A Method for Natural Regeneration of Beech

(*Fagus sylvatica* L.) practiced in Southern Sweden

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Abstract


In Sweden the most common way to regenerate beech forests is intensive natural regeneration combined with site preparation. However, the method has both economic and ecological drawbacks. On a large estate in southern Sweden a more non-intensive regeneration method is practised. Several catious cuttings regulate the forest floor conditions as well as the development of new seedlings originating from mast years occurring under a longer period. The aim of this study was to document this method and to study its regeneration dynamics. The seedling density recorded in the later phases of the regeneration period is considered to be sufficient for the development of new stands.

*Key words*: plant dynamics, pre-commercial thinning, regeneration-phase, regeneration quality, sapling, seed-fall, seed-tree, shelter-wood, site conditions, seedling establishment.

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Introduction

Traditional natural regeneration of beech is a common method for the regeneration of beech stands in Sweden and Denmark (Almgren et al. 1984, Henriksen 1996, Agestam et al. 2003) and in many European countries. The method can be summarized as follows:

- The forest manager awaits a mast year. On average in Southern Sweden this occurs every second or third year (Övergaard et al. 2007), however intervals are affected by the weather conditions.
- Site preparation is undertaken in late summer or early autumn in the mast year. After the seed fall it is recommended that the beech nuts are covered with mineral soil by superficial soil preparation.
- Heavy cutting is undertaken the following winter, removing c. 50 % of the canopy trees.
- The shelter-wood is gradually removed over a 10-30 year period, involving two or three cuttings.

Variations in the programme occur; a preparatory cutting is sometimes undertaken to stimulate seed production (Dengler 1972), especially in unmanaged stands. Some managers also prefer to wait for new seedlings to establish before significantly reducing the density of shelter trees. However, this may be a risk especially on poor sites where the competition from the shelter-trees is high.

The type and intensity of site preparation varies. The purpose is to facilitate the conditions for germination, establishment and early growth. Bare mineral soil mostly gives the best results (Madsen 1995). Field vegetation, competing for water, nutrients and light, is removed, the capillary force of the mineral soil brings water, soil temperature is increased and attacks of fungus are reduced. The disadvantage is that the seeds are easily found by different predators, but covering the seeds with soil will decrease the damage. Also the ectomycorrhizae composition is negatively influenced by removing the humus layer (Lazaruk et al. 2008). In areas where seed-eating and/or browsing animals are present, or the field-layer is thick and abundant, or the forest manager of other reasons expect low germination rate or high mortality in the new generation, big areas of bare mineral soil is needed. An intense site preparation method has to be chosen and the purpose is to get as many seedlings as possible.

When these big amounts of seedlings are not needed a disc-trencher or patch-scarifier is often used. This machinery creates rows or patches of bare mineral soil and in these often big quantities of seedlings appear while the number is much lower in the undisturbed parts of the regeneration area (Agestam et al. 2003). After seed-fall the beechnuts should be covered with mineral soil to enhance the over-wintering and germination of the seeds and to protect them from predation (Watt 1923, Huss and Burschel 1972). A less intense method is to use a rotary cultivator before the seed-fall, mixing the organic layer and the mineral soil to a depth of 5-10 cm. A second cultivation should be done after the seed-fall, but not deeper than 5 cm. A third way is to use the rotary cultivator only after the seed-fall and lightly mix the surface not deeper than 5 cm. Olesen and Madsen (2008) have in a study showed results in fenced areas of 160 germinates m⁻² in bare mineral soil, 100 germinates m⁻² in the intensively cultivated seedbed, and 40 germinates m⁻² in the lightly cultivated seedbed, compared to 5 germinates m⁻² in the untreated plots.

The intensive method is widely implemented by foresters and in most cases yields good results, although failures do occur. Nielsen (1977) found the pre-dispersal predation of seeds due to the beech seed moth *Cydia fagiglandana* varies from 7 to 55 % of the seed crop. A winter without the protection of snow cover provides opportunities for seed predators, including mammals and birds, to consume large quantities of seed (Harmer 1994). Big flocks of Brambling (*Fringilla montifringilla*) can consume huge amounts of beechnuts during winter (Lithner 2002). Linnard (1987) found 40 % of the seeds disappeared within one month after seed fall, and by March less than 3 % of the original seeds remained. During the years after germination, the number of seedlings is often reduced by voles, field mice and other mammals (Harmer 1994, Ravn et al. 2001) and in areas of high roe deer population fencing may be a way to regeneration success. Olesen and Madsen (2008) reported roe deer (*Capreolus capreolus*) browsing significantly decrease the number of newly germinated beech seedlings in bare mineral soil and also height growth was negatively influenced. In a German investigation about 60% of the germinates disappeared during the two first weeks after germination (Bressem 1998). Drought during spring and early summer will adversely affect germination and kill many seedlings. This is especially common...
Intensive site preparation is often believed to have a negative impact on biodiversity, recreation potential, and historical and cultural remains. Site preparation may also be difficult to carry out on sites with steep slopes or sites with abundant boulders.

A drop in timber prices can be expected if too large amounts of timber are harvested during mast years.

Long-term planning is difficult due to the irregularity of mast years.

If a regeneration attempt ends in failure, a second attempt will be more difficult due to competition from grasses and herbs on the site. There may be a lack of seed due to an uneven seed-tree distribution.

A rising water table and sun exposure often cause damage to shelter-wood trees. There is also a risk of epicormic branches developing on high quality trees.

The possibilities for maximizing the value of the old stand are limited since not all trees will reach the target diameters.

Site preparation involves an additional cost.

Sometimes abundant beech regeneration appears in gaps without any silvicultural measures (Bjerregaard and Carbonnier 1979). It is often questioned if advance growth can be used and whether the regeneration result is depending on site conditions (Collet et al. 2002). However, on some estates in Southern Sweden a regeneration method is employed, where the establishment of the new generation is less controlled than in the traditional method.

In the studied method the regeneration is not related to a special mast year but could be started at any time of the period. The regeneration will originate from several mast years and from limited seed-falls during intermediate years. When a well-managed mature stand has reached an age of 80-100 years, depending on site fertility, the stand is subjected to a preparatory cutting in order to achieve better soil conditions and to stimulate seed production. This is made without any consideration to advance regeneration. The change in light conditions should provide enough light for the establishment of new seedlings but should still inhibit the growth of competing field vegetation. By successive light-regulating cuttings, the most valuable trees close to their target diameters can be favoured. Other measures to stimulate the regeneration are undertaken only in exceptional cases e.g. site preparation could be carried out if a thick grass cover has established. At least 10-15 years will often be needed for the new generation to establish and to dominate the field vegetation. On poor sites particularly, the time span may be longer since factors such as a thick, inactive organic layer, a low nutrient content or a low pH often inhibit seedling establishment.

The spatial distribution of seedlings will be heterogeneous, with a considerable variation in height. An early pre-commercial thinning operation is, therefore, often needed. Similar non-intensive methods are used in Denmark (Bornebuch 1947, Henriksen and Bryndum 1996) and northern France (Evans 1982).

The studied method is associated with fewer of the disadvantages of the intensive method, listed above. However, regeneration is expected to be more uncertain. In Denmark the method has produced good results on high fertility sites (Henriksen and Bryndum 1996).

The aim of this study was to document the beech regeneration method and to study the dynamics of the seedling establishment. The hypotheses were:

- The method results in generally good regeneration.
- The abundance of seedlings in the new generation is dependant on the site fertility.
- The seedlings in the new generation will originate from several mast years.

**Materials & methods**

The study started in 1992 on a forest estate in Southern Sweden (56° 092 N; 14° 322 E), (Figure 1), where the method has been practised for many years. The climate conditions were favourable for growing beech, with an annual mean precipitation of 578 mm, precipitation during the growing season (April-Sept.) 300 mm, an average temperature of 7.1°C, a lowest average for a month in January of -1.1°C and highest in July of 16.2°C. The temperature sum (threshold value 5°C)
was 1 650 day degrees (SMHI). The highest altitude in the area was 150 m a. s. l., with small parts of the area located above the highest sea level during the latest glacial period.

Seven stands in different site index classes and regeneration phases were selected for the study. Three stands were chosen from the early regeneration phase (E-stands), two from the intermediate phase (I-stands) and two from the late phase (L-stands). According to the site’s forest management plan, site indices, i.e. the top height at a total stand age of 100 years (Kallstenius, 1971), varied between 22 and 30 m (Table 1). The stands were grouped into three site index classes; L (low), M (medium) and H (high), (Table 1). Silvicultural treatments, i.e. pre-commercial thinning and cuttings in the shelter-wood, were selected and carried out by the local forester. The two late regeneration-phase stands (LL and LH), had an acceptable level of regeneration in 2002 and 2000 respectively when the last shelter trees were cut. In stand EH and IH the last shelter-wood trees were cut in 2006.

Four sample areas were randomly selected in each stand. Within a radius of 25 meter different measurement were done in systematic design and with different plot sizes (Figure 2). Seed-fall, seed germination, seedling establishment and growth, field vegetation biomass and shelter-wood stand growth and cuttings were studied.

**Seed fall**

Three circular nylon seed traps (size 0.25 m²) were systematically placed in each sample area (Figure 2), giving a total of 12 traps in every stand. Every year, the traps were emptied at the end of December. Seed data from damaged traps were not used when compiling the results. Years with a seed fall of more than 50 seeds m⁻², which according to Henriksen (1988) is considered the lowest number of seeds required to establish a new stand of good quality, were defined here as mast years.

**Seedlings**

Seedlings of all tree species were measured every year, after the growing season, in nine 1 m² subplots arranged around the centre of each sample area (Figure 2), giving a total of 36 subplots in every stand. A frame divided into 16 subsections (25 × 25 cm) was used for seedling measurement. The frame was fixed to the ground by two plastic sticks through holes in the frame and into two metallic pipes driven down into the ground. When the study started, all existing beech seedlings, i.e. the advance regeneration established before the investigation started, in the frame were labeled, and the one situated in the most northerly position in each subsection was numbered and its height measured every year. In the same way, new seedlings were numbered and measured every year and every new cohort was marked with a label of a new colour. If possible, the cause of mortality or injury was noted as well as the vitality of the seedlings. Seedlings of other tree species were measured in the same way, but not labeled.
Table 1. *Site Index* and regeneration phase of the seven stands studied. Stand parameters of the initial stands, stands before and after cuttings, and stands at the end of the investigation period together with mean annual volume growth for the study period. Diameter corresponding to mean basal area.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Regeneration phase</th>
<th>Site index</th>
<th>Year</th>
<th>Initial stands and before cuttings</th>
<th>Cuttings</th>
<th>Stands after cuttings and in the end of the study period*</th>
<th>Volume growth 1993-2005 m³ ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Stems ha⁻¹</td>
<td>Mean diam., cm</td>
<td>Volume m³ ha⁻¹</td>
<td>Stems ha⁻¹</td>
</tr>
<tr>
<td>EL</td>
<td>Early</td>
<td>Low</td>
<td>1993</td>
<td>190</td>
<td>36.0</td>
<td>201</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2000</td>
<td>190</td>
<td>38.3</td>
<td>236</td>
<td>6.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EM</td>
<td>Early</td>
<td>Medium</td>
<td>1993</td>
<td>152</td>
<td>41.9</td>
<td>246</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<td>152</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EH</td>
<td>Early</td>
<td>High</td>
<td>1993</td>
<td>92</td>
<td>50.5</td>
<td>248</td>
<td>24</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>1996</td>
<td>91</td>
<td>52.1</td>
<td>264</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IL</td>
<td>Intermediate</td>
<td>Low</td>
<td>1993</td>
<td>117</td>
<td>42.8</td>
<td>176</td>
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<td></td>
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<td></td>
<td>2000</td>
<td>94</td>
<td>44.9</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>2005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IH</td>
<td>Intermediate</td>
<td>High</td>
<td>1992</td>
<td>110</td>
<td>47.5</td>
<td>239</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2002</td>
<td>90</td>
<td>50.8</td>
<td>234</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LL</td>
<td>Late</td>
<td>Low</td>
<td>1993</td>
<td>90</td>
<td>42.8</td>
<td>135</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2000</td>
<td>47</td>
<td>45.1</td>
<td>73</td>
<td>47</td>
</tr>
<tr>
<td>LH</td>
<td>Late</td>
<td>High</td>
<td>1992</td>
<td>82</td>
<td>55.4</td>
<td>282</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1997</td>
<td>53</td>
<td>55.6</td>
<td>182</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2002</td>
<td>26</td>
<td>56.8</td>
<td>84</td>
<td>26</td>
</tr>
</tbody>
</table>

¹Stand LL the period 1993-2000, stand LH 1993-2002
²Stand LL 2000, stand LH 2002
Field vegetation
All field vegetation was cut every fourth year from nine sample areas, each was rectangular and measured 0.5 m²; these subplots located systematically in different directions from the seedling measurement subplots (Figure 2). The vegetation was sorted according to species, dried at 70°C for 48 hours then weighed.

Pre-commercial thinnings
As a part of normal silvicultural practice, pre-commercial thinnings were conducted at the same time as the shelter-wood thinnings. The regeneration was tended mainly by cutting wolf-trees (low-quality trees, mainly with forks, spike-knots and thick branches, dominating and suppressing adjacent trees) and undesired species, such as hornbeam (*Carpinus betulus*) and birch (*Betula* spp.).

Potential quality of the new stand
In autumn 2006 the quality of all beech trees taller than 3 m was recorded in 12 circular plots (radius 4 m) in each of the two late regeneration stands cut in 2002 (LL and LH). For the dominant and co-dominant beech trees, stems were classified as potential final crop trees (undamaged trees with good growth and without thick branches, spike-knots or forks), wolf-trees and others. Mean height, suppressed beech stems, other species and the total number of stems were also recorded.

Shelter-wood trees
The diameter at breast height of the shelter trees was measured in 1993, 1996 and 2005, in four circular plots (radius 25 m) in each stand. The plots had the same centre as the sample areas were the new generation was observed. The tree height and height to the first living branch of selected sample trees (15-20 in each plot) were recorded. During cutting operations, the removed shelter trees were measured.

Analysis
The mean seed fall for the mast years and stands was calculated and analysed statistically using the Wilcoxon rank test (Wonnacott and Wonnacott 1985). To study differences between the years and stands with respect to the size of the mast years, pair-wise comparisons were made and Tukey’s test at the 5% level was used to determine significant differences (Quinn and Keough 2002). Stand

<table>
<thead>
<tr>
<th>Year</th>
<th>EL</th>
<th>EM</th>
<th>EH</th>
<th>IL</th>
<th>IH</th>
<th>LL</th>
<th>LH</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>327</td>
<td>657</td>
<td>497</td>
<td>285</td>
<td>927</td>
<td>420</td>
<td>578</td>
<td>527</td>
</tr>
<tr>
<td>1993</td>
<td>410</td>
<td>110</td>
<td>220</td>
<td>60</td>
<td>80</td>
<td>100</td>
<td>80</td>
<td>151</td>
</tr>
<tr>
<td>1994</td>
<td>0</td>
<td>0.3</td>
<td>0</td>
<td>0</td>
<td>2.4</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>850</td>
<td>900</td>
<td>1150</td>
<td>210</td>
<td>1270</td>
<td>330</td>
<td>740</td>
<td>779</td>
</tr>
<tr>
<td>1996</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
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<tr>
<td>1997</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>126</td>
<td>175</td>
<td>129</td>
<td>38</td>
<td>118</td>
<td>21</td>
<td>46</td>
<td>93</td>
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<tr>
<td>1999</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>1.5</td>
<td>0</td>
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<tr>
<td>2000</td>
<td>230</td>
<td>359</td>
<td>488</td>
<td>178</td>
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<td>2001</td>
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<td>0</td>
<td>0</td>
<td>0.9</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>2002</td>
<td>690</td>
<td>810</td>
<td>440</td>
<td>150</td>
<td>750</td>
<td>-</td>
<td>-</td>
<td>568</td>
</tr>
<tr>
<td>2003</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>50</td>
<td>130</td>
<td>130</td>
<td>10</td>
<td>120</td>
<td>-</td>
<td>-</td>
<td>88</td>
</tr>
<tr>
<td>2005</td>
<td>0.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.0</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>1042</td>
<td>923</td>
<td>819</td>
<td>74</td>
<td>860</td>
<td>-</td>
<td>-</td>
<td>744</td>
</tr>
<tr>
<td>Mean</td>
<td>466</td>
<td>508</td>
<td>484</td>
<td>126</td>
<td>577</td>
<td>189</td>
<td>305</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Seed fall (seed m⁻²) during the study period. In stands LL and LH the last seed-trees were cut in 2002 and 2000, respectively. Mast years are indicated by grey shading. Annual means followed by different letters are significantly different (P <0.05) based on the Wilcoxon rank test.
Figure 3. Change in number of seedlings in the early regeneration phase (stand EL, EM and EH), the intermediate regeneration phase (stand IL and IH), and the late regeneration phase (stand LL and LH). Red line shows the total number of seedlings, green line the number of seedlings established before the observation period 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.

Table 3. Seedling/seed ratio, i.e. percent of new seedlings ha\(^{-1}\) originating from the previous mast year divided by the number of fallen seeds ha\(^{-1}\). In stands LL and LH the last seed-trees were cut in 2002 and 2000, respectively

<table>
<thead>
<tr>
<th>Stand</th>
<th>1993</th>
<th>1994</th>
<th>1996</th>
<th>1999</th>
<th>2001</th>
<th>2003</th>
<th>2005</th>
</tr>
</thead>
<tbody>
<tr>
<td>EL</td>
<td>0.017</td>
<td>0.020</td>
<td>0.102</td>
<td>0.705</td>
<td>0.036</td>
<td>0.004</td>
<td>0</td>
</tr>
<tr>
<td>EM</td>
<td>0.017</td>
<td>0.210</td>
<td>0.186</td>
<td>2.444</td>
<td>0.402</td>
<td>0.103</td>
<td>0.124</td>
</tr>
<tr>
<td>EH</td>
<td>0.179</td>
<td>0.126</td>
<td>0.153</td>
<td>0</td>
<td>0.017</td>
<td>0.040</td>
<td>0</td>
</tr>
<tr>
<td>IL</td>
<td>0.205</td>
<td>0.377</td>
<td>0.606</td>
<td>1.462</td>
<td>0.125</td>
<td>0.057</td>
<td>0</td>
</tr>
<tr>
<td>IH</td>
<td>0.033</td>
<td>0.070</td>
<td>0.147</td>
<td>0</td>
<td>0.045</td>
<td>0.008</td>
<td>0</td>
</tr>
<tr>
<td>LL</td>
<td>0.020</td>
<td>0</td>
<td>0.011</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>LH</td>
<td>0.034</td>
<td>0.072</td>
<td>0.004</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<tr>
<td>Average</td>
<td>0.07</td>
<td>0.12</td>
<td>0.17</td>
<td>0.66</td>
<td>0.09</td>
<td>0.04</td>
<td>0.02</td>
</tr>
</tbody>
</table>
parameters for the shelter stands were calculated according to the standard routines for long term forest growth and yield experiments in Sweden (Karlsson 1998).

**Results**

**Seed fall**

Seven mast years occurred during the 14-years study period. Two consecutive mast years, 1992 and 1993, occurred (Table 2). Smaller quantities of seed were produced between mast years. There were no significant differences in the amount of seed produced between stands, site index classes or regeneration phases, despite the fact that there were fewer seed-trees in the later regeneration phases.

**Seedlings**

New seedlings were established after mast years in the early and intermediate phases but not in the late phase where a tendency to a slow reduction in number of seedlings could be noticed (Figure 3, Table 3). The number of seedlings observed the first autumn after seedling establishment decreased due to high mortality during the following years. Only small changes in the numbers of advance seedlings occurred during the observation period (Figure 3).

In stand EH there were an increased number of seedlings following the mast years in 1992 and 1995 (combined with a cutting in the shelter stand). After five years, the number of seedlings stabilised at a frequency of 15 000-20 000 seedlings ha⁻¹ (Figure 4). Sub-plots without seedlings tended to be colonised more frequently during the early regeneration phase than the later phases (Figure 5 and 6). After five to seven years after the stand was first opened-up, colonisation by new seedlings was low. A similar pattern was observed for stands in the intermediate regeneration phase. Almost no colonisation by new seedlings was observed in the two stands in the late phase.

There was no recorded relationship between site index and colonisation by new seedlings (Figure 5). Colonisation by new seedlings depends on mast years and conditions for establishment. The ratio between establishment of new seedlings on subplots without and with previous regeneration decreased over the observation period (Figure 6).

![Figure 4](image.png)

*Figure 4.* Change in number of seedlings in the seven stands. The diagrams show the total number of seedlings and how these are distributed in the four sample areas. An “x” indicates a mast year and an arrow a cutting in the shelter.
Figure 6. Number of subplots (out of a total of 36) with new seedlings established during the period 1993–2005 for stand EL, EM, EH, IL and IH and during 1993–2003 for stand LL and LH. Blue bars indicate subplots with previous regeneration and red bars indicate subplots without previous regeneration.
The proportion of subplots with no seedling did not appear to be related to regeneration phase or site fertility (Figure 5). Also for subplots with only beech seedlings, subplots with only other species and rate of admixture no relation with regeneration phase or site fertility was found.

**Seedling/seed ratio**

There was a high variation in the seedling/seed ratio, between both years and stands (Table 3). On average for the stands in the early and intermediate phases the seedling/seed ratio was 0.2 %. The ratio for the late phase stands was only 0.01 %. The highest seedling/seed ratio during the study period was 2.4 %, recorded during the autumn of 1999 in the early regeneration phase stand of medium site index, stand EM. In stand EH no new seedlings were found during this year, although the seed-fall was 1.3 million seeds ha⁻¹ anterior autumn. When comparing all years, 1999 had the highest seedling/seed ratio with an average for the seven stands of 0.66 %.

### Table 4. Seedlings of species other than beech ha⁻¹ in three height classes in autumn 2005 (stands EL, EM, EH, IL and IH) and autumn 2003 (stands LL and LH)

<table>
<thead>
<tr>
<th>Species</th>
<th>Height</th>
<th>Stand no</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>m</td>
<td>EL</td>
</tr>
<tr>
<td>Beech (Fagus sylvatica)</td>
<td>&lt;1 m</td>
<td>7 800</td>
</tr>
<tr>
<td></td>
<td>1-2 m</td>
<td>600</td>
</tr>
<tr>
<td></td>
<td>&gt;2 m</td>
<td>0</td>
</tr>
<tr>
<td><strong>Sum</strong></td>
<td></td>
<td>8 400</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Other species</th>
<th>Height</th>
<th>Stand no</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder (Alnus incana)</td>
<td>&lt;1 m</td>
<td>300</td>
</tr>
<tr>
<td>Ash (Fraxinus excelsior)</td>
<td>&lt;1 m</td>
<td>800</td>
</tr>
<tr>
<td>Birch (Betula sp.)</td>
<td>&lt;1 m</td>
<td>1 400</td>
</tr>
<tr>
<td></td>
<td>1-2 m</td>
<td>2 200</td>
</tr>
<tr>
<td></td>
<td>&gt;2 m</td>
<td>300</td>
</tr>
<tr>
<td>Hornbeam (Carpinus betula)</td>
<td>&lt;1 m</td>
<td>800</td>
</tr>
<tr>
<td></td>
<td>1-2 m</td>
<td>1 400</td>
</tr>
<tr>
<td></td>
<td>&gt;2 m</td>
<td>300</td>
</tr>
<tr>
<td>Oak (Quercus sp.)</td>
<td>&lt;1 m</td>
<td>300</td>
</tr>
<tr>
<td>Pine (Pinus sylvestris)</td>
<td>&lt;1 m</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td>1-2 m</td>
<td>1 100</td>
</tr>
<tr>
<td>Rowan (Sorbus aucuparia)</td>
<td>&lt;1 m</td>
<td>300</td>
</tr>
<tr>
<td>Spruce (Picea abies)</td>
<td>&lt;1 m</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td>1-2 m</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td>&gt;2 m</td>
<td>600</td>
</tr>
<tr>
<td><strong>Sum</strong></td>
<td></td>
<td>2 000</td>
</tr>
</tbody>
</table>

The proportion of subplots with no seedling did not appear to be related to regeneration phase or site fertility (Figure 5). Also for subplots with only beech seedlings, subplots with only other species and rate of admixture no relation with regeneration phase or site fertility was found.

**Seedlings of species other than beech**

The species and numbers of tree saplings and seedlings other than beech in autumn 2005 (stands EL, EM, EH, IL and IH), and autumn 2003 (stands LL and LH), were more frequent on subplots where no or very few beech seedlings were established (Table 4, Figure 7). Seedlings of other tree species were few and small in the early regeneration-phase stands and became more frequent and taller in the intermediate and late phases. The pattern of distribution varied between species and stands: in stands IL, IH and LH all hornbeam, birch and ash were found in one
Figure 7. Number of seedlings ha⁻¹ in different height classes in 2003 (stands LL and LH) and 2005 (stands EL, EM, EH, IL and IH). Greene bars show the average number of beech seedlings for each stand and blue bars show the number of seedlings of other species in the three height classes.

Figure 8. Height development of beech seedlings and saplings in the seven stands. The red lines indicate the mean height, the green lines the height of the seedlings established before 1993, and the black lines the height development of every new cohort. In stand LL and LH no measurements were made after 2003, since the regeneration periods were ended in these stands. An arrow indicates a cutting in the shelter.
single sampling area in each stand, while the pine in the intermediate and late regeneration phase stands of low site index, stands IL and LL, were spread across all four sampling areas. Species like ash (*Fraxinus excelsior*), hornbeam (*Carpinus betula*), oak (*Quercus sp.*), Scots pine (*Pinus sylvestris*) and rowan (*Sorbus aucuparia*) were unable to attain their growth potential as a result of browsing and pre-commercial thinning. For both pine and spruce there was abundant germination followed by high mortality.

**Height and height growth**

Seedlings established before the investigation started grew faster than newly established seedlings. The latter increased their height growth after two years (Figure 8). Mean seedling height for stand EH was 1.5 m in autumn 2005, while seedlings in the two other stands in the early regeneration phase did not attain a height of 50 cm. In the intermediate phase stands, the mean seedling height was between 1 and 2 m, and in the late phase between 2.5 and 4 m at the end of the observation period.

**Influence of shelter-wood density**

The average height growth of beech seedlings established at the start of the observation period was negatively correlated with the density of shelter expressed as the number of trees per hectare (Figure 9). However, the variation between individual years and stands was high and the correlation was low ($R^2 = 0.18$).

**Quality – potential crop trees and wolf trees**

The two stands in the late regeneration phase (stands LL and LH) contained 796 and 398 potential final crop trees ha$^{-1}$ respectively (Table 5). The proportion of wolf trees was low, about 4% in each stand.

**Field vegetation**

Stands IL and LL contained a high biomass of field vegetation (measured as dry mass) mainly consisting of *Vaccinium myrtillus* and *Rubus idaeus* (Figure 10). Other common field layer species were *Deschampsia flexuosa* and *Oxalis acetosella*.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Potential final crop trees no/ha</th>
<th>Other no/ha</th>
<th>“Wolf trees” no/ha</th>
<th>Total no/ha</th>
<th>Height average dm</th>
<th>Suppressed no/ha</th>
<th>Other no/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL</td>
<td>398 29</td>
<td>1310 73</td>
<td>66 4</td>
<td>1774 100</td>
<td>75</td>
<td>2437 1409</td>
<td></td>
</tr>
<tr>
<td>LH</td>
<td>796 42</td>
<td>995 53</td>
<td>83 4</td>
<td>1873 100</td>
<td>90</td>
<td>2106 381</td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Numbers, proportion and height of stems of the new generation in stand LL and LH divided into different categories, autumn 2006. All trees above 3 m were examined.
Shelter

The density of shelter varied between 92 and 190 stems ha\(^{-1}\) at the start of the experiment with no clear differences between stands in different regeneration phases or site index classes (Table 1). Removal of stems and volume during cuttings and final harvest over the course of the experimental period was regulated by the establishment and early growth of the new seedlings, and did not follow any clear pattern related to regeneration phase or site index. Volume growth of the shelter-wood stands was lower in the intermediate and late regeneration phases than in the early phase. Compared to the expected volume growth of beech stands (Carbonnier 1971) of corresponding ages, the volume growth of intermediate and late regeneration phases was surprisingly low.

Discussion

Seed-fall

The conditions for natural regeneration were favourable during the period investigated, including seven mast years. This frequency was higher than recorded previously (Övergaard et al. 2007). Mast years occurred in both 1992 and 1993. This contradicts the widely held opinion that the seed production is very small the year following an abundant mast year. Small amounts of seeds also resulted in new seedlings between the mast years (Figure 3 and 6). The differences in the quantity of seed produced in different mast years were probably due to variations in the weather: a warm summer favours the initiation of flower buds (Schmidt 2006), and spring frost reduces the number of flowers (Matthews 1955).

The number of seed-trees decreased in all stands over the observation period, but this did not seem to influence seed production. After a cutting, the crown size will increase as well as the exposure to solar radiation: this encourages seed production. It has also been shown that seed production is higher in open compared to more closed canopy layers (Dzwonko 1990). The low site index stand in the intermediate regeneration phase, stand IL, produced...
relatively few seeds. This may be explained by the high proportion of shelter-trees of other species.

Seed-fall before the study period
Seed-fall was not recorded before the study started. However, since 1974 mast years occurred at intervals of one to three years with the exception of a seven-year interval between 1976 and 1983 (Övergaard et al. 2007). The two late regeneration-phase stands may have been affected by this long interval: fewer seedlings would have been produced and field vegetation would have increased, thus adversely affecting seed germination from later mast years.

Important factors affecting the number of seedlings
Water and light are key requirements for seed germination and early seedling growth. A well-balanced shelter density regulates light, water and nutrients for new seedlings to grow, but adversely affects the growth of competing field vegetation. The shelter also provides protection against frost damage. A reduction in light and nutrients by the sheltering trees is also considered to favour new regeneration of high quality (Bjerregaard and Carbonnier 1979). Decreased incoming solar radiation adversely affects germination (Olesen and Madsen 2008). Low soil temperature reduce the decomposition of litter, and a thick humus layer is unfavorable since the nuts and initial roots will suffer from desiccation and/or frost damage (Watt 1923, Bressem 1998).

The 1995 mast year resulted in abundant establishment of new seedlings in the early and intermediate regeneration-phase stands (Figure 3). One explanation is that 1995, with a mean fall of 7.8 million seeds ha⁻¹ (Table 2), was followed by favourable conditions for germination and early growth in spring 1996. The early regeneration-phase stands
In the early regeneration-phase stand of low site index, stand EL, only a few seedlings established during the study period. This may be explained by the high number of stems left in the shelter stand (Table 1). It is recommended that areas with low site indices should have few shelter trees and a low basal area (about 15 m² ha⁻¹) (Bjerregaard and Carbonnier 1979). In 2005 the basal area in stand EL was 22 m² ha⁻¹. A large number of stems is known to decrease seed production (Dzwonko 1990), and EL had the highest number of stems of all the stands investigated. However, seed production was not suppressed (Table 2). Low light levels and a thick leaf-litter layer together with low soil temperatures are possible explanations for the low germination rate (Harley 1939, Bourne 1945, Madsen and Larsen 1997). The establishment of other woody species and field vegetation was also low (Table 4, Figure 10). Opening up the stand in 2000 did not increase the number of new seedlings, but probably benefited the survival of seedlings originating from the 1998 mast year. At the end of the study period, stand EL was still considered to be in the early regeneration-phase.

Both stand EM and EH exhibited a significant increase in the number of seedlings present. When the investigation started, both stands contained fewer shelter trees than stand EL (Figure 3, Table 1). In stand EM almost 43 000 new seedlings ha⁻¹ were
established following the cutting after the seed-fall 1998, but by 2005 only 20,000 of these remained. The mast years 1995 and 2000 contributed to increased seedling numbers and by the end of the period the stand contained about 47,000 seedlings ha\(^{-1}\). In stand EH a cutting was undertaken after the 1995 mast year, producing favourable conditions for the roughly 18,000 new seedlings ha\(^{-1}\) established. This number was reduced during the following years, but together with earlier cohorts, the total number of seedlings ha\(^{-1}\) remained at the same level. The fact that no new seedlings was found in stand EH after the abundant seed-fall 1999, when stand EM received 43,000 seedlings ha\(^{-1}\), is remarkable (Figure 3). The number of shelter-trees was quite low, 68 stems ha\(^{-1}\) compared to 119 in stand EM. The mean height of the new regeneration was about 50 cm in stand EH compared to about 10 cm in stand EM, but in stand EH about 7,000 seedlings, 4,000 advance regeneration and 3,000 emerged 1993, had a mean height of about 120 cm and 65 cm respectively (Figure 8). The remaining seedlings, originating from the mast year 1995, had a mean height of about 20 cm. The explanation that the competition for light from the 20,000 seedlings ha\(^{-1}\) prevented germination is not satisfying since seedlings were established both in 2001 and 2003, even if those were in small numbers.

At the end of the study period, stand EM was in the intermediate regeneration-phase, while stand EH had reached the late phase.

The intermediate regeneration-phase stands

Cuttings in the intermediate regeneration-phase stands IL and IH in 1993 and 1992 provided good opportunities for new seedlings to establish after the mast year in 1995 (Figure 3). After this, few new seedlings appeared. Cuttings in 2000 and 2002 did not influence the number of new seedlings, but the height growth of earlier established seedlings increased (Figure 3 and 8). The seedlings in stand IL grew relatively slowly as a result of competition with the abundant older seedlings and other field vegetation (Figure 8 and 10).

The late regeneration-phase stands

In the late regeneration-phase stands (LL and LH) almost no new seedlings appeared, probably due to competition from older ones and from established field vegetation. In stand LL a decrease in the number of seedlings was observed after a cutting in 1993; this was the result of both damage caused by harvesting the trees and the removal of wolf-trees in the new seedling generation.

Seedling distribution

The early regeneration phase stands initially had an uneven seedling distribution, with regeneration in only small areas (Figure 4, 5 and 6). Following mast years and cutting the shelter wood, a higher proportion of the area was colonized. The importance of the 1995 mast year is clear. Site index did not seem to influence seedling establishment. Some of the subplots were never colonized; new seedlings mostly established in subplots that were already colonized (Figure 6).

The seedling distribution seemed to be very variable between the four plots in some stands, e. g. EM and IL (Figure 4), but the numbers of seedlings ha\(^{-1}\) was sufficient in all sampling areas, and the numbers will probably increase in the future. More problematic is the situation in stand LH, which has only 2,200 seedlings ha\(^{-1}\) in one of the sampling areas. No other woody species were recorded in this sampling area (Table 4) but there was a large field vegetation biomass (Figure 10), which consisted mainly of different grasses that probably inhibited the germination and development of new seedlings.

Uneven seedling distribution is one of the disadvantages associated with the natural regeneration of beech (Bornebusch 1947, Huss 1972) and is generally expected to be more obvious as a result of the method described here than the more intensive approach, where site preparation facilitates germination and establishment. At the end of the investigation 38% of the subplots contained no seedlings. In an experiment at Skarhults experimental forest, situated in the central parts of Scania, natural regeneration of beech by using the traditional method including scarification was studied, the frequency of subplots without beech seedlings was recorded six years after the regeneration event. Under a sparse shelter with 54 stems ha\(^{-1}\) and a basal area of 15 m\(^2\) ha\(^{-1}\), 35% of the subplots on scarified ground and 65% of those on undisturbed ground contained no seedlings. Under a dense shelter with 106 stems ha\(^{-1}\) and a basal area of 23 m\(^2\) ha\(^{-1}\) the equivalent numbers were 35% and 75% respectively (Agestam et al. 2003). This indicates that a more even seedling distribution was achieved using the method described herein; this is the result of good soil conditions produced by carefully controlled cutting of the stands. Using the traditional regeneration...
method, seedlings were concentrated in the scarified areas, where they were often abundant, while there was poor regeneration in the unscarified areas.

**Advance regeneration**

Seedlings established before the study commenced had a mean survival of 76% over the investigation period. They were well established and had a higher mean height compared to later cohorts, thus suffered less from competition (Figure 3 and 8). Of the seedlings originating from the 1992 mast year, 36% were still alive in the autumn of 2005. However, these survival rates were also affected by a pre-commercial thinning and by damage caused by felling and the removal of timber from the plots.

**A comparison with the traditional approach**

Independent of regeneration method the goal is most often to get seedlings enough to establish a new stand of good quality. How many germinates that is needed differ between sites and the conditions of the area. After germination browsing is often the most severe damage and an abundant e.g. roe deer population calls for a high number of seedlings, and if the regeneration area is not fenced a more intense site preparation is needed. In areas where no specific calamities and high survival are expected it may be enough with a slight rotary cultivation. Some authors claim that the minimum acceptable number of seedlings at the end of the first growing season should be 200 000 ha⁻¹. This is considered sufficient to form a stand capable of producing high quality wood (Bonnemann and Burschel 1967, Huss et al. 1972). The high numbers of seedlings are expected to be reduced to about 20 000 ha⁻¹ before they reach a mean height of one meter (Huss and Burschel 1972).

In the study stands, the total number of seedlings never exceeded 60 000 ha⁻¹ (Figure 3), but these were supplemented by new seedlings after every mast year. At a mean height of one meter, the numbers of seedlings ha⁻¹ in stands EH, IL, IH and LL were about 18 000, 30 000, 20 000 and 17 000 (Figure 3 and 8).

In the traditional method, when it is time to regenerate, heavy cuttings are performed at mast years when the timber prices are acceptable. This may give large stocks to the industries, especially if the mast year interval has been long, and cause a fall in timber prices. In the here described method cuttings to promote regeneration and seedling growth can be done at any time when the timber prices are good, independent of mast years.

**Seedling/seed ratio**

The seedling/seed ratio was higher in the early and intermediate regeneration phase stands (0.2 %) than in the late regeneration phase stands (0.01 %). The variation indicated that competition had an influence on the germination and survival of new seedlings. The highest ratio, 2.4 %, was found for site EM in 1999. This can be explained by the heavy seed-fall in autumn 1998 followed by a cutting in the shelter-wood the following winter. The cutting and logging probably caused a light type of site preparation protecting the seeds and together with increased sun radiation and decreased competition germination was improved. The average ratio for the early and intermediate regeneration-phase stands for all years was 0.2 %. In another study of natural regeneration of beech in southern Sweden, the ratio was estimated to be 0.8 % without and 5.8 % with site preparation (Agestam et al. 2003). Site index class had no effect on this ratio.

**Height and height growth**

A slower height growth was recorded for beech seedlings in denser shelter wood stands in the early regeneration phase (Figure 8 and 9). Height growth was more rapid in the more widely spaced shelter-wood stands of the intermediate and late regeneration phases. Site index had no effect on beech seedling height growth. For some individual observations, a negative height growth was observed as a result of damage to seedlings and the removal of fast growing seedlings during pre-commercial thinning.

Increasing the shelter-wood density has also been shown to have a negative impact on beech seedling height growth under the traditional regeneration regime (Agestam et al. 2003). Height growth of sheltered seedlings was found to be a complex result of intercepted light, water stress, ground vegetation competition and other growth limiting factors. It was not possible to determine the contribution of the different growth factors in this study. The timing and intensity of cutting and the removal of shelter-wood trees is a complicated problem involving conflicting factors, and requires further experimental investigation.

Height growth of younger seedlings was gradually hampered by older seedlings and saplings as these grew taller. Consequently, the effect was more pronounced at the end of the intermediate phase and during the late regeneration-phase (Figure 8).
Initial stem quality
It is, of course, difficult at this early stage, based on the current regeneration results, to judge the likelihood of creating high quality stands. However, the proportion of wolf trees was low; about 4% in the two stands with the most advance regeneration. A much higher proportion of the stems were classified as potential crop trees in stand LH compared to stand LL (Table 5). This might be the result of better height development: the average height was about 1.5 m greater in stand LH than in stand LL. Tree quality may also be dependent on site quality.

Length of the regeneration period
There were longer regeneration periods for the stands with low site indices. In stand EL this could, however, be explained by the high numbers of shelter trees resulting in increased competition for light, water and nutrients. The low levels of solar radiation reaching the ground results in low soil temperatures and adversely affect mineralization; in addition, a thick leaf-litter layer impedes the germination and establishment of new seedlings (Watt 1923). The stand remained in the early regeneration phase at the end of the study period. A more open shelter-wood may have improved the regeneration result, but data do not exist to confirm this.

Other species
The abundance of other tree species is dependant on the distance to seed-sources and the dispersal capacity of the seeds (Karlsson 2001). Many of the stands had shelter-trees of other species within or close to the investigated stands.

In stand IL in 2005, 60% of the shelter-trees were beeches, 35% Scots pines and 5% oaks. The high proportion of Scots pine explains the high numbers of pine seedlings in the stand; the large numbers of birch seedlings originated from more distant seed sources (Table 4).

Conclusions
• Seed production was not influenced by site index, regeneration-phase or number of seed trees per hectare.
• The number of seedlings decreased with increasing regeneration time. Following mast years, new seedlings established in early but not in late regeneration phases. There was no tendency that site index influenced the colonisation of seedlings.
• A larger proportion of seeds produced seedlings in the early regeneration period than in the later phase; site fertility had no effect on this.
• Seedling height growth was negatively affected by increasing shelter-wood stand density, but unaffected by site fertility.
• Cuttings in the shelter-woods were determined when the economic outcome was profitable and were done to promote establishment and early growth of new seedlings, and did not follow any specific pattern related to regeneration phase or site index.
• Without using site preparation, the studied method resulted in adequate new beech regeneration following cautious light-regulating cuttings of the shelter stands, irrespective of site fertility and the timing of mast years.

References
Bornebuch, C. H. 1947. The management of the beech forests at Boller forest district The Danish Forest Experiment Station. 19:1. pp 1-80 (In Danish with French summary).
Photo appendix

In all stands photos were taken 1993, 1996, 2002 and 2008 to give an impression of the changes in number, growth and quality of seedlings and saplings, field vegetation and shelter stands. Only five of the stands are presented here since the late regeneration stands, LH and LL, many times gave an impression of a “green wall”, which made it impossible, on the photos, show some distinctive features that could be recognized all years.

Photo 1-3. Stand EH.
Photo 4-9. Stand EM.
Photo 10-12. Stand EL.
Photo 16-18. Stand IL.


Photo by:
E. Agestam photo 1-5, 7, 9-21
P-M Ekö photo 6, 8