# Natural Regeneration
# of Broadleaved Tree Species
# in Southern Sweden

## - Effects of silvicultural treatments and seed dispersal from surrounding stands

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# Abstract

The objective of the present thesis was to examine the effects of silvicultural treatments and seed dispersal from surrounding stands on the establishment of natural regeneration of broadleaved tree species in southern Sweden. Most of the broadleaved tree species that occur naturally in forests in southern Sweden were studied but birch (*Betula pendula* Ehrh./ *B. pubescens* Roth) was the most common species and present in equal numbers in all studies. The wind dispersal of seeds of seven species was studied and great variations were found. This could mainly be explained by differences in seed morphology. The effect of soil scarification was examined in all five studies and was generally found to be positive for the establishment of the studied broadleaved species. However, in some cases the scarification was not positive for the establishment. The reason for this was hypothesised to be that the seed supply was limited, or an effect of large and/or animal-dispersed seeds. The effect of shelterwood was examined in three studies and was found to be positive for animal-dispersed species but negative for shade-intolerant species, although a sparse shelterwood can be used to regenerate birch. Slash removal was included in one study and found to be positive for the establishment of birch. This thesis showed that regeneration treatments can be used to increase the establishment of naturally regenerated broadleaved tree seedlings, but the stand structure and species composition must be regulated with pre-commercial thinning. However, the effect of variations in seed production and seed dispersal must be closely examined from a time and a space perspective prior to any forecasts regarding the effects of regeneration treatments.

*Keywords:* Broadleaved tree species, Establishment, Natural Regeneration, Scarification, Seed dispersal, Shelterwood, Silvicultural treatments.

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## Lönnen

Hell de kämpar, som blöda i striderna,
trots ärr och sår strålande,
hell deras hårda kamp,
hell deras dyrköpta segrar!

Men o du unga träd, du blommande lönn,
dig älskar jag mer än kämpars ärr.
Din oförvärvade, lyckliga adel
är mer än deras vunna slag.

Frisk i livets morgon spirade du ur jorden,
frisk, frisk växte du lugnt i sol och regn;
ångest du kände ej, ånger ej,
intet av allt vårt sjuka.

Du blommar i guld och guldvin; i susningar skrattar du,
när vandraren kysser din stam.
Hans kyss är en bön till den eviga skönhet,
som tänkte i dagen din dejliga blom.

Välsignad du, välsignad du, skönväxande lönn!
De stridandes segrar behöver du ej.
Hos dig är ensliga skogars vila.
Hos dig är sol av gudom.

*Karin Boye*

# Contents

# Appendix

## Papers 1-5

This thesis is based on the following Papers, which will be referred to by the corresponding Roman numerals.

I.     Nilsson, U., Gemmel, P., Johansson, U. Karlsson, M. & Welander, T. Natural regeneration of Norway spruce, Scots pine and birch under Norway spruce shelterwoods of varying densities on mesic-dry site in southern Sweden. Forest Ecology and Management. In press.

II.     Karlsson, M. & Nilsson, U. The effect of scarification and shelterwood treatments on naturally regenerated seedlings of occurring tree species in southern Sweden. Manuscript.

III.     Karlsson, M., Nilsson, U. & Örlander, G. Natural regeneration in clearcuts – effects of scarification, slash removal and clearcut age. Submitted manuscript.

IV.     Karlsson, M. Seed dispersal from broadleaved stands and effects of scarification on seedling emergence. Manuscript.

V.     Karlsson, M., Vollbrecht, T. & Nilsson, U. Stand structure in naturally regenerated broadleaved stands - effects of shelterwood, scarification and pre-commercial thinning. Manuscript.

# Introduction

## Broadleaved trees in southern Sweden

### *Historical background*

Southern Sweden[1] belongs to the nemoral and boreonemoral zones (Sjörs, 1965). Therefore, broadleaved tree species would probably constitute a large proportion of the forests in southern Sweden if they had been left unmanaged (Björse & Bradshaw, 1998). Since modern forestry started to act in southern Sweden in the 19th century, Norway spruce (*Picea abies* (L.) Karst) has been favoured over broadleaved species. The proportion of pine has also decreased and given way to spruce (http://www-riksskogstaxeringen.slu.se: Accessed 22-Feb-2001). Spruce has been planted on abandoned agricultural land, but broadleaved stands have also been replaced by spruce. The forest industry prefers spruce to broadleaved species, since it offers great economy through simple management, an early net income from thinnings, a high wood production and short rotation periods (Carbonnier & Hägglund, 1969). In addition, spruce is less exposed to damage by browsing from roe deer and moose than broadleaved species, a major factor in southern Sweden which currently has high browsing pressure (Kullberg, 2000).

However, the decreasing trend of broadleaved trees existed before the rise of modern forestry in the 20th century (Eliasson & Nilsson, 1999). During the last millennia, anthropogenic influences through e.g. clearing of forests for agricultural land, grazing, fires and timber demand have altered the tree species composition and induced a rising percentage of conifers, mainly spruce, and decreasing amount of broadleaved tree species (Nilsson, 1997; Björse & Bradshaw, 1998; Lindblad et al, 2000). Research has shown that some broadleaved tree species, e.g. lime (*Tilia cordata* L.) and oak (*Quercus robur* L./ *Q. petrea* (Matt.) Liebl), have decreased more than others, e.g. birch (*Betula pendula* Ehrh./*B. pubescens* Roth). Modern forestry acted more uniformly against all broadleaved tree species.

### *The present state – need for a change?*

Is the present tree species composition in southern Sweden satisfactory or would it be preferable to change the forests to a species composition that better reflects paleoecological data and vegetation zones? Practically without exception, conventional cost estimates show that spruce and the present forests give the highest income, but with other approaches the answer may be different. Both society and individual forest owners may argue that it is hazardous to rely on the production of one type of raw material (spruce wood) with an uncertain market ahead of us. Moreover, a future shortage in the supply of wood from broadleaved tree species may result in higher prices. Furthermore, if forestry aims at a stable income, the

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[1] In this thesis "southern Sweden" corresponds to the region "Götaland" which is approx. delimited by the 59°N latitude.

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goal should be to minimise the risk for unpredictable losses due to e.g. wind throws or but rot. This would result in the selection of other species than spruce. A lower interest rate in the financial analysis would also be more beneficial to the advantage of broadleaved tree species.

An increment of the proportion of broadleaved tree species in the landscape of southern Sweden would be positive to biodiversity (Terstad, 1995; Nilsson, 1997). Because of the historical decrease of broadleaved trees (see above), the preferred or needed biotope or substrate has decreased for many species that depend on broadleaved trees. Many threatened species in southern Sweden are highly dependent on large living and/or dead broadleaved trees, and these populations are likely to be subjected to delayed extinction (Nilsson et al, 2001). To counteract the extinction of these threatened species, an increase in broadleaved trees should take place (Terstad, 1995; Nilsson, 1997). This would also benefit many species with a less threatened status, which prefer or depend on broadleaved tree species. However, the desired tree species is not so much the most common species, i.e. birch, but to a larger extent species recognised a carriers of biodiversity, i.e. principally oak and beech (Berg et al, 1994; Nilsson et al, 1994; Gustavsson, 1995; Fritz & Larsson, 1996; Jonsell et al, 1998).

The southern part of Sweden is one of the most densely populated regions in Sweden, something which causes high visiting pressure in the forests. This is further accentuated by the closeness to central Europe with large populations, many of which often visit southern Sweden as tourists. This means that the recreational value of the forests in southern Sweden has to be considered when managing the forests. It has been shown forest visitors prefer broadleaved stands and trees to dense spruce stands (Hultman, 1983; Gustafsson & Ingelöf, 1994; Lindhagen & Hörnsten, 2000). Due to its recreational value, the broadleaved tree component in the landscape should therefore be increased (Mattson et al, 1995).

Spruce affects the soil differently than many broadleaved trees, with higher podzolisation rates and lowered base cation availability (Hallbäcken & Tamm, 1986; Nordborg & Olsson, 1999). It has been indicated that spruce production is not sustainable due to the adverse effects on soil properties, and that forestry should hence replace spruce with broadleaved tree species that maintain a higher soil status (Thelin, 2000).

It has been forecast that spruce will move its natural distribution limit northwards in northern Europe in response to global change and that the plantation of spruce in southern Sweden should therefore be avoided (Bradshaw et al, 2000). This would also imply an increment of broadleaved trees in southern Sweden.

In conclusion, there are many reasons why the proportion of broadleaved trees should be increased. This recommendation has been implemented in FSC's certification rules for Sweden (FSC, 2000), and subsidies are given to promote the

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regeneration of broadleaved trees in previous spruce stands that have been wind-thrown (http://www.svo.se/aktuellt/press/budprop.htm: Accessed 20-04-2000). In addition, it has been implemented as declarations from the Nature Protection Agency (Terstad, 1995). Therefore, this study included natural regeneration of most occurring broadleaved tree species in southern Sweden (Table 1).

Table 1 *Tree species included in the present thesis*

| Common name | Scientific name | Present as seed data[A] or seedling data in paper | | | | |
| | | I | II | III | IV | V |
| --- | --- | --- | --- | --- | --- | --- |
| *Broadleaved species* | | | | | | |
| Aspen | *Populus tremula* L. | | x | | | x |
| Beech | *Fagus sylvatica* L. | | x | | x | x |
| Birch | *Betula pendula* Ehrh. / *B. pubescens* Roth. | x | x | x | x | x |
| Common alder | *Alnus glutinosa* (L.) Gaertner | | x | | x | |
| Elm | *Ulmus glabra* L. | | | | x[B] | |
| Hornbeam | *Carpinus betulus* L. | | | | x[B] | x |
| Norway maple | *Acer platanoides* L. | | | | x | |
| Oak | *Quercus robur* L./ *Q. petrea* (Matt.) Liebl. | | x | | (x)[B] | x |
| Rowan | *Sorbus aucuparia* L. | | x | | | x |
| Sallow | *Salix caprea* L. | | x | | | x |
| Swedish whitebeam | *Sorbus intermedia* (Ehr.) Pers. | | x | | | |
| Wild cherry | *Prunus avium* L. | | x | | | x |
| *Conifer species* | | | | | | |
| Larch | *Larix* sp. | | x | | | |
| Norway spruce | *Picea abies* (L.) Karst | x | x | x | | |
| Scots pine | *Pinus sylvestris* L. | x | x | x | | |

[A] Only in papers I and IV
[B] Only seed data

## Natural Regeneration

Today, the dominating regeneration method in southern Sweden is planting (Anon. 2000). Natural regeneration is common only for regeneration of pine and beech (Bjerregaard & Carbonnier, 1979; Karlsson, 2000). However, natural regeneration of broadleaved species occurs unintentionally in regeneration areas, which results in birch being the most common species in young stands in southern Sweden (diameter class 0–4 cm) (Anon., 2000). There are certain advantages with planting compared to natural regeneration. For example, planting is a technically well-

developed system. Furthermore, planting allows the use of genetically improved material and the outcome can easily be predicted. Natural regeneration requires more knowledge and great planning efforts. Knowledge about natural regeneration of broadleaved tree species are in general insufficient, and there is no great interest in planning regeneration of broadleaves since their potential is unknown. However, planting is expensive since it involves both seedling and site preparation costs, whereas natural regeneration only has site preparation costs. Another advantage of natural regeneration is that a high seedling density can be achieved. This is necessary if the goal is to produce high timber quality in the future stand (Persson, 1976; Bjerregaard & Carbonnier, 1979). Similarly, naturally regenerated seedlings can be used to increase the density or as nursery trees, and thus have a positive effect on the timber quality of planted seedlings (Klang, 2000). However, there are some financial drawbacks with natural regeneration: Since regeneration can be very dense, there are often additional costs for pre-commercial thinning. Furthermore, the shelterwood system is often used with natural regeneration. This increases the risk of wind-throws and creates higher cutting expenses. Natural regeneration has the benefit of providing a seedling population that may be genetically adapted to local conditions. However, it is still uncertain if it is better to use locally adapted trees or other, more southerly provenances to match global changes. In conclusion, natural regeneration may be a cost-efficient way to increase the proportion of broadleaved tree species, i.e. to use natural regeneration to establish broadleaved seedlings in areas previously occupied by conifers. However, if we want natural regeneration systems for broadleaved trees to compete with planting, it is essential that we acquire more knowledge about them and learn how to predict their outcome.

## Factors and processes of natural regeneration

It is possible to distinguish three processes, which limit the recruitment in forests – in other words processes, which control the success of natural regeneration: seed source strength, i.e. seed production or fecundity per adult tree unit; seed dispersal; and seedling establishment (Harper, 1977; Clark et al, 1998; Clark et al, 1999) (Fig. 1). The production of viable seeds, or the allocation of resources to reproduction, per tree unit depends on plant size, the proportion of resources devoted to seeds, and the seed weight respectively. Furthermore, there is a variation in time (between years and within years) that depends on factors such as climate and pre-dispersal predation (Harper, 1977). The seed production sets the size of the seed rain, but the seed dispersal controls the distribution of the seed rain together with the seed source density and distribution, i.e. the seed density or seed supply in a given area (cf. Fig. 2). The seed dispersal depends on factors such as species-specific morphological adaptations of the seeds to dispersal mechanisms, available dispersal agents like animal populations, wind conditions, and tree height (Harper, 1977; Augspurger & Franson, 1987). Post-dispersal predation of seeds may alter the amount of germinable seeds in an area (Janzen, 1971; Nystrand, 1998). Many studies working with natural regeneration in shelterwoods or recruitment in stands have not considered seed availability as a limiting factor (Clark et al, 1999). However, when applying natural
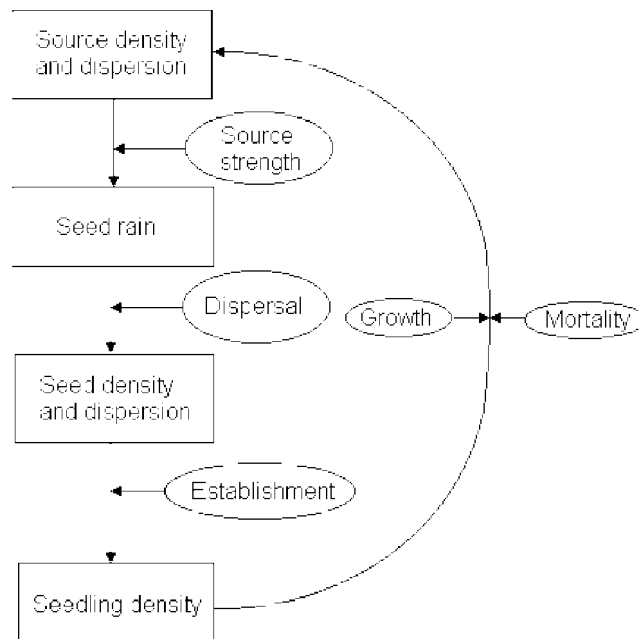
*Figure 1* A conceptual model of the recruitment limitations in forests adapted and modified after Clark et al (1998) and Clark et al (1999).

regeneration outside the seed-producing stand, there may not always be an excessive seed supply (LePage et al, 2000; Beach & Halpern, 2001).

The term "seedling establishment" has been defined as the germination and first-year survival of seedlings (Clark et al, 1999). However, the definition of the terms "seedling" and "establishment", are not evident. This study, however, chose to have a somewhat longer perspective on seedling establishment and therefore include the growth and survival of the seedlings during the first 3–5 years after germination. This was done since the seedlings have a very dynamic development during the first years and substantial changes may occur. Hence, longer study periods than one year are therefore more appropriate for silvicultural purposes.

The germination of viable seeds is controlled by physical conditions, e.g. temperature, moisture conditions, and in some cases light (Kozlowski et al, 1991). The growth of the germinated seedling relies on the amount of resources (light, nutrients and water) while survival primarily is controlled by predation and pathogens, although low levels of resources may have a predisposing effect (Kozlowski et al, 1991). Since it is possible to control the moisture conditions in a seed-bed (Oleskog, 1999), to increase the availability of water (Löf et al, 1998) or to add nutrients (Burgess & Wetzel, 2000) etc. through regeneration treatments (e.g. scarification, shelterwood, slash removal), it is also possible to control the establishment process and the success of natural regeneration. However, this control

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should pay attention to year-to-year climate shifts, since these may have great impact on the regeneration success (Oleskog, 1999). Site characteristics such as soil moisture, geology and microclimate also have large impact on the outcome of natural regeneration. The discussion above focused on regeneration from seeds and disregarded vegetative reproduction, i.e. root suckers and stump sprouting. Vegetative reproduction may constitute a large part of the regeneration in cut areas previously occupied by species that form suckers or sprouts (White, 1991; Wang & Nyland, 1993; Brown, 1994; Prevost, 1997). Another aspect of regeneration that may be overlooked in the above discussion is advance regeneration. According to previous studies, this may be an important factor during the regeneration of broadleaved stands (Bormann & Likens, 1979; Loftis, 1983; Björse, 2000).

## Seed dispersal

Seed dispersal is an essential part of the regeneration or recruitment of plants (e.g. Darwin, 1859; Harper, 1977; Willson, 1992; Ribbens et al 1994; Clark et al, 1999) (cf. Fig. 1). Seed dispersal has been studied in vegetation ecology for a long time. In recent years, however, a large number of studies have made progress in analysing, modelling and understanding the mechanisms of seed dispersal (cf. Nathan & Muller-Landau, 2000).

Seeds can be dispersed by various mechanisms such as wind, animals, water or active ejection from the parent plant, and seeds of most species have adapted to a certain dispersion mechanism (Howe & Smallwood, 1982; Willson, 1992). For forest tree species, wind dispersal is most common among canopy species, whereas understory species tend to be more dependent on animal dispersion (Waller, 1988). However, among the broadleaved forest tree species occurring in southern Sweden, several are regarded to be animal-dispersed (Grime et al, 1988).

Seed dispersal can be divided into short-distance and long-distance dispersal. This division is not clearly defined, but has been set to some hundred meters (Greene & Johnsson, 1995) or one hundred meters (Cain et al, 2000). In the present study, short-distance dispersal is used for seeds dispersed over distances up to one hundred meters, whereas long-distance dispersal refers to dispersal from seed sources on a landscape scale, i.e. seeds from other sources than those in the regeneration areas or neighbouring stands. The wind dispersal of seeds from a point source creates a dispersal curve (seed density over distance from source) that is convex close to the source, i.e. has a peak, and a long tail far from the source which depicts the long-distance dispersal (Harper, 1977; Okubo & Levin, 1989) (Fig 2). However, the dispersal curve from an area source will be less convex, or not convex at all, close to the source, since it summates a number of single seed sources and due to the leeward wind conditions close to the area source (Cremer, 1966; Greene & Johnsson, 1996) (Fig. 2). A negative exponential function can be fitted to the seed dispersion from an area source (Greene & Johnsson, 1996), but it has the disadvantage of underestimating the dispersal tail (i.e. the long-distance dispersal) (Nathan & Muller-
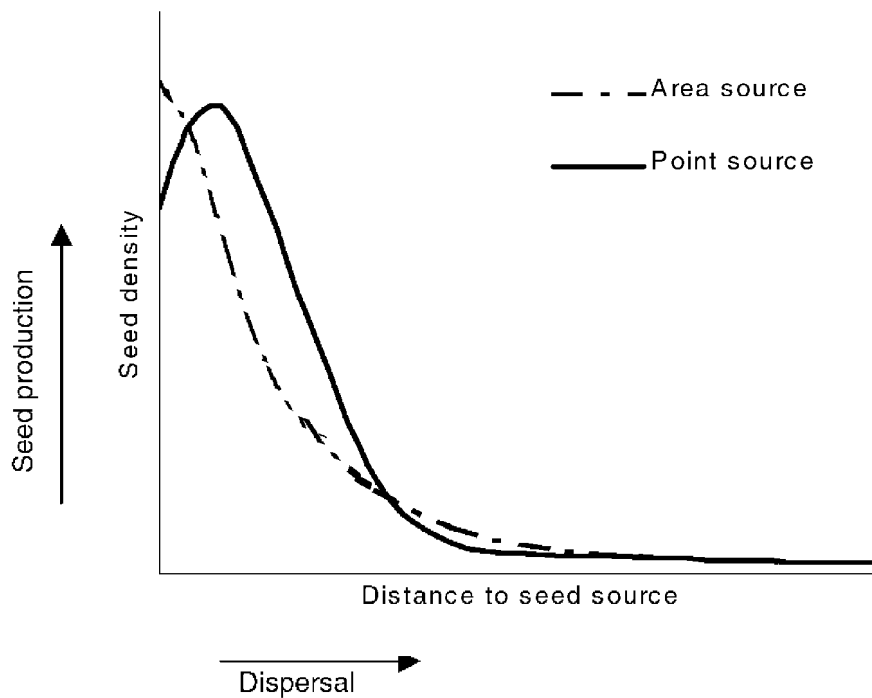
*Figure 2* Wind dispersal curves from point and area sources showing seed density over distance from source.

Landau, 2000). There is less information available concerning the dispersal curves for animal-dispersed seeds in temperate forests. In general, a dispersal curve generated by animals is believed to decrease with the distance from the source, similar to wind dispersal (Howe, 1986). However, seed dispersal is also believed to be controlled by the behaviour of the dispersing animal. This implies that e.g. environments are more or less preferred for caching or passive dispersal or that the dispersal is clumped and will result in aggregated seedling populations (Bossema, 1979; Jensen & Nielsen, 1986; Myster & Pickett, 1992; Kollmann & Schill, 1996; Vanha-Majamaa et al, 1996; Frost & Rydin, 2000). Furthermore, if the dispersing animal has a home range, the maximum dispersal distance is the diameter of the home range (cf. Nilsson, 1985).

When the seed has been dispersed from the parent tree and placed on the ground, it can be subjected to movement, i.e. secondary dispersal, caused by biotic or abiotic factors (Chambers & MacMahon, 1994). Biotic factors involve active or passive dispersal by animals and are generally controlled by the same conditions as described above. Abiotic factors are controlled by seed morphology, ground surface conditions and climate (Chambers & MacMahon, 1994) and primarily influence the seeds of wind-dispersed tree species. Among ground surface types, snow has been shown to

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be an efficient transport medium for secondary seed dispersal (Hesselman, 1934; Matlack, 1989; Greene & Johnsson, 1997). Secondary dispersal on snow of broadleaved tree species occurring in southern Sweden has to be regarded as minor, since only alder, and to some extent ash and hornbeam, disperse their seeds in winter (cf. Fig 7), when there may be snow cover in the region. Secondary dispersal on other ground surface substrates depends partly on the roughness of the surface (Chambers & MacMahon, 1994). It has been shown that seeds on bare mineral soil is transported longer distance than seeds on an more rough undisturbed ground surface (Vander Wall & Joyner, 1998). Another type of secondary seed dispersal is the vertical movements of seeds into the seed bank (Chambers & MacMahon, 1994). Mostof the occurring broadleaved tree species in southern Sweden have short viability or dormancy and may in general not form seed banks (Grime et al, 1988; Suszka et al, 1996). Birch seeds may form a seed bank with limited persistence, but only a few per cent of the buried seeds remain viable after one season (Granström & Fries, 1985). "The buried seed strategy" (sensu Bormann & Likens, 1979) is probably less important to tree species and sites in the present study.

## Establishment – effects of silvicultural treatments

The establishment process, or the "environmental sieve" (sensu Harper, 1977), may be manipulated through silvicultural treatments. The following section contains an introduction to known effects of some treatments commonly used in Sweden and investigated in this study.

### Soil scarification

"Soil scarification" mechanically removes the organic layers of the soil as well as the field vegetation, and exposes the mineral soil, or mix the organic layer and the mineral soil. "Site preparation" is a wider term, which includes methods that may involve techniques with prescribed fire, herbicide or steam (cf. Zackrisson et al, 1997). There are different types of soil scarification, e.g. disc trenching, patch scarification, mounding and ploughing. They all aim at changing or constructing different physical properties (Örlander et al, 1990). Physical properties may influence seed germination and seedling growth and survival, but physical properties that are positive to germination are not necessarily positive to seedling growth and survival, and vice versa (Marquis et al, 1964). Soil scarification can decrease the soil density or increase the soil temperature, soil moisture, gas exchange or soil nutrient availability respectively, but all changes depend on scarification type (Örlander et al, 1990). On bare mineral soil created through scarification, germination of seeds will often benefit from increased soil moisture and soil temperature (Örlander et al, 1990; Oleskog, 1999). However, scarification can sometimes result in a ground surface that is too dry for successful germination or an excess of water causing oxygen deficit (Örlander et al, 1990). Scarification types that remove the organic layer from the area around the seedlings, like disc trenching, may reduce seedling growth since nutrient concentrations are lower in mineral soil in the furrows than in or beneath a humus layer (Nohrstedt, 2000). However, competition from field

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vegetation is reduced in bare mineral soil and this has a positive effect on seedling growth (Beland et al, 2000). Seedling survival can generally be expected to increase following scarification. One reason is decreased attacks of pine weevil (*Hylobius abietis*) (Örlander & Nilsson, 1999) and less predation of voles that use field vegetation for protection (Bärring, 1963). However, broadleaved tree species are less affected by pine weevil feeding than conifer species (Löf, 2000). On sites with a high risk of frost heaving, scarification may be negative to survival (Goulet, 1995).

*Shelterwood*

A shelterwood is a stand of mature trees with a twofold purpose: to produce wood and to establish natural regeneration in the stand. The effect of the shelterwood on the latter can be divided in three parts: they guarantee a seed supply; they improve the microclimate for seedling establishment; and they reduce the field layer vegetation (Hagner, 1962). Compared to a clearcut, a shelterwood has higher minimum near-ground temperatures, and hence a decreased risk of frost damage (Ottoson Löfvenius, 1993; Blennow, 1998, Langvall, 2000). This is an effect of decreased net radiation, as the tree canopy obscures the sky, which also will reduce the maximum temperature. This, in combination with lower wind velocities (Chen et al, 1995), may reduce the evaporation from the seedlings and thus reduce the need for water uptake by the seedlings. Furthermore, the moisture conditions of the soil surface in shelterwood stands may provide a more continuous supply of water, something which improves seed germination (Oleskog, 1999). There is also research which shows that mortality in spruce seedlings caused by pine weevil is reduced in shelterwoods (von Sydow and Örlander, 1994). The field vegetation is increased and the species composition is altered after clear-cutting. This ingrowth is reduced in a shelterwood (Hagner, 1962; von Sydow and Örlander, 1994; Béland et al, 2000) and therefore seedling establishment may be better due to less competition and less predation of voles (Bärring, 1963). However, the development of field vegetation in a clearcut reflects an increased resource supply since the overstory trees and their resource uptake is removed. The increased supply of resources will not only favour the field vegetation but also the seedlings. Different tree species react differently to a certain resource supply depending on their tolerance to limited resource supplies. The reaction to light as a limiting resource, i.e. "shade-tolerant" and "shade-intolerant", is often used (Oliver & Larson, 1996) but might as well be an indirect measure of the reaction to water and nutrient availability.

Studies of shelterwoods in Sweden have mainly involved stands of pine, spruce and beech (Hagner, 1962; Sundqvist, 1993; Agestam, 1995; Holgén & Hånell, 2000; Karlsson & Örlander, 2000), while practical implementation primarily has been done for pine and beech stands. Spruce shelterwoods are seldom used. This study, however, used shelterwoods of pine, spruce, beech and oak, but focused on natural regeneration of tree species not present as seed trees in the shelterwoods.

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*Interaction between shelterwood and soil scarification*

Some interaction between shelterwood treatments and soil scarification has been found. Since the ingrowth of the field vegetation is slower, the scarified ground remains open and susceptible to seedling establishment for a longer period in shelterwoods than in clearcuts (Hagner, 1962; Beland et al, 2000). The physical properties of the obtained seed-beds after scarification have also been found to be different in shelterwoods than in clearcuts. Shelterwoods usually have a more continuous moisture availability in the mineral soil (Oleskog, 1999).

*Clearcut age*

Clear-cutting raises the level of available resources since mature trees and their uptake are removed. Furthermore, mineralisation increases as a result of increased soil temperature and substrate quality (Vitousek et al, 1992). However, different resources will act differently, e.g. water and light are increased immediately after clear-cutting, whereas available nutrients will increase more slowly peaking after some years (Bormann & Likens, 1979; Örlander et al, 1996). The ground vegetation will also increase gradually from an initially low biomass in the first year (Nilsson & Örlander, 1999). These changes after clear-cutting may affect the establishment of natural regeneration and probably leads to better conditions for establishment during the first years after clear-cutting. However, high mortality caused by pine weevil during the first years after clear-cutting can be expected (Örlander & Nilsson, 1999).

*Slash removal*

The applied cutting practices in Sweden include debranching of the timber, which leaves residual slash, i.e. branches and leaves/needles, on the site. However, slash is usually removed from clearcuts due to its value as biomass fuel and in order to facilitate regeneration treatments. Most tree nutrients trees are allocated in leaves or needles and the nutrient dynamics following slash removal may therefore be of interest. According to findings, the concentration of soil nutrients, which can either be leached or taken up by the field vegetation, is reduced when the slash is removed (Smethurst & Nambiar, 1990; Staaf & Olsson, 1994). However, the ingrowth of field vegetation has been reported to both increase (Fahey et al, 1991) and remain unaffected by slash removal (Olsson & Staaf, 1995; Bergquist et al, 1999). Another effect of slash removal is increased soil temperature caused by higher irradiation (Shethurst & Nambiar, 1990). The effect of slash removal on the establishment of naturally regenerated seedlings may also include the physical barrier that the slash forms for the seeds. Furthermore, slash removal may produce a more disturbed ground, since the removal operation in itself may create disturbed ground. It has also been shown that populations of some small mammal species (i.e. mice and voles) may be reduced after slash removal (Moses & Boutin, 2001)

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*Fencing*

Damage on broadleaved seedlings caused by browsing of large mammals can be substantial (Gill, 1992; Gill, 2000; Kullberg, 2000). With the present browsing pressure in southern Sweden, mainly from roe deer (*Capreolus capreolus*), moose (*Alces alces*) and hares (*Lepus timidus* and *L. europeus*), planting of broadleaved tree species should only be done after fencing (Kullberg, 2000). The possibility of regenerating broadleaved trees naturally with and without fences was studied by Björse (2000), who found no positive effect of fencing on the density of the studied broadleaved tree species. One explanation for the lack of effect of fencing was that the surrounding landscape was dominated by broadleaves and that broadleaved species therefore were less subjected to browsing. However, relatively rare species may experience a higher browsing pressure (cf. Bergquist, 1998) and this may imply increased browsing pressure on broadleaved species in a landscape dominated by conifers.

High browsing pressure may not necessarily result in high mortality or large growth reduction, since the plant's response to browsing may differ substantially between species (Eiberle, 1975; Hess et al, 1996). Responses in growth patterns have been observed e.g. for birch and oak, which may produce fewer but larger long-shoots when browsed (Bergström & Danell, 1987; Kullberg & Welander, 2000). Browsing-related mortality is higher in small than large seedlings (Hess et al, 1996) but this is probably also species-specific, since the proportion of below-ground nutrient storage differs between species.

Browsing may also affect the field vegetation, which may experience changed species composition and reduced biomass (Bergquist et al, 1999).

*Pre-commercial thinning*

When establishing broadleaved or mixed broadleaved/conifer stands through natural regeneration – the underlying objective of this study – it may be possible to control species density and composition respectively through the regeneration treatments described above and further evaluated in this study. Still, there will be a need to control species density, species composition and stand structure after natural regeneration has been established. A well-known "silvicultural rule" is that cutting in order to adjust the vertical and horizontal stand structure is only effective in young stands (Pretzsch, 1999). Pre-commercial thinning may therefore be a suitable way to adjust the structure and species composition for the future, mature stand. Combined with the regeneration treatments' effect on stand establishment, the stand treatment in young stands may provide an effective means of controlling the stand structure and diversity (Pretzsch, 1999). Therefore, the possibility of manipulating the stand structure of naturally regenerated stands in pre-commercial thinning was evaluated in this study.

# Ecological strategies and characters

Tree species can be classified and grouped into ecological strategies according to the species' characters. This has been done from different viewpoints. Clements (1916) classical grouping of the tree species' role in succession from a disturbed environment occupied by "pioneer" or early successional species to a climax state occupied by "climax" or late successional species is widely used today. Clements' view of climax forests was modified when the role of gap dynamics was recognised (Sousa, 1984; Runkle, 1985) and the group of gap-colonising tree species distinguished. Grime (1979) used a classification system with two factors, disturbance and stress. Disturbance is a process which removes plant biomass, whereas stress is the reduction of growth caused by unfavourable environmental conditions. This resulted in the classification of species as competitors (adapted to low disturbance and low stress), stress-tolerants (adapted to low disturbance and high stress) and ruderals (adapted to high disturbance and low stress). No viable strategy could be found for high disturbance and high stress. Other classifications of organisms, like the r- and K-strategies of MacArthur & Wilson (1967) have been less applied to tree species. Clements and Grime both created classifications that were based on the species' ecological character, such as their ability to grow fast with a large resource supply, their ability to grow and survive with a limited resource supply, regenerative strategies involving seed size, seed production and dispersion mechanisms, etc. However, Grime et al (1988) later seemed to somewhat revise the classification system described above to account for established plants only, whereas regenerative strategies were treated separately.

Silvicultural literature has often used the Clementsian viewpoint to predict and generalise the outcome of silvicultural treatments (e.g. Almgren & Brusewitz, 1990; Jäghagen & Sandström, 1994; Oliwer & Larson, 1996), since these treatments affect the supply of resources and resembles disturbance. A common approach in literature has also been to classify tree species according to single ecological characters like shade-tolerant – intermediate – shade-intolerant; or animal-dispersed – wind-dispersed; or small seed – large seed (Bormann & Likens, 1979; Oliwer & Larson, 1996). Brzeziecki & Kienast (1994) argued that the Grimian classification would be better for classifying forest tree species and used ecological attributes of north European tree species to ordinate them. This study discusses the use of the classification of tree species according to Clements or Grime respectively, and of single ecological characters, in order to predict the outcome of regeneration treatments. The following predictions of the outcome of natural regeneration using ecological categories and single characters may be hypothesised: Clear-cutting should favour pioneer, ruderal and shade-intolerant species whereas shelterwood should favour late successional, competitive, shade-tolerant and animal-dispersed species. Soil scarification should favour pioneer and ruderal species, and species with small seeds whereas late successional and competitive species, and species with large seeds should be less favoured or unaffected.

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## Objectives

The introduction above has shown that an increase of broadleaved trees is desired in southern Sweden and that natural regeneration may be a feasible regeneration method, but that additional knowledge is necessary. The objective of this study was to investigate the possibility of, and to expand the knowledge about, using natural regeneration to increase the proportion of broadleaved tree species in southern Sweden. The study focused on the processes "dispersal" and "establishment" (cf. Fig. 1) for broadleaved tree species in regeneration areas previously dominated by conifer species, although one study used broadleaved sites. The following specific hypotheses were addressed:

- The species composition in natural regeneration can be controlled with silvicultural treatments.

- The establishment of naturally regenerated seedlings is usually favoured by soil scarification, but tree species with small seeds are more favoured than tree species with large seeds.

- The effect of shelterwoods on the establishment of naturally regenerated seedlings is positive to shade-tolerant and animal-dispersed species.

- The seed dispersal of the studied tree species is different.

- The seed supply, which is a result of the seed source density and distribution, seed production and dispersal, interacts with silvicultural treatments and may sometimes overshadow the effect of these.

# Materials and methods

## Study sites

All sites used in this study, except the ones used in Paper V, were clearcuts or shelterwoods formerly occupied by coniferous stands. In Paper V, a beech and an oak site with clearcuts and shelterwoods were used.

Site productivity, soil texture and soil moisture for all study sites are given in Table 2. Dates of treatments, inventories and study periods for the study sites are shown in Figure 3, the locations of the sites are shown in Figure 4.

The mean annual temperature in southern Sweden varies between 5° C in the inland (300–400 m.a.s.l.) up to 8° C in the south. The mean temperature in January varies between -4° C and 0° C and in July between 15° C and 16° C. The mean

Table 2. *Descriptions of the study sites concerning site productivity, soil texture and soil moisture according to definitions by Hägglund & Lundmark (1977).*

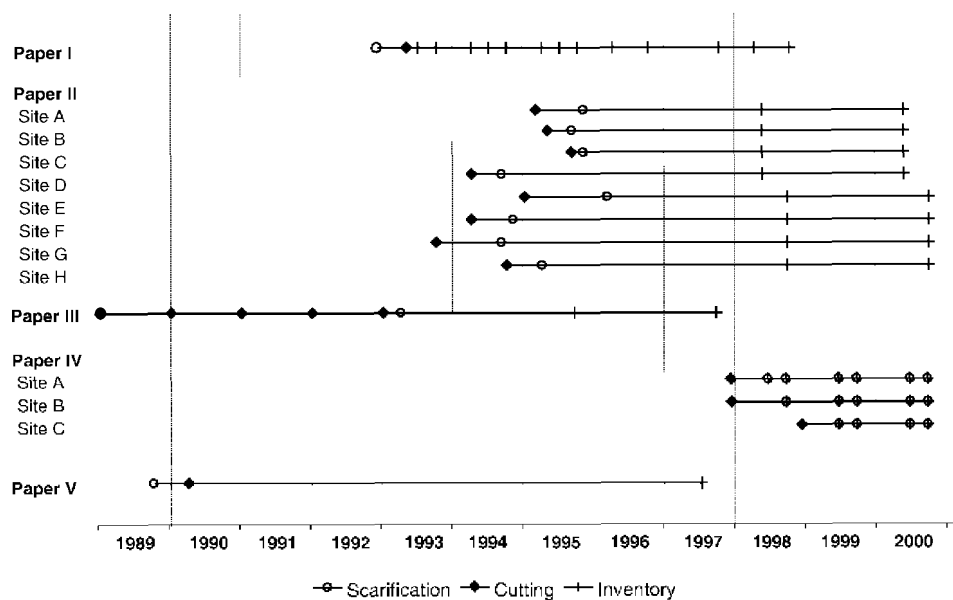| Paper | Site | $H_{100}$ | $m^3 \, year^{-1} \, ha^{-1}$ | Species | Soil texture | Soil moisture |
|-------|------|-----------|------------------|---------|--------------|---------------|
| | | | Site index/Productivity | | | |
| I | | 30 | 10.1 | spruce | coarse gravel | dry-mesic |
| II | A | 26 | 6.8 | pine | sandy silty till | mesic |
| | B | 26 | 6.8 | pine | sandy silty till | mesic |
| | C | 26 | 6.8 | pine | sandy silty till | mesic |
| | D | 24 | 5.9 | pine | sandy silty till | mesic |
| | E | 22 | 5.1 | pine | sandy till | dry |
| | F | 26 | 6.8 | pine | sandy silty till | mesic |
| | G | 25 | 6.5 | pine | clay-rich till | mesic |
| | H | 26 | 6.8 | pine | sandy silty till | mesic |
| III | 1 | 28 | 9 | spruce | silty sandy till | mesic |
| | 2 | 28 | 9 | spruce | sandy till | wet |
| | 3 | 31 | 10.7 | spruce | silty sand | dry |
| | 4 | 31 | 10.7 | spruce | silty sand | dry |
| IV | A | 33 | 12 | spruce | sandy till | mesic |
| | B | 32 | 11.3 | spruce | sandy till | mesic |
| | C | 32 | 11.3 | spruce | silty till | mesic |
| V | | 28 | 6.3 | beech | loam | mesic |
| | | 26 | 5.2 | oak | loam | mesic |



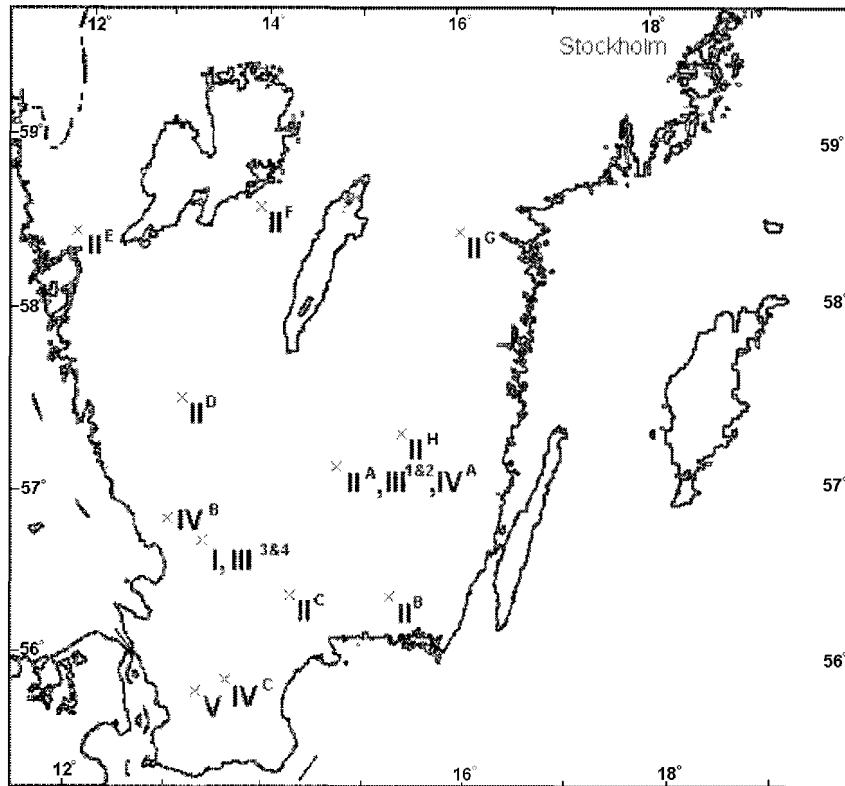*Figure 3* Dates for cutting and scarification at the study sites as well as seedling inventory occasions.

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*Figure 4* Locations for the study sites in southern Sweden.

annual precipitation varies from 500 mm year$^{-1}$ in the east up to 1,200 mm year$^{-1}$ in the west, but the range is normally between 600 and 1,000 mm year$^{-1}$. The prevailing wind directions are mainly westerly or south-westerly (Raab & Wedin, 1995). The mean length of the growing season (daily mean temperature >5° C) varies between 180 days and 240 days per year and the total mean temperature (total of daily mean temperature >5° C) varies between 1,100 and 1,500 day degrees (Nilson, 1996).

## Inventory methods

Seedling data (i.e. densities, distribution, growth, survival) were assessed on 1 m$^2$ quadrate plots (Papers I, II and IV) or circular plots (Paper III). In Paper V the inventory plots were rectangular (0.8 x 1.2 m). Furthermore, seedling densities for less common tree species in Paper II were assessed through strip inventories with an area of 330 to 540 m$^2$ per treatment combination. In Papers I, II and IV, seedlings in the inventory plots were mapped on a "seedling map" in order to enable reassessment for growth and survival estimates. In addition to seedling data, data for vegetation cover were assessed in the inventory plot in Paper I and in special plots (0.5 m$^2$) in Paper III. Seed-fall data were assessed with seed traps (0.25 m$^2$) in Papers I and IV.

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# Results and discussion

## Seed dispersal

### Short-distance dispersal

The found functions (negative exponential) for short dispersal of seeds by wind in Paper IV show that the dispersal efficiency could usually be predicted based on seed size and the occurrence of wings. However, the seed dissemination period seemed to improve the dispersal efficiency of maple seeds. The studied tree species were in the following order, starting with most easily dispersed species:

birch>elm=maple>alder>hornbeam>beech>(oak)

The importance of seed morphology for seed dispersal by wind is supported by earlier studies (Augspurger & Franson, 1987; Okubo & Levin, 1989; Willson, 1992)

### Long-distance dispersal

This study did not provide any direct estimates of long-distance seed dispersal. However, a approximate analysis was done by comparing the estimates of seedling densities in broadleaved species in Paper II (the mean based on all treatments and sites) with the proportion of these tree species in southern Sweden (i.e. Götaland). Birch was excluded because it occurs on or close to most sites, and beech was excluded since its distribution is restricted to the southern part of Götaland. The proportion was expressed as a percentage and calculated from the growing volume of each tree species in relation to the total growing stock in southern Sweden (Anon., 2000b). Thus, a "mean density" of naturally regenerated seedlings in all of southern Sweden could be compared to a "mean occurrence" of seed sources on a landscape scale in all of southern Sweden (Fig. 5), and the relative capacity for long-distance seed dispersal could be estimated. However, there are three major difficulties in this estimation: The tree species do not have the same source strength, i.e. different amounts of seeds are produced per tree unit. Furthermore, the tree species do not have the same success rate per seed. Finally, the tree species are not distributed in the same way in the landscape. Some species may be confined to special sites whereas others are more evenly distributed. These errors must certainly account for a part of the results shown in Figure 5 but with cautious interpretation some information can be derived: Alder and oak had low seedling densities in relation to the proportion of the growing stock compared to rowan, sallow, whitebeam and larch. The latter tree species could therefore be interpreted as having higher long-distance seed dispersal than the former. Although alder has wind-dispersed seeds, the efficiency was found to be intermediate (see section "short-distance dispersal"). Rowan and whitebeam are animal-dispersed just like oak. However, the two former species can be dispersed by more species and therefore be expected to have a more efficient long-distance dispersal. The seeds of sallow are very small and have a plume (Grime et al, 1988).
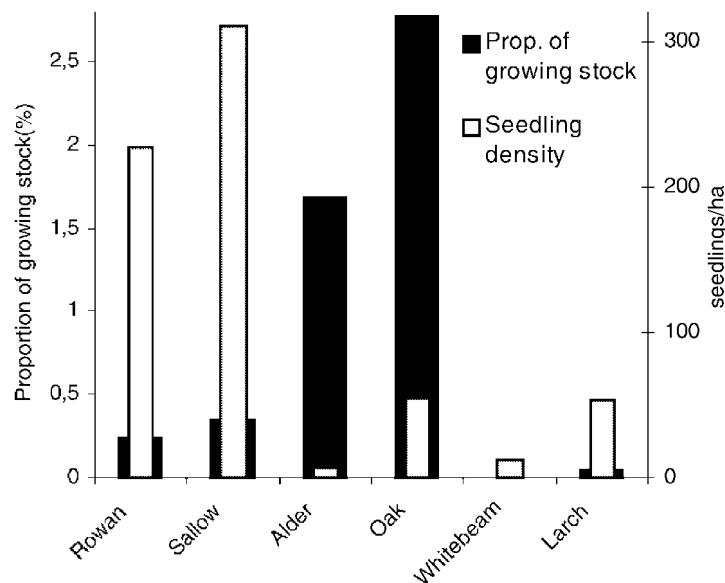
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*Figure 5*.Seedling densities for Stand-Enriching Tree Species in Paper II and their proportion of the growing stock in southern Sweden.

They are therefore expected to have highly efficient long-distance dispersal. The seeds of larch are wind-dispersed and winged but rather heavy. They were therefore not expected to have efficient long-distance dispersal.

## Variations in seed production

The size of the seed production per tree unit was not estimated in this study. However, variations in seed production between and within years could be seen from the seed rain data in Papers I and Paper IV, since they were compiled over several periods within each year and over several years. The production of birch seeds was ten times higher in 1993 compared to subsequent years as indicated by seed-fall data from 1993 to 1997 in Paper I (Fig. 6). Seed-fall data from 1998 to 2000 in Paper IV show that the production of seeds from broadleaved species was low in 1999, except some seed-fall of birch and alder in site C (Fig. 7). This irregularity between years in the seed production of birch has previously been found by e.g. Koski & Tallqvist (1978). According to Sarvas (1948) the germinability of birch seeds is higher in years with high seed production, something which should increase the variability. Masting of beech occurred in 1998 and weaker masting in 2000. For oak, masting was strong in 2000 (Fig. 7). The seed-fall period for the tree species within each year shows clear patterns: The seed-fall of elm peaks in early summer whereas birch seed-fall peaks in August – although it continues with declining intensity during autumn. The seed-fall of alder occurred during all autumn and winter. Beech,

*Figure 6.* Seed-fall for birch in the S275 shelterwood in Paper I.

oak and maple seed-fall peaked in October while the seed-fall of ash and hornbeam seemed to occur over a somewhat longer period in the autumn. These findings generally correspond to existing knowledge of seed dissemination periods (Almgren, 1986; Suszka et al, 1996) except for birch seed-fall in northern Sweden, which has been found to peak in September (Fries, 1984).

## Establishment – effects of silvicultural treatments

By manipulating the conditions that control the "establishment" process (cf. Fig. 1) including seed germination and seedling growth and survival, it may be possible to control the success of natural regeneration with silvicultural treatments. None of Papers I-V contain an explicit estimation of the germination success, since the time between germination and inventory was too long – from some months in Paper IV to eight years in Paper V. Therefore, the seedling density at the time of inventory, a figure which constitutes an integration of germination and survival until the time of inventory, is used to indicate establishment success. Data on growth and survival are available in Papers I and II. These are also measures of the establishment success. Furthermore, the possibility of controlling the tree species composition with pre-commercial thinning is discussed.

### Soil scarification

Seedling densities

The seedling densities of birch, which is the only species occurring as natural regeneration on all sites, were generally more than 2,000 per hectare (Table 3). The effect of scarification on birch establishment was positive in most studies. In Papers I, III and IV, the positive effect of scarification on birch densities was also statistically
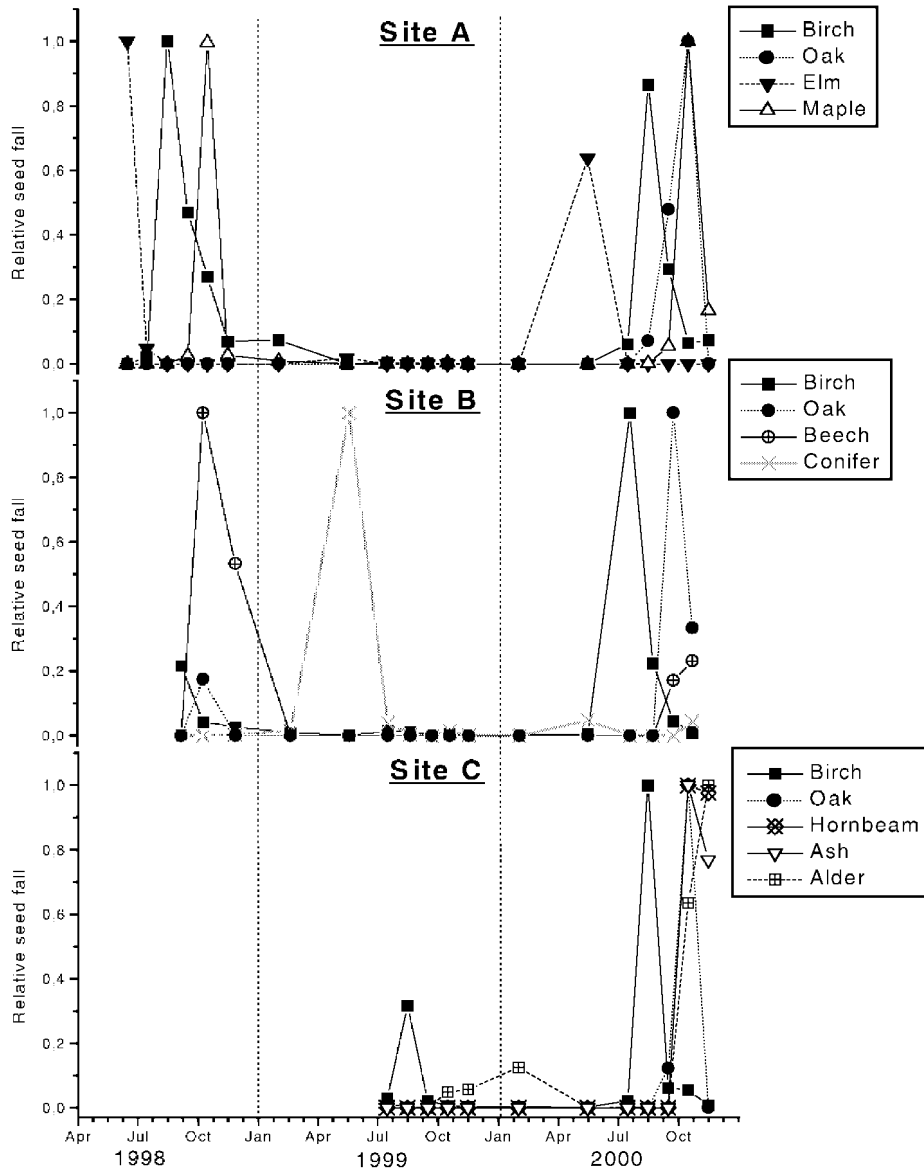
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*Figure 7*. Seed-fall data from the study in Paper IV. The relative seed-fall is the average seed-fall per trap and period in relation to the maximum average seed-fall per trap and period per tree species and site, for respective tree species and site.

significant (p<0.05). The positive effect of soil scarification, bare mineral soil and disturbed ground on establishment has been shown by many previous studies on silver birch and hairy birch (Sarvas, 1948; Hagner, 1962; Kinnaird, 1974; Raulo & Mälkonen, 1976; Fries, 1984; Palo, 1986; Karlsson, 1996a; Karlsson et al, 1998; Björse, 2000) as well as on the taxonomically close North-American species Paper

birch (*Betula papyrifera* March.) (Marquis et al, 1964; Perala & Alm, 1989; Prévost, 1997; Carlton & Bazzaz, 1998). Therefore, the most interesting results from the soil scarification treatment were the negative results in the clearcut (Paper II) and the sparse shelterwood (Paper V). This clearly shows that soil scarification does not always result in increased seedling density when regenerating birch. The reason that scarification can not be pointed out. However, the positive scarification effect in Papers I, III and IV occurred on bare mineral soil created shortly before a seed-fall in a year with high seed production (1993 – cf. Paper I). One possible reason for the negative scarification effect in Paper II can be that the scarification treatments were done just after the rich seed-fall in 1993 on several of the study sites (cf. Fig. 3). The seeds received and the seedlings established from the were established from the seed-fall, may have been removed, buried or destroyed by the scarification, whereas seeds and seedlings in the undisturbed ground were left to develop. If the birch seed production was low during following years, the scarified ground may have been degraded and colonised by field vegetation before a good seed-year occurred. This may be an explanation to the negative scarification effects, at least if the climatic conditions were favourable to establishment on undisturbed ground. Additional explanations for negative scarification effects may be the presence of favourable undisturbed moist ground and advance regeneration. Furthermore, when the sites are wet and there is favourable undisturbed and moist ground, the scarified seed-bed may be too wet, causing oxygen deficit to the seedlings (Örlander et al, 1990). Another reason may be frost heaving occurring on the scarified seed-beds (Goulet, 1995; Karlsson, 1996b; Carlton & Bazzaz, 1998). However, frost heaving, wet sites and advance regeneration were considered less important in Paper II compared to the importance of scarification timing versus seed-fall. The timing of scarification versus seed-fall shows that the interaction between seed abundance and favourable seed-beds (cf. LePage et al, 2000) must be considered in order to accomplish an apposite establishment result. However, this explanation of mismatching seed-fall and scarification timing may probably not hold true for the negative scarification effect in the sparse shelterwood in Paper V. The data in Paper V were rather small and probable explanations for the negative scarification effect could therefore be spatial variability of some factors: The undisturbed plots in Paper V may have had spots of favourable moisture conditions, known to exist on undisturbed ground (Perala & Alm, 1990), or patchy presence of advance regeneration.

The effect on birch establishment on different forms of seed-beds obtained through soil scarification was studied in Paper I and IV. The berms that was created in Paper I was turned organic layer and mineral soil, but since scarification was done by double crosswise passing, the berms were mixed with mineral soil and mostly in level with other ground surface. Therefore, the berms were comparable with the mixing treatment in Paper IV. In Paper I, the berms did not have higher birch densities than the undisturbed ground in the clearcut. In Paper IV, the mixing treatment increased the birch density compared to the undisturbed control but not significantly and less than the bare mineral soil. It has previously been shown that a mixture of

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Table 3. *Seedling densities (seedlings ha⁻¹) for birch in the included papers.*

| Paper | Clearcut Undisturbed | Clearcut Soil scarification | Sparse shelterwood (10-15 m² basal area) Undisturbed | Sparse shelterwood Soil scarification | Dense shelterwood (18-25 m² basal area) Undisturbed | Dense shelterwood Soil scarification | Uncut stand (28 m² basal area) Undisturbed | Uncut stand Soil scarification | Year of inventory |
|---|---|---|---|---|---|---|---|---|---|
| I | 5 000 | 13 900[A] (2 900)[B] | 4 400 | 18 800[A] (25 600)[B] | 1 900 | 16 900[A] (16 300)[B] | 300 | 12 300[A] (3 700)[B] | 1997 |
| II | 14 400 | 6 100 | 3 200 | 16 900 | | | | | 2000 |
| III | 3 000 | 19 400 | | | | | | | 1997 |
| IV | 2 100 | 15 000[A] (11 400)[C] | | | | | | | 2000 |
| V[D] | 4 100 | 19 800 | 13 500 | 8 200 | 2 000 | 3 400 | | | 1997 |

[A] Density is data on bare mineral soil
[B] Density is data on berms
[C] Density is data on mixed organic layer and bare mineral soil
[D] Densities are the mean for the oak and beech sites

the organic layer and the mineral soil is less favourable to the establishment of naturally regenerated birch seedlings than bare mineral soil (Raulo & Mälkonen, 1976). The scarification in Paper III was mounds on mineral soil, a method which is known to be less favourable and produce a drier seed-bed than flat and bare mineral soil (Örlander et al, 1990; Carlton & Bazzaz, 1998). The positive scarification effect found in Paper III may have been caused by climatic conditions that made the mounds humid enough for germination and growth of the small birch seedlings. Another explanation may be that seeds were gathered (through secondary dispersal) in the pits around the mound (c.f. Carlton & Bazzaz, 1998), a microsite that probably was better for seedling establishment than the top of the mounds.

The effect of scarification on other broadleaved tree species than birch was variable (Table 4). The only significant effect was for sallow in Paper II and for maple and alder in Paper IV. For maple and alder, the findings are supported by Seiwa & Kikuzawa (1996) for other species of the same genera. The density of beech was higher on bare mineral soil in Paper IV, although the effect was not significant. This was believed to be caused by the scarce dispersion of seeds into the clearcut, which resulted in few plots where seedlings could be established, rather than a lack of positive scarification effect, since such effects have been documented in earlier studies (Huss et al, 1972; Röhrig, 1975, Agestam et al, 2001), and was supported by higher densities in scarified plots in the beech site in Paper V. Aspen, hornbeam and wild cherry had higher densities in soil-scarified areas in Paper V, although the effects were unclear and not statistically tested because of too few values. Rowan and oak occurred in Paper II and in both sites in Paper V, but the densities were not increased in either study. This suggests that scarification is not favourable to the

establishment of rowan or oak. It is likely that this is an effect of the seed size and/ or dispersal mechanisms. It has been shown that species with a large seed reserve may show higher establishment on litter than species with small seed reserves (Marquis, 1975; Sciwa & Kikuzawa, 1996). Furthermore, since rowan and oak are animal-dispersed (Grime et al, 1988), the seeds may be cached in the soil, as for oak (Darley-Hill & Johnson, 1981; Kollmann & Schill, 1996), or ingested and defecated, as for rowan. This "dispersal effect" may result in establishment that is less dependent on ground conditions, something which has been shown for oak (Kollmann & Schill, 1996).

In general, the scarification effect on low-frequent tree species, like the Stand-Enriching Tree Species in paper II, were not visible. This is probably influenced by a low seed supply, owing to low amount of seed source, low seed production or low seed dispersal.

Considering the conifer establishment in Papers I, II and III, the scarification effect was significantly positive for both spruce and pine, except for spruce in Paper II. The positive scarification effect on spruce and pine establishment is well supported by other studies (Hagner, 1962; Béland et al, 2000; Karlsson & Örlander, 2000)

The density of the advance regeneration of birch observed in Paper II was lowered by the scarification treatment in the clearcut treatment. It is known from previous studies that scarification may destroy parts of the advance regeneration (Prévost, 1997; Björse, 2000).

Growth and survival

The growth estimates in Paper I can be analysed as seedling height five years after scarification. However, the analysis of birch and pine could not be done due to few values. For spruce, the height growth was lower in scarified areas. The reason for this can not concluded but possible reasons may be lower nutrient availability in the scarified ground (Nohrstedt, 2000) or higher browsing pressure. The height increment in Paper II did not show any significant effects of scarification treatments for either birch, pine or spruce. However, after the first inventory (1998), pine seedlings were significantly higher in scarified plots than in undisturbed plots, but this difference was not visible in the later inventory (2000). No effects on the height of birch and spruce were observed.

The survival of spruce was higher on bare mineral soil than undisturbed ground in Paper I, whereas the survival of birch and pine was unaffected. These findings may be an effect of a decreased attack of pine weevil on seedlings in scarified ground (Örlander & Nilsson, 1999). This would also explain the lack of effect on birch, since pine weevil damage on broadleaved tree species is less serious than on spruce (Löf, 2000). In Paper II, the survival of birch, pine and spruce between the inventory occasions was unaffected by scarification.

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Table 4. *Effects of scarification and shelterwood on the establishment of broadleaved tree species (except birch) found in Papers II, IV and V. The signs (+, - or 0) mean increased, reduced or equal seedling density caused by the treatment. A double sign (++) indicates a statistically significant (p=0.05) effect.*

| Tree species | Paper II | | Paper IV | Paper V | | | |
|---|---|---|---|---|---|---|---|
| | | | | Scarification | | Shelterwood | |
| | Scarification | Shelterwood | Scarification (bare mineral soil) | oak site | beech site | oak site[A] | beech site[A] |
| Aspen | | | | + | + | 0 | 0 |
| Beech | 0 | + | + | 0 | + | | |
| Common alder | 0 | 0 | ++ | | | | |
| Hornbeam | | | | 0 | + | | + |
| Norway maple | | | ++ | | | | |
| Oak | 0 | + | | 0 | 0 | | |
| Rowan | 0 | ++ | | 0 | 0 | 0 | + |
| Sallow | ++ | 0 | | 0 | 0 | - | 0 |
| Swedish whitebeam | 0 | + | | | | | |
| Wild cherry | 0 | + | | + | - | | |

## Shelterwood

### Seedling densities

The seedling densities of birch were lower in the densest shelterwoods, at least on undisturbed ground, compared to clearcuts and sparse shelterwoods (Table 3). No evident differences were observed in birch seedling density between sparse shelterwoods and the clearcuts. These findings somewhat correspond to Hagner (1962), who found a tendency for decreasing seedling density with increasing shelterwood density. However, Holgén & Hånell (2000) found no influence on birch seedling density from increased shelterwood density. For Paper birch (*Betula papyrifera* Marsh.), however, it has been shown that shady environments provide favourable moisture conditions for early establishment, although later growth is reduced. Therefore has shelterwoods, which should been removed after a short period, been proposed as a method to regenerate Paper birch (Marquis et al, 1964; Perala & Alm, 1989). A stronger negative influence by shelterwoods was expected in Papers I, II and V, since the birch species are considered shade-intolerant. However, this study can not evaluate why shelterwoods had no or very little effect, but it may be the same reasons as described for Paper birch above.

In Paper II, the seedling densities of rowan showed a statistically significant increase by shelterwood treatment. Higher densities of rowan in the shelterwoods were also observed in Paper V. Vanha-Majamaa et al (1996) found higher seedling densities of rowan where residual trees were left uncut. They suggested that the trees functioned as a preferred environment to the birds dispersing the rowan seeds.

This study supports this hypothesis; the shelterwoods may have provided a preferred environment to the dispersing birds. Since rowan is a shade-intolerant species, seedlings can not considered to suffer from the clearcut environment or benefit from the shelterwood. Although not statistically proven, the seedling densities of beech, oak and whitebeam were higher in the shelterwood treatment in Paper II. Since beech is considered a shade-tolerant species, higher densities were expected in the shelterwood. On the other hand, both oak and whitebeam are considered shade-intolerant. For these species, the dispersal mechanism (animal) may hence be a better explanation for the higher density in the shelterwoods, as for rowan.

The shelterwood effect on the conifer establishment found in Paper I shows a significant positive effect for spruce whereas no effect was found for pine. In Paper II, the shelterwood significantly increased the seedling density of pine but the effect of shelterwood on the physical conditions and the seed supply respectively can not be separated. However, the higher pine seedling densities are partly an effect of a larger seed supply to the ground in the pine shelterwoods. In general, the shelterwood effect was positive for the conifer establishment, as found in previous studies (Hagner, 1962; Holgén & Hånell, 2000)

Growth and survival

The growth estimates in Paper I show a reduction with increasing shelterwood density for spruce, pine and birch. However, birch was higher in the most sparse shelterwood (S95) than in the clearcut. In Paper II, the height of the pine seedlings was significantly decreased by the shelterwood treatment, whereas the height increment was unaffected between the inventory occasions. No effect on height or height increment for birch or spruce was found in Paper II. In Paper V, a decreasing effect of shelterwood treatment can be observed as lower seedling heights in the shelterwoods. Reduced growth in shelterwoods is known from earlier studies (Hagner, 1962)

Regarding survival in shelterwoods, Paper I shows that the survival of birch seedlings decreased with increased shelterwood density, while the survival of spruce seedlings was lower in the clearcut than in the shelterwoods. No shelterwood effects on the survival between inventory occasions were found in Paper II.

*Interaction between scarification and shelterwood*

Paper II shows a negative scarification effect for birch in the clearcut and a positive effect in the shelterwood. The negative effect in the clearcut may be explained by destruction of seeds and seedlings occurring prior to treatment and that low amounts of seeds may have been received by the fresh scarified ground. The positive scarification effect in the shelterwood could be explained by the fact that the resource supply was too low for the seedlings in undisturbed plots in the shelterwoods, resulting in high mortality and low seedling densities. Furthermore, the scarified ground in the shelterwoods could have remained susceptible to seedling establishment owing to delayed ingrowth of field vegetation. The scarified ground may also have served

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the seedlings with a higher resource supply than the undisturbed ground in the shelterwood, resulting in a higher survival. Hence, a rich seed-fall some years after scarification would still contribute seeds that could be established in the scarified ground. An illustration of this hypothesis is shown in Figure 8. If this hypothesis is true, this would mean that when no information of yearly seed production is available, the best way to establish high densities of birch would be to scarify in a sparse shelterwood. Since no prognosis tools for birch seed production exist to my knowledge, the scarification/sparse shelterwood combination may be regarded as convenient. The scarified ground in the shelterwoods in Paper I had slightly higher densities of birch seedlings than the scarified ground in the clearcut, whereas the densities on undisturbed ground were equal or lower in shelterwoods compared to the clearcut. This may indicate that bare mineral soil is a better seed-bed for seedling establishment in shelterwoods than in clearcuts (cf. Marquis et al, 1964). Furthermore, the birch seedling densities on berms (mix of organic layer and mineral soil) in Paper I were low in the clearcut, while the berms in the sparse and dense shelterwoods had about the same densities as the mineral soil. It is possible that a more humid environment in the shelterwoods would have reduced the drying out of the surface soil in the mixed seed-beds.
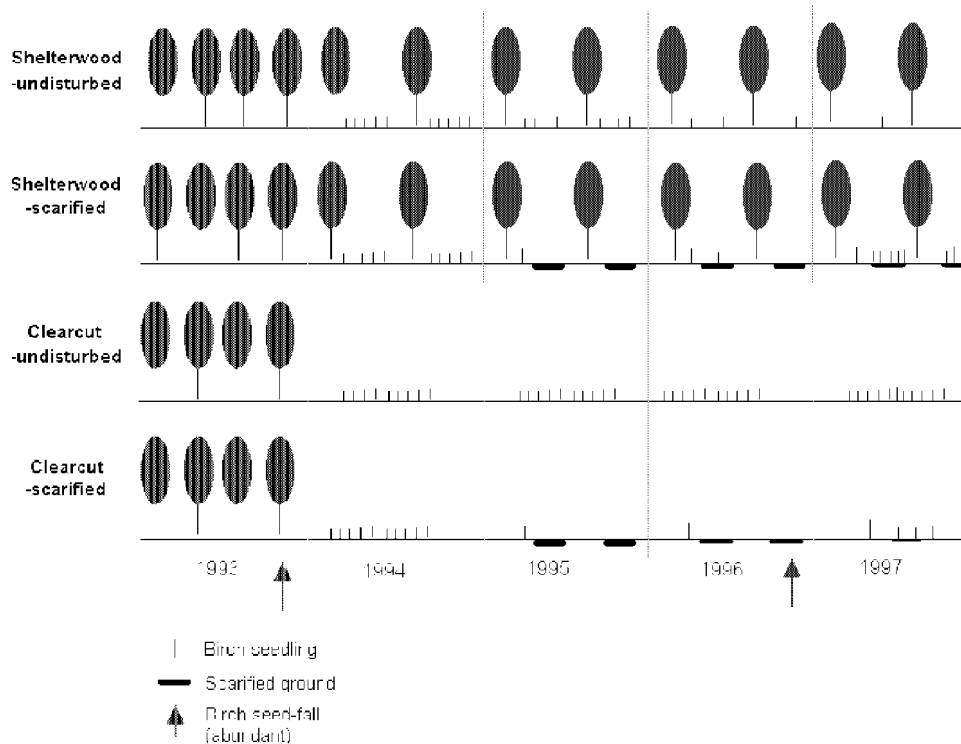


Figure 8. An explanatory figure for the interaction effect of scarification and shelterwood in Paper II, resulting in higher birch seedling densities in the undisturbed clearcut and the scarified shelterwood than in the scarified clearcut and the undisturbed shelterwood.

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## Clearcut age

The effect of clearcut age was investigated in Paper III. In undisturbed control plots and scarified plots, birch seedling densities were not significantly different between clearcuts of different age. Therefore, it may be concluded that only the timing of clear-cutting to an abundant seed-fall does not ensure higher seedling establishment. Unexpectedly, fewer birches were established in the fresh, scarified and undisturbed clearcuts than in one-year-old and older clearcuts, although not statistically proven. This could possibly indicate that high pine weevil abundance caused higher mortality in the fresh clearcut or that the field vegetation in older clearcuts provided better establishment conditions in the scarified plots through shading, and therefore higher soil moisture availability (cf. Marquis et al, 1964). In Paper III, neither seedling densities of spruce and pine showed any significant effects of clearcut age.

## Slash removal

The slash removal treatment in Paper III increased the birch seedling density and also the pine seedling density, although this was not statistically proven. Few other studies dealing with the effect of slash removal on natural regeneration were found. Boe (1956) found lower densities of Lodgepole pine (*Pinus contorta*) in concentrated slash than on the forest floor or scarified ground, but there was no difference when the slash was lopped and scattered. Concerning direct seeding, however, Tamm (1947) found higher pine seedling densities with slash removal. The observed positive effect in this study may be due to the fact that slash removal resulted in more disturbed ground and possibly also that the slash acted as a physical barrier.

## Fencing

The study sites in Papers I, II and III were not fenced, whereas the sites in Papers IV and V were fenced. None of the papers estimated the importance of browsing or absence of browsing. Although not presented in Paper IV, this study included scarified and undisturbed plots that were established just outside the fence. They could therefore be compared to plots treated the same way but just inside the fence, only a few meters away from the unfenced plots and with about the same seed supply. Only birch was analysed, since it alone occurred in large densities on all three sites. The General Linear Model (GLM) procedure for split plot designs of SAS (SAS Institute Inc., 1998) was used to perform statistical tests of birch seedling density and height. The model was:

$$Y = m + a_i + b_j + (ab)_{ij} + c_k + (bc)_{kj} + e_{ijk}$$

where m is the general mean, $a_i$ is the effect of the site, $b_j$ is the effect of the fencing treatment, $c_k$ is the effect of the scarification treatment, $(bc)_{kj}$ is the interaction effect of scarification and fencing, and $ab_{ij}$ and $e_{ijk}$ are error terms. The birch seedling densities analysed were the seedlings estimated to have germinated after the time of scarification and until autumn 1999 and still alive in autumn 2000. The birch seedling height was the height of these seedlings in autumn 2000.

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No effect on birch seedling height was found and the overall average seedling height was 20 cm. The birch seedling density was positively affected by fencing (p=0.0287) with 2.0 seedlings m$^{-2}$ in unfenced plots and 3.1 seedlings m$^{-2}$ in fenced plots. No significant scarification or interaction effect was found. A positive effect of fencing on the density of naturally regenerated birch seedlings has also been found by Hess et al (1996), but contradictory results have been presented by Björse (2000), who found larger birch densities in unfenced clearcuts. An explanation to the contrasting results may be that the present study was conducted in a landscape dominated by conifers, whereas Björse's site (2000) was situated in a surrounding dominated by broadleaves. An explanation used by Björse (2000) for the negative effect of fencing on birch density was that the dense field vegetation inside the enclosure might have been an obstacle to the seedlings. In the present study, the field vegetation in the enclosures was denser but also had a different species composition than outside the fence, where the vegetation was dominated by grasses. Inside the enclosures, the field vegetation had a higher percentage of herbs, e.g. *Rubus ideus* and *Epilobium angustifolium*. Therefore, the effect of fencing on birch densities may partly be explained by different competition or environmental conditions caused by the field vegetation inside and outside the fence. However, it is most likely that browsing on seedlings was also influencing the result, since browsing damage was observed on the seedlings on sites B and C. Another factor that may have affected the results was that the non-fenced plots were just outside the fences, and the movement of animals may therefore have been higher around the unfenced plots.

### Pre-commercial thinning

In Paper V, pre-commercial thinnings were simulated in young mixed broadleaved stands. The pre-commercial thinnings were simulated to achieve two different goals of the future mixed stand: timber production or maximised tree species diversity. The stands were established with or without combinations of scarification and shelterwood. This enabled an evaluation of the effect of regeneration treatments to achieve *a priori* stand goals. A majority of the stands were judged to be able to achieve the goals after pre-commercial thinnings and only two out of twelve cases were regarded as failures. However, differences in mean height after the simulated cuttings indicated that different regeneration treatments were more or less efficient in achieving the goals. Therefore, this study shows that the possibility to attain the *a priori* set stand structure is highly influenced by various combinations of regeneration treatments.

An approach similar to the one above may be discussed concerning planting of spruce and the establishment of naturally regenerated birch seedlings, i.e. to use regeneration treatments and pre-commercial thinning as a combined tool in order to reach a desired stand structure. This thesis has shown that it may be possible to establish large densities of birch seedlings with scarification and slash removal, given an adequate seed supply. If a forest manager would like to establish a mixed

spruce/birch stand or if the probability for mortality of the planted spruce seedlings is high due to e.g. frost damages or pine weevil attacks, then scarification and slash removal should be done to promote natural regeneration of birch. Later, when the success of planting and natural regeneration may be evaluated, the horizontal and vertical stand structure can be adjusted through pre-commercial thinning to reach a stratified spruce/birch stand with birch in higher height classes, or a one-layered mixed stand. By contrast, if the desired stand structure is a pure spruce stand and the probability of mortality for the planted spruce is low, scarification and slash removal should be avoided.

Another aspect of the establishment of mixed species stands was discussed in Paper I, where it was concluded that mixed stands of spruce, pine and birch could be established with a sparse shelterwood and soil scarification. These treatments encourage the establishment of all three species, but pre-commercial thinning was regarded as necessary to adjust the species composition.

A possible desired stand might contain low-frequent tree species like the Stand-Enriching Tree Species in Paper II. This thesis has shown that the possibility of controlling the natural regeneration of these low-frequent tree species is limited due to low seed supply. However, pre-commercial thinning offers a way to favour individuals of these rare tree species and hence increase the possibility for the tree species to be a component in a future stand. Several of these tree species, e.g. oak, are also sensitive to competition and may need repeated pre-commercial thinning to develop.

## Predicting natural regeneration using ecological strategies and characters

In Paper V, seedling density and height were used to estimate the dominance of tree species in the clearcut and shelterwoods. Based on this, ruderal species were found to dominate the clearcuts and competitive species in the dense shelterwood. The ruderal species that dominate in the clearcut are also regarded as pioneer species. Since oak is most often considered a pioneer species (Table 5), one would expect oak to be favoured by clear-cutting and disfavoured by shelterwood, but this was not the case in Papers II and V. Hence the Clementsian view seems less successful than the Grimian model in predicting the shelterwood effect on natural regeneration. Rowan is considered a ruderal as well as a pioneer species, but was not favoured by clear-cutting in either Paper II or V. Furthermore, Paper II showed that the group of animal-dispersed Stand-Enriching Tree Species tended to have a higher density in the shelterwood treatment. Out of these species, only beech may be considered as shade-tolerant. The positive shelterwood effect may therefore be explained by the dispersal mechanism (animal) and/or the seed size. A relationship between seed size and shade tolerance has been found for North-American broadleaved tree species (Hewitt, 1998). Even if this relationship may not be stated for broadleaved tree species positively affected by a shelterwood in this study, it may be stated for the

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Table 5. *Ecological categories and single ecological characters for the broadleaved tree species studied in the present thesis.*

| | Ecological categories | | Single ecological characters | | |
|---|---|---|---|---|---|
| | Grimian model[A] | Clements' model[B] | Dispersal agent[C] | Shade tolerant/ intolerant | Seed size (seed weight)[D] |
| *Acer plataniodes* L. | Competitive | Intermediate /Gap species | Wind | Tolerant | Large (140 mg) |
| *Alnus glutinosa* (L.) Gaertner | Ruderal | Pioneer | Wind-Water | Intolerant | Small (1.1 mg) |
| *Betula pendula* Ehrh. / *B. pubescens* Roth. | Ruderal | Pioneer | Wind | Intolerant | Small (0.15/0.12 mg) |
| *Carpinus betulus* L. | Competitive | Climax | Wind | Tolerant | Large (40 mg) |
| *Fagus sylvatica* L. | Competitive-Stress tolerant | Climax | Animal | Tolerant | Large (250 mg) |
| *Populus tremula* L. | Ruderal | Pioneer | Wind | Intolerant | Small ( no data ) |
| *Prunus avium* L. | Stress tolerant-Ruderal | Pioneer(?) | Animal | Intolerant | Large (150 mg) |
| *Quercus robur* L./ *Q. petrea* (Matt.) Liebl. | Competitive-Stress tolerant | Pioneer(?) | Animal | Intolerant | Large (4,000/3,000 mg) |
| *Salix caprea* L. | Ruderal | Pioneer | Wind | Intolerant | Small (0.09 mg)[F] |
| *Sorbus aucuparia* L.[E] | Stress tolerant-Ruderal | Pioneer | Animal | Intolerant | Small (2.58 mg)[F] |
| *Ulmus glabra* L. | Competitive | Climax | Wind | Tolerant | Small (3.5 mg)[F] |

[A] According to Brzeziecki & Kienast (1994)
[B] According to various sources
[C] According to Grime et al (1988)
[D] Data for seed weight from Suszka et al (1996) (Small <10 mg; Large >10 mg)
[E] Including S. intermedia since no data are available
[F] Data for weight of germinule (Grime et al, 1988)

tree species positively influenced by the clearcut, i.e. species with small seeds which also are shade-intolerant.

The scarification effect was positive for most tree species in the present study and negative for none. Therefore it is more difficult to evaluate the effect on different species, e.g. a more positive effect of scarification on ruderal species was expected, but not found. However, in both Papers II and V, rowan and oak were unaffected by scarification treatments. This could be interpreted as an effect of the dispersal mechanism for both species and the seed size for oak. Furthermore, the wind-dispersed group of Stand-Enriching Tree Species in Paper II was positively affected by scarification but not the animal-dispersed group. However, this can be interpreted as an effect of the small seed size of wind-dispersed species rather than the dispersal mechanism (wind). The influence of seed size on the effect from scarification has previously been found by Marquis (1975) and Seiwa & Kikuzawa (1996).

The discussion above shows that ecological categories like the ones included in the Clementsian or Grimian theory may predict the outcome of treatment effects on

natural regeneration, at least for the clearcut/shelterwood reactions. However, these predictions contain several exceptions, which may instead be better explained by single characteristics of the species in question. In every categorisation, one has to generalise the species' ecology, and this produces general answers. It is questionable if general answers are good enough for silvicultural aims. If the tree species' single ecological characters are used, less general and more precise knowledge is obtained. However, the original aim of this study did not include an evaluation of ecological knowledge, and a thorough evaluation should include a more systematic design for this purpose.

# Conclusion

This thesis shows that silvicultural treatments can to some extent be used to control the species composition of the natural regeneration, but since the effect of regeneration treatments is quite course and only can be used to increase or decrease a species' occurrence, pre-commercial thinning and possibly complementary planting will often have to be used to reach a target stand structure. The establishment of naturally regenerated seedlings was in general found to be promoted by soil scarification and only indications of stronger positive scarification effects on tree species with small seeds than on tree species with large seeds were found in the present study. The effects of shelterwood on the establishment of naturally regenerated seedlings were found to be positive for animal-dispersed species, but not necessarily for shade-tolerant species. Clear-cutting was found to favour shade-intolerant species. However, a sparse shelterwood did not decrease the birch seedling densities and may therefore be used to establish birch if other effects of a shelterwood are desired. The wind dispersal of seeds of the studied tree species was found to be clearly different between tree species and could in general be explained by seed morphology. The effect of silvicultural treatments was influenced by seed supply, which results from seed source density and distribution, production and dispersal. The effects of seed supply did in some cases overshadow the effects of treatments. This was notable in the lack of scarification effects on beech in Paper II due to low dispersal efficiency, and scarce treatment effects on the Stand-Enriching Tree Species in Paper II due to low seed supply. The confounding effect of scarification on birch establishment in Paper II was also believed to have been affected by the timing of seed supply in relation to scarification.

In conclusion, this study shows that silvicultural treatments can be used to establish and control natural regeneration after considering the surrounding seed sources and the variation in seed production and dispersal in time and space.

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