rest of the country. Many local communities rely socially and economically on forestry. In principle the full forest resource is utilised for timber production. Only 0.7 % of the forested area is protected for conservation purposes (Löfgren 1997). Economic private forestry is of less importance in the nemoral forest regions in central Europe.

Southern Sweden is densely populated and the forest ownership is scattered. 60% of the forest is owned by 172000 land owners with an average forest property size of 33 ha (Anon 1999 b). This causes problems for landscape planning opportunities for nature conservation and timber production (Carlsson 1998).

Silvicultural factors

Most south Swedish forests, both coniferous and deciduous, are intensely managed for economic timber production. Beech is the most economically used deciduous tree species. Current south Swedish harvesting methods include clearcutting and various shelterwood systems. The shelterwood produces seeds for natural regeneration (Hagner 1962) and reduces frost (Ottosson-Löfvenius 1993), vegetation competition (Helliwell and Harrison 1979, Béland in press) and insect attacks (von Sydow and Örlander 1994). Nemoral deciduous forests are primarily regenerated by using natural regeneration under a uniform shelterwood system (Henriksen 1988, Harmer 1994). Soil scarification is widely used for natural regeneration of beech (Bjerregaard 1979), and is believed to decrease competition from ground vegetation, improve microclimatological conditions for

seedlings (moisture, temperature, air circulation), enhance mineralization, and reduce insect attacks (Örlander et al. 1990).

Combining nature conservation and forestry in southern Sweden

Roberts and Gilliam (1995) regard the maintenance of biodiversity to be one of the main objectives of global sustainability. The protection of biodiversity is an urgent, often discussed question also with regard to southern Sweden (Berg et al. 1994 and 1995, Nilsson 1997). Meanwhile, economic timber production is of crucial importance to regional forestry and the socio-economic situation. Hence the combination of biodiversity protection and timber production is a major issue in southern Sweden. Mimicking natural conditions in the silvicultural measures within stands is one approach towards reaching this goal, while landscape models may be complicated due to the ownership structure. In conclusion, the mimicking approach is attractive as one possible way of solving the double demands in southern Swedish forestry.

However, the mimicking approach does raise obstacles. The massive human transformation of the south Swedish landscape has caused a lack of information about the natural forest conditions. No remnants of virgin forests exist as a reference for developing the mimic approach. The reference forest conditions have to be found in the past. Written sources do not reach back to the times when forests were unexploited by man, whereas palaeoecological methods can be used to investigate former habitats over thousands of years.

The opportunities for adapting silvicultural activities to natural conditions are greatest at harvest and in the following regeneration phase. Nemoral deciduous regeneration often needs to be fenced due to heavy ungulate browsing. We have limited information on the compatibility of these methods with nature-based forestry.

We need to acquire more information about the changes in southern Swedish forest over time and the driving forces behind these changes. It is important to carefully design and evaluate the mimicking approach to the local ecosystem. Silvicultural methods, especially for harvesting and regeneration, should be designed to promote both the cultivation and harvesting of wood products and the features important to biodiversity. Traditional methods may be used with small refinements, or questioned and abandoned if necessary. This has to be evaluated from both a silvicultural and ecological perspective.

Objectives of the thesis

The objectives of this thesis were to:

- 1) Map the changes in forest types in southern Sweden over the last 2000 years. The aims were:
 - a) to create a useful method of describing the former forest composition of a region over such a long period that written sources are insufficient;
 - b) to identify which tree species existed on a regional scale;
 - c) to quantify the relative amounts of these tree species.
- 2) Evaluate the driving forces for the changes in southern Swedish forests. The questions addressed were:
 - a) What were the major recent changes in the constitution of the southern Swedish forest?
 - b) What were the driving forces for these changes, in particular the balance between anthropogenic activities and 'natural' drivers?
 - c) When did these changes occur?
- 3) Identify current forest types with a large 'natural' component and a long continuity on the landscape. Such forest types are likely to be of interest for nature conservation and the mimicking approach to the combination of biodiversity protection and timber production in southern Swedish forests.
- 4) Start investigating silvicultural possibilities to regenerate stands of the identified forest types in accordance with the mimicking approach of combining biodiversity and timber production.
- 5) Start describing the effects of silvicultural activities on biodiversity in the identified forest types. The aspect of biodiversity studied was floristic diversity.

The overall purpose was to contribute to knowledge important for practical recommendations on, and to define the need for further research about, issues concerning nature-based silviculture in southern Sweden.

Background to and definitions of terms used in the thesis

Biodiversity (Biological diversity). There are many definitions, sometime with quite different meanings, attached to the term biodiversity (for review, see DeLong 1996). In this thesis I use: "Biological diversity means the variability among living organisms from all sources including inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part, this includes diversity within species, between species and of ecosystems." (UN 1992). I use the term "floristic diversity" as simply the numerical diversity of vascular plant species in the field layer. It is expressed as a number of species or with the Shannon index (Shannon and Weaver 1949).

Naturalness is reviewed by Peterken (1996) and Sprugel (1991), who both stress the difficulty of defining the term. Peterken (1996) defines natural as ‘absence of people’, but stresses the practical used application as being ‘close to’ this state. Sprugel (1991) concludes that there is not one single state of naturalness but a range of ecosystems in a region that can be considered ‘natural’. My way of using the term “natural” fits both these definitions. ‘Near-natural’ permits a freer application and is often used without a strict definition. The application varies significantly between regions and biotopes. In my work I define it myself in Paper III: ”Stands corresponding to historically common, mixed nemoral deciduous forests, though not ‘natural’ as defined by Peterken (1996) in that they show no direct signs of human impact.” Or, as in Paper IV: “The present area in southern Sweden still featuring a mixture of several nemoral deciduous tree species, cannot be considered as natural, where ‘natural’ is defined as showing no direct signs of human impact (Peterken 1996). However, these forests retain certain features of the primeval deciduous forests as regards species composition and occasionally structure.”

Nature-based silviculture is a theoretical and/or practical method of combining biodiversity protection and timber production on stand scale (Bradshaw et al. 1994). It strives to adapt silvicultural measures to the natural processes and the flexibility of the steadily changing forest ecosystem. The theory of mimicking the natural forest for the combination of biodiversity protection and timber production coincides with the concept of nature-based silviculture. Nature-based silviculture may be used as one component in the construction of a sustainable forestry.

Nemoral deciduous forest. A forest that consists of at least 70 % (basal area) of deciduous trees and at least 50 % of one or several nemoral deciduous tree species in at least 0.5 ha is defined as nemoral deciduous forest (Anon. 1999 a). The nemoral deciduous tree species are: oak (*Quercus robur*) and (*Q. petraea*), beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), maple (*Acer platanoides*), elm (*Ulmus glabra*), lime (*Tilia cordata*), hornbeam (*Carpinus betulus*) and sweet cherry (*Prunus avium*). This type of forest is also called “southern deciduous forest” (Sjörs 1965), “southern deciduous woodland” (Gustafsson 1994), “temperate deciduous forest” (Röhrig 1991), “noble forest”, “valuable hardwood” (Anon. 1994), “broad-leaved hardwood forest” (Diekmann 1994), “rich deciduous forest” (Papers I and II) or in Swedish “ädellövskog” (Almgren 1984).

Palaeoecology is the science of ecological conditions during the history of the earth (Birks and Birks 1980). It originated as a branch of palaeontology and is scientifically organised at the interface of biology and geology. It is the major source of knowledge about the ecosystems in the time prior to written sources, and includes studies of fossil pollen, spores and floristic and faunal macrofossils. The science has developed since the beginning of the twentieth century (for review, see Hannon 1999). The traditional pollen analysis (Birks and Birks 1980)

involves the collection of pollen samples from large basins (lake or bogs), reflecting an entire region. The fossil pollen grains can be preserved in the anaerobic environment of the sediment deposit for thousands or even millions of years due to their resistant outer crust. After extraction they can be analysed in a microscope and defined to family, genus or species, and dated with the help of C14 analysis. The intrinsic relation of pollen taxa and the variations over time are subjected to interpretation with the help of calibration methods to get an understanding of the former vegetation composition of the region (Davies 1963).

Silviculture concerns the management of forests and should be considered an academic term. It is sometimes defined as “the cultivation of trees and management of forests and woodland for timber” (Lawrence 1995), or “the raising, care and renewal of forest stands in such way that the production capacity of the site is sustainable and utilised most appropriately” (translated after TNC 96 1994). I prefer to consider it as “the science of” these definitions. Traditional Swedish silvicultural research has mainly dealt with timber production from conifer species in the boreal forest (e.g. Pettersson 1955, Jonsson 1962, Eriksson, 1976, Albrektsson, 1980, Nilsson, 1993). Silviculture is the main source of knowledge for rational forestry in Sweden. The present silvicultural research deals to some extent with questions about sustainable forestry.

Southern Sweden In contexts where “south Sweden” or “southern Sweden” are used without further explanation I refer to the regions of Götaland and Svealand with special emphasis on Götaland. This roughly corresponds to the nemoral and boreo-nemoral vegetation zones (Fig. 1). The term is used vaguely in some contexts.

Summary of the papers

Papers I and II concern forest vegetation history in southern Sweden. In these studies palaeoecological methods and data were used. Paper III is concerned with the regeneration of mixed near-natural nemoral deciduous forest stands from a silvicultural point of view. Paper IV describes the response of the ground vegetation to the silvicultural operations described in Paper III, with a vegetation ecological approach. Paper V puts the palaeoecological, silvicultural and vegetation ecological knowledge acquired in the previous papers into a conceptual approach to mimic the “natural” forests as a basis for nature-based silviculture in southern Sweden, but does not contribute with original results.

I. Calibration of regional pollen data to construct maps of former forest types in southern Sweden

The aim of the first study was to develop a method for constructing maps of former forest types using palaeoecological data. This method can serve as an effective tool when reconstructing historical forest composition on a regional scale in areas with little knowledge about the virgin forests.

The method was developed using 37 regional pollen analyses with pollen source areas of approximately 50 km radius, all located in Sweden south of 60°N. The pollen sites were lakes or peat deposits which were all of high quality: large pollen totals, well-dated and analysed after 1960. Pollen from all present tree taxa; *Alnus*, *Betula*, *Carpinus*, *Corylus*, *Fagus*, *Fraxinus*, *Juniperus*, *Picea*, *Pinus*, *Populus*, *Quercus*, *Salix*, *Tilia* and *Ulmus* were considered. Pollen percentage values of each site for five points in time - 2000 years Before Present, 1500 BP, 1000 BP, 500 BP and present - were calculated and converted into estimates of tree composition. An inverse distance weighted interpolation algorithm was used to generate maps for each species at each point in time, and a supervised classification routine was used to generate nine forest types common for all time intervals. The method was calibrated by comparing the core tops with present day inventory data and by comparing local pollen analyses with the regional ones forming these maps.

The results were presented on two types of map. Tree abundance maps where *Fagus* and *Pinus* were shown as examples, and forest type maps showing the correspondence of corrected pollen data to tree inventory data. Some tree species abundances were overestimated and others underestimated, but the overall estimates of abundance and patterns of distribution were well reflected by the maps. Difficulties and accuracy of the method were discussed. The most difficult tasks to solve were how to obtain accurate correction factors for pollen abundance – tree abundance, and how to make correct estimates for species with poor pollen dispersal, such as *Tilia* and *Acer*. Comparisons to overlapping small hollow pollen analyses helped us to make correction factors for lime. These correction factors are not very precise due to weak data support, but may be assumed to also represent ecologically similar tree species such as *Acer*, *Ulmus* and *Fraxinus*, which lack the possibilities of this type of correction.

II. 2000 years of forest dynamics in southern Sweden: suggestions for forest management

The aim of the second study was to give an overall description of the former forests in southern Sweden and to discuss the driving forces for forest change in the area. The method described in Paper I was used to generate forest type maps of southern Sweden every 500 years since 2000 BP.

The results show a dramatic conversion from deciduous forests to coniferous forests. Spruce entered the region from the north, and migrated rapidly southward,

as shown in many previous studies (Moe 1970, Tallantire 1972), but did not dominate the landscape as at present. Rich mixed deciduous forest dominated the most southerly part of the studied area during the first part of the study period. It was replaced by beech forest 500 BP, a forest type that was not at all represented until 1000 BP, although beech also occurred earlier as a minor element in several deciduous mixtures. Still, at 500 BP the beech forest was not a monocultural forest like most present south Swedish beech stands. Rich mixed pine forest was another abundant forest type that has practically disappeared. It consisted of a mixture of pine and several nemoral deciduous tree species such as oak, lime, birch and alder. Pine dominated coniferous forest is mainly represented in the eastern parts of the region.

This type of map helps to investigate the forest history before the period of written sources. The time period studied is chosen to reflect a forest under human influence. In fact the human influence, in the form of clearance for agricultural land, and manipulation of the natural fire and grazing regimes, is indicated to be the major driving force of forest change during the last 2000 years. Climate change, natural migration processes and soil degradation also contributed to the forest development.

Limitations of the method were discussed: it is not possible to distinguish the level of mixture of the tree species within a forest type; they can be mixed by stems or in small or larger stands, and also vary in different time periods. Nor do the maps tell how dense the described forests were, or what proportion of the landscape was forested. In one case out of the nine defined forest types, open mixed forest, the high abundance of juniper pollen suggests an open forest, but in other cases the openness and amount of open areas in the landscape probably varied both spatially and temporally.

The results have implications for the development of guidelines for sustainable forestry in the region, in accordance with the approach of mimicking the natural forest when performing silvicultural operations. All forest types present in the recent past of a region are important for maintaining high biodiversity, functioning ecosystems and the protection of threatened species. However, efforts to imitate former forest types should be concentrated to forest types that were common in the past and rare at present, in order to be the most effective and gainful to the protection of biodiversity. At least three such forest types were identified as valuable for southern Sweden: rich deciduous forest, rich mixed pine forest and open mixed forest.

III. Effects of shelterwood density, soil scarification and fencing on natural regeneration within a mixed near-natural nemoral forest stand in southern Sweden

The aim of the third study was to describe the early regeneration process within a near-natural nemoral forest stand in southern Sweden. This was done in relation to various silvicultural measures - shelterwood density, fencing and soil scarification - in order to enhance the general knowledge about regeneration of mixed nemoral deciduous stands in the nemoral zone.

A long-term experiment was established in a ca. 70-year-old, mixed near-natural nemoral forest stand in southern Sweden (55°53'N, 13°39'E). It had a split plot design with shelterwood density as main plots, and fence and soil scarification as sub plots. Ash and beech dominated the stand, which also had considerable elements of hornbeam, elm, hazel (*Corylus avellana*) and minor streaks of maple, lime, alder (*Alnus glutinosa*) and birch (*Betula pendula/pubescens*). The site factors were favourable. The levels of the treatment intensities were chosen to represent a range of disturbance intensities, assumed to be equivalent to, or exceed, the natural disturbance intensity of the nemoral ecosystem. The logging was performed so that the shelterwood would reflect the species composition of the original stand. Advance growth was registered from the start, and annual establishment of new tree seedlings and suckers (in common named saplings) was registered by species during the first four seasons after the treatments. Survival and death of previously recorded saplings were registered. The material was analysed statistically with analysis of variance.

The early results show overall good establishment. The highest total mean number of saplings/m² at the end of the study period was found in sparse shelterwood (27.9 saplings/m²) and on unscarified soil (25.5 saplings/m²) respectively. No difference was found between the fenced and unfenced areas except for birch, which had nearly four times as many saplings in the unfenced areas as in the fenced. No treatment or species showed a reduced amount of saplings during the study period and the ranking of treatments remained the same: the treatment with the highest number of saplings/m² in 1995 still had most saplings in 1998. Ash dominated the regeneration in all treatments, followed by hornbeam. Birch representation increased over time on the clearcut and the open mixed soil. Maple had best regeneration results in the dense shelterwood and on undisturbed soil. Elm had the most numerous regeneration results on undisturbed soil, and the lowest in sparse shelterwood.

Advance growth had higher survival than saplings established during the study period, and the most crucial factor for the final regeneration result was the amount of advance growth at the start. Hence the undisturbed soil had the best regeneration result as saplings were not removed by the treatment itself, as on the scarified plots. New establishment during the study period did not compensate the loss of advance growth on the scarified plots. Soil scarification is not

recommended as this impairs the final regeneration result by destroying the advance growth saplings.

IV. Effects of silvicultural treatments on the field layer vegetation and floristic diversity within a mixed, near-natural nemoral forest stand in southern Sweden

The aim of the fourth study was to describe the short-term effects of silvicultural treatments on the field layer vegetation in a near-natural mixed deciduous forest stand, hopefully contributing to knowledge about the silvicultural effects on floristic diversity in nemoral forests.

The same experimental setup as described for Paper III was used in the same 70-year-old, mixed near-natural nemoral forest stand in southern Sweden (55°53'N, 13°39'E). It had a split plot design with shelterwood density as main plots, and fence and soil scarification as sub plots. The site factors were favourable and the field layer vegetation was dominated by species common to the biotope, composed of a wide variety of species, including rare and threatened species. Number of species and species cover were investigated and statistically evaluated with analyses of variance. Floristic diversity was expressed as number of species and with the help of Shannon index. The early results covering investigations from the first three years after the silvicultural treatments were presented.

The experiment will be continued but the early results presented show that number of species, cover and Shannon index increase as a result of most treatments. Several species typical of the nemoral forest also increased but did not show the largest increase on the most disturbed areas (clearcut and open mineral soil). Other species typical of the nemoral forest decreased during the study period. Early successional species increased on the most severely disturbed soil. No trends were found as a result of fencing. My interpretation is that high floristic diversity in near-natural nemoral forests in southern Sweden may initially be conserved, or even improved by silvicultural operations. However, the ground flora typical of the nemoral forest may be disfavoured by the most intensive silvicultural treatments, for example by increased competition from increasing pioneer species. I recommend caution in the use of clearcutting and intensive soil scarification methods when managing mixed nemoral forests.

V. Regeneration of deciduous native tree mixtures with consideration to biodiversity in forest stands used for timber production

The aim of the fifth study (V) was to describe a silvicultural approach for combining economic production with the protection of biodiversity. The approach was developed to be applicable to existing nemoral mixed deciduous forest stands and focuses on regeneration of such stands.

The approach is scientifically anchored in the theory of mimicking the historical forest of the region for the combination of biodiversity protection and timber production. As no natural forests for reference are left in the nemoral part of Europe, palaeoecological data, partially from Papers I and II, was used for the reconstruction of former tree species composition. This helped us to suggest appropriate mixtures of tree species for the management for biodiversity and also to indicate fragments on the landscape for the study of internal forest dynamics. Data on forest regeneration in mixed near-natural nemoral forests was obtained from Paper III and further analysed. A good regeneration result was obtained with an even wider tree species diversity than in the old stand. Beech, which is the most economically used nemoral deciduous tree species, decreased its representation. Due to the good total regeneration result there were however enough beech saplings to presume an economically vital regeneration result. This will be subjected to further evaluations. The possible use of advance growth and vegetative sprouting for regenerating mixed stands was discussed. A rapid field recording system to estimate the biodiversity potential was presented, and applied to the regeneration trial experimental site. The biodiversity potential was somewhat decreased as a result of the silvicultural operations but not to the levels of traditional beech forest management. The approach combined palaeoecological, vegetation ecological and silvicultural knowledge on mixed near-natural nemoral forests. Natural regeneration under a mixed species sparse shelterwood was suggested for obtaining a similar tree species mixture in the secondary stand, a preserved biodiversity potential and high economic capacity.

Discussion

The constitution of southern Swedish historical forests

The historical dominance of deciduous species in southern Sweden has already been stressed. One interesting finding is that not only beech, oak and birch, at present the most common deciduous tree species of the region, were abundant in the landscape, but, until at least 500 BP, the currently rarer lime, ash, elm and alder were also present. This contradicts the view that pure beech forests were the major natural forest type in the south Swedish nemoral ecosystem. Brunet (1995) and Ellenberg (1988) stress the importance of beech forests in Sweden and central Europe. It is noteworthy that not even the forest type called “beech forest” (Fig 2, Paper II) is pure beech, but is, on average, supposed to contain up to 2/3 deciduous species other than beech. In reality the difference between “rich deciduous forest” and “beech forest” is slight. I recommend caution when interpreting the division of regions of the forest types. Firstly, the distinctions of the forest types are not always clear, and we must be aware that this is a crude model, and that the actual historical forests must obviously have showed a wide range of combinations and transitions between the suggested forest types.

Secondly, the underlying data does not exhibit such a level of detail that it is possible to properly confirm the location of each forest type. Though the presented pictures are more detailed than previous studies, we should not be tempted to overinterpret them.

The level of mixture of the forest types has been the object of discussion. No assessment of the level of mixture can be made from the maps produced with the help of the model described in Paper I. The stands may have been stem-wise mixed, or mixed by small or large single species groves. However, macrofossil analyses from Swedish and Danish nemoral stands suggest that at least the forest types with significant streaks of nemoral deciduous tree species were often mixed in a stem-wise manner (Hannon 1999). This probably varied in time and space and as a result of disturbance influence and internal dynamics. The pine-dominated coniferous forests, chiefly confined to the dry eastern parts of south Sweden (Fig 2, Paper II), were affected by repeated fires (Drakenberg and Niklasson in press, Axelsson 199X, Granström 1993). These forests are more likely to have been mixed in a stand-wise manner due to the large-scale disturbance regime.

Driving forces for the changes of forest composition

Changes in the forest composition may be a result of climatic change (Wright et al. 1993), natural migration processes (Huntley 1988, Bennett et al. 1991), soil development (Andersen 1970, Iversen 1973), or human influence (Behre 1988). The most likely explanation is a complex combination of all these factors. However, human influence seems to have had an outstanding role in the replacement of the deciduous forests. During the selected time span, anthropogenic influence radically increased in stages (Berglund 1969 and 1991). The results from Paper II show that the primary driving force was direct or indirect disturbance derived from human activities. In several local small hollow pollen analyses the *Tilia* decline coincides with the first major human indicators (Hannon et al. in press, Eriksson 1996, Björkman 1997, Lindbladh and Bradshaw 1995). The *Tilia* decline occurred at different times in the studied examples.

The human influence was direct and indirect. Direct influence included clearance for agricultural land, which was extended in stages from the first evidence of farming around 5000 BP (Berglund 1969) until the mid-nineteenth century (Emanuelsson and Bergendorff 1986). Rich deciduous forests were readily selected for clearance due to the favourable site conditions. Grazing regimes altered by man should be considered as an indirect influence (Bradshaw and Mitchell 1999). The large numbers of livestock kept in the forest in the Middle Ages and early modern time (Lagerås 1996) affected tree species composition in forest regeneration. However, the cattle grazing also facilitated the survival of many species, including presently threatened species associated with forest glades and openings (Andersson and Appelqvist 1990, Owen-Smith 1987). Slash-and-burn cultivation (Larsson 1995) can be considered to be both a direct and an

indirect human influence. The very removal of the trees is an obvious influence but also the alteration of the prevailing disturbance regime by introducing fire may be of great importance. The rapid expansion of spruce to southern Sweden is discussed as being a result of this disturbance regime alteration (Lindbladh 1999). However, the most important factor for the large amount of spruce introduced in the southernmost parts of Sweden is the rational forestry during the last 150 years. The total volume of growing spruce is four times greater today than 70 years ago (calculated from Svensson 1980, Anon 1986 and Anon 1999 b).

The breakpoint when human influence became a more significant factor for the development of the forest in southern Sweden is hard to identify. Human influence replaced climate as the major driving force for vegetation at least 1000 years ago (Lindbladh et al. 2000). There are no indications that any of the major historical forest types decreased due to primarily climatic fluctuations. The majority of the studied species are not limited by climate for their present growth in southern Sweden. Thus all detected forest types are theoretically possible to use as a basis for nature-based silviculture in southern Sweden.

Forest types of interest for nature-based silviculture in southern Sweden.

The benefit for the numerous aspects of biodiversity is the wide variation of forest communities in time and space. The decision about which state to mimic is not simple. A wide range of ecosystems and forest types should in the optimal situation be mimicked to oblige the multiple demands urgent to individual species and biotopes. In southern Sweden, maybe even more than in the boreal region, we must be humble to the diversity, variety and mosaics of the natural forest landscape. We must also consider the fact that some forest types, like the open mixed forest and the forest subjected to slash-and-burn rotations were originally created and maintained by human activities. Decision making in forestry and nature conservation must consider biological values originating both from the virgin state of the forests and from human activities, and realise the vital management differences these necessitate.

Nature conservation is expensive. It is imperative to develop models that maximise the conservation advantage. The mimicking efforts would be the most effective in forest types that were very common in the past but are very rare today. Species adapted to habitats within these forest types had formerly widespread living space. Thus no selection for adapting to restricted habitats, like specific dispersal strategies, has evolved. When these habitats decreased dramatically the associated species became threatened. Providing an opportunity to keep or reintroduce such habitats, for example by mimicking natural processes in silvicultural operations, is supposed to be beneficial to the protection of biodiversity (Hunter et al. 1988, Bradshaw et al. 1994). Scrutinising the maps, I find two forest types to be the most interesting in this respect: "rich deciduous forest" and "rich mixed pine forest" (Paper II). Both forest types were common in

southern Sweden 2000 years ago, but hardly exist at all at present. Both were mixed and contained considerable numbers of nemoral deciduous tree species. The legitimacy of the statement is supported by several studies finding the nemoral deciduous forest to be the most important habitat for threatened species in Sweden in spite of its very small area (Berg et al. 1994 and 1995, Gustafsson 1994). Tyler and Olsson (1997) and Brunet and von Oheimb (1998) discuss the poor dispersal capacity for species typical of these forest types. Several more arguments for the focus on these two forest types can be presented:

- 1) A growing economic interest and value of the timber from oak, beech, ash, elm, maple and alder.
- 2) Official conservation work focus on mixed near-natural deciduous forests (Norén et al. 1995). In the near future a serious problem will arise with the lack of scientifically evaluated management alternatives for these key habitats.
- 3) A growing need for forests with recreational value due to high population densities and a landscape dominated by agriculture. Mature nemoral deciduous forests are highly appreciated as recreational forests (Jensen and Koch 1997, Gustafsson and Wittrock 1997).
- 4) Several nemoral deciduous tree species are soil improving with an anti-acidification effect and nutritious litter (Nordén 1992 and 1994, Pigott 1991, Nielsen 1995). This may be used for solving forest management problems in the western humid areas of southern Sweden subjected to atmospheric pollution and acidification (Hallbäck and Tamm 1986).
- 5) Spruce planted outside its natural distribution range for economical forestry involves increased risk of windthrow and pests (cf Persson 1975 and Vollbrecht 1994). Silvicultural methods of limiting this risk should include management of nemoral deciduous forests.
- 6) Alarm reports presented about climate change predict a warmer and moister climate in the future in southern Sweden. If this scenario is true, the southern extension border of spruce may retreat to the north with severe problems for spruce outside this new theoretical natural distribution range as a result (Sykes et al. 1996). This threat can be dealt with in the southern boreo-nemoral zone by growing tree species such as oak, beech, ash, pine and alder, which have a climatic tolerance amplitude suitable to both nemoral and boreo-nemoral conditions, and this will once again raise demands for appropriate silvicultural methods.

“Rich deciduous forest” with its modern analogue “mixed near-natural nemoral forest” were selected to further silvicultural and vegetation ecological research (Papers III-V). The arguments listed above, in combination with the fact that there are hardly any remnants of the rich mixed pine forest in the present south Swedish landscape, were the bases of this decision.

Silvicultural aspects on the management of mixed near-natural nemoral forest

The treatments

The silvicultural treatments performed in Papers III and IV are chosen to represent a range of disturbance intensities, assumed to range from equal to or

exceeding the natural disturbance intensity of the nemoral ecosystem. In that way we wanted to mimic natural disturbance regimes, likely or unlikely to have occurred in the historically equivalent forest. However, we must be aware that this mimicking is very rough. The shelterwood densities represent a gradient of gap/clearance size, where the dense shelterwood corresponds to undisturbed forest. The sparse shelterwood is supposed to mimic a gap mosaic, which in the virgin forest corresponds to a small scale disturbance resulting in small gaps from the fall over of single trees or small groups of trees (cf Falinski 1978 and 1986). The clearcut aims to mimic a large-scale disturbance that in the virgin landscape could correspond to a forest fire, or perhaps a large wind throw (Zackrisson 1977, Schimmel 1993, Foster and Boose 1992). The alleged resemblance of the shelterwood densities to natural conditions mainly comprises the dimension of light (cf Emborg 1998). The soil scarification methods were supposed to mimic the natural disturbance regimes of rooting from wild boar or domestic swine (mixed soil) (Groot Bruinderink and Haezbroek 1996, Kardell and Kardell 1996, Welander 2000), and forest fires or windfellings (open mineral soil) (Zackrisson 1977, Schimmel 1993, Falinski 1978). The silvicultural treatments chosen are in common use in single species forestry. It was valuable to test their compatibility to nature-based silviculture.

Advance growth

The most interesting finding from the study in Paper III is the fact that advance growth plays such an important role for the start of the new stand after the regeneration cutting in a mixed near-natural nemoral forest stand. Further research could beneficially be focused on the development of silvicultural methods utilising this fact. Areas hard to re-establish with oak are found in the temperate region of eastern North America. Oak is a desired tree species so methods to establish enough saplings have been sought after. Several authors have found the use of advance growth from oak to be a fruitful method (Grisez and Peace 1973, Sander 1971, Loftis 1983 and 1992). The method is rarely used in Europe, however, and no original scientific work on the use of advance growth for the purpose of regeneration of European nemoral deciduous forests was found in a profound literature search. Some authors call for caution against the use of advance growth due to alleged high mortality among the advance saplings (Evans 1984). Supported by the results from Paper III this allegation may be questioned as the advance growth showed distinctly lower mortality than the saplings established after the treatments. However, as stressed earlier, it is of great importance to evaluate this and similar experiments over a long time period, to avoid drawing conclusions based on changing results.

Soil scarification

Comparing the soil scarification methods, the least numerous regeneration results were found on the open mineral soil (Paper III). This is in line with the statement that forest fires were of minor importance in the historical transition of the rich deciduous mixed forest (Nilsson 1997). The largest total number of saplings

established during the study period, in particular the nemoral species ash, beech and hornbeam, occurred on the mixed soil. This suggests the adaptation of the forest type to rooting as an important disturbance regime (Welander 2000). However, the mechanical performance of the mixing procedure is severe. The big establishment of new saplings during the study period could not compensate for the large amount of advance growth destroyed by the scarification itself.

Traditional silvicultural programmes for the regeneration of beech, oak, and ash stress the importance of soil scarification for satisfactory regeneration results (Bjerregaard 1979, Evans 1984, Harmer 1995). Löf (1999) suggests dense ground vegetation competition for water to be the crucial factor. The experimental stand in Paper III, like most mixed near-natural nemoral stands, has favourable soil conditions with rich access to ground water. Soil scarification may have a more pronounced effect on mixed near-natural nemoral stands on dry sites. General statements on the issue require replicate experiments.

The pioneer species birch, alder and sallow (*Salix caprea*), had the most numerous regeneration results on the open mineral soil. These species are not typical components of the rich mixed deciduous hardwood forest (Pettersson and Fiskesjö 1992, Pålsson 1994). The numerous birch regenerations on the most severely disturbed treatments is in accordance with the general knowledge of birch being a pioneer species with quick establishment on recently disturbed soil (Atkinson 1992, Perala and Alm 1990). When nemoral deciduous species are preferred in areas where they can be assumed to suffer from competition from pioneer species such as birch, it might be wiser to avoid severe silvicultural operations. This is also suggested, though in fact not studied, by Diekmann (1994). It also corresponds to the conclusion from Paper IV where caution is recommended against the use of clearcutting and intensive soil scarification for conservational reasons.

The soil scarification methods referred to as ‘open mineral soil’ and ‘mixed soil’ can in practice be obtained by patch scarification and scarification of harrow type respectively (Örlander et al. 1990). At this stage I would suggest avoidance of soil scarification in all forms in mixed near-natural forest for practical forestry, in order not to harass the regeneration of a new mixed near-natural nemoral stand or the vegetation composition typical of the nemoral forest.

Expansion of mixed near-natural nemoral deciduous forests in southern Sweden

The silvicultural experiment was performed within one of the rare remnants of the valuable mixed near-natural nemoral deciduous forests present in southern Sweden. It can be questioned whether this *per se* jeopardizes the values for biodiversity. However, once the knowledge of the function of these forests is obtained it is possible to develop scientific methods for the enlargement of the

forest type, if that is desirable. This work has already begun, partly based on the findings in this study (Karlsson in prep).

Effects of silvicultural activities on floristic diversity

The results from Paper IV indicate initially increased floristic diversity after all studied silvicultural operations, and there are also examples of species typical of the nemoral forest increasing. However, it is observed that several species typical to the nemoral deciduous forest tend to be disfavoured by the most intensive silvicultural operations, which is why I recommend caution in the use of clearcutting and heavy soil scarification in these forests. Increased floristic diversity after felling has been found in many other studies (Kirby 1988 and 1990, Swindel et al. 1984, Burchel et al. 1992), and is well known among vegetation ecologists (Ford and Newbold 1977, Bormann and Likens 1979, Canham and Marks 1985, Roberts and Gilliam 1995). We must be aware that the early results from this study may change over time as abiotic and biotic responses may affect the floristic diversity long after the disturbance occasion (Huston 1979, Collins et al. 1985). Dzwonko and Loster (1992), Tyler and Olsson (1997) and Brunet and von Oheimb (1998) discuss the low dispersal ability of many south Swedish species and hence the high risk of them becoming locally extinct after a large-scale disturbance. This supplements the results from Paper IV indicating that the most severe silvicultural operations tend to disfavour species typical to the nemoral forest, including threatened and rare species (cf Aronsson 1999 and Krok and Almquist 1994). Caution is therefore required when planning and performing silvicultural operations in near-natural nemoral forests.

In Paper IV I use floristic diversity, mathematically measured as number of species and with the Shannon index, as one indication of biodiversity. The early findings indicate increased diversity though a worrying trend of deteriorated conditions for the species typical of nemoral forest can also be seen. This trend cannot be reflected by the present definition of biodiversity. Therefore I question the widespread use of the term biodiversity as the most desirable state for all conservation work. Biodiversity has been used in practice to represent a conservational goal. However, the definition of the term does not include all features of this goal. Important biological processes are not included in the definition of biodiversity. Thus I recommend a somewhat altered focus from biodiversity to the concept of biological integrity. Biological integrity includes the function and intrinsic composition of ecosystems (Angermeier and Karr 1994, Hunter 1999).

Methodological aspects

The palaeoecological method

Knowledge about the southern Swedish natural forests was refined and shown with a higher degree of detail on a regional level in Papers I and II than in previous studies. A network of corrected regional pollen analyses has not been utilised in earlier works to obtain a total view of the historical forest of a region.

The study was possible as Southern Scandinavia is relatively well surveyed with palaeoecological studies, with a large number of pollen analyses performed (Birks 1985). On a continental scale, with its lower demand for detail, however, several fruitful attempts have been made (Jacobson et al. 1987, Huntley 1990, Delcourt and Delcourt 1981,1987), and also a regional view on the British Isles based on uncorrected pollen data (Bennett 1989). The method developed in Paper I has meanwhile been further developed, refined and utilised in other regions (Bradshaw and Holmquist 1999, Lindbladh et al. 2000).

The conversion of pollen percentage to tree volume percentage of the tree species with poor pollen production, dispersal capacity and/or preservation, e.g. *Tilia*, *Acer*, *Ulmus*, *Fraxinus*, *Fagus* and *Salix* (Birks and Birks 1980) is complicated. We were aware that *Tilia* was underrepresented in the regional pollen analyses compared to stand-scale pollen analyses performed within the same estimated pollen source area (Björkman 1996 a and b, Abrahamsson 1996, Lagerås 1996, Lindbladh and Bradshaw 1995 and 1998, Karlsson 1996, Andersson 1996). Therefore we upgraded the correction factor for *Tilia* in accordance with these local small hollow pollen diagrams, though better interpretation methods were desired. No adjustments of the correction factors were performed for *Ulmus*, *Acer*, *Fraxinus*, *Fagus* and *Salix*. Also *Picea* posed correction problems, which previous has been discussed by Prentice et al. (1987) and Parsons et al. (1980). More careful methods for this correction are desired. The correction factors should preferably be further developed before future use of the presented model.

The silvicultural method

The main advantage of the silvicultural trial described in Paper III is the long time horizon planned to be covered in the study. Prior to this study no silvicultural attempt has been made in Sweden to study the complex ecosystem of mixed deciduous nemoral forest. The study of species mixtures are complex so isolated experiments, *in situ* or in laboratory, on biotic and abiotic factors, would complement this study in an favourable way. The shelterwood densities are not repeated so proper evaluation of the effect from shelterwood density cannot be made and there was no inventory performed prior to the treatments that could be used as a start point reference. However, an additional series of similar experiments were laid out in the nemoral and boreo-nemoral zone (Björse and Vollbrecht 1996, 1999). Their design is somewhat altered due to the experience gained from this work, but are still designed in a way that they all can be evaluated together.

The silvicultural method may be questioned for a vegetation ecological study as performed in Paper IV. The absence of repetition of the shelterwood densities prevented comparisons related to cutting intensity, different inventory occasions in the three studied vegetation seasons complicated comparisons over time, and the reduced area of the inventory in the last year made comparisons of the absolute number of species impossible. As for Study III, a complementary series

of experiments is laid out (Björse and Vollbrecht 1996, 1999), which at the final revision will reduce these problems. Hannerz (1996) reported similar difficulties. This demonstrates the need for a unified and carefully worked through methodology for the study of vegetation changes after silvicultural operations. Furthermore, the Hult-Sernander inventory methodology (Andersen and Jørgensen 1995) may be replaced by a more efficient inventory method with increased possibilities to comment on a larger number of individual species. These aspects are considered when designing the above mentioned follow-ups of the experiments (Björse and Vollbrecht 1996, 1999). Nevertheless, the experiment constitutes a unique source of information on vegetation changes associated with silvicultural operations in mixed near-natural nemoral deciduous forests close to the northern limit of its distribution range. The early results presented are valuable for future evaluation, though the most interesting results are expected to be found after repeated evaluations.

Implications for nature-based silviculture in southern Sweden

The question of whether timber production and the protection of biodiversity is possible to combine in the mixed near-natural nemoral forest cannot be answered solely with the help of the results presented in this thesis. Elton (1979), Harmon et al. (1986), Kirby and Drake (1993), and Samuelsson et al. (1994) stress the importance of dead wood for the maintenance of biodiversity. Nilsson (1997), Berg et al. (1994 and 1995) and Hultengren and Nitare (1999) emphasise the importance of large old trees of various species. Nilsson and Baranowski (1993 and 1994), Fritz and Larsson (1997), Ohlsson and Tryterud (1999), Appelquist and Nordén (1998) and Kers(1977) call attention to continuity. All these features must be considered and evaluated in the development of a practicable silvicultural method. More studies on various species groups and their response to silvicultural operations within the ecosystem are necessary to obtain an overall idea of the effects of silviculture on biodiversity and biological integrity.

Silvicultural operations cannot fully mimic the natural disturbance regimes. The harvesting of woody biomass is the original purpose of forestry, while the natural disturbance regimes entail an increased amount of dead wood in the forest, which is identified as crucial to biodiversity. One urgent issue will be to balance these conflicting demands, and to define the essential amounts of dead wood, minimum proportion of deciduous tree species, number and importance of large and old trees. The balance should be adjusted to each forest type/ecosystem individually.

This study focuses on harvest and the regeneration phase with regard to silviculture. A complete silvicultural system encompasses an entire rotation period. Much knowledge has still to be added about the most appropriate way to maximise the benefit for biodiversity, combined with reasonable economic return in the phases of precommercial thinning, thinning, final cutting and shelterwood removal. The true economic potential and interest of the possible wood products, the effect of biological concern on the potential timber production and quality and

technical possibilities for sensitive harvesting and extraction of timber are also important questions to an approved model for nature-based silviculture.

The framework of one approach to handle all these aspects and demands is presented in Paper V. The knowledge acquired can gradually be incorporated in the approach. Recent scientific initiatives are presently stimulating research on those issues in the boreo-nemoral and nemoral vegetation zones (Bradshaw and Lindén 1999, Anon 1997). The approach described in Paper V is based on the mimicking approach to the combination of biodiversity consideration and timber production. Regeneration under a sparse shelterwood without soil scarification is suggested. The approach is designed to be flexible to the ongoing change of biotic and abiotic conditions of the forest ecosystems, by its take-off in the natural forest ecosystem and its processes, precisely as required in a nature-based silvicultural model (Bradshaw et al. 1994). However, the approach is not yet evaluated from various aspects of biodiversity.

Finally I want to stress the importance of areas solely preserved for the protection of biological values. Local extinction of species dependent on nemoral deciduous forests is severe due to the rarity of the forest type, and in many cases poor dispersal capacity (Peterken and Game 1984, Nilsson and Ericsson 1997 and Brunet and von Oheimb 1998). Several authors define the nemoral deciduous forest as a very important biotope to protect for the benefit of threatened species (Gustafsson 1994, Berg 1994). Before the proposed refinements of the statements in the thesis are implemented, the principle of caution suggests that any silvicultural operations performed in the remaining fragments of the near-natural nemoral forest primarily should be intended to protect the biological values.

Further research

Among the topics suggested for further research throughout the thesis, the following appear to be the most urgent to follow on from the presented results: i) the use of advance growth in practical forestry; ii) the long term validity of the presented results; iii) development of management methods for the benefit of the combined objectives in the growing and mature phases of the stands; iv) the influence of silvicultural operations on all present species groups and other aspects of biodiversity and biological integrity; v) the influence of silvicultural operations on biodiversity and biological integrity associated with mature and decaying phases of the ecosystem; vi) development of equivalent management possibilities for “rich mixed pine forest”, “open mixed forest” and other forest types defined in Paper II; vii) the economic results and technical possibilities for the combination of biodiversity protection and timber production.

Concluding remarks

This work has hopefully contributed to the knowledge important for practical recommendations on nature-based silviculture in southern Sweden. I have highlighted the historical dominance of the deciduous forests. Human activities were both significant for the transformation to coniferous forest and for maintained biodiversity. Today both timber production and protection of biodiversity are important issues in south Swedish forestry. I have discussed the opportunities to combine the two issues in the concept of nature-based silviculture. The approach of mimicking the historical forest composition and processes in the silvicultural measures was pointed out as one possible way to reach these combined goals. Caution was advised against severe silvicultural disturbance within near-natural nemoral deciduous forest stands. The results must be further examined and replicated to be generally valid, and there are several more questions to answer before a complete silvicultural system beneficial for the combined goals is attained.

Sammanfattning

Svensk skogspolitik likställer värdet av virkesproduktion och skydd av biologisk mångfald, som en följd av moraliska och funktionella aspekter. Trots detta saknas en stabil vetenskaplig grund för hur detta skall uppnås, och bristen på kunskap är särskilt uttalad i södra Sverige.

Naturnära skogsskötsel är ett sätt att kombinera virkesproduktion och hänsyn till biologisk mångfald på beståndsnivå och kan ses som en byggsten i begreppet uthålligt skogsbruk. Naturnära skogsskötsel baseras på områdets naturliga skogsekosystem och är tänkt att vara flexibelt för naturliga omvärdsförändringar (klimatiska svängningar, naturlig störningsdynamik etc). En modell för naturnära skogsskötsel är teorin om efterliknande av naturskogens struktur och dynamik i praktisk skogsskötsel. Om storlek, intensitet och tidsrymd mellan ingreppen vid skogsvårds- och avverkningsåtgärder kan härma den naturliga störningsdynamiken, trädslagsblandningen och strukturen i en viss region, skapas en "spelplan" där de biologiska processerna kan fungera trots mänskligt utnyttjade. I Sydsverige har hittills saknats utgångspunkter för ett dylikt efterliknande pga av människans utnyttjande och omformning av landskapet under flera tusen år. Idag finns inga naturskogsreferenser med bevarade biotoper av opåverkade ekosystem i Sydsverige. Kunskap om den naturliga skogen kan dock erhållas från pollenanalys.

I avhandlingen utnyttjar jag pollenanalys för att beskriva skogens historiska tillstånd och utveckling i Sydsverige. Den skoghistoriska utvecklingen och dess drivkrafter diskuteras. Kunskaperna tas upp i skogsskötsel försök där möjligheten

att efterlikna några av de ursprungliga strukturerna undersöks. Skötselmetodernas påverkan på floristisk diversitet undersöks. Ett konceptuell modell för att utnyttja dessa och andra kunskaper i ett system för naturnära skogsskötsel diskuteras.

Artikel I beskriver en metod för att utnyttja ett nätverk av pollenanalyser för att ge en översiktlig, regional bild av skogshistorien vart femhundra år sedan år 0. Pollen från alla närvarande trädslag; al, alm, ask, asp, avenbok, björk, bok, ek, en, gran, hassel, lind, sälg och tall från 37 högkvalitativa pollenanalyser från sjöar och mossar söder om 60°N utnyttjades. Pollenrepresentation på varje lokal omräknades för att spegla den relativa mängden träd. Genom avståndsvägd interpolation skapades regionala kartor för varje trädslags relativa representation, Dessutom beräknades nio olika "skogstyper" utbredning vid varje tidsnedslag. Metoden tillåter inga detaljstudier.

I artikel II utnyttjas metoden från artikel I att beskriva skogsutvecklingen i Sydsverige de senaste 2000 åren. För 2000 år sen dominerades Sydsverige av lövskogar, i stor utsträckning ädellövskog. Gran fanns bara i de norra delarna av studieområdet och inte heller bok var speciellt vanlig. Bok expanderade på de andra ädellövträdens bekostnad, trots att bokskogen länge hade stora inslag av andra ädla lövträd. Gran expanderade kraftigt söderut till följd av klimat och mänsklig påverkan för att idag fullständigt dominera Sydsveriges skogar. Ädellövskog är idag en viktig biotop för hotade växt- och djurarter. Rik blandad ädellövskog, rik tall-ädellöv-blandskog och öppen blandskog med barr- och ädellövträd utpekade som skogstyper intressanta för teorin om att efterlikna historiska skogar i ett naturnära skogsbruk.

Södra Sveriges ädellövskogar har stort naturvårdsvärde. Samtidigt är de ekonomiskt värdefulla och utnyttjas för rationellt skogsbruk. Artikel III beskriver ett skogsskötselexperiment som belyser möjligheten att sköta rika blandade ädellövskogsbestånd (near-natural mixed nemoral forest, jfr artikel II) på ett sätt som gagnar både biologisk mångfald och virkesproduktion. Effekter av skärmtäthet (inkl kalhygge), markberedning och viltstängsling på föryngringsprocessen studerades under fyra år efter avverkning av ett blandbestånd av bok, ask, avenbok, alm m fl trädslag. Det totala föryngringsresultatet i slutet av studieperioden var gott på alla behandlingar men högst i gles skärm. Ask, följt av avenbok dominerade det slutgiltiga föryngringsresultatet. Andelen björk ökade efterhand på områden med de kraftigaste ingreppen; hygge och kal mineral jord. Förekomst av beståndsföryngring var den mest avgörande faktorn för föryngringsresultatet. Beståndsföryngrade plantor uppvisade bättre överlevnad än plantor etablerade under studieperioden. Genomgående bättre föryngring återfanns på icke markberedda ytor eftersom markberedningsingreppen i sig skadade beståndsföryngringen. Ingen nämnvärd skillnad i föryngringsresultat kunde påvisas som en effekt av hägn. Försöket är ämnat att följas under en längre tidsperiod.

I artikel IV belyses skogsskötsels effekt på fältskiktsvegetationen i rik blandad ädellövskog. Försöksupplägget är detsamma som i artikel III. Fältskiktsfloran studerades med avseende på artantal, täckningsgrad och "floristisk diversitet" uppskattad m h a Shannon index. Resultaten visar att hög floristisk diversitet initialt kan upprätthållas eller till och med ökas till följd av skogsskötselåtgärder. Denna ökning beror framförallt på att nya, ofta störningsanpassade arter etableras. Dock syns en tendens att typiska ädellövskogarter kan komma att missgynnas på de störda ytorna, och att systemet på sikt förlorar sin ekologiska särart. Därför verkar kalhuggning och kraftig markberedning vara en olämplig åtgärd i rik blandad ädellövskog. Försöket försöket kommer att utvärderas efter längre tid.

Artikel V diskuterar kunskaper från artikel I - IV och andra studier i ett system för naturnära skogsskötsel, med blandad ädellövskog som referens. Systemet kompletteras av ett måttssystem för möjlig biodiversitetspotential. Systemet antas vara flexibelt för att möta långsiktiga naturliga förändringar som alltid pågår i ett skogsekosystem, och kan byggas på med vidare kunskap i framtiden.

Acknowledgements

I thank my supervisors Richard Bradshaw and Pelle Gemmel. Pelle shared his silvicultural knowledge and above all provided inspiration and go-ahead spirit. Thank you for believing in me when I almost didn't myself and for putting up with my tears and riots in times of frustration. Richard introduced me to palaeoecology, was a skilled co-author and patiently corrected my English. I was very pleased to share your visions and enthusiasm for vegetation history and nature conservation.

Ola Sallnäs had a central role in concluding this thesis. I cannot thank you enough for all time, courage, inspiration and patience you paid me during the process. Our discussions on both science and personal issues encouraged and enriched me deeply. I admire you for your humbleness and freedom of prejudices. Thanks.

I am deeply grateful to Urban Nilsson who kindly helped me with statistics, escorted me into SAS and contributed with fruitful discussions and valuable comments on my manuscripts. Thanks.

I thank *everybody* at The Southern Swedish Forest Research Centre for creating a wonderful place of work. I especially thank Matts Lindbladh for encouraging support and cooperation, Tove Vollbrecht for cooperation and small chats, Janet Boke for your organising and small chats, Rolf Övergaard for field assistance, Micke Andersson for computer aid, Elsy Ljungdell for cleaning, PM Ekö for fabulous stories.

Örjan Hallnäs, Karin Djurvall, Michelle Benyamine, Tove Vollbrecht, Katarina Månsson, Karin Svensson and Joachim Janninge, spent weeks with me in Fulltofta measuring plants and saplings. I got a lot of help and certainly had a much nicer time than being there alone. Unmentioned persons helped for a shorter time. Thanks.

Jan-Eric Englund taught me statistics and was always very helpful with questions. Lena Gustafson supported my vegetation ecological searching. Daniel Michelson contributed to fruitful co-operation. Leslie Walks kindly corrected my English. Nils Fahlvik helped with final layout. The personal at Alnarps-biblioteket was always very helpful. Thanks.

I am grateful to my parents, Ulla and Sven-Anders who let me grow up close to the nature and who built the foundation of my biological knowledge and interest.

Finally, most ardently, Magnus, thanks for all support, mainly privately but also scientifically. For sharing joy, visions and obstacles, for consoling me when everything seemed hopeless and for making my life happy.

Landstingets skogar and Skogssällskapet provided forest land and practical assistance for the experiments. The work was financed by The Southern Swedish Forest Research Program and The Faculty of Forestry (research program: "Managing Forests for Industrial Products and Environmental Quality").

References

- Abrahamsson, Å., 1996. Pollenanalytisk studie i Ryfors Gammelskog, Västergötland. B.Sc thesis, Lund Univ., Sweden, 24 pp. (In Swedish)
- Agestam, E. 1985. A growth simulator for mixed stands of pine, spruce and birch in Sweden. Department of forest yield. Report no 15. Swedish University of Agricultural Sciences, Garpenberg, Sweden. (In Swedish with English summary).
- Ahti, T., Hämet-Ahti, L. and Jalas, J., 1968. Vegetation zones and their sections in north western Europe. *Ann. Bot. Fenn.* 5, 169-211.
- Albrektsson, A. Biomass of Scots pine (*Pinus sylvestris* L.) amount- development-methods of mensuration. The Swedish University of Agricultural Sciences. Department of Silviculture. Umeå, Sweden. (In Swedish with English summary).
- Almgren, G., 1984. Ädellövskog. Ekologi och skötsel. Skogsstyrelsen, Jönköping, Sweden. 136 pp. (In Swedish.)
- Altrel, D., 1995. Vegetationsförändringar i bokskog och alkärr, orsakade av vildsvinsaktivitet. Swedish University of Agricultural Sciences, Department of Vegetation Ecology. Masters thesis. (In Swedish with English summary).
- Andersen, S.T., 1970. The relative pollen productivity of North European trees, and correction factors for tree pollen spectra. *Geological Survey of Denmark II* 96: 1-99.
- Andersen, U. V. and Jørgensen, B. B., 1995. Urtefloras sammensætning i to skovtyper. FSL, skovbrugsserien nr 12 1995. (In Danish.)

- Andersson, L. and Appelqvist, T., 1990. Istidens stora växtätare utformade de nemorala och boreonemorala ekosystemen. *Svensk Bot. Tidskr.*, 84, 355-368. (In Swedish with English summary.)
- Andersson, R., 1996. Från lind till gran på 2000 år. M.Sc. thesis, Swedish Univ. of Agricultural Sciences, Alnarp, Sweden. 38 pp. (In Swedish)
- Angelstam, P., 1996. The ghost of forest past - natural disturbance regimes as a basis for reconstruction of biologically diverse forests in Europe. In: DeGraaf, R. M. and Miller, R. I. (Eds.) *Conservation of faunal diversity in forested landscapes*. Chapman and Hall
- Angelstam, P., Rosenberg, P. and Rückler, C., 1993. Aldrig, sällan, ibland, ofta. *Skog och forskning* 93, 43-41. (In Swedish)
- Angelstam, P., Majewski, P. and Bondrup-Nielsen, S., 1995 a. West-east cooperation in Europe for sustainable boreal forests. *Water, air and soil pollution* 82, 3-11.
- Angelstam, P., Mikusinski, G. and Travina, S., (Eds.), 1995 b. *Research in eastern Europe to solve nature conservation problems in the Nordic countries*. Swedish university of agricultural sciences, Dept of Wildlife Ecology, report 28.
- Angelstam, P. and Pettersson, B., 1997. Principles of present Swedish forest biodiversity management. *Ecol. Bull.* 46, 191-203.
- Angermeir, P. L. and Karr, J. R., 1994. Biological integrity versus biological diversity as political directives. *BioScience* 44, 690-697.
- Ångström, A., 1974. *Sveriges klimat*. 3rd edition. Generalstabens litografiska anstalts förlag, Stockholm. 188 pp. (In Swedish)
- Anonymous, 1986. *Sydsvensk skogsforskning*. Sveriges Lantbruksuniversitet. Skogsvetenskapliga fakulteten rapport 2. Umeå, Sweden. (In Swedish.)
- Anonymous, 1994. *Skogsordlista – Forest vocabulary*. Tekniska nomenklaturcentralen (TNC). Sveriges skogsvårdsförbund, Solna, Sweden.
- Anonymous, 1997. *SUFOR – Sustainable forestry in southern Sweden*. Årsrapport, tema uthålligt skogsbruk och biologisk mångfald. Rahms boktr, Lund, Sweden. (In Swedish.)
- Anonymous, 1999 a. *Skogsvårdslagen*. Handbok. Skogsstyrelsen, Jönköping, Sweden. (In Swedish.)
- Anonymous, 1999 b. *Skogsstatistisk årsbok*. Sveriges officiella statistik. Skogsstyrelsen, Jönköping, Sweden. (In Swedish with English summary.)
- Appelqvist, T. and Nordén, B. 1998. Kontinuitet - ett mångtydigt begrepp. *Sv. Bot. Tidskr.* 92, 23-36. (In Swedish with English summary.)
- Aronsson, M. (Ed.), 1999. *Rödlistade kärlväxter i Sverige, artfakta*. Del 1 och 2. ArtDatabanken, Uppsala, Sweden. (In Swedish with English summary.)
- Atkinson, M. D., 1992. *Betula pendula* Roth (B. *Verrucosa* Ehrh.) and *B. Pubescens* Ehrh. Biological flora of the British Isles. No. 175. *Journal of Ecology* 80, 837-870.
- Attiwill, P. M., 1994 a. The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manage.* 63, 247-300.
- Attiwill, P. M., 1994 b. Ecological disturbance and the conservative management of eucalypt forests in Australia. *For. Ecol. Manage.* 63, 301-346.
- Axelsson, A., 199X. *Brandhistorien i Sydsverige under senare holocen*. Masters thesis. Ekologiska institutionen, Avd. för växtekologi, Lund University. Lund, Sweden. (In Swedish)
- Behre, K-E., 1988. The role of man in European vegetation history. In: Huntley, B. and Webb, T. III (Eds.), *Handbook of Vegetation Science*, Vol. 7, *Vegetation History*. Kluwer Academic Publishers, Dordrecht. p. 633-672.
- Béland, M., Agestam, E., Ekö, P-M, Gemmel, P. and Nilsson, U., in press. Effects of scarification and seedfall on natural regeneration of Scots pine under two shelterwood densities in southern Sweden. *Scand. J. For. Res.*
- Bennett, K. D., 1989. A provisional map of forest types for the British Isles 5000 years ago. *J. Quat. Sci.* 4, 141-144.

- Bennett, K. D., Tzedakis, P. C. and Willis, K. J., 1991. Quaternary refugia of north European trees. *J. Biogeogr.* 18, 103-115.
- Berg, Å. and Tjernberg, M., 1996. Common and rare Swedish vertebrates - distribution and habitat preferences. *Biodiv. and Cons.* 5, 101-128.
- Berg, Å., Ehnstöm, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. and Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. *Conserv. Biol.* 8, 718-731.
- Berg, Å., Ehnstöm, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. and Weslien, J., 1995. Threat levels and threats to red-listed species in Swedish forests. *Conserv. Biol.* 9, 1629-1633.
- Bergeron, Y., 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. *Ecology* 72, 1980-1992.
- Bergeron, Y. and Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. *For. Ecol. Manage.* 92, 235-242.
- Berglund, B. E., 1969. Vegetation and human influence in South Scandinavia during Prehistoric time. *Oikos Suppl.* 12, 9-28.
- Berglund, B. (Ed.), 1991. The cultural landscape during 6000 years in southern Sweden – the Ystad project. – *Ecol. Bull.* 41, 337-350.
- Birks, H. J. B., 1985. A pollen-mapping project in Norden for 0-13000 B.P. Nordmap 1. Botanisk institutt, Bergen, Norway, 41 pp.
- Birks, H. J. B. and Birks, H. H., 1980. Quaternary palaeoecology. Edward Arnold Ltd, London, 289 pp.
- Bjerregaard, J., 1979. Att sköta bok. Sveriges skogsvårdsförbunds tidskrift 77 (3), 6-37. (In Swedish.)
- Björkman, L., 1996 a. The late Holocene history of beech *Fagus sylvatica* and Norway spruce *Picea abies* at stand-scale in southern Sweden. Lundqua thesis, volume 39. Lund university, Department of Quaternary Geology, Lund, Sweden.
- Björkman, L., 1996 b. Long-term population dynamics of *Fagus sylvatica* at the northern limits of its distribution in southern Sweden: a palaeoecological study. *The Holocene* 6, 225-234.
- Björkman, L., 1997. The history of *Fagus* forest in south-western Sweden during the last 1500 years. *The Holocene* 7, 419-432.
- Björse, G., Vollbrecht, T. 1996. Föryngringsstudier i rik blandad ädellövskog - på väg mot ett naturvårdsanpassat skogsbruk. In: Väckande vetande om sydsvensk skog. Rapport. Skogskonferensen, SLU, Alnarp, Sweden. (In Swedish).
- Björse, G. and Vollbrecht, T., 1999. Naturlig föryngring av lövblandskog. In: Lindblad, M. and Gemmel, P. (Eds.) Nu är det slut. Slutrapport från programmet för sydsvensk skogsforskning 1988-1999, p. 57-60. (In Swedish).
- Bormann, F. H. and Likens, G. E., 1979. Pattern and processes in a forested ecosystem. Springer-Verlag, New York. 253 pp.
- Bradshaw, R. H. W., 1995. The origins and dynamics of native forest ecosystems: background to the use of exotic species in forestry. *Icel. Agr. Sci.* 9, 7-15.
- Bradshaw, R. and Holmquist, B., 1999. Danish forest development during the last 3000 years reconstructed from regional pollen data. *Ecography* 22, 53-62.
- Bradshaw, R. and Lindén, M., 1999. RENFORS - 3rd year report. SLU, Alnarp, Sweden.
- Bradshaw, R., Gemmel, P. and Björkman, L., 1994. Development of nature-based silvicultural models in southern Sweden: the scientific background. *For. Landsc. Res.* 1, 95-110.
- Bradshaw, R. and Mitchell, F. J. G., 1999. The palaeoecological approach to reconstructing former grazing-vegetation interactions. *For. Ecol. Manage.* 120, 3-12.
- Brunet, J., 1995. Sveriges bokskogar har gamla rötter. *Svensk Bot. Tidskr.* 89, 1-10. (In Swedish with English summary).

- Brunet, J. and von Oheimb, G., 1998. Migration of vascular plants to secondary woodlands in southern Sweden. *J. Ecol.* 86, 429-438.
- Burchel, P., El Kateb, H. and Mosandl, R., 1992. Experiments in mixed mountain forests in Bavaria. In: Kelly, M. J., Larson, B. C. and Oliver, C. D., (Eds.), *The ecology and silviculture of mixed species forests*. Kluwer academic publishers, Dordrecht. p. 183-215.
- Canham, C. D. and Marks, P. L., 1985. The response of woody plants to disturbance: patterns of establishment and growth. In: Pickett, S. T. A. and White, P. S. (Eds.). *The ecology of natural disturbance and patch dynamics*. Academic press, Inc. 197-216.
- Carlsson, M., 1998. On forestry planning for timber and biodiversity. *Acta Universitatis Agriculturae Sueciae, Silvestria* 64. Alnarp, Sweden.
- Collins, B. S., Dunne, K. P. and Pickett, S. T. A., 1985. Responses of forest herbs to canopy gaps. In: Pickett, S. T. A. and White, P. S. (Eds.). *The ecology of natural disturbance and patch dynamics*. Academic press, Inc. 217-234.
- Davis, M., 1963. On the theory of pollen analysis. *Am. Jour. Sci.* 261, 897-912.
- Delcourt, P. A., and Delcourt H. R., 1981. Vegetation maps for eastern North America: 40,000 yr B.P. to the present. In Romans, R. C. (Ed.), *Geobotany II*. Plenum Press, N.Y. 123-165.
- Delcourt, P.A and Delcourt, H. R., 1987. Long-term forest dynamics of the temperate zone. *Ecological studies* 63. Springer-Verlag, N.Y., 439 pp.
- DeLong, D. C. Jr., 1996. Defining biodiversity. *Wildl. Soc. Bull.* 24 (4), 738-749.
- Diekmann, M., 1994. Deciduous forest vegetation in Boreo-nemoral Scandinavia. *Acta Phytogeographica Suecica* 80. Editit svenska växtgeografiska sällskapet. Oplulus press, Uppsala, Sweden.
- Drakenberg, B. and Niklasson, M., in press. Skogsbrandhistorik i Norra Kivills Nationalpark. SNV rapport. Statens Naturvårdsverk, Stockholm. (In Swedish).
- Dzwonko, Z. And Loster, S., 1992. Species richness and seed dispersal to secondary woods in southern Poland. *J. Biogeogr.* 19, 195-204.
- Ellenberg, H., 1988. *Vegetation ecology of central Europe*. 4th edition. Cambridge university press, Cambridge.
- Elton, C. S., 1979. *The pattern of animal communities*. Chapman and Hall, London.
- Emanuelsson, U. and Bergendorff, C., 1986. History as a guideline to nature conservation and management in Scania, southern Sweden. In: Bradshaw, A. D., Goode, D. A. and Thorpe, E. H. P. (Eds.) *Ecology and design in landscape the 24th Symposium of the British Ecological Society*. Blackwell Scientific Publ., Oxford. 237-255.
- Emborg, J., 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manage.* 106, 83-95.
- Engelmark, 1984. Forest fires in the Muddus national park (northern Sweden) during the past 6000 years. *Can. J. Bot.* 62, 893-898.
- Eriksson, B., 1982. Data rörande Sveriges temperaturklimat. SMHI Reports Meteor. Climat. RMK 39, Norrköping, Sweden. 34 pp. (In Swedish.)
- Eriksson, B., 1983. Data rörande Sveriges nederbörds-klimat. Normalvärden för perioden 1951-1980. SMHI Rapport 1983:28. Norrköping, Sweden. 92 pp. (In Swedish.)
- Eriksson, G., 1996. Fulltofta, från ädellövurskog till granskog. En paleoekologisk studie av trädslagssammansättningen under de senaste 5000 åren. Report commissioned by Skogssällskapet, Göteborg, Sweden. (In Swedish.)
- Eriksson, H., 1976. Yield of Norway spruce in Sweden. Department of forest yield research. Research notes no. 41. Royal college of forestry, Stockholm. (In Swedish with English summary.)
- Evans, J., 1984. *Silviculture of broadleaved woodland*. Forestry commission bulletin 62. Her majesty's stationery office. London.

- Falinski, J. B., 1978. Uprooted trees, their distribution and influence on the primeval forest biotope. *Vegetatio* 38, 175-183.
- Falinski, J. B., 1986. Vegetation dynamics in temperate lowland primeval forests. *Geobotany* (8). Junk, Dordrecht. 537 pp.
- Ford, E. D., Newbold, P. J., 1977. The biomass and production of ground vegetation and its relation to tree cover through a deciduous woodland cycle. *J. Ecol.* 65, 201-212.
- Foster, D. R. and Boose, E. R., 1992. Patterns of forest damage resulting from catastrophic wind in central New England. *J. Ecol.* 80, 79-98.
- Franklin, J. F., 1992. Scientific basis for New Perspectives in forests and streams. In: Naiman, R. J. (Ed.), *Watershed management*. Springer, N.Y. 25-72.
- Fries, C., Johansson, O. and Pettersson, B., 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. *For. Ecol. Manage.* 94, 89-103.
- Fries, C., Carlsson, M., Dahlin, B., Lämås, T. and Sallnäs, O., 1998. A review of conceptual landscape planning models for multiobjective forestry in Sweden. *Can. J. For. Res.* 28, 159-167.
- Fritz, Ö. and Larsson, K., 1997. Betydelsen av skoglig kontinuitet för rödlistade lavar. En studie av halländsk bokskog. *Svensk botanisk tidskrift* 90, 241-262. (In Swedish with English summary.)
- Gibbons, A., 1992. Mission impossible: saving all endangered species. *Science* 256, 1386.
- Granström, A., 1993. Spatial and temporal variation in lightning ignitions in Sweden. *J. Veg. Sci.* 4, 737-744.
- Grisez, T. J. and Peace, M., 1973. Requirements for advanced reproduction in Allegheny hardwoods – an interim guide. U. S. Dep. Agric. For. Serv. Res. Note NE-180.
- Groot Bruinderink, G. W. T. A. and Hazebroek, E., 1996. Wild boar (*Sus scrofa scrofa* L.) rooting and forest regeneration on podzolic soils in the Netherlands. *For. Ecol. Manage.* 88, 71-80.
- Gustafsson, L., 1994. A comparison of biological characteristics and distribution between Swedish threatened and non-threatened forest vascular plants. *Ecography* 17, 39-49.
- Gustavsson, R. and Wittrock, S., Lunden till glädje och nöje. *Skog och forskning 1/97*, 28-37. (In Swedish).
- Hagner, S. 1962. Natural regeneration under shelterwood stands. *Meddelanden från statens skogsforskningsinstitut*. Band 52, nr 4. Stockholm, Sweden (In Swedish with English summary.)
- Hallbäcken, L. and Tamm, C. O., 1986. Changes in soil acidity from 1927 to 1982-1984 in a forest area of south-west Sweden. *Scand. J. For. Res.* 1, 219-232.
- Hannerz, M., 1996. Vegetation succession after clearcutting and shelterwood cutting. Licentiate thesis. Swedish University of Agricultural Sciences. Dept. of Ecology and Environmental Research. Report 84. Uppsala, Sweden.
- Hannon, G. E., 1999. The use of plant macrofossils and pollen in the palaeoecological reconstruction of vegetation. *Acta Universitatis Agriculturae Sueciae, Silvestria* 106. Alnarp, Sweden.
- Hannon, G. E., Bradshaw, R. H. W. and Emborg, J., in press. 6000 years of forest dynamics in Suserup Skov, a semi-natural Danish woodland. *Global Ecology and Biodiversity letters*.
- Hansson, L. and Larsson, T.-B., 1997. Conservation of boreal environments: a completed research program and a new paradigm. *Ecol. Bull.* 46, 9-15.
- Harmer, R., 1994. Natural Regeneration of Broadleaved Trees in Britain; I. Historical Aspects. *Forestry* 67; 179-188.
- Harmer, R., 1995. Natural Regeneration of Broadleaved Trees in Britain; III. Germination and establishment. *Forestry* 68; 1-9.

- Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K., Jr. and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in ecological research* 15, 133-302.
- Helliwell, D. R. and Harrison, A. F., 1979. Effects of light and weed competition on the growth of seedlings of four tree species on a range of soils. *Quart. J. For.* 80, 160-171.
- Henriksen, H. A., 1988. Skoven og dens dyrkning. Dansk skovforening. Nyt nordisk forlag, Arnold Busck, Copenhagen. (In Danish) 664 pp.
- Heybroek, H. M., 1980. Monoculture versus mixture: interactions between susceptibility and resistant trees in a mixed stand. In: Heybroek H. M, Stephan, B. R. and Weissenberg, K. (Eds.), *Proceedings of the third international workshop on the genetics of host parasites interactions*. Wageningen, Netherlands. 326-341.
- Hultén, E., 1950. Atlas of the distribution of vascular plants in NW. Europe. Generalstabens litografiska anstalts förlag. Stockholm. 512 pp.
- Hultengren, S. and Nitare, J., 1999. Inventering av jätteträd. Skogsstyrelsen. Jönköping, Sweden. 48 pp. (In Swedish).
- Hunter, M. L. Jr., 1999. Biological diversity. In: Hunter, M. L. Jr. (Ed.), *Maintaining biodiversity in forest ecosystems*. Cambridge university press. p. 3-21.
- Hunter, M. L. Jr., Jacobson, G. L. Jr. and Webb, T. III, 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conserv. Biol.* 2, 375-385.
- Hunter, M. L. Jr. and Calhoun, A., 1996. A triad approach to land use allocation. In: Szaro, R. C. and Johnston, D. W. (Eds.) *Biodiversity in managed landscapes*. Oxford Univ. Press, N.Y. 477-491.
- Huntley, B., 1988. Europe. In: Huntley, B. and Webb III, T. (Eds), *Handbook of Vegetation Science, Vol.7, Vegetation History*. Kluwer Academic Publishers, Dordrecht. 341-383.
- Huntley, B., 1990. European post-glacial forests: compositional changes in response to climatic change. *J. Veg. Sci.* 1, 507-518.
- Huss, J., 1987. Mischwald zwischen Wunsch und Wirklichkeit. *Forstwissenschaftliches Centralblatt*, 106(3), 114-132. (English summary).
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81-101.
- Iversen, J., 1973. The development of Denmark's nature since the last glacial. *Geological Survey of Denmark. V. Series. No. 7-C. Geology of Denmark III*. C. A. Reitzels forlag, Copenhagen, 126 pp.
- Jacobson, G.L. Jr., T. Webb III & E.C.Grimm, 1987. Patterns and rates of vegetation change during the glaciation of eastern North America. In W.F. Ruddiman & H.E. Wright, Jr. (Eds.), *North America and adjacent oceans during the last deglaciation. The Geology of North America, K-3*. Geological Society of America, Boulder, Colorado. 277- 287.
- Jensen F. S. and Koch N. E. 1997. Friluftsliv i skovene 1976/77 - 1993/94. Den Kgl. Veterinaer og Landbohøjskole. Forskningcentret for Skov og Landskab. København, Denmark. 215 pp. (In Danish with English summary.)
- Jonsson, B., 1962. Yield of mixed coniferous species. *Meddelanden från Sveriges skogsforskningsinstitut. Band 50, nr 8*. (In Swedish with English summary).
- Kardell, L. and Kardell, Ö., 1996. Ollonsvin. Historia samt försök med skogsgrisar på Tagel. The Swedish university of agricultural sciences. Department of environmental forestry. Report no. 65. 103 pp. (In Swedish).
- Karlsson, M., 1996. Vegetationshistoria för en artrik bokskog i Halland. M.Sc. thesis, Swedish Univ. of Agricultural Sciences, Alnarp, Sweden, 47 pp. (In Swedish)
- Kers, L. E., 1977. Floristic methods useful when evaluating continuity of stands. In: *Forest genetic resources, Ultuna 1976*. Department of forest genetics. Research notes no 24. Royal college of forestry, Stockholm. (In Swedish with English summary).

- Kirby, K. J., 1988. Changes in the ground flora under plantations on ancient woodland sites. *Forestry* 61, 317-338.
- Kirby, K. J., 1990. Changes in the ground flora of broadleaved wood within a clear fell, group fells and a coppiced block. *Forestry* 63, 241-249.
- Kirby, K. J. and Drake, M. (Eds.), 1993. Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. *English nature* no 7.
- Krok, Th, O. B. N, and Almquist, S., 1984. *Svensk flora*. 26th edition, Esselte Herzogs, Uppsala, Sweden.
- Lagerås, P., 1996. Vegetation and land-use in the Småland Uplands, southern Sweden, during the last 6000 years. Lundqua thesis, Lund university, Sweden, 112 pp.
- Larsen, J. B., 1995. Ecological stability of forests and sustainable silviculture. *For. Ecol. Manage.* 73, 85-96.
- Larsen, J. B., 1996. Ecosystem stability and sustainability. In: Larsen, J. B. (Ed.), *Sustainable forest management*. TemaNord 1996:578. Nordic Council of Ministers, Copenhagen.
- Larsen, D. R. and Johnson, P. S., 1998. Linking the ecology of natural oak regeneration to silviculture. *For. Ecol. Manag.* 106, 1-7.
- Larsson, B. (Ed.), 1995. *Svedjebruk och skogsbränning i Norden*. Nordiska museet, Stockholm. (In Swedish with English summaries.)
- Lawrence, E. (Ed.), 1995. *Hendersons dictionary of biological terms*. 11th edition. Longman, Essex.
- Liljelund, L.-E., Pettersson, B. and Zackrisson, O., 1992. Skogsbruk och biologisk mångfald. *Sv. Bot. Tidskr.* 86, 227-233. (In Swedish with English summary).
- Lindbladh, M., 1998. Long term dynamics and human influence in the forest landscape of southern Sweden. *Acta Universitatis Agriculturae Sueciae, Silvestria* 78. Alnarp, Sweden.
- Lindbladh, M., 1999. The influence of former land-use on vegetation and biodiversity in the boreo-nemoral zone of Sweden. *Ecography* 22, 485-498.
- Lindbladh, M. and Bradshaw, R. H. W., 1995. The development and demise of a Medieval forest-meadow system at Linneaus' birthplace in southern Sweden; implications for conservation and forest history. *Vegetation history and archaeobotany* 4, 153-160.
- Lindbladh, M. and Bradshaw, R. H. W., 1998. The origin of present forest composition and pattern in southern Sweden. *J. Biogeogr.* 25, 463-477.
- Lindbladh, M., Bradshaw, R. and Holmqvist, B. H., 2000. Pattern and process in south Swedish forests during the last 3000 years, sensed at stand and regional scales. *J. Ecol.* 88(1), 113-128.
- Löf, M., 1993. Relationen mellan miljörörelsen och skogsbolagen 1970-1993. Swedish University of Agricultural Sciences, Dept of Forest Economics. Report 176. (In Swedish.)
- Löf, M., 1999. Environmental stress on establishment and growth in *Fagus sylvatica* L. and *Quercus robur* L. seedlings. *Acta Universitatis Agriculturae Sueciae, Silvestria* 91. Alnarp, Sweden.
- Löfgren, R., 1997. Skogsreservat i Sverige. Rapport 4707. Naturvårdsverket, Stockholm. (In Swedish.)
- Loftis, D., 1983. Regenerating Southern Appalachian mixed hardwood stands with the shelterwood method. *Southern Journal of Applied Forestry* 7(4), 212-217.
- Loftis, D. L., 1992. Regenerating northern red oak on high-quality sites in the southern Appalachians. In: Loftis, D. L. and McGee, C. E. (Eds.) *Oak regeneration*. Symposium proceedings. Southeastern forest experiment station, Asheville, N. C. USA.
- Loiskekoski, M. and Halko, L. (Eds.), 1994. Ministerial conference on the protection of the forests in Europe, 16-17 June 1993 in Helsinki. Maa- ja metsätalousministeriö, Finland.

- Lundquist, T., 1994. Bedrock. In: Fredén, C. (Ed.), *Geology. National Atlas of Sweden*.
- Moe, D., 1970. The post-glacial immigration of *Picea abies* into Fennoscandia. *Botaniska notiser* 123, 61-66.
- Naiman, R. J., Johnston, C. A. and Kelly, J. C., 1988. Alteration of North America streams by beaver. *BioScience* 38, 753-762.
- Nielsen, K. E., 1995. Fra kredsløb til afløb. In: *Skovbrugets grønne alternativ*. Nepenthes forlag, Århus, Denmark. (In Danish with English summary).
- Nilsson, S. G., 1997. Forests in the temperate-boreal transition: natural and man-made features. *Ecol. Bull.* 46, 61-71.
- Nilsson, S. G. and Baranowski, R., 1993. Skogshistorikens betydelse för artsammansättning av vedskalbaggar i urskogsartad blandskog. *Ent. Tidskr.* 114(4), 133-146. (In Swedish with English summary.)
- Nilsson, S. G. and Baranowski, R., 1994. Indikatorer på jätteträdskontinuitet. *Ent. Tidskr.* 115 (3), 81-97. (In Swedish with English summary.)
- Nilsson, S. G. and Ericson, L., 1997. Conservation of plant and animal populations in theory and practice. *Ecol. Bull.* 46, 117-139.
- Nilsson, U., 1993. Competition in young stands of Norway spruce and Scots pine. Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, dissertation. Alnarp, Sweden.
- Nordén, U., 1992. Soil acidification and element fluxes as related to tree species in deciduous forests of south Sweden. Dissertation, University of Lund, Department of Ecology, Plant Ecology. Lund, Sweden.
- Nordén, U. 1994. Influence of tree species on acidification and mineral pools in deciduous forest soils of south Sweden. *Water, air and soil pollution* 76, 363-381.
- Norén, M., Hultgren, B., Nitare, J. and Bergengren, I., 1995. Instruktion för datainsamling vid inventering av nyckelbiotoper. Skogsstyrelsen, Jönköping, Sweden. 88 pp. (In Swedish).
- Ohlsson, M. and Tryterud, E. 1999. Long-term spruce forest continuity - a challenge for a sustainable Scandinavian forestry. *For. Ecol. Manage.* 124, 27-34.
- Örlander, G., Gemmel, P. and Hunt, J., 1990. Site preparation. A Swedish overview. FRDA Rep. 105. B. C. Ministry of Forests, Research branch, Victoria, Canada.
- Otto, H.-J., 1995. Natural forests as a model for silviculture. In: *Skovbrugets grønne alternativ*. Nepenthes forlag, Århus, Denmark. (In Danish with English summary).
- Ottosson-Löfvenius, M., 1993. Temperature and radiation regimes in pine shelterwood and clear-cut area. Swedish University of Agricultural Sciences. Department of Forest Ecology. Dissertation. Umeå, Sweden.
- Owen-Smith, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*, 13(3), 351-362.
- Parsons, R.W., I.C. Prentice & M. Saarnisto, 1980. Statistical studies on pollen representation in Finnish lake sediments in relation to forest inventory data. *Ann. Bot. Fennici* 17: 379-393.
- Perala, D. A. and Alm, A. A., 1990. Reproductive ecology of birch: A review. *For. Ecol. Manage.* 32, 1-38.
- Persson, P., 1975. Windthrow in forests, its causes and the effect of forestry measures. Research notes 36. Dept. of Forest Yield Research. Royal College of Forestry, Stockholm. 294 pp. (In Swedish with English summary.)
- Peterken, G. F. and Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J. Ecol.* 72, 155-182.
- Peterken, G. F., 1996. Natural woodland. Ecology and conservation in northern temperate regions. Cambridge university press. 522 pp.

- Pettersson, B. and Fiskesjö, A.-L., 1992. Flora and fauna in semi-natural deciduous forests - conservation evaluation, selection and management of stands. Naturvårdsverket rapport 3991, Solna. (In Swedish with English summary).
- Pettersson, H., 1955. Barrskogens volymproduktion. Meddelanden från statens skogsforskningsinstitut, 45:1. Stockholm. (In Swedish and German).
- Pigott, C. D., 1991. Tilia cordata, Miller. Biological flora of the British Isles. No 174. J. Ecol. 79, 1147-1207.
- Pott, R., 1988. Impact of human influences by extensive woodland management and former land use in North-Western Europe. In: Salbitano, F. (Ed.), Human influence on forest ecosystems development in Europe. ESF FERN-CNR, Pitagora Editrice, Bologna. 263-278.
- Prentice, I.C., B.E. Berglund & T. Olsson, 1987. Quantitative forest-composition sensing characteristics of pollen samples of Swedish lakes. Boreas 16: 43-54.
- Påhlsson, L. (Ed). 1994. Vegetationstyper i Norden. Tema Nord 1994:665. Nordiska rådet, Stockholm. 629 pp. (In Swedish with English summary).
- Rackham, O., 1980. Ancient woodland. Arnold, London. 402 pp.
- Roberts, M. R. and Gilliam, F. S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol. Appl. 5, 969-977.
- Runkle, J. R., 1985. Disturbance Regimes in Temperate Forests. In: Pickett, S. T. A and White, P. S. (Eds). The ecology of natural disturbance and patch dynamics. Academic press, Inc. 17-33.
- Röhrig, E., 1991. Vegetation structure and forest succession. In: Röhrig, E and Ulrich, B (Eds.) Ecosystems of the world 7. Temperate deciduous forests. Elsevier, Amsterdam. 35-49.
- Samuelsson, J., Gustafsson L. & T. Ingelög, 1994. Dying and dead trees - a review of their importance for biodiversity. Swedish Threatened Species Unit, Uppsala, 109 pp.
- Sander, I. L., 1971. Height growth of new oak sprouts depends on size of advance regeneration. J. For. 69, 809-811.
- Schimmel, J. 1993. On fire. Fire behaviour, fuel succession and vegetation response to fire in the Swedish boreal forest. Swedish university of agricultural sciences. Department of vegetation ecology. Dissertation no 5. Umeå, Sweden.
- Schmidt, R. A., 1978. Diseases in forest ecosystems: the importance of functional diversity. In: Horsfall, J. G. and Cowling, E. B. (Eds.), Plant diseases: an advanced treatise; vol. 2. How disease develops in populations. Academic press, New York. 287-315.
- Schnitzler, A., 1995. Successional status of trees in gallery forest along the river Rhine. J. Veg. Sci. 6, 479-486.
- Seitschek, O., 1989. Aufbau stabiler wälder - zentrale Aufgabe des Waldbaus. Forst und Holz 7, 163-169. (In German).
- Seymour, R. S. and Hunter, M. L. Jr., 1999. Principles of ecological forestry. In: Hunter, M. L. Jr. (Ed.), Maintaining biodiversity in forest ecosystems. Cambridge university press. 22-41.
- Shannon, C. E. and Weaver, W., 1949. The mathematical theory of communication. University of Illinois Press, Urbana.
- Sjörs, H., 1965. Forest regions. Acta Phytogeographica Suecica 50, 48-63.
- Slotte, H. and Göransson, H. (Eds.), 1996. Lövtäkt och stubbskottbruk. I and II. Kungl. Skogs- och Lantbruksakademien, Stockholm. 464 pp. (In Swedish, Danish, English and Norwegian.)
- SOU, 1992. Skogspolitiken inför 2000-talet. Statens offentliga utredningar 1992:76. Jordbruksdepartementet. Stockholm, Sweden. (In Swedish.)
- Sprugel, D. G., 1991. Disturbance, equilibrium, and environmental variability: what is 'natural' in a changing environment? Biol. Cons. 58, 1-18.

- Stener, L-G., 1998. Provincial statistics on the forest land area and growing stock of broadleaved trees in Sweden. Skogforsk, The forestry research institute of Sweden. Redogörelse nr 4, 1998. (In Swedish with English summary.)
- Svensson, S. A., 1980. The Swedish national forest survey 1973-1977. Swedish University of Agricultural Sciences. Dept. of Forest Survey. Report 30. Umeå, Sweden. (In Swedish with English summary.)
- Swindel, B. F., Conde, L. F. and Smith, J. E., 1984. Species diversity: concept, measurement, and response to clearcutting and site-preparation. *For. Ecol. Manage.* 8, 11-22.
- Sykes, M. T., Prentice, I. C. and Cramer, W., 1996. A bioclimatic model for the potential distribution of north European tree species under present and future climates. *J. Biogeogr.* 23, 203-233.
- Tallantire, P. A., 1972. Spread of spruce (*Picea abies* (L.) Karst.) in Fennoscandia and possible climatic implications. *Nature* 236, 64-65.
- Thirgood, J. V., 1989. Man's impact on the forest of Europe. *Journal of world forest resource management* 4, 127-1676.
- Tilman, D. and Downing J. A., 1994. Biodiversity and stability in grasslands. *Nature* 367, 363-365.
- TNC 96. 1994. Forest vocabulary. Tekniska nomenklaturcentralen; Sveriges skogsvårdsförbund. Solna, Sweden
- Troedsson, T. and Nykvist, N., 1973. Marklära och markvård. Almqvist & Wiksell läromedel AB, Stockholm. 403 pp.
- Tuhkanen, S., 1980. Climatic parameters and indices in plant geography. *Acta Phytogeographica Suecica* 67.
- Tyler, T and Olsson, K.-A., 1997. Förändringar i Skånes flora under perioden 1938-1996 - statistisk analys av resultat från två inventeringar. *Sv. Bot. Tidskr.* 91, 143-185. (In Swedish with English summary.)
- United Nations 1992. Convention on Biological Diversity. United Nations conference on environment and development, 2-14 June 1992, Rio de Janeiro, Brazil. United Nations, USA. 25 pp.
- Watt, A. D., 1992. Insect pest population dynamics: effects of tree species diversity. In: Canell, M G. R, Malcom D. C. and Robertson, P. A. (Eds.), *The ecology of mixed-species stands of trees*. British Ecology Society, Spec Publ. 11. Blackwell, Oxford. p. 267-275.
- Webb, D. A., 1985. What are the criteria for presuming native status? *Watsonia* 15, 231-236.
- Welander, J., 2000. Spatial and temporal dynamics of a disturbance regime. Wild boar *Sus scrofa* rooting and its effects on plant diversity. *Acta Universitatis Agriculturae Sueciae, Silvestria* 127. Uppsala, Sweden.
- Vollbrecht, G. 1994. Effects of silvicultural practices on the influence on the incidence of root and butt rot in Norway spruce with special emphasis on *Heterobasidion annosum*. Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre. Dissertation. Alnarp, Sweden.
- Vollbrecht, G., 1996. Fiberskog- förutsättningar samt forsknings- och utvecklingsbehov. SLU, Skogsvetenskapliga fakulteten, rapport 16. Alnarp, Sweden. (In Swedish.)
- von Sydow, F. and Örlander 1994. The influence of shelterwood density on *Hylobius abietis* (L.) occurrence and feeding on planted conifers. *Scand. J. For. Res.* 9, 367-375.
- Wright, H.E., Kutzbach, J.E., Webb, T. III, Ruddiman, F.A., Street-Perrot, F.A. and Bartlein, P.J. (Eds.), 1993. Global changes since the last glacial maximum. Univ. of Minnesota Press, Minneapolis, MN. 544 pp.
- Zackrisson, O., 1977. Influence of forest fires on the north Swedish boreal forest. *Oikos* 29, 22-32.