# Seed Production and Natural Regeneration of Beech (*Fagus sylvatica* L.) in Southern Sweden


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Cover: Newly established beech seedlings
(photo: R. Övergaard)

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## Abstract

When mature beech forests are harvested, the new regeneration is established by natural regeneration, which is by using the seeds from the old stand to create the new generation. Most often the seed from a single mast year is used preceded by site preparation. After seed-fall, a heavy thinning in the old stand is performed, leaving a protective shelter. Sometimes an alternative, less intense regeneration method is used, which involves the use of seed from several mast years and no site preparation. These methods usually result in adequate regenerations but sometimes failures occur in old stands with a low site index, a thick humus layer, and acid soils.

The occurrence of mast years and the size of the seed production in them are important factors when working with natural regeneration. The mean interval between mast years has been about five years since the end of the 17$^{th}$ century, but during the last 30 years this has decreased to 2.5 years. Seed production increased with increasing site index and mast years were usually preceded by a warm and dry July in the previous year.

An alternative, more extensive regeneration method is currently sometimes used in southern Sweden. The method has both economic and ecological advantages. Seed from several mast years are used and instead of site preparation, several judicious cuttings are made in the old stand in order to regulate the conditions of the forest floor in a way that promotes the establishment and growth of the new seedlings. The regeneration dynamics have been studied and documented and the method has resulted in good regenerations, independent of site index.

However, regeneration failures sometimes occur at old sites with low fertility and a low pH. In Europe, liming is an option to overcome these difficulties. To study the effect of liming, 12 sites in southern Sweden were limed in 1991 and 1993, and in 2007 three of these were regenerated using the traditional method, and three were regenerated with the alternative method. Neither the sizes of the seed-falls nor the height growth of new seedlings were influenced by liming. When the traditional method was used, liming improved the regeneration result in a stand of low site index, while the opposite effect was found in a stand of high site index. Seedling survival, the size of earthworm populations, and the concentrations of a potential defensive compound in seedling leaves, chlorogenic acid, all increased after liming.

In the alternative regeneration method, the numbers of germinates developing in years following mast years was negatively affected by liming in the first six years after liming. Thereafter the effect was positive. Liming shortens the regeneration period and increases the number of seedlings.

*Keywords:* Natural regeneration, *Fagus sylvatica*, mast year, seed production, extensive natural regeneration, site preparation, shelter, liming, earthworm, defensive compound.

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# Dedication

To my family, and to my friends, for always supporting me.

*Better late than never!*

# Contents

# List of Publications

This thesis is based on the work reported in the following papers, referred to by the corresponding Roman numerals in the text:

I Övergaard, R., Gemmel, P. and Karlsson, M. (2007). Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* 80(5), 555-565.

II Övergaard, R., Agestam, E., Ekö, P-M. and Johansson, U. (2009). A Method for Natural Regeneration of Beech (*Fagus sylvatica* L,) practiced in Southern Sweden. *Studia forestalia Suecica* 218, 1-30.

III Övergaard, R., Gemmel, P., Welander, N. T. and Witzell, J. (2009). Effects of liming on site properties and natural regeneration of European beech *Fagus sylvatica* L. in southern Sweden. *Ecological Bulletins*, accepted.

IV Övergaard, R., Gemmel, P. and Welander, N. T. Improving an alternative method for natural regeneration of beech (*Fagus sylvatica* L.) by liming in Southern Sweden. *Manuscript.*

Papers I-III is reproduced with the permission of the publishers.

The contribution of Rolf Övergaard to the papers included in this thesis was as follows:

I Övergaard and Gemmel were responsible for the experimental design. Övergaard was the corresponding author and the main author responsible for writing the text with contributions from the other authors. Övergaard was responsible for the field work; Karlsson and Övergaard were jointly responsible for processing the data.

II All authors were jointly responsible for the experimental design. Övergaard was the corresponding author and the main author responsible for writing the text, executing the field work and processing data, with contributions from the other authors. Photos were taken by Agestam and Ekö.

III Övergaard and Gemmel were responsible for the experimental design, Övergaard for the field-work (including sample collection) and data processing. Witzell was responsible for the chemical analyses. Övergaard was the corresponding author and the author mainly responsible for writing the text, with contributions from the other authors.

IV Övergaard and Gemmel were responsible for the experimental design. Övergaard was the corresponding author and the author mainly responsible for writing the text with contributions from the other authors. Övergaard was responsible for the field-work and data processing.

# Abbreviations

| | |
|---|---|
| °C | Temperature, (Degrees Celsius) |
| Ca | Calcium |
| F20 | Site index for *Fagus* (beech) defined as the average top-height of the 100 trees with the largest diameter at 100 years total age, e.g. F20 – top-height 20 m, F24 – top-height 24 m, *etc.* |
| ha | Hectare (1 hectare = 10 000 $m^2$) |
| K | Potassium |
| Kg | Kilogram |
| MAI | Mean Annual Increment |
| Mg | Magnesium |
| $m^3$sk | Volume of the tree above the stump in cubic meters: i.e. the stem with the bark and top included |
| N | Nitrogen |
| P | Phosphorus |
| pH | Potential of Hydrogen, indicating acidity |

# 1 Introduction

## 1.1 An overview on beech and beech management in Sweden

### 1.1.1 Beech – distribution, biology and physiology

Beech (*Fagus sylvatica* L.) belongs to the family Fagaceae, which includes 10 spieces of the genus *Fagus* (Anderberg and Anderberg, 2009). The European beech, *F. sylvatica*, is distributed from the west coast of Norway at 60° North in the north (Yakovlev and Myking, 2009), to Sicily in the south, and from northwestern Spain in the west, to Romania in the east (Figure 1). In Sweden, beech is most commonly found in the south of the country. The natural distribution of beech in Sweden is restricted by the occurrence of spring frosts during flowering, which damage flowers to such an extent that too few viable seeds are formed to produce an adequate new regeneration (Lindquist, 1931, Matthews, 1955). When planted, the beech can survive further north and separate individuals are said "to be comfortable" as far north as locations close to Umeå, 64° North (Wahlgren, 1922).

Beech grows well on slopes of fresh moraines with some limestone content and a good water supply. The ground should be well-drained and nutrient rich. A maritime climate with winters that are not too cold, together with high humidity and high precipitation are its preferred conditions (Almgren et al, 1984). In southern Sweden beech is often found on ridges up to about 200 m above sea level. Spontaneous mixtures occur with other broadleaved species, especially oak, ash and hornbeam, and in the northern parts of its range beech can also be found with pine and spruce, in both natural and managed stands.

In stands, the trees start to flower between the ages of about 60 and 70 years, and their seed production peaks between the ages of 100 and 150 years, after which it tends to decline, although some individuals continue to flower and produce seed up to the age of 300 years (Dzwonko, 1990). For solitary trees, flowering and seed production can start at an age as young as 40 years (Dzwonko, 1990). Flowering starts when the trees come into leaf (Nielsen and Schaffalitzky De Muckadeli, 1954), which in Sweden usually takes place during the first part of May (Anderberg and Anderberg, 2009).

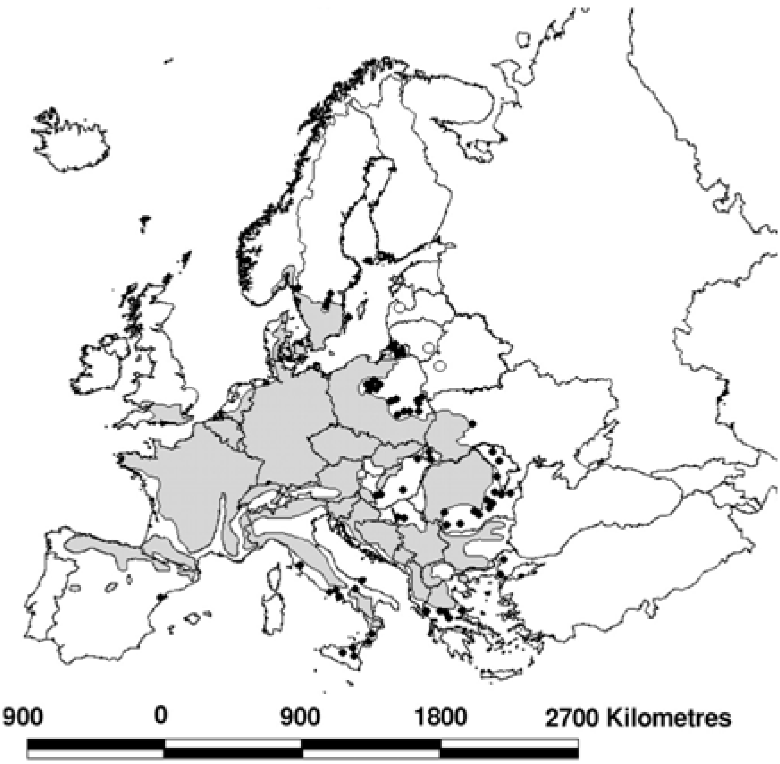


*Figure 1. Distribution of European beech (Fagus sylvatica L.), grey area. Isolated occurrences (filled dots) and additional occurrences of beech acc. to Gross (1934) and Dreimanis (2004) (unfilled dots) of European beech. From Bolte et al. (2007).*

Beech is a monoecious plant and self-pollination is avoided by individual trees spreading the time of coming into leaf and flowering, with the female flowers usually opening first, and the male flowers opening about a week later (Nielsen and Schaffalitzky De Muckadeli, 1954). Pollination is by wind, with the female flowers being receptive to pollination over a period of about two weeks. Usually less than 10 % of the seed originates from self-pollination (Nielsen and Schaffalitzky De Muckadeli, 1954). The time of flowering is a sensitive period; frosts, hailstorms, heavy rains, and strong winds can severely damage the flowers (Gruber, 2003,) and heavy rain in April has been shown to have a particularly negative effect on seed production (Holmsgaard and Olsen, 1960). The female flowers develop a protective bowl, a cupula, about 2.5 cm long, which protects the two oval, triangular beech nuts. These usually develop during the summer, but abortion can occur in the events of summer droughts or in particularly wet and cold summers (Lindquist, 1931, Röhrig et al., 1978). In autumn, often after the first frost, the cupulas open and the seeds start to fall (Simak, 1993).

### 1.1.2 Beech in Sweden

Pollen analyses show that beech was already present in restricted areas in southern Sweden as long as 4 000 years ago (Bradshaw and Lindbladh, 2005. At the same time as Norway spruce was migrating from the north, beech was spreading northward, probably partly due to human activity. The maximum distribution was reached about 1 000 years ago, since when there has been a southward movement of the farthest limits of its range to its present distribution, also brought by human activities (Bradshaw and Lindbladh, 2005). In the 17th century, beech and oak were the dominant tree species in the most southern provinces in Sweden, i.e. Scania, Halland, Blekinge and southern Småland (Figure 2). The sparse forests were at that time mostly used as pasture land for animals, and for fuel-wood (Lindbladh et al., 2008). In the 18th and 19th centuries the beech forests were also exploited for industrial purposes including the production of potash, which was used for making soap, glass and gunpowder. (Larsson, 1989). There was also a great need for barrels made from beech, which were used for storing herring (Simonsson and Larsson, 2007). Since there was a great need for arable land by farmers, large areas of beech forests were cut down, all this activities together causing the decline in the area of beech forest. Where beech persisted was mostly on properties belonging to the nobility, who could afford to keep forests for hunting purposes (Hultberg et al., 2010).

During the 20th century, many beech forests were converted to Norway spruce for economical reasons, and the area of beech forest again decreased dramatically (The Swedish Environmental Protecting Agency, 1982). In 1974 this prompted the Beech Forestry Act, the purpose of which was to preserve beech forests by appropriate management and by forbidding their conversion to other tree species (The Swedish Parliament, 1971). In 1984 the act was replaced by the Hardwood Tree Forestry Act, which had the same purpose, but also included measurements to protect other "noble" tree species such as ash (*Fraxius excelsior*), elm (*Ulmus glabra*), hornbeam (*Carpinus beula*), lime (*Tilia cordata*), maple (*Acer platanoides*), oak (*Quercus petrea, Q. robur*) and wild cherry (*Prunus avium*) (The Swedish Parliament, 1992). One implication of the Hardwood Tree Forestry Act is prohibition of the conversion of low-yielding beech stands into stands consisting of other tree species, even though they may potentially be better suited to local site conditions.

Today, the primary products of beech are materials used for flooring, furniture and carpentry. Pulpwood from beech is also used in the production of high quality paper. There is a large price differential between logs of different qualities, with coarse trunks (> 50 cm) receiving the largest financial returns.

In Sweden, beech forests, i.e. forests in which more than 70 % of the basal area consists of beech, cover about 58 000 ha and have a standing volume of about 21 million $m^3$sk, which represents 0.7 % of the standing volume in Sweden. In the counties of Scania, Halland and Blekinge, however, 11 % of the standing volume consists of beech. The annual increment is approximately 450 000 $m^3$sk, and the annual cut is approximately 400 000 $m^3$sk. Trees with diameters of at least 25 cm at 1.3 m above ground level, account for approximately 85 % of the total volume (Svensson, 1995, The Swedish Forest Agency, 2009).

### 1.1.3 Management of beech

In Sweden, beech forests are currently managed for several purposes. Beech forests often have a lengthy continuity and are, therefore, important for biodiversity. Many red-listed lichens and insects can be found in association with old beech trees (Jonsell et al., 1998, Müller et al., 2007, Fritz et al., 2009). To preserve and enhance these associations, special management attention is required (Fritz et al., 2009). Standing and lying dead wood, trees with nesting cavities and old trees favour these endangered species (Müller et al., 2007, 2008).

The recreational values of beech forests, in particular, are of big importance for society, today (Holgen and Bostedt, 2004). Normally no special management is needed; old, sparse, high quality "pillared halls" are the most preferred attributes among typical forest visitors (Jensen and Koch, 1997).

The aim of the economic sustainable silviculture of beech is, bearing in mind current costs and values, to produce high quality timber of large dimensions, namely trunks with a diameter of 50 cm or more in a profitable way. New beech stands are only established today to a limited extent, the dominant method for beech production being the regeneration of existing beech stands, mainly by natural regeneration with a shelter-wood. The shelter-wood is harvested concurrently with the growth of the new regeneration, followed by several pre-commercial thinnings. Usually the pre-commercial thinnings begin when the regeneration has a height of about two meters and involve the removal of undesirable species and fast-growing beeches, known as "wolf trees". Next, the pre-commercial thinning operation is performed at a stand height of about five to seven meters and characterized by a negative selection, i.e. removal of "wolf trees" and trees of bad quality in the uppermost crown layer. The following pre-commercial thinning favours trees of good quality as potential crop trees (Bjerregaard and Carbonnier, 1979). The pre-commercial thinnings makes this phase costly, but alternative methods, including fewer and less intensive operations, have also been evaluated (Ekö et al., 1995).

The thinning program is characterized by many thinnings, the first when the stand has reached a height of about 10 – 12 meters, followed by further thinnings at short intervals in the beginning, with the interval increasing with increasing age of the stand. As a rule of thumb the thinning interval is the stand age divided by ten. At every thinning, it is important to promote stems of good quality, and in the later thinnings to aim for a good, even distribution of the standing trees over the area. The thinning method used in Sweden today is crown thinning, in which the potential final crop trees are promoted. Today many forest owners do not use this intense forest management, but have increased the thinning intensity and prolonged the thinning intervals. A more extensive thinning program with three to six thinnings was suggested by Carbonnier (1971). On the other hand the increased demand for energy wood may increase the thinning intensity.

In the research program Sustainable Management in Hardwood Forests (2010), the possibilities for a more rational, but less intense thinning program, is investigated. The aim is to develop a thinning program resulting in a higher net income compared to the traditional approach.

The rotation period for a beech stand normally varies between 100 and 150 years, depending on the site index, but actual timber prices and target diameters have the strongest influence on the specific time of final cutting (Bjerregaard and Carbonnier, 1979).

### 1.1.4 Growth and yield of beech in Sweden

The growth and yield of beech in Sweden was studied by Carbonnier (1971), who constructed site index curves based on top-height (also called dominant height, defined as the mean height of the 100 trees $ha^{-1}$ with the largest diameter) and total age. Carbonnier (1971) also constructed yield tables, based on data from 39 permanent research plots, for site indices F20, F24, F28 and F32 (F20, for instance, standing for Fagus 20, i.e. beech with a top-height of 20 m at 100 years total age). The mean annual increments (MAI) up to 120 years total age were calculated to be 3.6, 5.1, 6.3 and 7.8 $m^3$sk $ha^{-1}$ $year^{-1}$ for the site index classes F20, F24, F28 and F32 respectively.

In the calculations of the yield tables Carbonnier (1971) used two thinning programmes; one intensive with between 5 and 12 thinnings for site indices from F20 to F32; and one more extensive programme with three to six thinnings during a rotation for the same site index classes. For the more productive site index classes production tended to be higher with a lower number of thinnings. The yield tables probably underestimate the total production for beech since, firstly Carbonnier only calculated up to the age of 120 years, at which age the increment had not yet culminated, and secondly, the removals in the first thinning were not included in the calculations. Today, the small dimension timber from the first thinning can be used for pulpwood to provide a net income. Another point to note is that the calculations of volume of beech used in Sweden (Hagberg and Matern, 1975) only include stem-wood, not branches.

Bjerregaard and Carbonnier (1979) also compared the production of stem-wood and dry matter for spruce and beech and found spruce to be superior to beech in volume production: 2.6 times higher for site index class F20 and 1.6 times higher for the best (F32) sites. However, for dry matter production the figures are evened out due to the higher basic density of beech. At unfertile (F20) sites, spruce produced 1.5 times more dry matter than beech, but on the best sites beech produced 1.1 more dry matter than spruce.

The yield studies by Carbonnier (1971) are results from research plots in pure beech stands. Beech in Sweden is mainly growing in pure stands, especially in the more productive sites.

## 1.2 Regeneration

### 1.2.1 Seed production of beech

Seed production of beech is irregular with a wide variation between years (Lindquist, 1931, Perrins, 1966, Jenni, 1987, Hilton and Packham, 2003). Mast years are defined as years in which the seed production is high, mostly several millions of seeds $ha^{-1}$, occuring over subcontinent- to continent-wide areas (Wachter, 1964, Perrins, 1966). According to the literature, mast years occur irregularly at intervals of between three an fifteen years (Matthews, 1955, Maurer, 1964, Bjerregaard and Carbonnier, 1979, Harmer, 1994), and it is impossible for beech to flower and produce seed in two consecutive years (Lindquist, 1931). The various factors that trigger the flowering of beech have been studied by several authors, most of who agree that a warm and dry summer initiates flower-buds for the next year's flowering and seed production (Matthews, 1955, Matyas, 1965, Schmidt, 2006). Records of the amounts of seed produced during mast years are rare and mostly qualitative.

### 1.2.2 Traditional regeneration

Natural regeneration is currently the most common method used to regenerate beech. In general, large quantities of seedlings are established, and as long as populations of ungulates in the area are not too large, fencing is not necessary. With the relatively high number of seedlings necessary to perform a future high quality stand, together with planting costs and complementary planting would result in high costs (Bjerregaard and Carbonnier, 1979). From Madsen and Löf (2005) the regeneration cost could be estimated to be at least 5 000 € $ha^{-1}$. Furthermore, even with only small herds of ungulates, planting without fencing would be a risky business. Seeding could be a cheaper alternative, but the method is currently unreliable, mainly due to predation by rodents (Birkedal et al., 2009).

One of the advantages with the natural regeneration of beech is the possibility to get a high number of seedlings established (Madsen and Larsen, 1997, Agestam et al., 2003). This is desirable since several factors contribute to high levels of mortality in the first years after seedling establishment (Huss, 1972, Agestam et al., 2003). High numbers of seedlings are also needed in order to generate a good quality new stand, since the high level of competition between seedlings favors high quality shape of trees in the new stand (Bjerregaard and Carbonnier, 1979) and provides opportunities to positively select the best trees in subsequent management operations such as thinnings. These factors highlight the importance of high germination and survival rates, since the failure of regeneration is difficult to rectify (Bjerregaard and Carbonnier, 1979).

Various measures are often undertaken to promote conditions that encourage seeds to germinate and aid seedling survival. To enhance seed production, the last thinning of the old stand, which is usually performed 10 to 20 years before the regeneration event, can be heavier than earlier thinnings (Dengler, 1972). A sparse stand allows bigger crowns to develop that are exposed to more solar radiation, which favors seed production (Topoliantz and Ponge, 2000).

In Sweden normally some kind of site preparation should be undertaken before seed-fall, especially if the organic layer is thick or the ground vegetation abundant (Agestam et al., 2003). This should be done in late summer or early autumn before the seed starts to fall, the aim being to make it easier for the beech seeds to germinate (Bressem, 1988, Madsen, 1995a). Bare mineral soil, or a mixture of mineral soil and humus, facilitates the resulting regeneration in many ways. For example: various fungi, which attack seeds during the winter, and germinates during the spring, are more abundant in humus than mineral soil (Bressem, 1998); soil temperatures are higher in bare mineral soil (Örlander et al., 1990), as is the availability of water (Löf, 2000); and competition from ground vegetation is reduced. The most common way of creating areas with a bare mineral soil surface is to use a disc-trencher or a patch-scarifier; equipment originally developed for the regeneration of conifers. The cost for site preparation under a shelter-wood with this type of machinery was calculated in 1996 by Westerberg and von Hofsten, and would today corresponds to about 260 € $ha^{-1}$. However, a disadvantage with this type of site preparation is that the fallen seeds are more visible to seed-eating animals, such as birds, rodents and ungulates. For this reason, it is good practice to cover exposed seeds with a protective layer of mineral soil or humus (Watt, 1923). This should be done when most seeds have already fallen and the ground is still unfrozen.

A less extensive site preparation method, using a rotary cultivator – the Lindenborger harrow - is sometimes used to mix the organic layer and the mineral soil to a depth of 5 cm to 10 cm before seed-fall occurs. After seed-fall, the ground is cultivated again, using the same machinery, but this time to a depth of only 5 cm, in order to cover the seed. Alternatively, the ground may be simply lightly cultivated with this machinery after seed-fall (Olesen and Madsen, 2008).

Ungulates are a common problem when establishing beech forests. The damage is most severe after germination (Madsen, 1995a) and the browsing pressure increase with increased seedling density (Olesen and Madsen, 2008). The regeneration is negatively influenced until it has reached the height when the top sprouts are not reached (Drexhage and Colin, 2003). To decrease the herds of ungulates by hunting does not seem to be a way to decrease the browsing. Hunting is a most appreciated recreational activity in Sweden and hunting rights provide a considerable income for the land owner. Often the land owner is a hunter and therefore has conflicting interests. Fencing, which is expensive to supply and erect, and requires continuous upkeep and repair during the regeneration phase, is the only effective way to protect areas from ungulates (Rosenquist, 2003).

The regeneration method using site preparation described above usually yields good results, but there can be disadvantages. Site preparation can be difficult at sites with boulders or steep slopes; it is thought to be unfavorable for biodiversity; it may be unsuitable in areas of historical or cultural interest, or areas used for recreation; and it involves an additional cost.

The regeneration described depends for its seed on a mast year, i.e. a year with high seed production. Since it can be difficult to predict exactly when mast years are likely to occur, planning regeneration can be problematic for forest managers. If there has been a long interval since the last mast year, a large amount of beech timber will be harvested at the same time, since many forest owners will probably want to begin regenerating their beech stands at the same time.. This sudden excess of supply may depress timber prices and cause a wide variability in primary products for other industries. The value of the old stand may also be limited because a final felling of most of the standing trees will prevent all trees from reaching a target diameter. It may also be difficult to find skilled workers and machinery in sufficient quantities since the demand for them during a mast year will be high.

If a regeneration attempt ends in a failure the only recourse is to try again in the next mast year. However, the second attempt may be even less likely, since the cutting of the shelter-wood for the first attempt may result in a rising water table, an increase in the competition for nutrients, and an increase in the solar radiation reaching the ground, resulting in increased ground vegetation, Altogether this will adversely affect the germination and establishment of the new regeneration.

### 1.2.3 An alternative regeneration method

Another, alternative regeneration method (Bornebuch, 1947, Evans, 1982, Henriksen and Bryndum, 1996), involves controlling the ground conditions and the establishment and development of the new regeneration, by several judicious cuttings in the old stand. In this way the incoming solar radiation and the competition from the old stand can be regulated to control the growth of the ground vegetation, the decomposition rate of the litter, as well as other factors that affect the establishment and growth of the new regeneration. In the alternative method, the new regeneration originates from the large quantity of seed produced over the course of several mast years, plus any seeds produced in small amounts between mast years. This inevitably implies a longer regeneration period, thus since the cuttings in the old stand do need not be done in any particular year, they can be performed when timber prices are at a peak, or when any other special requirements need to be fulfilled, including the possibility of leaving good quality trees to reach the target diameters.

The method is, however, sometimes considered to be unreliable. The regeneration period may be long, and the regeneration that develops from this method is also said to be too sparse and uneven in both distribution and height to give a good quality stand (Bornebuch, 1947, Evans, 1982).

### 1.2.4 Liming

In the last hundred years, acidification has increased in many regions of the world due to air pollution mainly from industrial activities and food production (Galloway, 2001). In Europe, the most affected areas are concentrated in the northeastern regions. For instance, 34 % of the forests in the former West-Germany were reported to be damaged, dying or dead due to acidification (Backiel, 1985). In southern Sweden the pH of forest soils has decreased by between 0.3 and 1.0 unit during the last 30 years, mainly due to acid pollution (The Swedish Environmental Protection Agency, 2009). Even though acid deposition in Sweden has decreased in recent years, it is still sufficiently high to continue to negatively influence the pH of Swedish forest soils in the future (The Swedish Environmental Protection Agency, 2009).

Acid soils hinder the natural regeneration of beech in many ways. Bressem (1998) found germination to be severely inhibited at pH(KCl) values lower than 3.5. Low pH values also seem to increase the aggressiveness and pathogenicity of soil fungi that attack the fallen beech seeds and developing germinates (Bressem, 1988); cause poor development of fine roots of beech seedlings (Ljungström and Stjernquist, 1993); and adversely affect soil fauna, e.g. earthworm communities (Ammer and Huber, 2007). The best germination and development of primary roots and cotyledons has been found to occur at pH values of around 4.3 (Bressem, 1988). Such observations have stimulated investigations of the effects of liming, several of which have shown improved regeneration results following liming (Bressem, 1998), which is now an option sometimes used to complement beech regeneration at acid soils (Bauhus et al., 2004).

In Sweden, natural regeneration of beech sometimes fail, especially when they are performed in old stands with low site indices and podzolic soils with a thick raw humus layer and a low pH. In an experiment in Sweden Ljungström et al., (1990) found liming had no effect on beech regeneration when liming was carried out at the time of seed-fall. The same experience was made in a German sowing experiment where Ammer et al. (2002) found no effect of liming on seedling numbers when liming was performed coincident with liming. However, other authors have claimed that, to be effective, liming should be done several years before the regeneration event (Röhrig et al., 1978, Bressem, 1988).

## 1.3 Objectives of the studies

The results of regeneration activities in beech stands are important because they have an influence over the whole rotation period, which is typically 100 - 150 years in Sweden. The large differential in the financial value of a good quality and a low quality beech stand, and the long rotation period, make the efficacy of regeneration activities particularly important.

This thesis deals with three main aspects and issues related to the natural regeneration of beech; 1) seed-fall and mast years; 2) possibilities for lowering the intensity of regeneration work; and 3) the utility of liming to improve the regeneration results.

Improved understanding of the masting behavior of beech, i.e. greater knowledge of the timing of mast years and the size of seed-falls during them, would be very helpful for good beech regeneration. Alternative regeneration methods that may simplify the planning, decrease the regeneration costs, and increase the value of the old stand, would also be of considerable importance. On acid soils the result of regeneration is often inadequate; a problem which may be further aggravated by decreasing pH values in the future (The Swedish Environmental Protection Agency, 2009). Liming may provide a way to overcome these obstacles.

The specific questions addressed in these thesis (and the studies it is based upon) are:

### 1.3.1 Mast years and seed production in beech forests (Paper I)

- Has there been a change in the interval between mast years over the last 30 years, compared to earlier periods?
- Does seed production differ between sites?
- What climate factors are most important for flower bud initiation?

### 1.3.2 An alternative regeneration method for beech (Paper II)

- Does site index influence the regeneration result, and is it possible to use the alternative method at a large variety of sites?
- How does the regeneration develop during the shelter period?
- Is an adequate regeneration achieved with the alternative method?

### 1.3.3 Liming to improve natural regeneration of beech (Paper III and IV)

- Does liming improve seed production, germination, early growth, and seedling survival?
- Does liming influence the ground flora and soil fauna?
- In what way does liming influence the results of the alternative method of regeneration?

# 2 Summary of papers

## 2.1 Paper I

For beech, a mast year is one in which there is an abundant production of seeds over a wide geographical area, as extensive as, for example, southern Sweden or Denmark (Perrins, 1966). The quantity of seed should be sufficient abundant to permit the creation of, with appropriate supplementary treatment, a new stand of good quality. Henriksen (1988) claims that at least 500 000 viable seeds $ha^{-1}$ (50 seeds $m^{-2}$) is necessary, and Huss (1972) states that 20 seedlings $m^{-2}$ to be a minimum for initial stock. Naturally, the number of seeds needed to establish a good regeneration varies between sites and the weather conditions during the establishment period. However, as can be seen in this paper, there is a big difference in amount of seeds between mast years and non-mast years. During mast years the seed production was counted in millions, or at least hundreds of thousands of seeds, while during non-mast years the seed production was counted in a few thousands of seeds.

When studying, or applying, practices involving the natural regeneration of beech, mast years are naturally of primary importance. Although earlier literature states that mast years occur at intervals of from three to ten years (Matthews, 1955, Maurer, 1964, Bjerregaard and Carbonnier, 1979), the general opinion among foresters and researchers is that the mast years currently occur more frequently (Hilton and Packham, 2003, Schmidt, 2006).

In late 1980s, new research on beech regeneration started within the newly established Southern Swedish Forest Research Centre. In an initial and several subsequent studies, seed-falls were recorded in both mast years and non-mast years. From these studies it became clear that the appearance of mast years did not follow the text book accounts in all respects. Mast years seemed to occur more often than expected from the accounts in the literature; they occasionally occurred in two consecutive mast years; and also there seemed to be a wide variation in seed production between sites and years.

The main questions in this study are:

- Has there been a change in the interval between mast years over the last 30 years, compared to earlier periods?
- Does seed production differ between sites?
- What climate factors are most important for flower bud initiation?

### 2.1.1 Materials & methods

To find out if there had been a change in the mean interval between mast years, a literature survey was performed, and the results from this survey were compared to records of seed-falls during the last 35 years. Information about mast years in Sweden since the end of the 17th century was obtained for the following periods; 1687 - 1711 and 1753 - 1795 (Osbeck, 1996), 1895 - 1929 (Lindquist, 1931), 1930 – 1933 (Tirén, 1931, 1932, 1933, 1934), 1944 - 1960 (Jenni, 1987), 1954 - 1964 (Perrins, 1966) and 1974 – 1983 (Simak, 1993). Information about mast years between 1974 and 1989 was also obtained from notes regarding two beech seed-orchards, Albjershus and Ramsåsa (Figure 2), which were established as plantations for seed production in the 1950s from grafts of good genetic material.

Records since 1989 are from different regeneration experiments performed by the Southern Swedish Forest Research Centre. Seed production has been measured at a total of 25 sites covering the most central parts of the beech distribution area (Figure 2), but continuous measurements covering the entire period are not available for any of the sites. In Skarhult experimental forest (Figure 2, no 6) a study of natural regeneration of beech was established in 1989 (Agestam et al., 2003) when the seed production was recorded from a total of 60 seed traps.

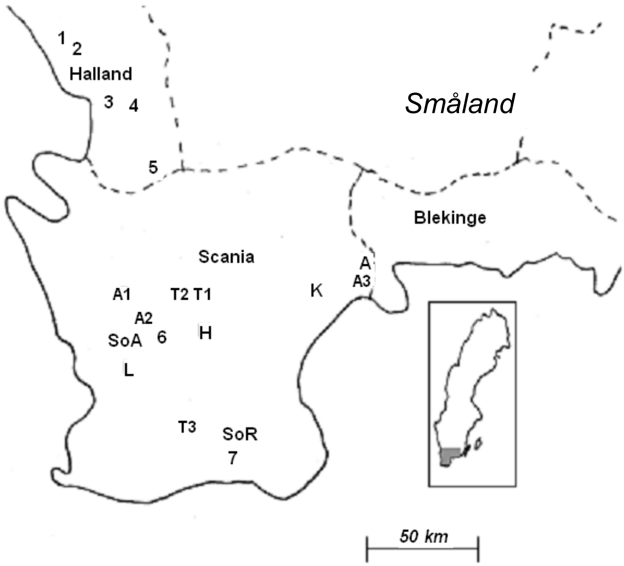


*Figure 2. Location of the sites where seed-falls have been recorded: 1 – 7, A, A1 – A3, T1 – T3. The experiment with the alternative regeneration method is situated at A (Paper II); the experiment combining liming and the traditional regeneration method is situated at T1 – T3 (Paper III); and the experiment combining liming and the alternative regeneration method at A1 – A3 (Paper IV). Other indicated locations are: the seed orchards Albjershus (SoA) and Ramsåsa (SoR), and the climate stations Lund (L), Hörby (H) and Kristianstad (K).*

In a study of an alternative method for the natural regeneration of beech (Paper II) the seed production was recorded at seven sites every year between 1992 and 2006 (Figure 2, A).

In a liming experiment (Papers III and IV) established in 1991 (Figure 2, Nos. 2 – 7, T1 – T3, A1, A2) and 1993 (Figure 2, No. A3) seed production in the mast years was recorded from 1993 (sites 2 –7, T1 – T3, A1, A2,) and 1995 (site A3) until 2006 using data from a total of 88 seed-traps.

In another natural regeneration experiment in a beech-dominated forest, seed production was recorded every year from 1998 to 2004 using 13 seed traps (Figure 2, No. 1).

To identify climate factors that had the strongest influence on flower bud formation, climate data recorded during the last 35 years by the Swedish Meteorological and Hydrological Institute (SMHI) at the climate stations of Lund, Hörby and Kristianstad (Figure 2, L, H and K) were used. The following variables were analyzed for the months May to September: mean temperature, duration of warmth (number of days with maximum temperature exceeding 20° C), intensity of warmth (the sum of maximum temperature exceeding 20° C), precipitation and potential evapotranspiration. The variation in seed production among mast years, and wether site index could explain the differences among sites, were also investigated.

### 2.1.2 Results

The information about mast years since the end of the 17$^{th}$ century revealed that the mean interval between mast years has varied between four and six years (Figure 3). Since 1974, however, the mean interval has been about 2.5 years, and since the mast year of 1983, which was preceded by a seven-year interval, there have never been more than three years between successive mast years. There have also been two occasions with two consecutive mast years; 1986 - 1987 and 1992 – 1993, which are rare events never previously reported in Sweden.

A range of climate factors that are thought to trigger the flowering of beech were investigated. The variables with the strongest influence were all variables for the climate in July: the duration and intensity of warmth and mean temperature when higher than their respective 30-year means, and for precipitation when lower than the 30 years mean, were all significantly positively correlated to high seed production in the following year. A weaker correlation was also found for mean temperature in September, when higher than the 30-year mean. However, even when all of these criteria were fulfilled, there were rarely two consecutive mast years. The year that was followed by a mast year, if that year was not itself a mast year, had an average July temperature of at least 15.8° C, and 16 days or more with a maximum temperature exceeding 20° C (Figure 4).

The variation in seed production between mast years was significant and varied from 1 million to 10 million seeds ha$^{-1}$. In non-mast years the seed production was zero or lower than 5 000 seeds ha$^{-1}$.

The seed crops were also influenced by site index, and an increase with 160 000 seeds ha$^{-1}$ per site index meter was found (Figure 5).

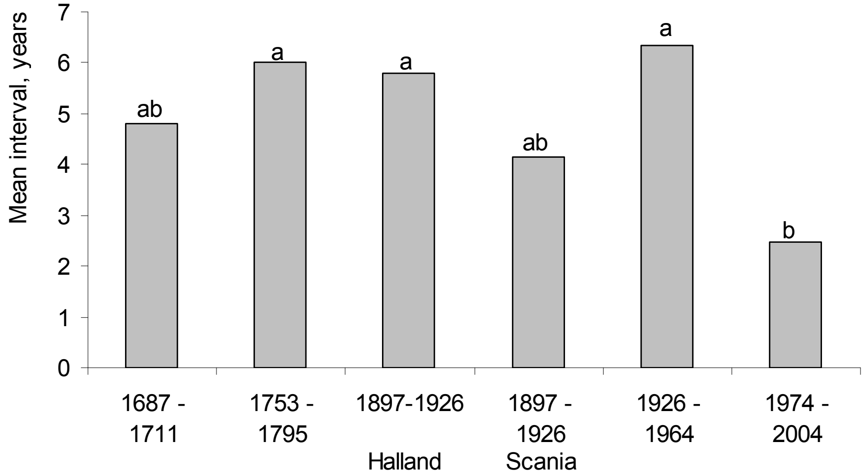


*Figure 3. Mean intervals between mast years in time periods with available data. Data for the period 1897 - 1926 from Halland and Scania are shown separately. Intervals with same letters are not significantly different ($p < 0.05$).*

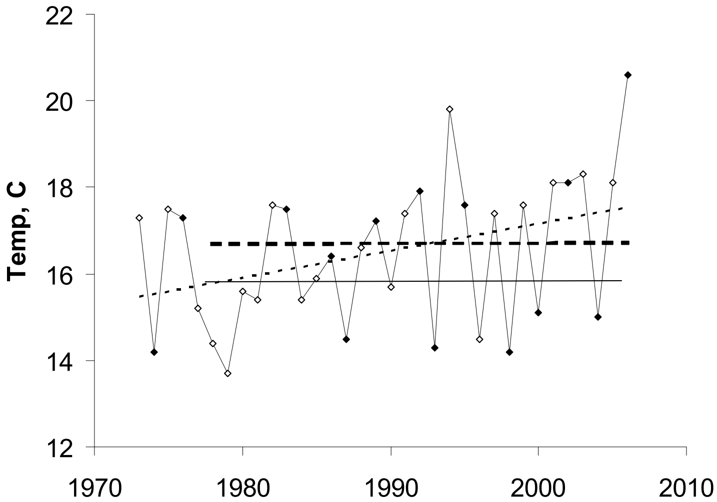


*Figure 4. Mean July temperatures at Hörby climate station for the period 1973 - 2006. The dashed line shows the mean July temperature for the period 1977 – 2006, the unbroken line shows the temperature 15.8° C and the dotted line shows the trend for July temperature for the period. Filled markers indicate mast years between 1974 and 2006.*

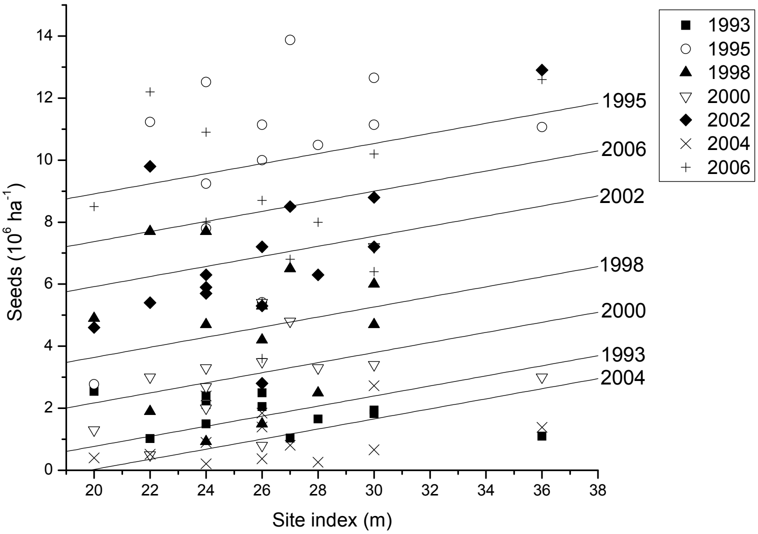


*Figure 5. The recorded seed-falls during mast years in relation to site index of the study sites. The lines indicate the least-square mean estimates of the models from the statistical analysis where site index was treated as a covariate. Record is missing from one F26 site in 1993, since this site was established late in 1993. Record from the F36 site is missing 1998 since all seed-tarps were damaged.*

## 2.2 Paper II

In Sweden, the overwhelmingly dominant method for regenerating beech forests is natural regeneration. The most common practice is to await a mast year, perform some kind of site preparation before the seed-fall, and after seed-fall undertake a heavy cutting, leaving a protective shelter. The method usually results in acceptable regenerations, but does have some drawbacks. Not all sites are suitable for site preparation due to physical or ecological hindrances, and the method gives rise to practical problems that prevent all trees from being left to reach the dimensions at which they attain their highest values. Furthermore, site preparation involves an additional cost and the method limits regeneration attempts to mast years. If the method fails to produce an adequate regeneration, severe difficulties may arise at the next regeneration attempt due to increased field vegetation after the shelter-wood cutting.

An alternative, less intense method is sometimes used in southern Sweden. In this approach the new regeneration originates from the accumulated seed production of several mast years, which implies a longer regeneration period. No site preparation is performed, the forest floor conditions and the establishment and early growth of seedlings instead being regulated by several judicious cuttings in the old stand. The method is however, thought to be less reliable than the traditional method. The aim of the present study was to map the method and to study the regeneration dynamics.

The main questions in this study are:

- Does site index influence the regeneration result, and is it possible to use the alternative method at a large variety of sites?
- How does the regeneration develop during the shelter period?
- Is an adequate regeneration achieved with the alternative method?

### 2.2.1 Materials & methods

Seven stands in different phases of regeneration were studied between 1992 and 2005. Seed-falls, the establishment of new seedlings in each new generation, early growth, mortality, and damage were recorded in these new regenerations, as well as potential quality of the new stand. The development of the ground vegetation and the shelter trees were also studied. Three stands were in the early regeneration phase, two in the intermediate, and two in the late phase. The early regeneration phase stands were situated at sites with low (< F24), medium (~ F24) and high (> F26) site indices, while one of each pair of stands in the intermediate and late regeneration phase were situated on a site with a low site index and the other on a site with a high site index.

Four plots were randomly selected in each stand. In each plot the seed-fall was recorded every year using three seed-traps, each with an effective area of 0.25 $m^2$ or 0.125 $m^2$. The area of each individual seed-trap was measured and seed-fall $ha^{-1}$ calculated. Each plot had nine 1 $m^2$ subplots in which the regeneration was studied. At the start of the experiment, seedlings that were already established were labeled and a sample was numbered. New seedlings were marked every autumn with a label of a new color to identify every new cohort, and a sample was numbered. The heights of, and injuries to, on numbered seedlings, and mortality among all seedlings in each subplot were recorded every year for each cohort.

Every fourth year, the ground vegetation was harvested, dried and weighed. The shelter trees around each plot were measured in 1993, 1996 and 2005 and shelter trees removed at cuttings were also measured. In autumn 2006 the quality and number of potential final crop trees was estimated in the two late regeneration phase stands.

The selection and cutting of trees from the old stand, and for the pre-commercial thinnings, which were performed simultaneously with the cuttings, were performed by the local forest manager.

### 2.2.2 Results

Seed production and the numbers of new seedlings were not significantly influenced by site index or the number of shelter trees. A small amount of seed production was also recorded in non-mast years. Seedling establishment was most pronounced in the early and intermediate phases of the regeneration period, but rarely in the late phase, during which a slow decrease in seedling number was observed (Figure 6). The mortality among new seedlings was high in the first years after establishment, but decreased thereafter. The height growth of the new regeneration was negatively influenced by seeding tree density, but was not influenced by site index. Cuttings in the shelter stands did not follow any particular pattern, but were undertaken when timber prices offered a good return and in order to promote the establishment and growth of new seedlings. The volume growth of the shelter stands was low. The number of shelter trees varied from 190 stems $ha^{-1}$ at the beginning of the regeneration phase in the low site index stand, to 26 stems $ha^{-1}$ before the last cutting in the high site index stand.

The method resulted in adequate regenerations with a sufficient number of potential final crop trees, regardless of site index and the timing of mast years.

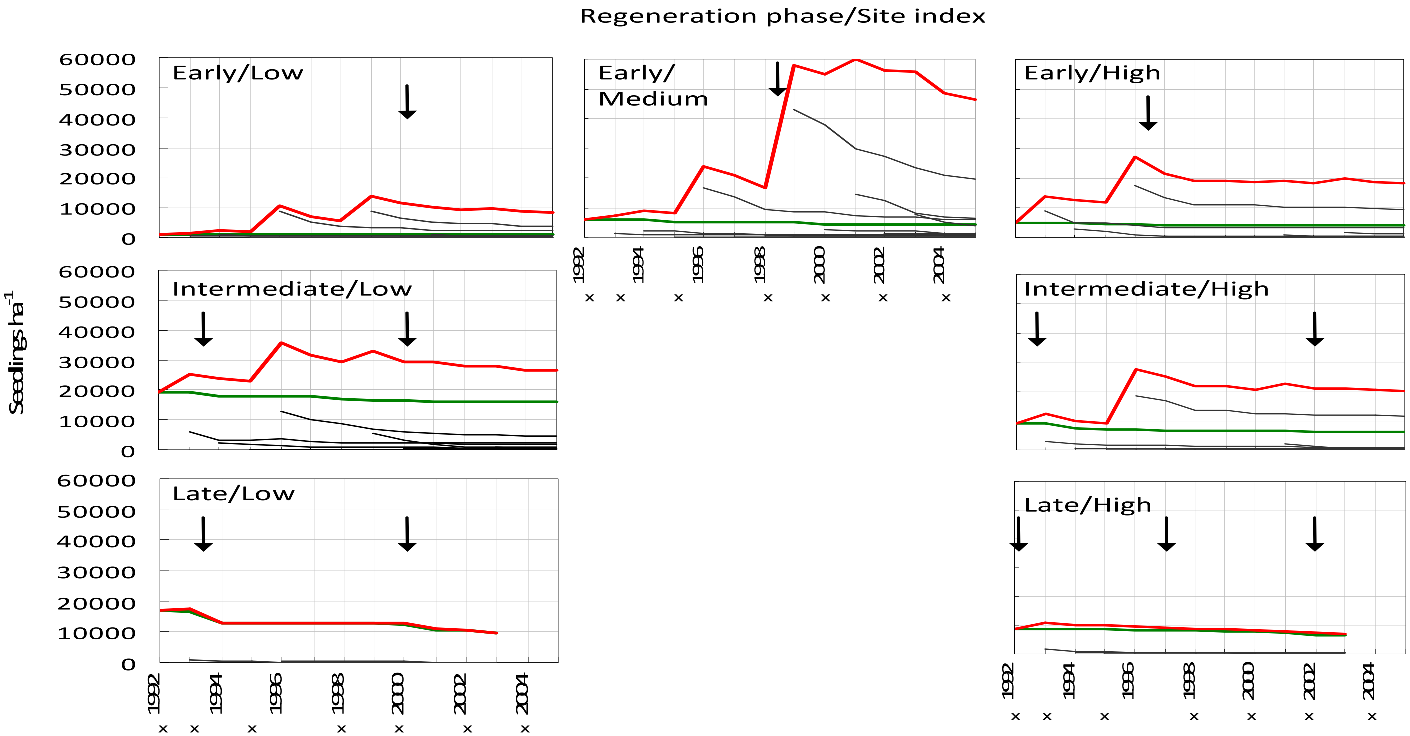


*Figure 6. Changes in numbers of seedlings in the early, intermediate and late regeneration phases. The red line shows the total number of seedlings, the green line the number of advance seedlings and black lines the number of seedlings of every new cohort. An "x" indicates a mast year and an arrow a cutting in the shelter.*

## 2.3 Paper III

Both methods of natural regeneration of beech described in Paper II usually result in good regenerations with an abundance of seedlings, but sometimes failures occur. Notably, at old sites with a low site index, often with a thick raw humus layer on iron podzol soils and a low pH, the number of seedlings is sometimes insufficient. Since several investigations in Europe have shown liming to improve seedling emergence on acid soils, the effect of liming on regeneration results and site properties was also analyzed at three sites in southern Sweden.

The main questions in this study are:

- Does liming improve seed production, germination, early growth, and seedling survival?
- Does liming influence the ground flora and soil fauna?
- Does liming alter the concentrations of defensive phenolics in leaves (both positive and negative alterations may be expected).

### 2.3.1 Materials & methods

Three sites were limed in 1991 with 5 000 kg of pulverized limestone $ha^{-1}$. The site indices of the three sites, T1 – T3, were F24, F26 and F30, respectively. Each site had four blocks, and each block had one limed and one un-limed plot of 25 m × 25 m. The sites were regenerated in the spring of 2007 after the rich mast year of 2006. Before seed-fall, site preparation was performed over the whole stand, in which the experiment was situated, resulting in areas of bare mineral soil, areas with a mixture of humus and mineral soil, and untreated areas. The seed-fall was measured at all three sites with one seed-trap in each plot. After seed-fall, a heavy cutting, performed by the local forest manager, in the adult stands was undertaken, leaving a sparse shelter.

In spring 2007, ten 1 $m^2$ subplots were systematically laid out along a diagonal across each plot. The percentages of the areas covered by the different site preparation types, including the untreated control areas, were recorded in spring 2007 together with 'impediment areas', defined as areas where it was physically impossible for seed to germinate. The number of seedlings in each area was also recorded, and in autumn 2008 their survival and height were recorded.

The numbers and weight of earthworms was recorded in autumn 2007. In August of the same year, a vegetation sample was harvested from each plot in all stands. The vegetation was dried and weighed. In the autumn of the same year, the thickness of the organic layer was measured and soils were sampled for chemical analyses. To find out if weather liming influenced the concentration of a potential defensive compound in seedlings, leaves were sampled in spring 2008 for chemical analysis.

### 2.3.2 Results

Neither liming nor site index influenced the size of the seed production. However, the number of seedlings and the effects of liming differed among the sites. At the site with the lowest site index, Site T1, more seedlings were found in the limed plots, even though the total number of seedlings was low. No significant difference in seedling numbers between limed and un-limed plots was recorded in the stand with intermediate site index, Site T2, while the stand with the highest site index, Site T3, had more seedlings in the un-limed plots. At Site T3 the seedlings were very abundant.

Site preparation did not influence the number of seedlings in limed or un-limed plots, the only significant difference was found in areas without site preparation at Site T3, where more seedlings emerged in the unlimed plots (Figure 7).

Liming increased the dry-mass of field vegetation at Site T3, while it decreased the thickness of the organic layer. No differences associated with liming in these respects were found at the other sites.

After two growing seasons, height growth was not found to have been influenced by liming.

The survival of seedlings on limed plots was significantly higher at Site T3. Liming also improved the survival of seedlings situated in mineral soil.

Liming increased the numbers of earthworms at Site T2 and T3 while it increased the mass of earthworms at all sites.

After liming, the concentration of a potential defensive compound, chlorogenic acid, which is thought to protect the cell walls of the leaves, increased in seedling leaves.

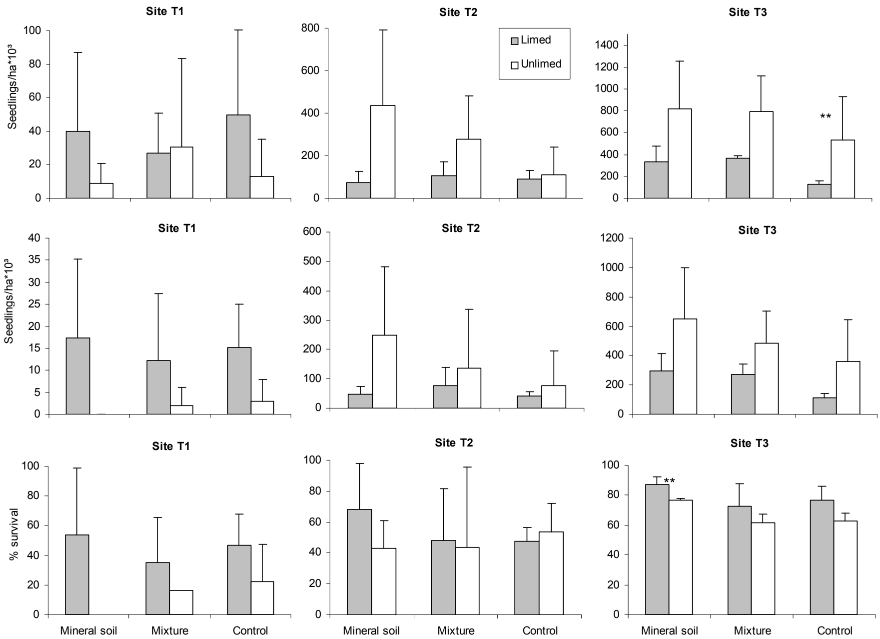


*Figure 7. Number of emerged seedlings in spring 2007 (upper graphs), number seedlings surviving in autumn 2008 (middle graphs), and percentage seedling survival in autumn 2008 (lower graphs) in limed (grey) and un-limed (white) plots subjected to different site preparation techniques. The mean values and SE are shown. Significant differences between limed and un-limed treatments are indicated by ⋆⋆ ($p < 0.01$). No seedlings survived in the un-limed plots with mineral soil at site T1. Note the different scales of the y-axes in the upper and middle graphs.*

## 2.4 Paper IV

The alternative method for regenerating beech (Paper II) is thought to be less reliable than the traditional method and to require a longer regeneration period in order to achieve acceptable result. On sites with a low site index the regeneration phase may be longer because a thick humus layer, a low nutrient content, and a low pH value, can all inhibit seedling establishment. Furthermore, the seedlings may be unevenly distributed with a wide variation in height. The combined effects of the alternative regeneration method and liming were investigated in Paper IV.

The main questions in this study are:

- In what way, and to what extent, is the time after liming influencing the seed production and the seedling emergence?
- In what way is liming influencing the regeneration result when the alternative regeneration method is used?

### 2.4.1 Materials & methods

To evaluate how liming might influence the regeneration resulting from using the alternative method, two sites (A1 and A2) that were limed in 1991, and one site (A3) limed in 1993, were monitored until the autumn of 2008. The liming treatment and experimental design were virtually identical to those of the experiment described in Paper III, i.e. the amount of added lime was 5 000 kg $ha^{-1}$ and each site had four blocks, each with one limed and one un-limed plot of 25 m × 25 m. However, no site preparation was carried out in this study. The regeneration status of the three sites was investigated by recording seed production in each mast year and the number of germinates in the following spring. Vegetation and soil samples were collected in the autumn 2007, and the number and height of seedlings and saplings were also recorded in the autumn of 2008.

### 2.4.2 Results

Liming increased soil pH mainly in the humus layer and to a lesser extent in the mineral soil. The concentration of Ca was highest in the humus layer in the limed plots. Liming did not influence the amount of ground vegetation or seed production. When the response was averaged over all three sites, liming had a negative influence on the number of germinates during the first six years, but thereafter the influence was positive. There was only a weak correlation between the number of seeds and the number of germinates the following spring.

By the autumn of 2008 liming had no influence on either the height growth or the dry-mass of ground vegetation. Liming had apparently increased the number of seedlings overall, but at the level of individual sites, a significant difference was only found at site A3 (Figure 8) where seedling numbers were lower than at the other two sites. Site A3 was younger, had a lower site index, a higher number of shelter trees $ha^{-1}$, and higher crown cover than the other two stands.

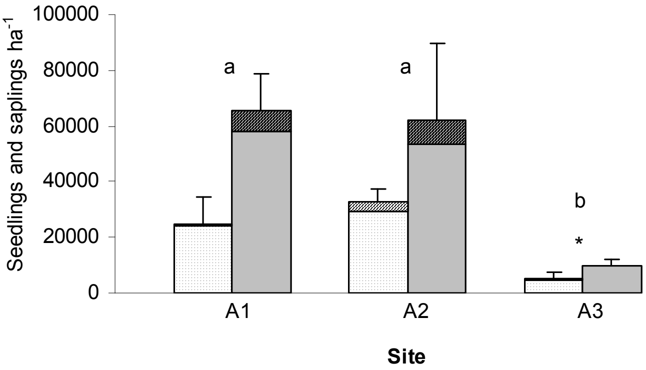


*Figure 8. Number of seedlings of beech and other tree species ha$^{-1}$ in autumn 2008 in un-limed plots (white columns) and limed plots (grey columns) at the three sites. Striped parts of columns indicate species other than beech. Columns indicate means, with SE bars above. Significant differences between limed and un-limed plots are indicated with an asterisk * ($p < 0.05$). At sites marked with the same letters there was no significant difference between numbers of seedlings.*

# 3 Discussion

## 3.1 Seed production of beech (Paper I)

The earliest records concerning mast years date from the 17th and 18th centuries and relate to the province Halland. A pupil of Carl Linné, Pehr Osbeck (1723 - 1805) (Fritz, 2000), declared that he had information "from reliable sources" about mast years (Osbeck, 1996). He also claimed that mast years did not always occur on the north side of the Hallandsås ridge, situated at the provincial border between Scania and Halland, at the same time as on the southern side. Linquist (1931) collected information on mast years for the period 1895 - 1929 in the forest districts of Halland and Scania, which also provided evidence of differences in the occurrence of mast years between the two provinces. However, such differences have not been observed in quantitative studies performed since 1993, including those conducted at four sites in Halland.

Information about mast years between 1926 and 1964 comes from four different sources, while the most recent period, 1974 - 2006, comprises information from three sources. Qualitative records from the beech seed-orchards, Albjershus and Ramsåsa (Figure 2), were compiled together with quantitative studies by Simak (1993) and the Southern Swedish Forest Research Centre.

Authors usually make their observations concerning mast years in different ways, using data from different sources (often second-hand information and hearsay), and sometimes one qualitative scale is transformed to another. Only two quantitative studies appear to have been performed in the most recent period. It should also be noted that there are some complete gaps in the data; for example, no records were found relating to the period from 1795 to 1895. However, even though this information may seem to be rather unreliable, a consistent trend has been revealed in all the periods covered by early investigations: e.g. the mean interval between mast years has been between four and six years since the end of the 17$^{th}$ century. Since 1974 this has decreased to 2.5 years, a decrease that is also evident in other European countries, e.g. in northern Germany the mean interval was eight years between 1869 and 1909, decreasing to only 2.8 years between 1987 and 2004 (Hase, 1985, Jenni, 1987, Bartsch et al., 1993, Lange, 1995, Schmidt, 2006).

The investigation into the influence of climate factors on flower bud initiation in the year preceding a mast year found strong correlation between higher than average temperatures and lower than average precipitation during July of the year preceding a mast year. However, Büsgen (1916) found the first indications of flower predispositions as early as in the end of May the year preceding the year of flowering. This implies that flower induction has already taken place by the end of April or beginning of May (Röhrig et al., 1978), and Kon et al. (2005) claim that low temperatures in late April to mid-May induce a productive mast in the following year for *Fagus crenata*. Is thus seems that the predisposition to flower is induced by April or May, but the further development of flowers depends on the weather conditions later in summer. This raises interesting questions worthy of further investigation.

The fact that a mast year did not always occur in Halland when it did in Scania is probably due to differences in climate. It has already been noted that several authors (Matthews, 1955, Matyas, 1965, Schmidt, 2006) state that a high summer temperature and low precipitation precedes a mast year, which was also confirmed in Paper I. It is also known that the more northerly sites have both a lower summer temperature and higher precipitation (SMHI, 2010). Thus, in some years, while these climate variables may not have been optimal for inducing flower buds in Halland, they may have been optimal in Scania. Another contributory factor may be the occurrence of frost during the time of flowering, since climate maps from SMHI show that May frosts occur more often in Halland than in Scania. The time of flowering is the most sensitive period, especially for the female flowers, and frosts or hard rains may destroy the flowers in some years. There is some evidence for this in the mast year 2004, in which there was relatively low seed production in Halland compared to Scania (Paper I). In that year there were several night frosts at the time of flowering in early May, which probably reduced the seed production in general and in particular at the sites in Halland. The mean seed production in Halland in that year was less than 300 000 seeds $ha^{-1}$ while in Scania 1 450 000 seeds $ha^{-1}$ were produced. However, no mast years that differ between these two landscapes in terms of timing or degree have been observed in any quantitative studies performed since 1993.

The reasons for the more frequent occurrence of mast years in the most recent period studied are probably changes in weather conditions at the time of flower initiation. Between 1974 and 2006 there have been 14 mast years, 11 of which were preceded by a July with a higher mean temperature than the 30-year July means (Figure 4). All non-mast years with a July mean temperature exceeding 15.8° C have been followed by a mast year.

A further factor that may contribute to the more frequent occurrence of mast years and increased seed production is nitrogen deposition. The annual deposition of nitrogen is currently approximately 20 kg $ha^{-1}$, which has resulted in a level of nitrogen storage of between 300 kg $ha^{-1}$ and 450 kg $ha^{-1}$ in southern Sweden (Westling, 2001). In Paper I it was shown that there is an increase of 160 000 seeds $ha^{-1}$ per site index unit (Figure 5). This corroborates the work of Nemec (1956) and Le Tacon and Osvald (1977), who found an increase in seed production and an increase in the frequency of mast years after fertilization, with the greatest impact resulting from nitrogen fertilizers. Further, in a study of beech forests in Sweden Falkengren-Grerup and Eriksson (1990) found there to have been a general (but very small) increase in beech site index over the period between 1947 and 1988.

Seed production in 1993 was low compared to 1992, which might be explained by a lack of sufficient nutrient resources for the production of seed in large quantities in a second, consecutive year (la Bastide and van Vredenburch, 1970), since resources had been heavily depleted by the production of seed in 1992. Flower and seed production make heavy demands on a tree's resources which would otherwise be allocated to the production of wood. Further evidence of resource depletion and re-allocation has been given by Hartig (1889), who has shown that nitrogen in the stem decreases after a mast year, and Holmsgaard (1955) who demonstrated that diameter growth decreases during a mast year and the two following years.

Although it has been claimed (Lindquist, 1931) that it is impossible for beech to flower and produce seeds in two consecutive years, it has been reported to have happened twice in Sweden during the most recently investigated period, and at least twice in other countries, e.g. in northern

Germany in 1989 - 1990 (Bartsch et al., 1993) and in the Netherlands in 1986 - 1987 (Hilton and Packham, 2003). Increased availability of nitrogen in the ground may have helped the trees to overcome the nitrogen deficit rapidly in these cases, and when the weather conditions were appropriate to flower and produce seed in a second year, even if seed production was somewhat lower. However, despite these recent observations, the occurrence of two consecutive mast years is still a very rare event that normally seldom happens.

In the study reported in Paper II, the stands in the late regeneration phase had relative low densities of shelter trees, but seed was nevertheless produced at the same level as in the stands in the early regeneration phase, which had a higher number of shelter trees. This may have been because in a sparse stand, after cuttings, the remaining trees develop and enlarge their crowns, which then receive greater amounts of solar radiation, thus enhancing the seed production (Dzwonko, 1990, Topoliantz and Ponge, 2000).

Seed production in mast years and non-mast years differs by several orders to magnitude. While the numbers of seeds during mast years are counted in millions, in non-mast years they are counted in thousands, making it easy to separate a mast year from a non-mast year.

When the mean July temperature exceeds the value necessary for flower formation, it also influences the amount of seed that will be produced (Schmidt, 2006). The higher the July temperature, the more flower buds are initiated and the more seeds will be produced in the following year, as long as other disturbances, such as frosts during the time of flowering, do not hamper the seed production. In recent years, there has been an increase in the temperature difference between warm and cold July months which would be expected to lead to increased seed production in mast years preceded by a year with a warm July. However, records of seed production since 1989 show only a slow increase in number of seeds $ha^{-1}$.

## 3.2 An alternative beech regeneration method (Paper II)

Seven mast years were recorded during the 14 years study. Naturally, this period of intense seed production provided good opportunities for good regeneration results. High frequencies of seedlings were also recorded in most of the early and intermediate regeneration phase stands (Figure 6).

Although this was mainly related to mast years, not all mast years gave rise to large frequencies of new seedlings. Regeneration results can improve if the shelter is cut in the winter following a mast year, since this reduces the competition for belowground resources (Bolte and Roloff, 1993, Bílek et al., 2009) and more ground vegetation has not yet established. This effect was most clearly observed in the early regeneration phase stands with medium and high site indices in 1999 and 1996, respectively. The 1995 mast year gave rise to many seedlings in both the early and intermediate regeneration phase stands where the seed-fall was abundant. More importantly, however, were the weather conditions in spring of 1996, which were characterized by high levels of precipitation, and probably enhanced germination and establishment of new seedlings (Piovesan and Bernabei, 1997).

In the early regeneration phase stand with the low site index few seedlings developed during the whole period of the investigation. The height development of the seedlings was also poor, with all cohorts having a mean height of less than 30 cm in 2005. This was probably due to severe competition from the adult stand, in which the density was only reduced from 190 stems $ha^{-1}$ to 164 stems $ha^{-1}$ in 2000. This most likely resulted in low amounts of solar radiation and competition for water, and, therefore, reduced the height growth of seedlings (Ammer et al., 2008). In general, the shelter stands on sites with low site indices should be sparser than those on sites with higher site indices (Bjerregaard and Carbonnier, 1979); however, despite its low site index, this early regeneration stand had the highest density of stems in the entire investigation, even after the cutting in 2000. A dense stand severely hampers the germination, establishment and early growth of seedlings (Agestam et al., 2003). The soil temperature remains low due to the reduction in incoming solar radiation (Burschel and Huss, 1964), and thus retards the decomposition of litter (Harley, 1939), which together with competition for water and nutrients hinders germination and establishment (Madsen, 1995b, Ammer et al., 2008). Low light levels, low soil temperatures, and competition from the adult stand, also lessen the height growth of new seedlings (Madsen and Larsen, 1997, Küssner and Wickel, 1998, Ammer et al., 2008). The fine-root growth of the seedlings is more limited to the uppermost parts of the soil, due to competition from the old stand, and has a lower fine-root weight compared to seedlings under a more sparse shelter stand (Bolte and Roloff, 1992). The early regeneration phase stands also yielded little field vegetation in 2005, at only 31kg dry weight $ha^{-1}$, which is also indicative of severe competition from the shelter trees. This highlights the importance of performing adequate thinnings in the stands as the time for initiating regeneration approaches (Dengler, 1972). This will tend to improve the site conditions and result in a thinner organic layer and increases in soil temperature, both of which improve seedling establishment. After a thinning, the crowns of the remaining trees enlarge and thus improve the prospects for good seed crops (Topoliantz and Ponge, 2000).

In the early regeneration phase stand with the high site index, the last shelter trees were cut late in 2006. This implies that it took 16 years from the start of the regeneration period, i.e. the time period from when seedling establishment started, until the last shelter trees were cut, to get an adequate regeneration. This cannot be considered as a particularly long regeneration period compared to that of regeneration by the traditional method, in which the shelter trees mostly are kept for a similar length of time.

The high density of shelter stems in the low site index stand in the early regeneration phase was due to the low cutting activity at this site. The reason for not reducing the number of shelter trees to any great extent might have been the poor regeneration, and a concern that a cutting might increase the growth of (and hence competition from) field vegetation, or it might have been due to the forest manager deciding to wait for better market conditions and for the shelter trees to increase in size.

The two intermediate regeneration phase stands did both pass into the late regeneration phase during the study period. Both had a seedling number between 20 000 and 30 000 seedlings $ha^{-1}$ in 2005, a result of good conditions for seedling establishment in the early and intermediate phase. In the low site index stand the last shelter trees were finally cut early in 2009 and in the high site index stand late in 2006. The amount of seedlings $ha^{-1}$ in these stands was probably higher at this point of time compared to the number of seedlings in the late regeneration phase stands when the shelter trees were cut.

In contrast to the intermediate regeneration phase stands practically no new seedlings were established in the late regeneration phase stands during the observation period. This was probably due to competition from the present regeneration, which had a mean height of about 1 m in 1992, and the fact that most of the areas where it was possible for seedlings to establish were already occupied by seedlings of beech or other species, or by ground vegetation. When the last shelter trees were cut, the regeneration in the low site index stand, which mainly originated from earlier regeneration phases, had reached a mean height of 2.5 m and consisted of about 10 000 beech saplings per hectare, together with 6 000 saplings of other species per hectare, mainly pine (*Pinus sylvestris*). In the high site index stand, the regeneration had a mean height of 3.5 m and was composed of about 7 000 beech saplings per hectare and 4 000 saplings of other species per hectare, mainly ash (*Faxinus excelsior*).

Pre-commercial thinnings, principally to remove "wolf-trees" and other undesirable species, were performed simultaneously with the cuttings in the adult stand. This reduced the number of saplings, especially in the low site index stand (Figure 6).

An important question is if the number of saplings can be considered to be high enough to build up a new stand of good quality. Huss (1972) claims that at the height of 1 m, 20 000 seedlings ha$^{-1}$ is a minimum, while Bjerregaard and Carbonnier (1979) had the opinion that 14 000 seedlings ha$^{-1}$ in the dominant tree class is needed. As can be seen in Paper II the number of seedlings in the low site index stand was between 15 000 and 20 000 beech seedlings ha$^{-1}$ at the height of 1 m, while the number in the high site index stand was about 9 000 beech seedlings at the height of about 1.2 m. To this comes the number of seedlings of other species. An additional factor is the quality of the new regeneration, in which the denser low fertility stand had about 400 potential final crop trees ha$^{-1}$, and the sparser high fertility stand had about 800 potential final crop trees ha$^{-1}$, but as is mentioned this number may change. The future low fertility stand will probably consist of a beech dominated stand mixed with mainly Scotch pine. This may be an advantage, since the mixture of the shade tolerant beech and the more shade-intolerant Scotch pine is shown to enhance the production (Bonnemann, 1939, Pretzsch, 2004). The high fertility site, however, may not receive this advantage, since the additional species in this stand mainly consists of ash, that suffer severely from the ash disease caused by the fungi *Chalaria fraxinea* (Barklund, 2008). However, in this stand the number of potential final crop trees was high, and must be considered to be enough for the new stand.

In the late phase stands, there may have been a problem with the establishment of new seedlings during the long period between the mast years of 1976 and 1983 (Paper I). During his period, these stands were probably in the early regeneration phase when any cuttings that might have been performed would not have enhanced the establishment of new beech seedlings, but may instead have encouraged ground vegetation and other tree species, which would have subsequently hindered the establishment of beech seedlings.

At the beginning of the regeneration period, seedling distribution was uneven, but as increasing numbers of the $1m^2$ subplots were gradually colonized, the seedlings became more even distributed. This process was most clearly seen in the early and intermediate regeneration phase stands after the mast year of 1995, when favorable weather conditions improved the establishment of seedlings in the subplots, including those in which it had previously been difficult to establish new seedlings. In the late regeneration phase the situation was more static, and after 1996 no new subplots were colonized. When the last shelter trees were cut about 60 % of the subplots in these stands were colonized. In another study of the natural regeneration of beech, in which the traditional method, including site preparation, was used (Agestam et al., 2003), only 35 % of subplots in undisturbed ground were colonized with beech seedlings seven years after establishing a shelter. However, although the subplots in the cited experiment were smaller, 0.67 $m^2$, the findings indicate that the site conditions are more conductive to germination and establishment when the alternative method is used than when the traditional method is used. With the traditional regeneration method, seedlings are most abundant where they have been concentrated in areas where site preparation has been performed. On undisturbed ground, however, they are few and unevenly distributed.

In the early regeneration phase, seedlings in the < 1 m height class dominated, with only few seedlings in the other height classes. In the intermediate regeneration phase, the height distribution was the widest with most seedlings in the < 1 m and > 2 m classes, while only a few seedlings were found in the 1 m – 2 m class. In the late regeneration phase stands, however, few seedlings were shorter than 2 m. Most of the smaller seedlings in the intermediate regeneration phase stands were probably out-competed when the stands reached the late phase. It seems probably that competition, together with the removal of fast-growing individuals during the pre-commercial thinnings, leads to a relatively even height distribution by the end of the regeneration period.

In the autumn of 2006 the numbers of potential final crop trees in the two late regeneration phase stands were estimated to be about 400 and 800 $ha^{-1}$ in the low and high site index stand, respectively. The proportion of wolf-trees was low, at about 4 % in both stands. The number of crop trees in the high site index stand may have been high, despite it having the lowest overall stand density, due to its high site index and better height development of saplings. Taller trees might also be more readily classified as potential crop trees. The dominant and co-dominant beech stems, which were selected for quality estimation, had a mean height of 7.5 m in the low site index stand, and 9.0 m in the high site index stand. Naturally, it is difficult to forecast the future quality at this early stage of the stands, since changes in quality are common in young beech stands (Bjerregaard and Carbonnier, 1979).

There is no fixed regeneration period within the alternative method. The forest manager has the possibility to choose the regeneration period not only depending on the regeneration result, but also to influence the value of the shelter trees. Higher income may be possible if the shelter trees reach higher diameters and if fluctuations in market can be used. On the other hand, the study presented in Paper II showed a low volume yield in sparse shelters. There is also a risk for damages to the shelter trees, especially red-heartwood which is a problem connected to long rotation periods for beech (Knoke and Schultz Wenderoth, 2001).

The main conclusion from Paper II is that the alternative natural regeneration method, regardless of site index, results in adequate regenerations that originate from the seed production during several mast years. Ground conditions, and the establishment and development of seedlings, are regulated by several judicious cuttings in the old stand. Short intervals between mast years, and adequate thinnings in the mother-stands, promote seedling establishment.

The alternative method for natural regeneration of beech has many advantages. A closer–to-nature regeneration method, without site preparation, is now more desirable than ever before, since it not only benefits biodiversity, but also helps to conserve the historical and cultural heritage as well as recreational areas that are highly appreciated. The method also has economic advantages; the cost of site preparation is avoided and it is possible, by increasing the length of time that shelter-wood is left in the old stand, to let more trees grow to dimensions at which they are most valuable. Sometimes the regeneration period can be lengthy, but the method renders it possible to adapt management interventions to the market situation, to increase the dimension of high quality shelter trees and thus increase the profitability of the regeneration. There are also several practical advantages such as the forest manager is not dependent on a single mast year and cuttings may be performed at the most suitable times.

## 3.3 Liming and the traditional method for natural regeneration of beech (Paper III)

Liming influences the forest ecosystem in many ways. It increases the soil pH (Ljungström et al., 1990, Bressem, 1998, Ammer and Huber, 2007) and concentrations of available nutrients (Bressem, 1998, Ljungström and Nihlgård, 1995), which in turn influences other processes, such as the growth, development and population dynamics of soil fauna (Muys, 1989) and ground vegetation (Hartmenn et al., 1956).

Seed production was not increased by liming. Other authors have found significant increases in seed production after fertilization (Führer and Pall, 1984), and Spellman and Meiwes (1995) showed that liming may continue to affect site index positively at least 58 years after liming. As is shown in Paper I, seed production increased with increasing site index, and a tendency in this direction was also observed in this study, but the increase was not significant, probably due to too few observations.

Liming positively influenced the amount of ground vegetation at Site T3, but it was also abundant in the un-limed plots at this site. At the other sites liming had no significant influence, probably because only small amounts of vegetation were present in them that could act as a source from which vegetation could spread further into the stand. The small amount of vegetation at these other sites may be explained by their lower site indices and other unfavorable conditions, e.g. a thicker humus layer (Falkengren-Grerup and Eriksson, 1990).

The effect of liming on seedling emergence differed between sites. A positive effect was only found at Site T1, the low fertility site (F 24), but the number of seedlings there was far too low for it to be considered as an acceptable regeneration (Huss, 1972, Henriksen, 1988). No difference in seedling emergence was found between limed and un-limed plots at Site T2, but at this site the number of seedlings was sufficient to form an adequate regeneration. At Site T3, however, although the number of seedlings was generally high, they were significantly higher in the un-limed than the limed plots. It should be noted that the results from Site T3 are not in accordance with those reported by other authors (Röhrig et al., 1978, Bressem, 1988) and they are difficult to explain in terms of the factors and variables considered in the present study.

Various factors may explain the low germination rate observed at Site T1. Firstly, this site had the thickest humus layer and a thick humus layer is known to adversely affect the germination of seedlings by making it difficult for the roots to reach the mineral soil where water is available (Madsen, 1995b). Secondly, a thick humus layer often harbors an abundance of diverse fungal pathogens, such as *Rhizoctonia solani* and *Cylindrocarpon destructans,* which are known to attack nuts and roots of newly germinated seedlings (Dubbel, 1989). Thirdly, even after shelter-wood cutting, the density of shelter-wood stems was highest at this site, and lowest at Site T3. Normally, the opposite would be expected since sites with high site indices generally carry more shelter-wood stems $ha^{-1}$ than sites with lower site indices (Bjerregaard and Carbonnier, 1979). The competition for water and the low amounts of solar radiation reaching the ground at Site T1 may therefore have hampered the germination there (Bourne, 1945, Bílek et al., 2009). Finally, the biomass of earthworms was higher in the limed than un-limed plots at all sites, which may have had some additional positive influence on seedling emergence at this site.

Liming negatively affected the number of seedlings emerging at Site T3, while un-limed plots had an abundant regeneration. At this site the humus layer was relatively thin in both limed and un-limed plots, and the competition from the shelter stand was low. The amount of field vegetation, however, was higher on the limed plots, where it probably competed both for solar radiation and water. This was most obvious in areas where no site preparation had been performed, i.e. the control areas, where the number of germinates was significantly higher on the un-limed plots, and the amount of competing ground vegetation was lower. On limed plots, more seedlings were found in areas that had had any type of site preparation, than in the untreated control areas. The reason for this enhanced difference between limed and un-limed plots on untreated ground may, again, be related to the amount of other vegetation present. It is also possible that the higher pH after liming increased the aggressiveness of the pathogen *Rhizoctonia solani,* a phenomenon that has been previously demonstrated by Perrin and Muller (1979) and Dimitri and Bressem (1988).

Generally, the influence of site preparation on seedling numbers was surprisingly low. No effect at all was seen at Site T1, at Site T2, site preparations seem to have had an effect on the un-limed plots but not on the limed plots, while a slight effect was observed for both treatments at Site T3. In contrast, Agestam et al. (2003) found significant differences among all types of site preparation (including the untreated controls), with the highest number of seedlings in mineral soil plots, and the lowest number in the untreated controls.

Height growth of the seedlings was not influenced by liming but was highly correlated with shelter stand density: the largest height growth occurring in the stand with the lowest number of shelter stems, and least in the stand with the highest number of shelter stems. These results are well in line with the findings made by Ammer et al. (2008), that height growth is most dependent on the incoming solar radiation and water supply.

Earthworms are known to improve soil conditions by lessening soil compaction and enhancing degradation processes (Muys, 1989). The mass of earthworms, and in some instances their numbers, increased after liming. This increase probably contributed to a tendency for the humus layer to be thinner in the limed plots at all sites, but the humus was only significantly thinner at Site T3, the stand with the high site index, which also had the highest number of earthworms. Accordingly, the low site index site, Site T1, had the thickest humus layer and the lowest number of earthworms.

By the autumn of 2008, survival rates at the different sites closely reflected the patterns of seedling emergence; the best survival rate being found at Site T3, which had the highest number of seedlings, and the lowest survival rate at Site T1, which also had the lowest number of seedlings. In general, seedling survival was higher in limed plots. This resulted in a change at Site T3, which no longer had significantly more seedlings in the un-limed plots in 2008. The higher seedling survival rate in limed plots could be related to the greater abundance of earthworms in the limed plots at all sites. Site T3, for instance, which had the highest survival rate, also had the highest number of earthworms.

A secondary chemical with defensive potential, chlorogenic acid was found in higher concentrations in beech leaves sampled from seedlings in the limed plots. This compound is thought to hinder fungal pathogenes' abilities to penetrate the cell walls of beech leaves, thereby reducing the rate of infection (Bahnweg et al., 2005). On the other hand, chlorogenic acid may also inhibit the growth of fungal endophytes that live in beech leaves without causing symptoms, but act as defensive agents against other pathogens and herbivores (cf. Arnold et al., 2003). Since the ecological consequences of variation in chlorogenic acid concentration may be diverse, complex, and partly counteracting, further research is needed to evaluate the practical effect of increasing chlorogenic acid in beech seedlings by liming.

The results from the experiment described in Paper III are partly unexpected, especially regarding the influence of liming on seedling emergence at the different sites, and the low effect of site preparation. The chemical analyses of soil samples showed that, 17 years after liming, pH values had increased both in the humus layer and in the mineral soil, but N, P and K contents had not increased in either the limed mineral soil or the limed humus layer. The Ca content was, however, high in the humus layer, indicating that the full effect of liming has not yet been reached.

Studies in Germany on the natural regeneration of beech (Becker, 1983, Dimitri and Bressem, 1988), and in a sowing experiment (Küssner and Wickel, 1998), have reported a positive effect of liming on seedling numbers. However, in another sowing experiment, in which liming and sowing were performed simultaneously, no effect of liming was found (Ammer et al., 2002). The similar result was recorded in a Swedish study on the natural regeneration of beech, in which the liming was performed at the same time as the seed-fall (Ljungström et al., 1990).

Bressem (1988) found the best germination and further development of seedlings to occur at pH(KCl) values of 4.3, while a pH of 3.0 severely inhibited plant development, and pH > 6.0, was unfavourable for the overwintering of the seeds, as was liming in the mast year itself. Bressem (1988) further recommends that liming should be done at least 3 - 5 years and preferably 15 – 20 years, before the time for regeneration. Similar recommendations are given by Röhrig et al. (1978) who suggest an interval of 10 - 30 years between liming and beginning a natural regeneration.

The conclusion from this paper is that liming may be a suitable method for improving the natural regeneration of beech at sites with a low site index. Liming resulted in an increase in earthworm abundance, and an increase in the ground vegetation at sites where it was already present at the time of liming. Liming also increased the decomposition rate of the humus layer and improved the survival of seedlings.

## 3.4 Liming and the alternative method for natural regeneration of beech (Paper IV)

The alternative natural regeneration method of beech is often said to be beset with certain drawbacks, namely a longer regeneration period and the establishment of insufficient seedlings. To evaluate the regeneration resulting from the alternative natural regeneration method combined with liming, three sites were studied, two of which were limed in 1991 and the other in 1993.

Liming positively influenced seed production significantly at only one site, in only one of the seven mast years during the study period; but at that site no difference was found in the number of germinates in different plots in the following spring. Moreover, the difference in the number of germinates on limed and un-limed plots in the years after mast years cannot be explained by differences in seed production in the respective preceding years. Furthermore, the correlation between numbers of seeds and numbers of germinates was low ($R^2$=0.20), a result which may be explained by the fact that most seeds never germinate due to damage caused by fungi or predators (Dubbel, 1989, Harmer, 1994); Linnard (1987), for instance, found that 40 % of seeds disappear within a month after seed-fall.

Seed production was higher at Sites A1 and A2, than at Site A3 in the years 1995 - 2002, probably for several reasons. The stand at Site A3 was just under 60 years old at the time of liming, and at this age the stand had just started to produce seed, while the peak of seed production occurs at ages of 100 - 150 years (Dzwonko, 1990). The stands at Sites A1 and A2 were 88 and 108 years, respectively at the time of liming, which at least partly explains the higher seed production in those stands. A further contributory factor is related to the high number of stems present at Site A3. Trees in a dense stand have small crowns that, nevertheless, shade each other, while trees in a sparser stand develop bigger crowns that receive more solar radiation, which positively affects the set of flower buds and seed production (Dzwonko, 1990, Topolintz and Ponge, 2000).

The accumulated effect of liming on seedling emergence was negative during the first six years, but after eight years or more liming had a positive effect. Several authors recommend a lengthy interval between liming and the regeneration event. For example, Röhrig et al. (1978) recommends an interval of 10 - 30 years, while Bressem (1988) suggests an interval of at least 3 – 5 years, and 15 - 20 years for the best effect. Bressem (1988) also state that liming in the mast year itself, and pH values above 6.0 impair the overwintering and vitality of seeds. The later may account for the observed negative effect of liming on seedling emergence during the first six years after liming. Site A3, for instance, which was limed in 1993, had significantly fewer germinates in limed plots one and three years after liming.

By the autumn of 2008 liming had significantly increased the number of seedlings of beech and other species (Figure 8). At the level of individual sites, however, the positive effect of liming was only significant at Site A3. The number of seedlings was similar at Sites A1 and A2, in both limed and un-limed plots, but significantly lower at Site A3. One explanation for this result might be the denser stand at Site A3; in 2009 Sites A1 and A2 had 102 and 108 stems $ha^{-1}$ respectively, while Site A3 had 148 stems $ha^{-1}$. Similarly Sites A1 and A2 had crown covers of 86 % and 84 %, respectively, while at Site A3 it was 93 %. According to Bílek et al. (2009) a crown cover exceeding 80 % reduces the survival of seedlings. The consequent decrease in the amount of solar radiation reaching the forest floor results in a low ground temperature, which retards the decomposition of litter (Harley, 1939), and a thick organic layer makes it difficult for the roots of the germinates, which have limited resources, to reach the mineral soil below (Bílek et al., 2009). There is also a stronger competition from trees in a dense shelter stand for water and nutrients.

Liming had no influence on seedling height growth, in contrast to the significant influence observed in other studies (Bressem, 1998). It is possible that the greater amount of ground vegetation in the limed plots at Site A1 and A2 competed more severely for water and nutrients, and thus reduced height growth to a level equal to that seen in the un-limed plots.

Liming generally increased the pH of the soil, but had no influence on its N, P or K contents. However, the concentration of Ca, was still high in the humus layer, indicating that liming not yet reached full effect. The length of time required for the treatment to take full effect has been stressed in several studies. For example Röhrig et al. (1978) suggests a time span up to 30 years for best effect and Bressem (1988) emphasize the importance of waiting at least 3 - 5 years before the regeneration event to avoid the negative influence that was observed the six first years in this experiment. This lack of effect on seedling emergence when liming was applied either at the time of seed-fall, or coincident with sowing, has also been observed in other studies (Ljungström et al., 1990, Ammer et al., 2002).

Crown cover seems to be a more important factor than seed production for generating an adequate number of germinates in years following mast years. Even though the number of seedlings increased in the limed plots, liming, *per se,* does not seem to be necessary to achieve an adequate regeneration.

The results reported here highlight the importance of an interval between liming and the start of the regeneration event. In this experiment liming was done too close to the start of the regeneration. However, liming performed at an appropriate time can probably shorten the regeneration period and result in a good regeneration. The results show that liming may be a good tool for improving the alternative beech regeneration method.

## 3.5 Final discussion

The only practical and economical reasonable way to regenerate beech stands in Sweden is by natural regeneration. Important factors for success are among others the occurrence of mast years and the seed production. In Paper I it is stated that mast years have occurred more often since 1974, compared to earlier time periods. This facilitates regeneration by giving the forest managers more frequent opportunities to regenerate, and fluctuations in the timber market might also be less dramatic. If a regeneration attempt ends in a failure, it will be easier to repair since the probability for a new mast year to appear before the regeneration area is occupied by ground vegetation, is higher. It will also be easier to fill in gaps where seedlings are missing after a regeneration event.

The alternative natural regeneration method, described in Papers II and IV, where the new regeneration originates from several mast years, is also favored by the more frequent mast years. This may decrease the regeneration period, which sometimes is considered to be long. The forest manager also has more frequent opportunities to find a density of shelter trees suitable for seedling establishment, which is important, even though it is expensive to perform several cuttings.

In Paper I it is stated that the seed production increases with increasing site index. This conclusion is drawn after analyzing seven mast year seed-falls from 12 sites with a site index varying from F20 to F36. It is logical that seed production increases with increasing site fertility and this study is suitable for this sort of question. This finding is not confirmed in any of the other studies, in which seed-falls were recorded as well. The reasons are inadequate site index classification (Paper II), too few stands (Paper III and IV) or too few mast years (Paper III).

In the literature there is no consensus of what quantities of seeds that should be produced during a year for the year to be considered as a mast year. Instead, a mast year is said to be a year when big amounts of seeds are produced over a wider geographical area and that it possible to regenerate a beech stand (Wachter, 1964, Perrins, 1966). Henriksen (1988) claims a minimum number of viable seeds $ha^{-1}$ needed, while Huss (1972) state a minimum number of seedlings $ha^{-1}$ after the first growing season. However, from the records of seed-falls in Paper I, it is quite clear that there is a large variation between mast years and the diminutive amount of seeds in the non-mast years. Up to these records, there is no reason to be in doubt if a year is a mast year or not, since the number of seeds in a mast year is counted in millions, and in a non-mast year in thousands.

No significant positive influence of liming on seed production was found in the studies where liming and natural regeneration were combined. Liming is considered to have a fertilizing effect since the amount of available nutrients increase (Bressem, 1998), and fertilizing has increased seed production in other studies (Nemec, 1956, Führer and Pall, 1984). However, the liming effect on seed production may have been restricted, since the treatment plots in both studies had a size of only 25 × 25 m. The seed traps were placed in the middle of each treatment plot, or as far away as possible from the opposite treatment, to catch the seeds from the trees affected by the treatment in the plot. It is possible that parts of the root system of a tree had been growing in both treatments, and also that the seed from a tree situated in a plot with one treatment had been caught by a seed-trap situated in the opposite treatment.

The number of seedlings after mast years was not highly correlated to the seed production the preceding year in any of the studies described in Paper II, III or IV. The amount of additional seedlings depends on a number of things, for example the amount of seeds, the climate and the stand management actions the first years after seed-fall. In the experiment of natural regeneration performed by the alternative regeneration method (Paper II), the highest seedling/seed ratio was found when a cutting had been done in the shelter-wood during the winter after the seed-fall. This improved the conditions for seed germination and establishment by decreasing both below- and above-ground competition. Also some kind of soil disturbance was caused by the cutting and the forwarding of the timber, resulting in slight site preparation enhancing the germination.

It is obvious from all three studies of natural regeneration (Paper II-IV) that the influence of the shelter-stand is important for seedling establishment and early growth. A sparse shelter-stand has low fine-root content (Bolte and Roloff, 1993) that competes less for below-ground resources, which are necessary for the new seedlings to establish (Ammer et al., 2008). In accordance to this, stands with a dense shelter compete severely for both below- and above ground resources, resulting in a low seedling establishment rate and also poor height growth among existing seedlings (Ammer et al. 2008, Wagner et al., 2009). However, below-ground resources are not the only factor influencing establishment of new seedlings; a thick humus-layer is also known to aggravate the germination (Bílek et al, 2009), but is also often a result of a dense shelter (Watt, 1923). A low seedling establishment is also observed in all three studies in the sites with a high shelter-wood density.

Bílek et al. (2009) stress the importance of having a shelter-wood of an adequate number of stems $ha^{-1}$ which should have a crown cover not exceeding 80 %. However, it is easy to understand a cautious attitude to cuttings in the shelter-woods. A very heavy cutting may lead to an invasion of ground vegetation that will be a severe threat to establishment of seedlings, and also hard to get rid of when it is well established. Leder et al. (2003), for example, found in a beech sowing experiment under a shelter of Norway spruce, the natural regeneration of Norway spruce to overgrow the beech seedlings when the crown cower was reduced to 60 %.

The conclusion from Papers II – IV, in the aspects of seedling establishment and height growth, is the importance of decreasing the below-ground competition to increase the germination and establishment of new seedlings, and to allow solar radiation to reach the ground to enhance height growth. These results are in accordance with the experiences of the forest manager responsible for the stands used in the study presented in Paper II. He stressed the importance of opening up the closed stands to facilitate the seedling emergence and development of established seedlings.

The mortality among new beech seedlings is high (Huss, 1972, Agestam et al., 2003). In Figure 6 from Paper II, in which the alternative beech regeneration method is studied, the numbers of new seedlings can be seen every year in the seven stands, It seems like the mortality was the highest when the contribution of new seedlings was the highest, which may be due to high competition and the fact that pests spread easier when the regeneration is denser, since the distance between the seedlings is shorter (Augspurger and Kelly, 1984). Ungulates seem to gather when the food availability is large (Olesen and Madsen, 2008), and the same may be true for rodents which also find shelter under a dense regeneration. This may be a disadvantage for the traditional approach of natural regeneration, in which there is a high concentration of seedlings in the bare mineral soil. Since it is shown that a sparser regeneration suffers less from pathogens, the alternative natural regeneration method has an advantage in a sparser but more even distributed regeneration.

In Paper III, liming significantly increased survival at one site and a tendency for higher survival can be observed in the other sites as well. The higher survival might be due to the increased earthworm community which is known to improve the soil conditions by decreasing the soil compaction and increasing litter decomposition, thereby facilitating germination of seedlings (Muys, 1989). Another factor may be the higher concentration of a secondary chemical with defense potential, chlorogenic acid, found in beech seedlings from limed plots. However, since the effect of this secondary metabolite is partly counteracting, no conclusions can be made so far but further research may increase the knowledge in this area.

Positive effects of liming on seedling emergence and seedling height growth, as well as increased nutrient availability in the ground, are reported by several authors (Spellmann and Meiwes, 1995, Bressem, 1998, Küssner and Wickel, 1998). The influence of liming found in Papers III and IV is weak and only partly positive for seedling emergence, and at Site T3 (Paper III) it is negative. No significant effect of liming was found for height growth in any of the studies.

Soil samples from limed plots showed increased pH values, both in the humus layer and in the mineral soil, but any increase in N, P, K or Mg contents were not detected, compared to the un-limed plots. The Ca content was, naturally, higher in the limed plots, especially in the humus layer. The high amount of Ca in the humus layer indicate that the pulverized limestone has not yet reached its full effect, 17 years after liming. Timing of the liming is decisive; Bressem (1988) recommends liming to be done 15 to 20 years before starting to regenerate, while Röhrig et al. (1978) recommends 10 to 30 years to be an appropriate time.

Liming of forests also has negative effects; it will initial lead to unnatural high pH values of the top soils which may disturb the soil ecosystem, like mycorrhiza community and diversity of pathogens, and it may increase nitrogen leakage and cause damage to ground flora (Bishop and Laudon, 2003). For these reasons liming of beech regeneration areas should be done with caution.

# 4 Future aspects

Seed production and mast years have been shown to be important factors in the natural regeneration of beech. To enhance the planning of regeneration, it would be useful to have a simple tool for forecasting mast years and the amount of seed that is likely to be produced. Such a tool could be developed from climate variables, site index, and historical records of the pattern of occurrence of previous mast years.

A decrease in beech wood production due to flowering and seed production was previously found by Burschel (1966) and Sawada et al. (2008) showed a decline of basal area increment during good seed years for *Fagus crenata* and *Fagus japonica*. With the apparent increase in the frequency with which mast years currently occur, a severe loss of increment may be expected. Whether the situation has altered due to increased nitrogen deposition (Westling, 2001), which may have reduced the loss in diameter growth, is a question that merits further investigation.

Quantitative data on seed production have been collected since 1989 from parts of southern Sweden where beech has its main distribution. These data form a unique series for Europe, and continuing the collection of these data is of vital importance since it will build on the existing 21-year data-series to form a valuable resource on which to base further research.

The alternative method for natural regeneration of beech has many advantages, but one of the drawbacks may be the longer time taken to establish an adequate regeneration compared with the traditional regeneration method. The shelter trees are increasing in diameter, but there may also be a risk for different calamities, like red-heartwood (a feature that often impairs the quality and value of beech timber) or wind-damages. However, this period may be shortened in several ways. Notably, it may be possible to adapt the end of the thinning program to the proposed method, in such a way that the ground conditions improve and thus enhance the germination and establishment of seedlings.

As shown in Paper IV, liming can shorten the regeneration period and this technique should be investigated further.

The shelter stand is an important tool that can be used to steer both seedling establishment and early growth. The way in which the density and other properties of the shelter stand could be managed to enhance the regeneration result are also worthy of further investigation.

The quality of wood from the shelter trees is highly important, since it is removed at the time in the rotation period when it has reached dimensions at which it is most valuable. However, the influences of possible treatments on the abundance of red-heartwood and other factors that influence the quality of the wood in the shelter stand warrant further investigation.

Stands of trees regenerated by the alternative method probably develop distribution patterns that differ from those of stands regenerated by the traditional method, both spatially but also in height. How this will influence the practice and costs of pre-commercial thinning programs is an important question.

The estimate of the quality of the new stands indicated that there would probably be an adequate number of crop trees at the final cutting, but at this early stage in the development of the new stands it is difficult to make accurate predictions of quality. It will therefore be necessary to undertake further studies on the future quality of the regeneration.

Even though the experimental studies presented here were large, being based on seven stands, it is important to apply the method experimentally to sites with a wider range of conditions, to evaluate responses to the method in other situations, before it is adopted at a large, commercial scale over a much broader variety of sites.

Since soil acidity continue to increase in Sweden (The Swedish Environmental Protection Agency, 2009), it is highly likely that the natural regeneration of beech on poor soils will be even more problematic in the future. Paper III showed a positive influence of liming on the number of germinates in a stand with a low site index, while at the two better sites liming had either no influence or a negative influence.

The six sites used in these studies form a part of a larger set of twelve sites which were all limed at the same time with the same dose of pulverized limestone. Of these twelve sites, five are to be regenerated in the near future. Further studies may help to explain some of the apparently conflicting results observed in the studies presented here. In addition to the factors and variables considered in the investigation presented in Paper III a range of other quantities should also be measured in the future studies, to shed further light on the subject. Additional data, which may help to explain the results already acquired include those that could be obtained from, for example:

- analyses of soil fungi and the mycorrhiza community
- further investigations into the presence and influence of secondary plant products as defense chemicals
- extended inventories of injuries
- chemical analyses of beech nuts, seedlings and ground vegetation
- more detailed measurements of solar radiation, edaphic factors such as soil water potential

Another important field of study that should be undertaken concerns whether the fertilizing effect of liming influences the growth and yield of beech.

Many of the aspects listed above also hold true in respect of the study presented in Paper IV, in which the influence of liming on the alternative natural regeneration method on beech was investigated. In that experiment, the interval between the application of the pulverized lime and the time when a positive effect on seedling emergence was detectable was six years. This time interval probably differs according to specific characteristics of various types of sites. The quantity of limestone applied and its grain size are also likely to be of important factors, relevant to both regeneration methods that should be investigated further in order for liming to be conducted as cost-effectively as possible.

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# Acknowledgements

The end.

Yes, this is the end of my thesis, but also the end of an almost 21 years long period at The Department working as a forest technician, which will be followed by a new, but shorter, period as a phd, if I pass, or otherwise continuing as a forest technician, if I fail.

When I started my employment her I never had a thought of any further studies, but after some years I was offered the opportunity to be a phd student, and after some persuasion I accepted. It was Pelle who pushed me to continue to work with the experiments I had worked with in the forests and who encouraged me in my studies. Pelle is a very honest man, he always tells you the true, and after his words of prudence: "Yes, Rolf, you are stupid, but there are those even more stupid who have became a phd", I saw some light in the tunnel. Anyhow, after a couple of years as my supervisor he could not take it anymore, left his position as a professor in silviculture, and moved far away.

My next supervisor to wear out was Eric. And he really has done a great work, especially the last days since it tomorrow is time to bring the thesis to the printing office. My first working week at the Department, Eric and I spent together in a mixed stand experiment close to Finspång. It was really cold, but from the very beginning it was very nice to work together with Eric. Sometimes you find a person to work with, when the work runs smoothly without to much of explanations, both just knows what to do and does it in the right moment. In this way it has continued for more than 20 years (!!) We have some nice days, even if the weather is bad, out in the forest now and then, and especially if we can convince the landowner that a stand has to be thinned immediately, so that Eric and I have to do it. I am looking forward to more of these days, isn´t it time for Bjersjölagård soon?

This was only two persons. There have been a lot of people at the Department during the years, many of them I have worked together with in field experiments, living at Youth hostels and cooking food together with. This is a very good way to learn to know people and I can´t remember any time when it has been unpleasant.

Magnus Pettersson at Asa experimental forest was the first forest technician to start with phd studies here in the south, followed by Kristina Wallertz. We had worked and laughed together a lot up in Asa earlier, and it was really good to see the development. Kristina and I have been phdstudents together and had the same courses, statistics for example, and it has been good to have her by my side, a long distance side, to share problems with and long back to "the good old days" as a forest technician, with. Also Oriana Pfister and I have studied together and encouraged each other. During the last year Maria Birkedal and I have been quite even in our studies and since we have our offices just the next door to each other, and we both work with hardwood species, we have shared joys and problems, more and more intense, since we decided to have our defenses the same day. It has really been great to see that it is not only me that is sweating over the statistics.

This chapter is not supposed to be too long, and I find it impossible to thank everyone for spurring and pushing me, I will just mention a few: Tove V. it was nice to work with you in your experiments, Tove H. you fond the biggest earthworm, didn´t you? PM, Urban and Torkel, we really had some nice days in Spain, Little Matts, thank´s for your help, and Janet, I wish you could have joined us the 26 March…

I will stop no with just saying thank you to everyone at the department for all nice days, for your help and for you believing in me!

But there are some other people and things as well, which have helped me to relax from my job and giving me inspiration and power to continue.

Sazed, your music and your help with the sitar has given me great pleasure and I am looking forward to continue.

Lars, Eva, Supriya and Andreas, thank´s for your support!

The dogs, horses and cats, which have been and are sources for relaxing and joy.

My dear old mother, who really cares for me to dress warm!

Nature, forest, garden; joyful things…

And last of all, but most important, my family, Kerstin, Ulla and Tuva-Lisa, who have supported me more than anyone could ask, and who has had a lot of understanding and patience for me and why I have been doing some things, instead of other things.

Rolf, 18 February 2010