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1 **Effects of tree size and position on pipe model ratios,**
2 **Scots pine**

3 **Frank Berninger^{1,2}, Lluís Coll³, Petteri Vanninen⁴, Annikki**

4 **Mäkelä¹, Sari Palmroth^{1,5}, Eero Nikinmaa¹**

5 1) Department of Forest Ecology, PO. Box 27, 00014 University of Helsinki, Finland

6 2) Present address: Département des sciences biologiques, Université du Québec à

7 Montréal, Case postale 8888, succursale Centre-Ville, Montréal, Québec, Canada,

8 H3C 3P8, Berninger.Frank@Uqam.Ca

9 3) Département des sciences biologiques, Université du Québec à Montréal, Case

10 postale 8888, succursale Centre-Ville, Montréal, Québec, Canada, H3C 3P8

11 4) Saima Centre for Environmental Sciences, Linnankatu 11, FIN-57130 Savonlinna

12 5) Present adress: Nicholas School of the Environment and Earth Sciences; Box 90328;

13 Duke University; Durham, NC 27708

1

2 **Abstract**

3

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

1

2 **Introduction**

3

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

14

15 The pipe model has been used to describe the functional balance between the foliage and
16 wood. Providing that this relationship between foliage and wood cross sections remains
17 constant, it allows the calculation of carbon allocation between different parts of the tree
18 (Valentine 1985, Mäkelä and Hari 1986, Nikinmaa 1992, Perttunen et al. 1996, Mäkelä
19 1997). Simulation studies (Nikinmaa 1992, Berninger and Nikinmaa 1997) have shown
20 that different foliage area to sapwood area ratios result in different stand dynamics due to
21 changes in allocation between foliage and woody parts of the tree. Indeed, Mäkelä and
22 Albrektson (1992) as well as Shelburne et al. (1993) have shown that suppressed trees
23 have lower foliage-to-sapwood area ratios than dominant trees. Size-dependent declines

1 of the pipe model ratios (i.e., fewer leaves for similar conducting areas) have been
2 proposed on theoretical grounds. A hydraulic theory of maximum tree height (Yoder et
3 al. 1994) was proposed since hydraulic pathways from the soil to the foliage get longer
4 with tree height, increasing the hydraulic resistance to water flow from the roots to the
5 foliage. This could be compensated for by a lower foliage to sapwood area ratio. This
6 theory has received support in the literature (e.g. McDowell et al. 2002 for a review).
7 However, for example, Monserud and Marshall (1999) found that the allometric relations
8 for Douglas-fir did not show any decrease in foliage to sapwood ratio with increasing tree
9 size.

10

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

14

15 **Materials and Methods**

16

17 The materials of this article originate from a database of tree measurements that allowed
18 estimation of the pipe model ratios from different stands from southern Finland and
19 adjacent areas. The database contained data from 36 stands with 199 sample trees. Data
20 were originally collected for different purposes by different researchers (mostly related to
21 the estimation of biomass or the testing of ecophysiological hypotheses). A description of
22 the stand variables is in Table 1. Some of the data have been published before. The data
23 were collected during three different sampling efforts:

1

2 Berninger, Nikinmaa and Palmroth (Berninger and Nikinmaa 1994, Palmroth et al. 1999)
3 focused on a more detailed structural analysis of trees and estimation of foliage mass of
4 stands (stands 1-4 or Dataset 1 in Table 1). They were derived from sample plots
5 typically containing 30-60 trees. Six to fifteen trees were felled for biomass
6 measurements from two strata; half larger than the average and half smaller than the
7 average tree. Branches were sampled in relation to size (about 10 branches per tree).

8

9 Ärölä (1996) collected data from 20 different stands (Dataset 2 in Table 1). From each
10 stand, a sample plot was established in the centre of the longest diagonal line traversing
11 the stand. Sample plots were circular plots and each contained about 40 trees. 2-4
12 randomly sampled trees were felled with similar selection criteria as above. The
13 diameters of all branches were measured and 10 branches per tree were used for the
14 biomass analysis. Branches were sampled systematically across the whole crown (e.g.,
15 10th branch).

16

17 Vanninen and Mäkelä's Dataset (3 in Table 1) consists of 114 trees measured for biomass
18 and dimensions using similar techniques to Ärölä (1996). The stands covered an age
19 gradient from seedlings to mature trees, and included both heavily thinned and unthinned
20 stands. Stands represented both fertile and poor sites. Within each stands, trees were
21 selected to cover the variation in the competitive status of trees.

22

1 Dataset 3 was sampled in August at the time of maximum foliage biomass whereas
2 Datasets 1 and 2 were collected in early summer before stem diameter growth (Vanninen
3 and Mäkelä 1999). Since Scots pine in Finland drops most of its four-year-old foliage in
4 early autumn this should lead to higher foliage per biomass estimates in Dataset 3
5 compared to datasets 1 and 2, which were measured after the oldest needle cohorts had
6 fallen but before there had been new wood thickness growth. Most of the old foliage in
7 Scots pine senesces in Finland during September and drops during autumn and winter.
8 New foliage grows in June-July (Pietarinen et al. 1982). To account for this, foliage
9 biomass in Dataset 3 was multiplied with 0.75. Analysis showed that the averages of the
10 ratios between the two datasets did not differ after the multiplication (mean of foliage per
11 stem cross sectional area ratio for the Vanninen and Mäkelä dataset 497 kg m^{-2} and for
12 the other data 475 kg m^{-2}). Branch diameters were measured in a different way in the
13 Vanninen and Mäkelä data and therefore we analyze only the foliage mass to stem cross-
14 sectional area ratio from this data (see below).

15

16 In all the data sets the diameters of all trees in each sample plot were measured. Tree
17 height was measured either from all the trees in the plot or from a large enough sample so
18 that representative height and diameter variation at each stand could be determined. The
19 measured variables from all the felled sample trees included diameters at breast height,
20 diameter below the living crown, the number of living branches as well as the diameter of
21 all living branches below the first living bifurcation of the branch (Fig 1). Foliage was
22 dried at $105 \text{ }^{\circ}\text{C}$ for 24 hours before dry weight determination. Diameters below the living

1 crown and branch diameters are diameters below bark. Diameters at breast height are
2 above the bark. The measurements were made during 4 different summers in 1990's.

3

4 **Analysis**

5

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

7
$$R_{FB} = \frac{\sum_{Tree} M_F}{\sum_{Tree} A_{BS}}$$

8

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

13

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

16
$$R_{BS} = \frac{\sum_{Tree} A_B}{A_{SC}}$$

17

18 where A_{SC} is the stem cross sectional area below the living crown (and below the bark)
19 and A_B the below bark cross sectional area of each living branch of the tree.

20

1 The foliage to stem cross sectional area ratio (R_{FS}) (i.e. the “classical pipe model ratio”)
2 was calculated as:

3

$$4 \quad R_{FS} = R_{BS} R_{FB}$$

5

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

9

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

12

$$13 \quad R_{Xij} = S_i + aQ_j + \varepsilon_{ij}$$

14

15 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
16 site i , a is the slope of the regression between Q and R_x and Q_j is a continuous tree-wise
17 measured variable (i.e. tree height or diameter) from tree j . a can be interpreted in the
18 context as the average **within-stand** regression slope between Q_j and R_x . ε_{ij} is the error of
19 the ratio estimate for tree j in stand i . **Between-stand variation** can be explored
20 calculating least square means of R_x . Least square means are the estimates of R_{Xij} at a
21 fixed value of the continuous variable Q_j .

22

1 The calculations were done using the SAS statistical package using the *Proc GLM* for
2 general linear models. Probabilities and least square means account for unbalanced
3 experimental designs.

4 **Results**

5

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

11

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

15

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

21 In the combined data there seemed to be a relation of R_{FS} and R_{BS} to tree height and Φ
22 (Figure 5).

23

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

12

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

21

22 Stand quality affected the ratios. For the worst site type (CT in the Finnish growth
23 classification system (Cajander 1949)) the estimate of foliage to stem cross sectional area

1 ratio was 565 kg m^{-2} , while it was 436 kg m^{-2} for the medium site class (VT) and 465 kg
2 m^{-2} for the better site class MT. Differences between the CT and the other site classes
3 were significant ($p < 0.05$). Differences between MT and VT were not significant.

4

5 **Discussion**

6

7 The close correlations between foliage mass and stem and branch area show that the pipe
8 model theory is a good approximation of tree structure in our data. The estimate of
9 foliage mass to stem cross sectional area ratio (488 kg m^{-2}) for the annual minimum
10 foliage mass is close to the previous published values in Southern Finland (i.e. Nikinmaa
11 1992). Also previous research showed that the branch cross sectional area to stem cross
12 sectional area ratio (R_{BS}) was only slightly higher than the one published before (i.e.
13 Berninger and Nikinmaa 1994, Berninger et al. 1995). Between-tree variation of the pipe
14 model ratios was similar in the study of Mencuccini and Grace (1995).

15

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

21

22 For interpreting the GLM results, slopes between variables are based on *within-stand*
23 variation, while relations of stand-specific Least Square Means (LSM) of a variable with

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

11

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

19

20 This suggests that the relative position of the trees in the stand is the dominant factor
21 explaining the variation in foliage to stem cross-sectional area in our data. In the presence
22 of Φ , effects of stand height were not statistically significant. This contrasts with a
23 number of other studies on Scots pine that claim large effects of tree size on foliage

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

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

17

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

1 3). Nevertheless, correlations between foliage mass and stem cross sectional areas were
2 tight and probably sufficient to estimate foliage biomass for most purposes (Fig 1).

3

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

14

15 Another possible reason for the low foliage area to stem area relationship in suppressed
16 trees could be differences in turnover of foliage, branchwood and stemwood, or higher
17 areas of heartwood, especially in low canopy branches. Sapwood area was not separated
18 from heartwood in all studies and definitions of sapwood and heartwood were not
19 consistent among the studies. However, staining experiments (Hari et al. 1985) indicate
20 that there is little heartwood at the crown base in the young Scots pine stands. We did not
21 consider heartwood and sapwood separately here, since it was not measured in some
22 studies and definitions of sapwood differ between the datasets. Previous research with
23 Scots pine has shown that different methods to determine heartwood area give quite

1 different results (Rust 1999). For these reasons we did not consider heartwood and
2 sapwood separately. In some of the material a visual determination of the heartwood
3 proportion was made from a thin disk cut at the crown base. The moist proportion of the
4 sample could was always below 15% of the cross sectional area where it was measured.

5

6 The GLM analysis showed that several factors modify the ratios. Changes in the ratio of
7 the cross-section of woody parts (R_{BS}) could be explained while variation in the ratio
8 between foliage mass and branch area (R_{FB}) was considerable but was not explained by
9 our statistical models. A better understanding of the factors that determine R_{FB} would be
10 important, since the ratio caused about half of the variation in the foliage to stem area
11 ratio. Also the coefficient of variation was larger for the foliage to branch area ratio than
12 for the branch to stem area ratio. However, it seems logical that the foliage to branch
13 area is harder to explain and more variable: Stem and branches are both woody tissues
14 and their diameter growth is controlled by the activity of the cambium. Cambial growth
15 seems to be largely controlled by temperature and flows of plant hormones from buds to
16 the roots (Aloni 2001). Empirical studies have shown that the weather conditions of the
17 current year largely determine the diameter growth of stems (although there are carryover
18 effects from previous years) (Mielikäinen et al. 1996). Foliage, in contrast, is grown from
19 primary meristems in the buds. The number of new needle fascicles in each shoot is
20 determined during bud formation (i.e. in the previous year) and extension growth of
21 shoots depends on weather conditions of the previous year (e.g. Junttila 1986). This
22 suggests that coordination between branch and stem diameter growth should be closer
23 than that between foliage and branch diameter growth.

1

2 Trees in our stands typically had eight to more than forty rings of sapwood below the
3 living crown. Therefore, the relation between branch to stem cross-sectional areas are the
4 average of many years of growth while there are only about four years of living foliage
5 branches. This foliage is more prone to herbivory (especially sawflies like *Neodiprion*
6 *pini*), fungi (e.g. *Greminella abietina*) and climate-induced damage than branch wood.
7 These biotic factors could cause some of the random variation we have observed in our
8 data although we tried to select healthy looking trees for our study. This needle loss
9 directly reflects in the foliage biomass but there are indications that wood area would not
10 change as quickly (Sievänen et al. 1997).

11

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

16

17 At the poorest sites (CT site class in the Finnish site classification system) the values of
18 R_{FS} were significantly higher than on the better VT and MT sites. Since CT sites only
19 existed in the dataset 3 we cannot test if changes are due to changes in the woody
20 structure of trees (i.e. R_{BS}) or due to changes between foliage and branches (i.e. R_{FB}). Site
21 quality has not been investigated much and much of the results on site fertility stand
22 allometry relations are conflicting. In a previous publication using the same data
23 Vanninen et al. (1996) found that CT sites have higher pipe model ratios, however,

1 Ärölä's work (1996), using one subset of our data, did not find a significant site quality
2 effect in a mixed model where stand and tree-level variation was considered. Long and
3 Smith (1988) found that higher growth rates increased foliage to sapwood area ratios.
4 However, Hacke et al, (2000) and Schäfer et al. (2002) found that trees growing on high
5 fertility sites trees have a larger proportion of their hydraulic resistance in the root
6 system. This is due to changes in allocation, since trees on high fertility sites allocate
7 more carbon to foliage and less to the root. According to them these changes are
8 compensated by lower foliage per sapwood area ratios (i.e. lower values of R_{FS}). Also,
9 Scots pine foliage to fine root ratios on good sites are higher than on bad sites (Vanninen
10 and Mäkelä 1999) and our data.

11

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

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- 1 Zimmermann M.H. 1983. Xylem structure and the ascent of sap. Springer Verlag. Berlin.
- 2 Germany. 143pp.

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

Site Name/ Abbreviation	Coordinates	Stand Density Trees/Ha	DBH Cm	H m	N measured trees	N sample trees	Data Set	
Hyytiälä Hy	62N 24E	1033	16.0	13.6*	40	15	1	
Juupajoki J	62N 24E	2330	10.7	10.5*	30	6		
Siuntio 1 S1	60N 24E	1950	7.3	4.9*	100	7		
Siuntio 2 S2	60N 24E	3400	7.8	6.1*	100	7		
Leivonmäki 1 LE1	62N 25.5E	1770	15.8	19.4	40	2	2	
Leivonmäki 2 LE2	62N 25.5E	890	19.2	20.6	40	2		
Leivonmäki 3 LE3	62N 25.5E	830	20.4	21.1	40	2		
Lammi 1 LA 1	61N 25E	630	21.1	20.5	40	2		
Lammi 2 LA 2	61N 25E	4700	8.2	12.2	40	4		
Mänttä 1 M1	62N 24.5E	2370	13.9	17.2	40	2		
Mänttä 2 M2	62N 24.5E	1050	16.8	16.3	40	2		
Mänttä 3 M3	62N 24.5E	1850	13.7	15.3	40	2		
Mänttä 4 M4	62N 24.5E	2120	13.7	15.7	40	2		
Mänttä 5 M5	62N 24.5E	730	19.4	16.3	40	2		
Juupajoki 1 J1	62N 24E	1080	16.3	14.2	40	2		
Juupajoki 2 J2	62N 24E	2790	10.2	10.9	40	4		
Tammela 1 T1	60.5N 23.5E	1000	20.3	23.9	40	2		
Tammela 2 T2	60.5N 23.5E	630	17.9	15.7	40	4		
Tammela 3 T3	60.5N 23.5E	500	24.9	20.9	40	2		
Heinola H	61.5N 26E	1940	13.6	16.1	33	4		
Puumala 1 P1	61.5N 28E	1500	18.6	23.8	40	4		
Puumala 2 P2	61.5N 28E	1840	16.1	21.6	40	2		
45a	61.3N, 27°E	1070	19	20.8	247	14		3
45b	61.3N 27°E	455	23	22.3	28	5		
47a	61.3'N, 25E	2914	35	11.7	271	7		
47b	61.3N, 25E	693	23	16.3	32	5		
23	62N, 23E	2079	9	8.4	145	4		
218	62N, 24E	1234	10	8.6	133	4		
224	62 N, 24E	1657	11	10.9	149	4		
153	62N, 24E	682	13	11.47	65	4		
223	62N, 24E	199	37	24.0	35	1		
157	62 N, 23E	2176	8	5.8	225	4		
167	60N, 25E	812	21	1840	82	4		
188	60N, 25E	390	29	2380	42	4		
5a	61.8N, 24.3E	18727	4	4.1	354	9		
5b	61.8N, 24.3E	2584	7	5.8	358	15		
1	61.8N, 24.3E	2675	12	11.7	122	15		
2	61.8N, 24.3E	1033	16	13.6	73	15		

1 **Table 2**

- 2 Properties of different models fit to the data with different variables as Q (equation 4).
 3 RMSE means Root Mean Square Error. Significances are based on type III model
 4 estimates.

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

5

1

2 **Table 3**

3

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

		R _{BS}	R _{FB}	R _{FS}
Model {	Φ	0.67	0.03	0.1
	Site	1.12	0.53	1.43
Error		1.87	0.55	3.35
Total		3.66	1.10	4.87

6

7

1 **Figure legends**

2

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

5

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

8

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

12

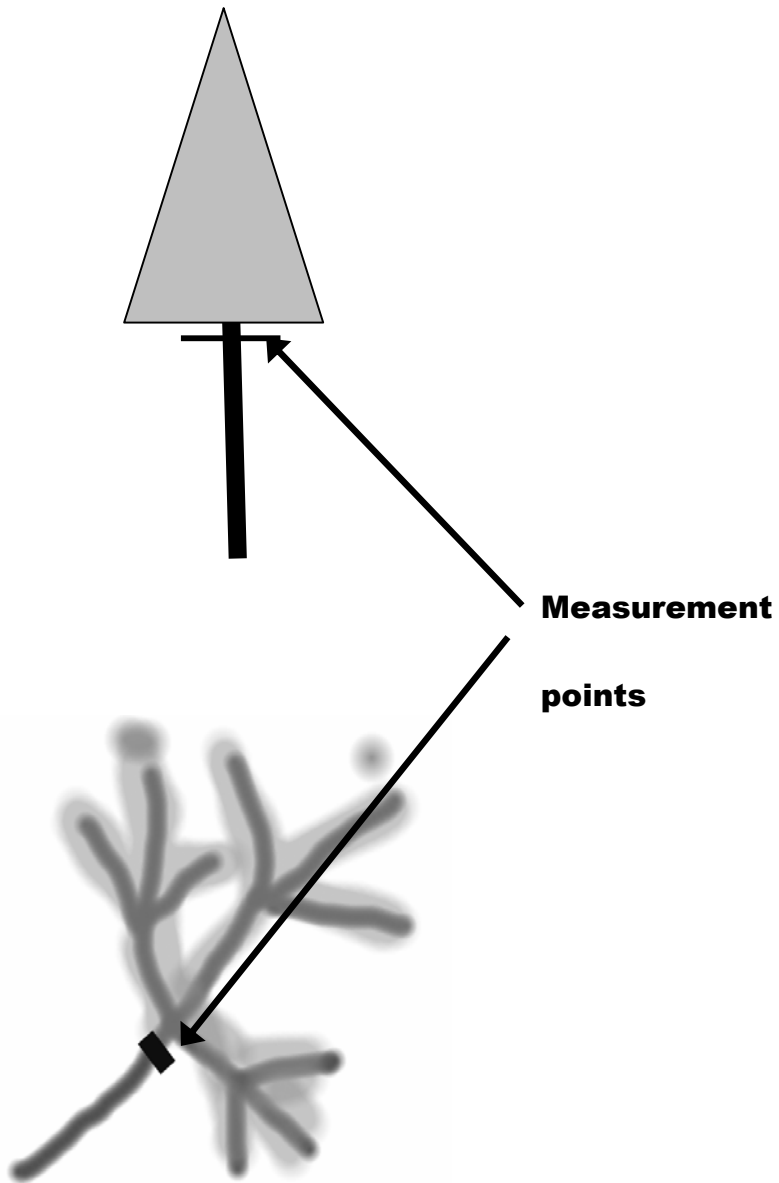
13 Figure 4) Correlation between the pipe model ratios R_{FS} , R_{FB} and R_{BS} .

14

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

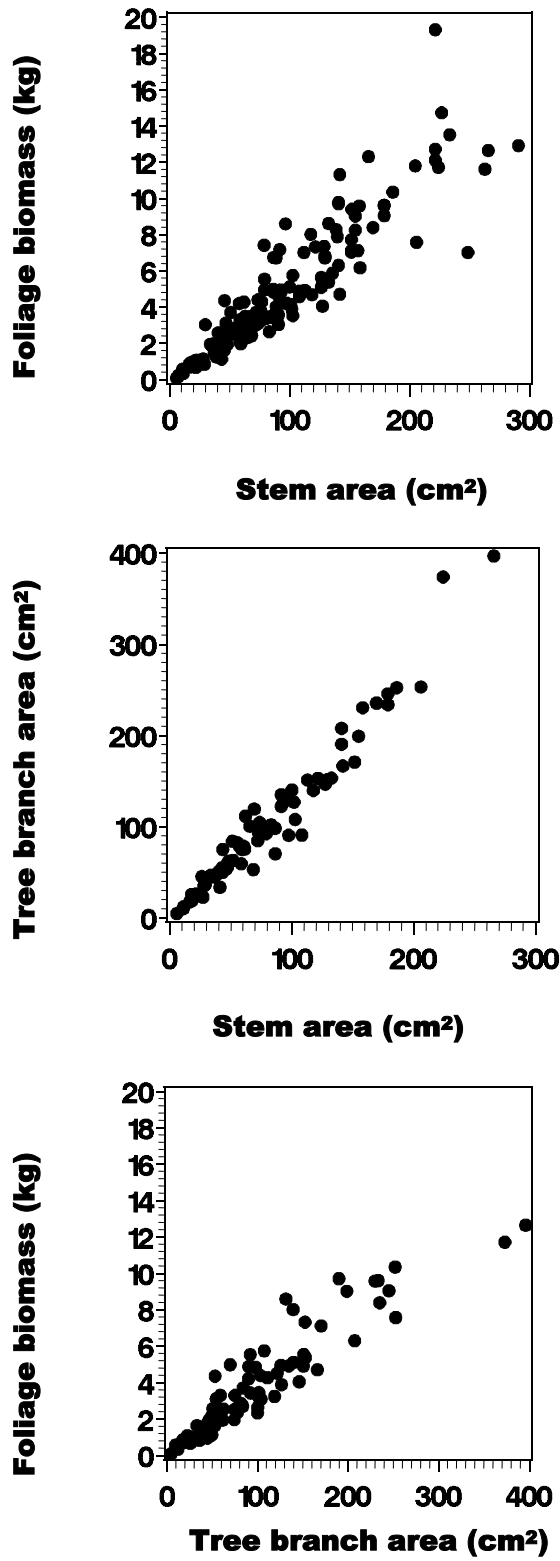
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19 Figure 6) Least square means of the pipe model ratios (R_{FS} (first row) , R_{FB} (second row),
20 R_{BS} (third row)) as a function of tree height. Least square means are either calculated for
21 a dominant tree ($\Phi=1$) with Φ as a continuous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



1
2 Figure 1
3

Figure 2



1

Figure 2

1

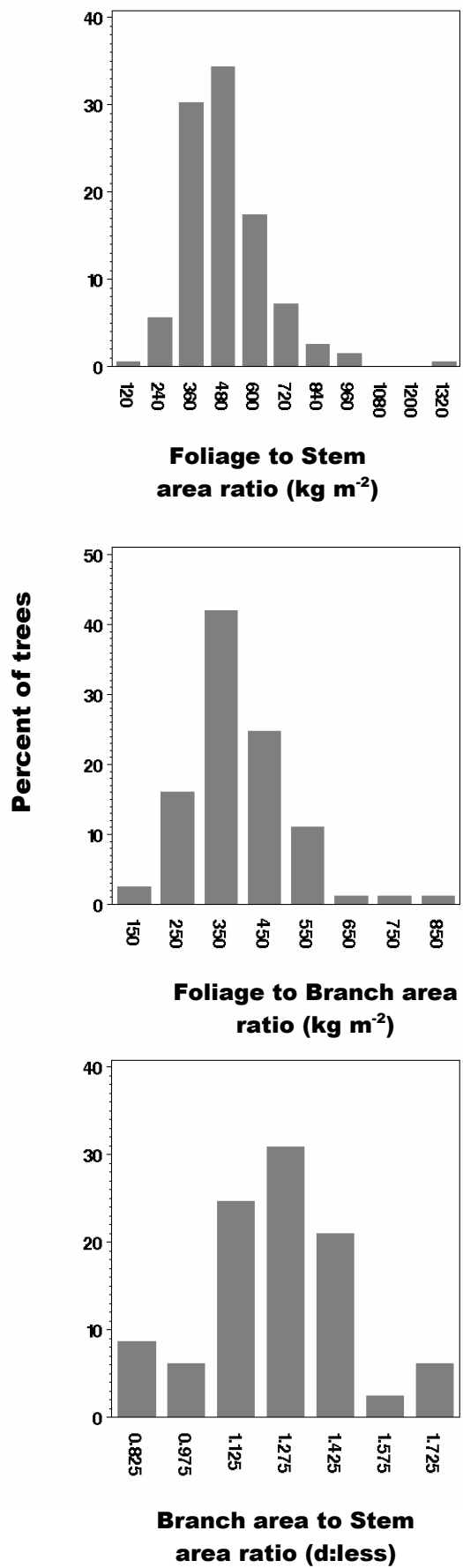


Figure 3

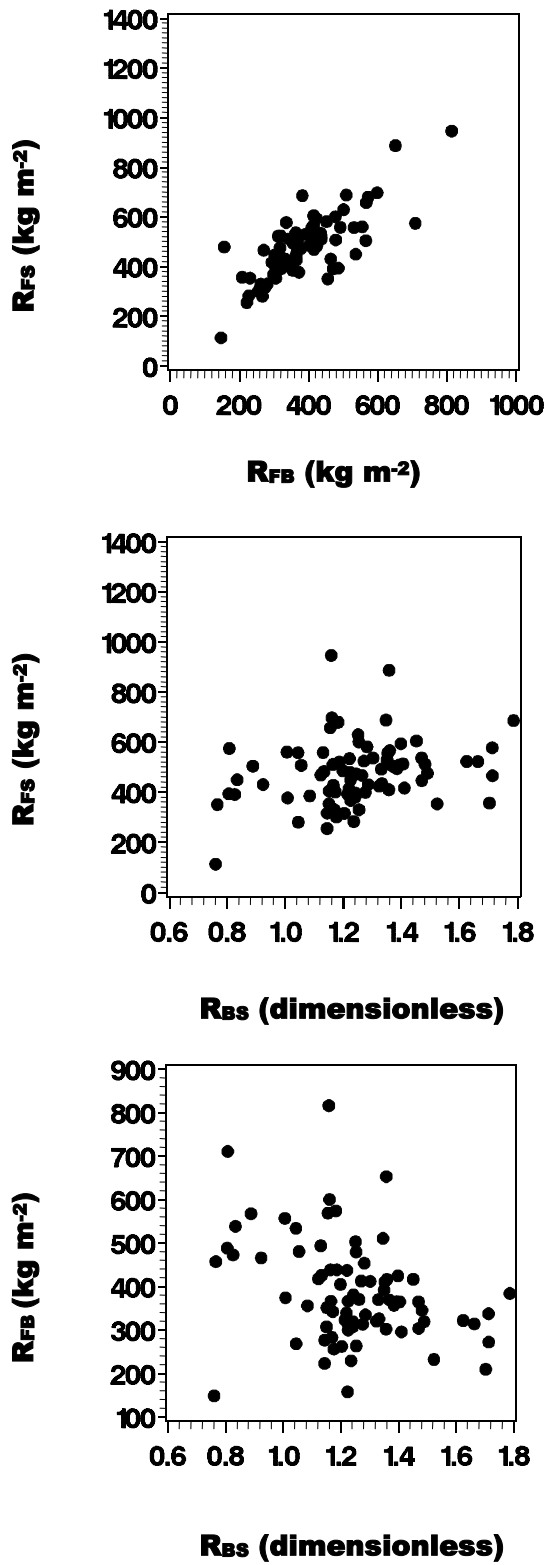
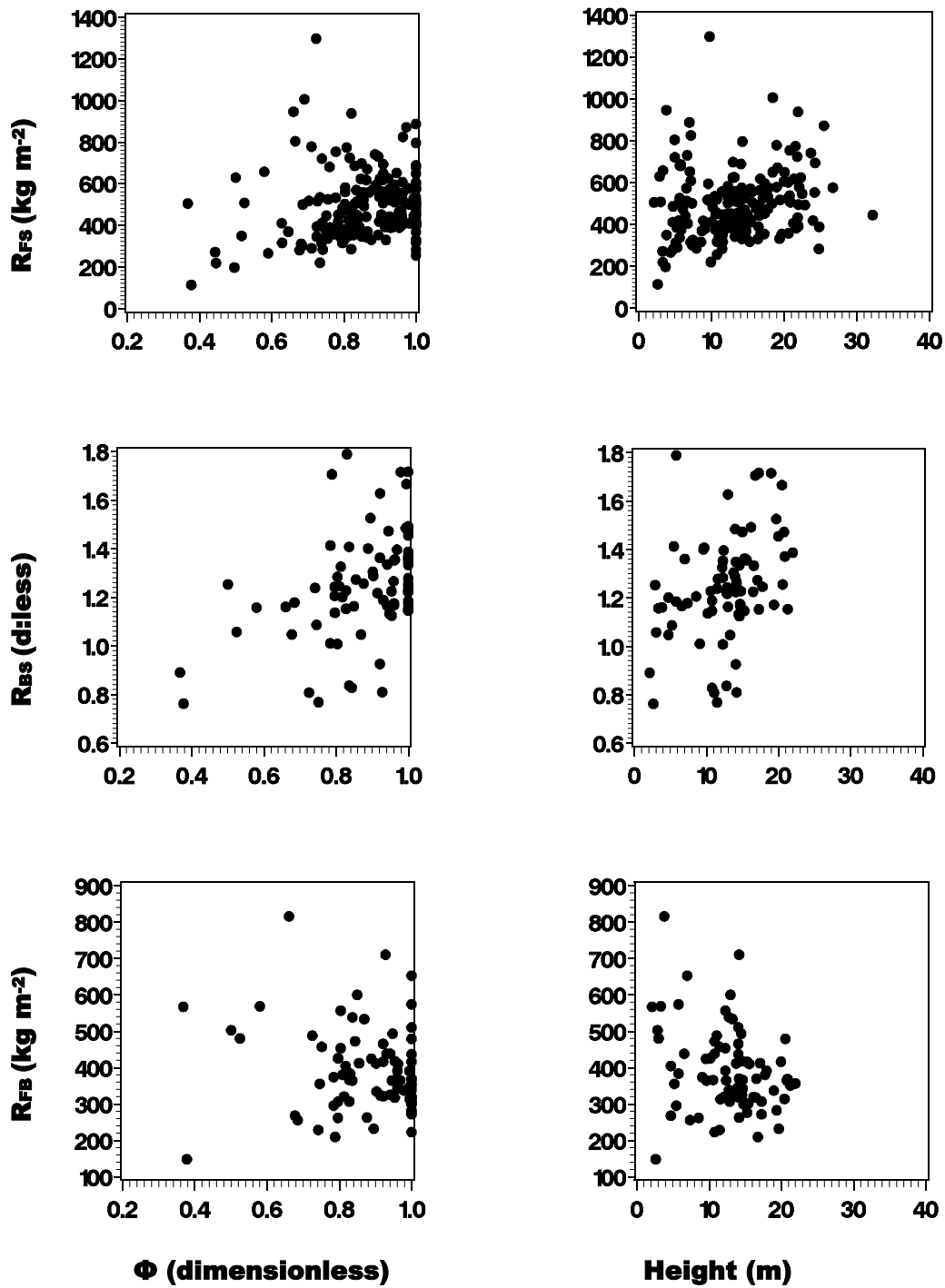


Figure 4

1 Figure 5



2

1 Figure 6

2

3

