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Allometric equations for two South American conifers: Test of a non-destructive method

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Abstract

Non-destructive biomass estimation for protected tree species is necessary to understand their population dynamics and the ecological factors affecting species scarcity. We present a method for estimating aboveground biomass of bole, branches and foliage, using data obtained by climbing live trees to collect limited samples and measurements. This method was applied to 26 individuals of *Fitzroya cupressoides* (Mol.) Johnston, a protected Chilean conifer, and to 12 individuals of a second, morphologically similar, but unprotected species, *Pilgerodendron uviferum* (D. Don.) Florín. Trees were climbed, basal diameter of all branches > 1 cm were recorded and four branches per tree were removed for further measurement. The sampled branches were used to develop allometric equations predicting branch, twig and foliar biomass from branch basal diameter. These equations were used to generate whole tree canopy biomass estimates based on climber's measurements of branch basal diameter. Bole biomass was estimated from serial measurements of height, diameter and wood density. Whole tree canopy and bole biomass estimates were then used to develop allometric equations predicting wood and foliar biomass from diameter at breast height. Five of the *P. uviferum* trees were felled and weighed by conventional methods, and the data used to evaluate error in the non-destructive technique. Although the technique was labor intensive, it was found to yield mean estimates for canopy components that are expected to be within 10% of the true mean for large populations of trees (watershed level studies). Accurate estimation of individual trees may be less reliable, as the amount of dispersion about some of the regressions was quite high (> 20%). © 1998 Elsevier Science B.V.

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1. Introduction

Estimates of aboveground biomass are important measures in ecological studies because they are commonly considered to be one index of primary productivity and nutrient cycling (Whittaker et al., 1974). Total harvesting is generally impractical or inappropriate in forest studies, so allometric methods have been developed to estimate total biomass from non-destructive surrogate measurements such as diameter of the bole at breast height (dbh). Such estimates are clearly most precise when they are calibrated with samples from the species of interest. Sometimes, the

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species of interest are rare or protected and cannot be destructively sampled to determine allometric relationships.

This is the case for an ongoing study examining how climatic and edaphic factors control productivity and dynamics in a temperate montane cloud forest (Hedin et al., 1995). The dominant species in moist upland valleys at this study site is the Andean Larch 'alerce andino' (*Fitzroya cupressoides* (Mol.) Johnston). This species is currently classified as endangered (Anon, 1974, 1977; US Dept. of Interior, 1979, 1984; USA, 1979). As a protected species, living trees cannot be cut down, although historically it has been an important timber species for the region (Veblen et al., 1976).

One objective of the Hedin et al. study is an understanding of nutrient cycling in this ecosystem, necessitating an evaluation of the biomass in each of several components of the forest canopy. This had to be accomplished in a non-destructive manner. We elected to climb the trees, making successive measurements on bole and limbs, along with limited sampling of limbs, which were then weighed. Bole weight estimates were derived from wood density measurements from cores and sections from dead boles.

At this site there is a morphologically similar species in the same family (Cupressaceae), *Pilgerodendron uviferum* (Don) Florín. This tree is not protected; consequently we used it to test the reliability of the non-destructive measurement technique.

2. Materials and methods

2.1. Study site

This study was conducted adjacent to a watershed located on the western slope of the Cordillera de Piuchué (CP), along the eastern edge of the Chiloé National Park (Parque Nacional de Chiloé, Chiloé, Chile, approx. 74°W, 42.7°S). It is at approximately 700 m elevation at the upper end of a shallow dendritic drainage slope (overall change in elevation 50 m). This site is characterized in detail elsewhere (Hedin et al., 1995). The purpose of this study was to derive equations to estimate the total conifer biomass of the CP watershed. Because this watershed is a site of long-term studies beginning in 1989, no destructive or intrusive measurements could be taken. Consequently, we measured trees in the adjacent drainage.

2.2. Tree selection

In the center of its range, *F. cupressoides* is a long-lived tall conifer, measuring up to 50 + m high and 4 m across at the base (Veblen et al., 1976). On our site in the Cordillera de Piuchué, we measured trees 13–65 cm in diameter and 7–17 m tall.

Initial visual inspection of the site suggested that *F. cupressoides* became shorter and squatter with elevation, therefore, trees were selected along an elevational transect. The transect began at the base of a small first-order stream in an area dominated by *F. cupressoides* (Alerce Forest, AF). As the elevation increased, the dominant species became *P. uviferum* and *Nothofagus nitida* ((Phil.) Krasser) (Transition Forest, TF). Trees with split tops were rejected. Thirteen *F. cupressoides* and six *P. uviferum* were measured in each forest type. Five of the *P. uviferum* were subsequently harvested to check the accuracy of the measurements with actual weights.

2.3. General sampling design and measurement procedure

For purposes of measurement and analysis, the trees were divided into separate architectural elements as in Table 1. Foliage, twig, and branch wood weight were predicted from limb basal diameter, based on regressions developed from stratified random samples of 48 limbs in *P. uviferum* and 102 limbs in *F. cupressoides* (generally four per tree). Bole weight was estimated from serial measurements of height, diameter and wood density using parabolic estimation of bole shape. These estimates were used to develop whole-tree regressions of bole and canopy component weight on dbh. To assess accuracy, five trees were subsequently felled and all elements weighed in the field.

The dbh was determined for each tree; which was then climbed to a point within reach of the apex using standard tree spikes, climbing harnesses and ropes. *F. cupressoides* has thick (up to ca. 5 cm), loose, fibrous bark, which was formerly stripped by

Table 1
For purposes of measurement and analysis, the trees were divided into separate architectural elements as follows

Bole	the main trunk of the tree, less the top
Top	the distal portion of the trunk containing limbs below 1 cm diameter
Limb	side shoots from the bole, greater than 1 cm in diameter
Branch	shoots arising from limbs, greater than 1 cm in diameter
Twig	shoots arising from branches or limbs; less than 1 cm in diameter
Foliage	apical shoots retaining foliage, whether green or brown

native boat builders for use as caulking (J. Armesto, pers. comm.). Evidence of such bark stripping is common, and the trees do not usually appear to be affected by this treatment. Consequently, we judged that the use of tree spurs to climb the trunks would not substantially injure the trees.

The upper meter of the crown consisted of small limbs, mostly <1 cm in diameter. These crown tips were considered separately (top), and a point at which limb diameters exceeded 1 cm was selected along the bole, at which point, the bole diameter, distance to the apex and height above the ground were determined. This diameter was used in the analysis of top characteristics, and was considered the upper end of the bole. Tree height was determined by summing the bole and top lengths.

The diameter of each limb below the top was measured and recorded. The climber then moved down 1–2 m, measured the bole diameter, height at that point, and the basal diameters of all limbs in the section between bole measurements. Exact distances were determined by height, canopy density and safety of the climber. This operation was repeated until the climber reached the base of the live crown. Limb diameters were determined at the first point at which the limb became cylindrical, typically within 5 cm of the trunk. The bole diameter and height were measured at the base of the live crown and at one-meter intervals along the remaining length of the trunk.

During the climb, four limbs of varying diameters were removed randomly from different levels of the canopy. Sampled limbs (SL) were then lowered to the ground and dissected. Total limb weight, longest limb length, weight of foliage, weight of limb elements less than 1 cm diameter (twigs) and weight of limb elements greater than 1 cm (branches) were determined and recorded. In addition, the canopy was divided into quadrants vertically, and the quadrant from which the branch was sampled was noted (CQ). Foliage, twig and branch tissues were subsampled for dry weight determination and nutrient analysis. Tissue subsamples were field weighed and brought back to the laboratory in plastic bags. The subsamples were then dried at 65°C for 48 h or until constant weight (bole sections). These data were used to develop regressions between limb diameter and limb component weight.

For *P. uviferum* subsequent to climbing and measuring as described above, five trees were cut down and dissected into bole and limbs. The total weight of each limb was recorded, along with its basal diameter and length, yielding a population of 271 limbs (TL) to test the accuracy of the equations determined from the dissected SL limbs. The bole was cut into segments. The diameter at each cut, segment length and weight were recorded. This allowed a reconstruction of the bole using measured values. Equations for limb components were determined by the same estimation technique used for *F. cupressoides*. Predictions from the diameter–weight relationship based on weighed limbs were compared to predictions based on the estimated value. Bole weight predictions based on bole shape calculations and wood density were compared to those based on the field measured weights and dimensions.

Measurements were conducted using standard dbh tapes for bole and large limb diameters (>10 cm). Smaller diameters were determined using vernier calipers. Heights were measured with 30-m measuring tapes. Limb component weights were determined using a 5-kg capacity portable electronic scale. Total limb weights and bole weights were determined using a 50-kg spring scale.

Four trees were climbed and measured by more than one climber to compare climbers. One recently dead (defoliated) *F. cupressoides* was found; it was cut down and dissected to provide direct measurements of bole, limb and bark dimensions. This tree had been stripped of its bark, and appeared to have been girdled in the process, which we determined to be the cause of death.

All trees were cored with an 11-mm increment corer. Core depth varied with tree diameter, smaller trees were cored through, larger trees were cored at least to the pith. Bole slices (ca. 2 cm-thick) were collected from 3–6 points along the boles of the felled trees. Cores and bole slices were used to calculate wood density. Sample volume was determined via displacement (Archimedes' principle). Cores were immersed in water in a 100-ml graduated cylinder. Although this limited precision to ± 0.5 ml, core volumes were > 13 ml, and consequently accurate within 4%. Density was determined using volume and oven-dry weight.

2.4. Analysis

Relationships between measured weights and diameters or lengths were evaluated using the standard allometric formula $y = \alpha x^{\beta}$. Linear regression models were fit to the equation

$$\log(\text{weight}) = \beta \cdot \log(\text{diameter}) + \gamma + \varepsilon,$$

where $\varepsilon =$ error term equal to $1/2$ the Mean Squared Error from the regression analysis. The error term is used to compensate for a slight downward bias when the regression estimates are back-transformed, arising from the fact that the mean of a log value is equal to the median of the untransformed value (Bell et al., 1984; Niklas and Buchman, 1994).

Sampled SL limbs were used to create a regression between limb basal diameter and limb fresh weight. This regression was used with the climber-measured limb diameters to estimate fresh weight of all limbs. The accuracy of this regression was checked by comparing predicted values with the TL field weights measured for the felled trees. The dissected SL were used to develop limb diameter vs. dry weight regressions for foliage, twig and branch components for each species. The regressions were then used with the limb diameters measured by the climbers to obtain estimates for the total canopy weight for each component. Total canopy component weights were used to obtain allometric equations using dbh.

Bole shape was calculated using data from height and diameter measurements collected as described above. These data were fit to individual parabolic curves, on a tree-by-tree basis. This result was then rotated through the X-plane to obtain a paraboloid. The parabolic volume was then multiplied by the density of wood samples collected for that tree.

Sum of bole weight and limb weights gives total tree weight. Estimated total tree weight and bole weight was regressed against easily obtained measurements such as dbh and tree height to obtain an allometric equation for the whole tree. For the felled trees, the predicted weights were then compared with the values from the regression to test the reasonableness of the values.

Statistical analyses for linear and multiple linear regressions, as well as Pearson's Product–Moment correlations, were performed using the computer program SigmaStat™ (Jandel Scientific, San Raphael, CA). Comparisons of slopes were performed manually following Sokal and Rohlf (1981). Regression correlation coefficients for limb regressions and bole regressions were tested via Turkey's jackknife procedure (Sokal and Rohlf, 1981) to evaluate sensitivity of the results to deletion of portions of the data set. Limb regressions were jackknifed by deleting randomly selected groups of 30 branches; this test was run 30 times. Bole regressions were tested using deletions of single samples and were run 12 (*P. uviferum*) or 26 times (*F. cupressoides*). Jackknifed regressions were then used to estimate values for the missing variates.

3. Results and discussion

3.1. Data collection

Initial data examination focused on determining whether the data collection techniques were consistent. One possible error source were differences between measurements taken by individual climbers. Four trees were climbed by more than one person; all results agreed within 5%. Another error source arose from differences between measurements made by climbers and those made on the ground. Results from the felled trees were compared with the values obtained by climbing them; again, these agreed well, although one tree's canopy weight was over-predicted by the climber by about 7%. This was due to a larger mean limb diameter in the climber's values compared with that obtained on the ground. In this case, the climber was using a diameter tape to measure small limbs, whereas the ground personnel were using calipers.

Similarly, an opportunity arose for error in the cut limb measurements used to develop the regressions for diameter versus component weight. The SL limbs were not necessarily cut at the exact point where diameter was measured by the climber. These cut limbs were remeasured on the ground prior to weighing. When the two measured diameters were compared, they were found to be significantly different (paired T-test: $T = -5.35$, $P < .00001$; Wilcoxon Signed Ranks: $W = 3069.0$, $P < 0.00001$; $n = 144$).

Table 2
Formulae and regression coefficients for limb component dry weight (DW) versus limb basal diameter (BD)

	α	β	s.e.	γ	s.e.	2ε	adjR^2	n
P. uviferum								
Climbers								
Branch	7.50	3.06	0.140	0.852	0.0619	0.0253	0.931	36
Twig	14.1	1.96	0.0840	1.15	0.0323	0.0210	0.921	48
Foliage	29.0	1.88	0.0916	1.45	0.0352	0.0250	0.899	48
Ground								
Branch	6.67	3.25	0.1384	0.813	0.0590	0.0220	0.940	36
Twig	15.0	1.99	0.0721	1.17	0.0271	0.0142	0.942	48
Foliage	30.3	1.92	0.0892	1.47	0.0332	0.0228	0.908	48
F. cupressoides								
Branch	9.85	2.87	0.0915	0.976	0.0469	0.0346	0.915	92
Twig	16.5	1.79	0.0492	1.21	0.0234	0.0159	0.929	102
Foliage		1.94	0.0820	1.73	0.0411	0.0334	0.867	102

CQ: $d = -0.0518^*$, s.e. = 0.0171, s.e.e. = 0.1828.
Dry weight values (g) were regressed against diameters (cm) measured by climbers (Climbers) and against those measured by ground crew (Ground) on sawed-off limbs.
Canopy quadrant (CQ) explained significant additional variance only for *F. cupressoides* foliage.
Formulae: $DW = \alpha \cdot BD^{\beta}$. Regression: $\log(DW) = \beta \cdot \log(BD) + \gamma + \varepsilon\{+\delta \cdot CQ\}$ where $\log(\alpha) = \gamma + \varepsilon\{+\delta \cdot CQ\}$. β = slope, γ = y-intercept, ε = error term., s.e. is standard error of the coefficient, 2ε is the regression mean squared error, adjR^2 is the degrees of freedom adjusted coefficient of determination, s.e.e. is the standard error of the estimate. All regressions significant at $P < 0.0001$ except *, $P < 0.005$.

Since the limb diameters were potentially different depending on where they were measured, the weighed values for the limb components were regressed against both diameter measurements to create two equations (Table 2). These equations were applied based on the measurement used. That is, when felled trees were measured on the ground, the ground-based diameter equation was used to predict canopy component weight; measurements made by climbers used the second equation to predict canopy component values.

The results for each species are examined separately below. The analyses are presented in the order they were analyzed to reconstruct a whole tree from its parts.

3.2. Limb analysis

3.2.1. *P. uviferum*

Forty-eight SL limb samples (four per tree) were used to develop the regression between limb diameter and limb component dry weight. The data used for regressions and the regressions themselves are shown graphically in Fig. 1. Foliage and twig make similar contributions to the overall weight of the limb, however, foliage is considerably more variable. We observed in the field that small diameter limbs in the lower canopy of the trees appeared to have less foliage and greater length. In performing the analysis, a multiple linear regression including either limb length or CQ did not significantly account for any added variance beyond that accounted for by simple regression against diameter, nor were canopy quadrant and limb length significantly correlated (data not shown). Consequently, limb weights were calculated using the regression for component dry weight against limb diameter. Coefficients and errors for the equations used are shown in Table 2.

Reliability of the estimates provided by the SL regressions was checked by comparison of total limb weight estimated from summing component regressions with TL weights measured in the field. TL diameters were used to calculate individual limb component dry weights using the SL-derived regressions. These values were divided by the dry weight percentage determined from sampled limbs for individual trees and CQ for each limb, to give a fresh weight estimate compensated, at least in part, for

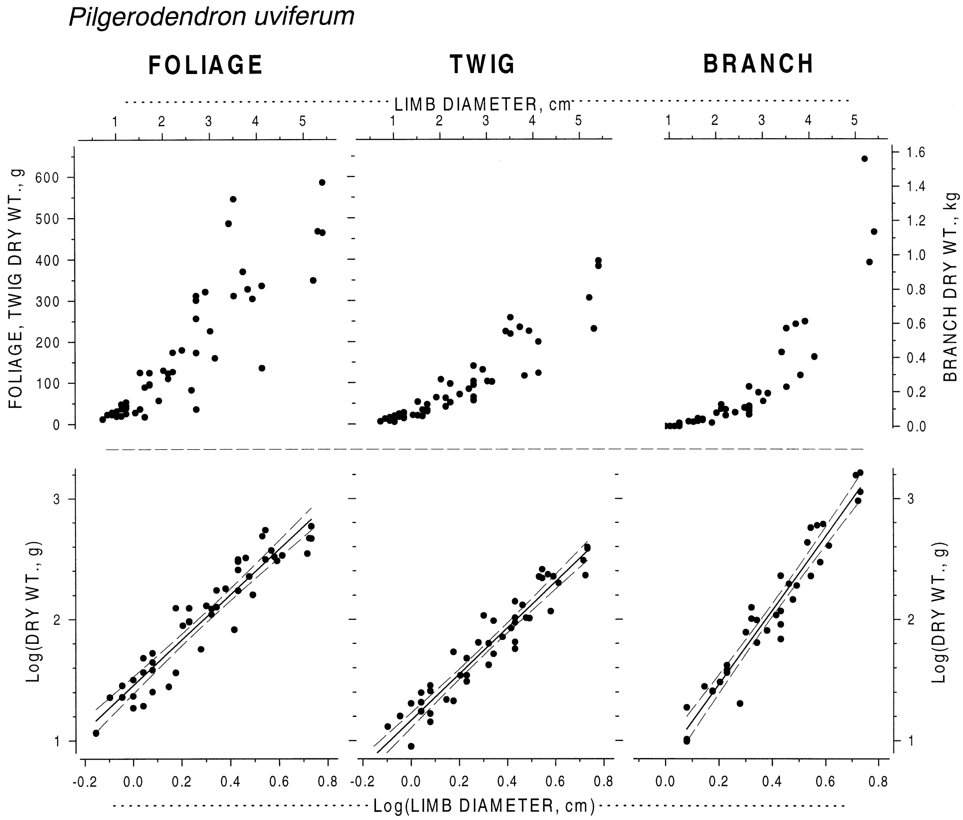

Fig. 1. *Pilgerodendron uviferum.* Data and regressions shown for dry weight of limb components against basal diameter of limb. Solid line is regression; dashed line represents 95% c.i. for the estimate. Note different units for Branch Dry Wt.

variation in water status between individual trees and within tree canopies. The values for component fresh weight estimates were then summed to yield a limb total fresh weight estimate.

This limb total fresh weight was then compared to the field weighed values for the limbs. The results of this comparison are shown graphically in Fig. 2. Field and estimated fresh weights were strongly correlated (Pearson's $R = 0.926$, $P < 0.0001$, $n = 273$), indicating that the regression does a good job predicting the test limbs. Some error may arise from the dry weight percentage used to estimate limb fresh weight. When the field weighed values for the sampled limbs were compared with the values predicted from the diameters (summed and calculated as above) a similar result was obtained ($R = 0.953$, $P < 0.0001$, $n = 48$). This is not unexpected, given the high coefficients of determination for the regressions.

If the weighed and predicted values are regressed against each other for the two limb groups, and the slopes compared, the test limb regression has a slightly greater slope ($m = 1.0005$ vs. $m = 0.9559$), but there is no statistical difference between them ($P < 0.87$). This indicates that the regression is predicting the test limb weights as well as it predicts the weights of limbs used to develop the regression.

This suggests that the upward bias in predicted values was not due to errors in the dry to wet weight conversions, but may have occurred as an artifact of our sampling procedure. Limb diameter is log-normally distributed, with the majority of the limbs in the 0.8–1.8 cm size class (Fig. 3A). We sampled a fairly consistent number of limbs across the range of diameters (Fig. 3A). Additional sampling of the smaller size limbs might have balanced an excessive contribution to the slope by the larger branches. However, when the five largest branches were re-

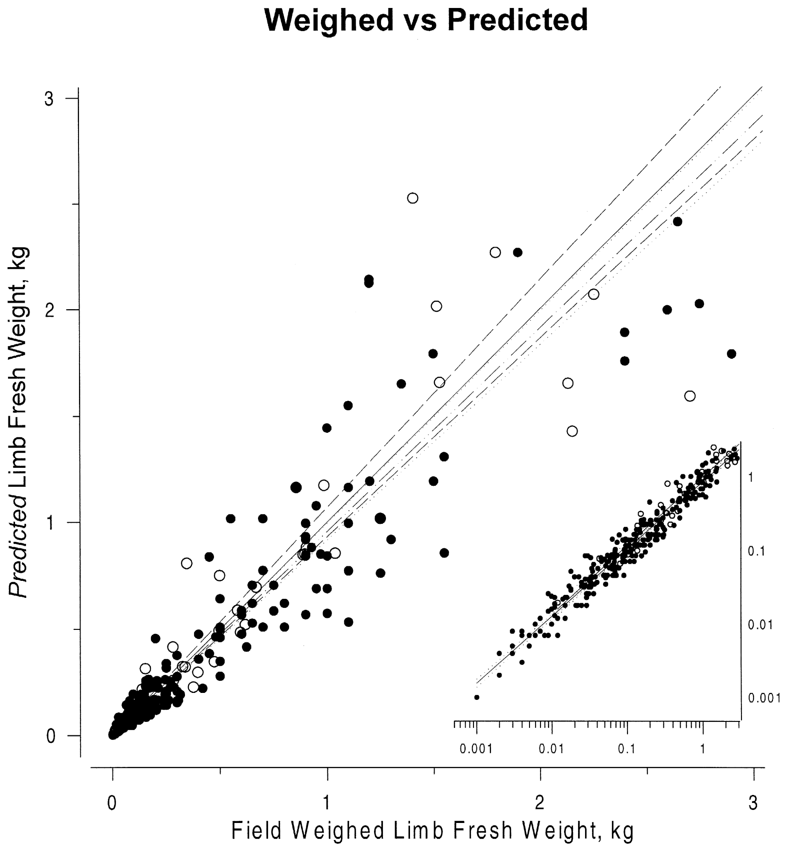

Fig. 2. *P. uviferum*. Comparison between field weight of entire limbs and weight predicted from regression. Open circles ($n = 48$) are data points used to develop regression between limb diameter and limb component. Solid circles ($n = 273$) are whole limb weights from felled, dissected trees used to test the regression. Pearson's $R = 0.926$, $P < 0.0001$ for this test. Solid line is the regression between weighed and predicted values for solid points; dashed line is the 95% c.i. for this estimate ($y = 1.0005x$). Dashed–dotted line is the regression between values for open circles; dotted lines are 95% c.i. ($y = 0.95559x$). Inset shows the same data on log scaled axes to show data distribution.

moved from the regression the values of the limb regression coefficients did not change (data not shown).

The percent difference between predicted and weighed values for the 273 test limbs is shown in Fig. 3B. The prediction error is consistently large or small across the range of diameters, indicating that the regressions do perform a good job of predicting mean weights for limbs not used to create the regressions. However, there is a tendency to overpredict the smaller diameter limbs to a greater extent than larger limbs. As there are large numbers of small limbs, there exists a possibility for overestimating the canopy totals. The contribution of the total number of limbs in each diameter class to the overall total weight of limbs is shown in Fig. 3C. The small diameters most likely to be overpredicted total less than 2% of the total limb weight. Consequently, this error was deemed to be small enough to ignore, and likely smaller than other errors in measurement.

3.2.2. *F. cupressoides*

Data and simple linear regressions for 102 limbs from 26 trees are shown in Fig. 4. Variability is similar to *P. uviferum*, a result only emphasized by the larger sample. In contrast to *P. uviferum*, this species has more foliage than twigs on a limb, nearing an equal weight for both branch and foliage components. The simple regressions shown in Fig. 4 indicate that many limbs have lower foliage weight

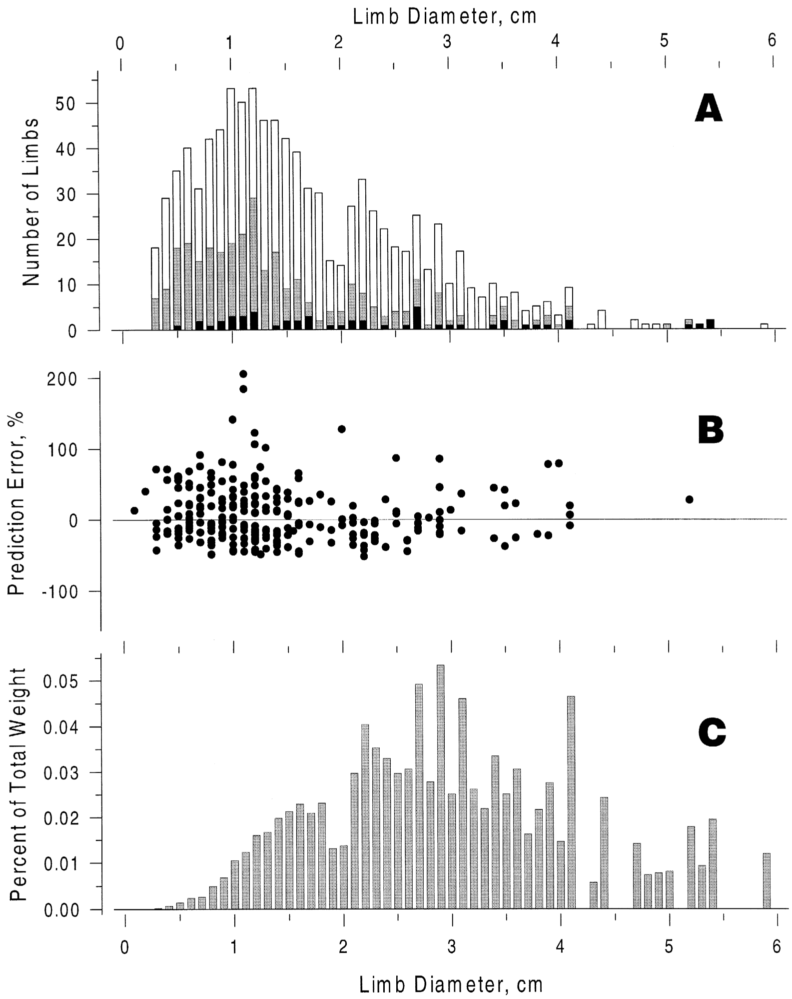

Fig. 3. *P. uviferum*. Limb diameter distributions for several variables. (A) Frequency of limb diameters. Open bars are all limbs measured. Shaded bars show data for test limbs (TL) from felled trees. Solid bars represent limbs used for developing the limb regressions (SL). (B) Percent difference between predicted and weighed value for test limbs from felled trees. (C) Percent of the total limb weight contributed by limbs of each diameter.

than would be expected from the regression ($\alpha = 45.7$, $\beta = 1.82$, $\gamma = 1.66$, $2\varepsilon = 0.0362$, adj$R^2 = 0.856$, $P < 0.0001$). The equation and regression coefficients are shown in Table 2.

Since we did not fell these trees or remove any additional branches for testing purposes, the robustness of the simple linear regressions were tested via Turkey's jackknife procedure. A group of thirty branches were randomly removed each recalculation of the regression. The results compare well with the values obtained for the whole sample regression (WSR). For example, the jackknifed correlation coefficient for the foliage regression is 0.898 (95% c.i. 0.56–0.98, $P < 0.002$, $n = 30$). Values for the regression coefficients were very close to the WSR: $\beta = 1.86 \pm 0.05$ (s.d. range 1.72–2.02); $\gamma = 1.66 \pm 0.01$ (s.d. range 1.62–1.77). The data for branch and twig regressions is similar (data not shown). The equations generated by each jackknife were used to calculate the weight of the excised samples, which was then compared to the value obtained from the WSR. Of the thirty jackknifes run, only two pro-

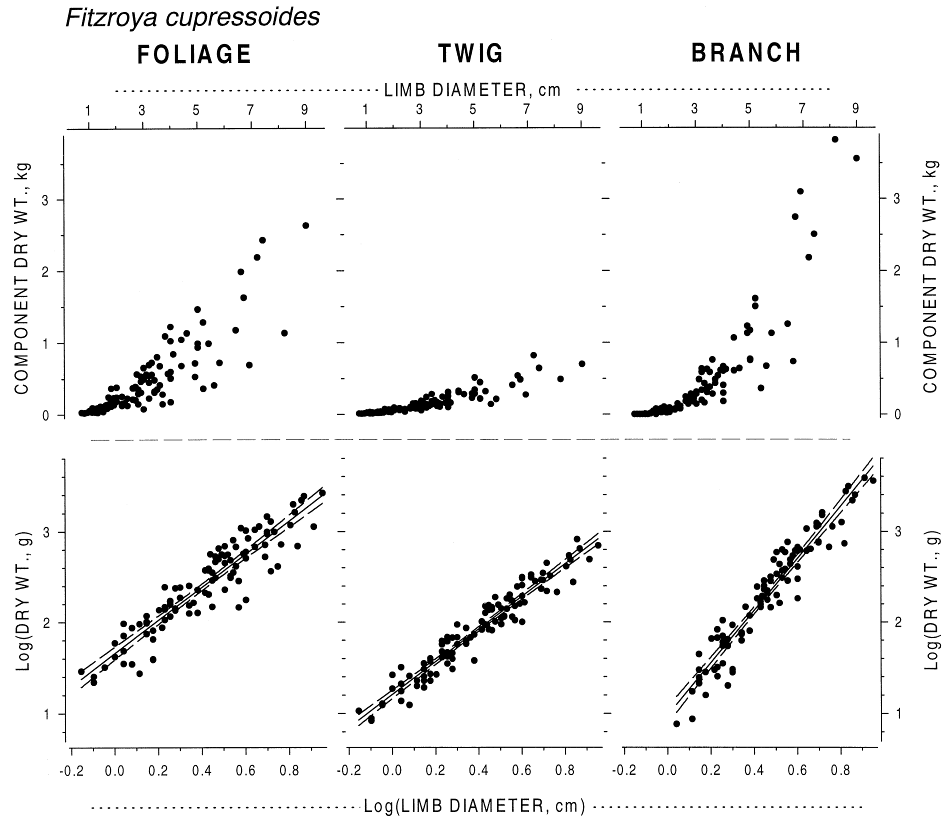

Fig. 4. *Fitzroya cupressoides*. Data and regressions shown for dry weight of limb components against basal diameter of limb. Solid line is regression; dashed line represents 95% c.i. for the estimate.

duced equations that failed to predict weights within the 95% prediction interval for the WSR (data not shown).

As with *P. uviferum*, we observed that smaller diameter branches lower in the canopy tended to have less foliage and longer limbs. Unlike *P. uviferum*, these factors did account for a significant amount of added variance in a multiple regression for foliage. Length and CQ were correlated; only CQ was used in the final regression, since we did note canopy position, but did not measure length. Although it accounted for only a small amount of variance in the regression it was sufficient to correct the limbs appearing below the simple regression line. Consequently, foliage weights for these limbs were calculated using CQ as a variate, according to the formula in Table 2.

Dead limbs for both species were calculated as having only the branch portion of the limb unless otherwise noted in the field. These limbs were generally overestimated by the equations. This was expected, as limbs in the field have lost some portion of their original size due to rot or breakage. However, there were very few dead limbs on trees, so this error was ignored in the estimates.

3.3. Canopy analysis

3.3.1. P. uviferum

Using the formulae above and the limb diameters measured for the climbed trees, estimated mean weights for each of the canopy components was calculated by summing the values for each limb. These values were then regressed on bole dbh. The apparent variability in the weight of the canopy components with respect to bole diameter is considerably greater than that seen for limb diameters. The sample size is small and biased towards trees in the middle of the size range, as there are few large trees in the field. The data and regressions are shown graphically in Fig. 5. Table 3 summarizes the coefficients for the regressions and the allometric formulae. Two of the trees lie noticeably outside the 95% c.i. for the estimate. One of these trees had grown in a small clearing and had a tall canopy relative to its diameter, typical of open-grown trees. The other tree had a large crook in its bole, having lost its leader when younger. This amount of variability was not unexpected, as trees in the field were observed to be subject to diverse injuries, from split boles to dead tops, as well as varying degrees of suppression.

The small sample size contributed to lower R^2 and higher ERE values than seen in other regressions in this study. The ERE values, in particular, suggest that dbh may only predict the weight of a particular canopy component within 50–100% (Table 3.) The predictive reliability of the regression was tested using values from the felled trees. Values for the total canopy (summed components) were compared to the summed field weighed limbs. The results are shown in Table 4 and Fig. 8. In three out of five cases, the regressed estimate is within 5% of the weighed value. The remaining two are about 20% above and below, respectively. Consequently, we believe that the mean value estimated for the canopy and its components probably reflects the true mean for the watershed forest as a population. Note, however, that since foliage and branch weights tend to

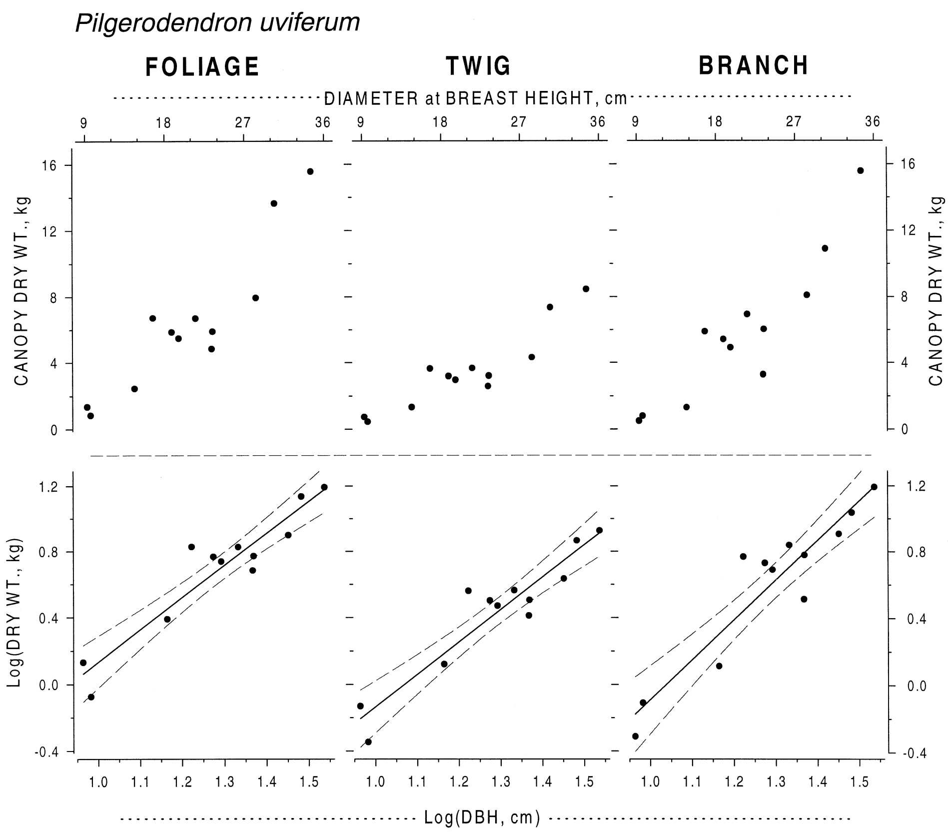

Fig. 5. *P. uviferum*. Data and regressions shown for dry weight of canopy components against bole diameter at breast height (dbh). Solid line is regression; dashed line represents 95% c.i. for the estimate.

Table 3
Coefficients for the allometric equation

	α	β	s.e.e.	ERE	adj R^2
P. uviferum					
Foliage	0.0158	1.94	0.1305	1.54	0.882
Twig	0.00828	1.95	0.1320	2.04	0.881
Branch	0.00358	2.38	0.1714	1.93	0.873
Canopy	0.0269	2.07	0.1340	1.33	0.885
Bole	0.0836	2.25	0.0669	1.09	0.974
Tree	0.1092	2.21	0.0640	1.08	0.975
Fitzroya cupressoides					
Foliage	0.02914	1.83	0.0947	1.20	0.883
Twig	0.01033	1.80	0.0913	1.36	0.927
Branch	0.00146	2.63	0.1719	1.47	0.924
Canopy	0.0227	2.12	0.1173	1.20	0.914
Bole	0.1311	2.21	0.0588	1.06	0.979
Tree	0.1542	2.20	0.0495	1.05	0.985

Dry weight (kg) = $\alpha \cdot \text{dbh}^{\beta}$. Dbh = diameter (cm) at breast height (1.37 m). s.e.e. is the standard error of the estimate for the fitted regression. Adj R^2 is the coefficient of determination adjusted for degrees of freedom. ERE is the 'estimate of relative error' (Whittaker and Woodwell, 1968).

covary inversely, some of the variability in component weight is masked in comparing the whole canopy weights. Although prediction error for a single tree's foliage weight may be somewhat high, it is expected that this effect is less serious as the number of trees increases, as in a watershed scale study.

3.3.2. *F. cupressoides*

Total weights for canopy components and regressions are shown in Fig. 6. Coefficients for the regressions and allometric equations are shown in Table 3. These regressions are somewhat more precise than those for *P. uviferum*. The data points include a tree with a split top, a suppressed tree and a flagged tree at a clearing edge. Although an effort was made to avoid disfigured trees due to the difficulty inherent in estimating their bole volume, damage was not always apparent from the ground. Removing these points does improve the R^2 for the canopy regressions somewhat. Since the points are near the midpoint of the values used for the regressions, their removal does not materially affect the coefficients (data not shown). It is, however, useful to have some idea of the actual variability seen in the field reflected in the data. Total canopy weights regressed on dbh had a similar amount of variability as seen in individual components (Fig. 9 and Table 3).

Table 4
Measured and predicted values of whole tree variables for six felled trees

Tree	Dbh (cm)	Height (m)	Crown (m)	DGL (cm)	Canopy (kg)	Tree (kg)	Limb (number)	Density (g cm^{-3})
1	18.8	7.8	3.4	29.7	15.1	68.9	103	0.480
2	28.3	10.86	5.16	37	21.3	153.7	43	0.469
3	9.2	4.63	1.79	13.7	2.7	12.7	54	0.444
4	9.6	6.5	1.7	14.6	2.2	19.1	29	0.424
5	19.6	8.87	3.2	29.3	14.0	76.6	39	0.415
A	33	15.2	5.1	45.2	–	–	22	0.41

Tree	Canopy			Bole				
	Weighed	Regressed	Ratio	Weighed	Calculated	Ratio	Regressed	Ratio
1	20.119	20.876	1.04	91.2	92.6	0.98	61.5	1.14
2	32.871	34.642	1.05	225.2	263.8	0.85	154.4	1.17
3	3.871	4.737	1.22	16.5	16.7	0.99	12.3	1.23
4	4.515	4.425	0.98	28.4	27.1	1.05	13.6	0.80
5	32.761	25.715	0.78	120.4	125.1	0.96	67.6	1.08
A	–	–	–	623.3	611.1	1.02	569.7	1.09

Numbers 1–5 are *P. uviferum*; A is dead *F. cupressoides* (tree has no canopy).
Dbh = bole diameter at breast height; Height = total tree height; Crown = height of live canopy; DGL = basal diameter of tree; Canopy = total dry weight of tree canopy; Total = total dry weight of tree (canopy + bole); Limb = number of limbs on tree; Density = bole wood density.
Second part of table presents data comparing field weighed whole canopy and bole weights to the values predicted by regressions (regressed) and calculated from bole volume and density measurements (calculated). See text for details.

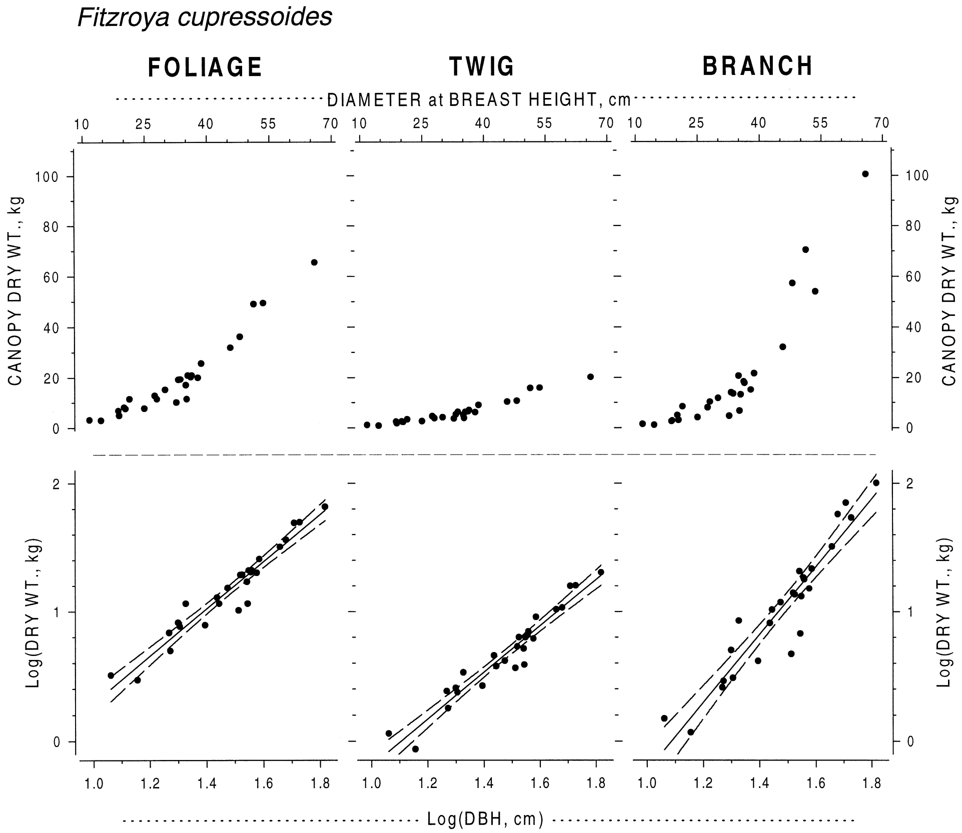

Fig. 6. *P. uviferum*. Data and regressions shown for dry weight of tree components against bole diameter at breast height (dbh). Solid line is regression; dashed line represents 95% c.i. for the estimate.

Generally speaking, damaged trees tend to have lower weights than would be predicted from bole diameter, as foliage or wood are lost due to storms or suppression. Thus, equations derived from undamaged trees are more likely to result in an overestimate of the real quantities in the field. This is supported in the data in that more individual data points are underestimated than overestimated (Figs. 5 and 6).

The use of additional variables to estimate canopy component weights might permit a more precise estimation of the weight. In this study, both canopy depth and bole diameter at the base of the live canopy (DBLC) predicted canopy components as effectively as did dbh (data not shown), but these values were significantly correlated (e.g. canopy depth vs. dbh $R \cong 0.738$, $P < 0.0001$, $n = 26$). Sapwood area has been shown to improve foliar estimates (Bormann, 1990). However, estimation of canopy depth or DBLC from the ground using geometric methods would probably introduce as much error as in the estimate based on the more readily obtained dbh. Coring each tree in a large plot to measure sapwood is labor-intensive, and could open the trees to infection and is consequently not a practical alternative.

3.4. Bole analysis

Typical bole profiles derived from climbers' measurements are shown in Fig. 7 for both species. The parabolic curves fit to these data points had R^2 values between 0.85 and 0.99 ($P < 0.001$), but tended to predict lower heights than actually recorded for

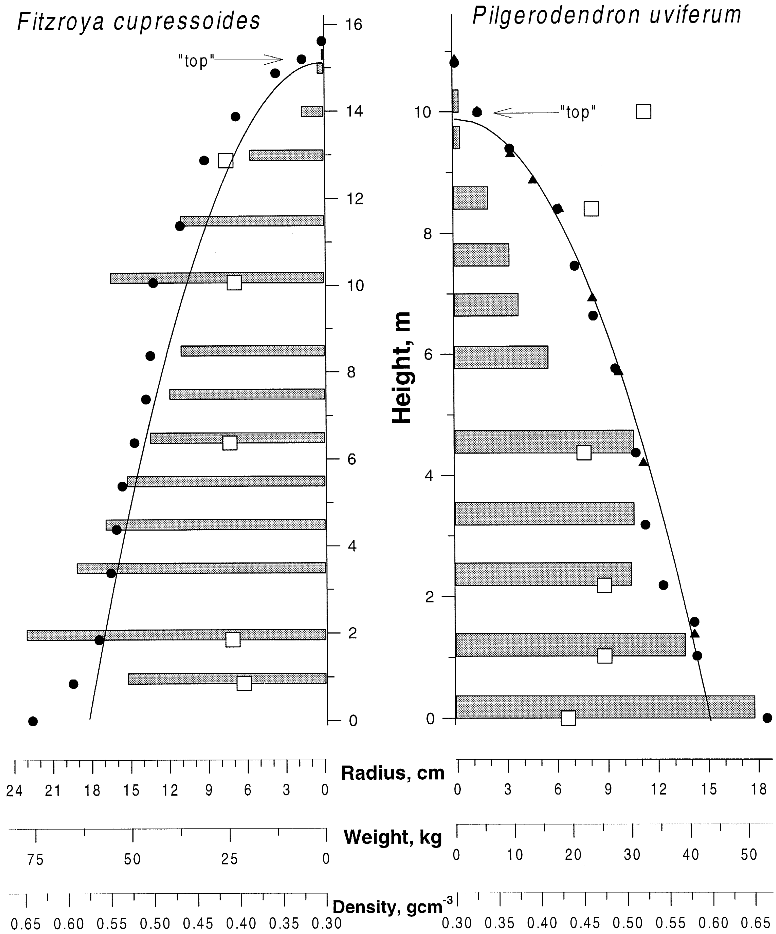

Fig. 7. *F. cupressoides*. Data and regressions shown for dry weight of canopy components against bole dbh. Solid line is regression; dashed line represents 95% c.i. for the estimate.

the trees (Fig. 7). Tree height included the portion of twig and foliage designated ‘top’. The point at which the ‘top’ was defined in each tree was the same as or very close to the bole shape *Y*-intercept calculated for that tree. The ‘top’ was then calculated as an added branch, although the regression generally underestimated the actual foliage/branch weight ratio (data not shown). Tree height values were not used in fitting the parabolic curves, nor were tree basal diameters, as they were obtained only for felled trees. In order to measure tree basal diameter, it would have been necessary to destroy the thick epiphyte mat surrounding the tree’s base to a height of 2 or more meters. In addition, larger trees show a considerable amount of butt flare. Inclusion of this point in the parabolic regression resulted in erroneous overestimates of volume. Although extending the parabola to the ground ignores the volume in the butt flare, the tendency of the parabolic form to overestimate the middle section of the trunk (Bell et al., 1984) compensates in part for this.

Careful examination of the bole shape data indicated that the shape was probably more accurately represented as a bicomponent shape, with a cone for the portion within the living canopy and a neiloid for the bole below the canopy. Although this form is probably more consistent biologically and mechanically, there was no statistically significant difference between bole weights calculated using the combined shape and the simpler paraboloid (data not shown).

Bole volume was calculated from the parabolic curves using the formula $V = 1/2\pi \cdot r^2 h$, where $h = y$-intercept from the parabolic equation and $r =$ radius at x-intercept (ground). This volume was then multiplied by bole wood density to obtain bole weight. Bole sections from felled trees brought back to the lab and dried were used to estimate dry to field weight conversion for the whole bole. The resulting estimated bole fresh weights were then compared to the actual field weighed values (Table 4). The values calculated in this manner agreed with the field weights within 5%. It was assumed that the remaining bole weight estimates were similarly close to the true values.

Errors in the bole weight estimates could occur due to inaccurate assessments of wood density, and due to the presence of bark. To test the former, felled trees were cored prior to felling and a section was cut from the bole just above dbh. Density values for the cores agreed with the larger bole slices within 3%, except in one case (7%). Bole sections and cores taken at different heights from felled or climbed trees indicated that bole density varies throughout the tree (cf. Fig. 7). In particular, the density increases near the top of the tree, where the bole is essentially all sapwood. The upper bole accounts for a very small percentage of the total bole weight (Fig. 7), so the error introduced by using a single density from low in the bole may not be significant. The variation in density due to age and amount of sapwood does suggest that care should be taken to maintain an appropriate ratio of sapwood to heartwood in the core used to test density.

The second source of error in estimating bole weight is the bark. It contributes to the diameter of the tree, but has a different density. In *F. cupres-*

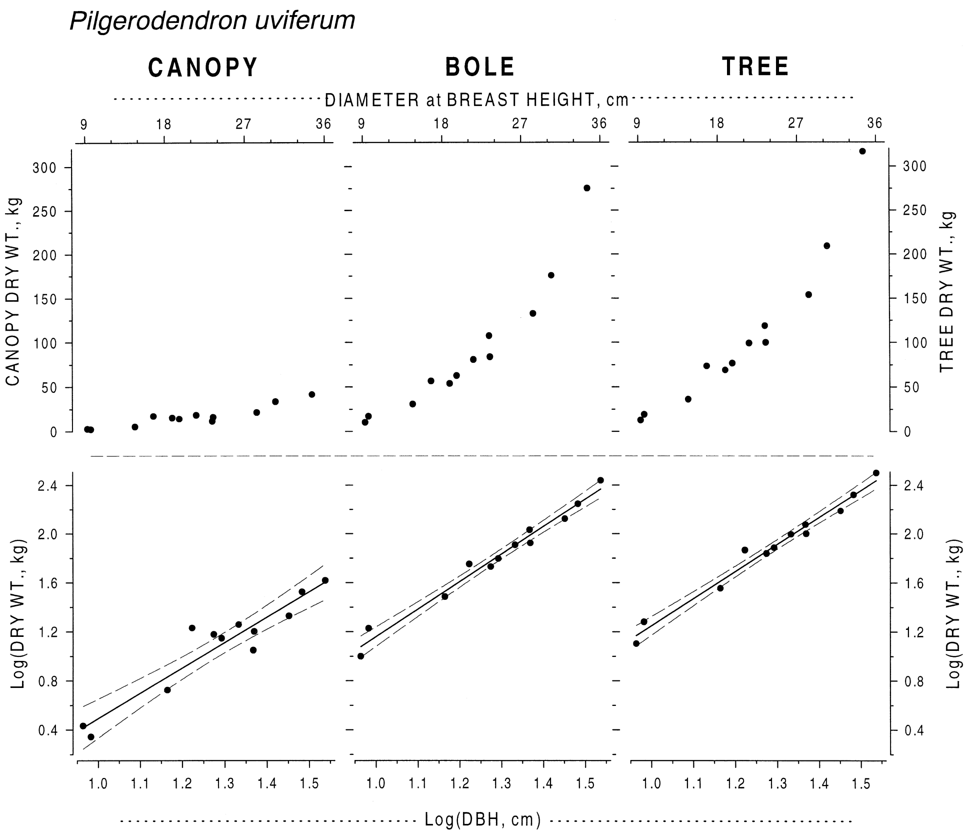

Fig. 8. *F. cupressoides*. Data and regressions shown for dry weight of tree components against bole diameter at breast height (dbh). Solid line is regression; dashed line represents 95% c.i. for the estimate.

soides the thick bark may contribute 10% of the diameter. Although it was possible to fit hyperbolic curves to bark thickness data for felled trees, the number of sample points available did not provide a high degree of precision in the estimate. In order to apply these curves, two data points were required, bark thickness at dbh and tree height. Although all trees in this experiment had height values, few had bark depth measures, as increment cores did not provide useful measures of bark depth. In addition, the curve assumes a consistent volume without voids. Attempts to directly measure volume via displacement produced erratic results due to void volumes within the bark. As a result, it was not possible to get an accurate measure of density. Since tree height and bark depth were not measured for all trees in the CP watershed, we chose to abandon attempts to separate the bole into bark and wood. Consequently, all references to 'bole' in this paper refer to wood plus bark.

The final step in bole analysis was the calculation of the regressions. As with the other derivations, the data and regressions are presented graphically, with *P. uviferum* presented in Fig. 8, and *F. cupressoides* Fig. 9. Equation coefficients and statistical data are summarized in Table 3. The values are closely clustered, resulting in a highly predictable relation between dbh and bole weight ($R^2 > 0.95$, ERE $< \pm 10\%$). This is not surprising, as tree bole architecture tends to be mechanically constrained (Bertram, 1989; Niklas, 1992). In addition, using calculated bole weights in the regression may obscure some of the natural variation. Since dbh is not a driving

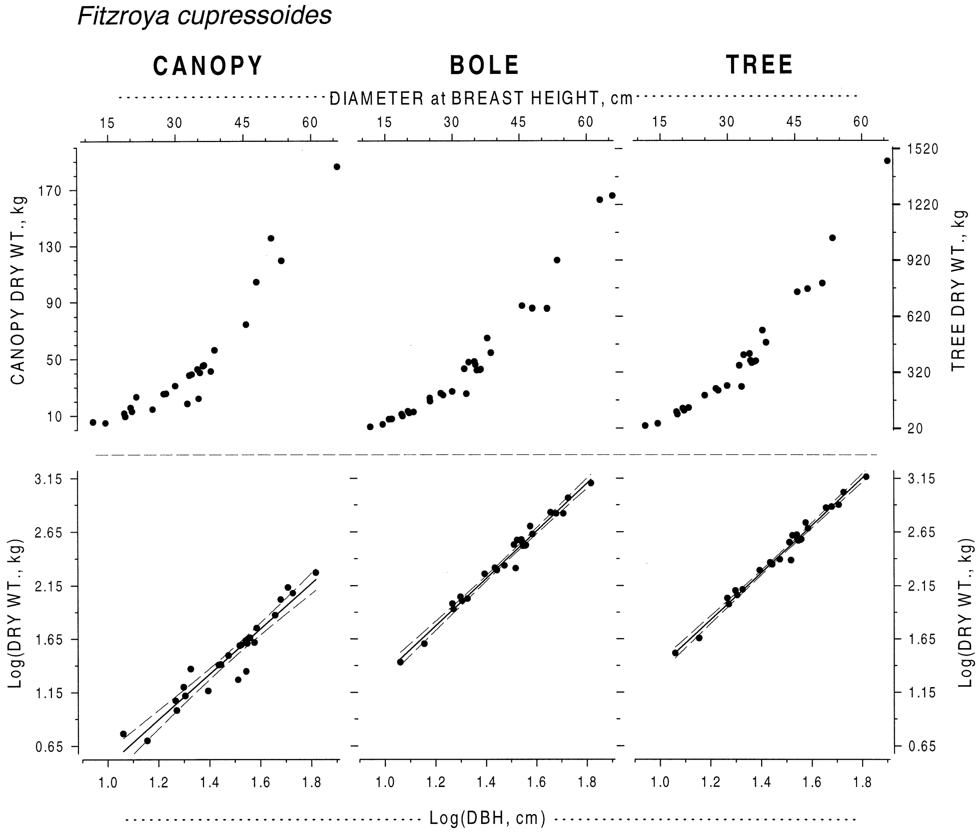

Fig. 9. Bole dimension values shown for a representative individual of each species. Solid circles represent data measured after felling tree (*F. cupressoides* was dead individual). Solid triangles show data measured by tree climbers. Solid line is parabolic regression line fit to these points. White squares represent density at a given height in the tree. Grey bars show field weight of the bole sections cut at measured intervals.

variable in the bole weight calculation, the parameters dbh and weight are not structurally correlated in the formula. Comparing the values predicted from the regression with those for the weighed trees suggests that, in practice, bole weight can vary up to 20% with respect to dbh (Table 4).

Because the bole weight is about 80% of the total tree weight, it is important to predict it as accurately as possible. We evaluated the robustness of the regression formula by jackknifing each value. The jackknifed correlation coefficient varied little, indicating that individual points did not affect regression variability (jackknife, $R=0.989$; 95% c.i., 0.969–0.996; $T=10.64$, $df=11$, $P<0.001$). Three of the jackknifed regressions produced slope coefficients different from the mean by more than 5%. In these cases, the trees removed were either of the two smallest trees measured; the third a tree growing adjacent to a clearing with a fuller canopy. Jackknifed regressions still predicted the missing variate within the 95% prediction interval for the mean regression.

Although height was a likely covariate explaining some of the variation in bole weight, it failed to do so (data not shown). We had initially observed that trees in the transition forest appeared shorter for a given dbh than trees in the alerce forest, suggesting that we might need to develop sets of equations for each forest type, or a set incorporating an elevational term. In the analysis, however, there was no evidence for a difference in the data collected. Total weights and component weights for the trees at both sites were similar for a given diameter. There was no readily apparent difference in the coefficients for the bole equations.

4. Conclusions

In summary, this approach to deriving allometric regressions using indirectly calculated weights appears to be as robust as regressions using actual weights. The largest sources of error lie in natural variability, rather than in the model or technique. This is consistent with the findings of others (Woods et al., 1991). The variance about the estimates are similar for both species. The equations herein are expected to predict the true mean weight for tree components within about 10% (based on ERE). Individual trees and component estimates are less precise, but the intended application for these equations is calculation of biomass for large areas. We propose that this technique is satisfactory for estimating biomass for tree species whose conservation status prohibits harvesting for calibration of allometric regressions.

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