

Use of branch cross-sectional area for predicting pruning dose in young field-grown *Quercus virginiana* ‘Cathedral’ in Florida, US

Jason Grabosky^{a,*}, Edward Gilman^b, Chris Harchick^c

^aDepartment of Ecology Evolution and Natural Resources, Rutgers University; New Brunswick, USA

^bDepartment Environmental Horticulture, University of Florida; Gainesville, USA

^cTechnician, Department Environmental Horticulture, University of Florida; Gainesville, USA

Abstract

Allometric relationships for trunk, first order branches and associated foliage were developed to develop a repeatable pruning dose for wind interception studies on *Quercus virginiana* Mill ‘Cathedral’. Three trees were dissected to develop relationships. It was determined that leaf mass was linearly related to the basal area of the primary branch, consistent with pipe model expectations. A pruning dose for leaf mass removal was defined by tracking basal branch areas and removing entire first order branches. Leaf mass was closely related to leaf surface area, however leaf mass varied with compass orientation while leaf area remained unchanged. The use of wood cross-section area conservation rules for branching in Lindenmayer (L-system) computer modeling is shown to be inconsistent with the data set, as is often observed in the field. The area conservation assumption is made to force taper into computer models, and departures are accepted by assuming heartwood formation forces imbalance into the model. The data set was developed from 3 year old or younger wood. The species is known to retain viable vessel elements in sapwood for at least 3 years in the areas surrounding the testing site. Since it is doubtful that there was heartwood or non-functional sapwood in the test trees, use of the area balance assumption for modeling by asserting heartwood influence is questionable.

© 2007 Elsevier GmbH. All rights reserved.

Keywords: Branch size; Leaf area; Pipe model; Taper

Introduction

Quercus virginiana Mill. makes up a very significant portion of many Floridian urban tree canopies and is subject to winds from tropical storms. Pruning is common on live oak in municipal landscapes for utility clearances in energy corridors, visual clearance in transportation corridors and for aesthetic reasons in private landscapes. Guidelines for maximum pruning activity are based on visual estimation of the relative

percentage of canopy leaf biomass removed. Initial studies on 8 cm trunk diameter (at 15.24 cm elevation) *Q. virginiana* ‘Highrise’ have observed the change in tree loading response to imposed wind fields in a static analysis of trunk deflection (Jones, 2006; Gilman et al., in press). The initial studies manipulated pruning dose (amount of biomass removed) and pruning method (location of biomass removed). The doses and methods were varied to test current ANSI A-300 Part 1-2001 standards for the tree care industry (ANSI, 2001) in relation to canopy wind interception and resultant trunk loading (Gilman et al., in press). Variability in visual estimation of pruning dose as verified by

*Corresponding author. Tel.: 11 732 932 0050; fax: 11 732 932 8746.
E-mail address: grabosky@aesop.rutgers.edu (J. Grabosky).

foliar mass measures (Jones, 2006) was a limitation in developing straight-forward dose–wind analyses. Consistency of foliage removal dose has been problematic in similar studies (Smiley and Kane, 2006) with *Acer rubrum* L.

A wind interception study was designed to use larger, established *Q. virginiana* ‘Cathedral’ trees (3.5 years post-transplant) with a larger mobile wind field generation system that had more efficient data acquisition and wind field definition control. Allometric relationships applied pipe model theory (Shinozaki et al., 1964a, b) to primary branches to define a consistent pruning dose protocol. The relationship linked hydraulic demand of leaves expressed as foliage mass to hydraulic capacity expressed as branch basal area to provide an estimator, conceptually similar to a Huber value (cross-section area of stem or sapwood per unit area of leaves) as discussed by Tyree and Zimmermann (2002). The primary purpose of this study was to develop a repeatable pruning dose using allometric relationships of branch size to leaf biomass. Secondarily, development of stem taper and branch segmentation data presented the opportunity to consider several aspects of tree modeling in the young live oak canopy.

In describing tree architecture with consideration of hydraulic and mechanical constraints several tree canopy architecture computer-modeling methods (such as MORPHO, LIGNUM and SIMFORG) employ a major simplifying assumption in the conservation of sapwood area. This is done to quantitatively deal with tree stem tapering effects while avoiding complications of heartwood development and influence within a mathematic modeling rule (Perttunen et al., 1996, 2001, Perttunen and Sievanen, 2005; Berezovskaya et al., 1997; Berninger and Nikinmaa, 1997). In short, the sapwood area of the tree below the branch connection is assumed equal to the sum of the sapwood area above the branch and the sapwood area at the branch base. Departures from this balance might be considered a consequence of disuse of xylem vessel elements (or tracheids) in the form of heartwood, as described in supplementary explanations and treatments of the pipe model (Shinozaki et al., 1964a; Chiba, 1998). Mäkelä (2002) explicitly states that the sapwood conservation assumption is inconsistent with field observation. The TREE and WHORL models alternatively assume a transition role in wood from sapwood to heartwood and varied ratios of foliage to sapwood to reconcile taper (Mäkelä, 2002).

Flow capacity in confined tubes is more reasonably modeled by the Hagen–Pouselle law as a function of radius raised to the fourth power, and is often considered when discussing hydraulic conductivity (Zimmermann, 1978; Tyree and Ewers, 1991; Tyree and Zimmermann, 2002). There are vertical limitations to the ascent of sap through a raw pipe flow model

under the cohesion–tension theory of sap ascent in trees. Difficulties in explaining hydraulic supply in trees have yielded new explanations; for example the WBE model of xylem conduit taper with tree height which modulates hydraulic resistance within the tree xylem to enable hydraulic supply ability (West et al., 1999; Anfodillo et al., 2006).

While the trees in consideration for developing pruning dose estimation methods are young and significantly smaller than those considered by many of the aforementioned models, they provide the ability to check some assumptions of balance and taper while providing data on a deciduous tree species. One significant limitation of many of the models is the lack of data on angiosperms. This investigation developed the protocol for estimating pruning dose in a quantitative, repeatable manner using branch cross-sectional area in consideration of the pipe model, and then used the data to investigate the assumptions of canopy architecture models for use in future studies of open grown deciduous trees under 25 years of age.

Methods

Eighty *Q. virginiana* ‘Cathedral’ 60 cm height liners were planted in August 2001 in a 2.4 by 3.6 m grid as part of a low branch management pruning study for nursery production (Gilman et al., 2006). The trees were established in a well-drained Millhopper sand (loamy, siliceous, hyperthermic, Grossarenic *Paleudults*) soil with supplemental irrigation at the Environmental Landscape Horticulture Experimental Laboratory at the University of Florida in Gainesville (29.4°N, USDA hardiness zone 8a). The block was thinned to 40 trees in November 2004 removing every other tree for a spacing of 4.8 m within row and 3.6 m between rows in a staggered block pattern. In 2006, the block was chosen for a planned wind interception study, since the species, size, and consistency of field grown replicates was extremely desirable (Table 1). Twenty trees were condemned to provide clearance for the moving walls and the needed wind-field clearance between testing

Table 1. Description of the study block of *Quercus virginiana* ‘Cathedral’ trees under consideration in proposed pruning-wind interception studies

Tree count = 39	Trunk diameter (cm) @ 15.25 cm elevation	Tree total height (cm)	Canopy spread (cm)
Mean	11.5	583.6	347.5
Max	13.5	676.7	405.4
Min	9.1	487.8	269.8
S.E.	0.178	7.5	5.2

replicates for the wind study equipment. Three of the 20 trees were randomly chosen to develop allometric relationships to guide pruning dose protocol for the remaining experimental trees.

Each tree was dissected standing in the field. The canopy was segmented into three sections based on branch origination on the trunk (Table 2). Canopy section was assigned in one-third increments defined by elevation of the first branch to the top of the central growth axis (hence-forth lower, middle, and upper canopy). Branches were removed at the trunk and placed onto a cloth marked with a 4 in (10.2 cm) grid. Branch length was measured along its main growth axis to the nearest inch (2.54 cm) and converted to centimeters. Branch diameter was recorded at the base of the removed branch with calipers at the widest dimension and in the perpendicular dimension for an average diameter to the nearest millimeter. Branch area in foliage was measured by the number of grids intersected by the leaves on the grid cloth.

Five branches in each of the three canopy sections were randomly selected from each of the three trees ($n_{T\text{subsample}} = 0\ 45$). Branches were immediately defoliated and wet mass of leaves determined. Bulk foliage fresh weight was regressed on branch basal area for development of a repeatable pruning dose protocol. The foliage was parsed into percentiles from tip of branch inward to reflect the percentage of influence by grid intersect to remove 15, 25, 33, and 40 percent of the foliage. The fresh weight and branch length removed for the foliage percentage reduction was noted. At each removal, the diameter of the branch present was noted to account for the partial percentile of canopy on the branch.

All remaining branches in the tree section were then removed and measured for branch basal diameter and length. All branches were catalogued (325 and the 45 foliage massing sub sample) for elevation and canopy section in the tree. Trunk diameter was measured at each 15.24 cm elevation and a stem taper function of trunk diameter with elevation was developed. Total foliage mass and grid count was noted for developing whole canopy pruning dose. In the upper-most section of the tree, the main axis of growth was defined at a chosen point as an equivalent to a lateral branch. The chosen point was identified when the trunk diameter approached the mean diameter of the subtending lateral branches in the upper section of the tree.

Once the data was processed, a protocol based on branch diameter was developed to impose a pruning dose that regulated the amount of foliage removed as a percentage of the total canopy, which followed the current industry methods of determining field dose (Gilman, 2002; Gilman and Lilly, 2002; Harris et al., 2004; ANSI, 2001). Three additional trees were subject to the targeted pruning types with a constant foliage removal dose. At each cut, branch diameter was noted in a field spreadsheet to track the number and foliage of the branches removed relative to the target-pruning dose.

Relationships were developed to compare data with the pipe model theory. A leaf surface area to leaf fresh weight relationship was established on a separate block of ‘Cathedral’ live oak of similar size growing within 100 m of the trees used for this study. Leaves were collected from the exterior 60 cm of canopy in the middle section of the canopy. Five trees were sampled on four cardinal compass directions with batch samples

Table 2. Description of three dissected *Quercus virginiana* ‘Cathedral’ trees to define lower, middle, and upper canopy elevations used in developing allometric relationships

Tree	Trunk diameter (cm)	Tree total height (cm)	Elevation of first branch from ground (cm)	Live canopy elevation range (cm)	Lower canopy elevation (cm)	Middle canopy elevation (cm)	Upper canopy elevation (cm)
19	11.6	585	143	442	143-291	291-438	438-585
26	12.7	582	125	457	125-277	277-430	430-582
38	11.3	591	134	457	134-287	287-439	439-591

Table 3. The relationship of trunk diameter and elevation to establish taper models on transplants of *Quercus virginiana* ‘Cathedral’

Tree	Regression model	Elevation range	r ²
19	Stem diameter (cm) = 12.7238–0.0224 stem elevation (cm)	15–549 cm	0.968
26	Stem diameter (cm) = 13.2574–0.0227 stem elevation (cm)	15–579 cm	0.967
38	Stem diameter (cm) = 11.7844–0.0204 stem elevation (cm)	15–564 cm	0.983
Combined	Stem diameter (cm) = 12.5821–0.0218 stem elevation (cm)	15–579 cm	0.962

of 10 leaves per side. Individual leaf area was measured with a digital planimeter (Lasico #1282W-24, Los Angeles, CA) to the nearest 0.001 in², totaled, converted to cm² total area, and compared with fresh weight of the total batch sample (due to low total mass on per-leaf basis). Leaf mass to area ratios were checked for orientation influence (side of tree) and tree individual influence. The mean leaf mass to area ratio was then used in developing the pipe model discussion, linking branch size–foliage mass relationship to foliage area.

Simple linear regression models for foliage mass as a function of branch basal area were developed to link with the leaf mass/surface area data. Data analyses were processed in Minitab 14. No heartwood was observed in the fourth year dissected wood. Studies on oak hydraulics in Central Florida including *Q. virginiana* suggest third year branch wood has hydraulic conductance capacity, although contribution is low as a consequence of additive sapwood areas in increasing trunk diameters (Cavender-Bares and Holbrook, 2001). As fourth year transplants from liner stage, the trunk and branches in the zone of interest (all occurring above initial transplanting dimension) consisted almost exclusively of 3-year-old wood.

The relationship between the trunk dimension below the branch with the combined dimension of the trunk above the branch and the branch was developed. Due to the high density of small branches on the trunk of the tree, few internode zones were available to directly test individual branch connections. The first attempt for a mass balance yielded the following hypotheses: The data equals zero (H_0 , model successful) or does not equal zero (H_a , model failure).

$$0 = r_b^x - (r_a^x + \sum r_l^x),$$

where r is the radius, b the trunk below branch section occurrence, a the trunk above branch section occurrence, l the lateral branches in trunk section, x the exponent in model (either 2 or 4)

The multi-branch zonal data were plotted against occurrence in the canopy by elevation. Data models on radius squared (sapwood area) and to the fourth power (flow capacity) were developed.

In the second attempt for a mass balance model, the trunk taper equations were used. The method was chosen to take full advantage of each of the 370 branches catalogued in the dissection process. The taper models were built from 6 in (15.25 cm) increments independent of node/internode position and deemed robust, and thus used to generate data to test the model. The trunk dimension as a radius was developed from the individual tree regression models for trunk taper (Table 3). Branch elevation was defined as the center point of branch attachment. Trunk dimensions below and above the branch were calculated at elevations equivalent to one branch diameter above and below each specific branch.

$$0 = r_b^x - (r_a^x + r_l^x),$$

where r is the radius, b the trunk below branch from taper model, defined by branch elevation and diameter, a the trunk above branch from taper model, defined by

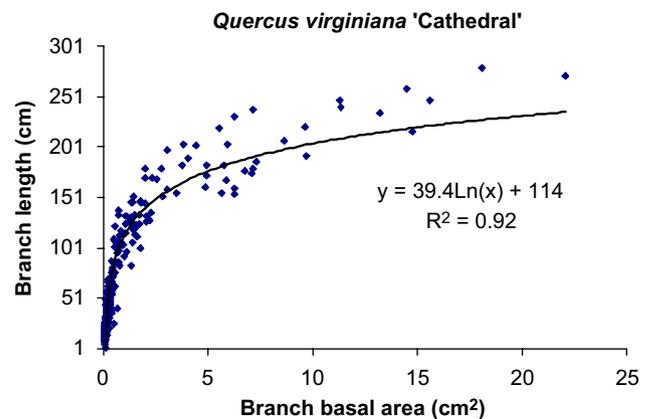


Fig. 1. The relationship of branch basal area and branch length in *Quercus virginiana* ‘Cathedral’.

Table 4. Branch counts, locations and size distribution on 3 *Quercus virginiana* ‘Cathedral’ transplants. Sizes were defined by caliper at point of attachment to main growth axis

Tree number	Section designation	Number of branches	Branch class: <5 mm	Branch class:5-10 mm	Branch class: >10 mm
19	lower	42	9	11	22
	middle	46	16	14	16
	upper	41	29	10	2
26	lower	42	4	15	23
	middle	33	16	7	10
	upper	47	31	12	4
38	lower	30	7	4	19
	middle	44	15	11	18
	upper	44	25	16	3

branch elevation and diameter, l the lateral branch, x is the exponent in model (either 2 or 4)

Since data in the model reflect taper equation radii from trunk elevation influenced by branch size, the data are auto-correlated. The data is used only to test the model hypotheses, as the curvature of the model data in the scatter plot reflect the mathematics in the dimensioning relationships used in data development.

Results

Stem taper was determined as change in diameter with increasing trunk height. The trees were consistent in

trunk taper within and between tree individuals; no differences were found between trees. For the purposes in wind interception analysis proposed, the data provided a consistent slenderness ratio (length to basal radius) to be used in mechanical analysis along the trunk of the tree, as it was envisioned to experience significant wind loading and potential trunk failure.

The number of branches in each section was variable (Table 4). As expected in a young live oak larger diameter branches occurred lower in the canopy, while smaller diameter branches occurred throughout the canopy.

Branch basal area was predictive of branch length (Fig. 1). There was no relationship between tree replicate and branch slenderness ratios (branch length: basal branch radius) or any relationship between branch slenderness ratio and point of branch origin in canopy section (low, middle or top third of canopy). After ranking branches on 4 mm radius size increments, there were no differences in slenderness ratio. Slenderness ratio data were observed to follow a $2/3$ power relationship in branches with less than 2 cm^2 of branch basal area, which is often employed in scaling analysis, but did not reflect the relationship in larger sized branches. Since the larger branches were kept in the data set, a better-fit relationship between branch basal area and branch length was described by a natural log function (Fig. 1).

Data from leaf-grid intersections over the length of the branch to suggest branch level dosing of foliage removal was found to be impractical, and the data provided no useful relationships. Leaf fresh weight was regressed against branch basal area, canopy location, and tree individual. Tree individual was not significant

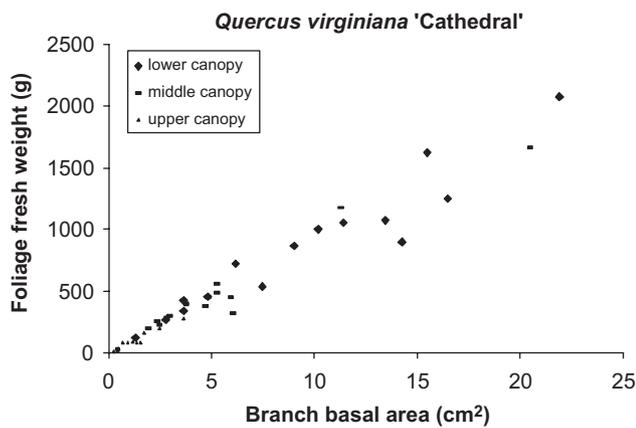


Fig. 2. Foliage fresh weight of branches from 3 *Quercus virginiana* ‘Cathedral’ as related to their respective branch basal areas. Data was presented as lower, middle and upper canopy positions of branch origination defined as one-third increments of the live canopy height.

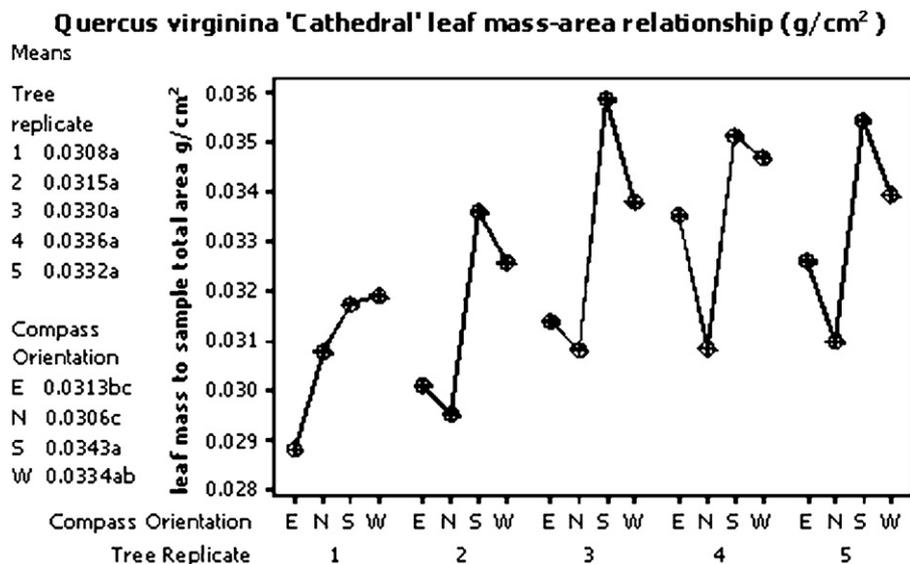


Fig. 3. Leaf mass to leaf area relationships on *Quercus virginiana* ‘Cathedral’ to link branch basal area to leaf area through the intermediate step of leaf mass collected in the field. Letter subscripts following means derived by Tukey means separation ($\alpha = 0.05$) used in general linear model analysis.

($p = 0.599$) and canopy location was not significant ($p = 0.223$) as parameters so data were treated as a simple linear model (Fig. 2):

$$\begin{aligned} \text{leaf fresh weight} &= 15 + 0.867 \text{ branch basal area;} \\ r^2 &= 0.954; \\ \text{branch basal area range: } &23.7\text{--}2192.6 \text{ mm}^2. \end{aligned}$$

To link leaf surface to branch basal area, a multiplier of leaf fresh weight to area (mean 0.0324 S.E. 0.0020 g cm^{-2}) was developed from the 20 leaf batch samples. The 20 leaf g cm^{-2} data were determined to be normally distributed from an Anderson–Darling normality test ($A^2 = 0.26, p = 0.667$). The data analyzed as a general liner model using Tukey mean separation ($\alpha = 0.05$) revealed a significant influence in canopy location by compass orientation (Fig. 3). Two-way AOV of the 200 leaf individual areas showed no influence in

tree individual ($p = 0.12$) or canopy section ($p = 0.73$) with no significant interaction ($p = 0.79$). It was then assumed that changes in leaf g cm^{-2} represented changes in leaf thickness or structural density corresponding to solar exposure in canopy location. Leaves with southern exposures were heavier per unit area than eastern and western exposures with northern leaves being lighter per unit area. Pruning dose estimation is a visual process relying on area to estimate biomass removal. The data was stable enough to suggest that leaf fresh weight is an effective indicator of leaf surface for evaluating the dissection data. The pruning protocol for the anticipated study was acknowledged as having the variability in biomass dosage by compass orientation of removed branches, but since the pruning was to occur uniformly around the tree, this error was deemed acceptable for implementation logistics. When pruning, the tree care professional more likely judges foliage removal by visual

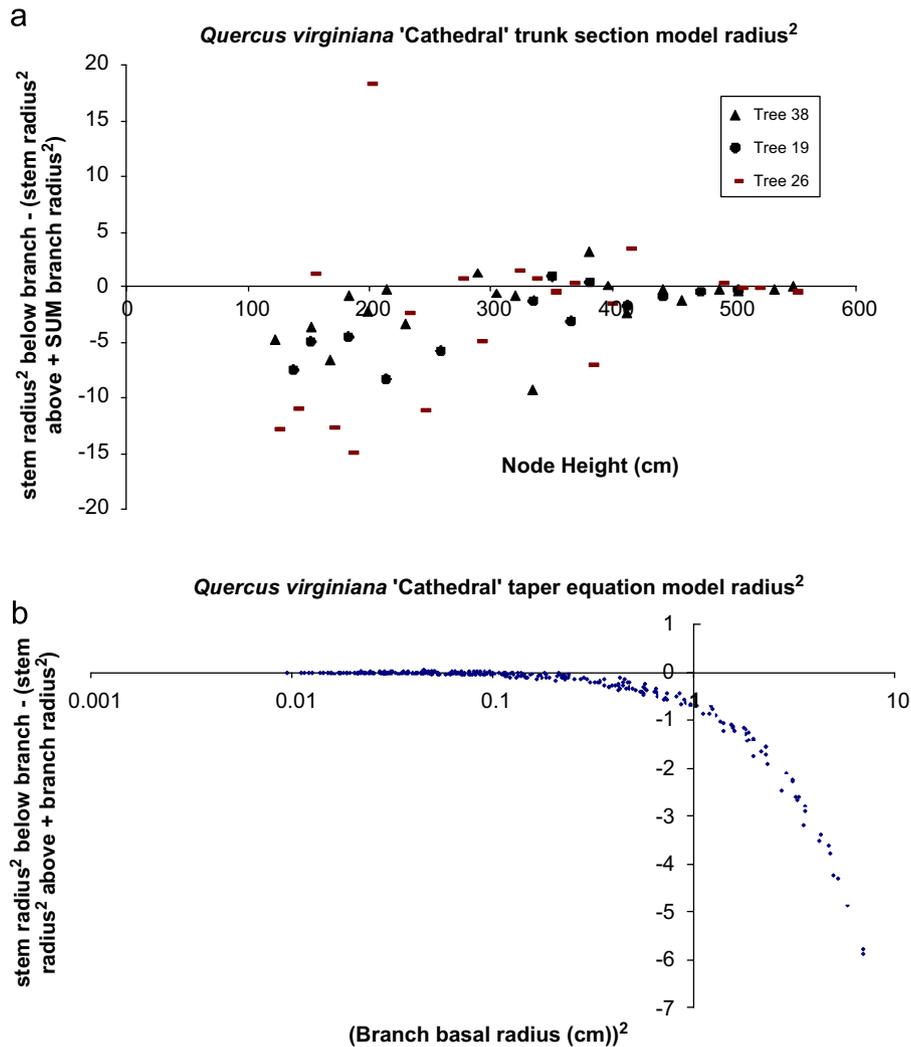


Fig. 4. (a, b). Graphic test of balance equations for data based on radius squared in the model. Fig. 4a shows real data in branch summations within sections of tree (termed a node). Fig. 4b shows all branches in data set in model developed in the taper equation thus are used only to demonstrate the direction of the model failure.

area estimation rather than biomass removal estimation; thus changes in leaf density and canopy location certainly entered into the dosing estimator of the previous studies (Gilman et al., in press b).

The branch data parsed to estimate foliage removal over individual branch length did not yield consistent relationships useful for developing a pruning treatment protocol. The grid system was too coarse for establishing foliage removal percentages based on grid totals when translated into weight or length criteria. Accordingly, the parsed data was discarded and the pruning protocol adopted whole-branch removal to administer dosage in removed foliage fresh weight. Using the branch basal area/foliage fresh weight model, a thirty three percent pruning dose was developed from the whole-tree branch basal diameter data to estimate total foliage fresh weight over the three sample trees and was imposed on the experimental treatment block. This was done by removing individual branches and using their basal area to predict foliage mass contribution to meet the target for foliage weight removal until the dose

requirement had been met. Total dose across the research block varied within 3 percent total foliage estimated mass, as pruning was limited to removal of whole branches.

At the within-branch level on these young oaks, use of the pipe model was useful to estimate foliage removed pruning dose. This represented a small range in size on young primary branches, suggesting the complications found in older trees is at least in some manner related to a critical size dimension, possibly the development of reaction woods or heart woods as a function of age. In general, for the pipe model to meet assumptions, sapwood area is related to leaf water demands, thus the supply capacity must be greater from below as it is divided into the multiple branch axes (additive area assumption).

In Figs. 4a and b, the use of squared radii shows greater total sapwood area of the branch and distal trunk section compared to the trunk area from which they originate. Data was then plotted as the radii to the fourth power to scale the systems toward hydraulic

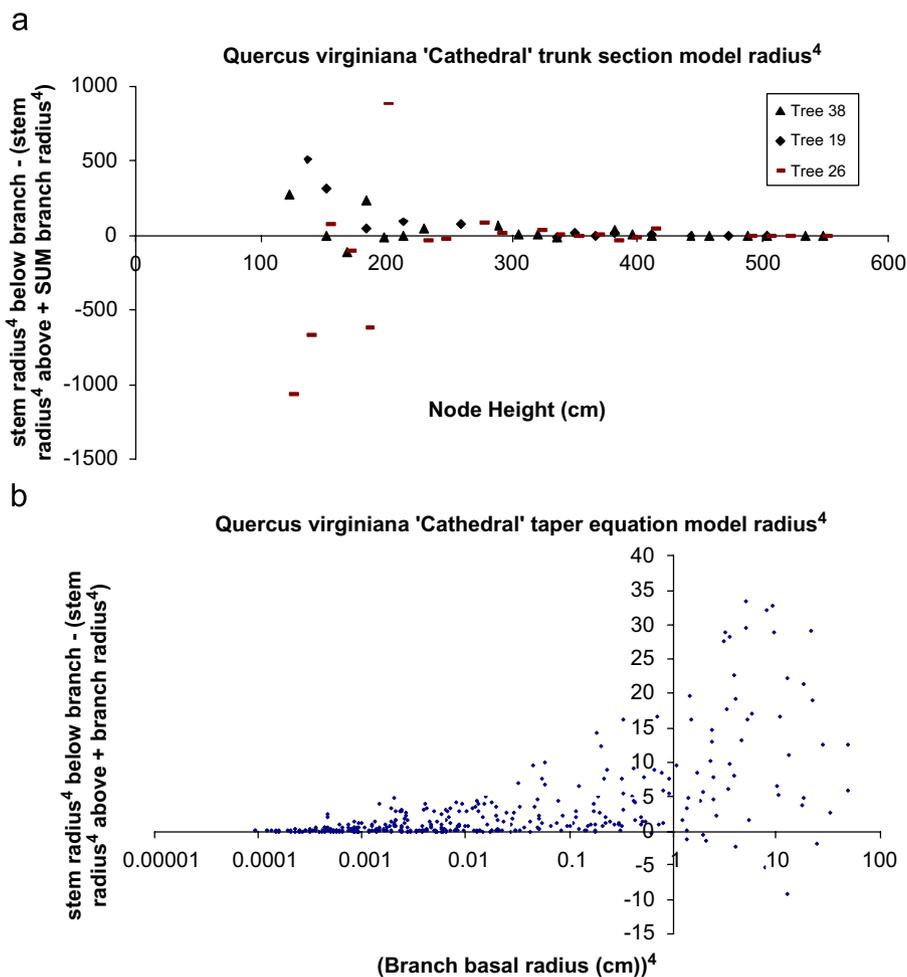


Fig. 5. (a, b). Graphic test of balance equations for data based on radius to the fourth power in the model. Fig. 5a shows real data in branch summations within sections of tree (termed a node). Fig. 5b shows all branches in data set in model developed in the taper equation thus are used only to demonstrate the direction of the model failure.

confined flow capacity through pipes (Figs. 5a and b). In the flow capacity case, the data would support greater capacity at the base as it is allocated through xylem segmentation points in branch connection zones (Zimmermann, 1978; Tyree and Ewers, 1991; Eisner, 2001; Eisner et al., 2002). In both radii modeling cases, the intensity of the differential value increased with increasing branch size. In the case of the radius squared data (area), the model failure (departure from zero) is suggested to be at least partially a function of the vessel element to fiber ratio in the branch connection zone under self-loading, increasing the cross sectional area as a result. For the radius to the fourth (flow capacity) data, there may be an influence in the nature of segmentation through the branch protection zone.

Discussion

From a practical standpoint, it is clear that in smaller dimensioned branches in live oak that branch basal area can act as a surrogate for estimating foliage area as a pruning dose when imposing treatments in the field. It is also very evident that treating branches as smaller iterative units of trees is not advisable even at a young age. From a modeling standpoint, it is clear that models asserting an area balance to deal with taper are flawed not only in field observation, but in the proposal in simplification to deal with heartwood development, since there was not heartwood in these young oaks. Indeed, live oak in the study region have been observed to have functioning sapwood for 3 years without significant decreases in vessel element functionality (Cavender-Bares and Holbrook, 2001), thus calling into some question the utility of phasing sapwood-heartwood ratios in other models since the model failure is independent of heartwood formation. Further studies are focusing on reconciling observations of branch hydraulic segmentation, the mechanics of branch connection zones, and within branch shifts in slenderness ratios on larger branches with the WBE model observations of vessel element geometry.

References

- American National Standards Institute, (ANSI), 2001. ANSI A300 (Part 1)—2001 American National Standard for tree care operations standard Practices (Pruning). ANSI, New York, NY.
- Anfodillo, T., Carraro, V., Carrer, M., Fior, C., Rossi, S., 2006. Convergent tapering of xylem conduits in different woody species. *New Phytologist* 169, 279–290.
- Berezovskaya, F.S., Karev, G.P., Kisliuk, O.S., Khlebopros, R.G., Tsel'niker, Y.L., 1997. A fractal approach to computer-analytical modeling of tree crowns. *Trees-Structure and Function* 11, 323–327.
- Berninger, F., Nikinmaa, E., 1997. Implications of varying pipe model relationships on Scots pine growth in different climates. *Functional Ecology* 11, 146–157.
- Cavender-Bares, J., Holbrook, N.M., 2001. Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. *Plant Cell and Environment* 24, 1243–1256.
- Chiba, Y., 1998. Architectural analysis of relationship between biomass and basal area based on pipe model theory. *Ecological Modelling* 108, 219–225.
- Eisner, N.J., 2001. The effect of branch junction morphology on tree wound compartmentalization and hydraulic segmentation. Masters Thesis, University of Florida, p. 74.
- Eisner, N.J., Gilman, E.F., Grabosky, J.C., Beeson, R.C., 2002. Branch junction characteristics affect hydraulic segmentation in red maple. *Journal of Arboriculture* 28 (6), 245–251.
- Gilman, E.F., 2002. *An Illustrated Guide To Pruning*, second ed. Delmar Publishing, Albany, NY, p. 330.
- Gilman, E.F., Anderson, P.J., Harchick, C., 2006. Pruning lower branches of live oak (*Quercus virginiana* Mill.) cultivars and seedlings during nursery production balancing growth and efficiency. *Journal of Environmental Horticulture* 24 (4), 201–206.
- Gilman, E. F., Grabosky, J., Jones, S., Harchick, C., Effects of pruning dose and type on trunk movement in tropical storm winds. *Arboriculture and Urban Forestry*, in press.
- Gilman, E.F., Lilly, S., 2002. *Best Management Practices: Tree Pruning*. Int. Soc. Arb., Champaign, IL, p. 35.
- Harris, R.W., Clark, J.R., Matheny, N.P., 2004. *Arboriculture: Integrated Management of Landscape Trees, Shrubs, and Vines*, fourth ed. Prentice-Hall, Upper Saddle River, NJ, p. 579.
- Jones, S., 2006. Effect of pruning type pruning dose and wind speed on tree response. Master Thesis, University of Florida, Gainesville FL.
- Mäkelä, A., 2002. Derivation of stem taper from the pipe theory in a carbon balance framework. *Tree Physiology* 22, 891–905.
- Perttunen, J., Sievanen, R., Nikinmaa, E., Salminen, H., Saarenmaa, H., Väkeva, J., 1996. LIGNUM: a tree model based on simple structural units. *Annals of Botany* 77, 87–98.
- Perttunen, J., Nikinmaa, E., Lechowicz, M.J., Sievänen, R., Messier, C., 2001. Application of the functional-structural tree model LIGNUM to sugar maple saplings (*Acer saccharum* Marsh) growing in forest gaps. *Annals of Botany* 88, 471–481.
- Perttunen, J., Sievanen, R., 2005. Incorporating Lindenmayer systems for architectural development in a functional-structural tree model. *Ecological Modeling* 181, 479–491.
- Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964a. A quantitative analysis of plant form: the pipe model theory I. Basic analysis. *Japanese Journal of Ecology* 14 (3), 97–105.
- Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964b. A quantitative analysis of plant form: the pipe model theory II. Further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology* 14 (3), 133–139.
- Smiley, E.T., Kane, B., 2006. The effects of pruning type on wind loading of *Acer rubrum*. *Arboriculture and Urban Forestry* 32 (1), 33–40.

- Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. *New Phytologist* 119, 345–360.
- Tyree, M.T., Zimmermann, M.H., 2002. *Xylem Structure and the Ascent of Sap*, second ed. Springer, New York, NY.
- West, G.B., Brown, J.H., Enquist, B.J., 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400, 664–667.
- Zimmermann, M.H., 1978. Hydraulic architecture of some diffuse porous trees. *Canadian Journal of Botany* 56, 2286–2295.