Effects of tree size and position on pipe model ratios,

Scots pine

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**Abstract**

We investigate how the foliage-to-wood area ratios depend on tree and stand characteristics previously collected data from Scots pine. Our analysis allowed a separation of the relationship between stem and branch cross-sectional areas and the relationship between the branch cross-sectional area and foliage mass. We studied how these relationships varied within and between stands. The lowest site fertility class had a higher foliage mass to stem area ratio than better sites. The relative height of a tree in the stand ($\Phi$) was the major factor that determined the variation in the relationship between the branch cross-sectional area to stem cross-sectional area. Models based on absolute height or tree diameter were usually weaker. Models based on $\Phi$ were simpler since no other variables were able to explain between stand variation in the presence of $\Phi$. We were able to predict changes in the branchiness of the tree but not in the foliage mass supported per unit of branch area.
Introduction

The pipe model of Shinozaki et al., (1964) is a widely used allometric model to describe relations between sapwood area and tree foliage mass (or area). The original ideas of Shinozaki assumed a set of cylindrical pipes connecting the foliage with the roots. This observation has been interpreted in terms of a hydraulic theory of tree functioning (e.g. Whitehead 1978) even if has been shown that it holds only approximately true (Zimmermann 1983). As a consequence, it has been observed that the pipe model ratio, i.e. the ratio between foliage biomass and sapwood area, is different for branches, stems and roots (Nikinmaa 1992, Berninger and Nikinmaa 1994) and sapwood cross-sectional area is not constant along the whole length of the stem below crown (Ojansuu and Maltamo 1995).

The pipe model has been used to describe the functional balance between the foliage and wood. Providing that this relationship between foliage and wood cross sections remains constant, it allows the calculation of carbon allocation between different parts of the tree (Valentine 1985, Mäkelä and Hari 1986, Nikinmaa 1992, Perttunen et al. 1996, Mäkelä 1997). Simulation studies (Nikinmaa 1992, Berninger and Nikinmaa 1997) have shown that different foliage area to sapwood area ratios result in different stand dynamics due to changes in allocation between foliage and woody parts of the tree. Indeed, Mäkelä and Albrektson (1992) as well as Shelburne et al. (1993) have shown that suppressed trees have lower foliage-to-sapwood area ratios than dominant trees. Size-dependent declines
of the pipe model ratios (i.e., fewer leaves for similar conducting areas) have been proposed on theoretical grounds. A hydraulic theory of maximum tree height (Yoder et al. 1994) was proposed since hydraulic pathways from the soil to the foliage get longer with tree height, increasing the hydraulic resistance to water flow from the roots to the foliage. This could be compensated for by a lower foliage to sapwood area ratio. This theory has received support in the literature (e.g. McDowell et al. 2002 for a review). However, for example, Monserud and Marshall (1999) found that the allometric relations for Douglas-fir did not show any decrease in foliage to sapwood ratio with increasing tree size.

The objective of this study is to test the effects of social position, site quality and tree size on the pipe model ratio and its components in Scots pine, using data collected during the past 15 years at the Department of Forest Ecology, University of Helsinki.

**Materials and Methods**

The materials of this article originate from a database of tree measurements that allowed estimation of the pipe model ratios from different stands from southern Finland and adjacent areas. The database contained data from 36 stands with 199 sample trees. Data were originally collected for different purposes by different researchers (mostly related to the estimation of biomass or the testing of ecophysiological hypotheses). A description of the stand variables is in Table 1. Some of the data have been published before. The data were collected during three different sampling efforts:
Berninger, Nikinmaa and Palmroth (Berninger and Nikinmaa 1994, Palmroth et al. 1999) focused on a more detailed structural analysis of trees and estimation of foliage mass of stands (stands 1-4 or Dataset 1 in Table 1). They were derived from sample plots typically containing 30-60 trees. Six to fifteen trees were felled for biomass measurements from two strata; half larger than the average and half smaller than the average tree. Branches were sampled in relation to size (about 10 branches per tree).

Ärölä (1996) collected data from 20 different stands (Dataset 2 in Table 1). From each stand, a sample plot was established in the centre of the longest diagonal line traversing the stand. Sample plots were circular plots and each contained about 40 trees. 2-4 randomly sampled trees were felled with similar selection criteria as above. The diameters of all branches were measured and 10 branches per tree were used for the biomass analysis. Branches were sampled systematically across the whole crown (e.g., 10th branch).

Vanninen and Mäkelä’s Dataset (3 in Table 1) consists of 114 trees measured for biomass and dimensions using similar techniques to Ärölä (1996). The stands covered an age gradient from seedlings to mature trees, and included both heavily thinned and unthinned stands. Stands represented both fertile and poor sites. Within each stands, trees were selected to cover the variation in the competitive status of trees.
Dataset 3 was sampled in August at the time of maximum foliage biomass whereas Datasets 1 and 2 were collected in early summer before stem diameter growth (Vanninen and Mäkelä 1999). Since Scots pine in Finland drops most of its four-year-old foliage in early autumn this should lead to higher foliage per biomass estimates in Dataset 3 compared to datasets 1 and 2, which were measured after the oldest needle cohorts had fallen but before there had been new wood thickness growth. Most of the old foliage in Scots pine senesces in Finland during September and drops during autumn and winter. New foliage grows in June-July (Pietarinen et al. 1982). To account for this, foliage biomass in Dataset 3 was multiplied with 0.75. Analysis showed that the averages of the ratios between the two datasets did not differ after the multiplication (mean of foliage per stem cross sectional area ratio for the Vanninen and Mäkelä dataset 497 kg m$^{-2}$ and for the other data 475 kg m$^{-2}$). Branch diameters were measured in a different way in the Vanninen and Mäkelä data and therefore we analyze only the foliage mass to stem cross-sectional area ratio from this data (see below).

In all the data sets the diameters of all trees in each sample plot were measured. Tree height was measured either from all the trees in the plot or from a large enough sample so that representative height and diameter variation at each stand could be determined. The measured variables from all the felled sample trees included diameters at breast height, diameter below the living crown, the number of living branches as well as the diameter of all living branches below the first living bifurcation of the branch (Fig 1). Foliage was dried at 105 °C for 24 hours before dry weight determination. Diameters below the living
crown and branch diameters are diameters below bark. Diameters at breast height are above the bark. The measurements were made during 4 different summers in 1990’s.

**Analysis**

We estimated the ratio of foliage mass to branch area of each tree separately ($R_{FB}$) as:

$$R_{FB} = \frac{\sum_{Tree} M_F}{\sum_{Tree} A_{BS}}$$

$M_F$ is the foliage mass of a sample branch and $A_{BS}$ is the cross sectional area of the sample branch. Sums were calculated for each tree separately. Branch cross sectional areas were summed only for sample branches (i.e. branches from which foliage biomass was determined).

The ratio of branch cross sectional area to stem cross sectional area below the living crown ($R_{BS}$) was calculated as:

$$R_{BS} = \frac{\sum_{Tree} A_B}{A_{SC}}$$

where $A_{SC}$ is the stem cross sectional area below the living crown (and below the bark) and $A_B$ the below bark cross sectional area of each living branch of the tree.
The foliage to stem cross sectional area ratio ($R_{FS}$) (i.e. the “classical pipe model ratio”) was calculated as:

$$R_{FS} = R_{BS} R_{FB}$$

We defined the relative position of a tree in a stand ($\Phi$) as the ratio of the height of the sample tree to the height of the largest tree in the sample plot (including trees not used for biomass analysis) and use $\Phi$ as an indicator of dominance or suppression of the trees.

Pipe model ratios ($R_{FS}$, $R_{FB}$, $R_{BS}$) were predicted for different trees in different stands using general linear models. Our analysis was set up similarly an analysis of covariance:

$$R_{Xij} = S_i + aQ_j + \epsilon_{ij}$$

Where $R_{Xij}$ is a pipe model ratio ($R_{FS}$, $R_{FB}$, $R_{BS}$) of tree $j$ on site $i$ and $S_i$ is the effect of the site $i$, $a$ is the slope of the regression between $Q$ and $R_x$ and $Q_j$ is a continuous tree-wise measured variable (i.e. tree height or diameter) from tree $j$. $a$ can be interpreted in the context as the average within-stand regression slope between $Q_j$ and $R_x$. $\epsilon_{ij}$ is the error of the ratio estimate for tree $j$ in stand $i$. Between-stand variation can be explored calculating least square means of $R_X$. Least square means are the estimates of $R_{Xij}$ at a fixed value of the continuous variable $Q_j$. 
The calculations were done using the SAS statistical package using the *Proc GLM* for general linear models. Probabilities and least square means account for unbalanced experimental designs.

**Results**

The correlations between foliage mass and branch cross sectional area, foliage mass and stem cross sectional area as well as the correlation between branch cross sectional area and stem cross sectional area were relatively tight (Fig 2). The foliage to stem cross sectional area ratio was approximately normally distributed for all data (Fig 3). The coefficients of variation $R_{FS}$, $R_{FB}$ and $R_{BS}$ were 0.25, 0.29 and 0.17 respectively.

There was little correlation between the $R_{BS}$ and $R_{FS}$ ($r=0.20$ *n.s.*) but the coefficient of correlation between $R_{FS}$ and the $R_{FB}$ was high ($r=0.78$ *p*<0.0001) (Fig. 4). There was a negative correlation between $R_{FB}$ and $R_{BS}$ ($r=-0.44$ *p*<0.0001).

In the combined data, $R_{FS}$ did not show much correlation with tree height, tree diameter and tree age or stand density. There was a close correlation between tree height and diameter ($r=0.81$) which makes it difficult to differentiate height and diameter effects on the ratios on statistical grounds. Stand density was correlated with the height or average diameter of the trees ($R=-0.74$ for average height and $R=-0.64$ for average diameter).

In the combined data there seemed to be a relation of $R_{FS}$ and $R_{BS}$ to tree height and $\Phi$ (Figure 5).
The GLM analysis revealed that there were always statistically significant inter-stand differences in all the ratios ($R_{FS}$, $R_{BS}$ and $R_{FB}$) (i.e. the values of the parameter $S_i$ were statistically significant). Tree height, diameter and $\Phi$ did not have a statistically significant effect on $R_{FB}$ (Table 2). However, $R_{BS}$ was sensitive to tree height, $\Phi$ and tree diameter (Table 2). All three independent quantitative variables explained the variation of the ratios similarly but $\Phi$ was the most significant. The same relations were found for $R_{FS}$. For all models the values of the parameter $a$ were positive, i.e. the ratios ($R_{FS}$, $R_{FB}$, and $R_{BS}$) increased within a stand with tree size. Models using more than one quantitative variable (i.e. tree height and tree diameter) were not statistically significant. The stand was the most important variable in the general linear model (Table 3), i.e. differences between stands were relatively important.

Least Square Means (LSM) were used as estimates of standwise values of the pipe model ratios ($R_{FS}$, $R_{BS}$, $R_{FB}$) at a fixed level of the covariate ($Q$) to check how standwise estimates of the ratios depend on average stand tree size, site quality or stand density. The results show that if tree diameter or tree height were chosen as continuous variables ($a$ in equation 4) there was generally a negative correlation between the LSM estimate of a pipe model ratio and average tree size in a stand (expressed as DBH or tree height) (Fig 6). If relative height ($\Phi$) was used as continuous variable the correlations between average tree size and the LSM estimate of a pipe model ratio were not observable.

Stand quality affected the ratios. For the worst site type (CT in the Finnish growth classification system (Cajander 1949)) the estimate of foliage to stem cross sectional area...
ratio was $565 \text{ kg m}^{-2}$, while it was $436 \text{ kg m}^{-2}$ for the medium site class (VT) and $465 \text{ kg m}^{-2}$ for the better site class MT. Differences between the CT and the other site classes were significant ($p<0.05$). Differences between MT and VT were not significant.

**Discussion**

The close correlations between foliage mass and stem and branch area show that the pipe model theory is a good approximation of tree structure in our data. The estimate of foliage mass to stem cross sectional area ratio ($488 \text{ kg m}^{-2}$) for the annual minimum foliage mass is close to the previous published values in Southern Finland (i.e. Nikinmaa 1992). Also previous research showed that the branch cross sectional area to stem cross sectional area ratio ($R_{BS}$) was only slightly higher than the one published before (i.e. Berninger and Nikinmaa 1994, Berninger et al. 1995). Between-tree variation of the pipe model ratios was similar in the study of Mencuccini and Grace (1995).

As figure 5 shows there seems to be a relation between either tree height or relative tree height and the ratios (except $R_{FB}$). Since trees were sampled from different stands and there is the possibility of stand effect on the pipe model ratios, we used the GLM:s to analyse the relations. Simple regressions would, in that case, not be valid, since the principle of independence of data points from each other would be violated.

For interpreting the GLM results, slopes between variables are based on *within-stand* variation, while relations of stand-specific Least Square Means (LSM) of a variable with
another variable are based on *between-stand variation at fixed level of all covariate variables*. For example, a LSM of $R_{BS}$ using $\phi$ as a covariate is an estimate of the branch-to-stem area ratio ($R_{BS}$) for a hypothetical dominant tree ($\phi = 1$) in the stand (Figure 6 left column). A LSM using tree height as a covariate should be interpreted as pipe model estimates for a hypothetical tree of the average height (15 m for the whole dataset) in the stand (figure 6 right column). We acknowledge that these hypothetical trees would be an unrealistically large tree in a small stand and a very suppressed tree in large stands. We believe that the opposite correlations of height with tree height and stand height are partly artifacts of this method. The use of relative height as quantitative variable (left column, figure 6) can be interpreted as estimates for a dominant tree in each stand.

We can see from figure 6 that the LSM that use absolute height as a covariate are correlated with average stand height. Least square means of ratios using $\phi$ as a covariate were not correlated with tree height. Models using $\phi$ as a covariate are, in addition, slightly better statistically (Table 2) than the other models. In other words, models based on absolute height and diameter (diameter data not shown) as covariates required that there exist two different trends, a within-stand increase in the ratio with increasing tree height and a between-stand decreasing trend in the ratio with increasing stand height.

This suggests that the relative position of the trees in the stand is the dominant factor explaining the variation in foliage to stem cross-sectional area in our data. In the presence of $\phi$, effects of stand height were not statistically significant. This contrasts with a number of other studies on Scots pine that claim large effects of tree size on foliage
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1 sapwood ratios (Mencuccini and Grace 1996). A notable difference is that many of these
2 studies measured sapwood area at breast height, while we measured stem cross-sectional
3 area below the living crown. Tapering of the sapwood be, why our results differ from
4 those of Ojansuu and Maltamo (1995). On the other hand, Shelburne et al. (1993) found
5 that suppressed loblolly pines were hydraulically more limited than dominant ones and
6 had higher pipe model ratios. Furthermore Vanninen and Mäkelä (2000) as well as Naidu
7 et al. (1998) (for loblolly pine) found that suppressed pines allocate more carbon to stem.

8 Although the changes in the foliage mass to stem area ratio could be attributed to the
9 competitive status of trees, physical and biological theories predict that water transport in
10 large trees is more difficult and more limiting. McDowell et al. (2002) provided evidence
11 that these increasing limitations often lead to decreased foliage area to sapwood area ratio
12 with increase tree size. However, there are notable exceptions to this: Monserud and
13 Marshall (1999) failed to find decreases in all species they examined. In a study by Irvine
14 et al. (2004), foliage area to sapwood area ratios did not decline with tree age, but
15 transpiration per leaf area did decline.

16 The present study shows that there are different components in the foliage mass to stem
17 cross sectional area ratio. Of these components the branch area to stem area ration ($R_{BS}$)
18 seems also predictable, but the foliage mass to branch area ration ($R_{FB}$) was not explained
19 by our analysis. Nevertheless, all the ratios had a substantial, random, between-site
20 variation. For exact determinations of foliage masses, it is therefore important to calibrate
21 pipe models or other allometric equations with on-site measurements (Ärölä 1996) (Table
Nevertheless, correlations between foliage mass and stem cross sectional areas were tight and probably sufficient to estimate foliage biomass for most purposes (Fig 1).

The negative correlation between $R_{BS}$ and $R_{FB}$ suggest that trees with higher branch per stem area ratio (high values of $R_{BS}$) tend to have less foliage per branch area (low values of $R_{FB}$). These differences compensate one another, such that the branch area - stem area relationship changes did not reflect the foliage mass stem area relationship. It seems that increases in branchiness ($R_{BS}$) may be compensated by having less foliage per branch area (lower values of $R_{FB}$) and vice versa. Foliage area was not measured in most datasets, and here it was measured the values where slightly above 10 m$^2$ kg$^{-1}$ (based on total area). In the same region Palmroth and Hari (2001) reported that SLA varied between 12 and 16 m$^2$ kg$^{-1}$. However Palmroth et al. (1999) reported values of SLA of about 10 m$^2$kg$^{-1}$ for some of the stands.

Another possible reason for the low foliage area to stem area relationship in suppressed trees could be differences in turnover of foliage, branchwood and stemwood, or higher areas of heartwood, especially in low canopy branches. Sapwood area was not separated from heartwood in all studies and definitions of sapwood and heartwood were not consistent among the studies. However, staining experiments (Hari et al. 1985) indicate that there is little heartwood at the crown base in the young Scots pine stands. We did not consider heartwood and sapwood separately here, since it was not measured in some studies and definitions of sapwood differ between the datasets. Previous research with Scots pine has shown that different methods to determine heartwood area give quite
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different results (Rust 1999). For these reasons we did not consider heartwood and
sapwood separately. In some of the material a visual determination of the heartwood
proportion was made from a thin disk cut at the crown base. The moist proportion of the
sample could was always below 15% of the cross sectional area where it was measured.

The GLM analysis showed that several factors modify the ratios. Changes in the ratio of
the cross-section of woody parts ($R_{BS}$) could be explained while variation in the ratio
between foliage mass and branch area ($R_{FB}$) was considerable but was not explained by
our statistical models. A better understanding of the factors that determine $R_{FB}$ would be
important, since the ratio caused about half of the variation in the foliage to stem area
ratio. Also the coefficient of variation was larger for the foliage to branch area ratio than
for the branch to stem area ratio. However, it seems logical that the foliage to branch
area is harder to explain and more variable: Stem and branches are both woody tissues
and their diameter growth is controlled by the activity of the cambium. Cambial growth
seems to be largely controlled by temperature and flows of plant hormones from buds to
the roots (Aloni 2001). Empirical studies have shown that the weather conditions of the
current year largely determine the diameter growth of stems (although there are carryover
effects from previous years) (Mielikäinen et al. 1996). Foliage, in contrast, is grown from
primary meristems in the buds. The number of new needle fascicles in each shoot is
determined during bud formation (i.e. in the previous year) and extension growth of
shoots depends on weather conditions of the previous year (e.g. Juntila 1986). This
suggests that coordination between branch and stem diameter growth should be closer
than that between foliage and branch diameter growth.
Trees in our stands typically had eight to more than forty rings of sapwood below the living crown. Therefore, the relation between branch to stem cross-sectional areas are the average of many years of growth while there are only about four years of living foliage branches. This foliage is more prone to herbivory (especially sawflies like *Neodiprion pini*), fungi (e.g. *Greminella abietina*) and climate-induced damage than branch wood. These biotic factors could cause some of the random variation we have observed in our data although we tried to select healthy looking trees for our study. This needle loss directly reflects in the foliage biomass but there are indications that wood area would not change as quickly (Sievänen et al. 1997).

Foliage to branch area ratios are also more uncertain than branch to stem cross-sectional area ratios, since they are based on a sample of branches, i.e. contain a sampling error. Branch to stem cross-sectional area ratios are based on all branches of a tree, so there is no sampling error associated with the treewise estimates $R_{BS}$.

At the poorest sites (CT site class in the Finnish site classification system) the values of $R_{FS}$ were significantly higher than on the better VT and MT sites. Since CT sites only existed in the dataset we cannot test if changes are due to changes in the woody structure of trees (i.e. $R_{BS}$) or due to changes between foliage and branches (i.e. $R_{FB}$). Site quality has not been investigated much and much of the results on site fertility stand allometry relations are conflicting. In a previous publication using the same data Vanninen et al. (1996) found that CT sites have higher pipe model ratios, however,
Ärölä’s work (1996), using one subset of our data, did not find a significant site quality effect in a mixed model where stand and tree-level variation was considered. Long and Smith (1988) found that higher growth rates increased foliage to sapwood area ratios. However, Hacke et al. (2000) and Schäfer et al. (2002) found that trees growing on high fertility sites trees have a larger proportion of their hydraulic resistance in the root system. This is due to changes in allocation, since trees on high fertility sites allocate more carbon to foliage and less to the root. According to them these changes are compensated by lower foliage per sapwood area ratios (i.e. lower values of $R_{FS}$). Also, Scots pine foliage to fine root ratios on good sites are higher than on bad sites (Vanninen and Mäkelä 1999) and our data.

Altogether, the results indicate that dominance or supression of trees are important factors that determine the structure of trees. Beyond the classical pipe model we could show that some relations between branch area and stem area seem to be tighter than relations between foliage mass and branch area, i.e. some parts of the structure of trees change more easily than others do. Figures 2 through 4 show that the pipe model remains a valid approximation of tree structure but it can be improved and calibrated to give more accurate estimates of foliage biomass. Variation between stands in pipe model parameters was important and we need further research to explain this variation.

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References


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daily growth of shoots, needles, and stem diameter in Scots pine trees. For. Sci. 28: 573-
581.

5 Rust, S. 1999. Comparision of three methods for determining the conductive xylem area

intact temperate forest ecosystem under ambient and elevated atmospheric CO2

and sapwood permeability on the relationship between leaf area and sapwood area in


sapwood senescence on tree growth using the model LIGNUM. Silva Fennica, 31:329-
340.


Table 1 Site names and characteristics. Datasets refer to the collectors. Average diameters and heights are based in the whole dataset (or just the sample trees when marked with an asterisk).

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<td>358</td>
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<td>61.8N, 24.3E</td>
<td>1033</td>
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<td>73</td>
<td>15</td>
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</table>
**Table 2**

Properties of different models fit to the data with different variables as $Q$ (equation 4).

RMSE means Root Mean Square Error. Significances are based on type III model estimates.

<table>
<thead>
<tr>
<th></th>
<th>Continuous Variable ($Q$)</th>
<th>RMSE</th>
<th>$R^2$</th>
<th>Value of the continuous parameter ($a$)</th>
<th>Significance of the continuous variable ($a$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Foliage to branch ratio ($R_{FB}$)</strong></td>
<td>H (m)</td>
<td>98 kg m$^{-2}$</td>
<td>0.49</td>
<td>9.7 kg m$^{-3}$</td>
<td>n.s</td>
</tr>
<tr>
<td></td>
<td>DBH (cm)</td>
<td>100 kg m$^{-2}$</td>
<td>0.49</td>
<td>2.5 kg m$^{2}$cm$^{-1}$</td>
<td>n.s</td>
</tr>
<tr>
<td></td>
<td>Φ (d:less)</td>
<td>97 kg m$^{-2}$</td>
<td>0.5</td>
<td>172 kg m$^{-2}$</td>
<td>n.s</td>
</tr>
<tr>
<td><strong>Branch to stem ratio ($R_{BS}$)</strong></td>
<td>H (m)</td>
<td>0.186 (d:less)</td>
<td>0.56</td>
<td>0.046 (d:less)</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>DBH (cm)</td>
<td>0.180 (d:less)</td>
<td>0.49</td>
<td>0.22(d:less)</td>
<td>0.01</td>
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<tr>
<td></td>
<td>Φ (d:less)</td>
<td>0.181 (d:less)</td>
<td>0.49</td>
<td>0.62 (d:less)</td>
<td>0.01</td>
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<tr>
<td><strong>Foliage to stem ratio ($R_{FS}$)</strong></td>
<td>H (m)</td>
<td>142 kg m$^{-2}$</td>
<td>0.32</td>
<td>16.4 kg m$^{-3}$</td>
<td>0.05</td>
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<td></td>
<td>DBH (cm)</td>
<td>142 kg m$^{-2}$</td>
<td>0.34</td>
<td>8.6 kg m$^{2}$cm$^{-1}$</td>
<td>0.01</td>
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<tr>
<td></td>
<td>Φ (d:less)</td>
<td>141 kg m$^{-2}$</td>
<td>0.35</td>
<td>338 kg m$^{-2}$</td>
<td>0.001</td>
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</tbody>
</table>
Table 3

The sum of squares for the general model with $\Phi$ as a quantitative variable. Model terms are divided into the effects of relative height ($\Phi$) and site using Type I sum of squares.

<table>
<thead>
<tr>
<th>Model</th>
<th>$R_{BS}$</th>
<th>$R_{FB}$</th>
<th>$R_{FS}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi$</td>
<td>0.67</td>
<td>0.03</td>
<td>0.1</td>
</tr>
<tr>
<td>Site</td>
<td>1.12</td>
<td>0.53</td>
<td>1.43</td>
</tr>
<tr>
<td>Error</td>
<td>1.87</td>
<td>0.55</td>
<td>3.35</td>
</tr>
<tr>
<td>Total</td>
<td>3.66</td>
<td>1.10</td>
<td>4.87</td>
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</tbody>
</table>
Figure legends

Figure 1) Illustration of the measurement points for branches and stems. (a) Below the living crown above and (b) at the first living bifurcation of a branch.

Figure 2) Relations between estimated tree foliage biomass (and measured stem area) (a) branch area and the relation between branch area of a tree and stem area of a tree.

Figure 3) Distribution of the foliage mass stem cross sectional area ratio ($R_{FS}$) (a), the foliage mass branch cross sectional area ratio ($R_{FB}$) (b) and (c) the branch cross sectional area stem cross sectional area ratio ($R_{BS}$).

Figure 4) Correlation between the pipe model ratios $R_{FS}$, $R_{FB}$ and $R_{BS}$.

Figure 5) Treewise values of the pipe model ratios ($R_{FS}$ (first row), $R_{FB}$ (second row), $R_{BS}$ (third row)) as a function of relative tree height ($\Phi$) (left column) and tree height (right column).

Figure 6) Least square means of the pipe model ratios ($R_{FS}$ (first row), $R_{FB}$ (second row), $R_{BS}$ (third row)) as a function of tree height. Least square means are either calculated for a dominant tree ($\Phi=1$) with $\Phi$ as a continuous variable ($Q$ in equation 4) (left column) or for a hypothetical tree of 20 m with height as a continuous variable.
Figure 1
Figure 2
Berninger et al. Pipe model ratios in Scots pine

Figure 3

Foliage to Stem area ratio (kg m\(^{-2}\))

Foliage to Branch area ratio (kg m\(^{-2}\))

Percent of trees

Branch area to Stem area ratio (d:less)
Figure 4
Figure 5
Figure 6

Berninger et al. Pipe model ratios in Scots pine

Stand height (m)

$R_{FS}$ (kg m$^{-2}$)  

$R_{BB}$ (kg m$^{-2}$)  

$R_{BS}$ (m$^2$m$^{-2}$)  

Tree height

$\Phi$