Growth analysis of Scots pine and lodgepole pine seedlings

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Abstract

Possible reasons for the superior growth rate of lodgepole pine (LP) (Pinus contorta Dougl. var. latifolia Engelm.) compared to Scots pine (SP) (Pinus sylvestris L.) were investigated in a trial where the species were grown in large pots with sand, till or topsoil, during 4 years following sowing. Although starting with lower seed mass, LP seedlings had greater mass than those of SP at the end of the study period. There was, however, a species x growing media interaction and the difference in final mass was greatest for seedlings growing in topsoil. Growth analyses showed that the faster relative growth rate in LP seedlings was linked with a higher leaf area ratio, specific leaf area and nitrogen use efficiency. A higher relative allocation to thin roots was another trait of LP that may contribute to its superior productivity. The fast root growth suggests shorter cultivating time of potted LP seedlings to avoid root deformation. SP allocated relatively more to stem and thick roots, components associated with physical stability. There was no species difference in allocation to needles when relating to total biomass, but LP had a larger proportion of needles in relation to above-ground biomass.

Keywords: Biomass allocation; Growth analysis; Lodgepole pine; Relative growth rate; Scots pine

1. Introduction

Lodgepole pine (LP) (Pinus contorta Dougl., var. latifolia Engelm.) produces 30–40% more stemwood than Scots pine (SP) (Pinus sylvestris L.) when these species are growing on adjacent comparable sites in Sweden (Elfving and Norgren, 1993). This higher stemwood production can be achieved through a faster rate of total biomass production and/or by allocating a larger proportion of the biomass produced to stem growth. A study of above ground biomass in young and middle-aged SP and LP trees indicated that LP allocates a lower proportion to the stem while still producing a greater total stem mass (Albrektson et al., 1995). In another biomass study of 9-year-old SP and LP trees, LP had a larger proportion of root mass in relation to total tree mass (Martinsson, 1986). Based on these studies it seems probable that the higher stemwood production of LP is accomplished through a faster total biomass development. LP starts with a lower seed mass but soon outgrows SP, and consequently has a faster relative growth rate (RGR) (Ingestad and Kähr, 1985). A detailed study of the early growth development of the two species could help interpret the basis for this growth superiority.

A fast RGR can be achieved through an efficient uptake and/or use of resources such as water, nutrients and light. Biomass allocation, morphology, chemical composition and rate of assimilation repre-
sent physiological functions of seedlings that affect uptake and use of resources and have been used as components of RGR in growth analysis (Margolis and Brand, 1990, Lambers and Poorter, 1992). The use of RGR in growth comparisons can compensate for differences in size, but does not function well unless growth is exponential (South, 1992). Seedlings seldom grow at an exponential rate over a period of several years. RGR consequently decreases with time (Van den Driessche and Wareing, 1966; Brand et al., 1987, Britt et al., 1991), and smaller plants have higher RGR than larger ones (Britt et al., 1991; Van den Driessche, 1992). In the growth analysis, comparison of the components of RGR should therefore be conducted with seedlings of similar size. As biomass partitioning also changes with tree size (Kira and Shidei, 1967), total seedling mass should be presented along with RGR and relative allocation to different biomass components in order to enable proper comparisons.

The objective of this study was to compare biomass development of SP and LP during the establishment phase (4 years following sowing) and to relate differences in growth rate to factors affecting it. Therefore, growth analysis was conducted, in which RGR was subdivided into components representing physiological functions of seedlings.

2. Materials and methods

Scots pine (SP) and lodgepole pine (LP) seedlings were grown for 4 years following sowing in pots filled with sand, till or topsoil on a cleared site at Umeå, Sweden, latitude 63°49’N, longitude 20°19’E and elevation 37 m. The pots contained one seedling each and were arranged in a totally randomised design. SP and LP were represented by three provenances each (Table 1) to enable a general species comparison. All seed sources were collected from natural stands. There were initially 480 seedlings included in the experiment distributed on 15-42 replications per species, growing media and harvest. Due to mortality, only 379 seedlings were analysed (Table 2). Number of seedlings per provenance were evenly distributed on species and growing media.

To mimic growing conditions on poor, medium and rich sites, three growing media were used, differ-

<table>
<thead>
<tr>
<th>Provenance</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation (m)</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Mixture</td>
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<td>18°30’E</td>
<td>360</td>
</tr>
<tr>
<td>Mixture</td>
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<td>16°10’E</td>
<td>300</td>
</tr>
<tr>
<td>Mixture</td>
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<td>15°50’E</td>
<td>300</td>
</tr>
<tr>
<td>Lodgepole</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pine</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carmacks</td>
<td>62°10’N</td>
<td>136°08’W</td>
<td>680</td>
</tr>
<tr>
<td>Watson Lake</td>
<td>60°07’N</td>
<td>129°45’W</td>
<td>725</td>
</tr>
<tr>
<td>Wonowon</td>
<td>56°43’N</td>
<td>121°15’W</td>
<td>900</td>
</tr>
</tbody>
</table>

1 Latitude 63°49’N, longitude 20°19’E and elevation 37 m; 2 All seed sources were collected from natural stands ing in nutrient availability (Table 3). Chemical analyses were conducted on samples of the growing media before sowing. Ammonia-N and nitrate-N were analysed with flow injection analysis (FIA) following KCl-extraction. Phosphate-P was analysed with FIA following extraction using anion-exchange resin (Sibbesen extraction). Concentrations of total nitrogen and carbon in the growing media were determined in a Perkin-Elmer 2400 CHN elemental analyser. All chemical extraction and analysis methods are described in detail by Emteryd (1990).

Table 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Growing seasons</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topsoil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP</td>
<td>15 (15)</td>
<td>14 (15)</td>
<td>15 (15)</td>
<td>21 (42)</td>
<td></td>
</tr>
<tr>
<td>SP</td>
<td>15 (15)</td>
<td>13 (15)</td>
<td>15 (15)</td>
<td>20 (42)</td>
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</tr>
<tr>
<td>Till</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP</td>
<td>15 (15)</td>
<td>15 (15)</td>
<td>15 (15)</td>
<td>11 (21)</td>
<td></td>
</tr>
<tr>
<td>SP</td>
<td>15 (15)</td>
<td>13 (15)</td>
<td>15 (15)</td>
<td>15 (21)</td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>LP</td>
<td>15 (15)</td>
<td>14 (15)</td>
<td>15 (15)</td>
<td>22 (42)</td>
<td></td>
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<tr>
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<td>15 (15)</td>
<td>25 (42)</td>
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<td>Σ</td>
<td>90 (90)</td>
<td>81 (90)</td>
<td>90 (90)</td>
<td>118 (210)</td>
<td></td>
</tr>
</tbody>
</table>

LP, lodgepole pine; SP, Scots pine.

* Seedlings growing in 2 dm² pots were harvested after 1 or 2 years, 5 dm² pots after 3 years and 15 dm² pots after 4 years.
Table 3

<table>
<thead>
<tr>
<th>Growing media</th>
<th>NH₄-N (mg (100g)⁻¹)</th>
<th>NO₃-N (mg (100g)⁻¹)</th>
<th>PO₄-P (mg (100g)⁻¹)</th>
<th>N (%)</th>
<th>C (%)</th>
<th>Density (kg (dm³)⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand</td>
<td>0.05</td>
<td>0.00</td>
<td>0.13</td>
<td>0.029</td>
<td>0.16</td>
<td>1.38</td>
</tr>
<tr>
<td>Till</td>
<td>0.21</td>
<td>0.01</td>
<td>0.14</td>
<td>0.075</td>
<td>1.09</td>
<td>1.35</td>
</tr>
<tr>
<td>Topsoil</td>
<td>2.29</td>
<td>1.14</td>
<td>1.77</td>
<td>0.758</td>
<td>5.34</td>
<td>1.07</td>
</tr>
<tr>
<td>Humus</td>
<td>0.80</td>
<td>0.047</td>
<td>3.13</td>
<td>1.29</td>
<td>46.6</td>
<td>1.02</td>
</tr>
</tbody>
</table>

To monitor seedling development over time, a sample of seedlings was harvested each autumn. To allow root systems to expand exponentially with time without reaching too high rooting intensity (Endean and Carlson, 1975), three different pot sizes were used: 2 dm³ pots were used to cultivate seedlings to be harvested after one or 2 years, 5 dm³ pots after 3 years and 15 dm³ pots after 4 years.

A plastic mesh was fastened in the bottom of the pot, allowing water but neither soil nor roots to pass. In 27 randomly chosen pots, gypsum blocks (Soilmoisture Inc., USA) were installed to monitor soil water potential. After filling the pots with sand, till, or topsoil, 10 g humus was added (Table 3) and mixed with the growing media at the sowing point. The humus, collected from the nearby forest and homogenised, served as mycorrhiza inoculant.

Seeds were weighed individually to the nearest milligram and three seeds per milligram class and provenance were sown in each pot in triangular indentations to improve conditions for germination (Bergsten, 1988). Seeds were germinated and grown for 1 month in a greenhouse having a photoperiod of 16 h and temperatures of 22/12°C (day/night).

The number of cotyledons were counted on all germinants that had dropped their seed shells within 2 weeks from sowing. One of these germinants was randomly chosen for further growth and the other two germinants were removed after 1 month. At this time, the top of the pot was covered with a 2 cm layer of brick pellets (AB Svenska Leca, Sweden) to decrease evaporation. Pots were then transferred to the field and placed in a sandbed with pot and sand surface in level. Seedlings were thereafter exposed to the weather at the site, no fertiliser was added and

Fig. 1. Soil water potential in topsoil (-----), till (-----) and sand (-----) measured weekly or biweekly using gypsum blocks (a) and daily mean temperature (line graph) and precipitation (columns) (b) during the four growing seasons. Temperature and precipitation data was obtained from a meteorological station 3 km from the experimental site.
pots were only irrigated to field capacity if water potential in any of the monitored pots dropped below \(-200\) kPa (Fig. 1). Weeds were carefully removed from the soil at short intervals throughout the experimental period and placed on the soil surface.

Current leader length, width and length of the terminal bud of the leader, and stem diameter 1 cm above ground level, were measured on all seedlings in the autumn each year, after growth had ceased. Number of needles were counted on 1-year-old seedlings and the vertically and horizontally projected above-ground seedling area was measured on 2- and 3-year-old seedlings, respectively, using video and computer based image analysis (Norgren et al., 1995).

In October each year, after growth had ceased, seedlings to be harvested (Table 2) were cut at ground level and the soil was carefully rinsed off the roots. Shoots were divided into stem, branches including buds, terminal bud and needles. Projected leaf area was measured with a leaf area meter (Li-3000, USA) on a sample of ten single needles randomly collected among all needles in a seedling. The root system was divided into thin roots (\(\leq 2.5\) mm) and thick roots, consisting of the part above the first lateral root and roots thicker than 2.5 mm. This division was conducted as mycorrhizal root tips were mainly found on roots thinner than 2.5 mm. One-year-old seedlings were only divided into roots, needles and stem, as branches and buds were very small or absent, and no roots were thicker than 2.5 mm. Frequency of mycorrhizal root tips was estimated on a sample of each seedling at the harvest each year. Root tips were classified as mycorrhizal when they were covered by a mantle of hyphae.

Biomass components were dried at 70°C for 24 h before being weighed; mass decreased no more when dried for longer time. Nitrogen concentration, as a percentage of total seedling dry weight, was measured with NA 1500 automatic analyser (Carlo Erba Instruments, Milan, Italy).

2.1. Growth analysis

Growth analysis was conducted as described by Margolis and Brand (1990). Mean relative growth rate (RGR) was subdivided into indices of foliar efficiency, biomass partitioning, foliage morphology and nitrogen use efficiency and availability. Mathematical derivations of the equations are described in more detail by Radford (1967).

Calculations of temporal development of total mass and RGR (Fig. 2 and Fig. 3) were based only on seedlings remaining until the final harvest. Total mass was estimated for each seedling as a function of number of needles on 1-year-old seedlings \((r^2 = 0.71)\), and as a function of stem diameter and the vertically and horizontally projected above-ground seedling area on 2- and 3-year-old seedlings, respectively \((r^2 = 0.97)\). The functions used were developed using linear and multiple regression, respectively, on seedlings harvested during the experimental period. The technique used was thus identical to the one described by Norgren et al. (1995) except that in the present study mass of the entire seedling, including the root system, was estimated.

RGR, defined as the increase in seedling mass per unit of mass present per unit time, was calculated as:

\[
RGR = \frac{(\ln W_2 - \ln W_1)}{(t_2 - t_1)}
\]  

Fig. 2. Development of total seedling mass during the first four growing seasons for lodgepole pine in topsoil (--- □ ---), till (--- ○ ---) and sand (--- × ---) and Scots pine in topsoil (--- ■ ---), till (--- ● ---) and sand (--- ◆ ---) Values are based on seedlings remaining until the final harvest (see Table 2). Error bars shown for the second, third and fourth growing season denote ± one standard error.
where \( W \) is seedling mass and \( t \) seedling age at start (1) and end (2) of a growing season.

RGR can be divided into one component describing the rate of increase in seedling mass per unit leaf area, Net Assimilation Rate (NAR) (g cm\(^{-2}\) year\(^{-1}\)), and another component describing the leaf area per unit seedling mass, Leaf Area Ratio (LAR) (cm\(^2\) g\(^{-1}\)).

\[
RGR = NAR \times LAR \tag{2}
\]

\[
NAR = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{\ln LA_2 - \ln LA_1}{LA_2 - LA_1}
\]

\[
LAR = \frac{LA_1 + LA_2}{2}
\]

where \( LA \) is total projected needle area per seedling.

These components were calculated under the assumption that \( LA \) and \( W \) are linearly related over the period \( t_1 \) to \( t_2 \) (Radford, 1967). LAR can be split further into Specific Leaf Area (SLA) (cm\(^2\) g\(^{-1}\)) and biomass allocation to leaves, termed Leaf Weight Ratio (LWR) (g g\(^{-1}\)):

\[
LAR = SLA \times LWR \tag{3}
\]

\[
SLA = \frac{LA_1 + LA_2}{2}
\]

\[
LWR = \frac{LW_1 + LW_2}{2}
\]

where \( LW \) is total needle mass per seedling.

For a resource such as nitrogen, RGR can be expressed as the product of Root Weight Ratio (RWR) (g g\(^{-1}\)), Nitrogen Availability (\( \frac{N}{RW} \)) (g g\(^{-1}\)) and Nitrogen Use Efficiency (NUE) (g g\(^{-1}\) year\(^{-1}\)):

\[
RGR = RWR \times \left( \frac{N}{RW} \right) \times NUE \tag{4}
\]

\[
RWR = \frac{RW_1 + RW_2}{2}
\]

\[
N = \frac{N_1}{RW_1} + \frac{N_2}{RW_2}
\]

\[
NUE = \frac{(W_2 - W_1)}{(t_2 - t_1)} \times \frac{(\ln N_2 - \ln N_1)}{(N_2 - N_1)}
\]

where \( RW \) is total root mass and \( N \) is total nitrogen content (g) per seedling.

In calculations, \( LA_1 \), \( LW_1 \), \( RW_1 \) and \( N_1 \) were represented by means for species and growing media for seedlings harvested after the first growing season, whereas \( W_1 \) was estimated non-destructively for each seedling as described above. \( LA_2 \), \( LW_2 \), \( RW_2 \), \( N_2 \) and \( W_2 \) were all measured on individual seedlings harvested the second autumn. Eq. (2), Eq. (3) and Eq. (4) were only applied to seedlings harvested after the first and second growing seasons, i.e. seedlings growing in the smallest pots (Table 2).

Allocation to the different seedling components, thin roots, thick roots, stem, branches, needles and terminal bud was calculated as percentage of total seedling mass at each harvest. Measurements of
length, mass and projected area of individual needles current in the last growing season (1994) and calculation of their corresponding SLA were conducted at the final harvest.

2.2. Statistical analyses

Analyses of variance for unbalanced design (Procedure GLM, Statistical Analysis Systems Institute Inc., 1989) were conducted to test species differences in the variables studied, according to the following model:

\[ Y_{ijk} = \mu + S_i + G_j + P_{k(i)} + (S \times G)_{ij} + (G \times P)_{k(i)} + e_{ijk} \]

where \( Y_{ijk} \) is any variable measured or estimated on the seedlings, \( \mu \) is the grand mean, followed by the effect of species \( (S_i) \), growing media \( (G_j) \), provenance (within species) \( (P_{k(i)}) \), interaction of species \( \times \) growing media \( ((S \times G)_{ij}) \) and growing media \( \times \) provenance \( ((G \times P)_{k(i)}) \), and error \( (e_{ijk}) \). The same model was used for all variables tested and Type III sums of squares were used in the analysis of variance (Statistical Analysis Systems Institute Inc., 1989). Provenance and interaction terms were excluded from the models unless they were statistically significant \( (P < 0.05) \). If the provenance effect was significant, Tukey’s studentized range test was used post hoc to determine which provenances differed.

3. Results

3.1. Biomass development

Mass of LP seeds ranged from 2 to 5 mg with an average of 3.0 mg, while average seed mass of SP was 4.7 mg, ranging from 3 to 8 mg. LP germinants had on average 3.6 cotyledons and SP 5.5 cotyledons. There was a positive correlation \( (P < 0.05) \) between seed mass and 1-year-old seedling mass for both species and all growing media, but this effect disappeared when seedlings grew larger (data not shown). The initial species difference in mass levelled out during the first growing season and LP continued to grow at a faster RGR that resulted in higher total mass than SP at the end of the study period (Fig. 2). Analysis of variance showed a significant effect of all terms tested in the model explaining total seedling mass after four growing seasons \( (P < 0.01) \). Increasing differences between species with increasing fertility of the growing media ex-

### Table 4
Mean values (and standard deviation) of components of relative growth rate of lodgepole pine and Scots pine seedlings growing in topsoil, till and sand

<table>
<thead>
<tr>
<th>Species</th>
<th>RGR (^a)</th>
<th>NAR (g cm(^{-2}) year(^{-1}))</th>
<th>LAR (cm(^2) g(^{-1}))</th>
<th>SLA (cm(^2) g(^{-1}))</th>
<th>LWR (g g(^{-1}))</th>
<th>RWR (g g(^{-1}))</th>
<th>N/RW (g g(^{-1}) years(^{-1}))</th>
<th>NUE (g g(^{-1}) year(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Topsoil</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP</td>
<td>3.05 (0.30)</td>
<td>0.127 (0.019)</td>
<td>24.8 (1.7)</td>
<td>56.7 (3.9)</td>
<td>0.45 (0.014)</td>
<td>0.47 (0.015)</td>
<td>0.039 (0.0038)</td>
<td>198 (54)</td>
</tr>
<tr>
<td>SP</td>
<td>2.74 (0.38)</td>
<td>0.126 (0.023)</td>
<td>22.3 (2.0)</td>
<td>50.9 (3.2)</td>
<td>0.44 (0.030)</td>
<td>0.47 (0.029)</td>
<td>0.041 (0.0036)</td>
<td>154 (46)</td>
</tr>
<tr>
<td><strong>Till</strong></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>LP</td>
<td>2.04 (0.43)</td>
<td>0.072 (0.015)</td>
<td>27.4 (2.8)</td>
<td>64.3 (4.1)</td>
<td>0.45 (0.031)</td>
<td>0.46 (0.033)</td>
<td>0.033 (0.0018)</td>
<td>166 (52)</td>
</tr>
<tr>
<td>SP</td>
<td>1.88 (0.52)</td>
<td>0.066 (0.025)</td>
<td>25.6 (1.8)</td>
<td>60.2 (3.8)</td>
<td>0.44 (0.025)</td>
<td>0.47 (0.028)</td>
<td>0.034 (0.0032)</td>
<td>115 (49)</td>
</tr>
<tr>
<td><strong>Sand</strong></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>LP</td>
<td>1.59 (0.34)</td>
<td>0.061 (0.018)</td>
<td>25.8 (1.4)</td>
<td>69.4 (4.7)</td>
<td>0.38 (0.020)</td>
<td>0.55 (0.025)</td>
<td>0.022 (0.0025)</td>
<td>142 (46)</td>
</tr>
<tr>
<td>SP</td>
<td>1.52 (0.37)</td>
<td>0.053 (0.017)</td>
<td>26.0 (1.4)</td>
<td>70.8 (2.3)</td>
<td>0.37 (0.020)</td>
<td>0.55 (0.021)</td>
<td>0.024 (0.0026)</td>
<td>109 (31)</td>
</tr>
</tbody>
</table>

LP, lodgepole pine; SP, Scots pine; RGR, relative growth rate; NAR, net assimilation rate; LAR, leaf area ratio; SLA, specific leaf area; LWR, leaf weight ratio; RWR, root weight ratio; N/RW, nitrogen availability; NUE, nitrogen use efficiency.

\(^a\) The components represent physiological functions of seedlings that affect the rate of uptake and the efficiency in use of resources through rate of photosynthesis and respiration (NAR), needle morphology (LAR, SLA), biomass allocation to needles (LAR, LWR) and roots (RWR) and the rate of uptake and efficiency in use of nitrogen (N/RW, NUE); values are based on seedlings harvested after one and two growing seasons (see Table 2)
explained the species × growing media interaction. The provenance effect was a result of the southernmost LP provenance having a higher mass than any other provenance (P < 0.05). Stem diameter and seedling height did not differ between species or provenances within each growing media at the final harvest. All seedlings were colonised by mycorrhiza at the end of the first growing season and frequency of mycorrhizal root tips was higher than 90% for all treatments (species and growing media) at all harvests. There were no differences between species or growing media.

3.2. Growth analysis

RGR decreased with increasing seedling mass and LP had generally higher values for a given seedling mass (Fig. 3). Measurements of components of RGR are presented in Table 4 for seedlings harvested after the first and second growing season. Analyses of variance showed that LP had higher RGR than SP (P = 0.04) which can be associated with a higher LAR (P = 0.0022) and/or NUE (P = 0.0001). The higher LAR could be attributed to higher LWR (P = 0.025) and SLA (P = 0.0019). SLA was also affected by a growing media × species interaction, as species difference decreased with decreasing fertility of the growing media. SP had higher N/RW (P = 0.023) whereas NAR and RWR did not differ between species. Differences in RGR between growing media were mainly associated with differences in NAR and/or N/RW and NUE (Table 4).

Analysis of needles current in the fourth growing season (1994) showed that LP needles were longer (P = 0.0001), larger in area (P = 0.0001), greater in mass (P = 0.042) and had higher SLAs (P = 0.0018) than those of SP (Table 5). LP had also more needles per cm on the terminal shoot in 1994 than SP.

Table 5
Mean values (and standard deviation) of length, mass, projected area and specific leaf area of Scots pine and lodgepole pine needles current in the fourth growing season (1994), and number of needles per centimetre terminal shoot in 1994 for seedlings growing in topsoil, till or sand a

<table>
<thead>
<tr>
<th>Species</th>
<th>Length (mm)</th>
<th>Mass (mg)</th>
<th>Projected area (cm²)</th>
<th>SLA (cm² g⁻¹)</th>
<th>Needles (number cm⁻¹ shoot)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topsoil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP</td>
<td>85 (17)</td>
<td>24 (7.0)</td>
<td>0.96 (0.25)</td>
<td>41 (2.5)</td>
<td>18 (3.2)</td>
</tr>
<tr>
<td>SP</td>
<td>58 (11)</td>
<td>22 (8.0)</td>
<td>0.74 (0.22)</td>
<td>34 (3.3)</td>
<td>13 (3.9)</td>
</tr>
<tr>
<td>Till</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP</td>
<td>85 (11)</td>
<td>17 (3.0)</td>
<td>0.86 (0.11)</td>
<td>50 (3.7)</td>
<td>20 (5.1)</td>
</tr>
<tr>
<td>SP</td>
<td>51 (10)</td>
<td>12 (2.4)</td>
<td>0.54 (0.14)</td>
<td>45 (6.9)</td>
<td>14 (3.6)</td>
</tr>
<tr>
<td>Sand</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP</td>
<td>56 (14)</td>
<td>8.5 (3.4)</td>
<td>0.49 (0.16)</td>
<td>59 (11)</td>
<td>23 (4.8)</td>
</tr>
<tr>
<td>SP</td>
<td>38 (8.5)</td>
<td>6.8 (3.5)</td>
<td>0.33 (0.10)</td>
<td>52 (9.5)</td>
<td>17 (7.6)</td>
</tr>
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SLA, specific leaf area; LP, lodgepole pine; SP, Scots pine.

a Nine seedlings per species and growing media were measured.
This is compatible with results showing a tendency of SP producing longer shoots per mm bud length (Fig. 4(a)) or bud width (Fig. 4(b)). Number of needles produced per mm bud length (Fig. 4(c)) or bud width (Fig. 4(d)) differed less between species. LP seedlings produced longer and wider terminal buds than SP (Fig. 4; P < 0.0001). The statistical analysis also showed an effect of provenance and a species × growing media interaction (P < 0.05). Length and width of terminal buds generally increased with latitude for SP provenances but decreased for LP provenances. Species differences increased with fertility of the growing media.

3.3. Biomass allocation

For a given seedling mass, LP allocated relatively more biomass to thin roots and terminal bud, but less to thick roots, stem and branches when compared to SP (Figs. 5–9 and Fig. 10). LP had a higher root/shoot ratio than SP after the first growing season (P < 0.01). In 1994, there was no species difference in relative allocation of biomass to needles, but when relating needle area instead of needle mass to total seedling mass, LP had a higher ratio (P = 0.008) owing to a higher SLA. LP had more than twice the total needle area as SP grown in

<table>
<thead>
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<th>Thin roots</th>
<th>Thick roots</th>
<th>Stem</th>
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<tbody>
<tr>
<td>A. Topsoil</td>
<td>B. Till</td>
<td>C. Sand</td>
</tr>
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</table>

Fig. 5. Relative biomass allocation to thin roots for lodgepole pine (+) and Scots pine (·) growing in topsoil (A), till (B) and sand (C). Values are based on harvested seedlings and presented in percent of total seedling mass and plotted against total seedling mass. Error bars denote ± one standard error.

Fig. 6. Relative biomass allocation to thick roots for lodgepole pine (+) and Scots pine (·) growing in topsoil (A), till (B) and sand (C). Values are based on harvested seedlings and presented in percent of total seedling mass and plotted against total seedling mass. Error bars denote ± one standard error.

Fig. 7. Relative biomass allocation to stem for lodgepole pine (+) and Scots pine (·) growing in topsoil (A), till (B) and sand (C). Values are based on harvested seedlings and presented in percent of total seedling mass and plotted against total seedling mass. Error bars denote ± one standard error.
Relative biomass allocation to thick roots, stem and branches generally increased with increasing seedling mass (Figs. 6–8). Relative allocation to thin roots and the terminal bud decreased with increasing seedling mass after the first growing season (Fig. 5 and Fig. 10), whereas relative allocation to needles showed no trend of change with seedling size (Fig. 9). For a given total seedling mass, biomass partitioning differed little between growing media (Figs. 5–10).

4. Discussion

By using three provenances per species, the study material was broadened which enabled a more general species comparison. There were generally no provenance effects within species on the variables studied, although the southernmost LP provenance had higher seedling mass than any other provenance at the end of the study. The reason for this growth.
superiority could not be detected in the growth analysis.

A phenology study, including the same provenances as were used in the present study, showed that all provenances started and ceased growth at about the same time, although the latitudinal span between the southernmost LP and northernmost SP provenances exceeded eight degrees (Norgren et al., 1996). LP provenances produced longer shoots, needles and terminal buds than those SP owing to a faster rate of growth. Duration of growth did not differ significantly between species or provenances. The faster RGR of LP compared to SP in the present study would thus mainly be a result of faster instant growth and less owing to a longer growing season.

Van den Driessche and Wareing (1966) found no differences in RGR between SP and LP, and SP seedlings had greater mass than those of LP after 96 days of growth owing to a higher initial seed mass. The faster RGR of LP compared to SP in the present study, however, is in agreement with Ingestad and Kähr (1985), where the two species were cultivated in a nutrient solution with variable relative nitrogen addition rate. LP had faster RGR than SP when given low as well as free access to nitrogen. The superior RGR of LP in the present study was achieved mainly during the first growing season and particularly for seedlings growing in topsoil (Fig. 2 and Fig. 3). This difference in growth rate superiority between growing media contradicts results from another study where the superior stemwood production of LP over SP was independent of site index (Elfving and Norgren, 1993). Site index, however, is a complex measure of which soil fertility is only one component, and effects of soil fertility may have been counteracted by climatic effects in that field study. Further experiments have to be conducted where these effects are separated. Longer study periods are also needed to manifest this possible species × growing media interaction, particularly when development is slow as for seedlings growing in nutrient poor sand.

The decrease in RGR with increasing seedling mass shown in Fig. 3 proves that a correct RGR-analysis should be conducted when the seedlings to be compared have approximately the same initial mass. Therefore, analysis of components of RGR in the present study was conducted only on seedlings harvested after the first and the second growing season when difference in mass between species was small (Table 4). According to Lambers and Poorter (1992), differences in RGR between plants grown under identical conditions are mainly associated with differences in LAR and SLA and less to NAR. The same relation was shown by Seibert and Pearce (1993), but Van den Driessche (1968) indicated the opposite. In the present study, LP had higher values of LAR and SLA than SP whereas there were no differences in NAR, thus supporting the statement by Lambers and Poorter (1992). Differences between growing media were associated with differences in NAR, as NAR increased with nutrient availability of the growing media. This is compatible with results showing that seedlings increase their NAR after fertilisation (Margolis and Waring, 1986). The high SLA may be an important characteristic contributing to the fast relative growth rate of LP, as a large needle area is exposed for light capture for a given investment in needle biomass.

The higher NUE of LP compared to SP is achieved through a lower investment in N per unit biomass. A lower N concentration in LP compared to SP has earlier been reported for needles of the two species (Watt, 1989, Sjöberg and Lindén, 1991, Norgren and Elfving, 1994, Albrektson et al., 1995). Consequently, the higher N/RW of SP is a result of a higher N concentration. A high NUE is an important trait where N is a limiting factor for growth, which is common in forest ecosystems (Tamm, 1991).

RWR did not initially differ between species, according to the growth analysis (Table 4), but LP allocated a larger proportion to thin roots after the first growing season (Fig. 5). This fast growth of thin roots increases the rate of soil penetration and most likely the rate of water and nutrient uptake of LP compared to SP. This characteristic of LP would be extra favourable for planted seedlings which often are subjected to water stress following outplanting in the field (Örlander, 1986). The fast rate of root growth of LP suggests a short cultivating time for container stock to avoid root deformation and subsequently instability after outplanting.

The high relative allocation to thick roots and stem of SP (Fig. 6 and Fig. 7) indicate a strategy for improving the physical stability to withstand strong winds and heavy snowloads when trees grow taller.
Martinsson (1986) also concluded that SP is more windfirm than LP based on his studies of seedlings and 9-year-old trees showing that SP has a deeper root system, higher frequency of tap roots, and a larger proportion of root burl and thick roots in relation to total root mass. LP, however, had a larger total root mass in relation to total tree mass. A higher frequency of snow and wind related damage is also the main reason for higher natural mortality in mature LP stands compared to SP (Elfving and Norgren, 1993).

Relative biomass allocation changed with seedling mass for most seedling components (Figs. 5–10) emphasising that comparison between seedlings or treatments should be based on size instead of time. In this respect, it is interesting to notice that relative biomass allocation seems to differ little between growing media when comparing seedlings of equal mass.

A higher relative allocation to terminal buds in LP (Fig. 10) should give an advantage over SP for next years shoot growth as there is strong correlation between bud size and the length of the shoot formed by that bud (Little, 1970, Kozlowski et al., 1973). However, in the present study, LP elongating from larger buds produced in 1993 did not produce longer shoots than those of SP in 1994 (Fig. 4). It seems probable that elongation of stem units was hampered in LP seedlings in 1994, as indicated by the results in Table 5 showing that LP needles were more closely spaced on the shoot. The water potential decreased rapidly in the pots, particularly in those with topsoil, and water had to be added four times (Fig. 1). The dry summer of 1994 compared to the previous years (Fig. 1), in combination with higher transpiration of the larger seedlings, may have resulted in this drought and hence reduced elongation of stem units (Cannell et al., 1976). Despite addition of water, seedlings were probably stressed and particularly those of LP growing in topsoil which had large root systems and large transpiring needle areas. The larger LP seedlings may also have consumed a greater part of the available nutrients in the pots resulting in a more pronounced reduction in relative growth rate. The tendency of decreasing species difference in growth rate during the fourth growing season (Fig. 2) may thus be a result of LP seedlings suffering more than SP from drought and depletion of nutrients.

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