Crown density of spruce trees related to needle biomass

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Abstract

Several monitoring programmes for the 'new forest damage' in Europe are based on visual assessment of crown density. In this report crown density is related to measured crown characteristics. The material comprised 100 old and 25 young Norway spruce trees visually assessed by crown density relative to a fully-foliaged tree. All branches were recorded by diameter class, and branch weight, needle weight, needle retention and shoot length, were measured in a sample of about 8%.

Crown density increased with increasing number of living branches per tree, especially in the lower branch diameter classes, and with increasing needle weight per branch. The ratio of needle dry-weight to branch basal area was curvilinearly related to crown density. In combination these effects implied that the visual assessment of slightly defoliated trees tended to underestimate the actual reduction in foliage biomass. Stem sapwood area and needle biomass were to some extent, but not completely mutually adjusted. Crown density increased with increasing needle retention and shoot length, but less pronouncedly so than with needle biomass.

Introduction

In recent years widespread forest damage has occurred in several European countries. Damage to silver fir has been observed in Germany since the early 1970s, and from 1980 onwards Norway spruce and other conifers, and deciduous species as well, have been affected to an alarming extent. The general symptoms are abnormal thinning and yellowing of the tree crowns (Schütt et al., 1983; Schütt and Cowling, 1985). Abnormal growth symptoms are also frequent. No definite causes have yet been established, but most hypotheses include air pollution as a cause or contributory factor.

A large-scale international cooperative programme for the assessment and monitoring of the damage has been established, including most of the European countries (Economic Commission for Europe, 1989; Aamlid et al., 1990; Horntvedt et al., 1992). The assessment of the damage is very reliant on visual observation of crown defoliation and discoloration of individual sample trees in representative regional surveys or at selected permanent plots.

The widespread use of visual assessment of symptoms like defoliation and
discoloration has been questioned for various reasons: (1) trees vary in appearance even in the absence of abnormal stress, because of genetic and site variation, and individual competition. To agree upon a ‘normal’ tree for reference is often difficult. (2) The assessment is subjective, and systematic differences between observers must be expected. In most countries training courses are arranged to reduce this source of error.

Several studies have been published on the relations between the decline symptoms and growth, nutrient status and other parameters (see e.g. Bucher and Bucher-Wallin, 1989; Thomsen, 1991). However, there seems to be remarkably little information about the crown decline symptoms as such. What does, for example, a 10% reduction in visually assessed crown density mean in terms of foliage biomass?

In Norway a wave of decline and bark beetle damage in Norway spruce, starting around 1971, was accelerated by the extremely dry summers of 1974–1976. The symptoms of decline were the same as those of the later ‘new forest damage’, namely defoliation and discoloration of the tree crowns.

Important research topics in this period were: (1) the importance of visual symptoms like defoliation and discolouration for tree and stand survival and resistance against pests, pathogens and other stresses; (2) the relation of visual to measurable criteria (Horntvedt and Christiansen, 1979).

This paper describes our efforts to relate visually assessed crown density of individual trees to measured crown characteristics like number of living branches, foliage biomass, needle retention and shoot length.

Materials and methods

Ten plots located within spruce stands in southeastern Norway were included in the investigation (Table 1). Seven of the plots represented mature stands from a silvicultural viewpoint, and three plots represented young- to medium-aged stands. Trees from the two stand types are referred to as ‘old’ and ‘young’, respectively.

Crown density of all trees was assessed in percent of what was considered a normal, fully-foliaged crown for the tree in question. Classes of 10% were used. The assessment refers to the upper half of the crown.

A total of 125 sample trees were randomly selected to represent different diameter and crown density classes. For the old trees the crown density ranged from 20 to 100%, but there were few trees in the lowest classes. All the young trees had crown densities of 90–100%.

All measurements were done on standing trees. A crucial point was that the sample trees should suffer as little damage as possible as a result of sampling.

The trees were climbed to a height of 1–3 m below the top. The stem diameter at this height was recorded, as was the basal diameter of all living branches below. Diameter classes of 5 mm were used. The inaccessible top
Table 1
Characteristics of the plots and sampled trees. Average values

<table>
<thead>
<tr>
<th>Plot</th>
<th>Alt. (m)</th>
<th>Yield class</th>
<th>Time of sampling</th>
<th>No. of sample trees</th>
<th>Age at bh (yr)</th>
<th>Diam. at bh (cm)</th>
<th>Height (m)</th>
<th>Crown length (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ås 1</td>
<td>120</td>
<td>G19</td>
<td>October 1978</td>
<td>12</td>
<td>98</td>
<td>32.9</td>
<td>25.6</td>
<td>57</td>
</tr>
<tr>
<td>Ås 2</td>
<td>120</td>
<td>G16</td>
<td>October 1978</td>
<td>14</td>
<td>105</td>
<td>31.4</td>
<td>23.6</td>
<td>52</td>
</tr>
<tr>
<td>Monsrud 1</td>
<td>400</td>
<td>G18</td>
<td>November 1980</td>
<td>11</td>
<td>116</td>
<td>36.2</td>
<td>28.4</td>
<td>65</td>
</tr>
<tr>
<td>Monsrud 4</td>
<td>500</td>
<td>G13</td>
<td>September 1979</td>
<td>19</td>
<td>124</td>
<td>27.3</td>
<td>22.5</td>
<td>68</td>
</tr>
<tr>
<td>Vardal</td>
<td>400</td>
<td>G17</td>
<td>May 1980</td>
<td>18</td>
<td>93</td>
<td>29.1</td>
<td>21.7</td>
<td>75</td>
</tr>
<tr>
<td>Lardal n</td>
<td>260</td>
<td>G20</td>
<td>June 1979</td>
<td>14</td>
<td>73</td>
<td>35.4</td>
<td>25.8</td>
<td>71</td>
</tr>
<tr>
<td>Lardal ö</td>
<td>260</td>
<td>G20</td>
<td>September 1979</td>
<td>14</td>
<td>80</td>
<td>39.4</td>
<td>25.8</td>
<td>79</td>
</tr>
<tr>
<td>Vardal</td>
<td>400</td>
<td>G20</td>
<td>May 1980</td>
<td>9</td>
<td>25</td>
<td>16.8</td>
<td>13.2</td>
<td>89</td>
</tr>
<tr>
<td>Lardal n</td>
<td>260</td>
<td>G20</td>
<td>June 1979</td>
<td>7</td>
<td>40</td>
<td>24.1</td>
<td>17.3</td>
<td>90</td>
</tr>
<tr>
<td>Lardal ö</td>
<td>260</td>
<td>G20</td>
<td>September 1979</td>
<td>7</td>
<td>54</td>
<td>28.5</td>
<td>18.7</td>
<td>92</td>
</tr>
</tbody>
</table>

was recorded as one branch with a diameter equal to the stem diameter at the uppermost accessible point.

The number of recently dead branches in the living crown was also recorded. 'Recently dead' implies that they still had bark, and a reasonable number of side branches.

The uppermost accessible whorl and every 12th whorl downward were taken as sample branches. The uppermost whorl represented crown Level 1, the next whorl crown Level 2, and so on. Most trees had four crown levels, some had only three, and some had five or six. The sample branches were cut at the base and thrown down. Basal diameter, length, fresh weight and length of the last five shoots were measured. Needle retention was recorded, i.e. the age of the oldest shoot retaining more than 50% of needles.

The green part of the branch was put in a paper bag, brought to the laboratory and dried. The needles were separated from the shoot axes, and weighed.

A total of 1885 sample branches was obtained, that is on average 15 per tree. A summary of the measured variables is given in Table 2. To compare branches of different size with regard to biomass, the ratios branch fresh weight/branch basal area (BFW/BBA) and needle dry weight/branch basal area (NDW/BBA) were calculated. Their statistics are included in Table 2.

The total needle biomass was calculated for each tree. An example is given in Fig. 1. Needle biomass was related to stem basal area at breast height, and at two plots also to sapwood area estimated from increment cores.

**Results**

**Branch variables**

Analyses of variance between and within trees are presented in Table 3. The analyses are based on the sample branches from the upper half of the crown.
Table 2
Summary of measurements on sample branches from spruce trees

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Avg</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch length (cm)</td>
<td>1884</td>
<td>172</td>
<td>92</td>
<td>12</td>
<td>532</td>
</tr>
<tr>
<td>Branch basal diameter (mm)</td>
<td>1885</td>
<td>20.8</td>
<td>9.1</td>
<td>3</td>
<td>53</td>
</tr>
<tr>
<td>Branch fresh weight BFW (g)</td>
<td>1885</td>
<td>1160</td>
<td>1180</td>
<td>10</td>
<td>10320</td>
</tr>
<tr>
<td>Needle dry weight NDW (g)</td>
<td>1729</td>
<td>201</td>
<td>197</td>
<td>2</td>
<td>1442</td>
</tr>
<tr>
<td>Length of last shoot (cm)</td>
<td>1561</td>
<td>5.2</td>
<td>3.2</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>Length of last five shoots (cm)</td>
<td>1839</td>
<td>25.1</td>
<td>14.3</td>
<td>5</td>
<td>116</td>
</tr>
<tr>
<td>Needle retention (years)</td>
<td>1876</td>
<td>7.6</td>
<td>2.4</td>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td>NDW/Branch basal area (g mm⁻²)</td>
<td>1729</td>
<td>0.51</td>
<td>0.26</td>
<td>0.03</td>
<td>2.07</td>
</tr>
<tr>
<td>BFW/Branch basal area (g mm⁻²)</td>
<td>1880</td>
<td>2.58</td>
<td>0.98</td>
<td>0.18</td>
<td>6.50</td>
</tr>
</tbody>
</table>

Fig. 1. An example of the relation between needle dry weight (NDW) and basal area of sample branches (BBA) from an old spruce tree. The regression equation is NDW = 17.3 + 0.506 BBA, \( s = 96.72, \ R^2 = 71.1\% \). The weighted average BBA of the tree is 530.05 mm². Fitted needle dry weight at this value is 285.5 g, with 95% confidence interval 246.2–324.8 g. The tree has 264 living branches, and the estimated foliage dry weight is 75.4 kg.

Although all variables showed significant differences between trees, the variation within trees was considerable. For example, the ratio needle dry weight/branch basal area had a pooled standard deviation within trees of 0.205, compared with a total standard deviation of 0.257. The length of the five last shoots was much higher in the young than in the old trees; this is the reason for the high \( F \)-value in this analysis.

There were significant effects of crown level on all the four branch variables. Branch fresh weight/branch basal area decreased from the base to the top of the crown, especially towards the uppermost level. Needle dry weight/branch basal area did not differ significantly between the three upper levels, but it was lower below. Needle retention decreased from base to top, whereas length of the five last shoots increased in the same order.
Table 3
Analyses of variance on branch variables between and within spruce trees

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source</th>
<th>DF</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branch fresh weight/branch basal area (g mm⁻²)</td>
<td>Between</td>
<td>124</td>
<td>2.854</td>
<td>4.10</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Within</td>
<td>1100</td>
<td>0.697</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Needle dry weight/branch basal area (g mm⁻²)</td>
<td>Between</td>
<td>124</td>
<td>0.276</td>
<td>6.58</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Within</td>
<td>993</td>
<td>0.042</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Needle retention (years)</td>
<td>Between</td>
<td>124</td>
<td>22.56</td>
<td>6.85</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Within</td>
<td>1097</td>
<td>3.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Five last shoots (cm)</td>
<td>Between</td>
<td>120</td>
<td>1510</td>
<td>11.47</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Within</td>
<td>1077</td>
<td>132</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The branch variables also showed significant differences between plots, even when only trees in crown density class 90–100% were considered. Except for the length of the five last shoots, these differences were not related to yield class or other observed variables.

Average and standard deviation of branch variables by crown density classes are given in Table 4. These figures are based on average values of all sample branches from the upper half of the crown of each tree, that is about ten branches per tree. Table 4 also contains pooled standard deviations and F-values taken from analyses of variance between and within the crown density classes of old trees. The F-values are all highly significant. Needle dry weight/branch basal area had the highest F-value, indicating that this variable discriminates best between the crown density classes, followed by branch fresh weight/branch basal area, length of the last five shoots, and needle retention.

In this study the needles were separated from the dried branches and weighed. This is a laborious procedure. A regression analysis of needle dry weight (NDW) on branch fresh weight (BFW) and branch basal area × length (BV) gave the following result

\[
NDW (g) = 10.5 + 23.5BFW (g) - 0.0948BV (cm^3)
\]

\[
s = 60.2, R^2 = 90.3, n = 1525
\]

Needle weight can thus be fairly precisely estimated from measurement of branch weight, diameter and length.

Tree variables

The average number of branches per tree increased from about 100 in the old trees of lowest crown density to 200 and 250 in the old and young fully foliaged trees, respectively.

Branch diameter distributions within four groups of crown densities are
Table 4
Branch and tree variables related to crown density of spruce trees. Upper half crown

<table>
<thead>
<tr>
<th>Tree age</th>
<th>Crown density class (%)</th>
<th>No. of trees</th>
<th>Needle d.w./branch basal area (g mm⁻²)</th>
<th>Branch f.w./branch basal area (g mm⁻²)</th>
<th>Needle retention (year)</th>
<th>Last five shoots (cm)</th>
<th>Needle d.w./stem basal area (g mm⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$\bar{x}$ $s$</td>
<td>$\bar{x}$ $s$</td>
<td>$\bar{x}$ $s$</td>
<td>$\bar{x}$ $s$</td>
<td>$\bar{x}$ $s$</td>
</tr>
<tr>
<td>Young</td>
<td>90–100</td>
<td>23</td>
<td>0.73 0.13</td>
<td>2.68 0.44</td>
<td>6.93 0.92</td>
<td>47.9 11.7</td>
<td>0.82 0.27</td>
</tr>
<tr>
<td>Old</td>
<td>90–100</td>
<td>46</td>
<td>0.62 0.13</td>
<td>2.72 0.46</td>
<td>7.57 1.47</td>
<td>25.6 5.9</td>
<td>0.53 0.19</td>
</tr>
<tr>
<td>Old</td>
<td>80–90</td>
<td>14</td>
<td>0.50 0.10</td>
<td>2.43 0.56</td>
<td>7.57 1.69</td>
<td>21.2 5.0</td>
<td>0.38 0.13</td>
</tr>
<tr>
<td>Old</td>
<td>70–80</td>
<td>15</td>
<td>0.41 0.11</td>
<td>2.31 0.45</td>
<td>6.48 1.44</td>
<td>19.7 3.6</td>
<td>0.29 0.11</td>
</tr>
<tr>
<td>Old</td>
<td>60–70</td>
<td>12</td>
<td>0.38 0.07</td>
<td>2.15 0.48</td>
<td>6.60 0.97</td>
<td>22.9 4.1</td>
<td>0.32 0.09</td>
</tr>
<tr>
<td>Old</td>
<td>50–60</td>
<td>4</td>
<td>0.28 0.10</td>
<td>1.73 0.38</td>
<td>5.54 1.96</td>
<td>18.4 2.7</td>
<td>0.22 0.04</td>
</tr>
<tr>
<td>Old</td>
<td>40–50</td>
<td>7</td>
<td>0.29 0.07</td>
<td>1.60 0.17</td>
<td>4.96 1.30</td>
<td>15.1 2.2</td>
<td>0.19 0.05</td>
</tr>
<tr>
<td>Old</td>
<td>30–40</td>
<td>3</td>
<td>0.33 0.06</td>
<td>1.81 0.37</td>
<td>5.75 1.48</td>
<td>17.5 1.2</td>
<td>0.19 0.02</td>
</tr>
<tr>
<td>Old</td>
<td>20–30</td>
<td>1</td>
<td>0.17 0.00</td>
<td>1.46 0.00</td>
<td>4.86 0.00</td>
<td>15.4 0.0</td>
<td>0.14 0.00</td>
</tr>
<tr>
<td>Pooled SD</td>
<td></td>
<td></td>
<td>0.114 0.456</td>
<td>1.46 4.92</td>
<td>6.70 19.38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$F = \frac{MS_{CDC}}{MS_{error}}$

17.80 9.46 4.82 6.70 19.38
Fig. 2. The number of branches in spruce trees. Average values per tree, by branch diameter and crown density class.

Fig. 3. The relation of needle weight to crown density class in old spruce trees. Needle weight is expressed as: (1) the ratio of needle dry weight to basal area of sample branches from the upper half of the crown; (2) the ratio of estimated needle dry weight of the whole tree to its stem basal area. Both lines represent predicted values from regression analyses of ln(NDW/BA) on crown density class.

presented in Fig. 2. The young trees had a large number of branches in the two lower diameter classes. These were mostly internodal branches in the upper crown level. Such branches were fewer in the old trees, and decreased with decreasing crown density. In the young tree crowns there were seldom any dead branches except at the lowest whorls. With decreasing crown density of
the old trees the number of recently dead branches in the crown increased and they extended to higher crown levels.

The estimated needle dry weight of the average tree was 36.1 kg, with a 95% confidence interval of 24.4–47.2 kg. The ratio of needle dry weight to stem basal area is included in Table 4.

Smoothed values by crown density class of the ratios: (1) tree needle weight to stem basal area; (2) the average needle weight of branches from the upper half crown to their basal area, have been estimated by regression analyses. The best fit was obtained by using log-transformation of the y-variable. Predicted values are shown in Fig. 3.

In Fig. 4 stem sapwood area and stem basal area at breast height are compared as regressors for needle weight. The use of sapwood area instead of total basal area reduced the residual variation in needle dry weight.

At Vardal young trees and old trees in crown density class 90–100 had comparable needle weights, when related both with total area and sapwood area. At Lardal, young trees had higher needle weight than old fully foliaged trees when related to total area, but they fitted better into the same regression when related to sapwood area.
Discussion

The study demonstrated that when making a visual assessment of crown density one tends to underestimate the actual reduction of needle biomass in slightly defoliated trees. A tree assessed to have 10% lower crown density than a fully-foliaged tree had a 17% lower needle biomass. Branches in the upper half crown of that tree had a 14% lower biomass.

A curvilinear relation of needle biomass to crown density class was indicated. This implied that the percentage values given above hold for the whole range of crown density classes when comparing with the neighbouring class instead of a fully foliaged tree. However, there was a wide variation both within trees and between trees of the same crown density class.

The crown density was reduced by the dieback of entire branches, especially the smaller ones, as well as by partial defoliation of living branches. This should be taken into account when making a visual assessment of crown density.

Needle retention has been suggested as a criterion of tree vigour, measured either by hands-on counting (Knabe, 1981) or by visual assessment from the ground (Innes and Boswell, 1990).

This may be a useful criterion in younger trees. In old trees, however, the branch geometry is often very complex, and it can be difficult to decide where to count. If first a sample branch is obtained, the best vigour measurement is doubtless its total weight or needle weight related to its basal area, and counting of needle years adds little to this.

In conclusion, for single trees none of these criteria can fully replace an integrating criterion like visual assessment of crown density. The ratio of needle or branch weight to branch basal area may, however, be a useful criterion for controlling a possible long-term drift in the visual assessment. In visual assessments, the tree should be compared with what is considered normal crown density for the tree in question, rather than with some other reference tree.

The relations between sapwood area and needle biomass in the present study support the pipe model theory (see Waring et al., 1982), which implies that there is a homeostatic relation between the leaf weight or leaf area of a tree and the cross-sectional area of the water conducting part of the stem. A reduction in leaf biomass will cause a reduction in sapwood area, and vice versa.

The adjustment of the sapwood to a reduced crown has been demonstrated in pruning experiments. Margolis et al. (1988) state that this adjustment was caused primarily by a reduction in basal area growth. Only after very severe pruning, removing 95% of the foliage, was an increased heartwood formation observed.

The larger residual variation in needle weight over sapwood area at Lardal than at Vardal fits with our general impression that the Vardal plot was in a
Table 5
Needle biomass vs. stem sapwood area in spruce trees. Coefficients from different studies of the regression: Needle d.w. (kg) = a + b stem sapwood area (cm²)

<table>
<thead>
<tr>
<th>Species</th>
<th>a</th>
<th>b</th>
<th>R²</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. engelmannii</td>
<td>-</td>
<td>0.072</td>
<td>0.99</td>
<td>Kaufmann and Troendle (1981)</td>
</tr>
<tr>
<td>P. rubens</td>
<td>-0.41</td>
<td>0.072</td>
<td>0.84</td>
<td>Marchand (1984)</td>
</tr>
<tr>
<td>P. abies</td>
<td>-</td>
<td>0.122</td>
<td>0.97</td>
<td>Oren et al. (1986)</td>
</tr>
<tr>
<td>P. abies</td>
<td>1.51</td>
<td>0.083</td>
<td>0.85</td>
<td>Vallevik (1985)</td>
</tr>
<tr>
<td>P. abies</td>
<td>0.15</td>
<td>0.104</td>
<td>0.82</td>
<td>Holen (1986)</td>
</tr>
<tr>
<td>P. abies</td>
<td>-2.8</td>
<td>0.103</td>
<td>0.75</td>
<td>This study, Vardal</td>
</tr>
<tr>
<td>P. abies</td>
<td>-1.9</td>
<td>0.104</td>
<td>0.59</td>
<td>This study, Lardal</td>
</tr>
</tbody>
</table>

fairly stable state, so that the sapwood area and needle mass had mutually adjusted. At the Lardal plot changes in crown density apparently had occurred more recently, and sapwood may not yet have been adjusted. In pruning experiments in Scots pine Långstöm and Hellqvist (1991) observed that, “the adjustment of conducting sapwood was still incomplete four years after treatment”.

In Table 5 the needle dry weight to sapwood area relations found in this study are compared with some other studies in spruce. Regressions for foliage biomass are often presented as total or projected leaf area per unit of sapwood area. In Norway spruce the ratio of total needle area to needle dry weight was found to be 10 m² kg⁻¹ (Horntvedt, 1988). Waring et al. (1982) used a factor of 0.4 to convert total area to projected area in spruce. Thus, the ratio of total needle area to sapwood area at breast height in Norway spruce is about 1 m² cm⁻², and projected area to sapwood area is about 0.4 m² cm⁻².

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