Broadleaved tree species in conifer-dominated forestry: Regeneration and limitation of saplings in southern Sweden

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Abstract

Forests and forestry in Sweden are dominated by conifers. Silviculture using mixed or broadleaved stands is often recommended, but the degree to which broadleaves regenerate naturally needs to be clarified. The Swedish National Forest Inventory is here used for a region-wide study of broadleaved saplings (1.3 m tall to 4.9 cm dbh) regenerated naturally. For 12 species (taxa) in young forests (<7 m tall) and high forests (≥7 m), sapling densities were related to seven forest types and three productivity classes. Birch had highest densities in all but two broadleaved forest types. Birch, oak, rowan and sallow had 70–85% of their total sapling populations in conifer-dominated forest types, indicating good potential for mixed stands. Beech, lime, hornbeam, ash and elm were mostly restricted to ‘noble’ (hardwood) forests. The regeneration success (saplings per mature tree) for birch, rowan and oak was highest in conifer-dominated forest types; beech was about equally successful in conifer-dominated and broadleaved forests, and ash was very successful in broadleaved forest. Oak regeneration may be problematical in broadleaved forests, but we suggest this is not the case in conifer-dominated forests (where oaks have rarely been studied). Sapling densities of the species in the forest types were not consistently correlated with productivity, but birch and aspen generally regenerated strongest at intermediate and at high productivity, respectively. In noble forests, oak, ash and elm regenerated strongest at low productivity. The role of asexual regeneration (sprouting) remains to clarify. Our results suggest that lime, elm, ash and some other trees currently are limited mainly by poor dispersal, rather than habitat availability. The results are promising for various forms of mixed-species forestry that does not require planting (or little planting) and that would be beneficial for nature conservation.

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1. Introduction

In many parts of Europe and elsewhere, forestry is based mostly on even-aged conifer stands harvested under short rotations by clearcutting (or removal of...
almost all large trees). In repeated thinnings, most of the broadleaved trees are cut or harvested. There are disadvantages with such forestry, if it comes to dominate as in Sweden. Even-aged conifer stands generally have low value for wildlife (Persson, 1990; Gustafsson, 1996; Hunter, 1999), may be susceptible to pests and global warming (Young and Giese, 2003; Sykes and Prentice, 1996; Bradshaw et al., 2000) and may create more acid soils (Nordborg and Olsson, 1999). Norway spruce (Picea abies), common in Europe, is also susceptible to wind-throw. Forest owners have been encouraged to plant or to favour native broadleaved trees for forestry and biodiversity purposes (Persson, 1990; Gustafsson, 2000; Zerbe, 2002). In these contexts, the benefits of mixed coniferous-broadleaved forests are often mentioned (Mosandl and Kleinert, 1998; Olsthoorn et al., 1999; Thelin et al., 2002; Johansson, 2003).

In northern Europe, the most common broadleaved trees are silver birch (Betula pendula) and hairy birch (B. pubescens), forming 10% of the total wood volume and 53% of the volume of broadleaves in southern Sweden (see below). High seed production and rapid growth in open clear-cut areas favour birches; however, they are mostly eliminated in repeated thinnings (Simard et al., 2004, and references therein). In Sweden, usually only a few mature trees per hectare (mainly birch, aspen Populus tremula, and/or Scots pine Pinus sylvestris) are retained for biodiversity at clearcutting. Given the goal of changing the forest composition to resemble more natural conditions (SOU, 1992), the broadleaved trees need more attention. For both forestry and conservation work, the factors limiting regeneration of broadleaved tree species are of interest. Beside historical human use of forests (Peterken, 1996; Lindbladh et al., 2000), tree species may be limited by, e.g., seed production, seed dispersal, and availability of habitat for growth (Clarke et al., 1999). Most of the present south Swedish forest consists of planted coniferous trees, whereas natural forests in this region were dominated by broadleaves, or mixed coniferous-broadleaved forests (Lindbladh et al., 2000 and references therein). Conversion of especially spruce forest to mixed or broadleaved stands is desirable (SOU, 1992; Spiecker et al., 2004). Here we analyse regeneration of 12 broadleaved tree species that occur in or have colonized the forests of southern Sweden. Moreover, to examine habitat limitation in these species, we analyse regeneration in relation to site productivity (site index).

Below, we first briefly present regeneration patterns (sapling densities) of broadleaves in the forests. The data are then used to answer the following three questions: (1) do the 12 broadleaved tree species differ in regeneration (i.e. production of small trees, saplings) in the forest types; in particular, does regeneration differ in coniferous versus broadleaved forests, indicating conditions that limit some species? (2) Are some species more successful in producing saplings (per capita mature trees) in coniferous than in broadleaved forest? (3) To what extent is regeneration in the species related to, or limited by site productivity?

Broadleaved trees in conifer-dominated forestry occur naturally as seedlings and saplings, while their densities as larger trees are determined mainly by the cutting regime, where thinning is important. In Sweden, regeneration of broadleaves has not been analysed at regional level, which is done here for saplings using data from the Swedish National Forest Inventory (NFI). We selected the southern part of Sweden for study, where most of the broadleaved tree species occur. Although seedlings of trees (<50 cm tall) may be ‘persistent juveniles’ for long periods (Grime et al., 1988; Tapper, 1992), saplings more reliably indicate regeneration potential of the species, as mortality is lower for saplings than for seedlings. We studied saplings defined as stems from breast height (1.3 m) up to stem diameter of 4.9 cm, dbh (referred to as 0.1–4.9 cm dbh). The majority of these saplings had not been affected by thinning (the cohort is dominated by small saplings about 0.1–2.5 cm dbh; see also below), and so regeneration was mainly determined by the natural processes of seed production, seed dispersal, germination, growth, or sprouting from cut stems or roots. For larger saplings (diameter interval 5.0–9.9 cm dbh in our data sets), densities were much lower, mainly due to thinning. We compared regeneration in all major forest types in the landscape of southern Sweden; three coniferous ones (strongly predominating in area), one mixed, and three broadleaved forest types. We analysed regeneration in young forest and in higher forest where saplings form advance regeneration that may be important for the stand after cutting (Greene et al., 1999; Nyland, 2002). We end by discussing factors limiting the broadleaved tree species in relation to
their ecological traits, and by considering implications for forestry and conservation.

2. Materials and methods

2.1. Study area and tree species selected

The study area of southern Sweden (Fig. 1) is a transition zone between the boreal forest in central and northern Scandinavia and the temperate (nemoral) forest in continental Europe; nemoral forest also occurs in southernmost Sweden (Fig. 1; Diekmann, 1994; SEPA, 1994; Nilsson, 1997). The northern limit of our study area coincides with the approximate limit of the distribution of oak (Fig. 1; the northern counties Uppsala, Västmanland, Örebro, and Värmland except the municipalities Torsby, Hagfors and Filipstad, are included). North of this limit, species richness and abundance of broadleaves is much lower than to the south (Gustafsson and Ahlén, 1996; Nilsson, 1990).

The study area is lowland (less than 300 m above sea level) where glaciation ended 15,000–10,000 years ago, containing mostly moraine soils on granite or gneiss (bedrock sometimes exposed, in a mosaic landscape of forest, small fields, wetlands and lakes). There are several larger lowland agricultural areas with fertile soil. In July, the mean precipitation decreases from about 100 mm in the west to about 55 mm in the east, and the temperature varies from about 14–17 °C. About 80% of the land area would be forested in the absence of human influence (Gustafsson and Ahlén, 1996) and the present forest proportion is about 56% (Forestry Statistics, 2000). Several thousand years ago, oaks (Quercus spp.), small-leaved lime (Tilia cordata), hazel (Corylus avellana) and other species probably dominated the forests, but during the last thousand years human influence is thought to have strongly favoured conifers, especially so in the last 150 years (Lindbladh et al., 2000). Presently, most stands are less than 60 years old; about 10% of the stands are 100 years or older (Forestry Statistics, 2000). Table 1 (see ‘Total’) shows the current tree species composition by wood volume in the study area.

In Swedish forest legislation, 13 broadleaved trees are ‘noble’ (historical term) and important for wood production and biodiversity (Berg et al., 1994; Gustafsson and Ahlén, 1996; Lof, 2001). Four of these trees have very limited distribution and were excluded. We included the following nine noble trees: pedunculate oak (Q. robur), sessile oak (Q. petraea), beech (Fagus sylvatica), common ash (Fraxinus

Fig. 1. Map of the study area in southern Sweden, coinciding approximately with the distribution of noble broadleaved forest or tree species, especially oaks. The northern counties Uppsala, Västmanland, Örebro, and Värmland except municipalities Torsby, Hagfors and Filipstad, were included, forming the northern limit of the study area. The area includes two (temperate) vegetation zones in Sweden, the nemoral and boreonemoral zone. Beech and hornbeam are largely restricted to the southern (nemoral) zone, to which we added the county of Kronoberg in south central Sweden where these trees also occur. The largest easternmost island, Gotland, is not included in the study.
small-leaved lime (*Tilia cordata*), Norway maple (*Acer platanoides*), hornbeam (*Carpinus betulus*), wych elm (*Ulmus glabra*), and gean (wild cherry) (*Prunus avium*). Beech and hornbeam are mainly restricted to the southern part of the study area (see Fig. 1, and Lindgren, 1970; Björkman, 1998) and sapling densities given below are based on this part. Of other broadleaved trees, we included silver and hairy birch, aspen, sallow (*Salix caprea*) and rowan (*Sorbus aucuparia*). Although *Q. petraea* is more common than *Q. robur* in xeric-mesic forest, the two oaks overlap considerably in range, stand types and traits, and were pooled. *B. pubescens* is more common in mesic-moist forest than *B. pendula*, otherwise the two birches overlap and are similar, and were pooled. In total, 12 species (taxa) were included, and studied in forest producing at least 1 m$^3$ per hectare and year (Swedish definition of ‘forest land’). Xeric and wet forests of lower productivity were excluded. We also excluded broadleaves mostly occurring in forested wetland (alder *Alnus glutinosa* and *Salix* spp.).

Ecological traits relevant to regeneration of the species are summarized in Table 2. Asexual regeneration by sprouting may be important for seedlings/saplings (Del Tredici, 2001), but has generally been neglected (Bond and Midgley, 2001) and little is known about less common species (Table 2). Classification of shade-tolerance tends to vary among studies; we focused on saplings (young trees) and Scandinavian conditions (Table 2).

### 2.2. The national forest inventory (NFI) and analyses

The Swedish NFI was established in 1923 (Thorell and Östlin, 1931). In 1983, a new design was introduced (Ranneby et al., 1987) and has been used since. The information recorded in the NFI is detailed and comprises tree, stand, and site data (Lindroth, 1995; SLU, 1997). The inventory covers the whole of Sweden with a stratified systematic cluster sample. Each cluster consists of permanent or temporary circular sample plots with radius 10 and 7 m, respectively, located along the sides of a square or rectangle. Certain measurements, such as forest type, height and closure are made with plot radius of 20 m, others such as sapling counts are made with radius 5 or 3.5 m (SLU, 1997). The permanent plots are
inventoried in 5–10 year intervals. In general, a 5-year period is needed to attain acceptable precision in the estimates. We present data based on all available plots in the study area during 1998–2002 (in total 15,082 plots). For calculation of volumes, forest areas, and standard error of means from NFI, see formulas in Fridman (2000) and Fridman and Walheim (2000).

We excluded forest land (plots) containing no or very few saplings/trees (stand closure in NFI equal to 0). Such forest land, for instance recent clear-cuts, is not included in estimates of forest areas. Data from the NFI plots were divided into (1) young forest, on average less than 7 m tall, and (2) high forest, on average 7 m or more (usually not very ‘old’, thus referred to as ‘high’). In plots (area within 20 m radius from center), if the average tree height weighed by basal area is higher than 7 m, weighing of height by basal area is used, but if it is lower, height is the arithmetic mean of the main trees assumed to be used in a crop. The forest types used in our analyses are defined by tree basal area (Table 3).

### Table 2

Ecological traits relevant to regeneration of the broadleaved tree species (taxa) included in the present study (for latin names, see Table 1)

<table>
<thead>
<tr>
<th>Species</th>
<th>Shade-tolerance</th>
<th>Seed weight (mg)</th>
<th>Seed production/mature tree</th>
<th>Dispersal agent</th>
<th>Sprouting capacity</th>
<th>Distribution in Sweden</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birches</td>
<td>Intolerant</td>
<td>0.14</td>
<td>Very high</td>
<td>Wind</td>
<td>Moderate</td>
<td>Country-wide</td>
</tr>
<tr>
<td>Aspen</td>
<td>Intolerant</td>
<td>Low</td>
<td>Very high</td>
<td>Wind</td>
<td>Very high</td>
<td>Country-wide</td>
</tr>
<tr>
<td>Sallow</td>
<td>Intolerant</td>
<td>0.09</td>
<td>Very high</td>
<td>Wind</td>
<td>Very high</td>
<td>Country-wide</td>
</tr>
<tr>
<td>Oaks</td>
<td>Intolerant/mid tol.</td>
<td>3500</td>
<td>Low/moderate</td>
<td>Animals</td>
<td>High</td>
<td>South-central</td>
</tr>
<tr>
<td>Rowan</td>
<td>Mid tolerant</td>
<td>2.6</td>
<td>High/moderate</td>
<td>Animals</td>
<td>Moderate/high?</td>
<td>Country-wide</td>
</tr>
<tr>
<td>Beech</td>
<td>Very tolerant</td>
<td>250</td>
<td>Low/moderate</td>
<td>Animals</td>
<td>Moderate?</td>
<td>South</td>
</tr>
<tr>
<td>Hornbeam</td>
<td>Tolerant</td>
<td>40</td>
<td>Moderate</td>
<td>Wind</td>
<td>High</td>
<td>South</td>
</tr>
<tr>
<td>Maple</td>
<td>Tolerant</td>
<td>140</td>
<td>Moderate</td>
<td>Wind</td>
<td>Moderate/high</td>
<td>South-central</td>
</tr>
<tr>
<td>Ash</td>
<td>Tolerant</td>
<td>80</td>
<td>Moderate</td>
<td>Wind</td>
<td>High/very high</td>
<td>South-central</td>
</tr>
<tr>
<td>Elm</td>
<td>Very tolerant</td>
<td>3.5</td>
<td>High</td>
<td>Wind</td>
<td>High</td>
<td>South</td>
</tr>
<tr>
<td>Lime</td>
<td>Tolerant</td>
<td>35</td>
<td>Moderate</td>
<td>Wind</td>
<td>Very high</td>
<td>South-central</td>
</tr>
</tbody>
</table>

* Based on Rinne et al. (1987), Grime et al. (1988), Kauppi et al., 1988, Mossberg (1992), Johansson (1992), Suszka et al. (1996), Karlsson (2001; pers. comm.), Deiller et al. (2003), Fältman et al. (2003), and own studies (Götmark, pers. obs.) of closed canopy broadleaved forest, and cutting in such forest (shade-tolerance, sprouting). The two species of birches and oaks were pooled (Table 1).

* Refers mainly to shade tolerance of seedlings/saplings; this trait may change with age/height of trees (e.g. Diekmann, 1996).

* For sallow, rowan and elm, weight of germinule (Grime et al., 1988).

* Number of seeds per tree.

* Refers to small individuals (seedlings/saplings/poles), sprouting capacity or importance generally declines with stem diameter (Del Tredici, 2001; Johnson et al., 2002).

* Sprouting by root suckers.

* Relatively small trees (occasionally high, 15 m or more).

We report mean sapling densities (stems, 0.1–4.9 cm dbh, per hectare), but areas of the forest types differed considerably and we also estimated total number of saplings per forest type, using these data for further analyses. Number of saplings (population size) was calculated as sapling densities per ha times the estimated area (ha) of each forest type. For comparison and for analyses, mean densities of large trees of the 12 species in high forest (>7 m) were estimated. Densities of saplings may be affected by thinning, but in young forest only 23% of the stand area had been thinned since stand establishment. In high forest, 57% of the area had evidence of thinning from after 1975. We cannot estimate the number or proportion of cut stems, but thinned stands had about equal or higher sapling densities than unthinned stands (Götmark et al., unpublished data).
For each tree species, we calculated per capita regeneration success, which is the ratio between density of saplings and density of large (mature) trees. For high forest, we compared two groups: the four coniferous/mixed forest types (pooled), and the three broadleaved types (pooled), calculating means that were weighed by the areal extent of forest types included within each group. Our success measure indicates the relative (approximate) production of saplings per mature tree in the species. In the first analysis, mature (reproductive) trees were defined as stems ≥15 cm dbh; for sallow and rowan, smaller trees starting to reproduce earlier, we set the limit lower (≥10 cm dbh). In the second analysis, we included stems ≥20 cm for all species except sallow and rowan [we could not find useful data for size at maturity, but Loehle (2000) reported that the typical age at sexual maturity in small trees (mean height 11 m) was 14 years, whereas medium-sized trees (height 21 m) and tall trees (30 m) did not differ much in this respect (typical reproductive age 33 and 35 years, respectively)]. We did not calculate per capita regeneration success for trees in young forest. Although there are scattered larger trees in young forest (retained for conservation or shelterwood), most seed trees would be at the edge of higher forest nearby (Karlsson, 2001) and cannot be estimated from the NFI.

Site productivity was based on the site index for each study plot, determined from curves relating tree age to tree height (based on conifers), and/or from the type of lower forest vegetation (SLU, 1997). In the NFI, the site index is translated into a productivity measure (m³ tree volume per ha and year). We studied regeneration of broadleaved trees in three classes (intervals) of productivity, as follows: (1) low: 1–5.9 m³ per ha and year, (2) intermediate: 6.0–8.9 m³, and (3) high productivity: ≥9.0 m³.

Since the NFI is based on sampling with partial replacement, the estimators are complex (see Fridman et al. / Forest Ecology and Management 214 (2005) 142–157).
and Walheim, 2000 for explanations and formulas). Although systematic sampling is used in the NFI, for this study standard error (S.E.) was estimated assuming random sampling of tracts, which is conservative as it might overestimate the true S.E. Confidence intervals (95%) for means were based on S.E., and significant differences reported below ($P < 0.05$) based on these confidence intervals.

### 3. Results

#### 3.1. Sapling densities

Table 4 shows estimates of sapling densities for the 12 species (taxa) in each forest type. Birch generally had highest sapling densities, but in noble and in other broadleaved forests other species dominated, and had relatively high sapling densities. The density of birch saplings was higher in young than in high forest (e.g. $P < 0.05$ for both spruce and in pine forest), but birch predominated among the saplings also in high forest. Some species, such as aspen and rowan, regenerated in most forest types, while saplings of other species mostly were restricted to one or a few forest types (Table 4). In young forest, saplings of oak were more common than those of beech ($P < 0.05$); in high forest, densities of these two species were more similar, but in noble forest beech had higher sapling densities than oak, ash and rowan ($P < 0.05$ in all cases, data from southern part of study area used, Fig. 1).

#### 3.2. Sapling populations in coniferous and broadleaved forests

Total sapling populations were estimated from Tables 3 and 4 (area $\times$ densities). Birch formed 81% (about $3.065 \times 10^9$ saplings) of all saplings in young forest and 66% (about $3.107 \times 10^9$) of all saplings in high forest. Birch was the major broadleaf element in

<table>
<thead>
<tr>
<th>Species/taxa</th>
<th>Forest height (m)</th>
<th>Spruce</th>
<th>Pine</th>
<th>Spruce-pine</th>
<th>Mixed</th>
<th>Birch</th>
<th>Noble</th>
<th>Other broadleaved</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birches</td>
<td>$&lt;7$</td>
<td>1896</td>
<td>1426</td>
<td>2582</td>
<td>4077</td>
<td>5123</td>
<td>363</td>
<td>1426</td>
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<tr>
<td></td>
<td>$\geq 7$</td>
<td>358</td>
<td>618</td>
<td>640</td>
<td>776</td>
<td>1097</td>
<td>81</td>
<td>305</td>
</tr>
<tr>
<td>Aspen</td>
<td>$&lt;7$</td>
<td>197</td>
<td>23</td>
<td>45</td>
<td>306</td>
<td>381</td>
<td>199</td>
<td>3698</td>
</tr>
<tr>
<td></td>
<td>$\geq 7$</td>
<td>31</td>
<td>30</td>
<td>44</td>
<td>117</td>
<td>103</td>
<td>87</td>
<td>452</td>
</tr>
<tr>
<td>Oaks</td>
<td>$&lt;7$</td>
<td>32</td>
<td>43</td>
<td>36</td>
<td>462</td>
<td>29</td>
<td>1600</td>
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<td>32</td>
<td>60</td>
<td>40</td>
<td>85</td>
<td>56</td>
<td>146</td>
<td>136</td>
</tr>
<tr>
<td>Beech</td>
<td>$&lt;7$</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>137</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\geq 7$</td>
<td>23</td>
<td>8.8</td>
<td>71</td>
<td>56</td>
<td>16</td>
<td>364</td>
<td>66</td>
</tr>
<tr>
<td>Elm</td>
<td>$&lt;7$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>294</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\geq 7$</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>2.3</td>
<td>1.2</td>
<td>37</td>
<td>8.5</td>
</tr>
<tr>
<td>Ash</td>
<td>$&lt;7$</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>163</td>
<td>784</td>
<td>214</td>
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<td></td>
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<td>4.0</td>
<td>4.0</td>
<td>0.7</td>
<td>5.5</td>
<td>91</td>
<td>234</td>
<td>137</td>
</tr>
<tr>
<td>Lime</td>
<td>$&lt;7$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>24</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$\geq 7$</td>
<td>0</td>
<td>0.9</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>38</td>
<td>0</td>
</tr>
<tr>
<td>Maple</td>
<td>$&lt;7$</td>
<td>1.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>80</td>
<td>193</td>
</tr>
<tr>
<td></td>
<td>$\geq 7$</td>
<td>5.1</td>
<td>0.8</td>
<td>5.4</td>
<td>2.0</td>
<td>8.3</td>
<td>33</td>
<td>42</td>
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<tr>
<td>Maple</td>
<td>$&lt;7$</td>
<td>8.2</td>
<td>30</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>201</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>$\geq 7$</td>
<td>3.9</td>
<td>1.3</td>
<td>7.7</td>
<td>16.2</td>
<td>44</td>
<td>95</td>
<td>0.9</td>
</tr>
<tr>
<td>Hornbeam</td>
<td>$&lt;7$</td>
<td>0.8</td>
<td>0</td>
<td>0</td>
<td>3.9</td>
<td>0</td>
<td>0</td>
<td>6.2</td>
</tr>
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<td></td>
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<td>1.8</td>
<td>1.6</td>
<td>1.2</td>
<td>0</td>
<td>17</td>
<td>23</td>
<td>14</td>
</tr>
<tr>
<td>Sallow</td>
<td>$&lt;7$</td>
<td>28</td>
<td>21</td>
<td>23</td>
<td>34</td>
<td>54</td>
<td>21</td>
<td>167</td>
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<td>$\geq 7$</td>
<td>7.8</td>
<td>11</td>
<td>28</td>
<td>34</td>
<td>31</td>
<td>3.3</td>
<td>50</td>
</tr>
<tr>
<td>Rowan</td>
<td>$&lt;7$</td>
<td>107</td>
<td>27</td>
<td>71</td>
<td>235</td>
<td>128</td>
<td>71</td>
<td>893</td>
</tr>
<tr>
<td></td>
<td>$\geq 7$</td>
<td>54</td>
<td>57</td>
<td>60</td>
<td>208</td>
<td>157</td>
<td>162</td>
<td>274</td>
</tr>
</tbody>
</table>

$^a$ Zero does not necessarily mean that there were no trees (rounded numbers).

$^b$ For full name, see Table 1.

$^c$ Based on the southern part of the study area, where these two species occurred (see Fig. 1).
five of the seven forest types (Table 4). High forest contained more than twice as many saplings as young forest (67.8% of all saplings), due to its large area. The broadleaved tree species differed considerably in the extent to which their sapling population occurred in or had colonized coniferous and mixed forest (Fig. 2). In high forest, birch, oak, sallow and rowan had highest population proportion in coniferous and mixed forest, whereas lime, hornbeam, ash and elm had lowest population proportion there. In young forest, the result was generally similar but gean, beech and hornbeam were more common in conifer and mixed forest (Fig. 2). In young forest, several species had small populations and the estimates may partly be influenced by chance, but for lime, ash and elm 70–100% of the saplings grew in broadleaved forest (Fig. 2).

### 3.3. Regeneration success of the tree species in coniferous and broadleaved forests

Table 5 shows estimates of densities of large trees, used to calculate per capita regeneration success in high forest. Fig. 3a (mature trees >15 cm dbh, for rowan and sallow >10 cm) shows that in coniferous forests, rowan had the highest per capita regeneration success, followed by oak and birch that had similar value, and then aspen, beech and sallow in this order. In broadleaved forests, ash was outstanding with a value of 66, followed by maple and rowan; birch and sallow had weakest per capita regeneration success there. Birch was especially successful in coniferous forests, compared to in broadleaved forests (Fig. 3a); oak and sallow had about twice as high per capita regeneration success in coniferous than in broadleaved forests, whereas aspen and beech had relatively similar regeneration success in coniferous and broadleaved forests.

Fig. 3b (mature trees >20 cm dbh) shows largely the same picture, but regeneration success of birch, aspen and oak became higher in coniferous forests, and the values for beech were similar in coniferous and broadleaved forests. Again, regeneration of ash was outstanding in broadleaved forests (Fig. 3b). Sallow and rowan were not included in Fig. 3b as they mature as small trees, and the data for gean was too uncertain to include in Fig. 3b.
3.4. Regeneration of the tree species in relation to productivity

For the forest types studied, we found complex relationships between sapling densities of the species and forest productivity (see Figs. 4–6, with significance of differences). For young forest, only data for coniferous forest types were meaningful to analyse, whereas for high forest six forest types were analysed. For birch, sapling densities peaked at intermediate productivity in six of nine comparisons, and in eight of nine comparisons densities decreased from intermediate to high productivity conditions (Figs. 4-6). For aspen, densities increased with increasing productivity or peaked at high productivity in six of nine forest type comparisons, and similarly for rowan in five of nine comparisons. Sallow and especially oak sapling densities showed highly variable relationships to productivity. Surprisingly, in noble forest, densities of oak, elm and ash saplings decreased with increasing productivity (Fig. 6a). For beech, sapling density was highest at high productivity in noble forest (Fig. 6a), though this was not the case in the two other broadleaved forest types.

At high productivity, seedlings and saplings might grow at higher density, but thinning of the forest may be more common, explaining, for instance, the pattern observed for birch. We re-analysed the data using only unthinned forest (plots) and found almost identical patterns as those presented in Figs. 4–6 (data not shown), so thinning did not influence these results. Thinning generally had weak influence on sapling densities in 1998–2002 (Götmark et al., unpublished data).

4. Discussion

4.1. Regeneration of broadleaves: the role of dispersal and persistence

Four species (birch, oak, sallow and rowan) had a large proportion of their total sapling population in coniferous and mixed forests, for oak almost 75%. These four species represent two different modes of seed dispersal; production of many small seeds easily dispersed by wind (birch, sallow) or production of fewer seeds dispersed by animals (acorns or in rowan seeds in fleshy fruits). If seed dispersal is important for the present occurrence of these trees in southern Sweden, both strategies seem to be successful (cf. Willson, 1993). Birch, sallow, oak, and rowan are also favoured by the initially open conditions on clear-cuts (cf. Table 2). The major dispersal agent of acorns in Sweden and other parts of Europe, the jay Garrulus glandarius (Bossema, 1979), usually nests in high densities in conifer-dominated forests, which offer good protection for their nests. Jays hoard acorns

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**Table 5**

Mean density of large mature trees (stems, >15 cm dbh, per hectare) for 12 species (taxa) in high forest (≥7 m), of seven types defined in Table 3 (NFI, 1998–2002)

<table>
<thead>
<tr>
<th>Species/taxa</th>
<th>Spruce</th>
<th>Pine</th>
<th>Spruce-pine</th>
<th>Mixed</th>
<th>Birch</th>
<th>Noble</th>
<th>Other broadleaved</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birches</td>
<td>26.5</td>
<td>17.7</td>
<td>67.9</td>
<td>102</td>
<td>207</td>
<td>24.8</td>
<td>93.7</td>
</tr>
<tr>
<td>Aspen</td>
<td>4.3</td>
<td>1.0</td>
<td>7.6</td>
<td>30.9</td>
<td>5.0</td>
<td>7.5</td>
<td>79.0</td>
</tr>
<tr>
<td>Oaks</td>
<td>1.9</td>
<td>1.9</td>
<td>4.2</td>
<td>12.7</td>
<td>3.4</td>
<td>107</td>
<td>15.3</td>
</tr>
<tr>
<td>Beech</td>
<td>2.0</td>
<td>1.6</td>
<td>2.1</td>
<td>19.1</td>
<td>1.0</td>
<td>123</td>
<td>5.9</td>
</tr>
<tr>
<td>Elm</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0.1</td>
<td>5.7</td>
<td>1.0</td>
</tr>
<tr>
<td>Ash</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>1.1</td>
<td>0.8</td>
<td>20.6</td>
<td>3.3</td>
</tr>
<tr>
<td>Lime</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>3.2</td>
<td>0.5</td>
</tr>
<tr>
<td>Maple</td>
<td>0</td>
<td>0.1</td>
<td>0</td>
<td>0.3</td>
<td>0.2</td>
<td>3.6</td>
<td>1.5</td>
</tr>
<tr>
<td>Hornbeam</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>6.3</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Gean/Cherry</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>10.0</td>
<td>0.9</td>
<td></td>
</tr>
<tr>
<td>Sallow</td>
<td>0.8 (2.0)</td>
<td>0.2 (0.8)</td>
<td>1.7 (3.7)</td>
<td>2.8 (7.7)</td>
<td>3.7 (9.0)</td>
<td>2.9 (3.7)</td>
<td>17.1 (34.2)</td>
</tr>
<tr>
<td>Rowan</td>
<td>0.6 (1.7)</td>
<td>0.1 (0.9)</td>
<td>0.9 (2.6)</td>
<td>2.7 (6.1)</td>
<td>1.2 (3.9)</td>
<td>3.7 (7.9)</td>
<td>5.4 (18.0)</td>
</tr>
</tbody>
</table>

*a* Zero does not necessarily mean there were no trees (rounded numbers).

*b* For full name, see Table 1.

*c* Based on the area where these species mainly occurred (Fig. 1).

*d* In parenthesis, estimates based on stems >10 cm dbh, used in analyses (see text).
hundred of metres or kilometres from oak trees, preferring open conditions or forest edges where some of the hoarded acorns germinate (Bossema, 1979). Clear-cutting combined with jays may be a major reason for oak colonization of coniferous forest. In addition, Frost (1997) (see also Nilsson, 1985) found higher survival of oak seedlings in coniferous than in broadleaved forest, which is consistent with our finding of higher per capita regeneration success in...
coniferous forest. Mosandl and Kleinert (1998) stated that jays were the major reason for successful regeneration of oak in pine forests in Germany, where hoarding by jays apparently takes place also under pine canopy cover. A comparison of our three conifer-dominated forest types shows that average oak densities were highest in pine forests, because jays often hoard there, because the availability of light in these stands is relatively good, and/or because oaks compete well in the soil of pine stands.

The fruits of rowan are often eaten by migrating birds in the autumn, mainly thrushes and waxwings. The seeds survive passage through the birds’ digestive system, leading to effective long-distance seed dispersal. Many migrating birds roost or seek cover in coniferous forest that covers a much larger area than broadleaved forest.

Beech colonized southern Sweden late (about 3000 years ago) and seems slow in its range expansion (Björkman, 1998). Beech apparently lacks efficient dispersal agents, though Nilsson (1985) reported that in years with few acorns and many beech nuts, jays dispersed nuts, which may explain northward migration. In high noble forest in the south, sapling density of beech was high, and shade-tolerance probably contributes to its success there. However, to some extent beech is colonizing spruce and coniferous forest, in agreement with Nilsson’s (1985) indication of high sapling survival in such forest, and occasional dispersal by jays.

Most of the trees with very low proportion of their saplings in coniferous forest are shade-tolerant and wind-dispersed (lime, hornbeam, ash, elm, maple).
Compared to birch and sallow, seed production per tree is lower and the seed and its appendage is heavier/larger in these species (Table 2), probably making long-distance wind dispersal more difficult. Therefore, beside historical factors (Lindbladh et al., 2000), dispersal limitation is one plausible or contributing reason why these species currently are uncommon as saplings in coniferous forest. The rates of seed fall in still air for aspen, maple, hornbeam and ash (terminal velocity) were 11, 107, 120 and 200 cm/s, respectively (Levin and Kerster, 1974), which is consistent with dispersal limitation and our findings. In southern Sweden, birch seeds were more readily dispersed into a clear-cut than seeds of elm and maple, which dispersed better than hornbeam seeds (but elm and birch did not differ much in dispersal distance; Karlsson, 2001). For long-distance dispersal (rare) updrafts are critical (Greene and Johnsson, 1995). Southern Sweden is dominated by forest, lakes and mires that may impede wind dispersal of heavy seeds.

An alternative or contributing factor explaining sapling regeneration is sprouting, the main form of regeneration in aspen, where sexual reproduction currently is rare. Limited knowledge about this ‘persistence niche’ (Bond and Midgley, 2001) for several species (Table 2) makes it difficult to evaluate its role. Sprouting in (cut) saplings is more common and important than sprouting in (cut) larger trees (review in Del Tredici, 2001). Precommercial and commercial thinning imply cutting of sapling and pole trees of broadleaves, but the degree to which plants die or become seedling sprouts has mainly been studied in birch and aspen in Scandinavia. In hardwood forest in US (three studies), 58–78% of “seedlings” were sprouts that may survive for long (Del Tredici, 2001). To judge from closely related American broadleaves, saplings of oak in Europe should have higher sprouting capacity than saplings of birch and maple in Europe (Del Tredici, 2001, pp. 131–134; Johnson et al., 2002; Table 2). If true, oak regeneration is produced, or maintained also in this way.

The trees with low proportion of saplings in coniferous forest, such as lime, ash and elm, sprout readily when pruned or cut (Table 2). Historically, sprouting probably facilitated their survival under pressure from human exploitation; pollarding for forage was common, so not all mature trees of these species were eliminated (SEPA, 1994; Nilsson, 1997).

4.2. Regeneration success of broadleaved trees

For high forest, the per capita regeneration success was higher in coniferous than in broadleaved forests for birch, oak, rowan, sallow and to some extent aspen. Between 1985 and 2000 in coniferous forests, birch sapling densities remained approximately constant while sapling densities of both oak and beech declined about 50%, probably mainly due to deer browsing (Götmärk et al., unpublished data). If data from 1985 had been used, per capita regeneration success for oak would have been much higher than for birch in coniferous forest, and beech would also have had higher success in coniferous forests.

For birch, oak, rowan, sallow and aspen there are several alternative explanations for higher regeneration success in coniferous than in broadleaved forests. First, light availability may be lower in high broadleaved forests than in high coniferous forests. As the four species are mainly shade-intolerant, their regeneration may be poor in darker broadleaved forests. Most high conifer stands have been thinned in forest management, which may keep stands relatively open, and allow regeneration of these species. But the broadleaved forests contained much birch and aspen, and were probably relatively open (and also partially cut, for e.g. fuel-wood). Noble forest is likely to be darker, because there is presently little management activities in these stands (Hamilton and Mirton, 1998). Light availability may play a role, but is probably not a major factor.

Second, in contrast to the broadleaves, Norway spruce and Scots pine die after cutting, and lower competition in conifer stands may facilitate regeneration of birch, oak, rowan and aspen there after thinning. In addition, clear-cutting is less common in broadleaved stands, which means less ground disturbance in the stands over time, and probably reduced regeneration of birch and rowan. For oak, it would be interesting to study whether jays prefer hoarding acorns on ground disturbed during clear-cutting. Aspen had somewhat higher per capita regeneration success in coniferous forests, possibly due to lower competition there.

The shade-tolerant maple and especially ash had high per capita regeneration success in broadleaved forest, but unfortunately these trees were too rare in coniferous forest to estimate regeneration success.
there. Ash has recently been reported to be successful in Europe (Tapper, 1996; Harmer et al., 1997; Marigo et al., 2000; Kerr and Cahalan, 2004). In lime, regeneration through seeds is weak compared with for instance ash and maple (pers. obs.). In addition to poor dispersal, lime may be limited by factors controlling sexual reproduction, as in north-western England (Pigott and Huntley, 1981). In elm, with good seed dispersal in Karlsson’s (2001) study, mortality through Dutch elm disease might influence sapling densities.

4.3. The influence of habitat productivity on regeneration

In studies of regeneration of trees in relation to productivity, one potential problem is non-random selection of study stands; in other words, the full range of productivity conditions for a species may not be represented. The NFI offers an advantage in its systematic sampling that covers whole regions. For the forest types studied, we found that birch sapling densities were reduced at high productivity levels, which may be due to increased competition from herbs, shrubs and other trees (Harvey and Bergeron, 1989; review in Greene et al., 1999). A similar relationship was found for essentially all forest types, suggesting that under the current conditions birch regenerate best in soils of intermediate productivity. At high productivity, herbs, grasses and dwarf-shrubs may suppress germination and growth of birch seeds that have small nutrient reserves. Thinning did not influence, or bias our results (see above).

Interestingly, the tree species that most strongly rely on regeneration by sprouting (aspen) showed the strongest positive association between productivity and regeneration. The root suckers of aspen are tied physiologically to the root system of the parent tree, at least initially. Possibly, during such linked conditions, regeneration and productivity will usually be positively correlated, under the assumption that the shoots (sprouts) are less influenced by other vegetation surrounding them than are shoots growing from seeds.

In high noble forest, sapling densities were generally highest at low and intermediate productivity, except for beech. For ash, we found a negative correlation between sapling density and productivity. Undergrowth of competing shrubs such as hazel is common in noble forests of high productivity, and may reduce tree sapling densities there. Alternatively, productive noble forest have more closed canopies and subcanopies (due to, e.g., limited cutting) leading to lower sapling recruitment. However, ash seedlings and saplings in southern Sweden are shade-tolerant (pers. obs.). Our results indicate that regeneration of ash, elm, maple and oak can be relatively high on forest land of low and intermediate productivity, but further studies of stem distributions and growth rates in noble forests are of interest. Ash was considered “very demanding with respect to soil moisture, pH and nitrogen” in southern Sweden by Diekmann (1996). The variables in Diekmann’s study should reflect productivity, though his conclusion for ash might be influenced by the particular stands selected for that study.

In the study area, most trees regenerate under a wide range of conditions. Scots pines are common on xeric forest land, but also on moist-wet mires. Alders are common in swamp forest, but also on mesic soils (Table 1). For beech, there are four stand types, differing markedly in soil pH and nutrient level (Lindgren, 1970). We found regeneration of the tree species under a wide range of nutrient (productivity) levels. There are probably several reasons for these broad habitat distributions. We suggest that the extinction of the great majority of the European tree species during the last ice age (Latham and Ricklefs, 1993) led to broader habitat distributions of remaining species. Generalist species might have survived the ice age better than specialists, contributing to the present wide distributions.

4.4. Implications for forestry and conservation

Naturally grown saplings of broadleaves in coniferous forests should be re-considered, as resources for future forests. Under certain conditions, forestry based on mixed species stands is productive (Mosandl and Kleinert, 1998; Olsthoorn et al., 1999; Thelin et al., 2002; Johansson, 2003; Simard et al., 2004 and references therein). Since conifer and hardwood trees partly have different species communities, mixed forests are favourable also for biodiversity (e.g. Gustafsson and Ahlén, 1996).

Our results suggest that birch, aspen, oak and rowan would be easy to favour in forestry by natural regeneration from present conditions. In high forest,
careful thinning or partial cutting is required, as advance regeneration may be damaged or die from exposure (discussion and references in Laiho et al., 1994; Greene et al., 1999; Nyland, 2002, pp. 283–285). One problem in southern Sweden is browsing of oak, beech and some other trees by roe deer and moose (Götmark et al., 2005; unpublished data). Thinning of birch, oak, and beech saplings in young coniferous forest may be reduced and relatively dense broad-leaved-dominated stands created, potentially swamp- ing foraging ungulates and reducing damages per tree (Vivás and Saether, 1987). Dense stands potentially give good timber quality, but even if trees are damaged, they may be used, for e.g. biofuel.

For long, oak regeneration has been weak and considered a problem in temperate forest (e.g. Watt, 1919; Kelly, 2002; Abrams, 2003). This seems to be the case in broadleaved forests in Sweden, when oak is compared to other trees. However, our data indicate, and we suggest that oak regeneration is stronger and generally not problematical in conifer-dominated forests, a hypothesis that should be tested in future studies.

Among the tree species largely limited to broad-leaved forest, the high per capita regeneration success of ash under natural conditions is promising for various forms of forestry (see also Kerr, 2004). Between 1985 and 2000 in the study area, for a group of trees where ash formed more than 50% of the saplings, stem densities (0–10 cm dbh) more than doubled (Götmark et al., unpublished data). Thus, deer browsing had little effect on recruitment of ash saplings (see also Götmark et al., 2005).

Forestry based on broadleaves requires integration with conservation work (e.g. Nilsson et al., 2001, 2002). For instance, old hollow oaks contain endangered species of lichens and beetles (Ranius and Jansson, 2000), so planning for oak regeneration is especially important in areas where such oaks occur. Pure or mixed stands arising from regeneration described here may be used for harvesting of energy-rich hardwood for biofuel (Johansson, 2003), which has environmental advantages compared to fossil fuel. To strengthen biodiversity values, natural succession and self-thinning in some proportion of the stands is motivated (Nordén et al., 2004a,b).

Our study suggests that natural regeneration of broadleaves offers a good potential for creating mixed stands in conifer-dominated forests in the future, at least in Sweden. This would reduce the costs of tree planting. Initially, changes in pre-commercial thinning regimes should be implemented, to favour broad-leaved trees.

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