

Allometric patterns in *Acer platanoides* (Aceraceae) branches

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Abstract *Acer platanoides* L. individuals were dissected to determine if branch allometry changed as branches increased in length. Branches were found to transition from a log–log curvilinear relationship to a linear relationship when above 3,000 mm in length. The log–log linear relationship was best modeled with the elastic similarity model. The total number of subordinate lateral branches was found to increase rapidly after the primary branch length surpassed 3,000 mm, suggesting that branches are transitioning to a structural role as size increases. The shift in allometry appears to correspond to a shift from increasing slenderness ratio (length/radius) with increasing branch length to decreasing ratio, and is likely due to a transition from flexible sun branches to stiffer structural branches.

Keywords Allometry · Branches · Elastic similarity · Slenderness · Length · Radius

Introduction

Plant biomechanics integrates principles of plant biology and engineering in order to better understand how organisms such as trees develop and withstand loading events over time. One of the important functions of secondary growth in trees is to provide the mechanical support for the trunk or branches against the constant force of gravity and

periodic additional loading events such as wind or ice storms. Most of the work in plant biomechanics appears to be concentrated on trees in the natural setting, where mechanical failure might lead to plant death with minor risk to other plants or objects in the surrounding environment. In the case of open-grown amenity trees, understanding how trees survive, or fail, during such loading events is important as the risk of serious personal or property damage increases in the urban setting.

Sullivan (1896) suggested building designers could turn to nature to learn how form follows function. He noted that if function holds steady, so should overall form. Researchers have utilized allometric relationships to describe and relate tree form and function, and a log–log relationship between length (L), or height, and radius (R) is often used in these models. McMahon (1975) forwarded three similarity models that describe growth patterns in trees as power law functions ($L \propto aR^b$). The geometric similarity model uses a scalar of $b = 1.0$, whereas the elastic similarity model uses $b = 0.67$, and the static stress similarity model $b = 0.5$. Previous workers have found different outcomes for allometric patterns in different forest species and it remains unclear which model is most applicable for trees in the natural or urban setting.

A large body of literature suggests that the elastic similarity model is best suited when scaling tree height relative to trunk radius (McMahon 1973; McMahon 1975; King 1986, 1996; Rich et al. 1986; Niklas 1994b, 1995, 2007; O'Brien et al. 1995; Niklas and Spatz 2004; Osunkoya et al. 2007). Dean and Long (1986) found that the static stress similarity model worked for both mature (>13 m) and sapling (<2.2 m) *Pinus contorta* Doug. Ex. Loud. trees, while the mature trees also fit the elastic similarity model apparently due to large variance about the slope coefficient. The geometric similarity model was found to fit

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Cecropia spp. trees (Sposito and Santos 2001), understory rainforest trees (Osunkoya et al. 2007) and gymnosperms (Niklas 1994a). Finally, there is a suggestion that allometry might transition from the elastic to the stress similarity model at very large sizes suggesting that function changes with size, yet the authors do not list a specific size (Niklas 1997, 2007; Niklas and Spatz 2000).

The allometry of branches has been found to be plastic, with smaller branches fitting a curvilinear pattern in *Quercus alba* L. and *Acer saccharinum* L., until they reach approximately 3,000 mm where they are best modeled with elastic similarity model (McMahon and Kronauer 1976; Bertram 1989). Suzuki and Hiura (2000) report that the elastic similarity model fits first order branches (arising from the central trunk), but not current-year shoots of broad-leaved trees growing forests. It has been suggested that branches move from a curvilinear log–log relationship to the elastic similarity relationship as the function of branches transition from smaller, more flexible branches, to stiffer scaffold branches that provide the structural support to the smaller lateral branches (Bertram 1989). In order to maintain or increase photosynthetic capacity over time, a shift in form and function would likely coincide with an increase in the number of lateral branches.

If branches shift from a curvilinear relationship to the elastic similarity relationship where the scalar is less than 1, slenderness ratio (branch length/branch basal radius) will move from a positive to a negative relationship with branch size. Bertram (1989) plotted slenderness against branch radius and showed that slenderness increased in small peripheral branches (radius ≤ 10 mm), while decreasing in non-peripheral branches (radius ≥ 10 mm), but did not indicate if a similar trend was seen between slenderness and branch length. Whether branch radius or length provides the best explanation of the apparent shift in slenderness remains untested.

This research was designed to determine whether branch allometric patterning shifts with size in amenity trees. We hypothesize that form will change from a curvilinear nature to linear, fitting the elastic similarity model. Investigation will explore which variables best explain any allometric shift in branch form. *Acer platanoides* L. (Aceraceae) (Norway maple) was chosen as a test species as it is common component in urban forests throughout the United States and Europe (Sæbø et al. 2002; Nowak and Rowntree 1990; Manion 1981; Valentine et al. 1978) and has a decurrent growth form that is frequently found in open-grown trees.

Methods

Sampling was done at Rutgers University Horticultural Farm III, located in East Brunswick, Middlesex County,

New Jersey, USA. Four *A. platanoides* trees growing on the perimeter of a mixed species plantation were randomly selected. A total of four trees were sampled during summers of 2005 and 2006. All sampling began after terminal bud set.

This study was designed to investigate the allometry of open-grown urban canopies. Therefore, only branches growing on the exterior half of the trees were sampled encompassing the complete vertical height of the trees. Branches were labeled as first order (arising from the central trunk), second order, or third order. A branch was subordinated to a lower order when the aspect ratio (branch basal radius/parent stem radius above the branch) was less than 0.8, following protocol set by Eisner et al. (2002). A condition rating was assigned using the following system: excellent (0–33% defoliated), fair (34–66% defoliated), poor (67–99% defoliated) and dead (dead or completely defoliated), where defoliation was estimated by looking for branchlets that were dead or without leaves.

Branch angle (with zero being parallel to the ground) and compass azimuth were measured for first order branches prior to removal from the tree. First order branches were removed from the tree and lowered to the ground using a rope to minimize breakage. Once on the ground, second and third order branches were subsequently removed and measured. Overall branch length was measured using a string to follow the contour of the given branch. Branch basal diameters were measured distal to any branch collar and converted to radius for analysis. Slenderness ratio was calculated as the branch length divided by branch radius. Due to time limitation in the field, any branch that was less than 100 mm in length and 1.5 mm in radius was considered a short shoot (Harris et al. 2004; Gradziel et al. 2002) and not included during data collection. Only branches rated in excellent condition were used during allometric analysis.

All data were analyzed in SAS 9.1 (SAS Institute) except standardized major axis (SMA) regression which was analyzed using SMART 2.0 (Falster et al. 2006; Warton et al. 2006). Ordinary least squared (OLS) and polynomial were run using Proc Reg. ANOVAs were conducted with Proc GLM and means separations were analyzed using Tukey adjusted mean separation LSD by hand to adjust for unequal sample sizes. Proc Univariate was used to verify normality of the data and residuals using a Kolmogorov–Smirnov test. Residuals and mean squared error (MSE) for SMA regressions were calculated in MS Excel 2003 (Microsoft Corporation). Mean (\bar{x}) and standard deviation \bar{S} for compass azimuth were derived in MS Excel as $\bar{x} = V + \text{ArcSin}(\bar{S}/\bar{R})$, where $\bar{R} = (\bar{C}^2 + \bar{S}^2)^{0.5}$, $\bar{C} = (\sum \text{Cos}\theta_i)/n$, $\bar{S} = (\sum \text{Sin}\theta_i)/n$, and $V = 0$ if $\bar{S} > 0$ and $\bar{C} > 0$, $V = 180$ if $\bar{C} < 0$ or $V = 360$ if $\bar{S} < 0$ and $\bar{C} > 0$ (Mardia 1972). All statistics used $\alpha = 0.05$. Data

were determined to be approximately normally distributed, and residuals were normally distributed unless otherwise stated. Graphical output was produced in MINITAB® Release 14.20.

Results

A total of 2,023 branches were collected from four trees between the two field seasons, with 1,735 (85.8%) in excellent condition, 71 (3.5%) fair, 31 (1.5%) poor and 186 (9.2%) dead. Heights (m) and diameters (cm), measured at 1.4 m above ground were: tree 31 (18.3 m, 41.8 cm), tree 92 (20.1 m, 35.7 cm), tree 96 (16.7 m, 32.6 cm) and tree 97 (17.4 m, 24.4 cm). Neither mean branch length ($P = 0.7883$, $N = 1,735$) nor branch radius ($P = 0.1174$, $N = 1,735$) were found to differ between trees.

Mean compass bearing for first order branches collected from tree 31 was $0.1^\circ \pm 6.97$ SE, tree 92 was 178.6 ± 5.92 SE, tree 96 was 178.7 ± 4.67 SE and tree 97 was 179.4 ± 7.20 SE. Significant OLS regressions were not found between compass bearing and log branch length ($P = 0.3762$, $N = 85$) nor log branch radius ($P = 0.3295$, $N = 85$). The change in compass bearing from a southern aspect (trees 92, 96 and 97) to a northern aspect (tree 31) did not influence branch form.

Branch angle did not appear to influence first order branch form, as mean branch angle (90° being perpendicular to the ground) did not vary between the trees ($P = 0.4227$, $N = 85$). Additionally, significant OLS regressions were not found between branch angle and log branch length ($P = 0.4528$, $N = 85$) nor log branch radius ($P = 0.1148$, $N = 85$).

A log–log plot of length (mm) versus radius (mm) for first, second and third order branches in excellent condition, depicts a curvilinear relationship (Fig. 1), yet a significant polynomial model was not identified as the residuals were not normally distributed ($P = 0.010$). As previous reports suggest a shift in branch form when branches reached 3,000 mm (Bertram 1989; McMahon and Kronauer 1976), therefore we grouped our branches as either sun (length < 3,000 mm or log 3.48) or structural branches (length \geq 3,000 mm). Significant log–log regressions were not found for sun branches, as the residuals were not normally distributed for SMA linear regression ($P = 0.010$) or quadratic regression ($P = 0.010$). A significant linear log–log SMA regression was found for structural branches, ($P < 0.0001$, $MSE = 0.0039$, $N = 123$, Fig. 1) fitting the elastic similarity model with a slope of 0.68.

An increase in the number of second order branches growing upon first order branches can be seen around a radius of 9–14 mm (Fig. 2) or branch length of 2,000–3,000 mm (Fig. 3). A significant linear regression (OLS)

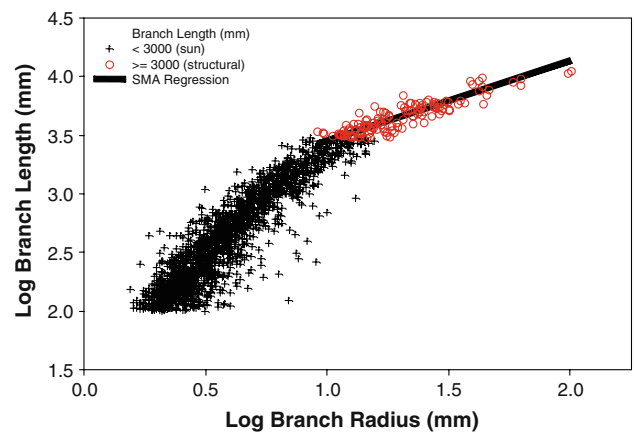


Fig. 1 Log–log plot of length (mm) versus branch radius (mm) of *Acer platanoides* first, second and third order branches. Branches are split into sun branches (length < 3,000 mm, log 3.48) and structural (length \geq 3,000 mm) based on results of McMahon and Kronauer (1976) and Bertram (1989). Standard major axis (SMA) regression line for structural branches is presented; $Y = 2.778 + 0.678X$, $r^2 = 79.9\%$, $N = 123$

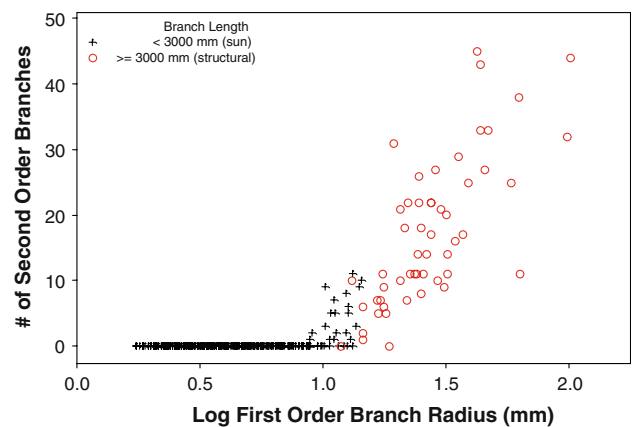


Fig. 2 Plot of the number of second order branches plotted against the log of first order branch radius

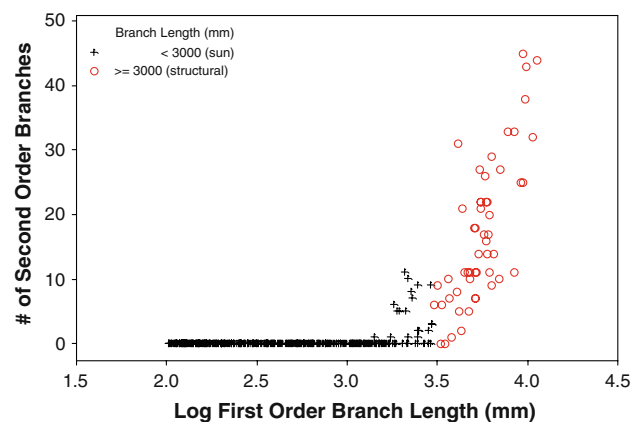


Fig. 3 Plot of the number of second order branches plotted against the log of first order branch length

was identified between the number of lateral branches and the log of branch radius ($P < 0.0001$, $MSE = 46.37$, $N = 70$, Fig. 4), yet this linear relationship does not suggest a shift in form. If primary branch length slows, investment in elongation would likely turn towards the lateral branches and a significant quadratic regression was found between the number of second order and the log of first order branch length ($P < 0.0001$, $MSE = 42.19$, $N = 70$, Fig. 5). This quadratic regression shows that the number of laterals will increase from 4 to 5 when 2,000 mm long, to 5–6 at 3,000 mm length, and then 9–10 by 4,000 mm length. Changes in branch form (allometric scaling) appear correlated with a change in branch length extension as branches reduce investment in elongation along the primary axis and redirect elongation into the lateral branches.

If the slope of length versus radius relationship changes with size then the relative growth rate of length to the

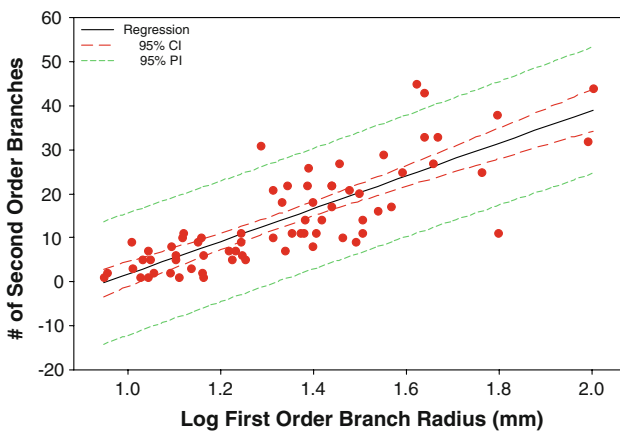


Fig. 4 Ordinary least squared regression of the number of second order branches versus the log of first order branch radius with one or more lateral branch, $Y = -35.40 + 37.13X$, $r^2 = 64.0\%$, $N = 70$

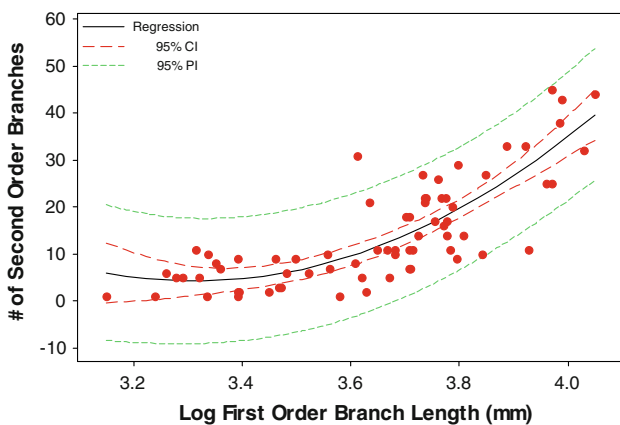


Fig. 5 Quadratic regression of the number of second order branches versus the log of first order branch length with one or more lateral branch, $Y = 726.0 - 436.0X + 65.76X^2$, $R^2 = 67.7\%$, $N = 70$

relative growth rate of radius also changes. Although this study did not measure annual growth, it is likely that the rate of annual growth in length reduces as a branch increases in size. Slenderness ratio (length/radius) may provide insight into the shift in branch form and useful in field evaluation by practitioners. Log slenderness ratio for all first, second and third order branches, used in the elastic similarity test, is plotted against the log of branch radius (Fig. 6) and the log of branch length (Fig. 7). Log slenderness increases in both plots until around 300 (log 2.5) when it peaks and begins reducing; indicating that branch form is altered as branch size increases. Analysis could not identify significant regressions between log slenderness and log branch radius as the residuals were not normally distributed ($P = 0.10$). A significant relationship was

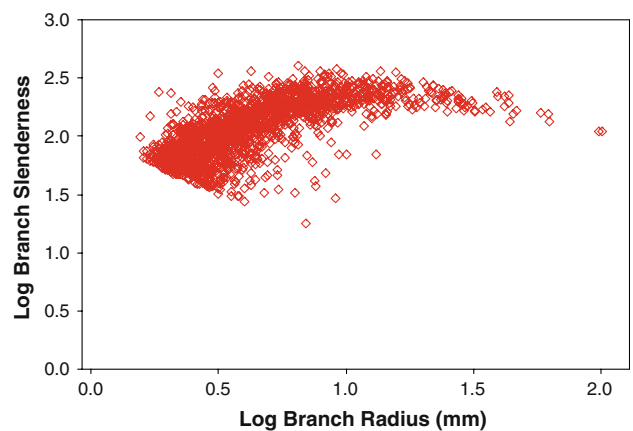


Fig. 6 Log–log plot of slenderness (branch length/radius) versus branch radius (mm) for *Acer platanoides* first, second and third order branches

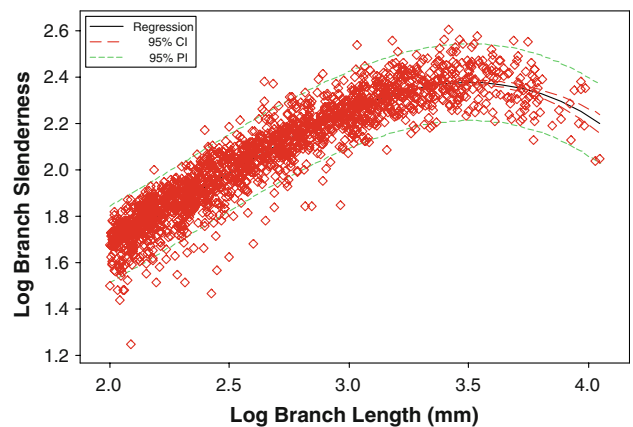


Fig. 7 Third order polynomial regression of log slenderness (branch length/radius) versus log branch length (mm) for *Acer platanoides* first, second and third order branches, $Y = 2.341 - 1.854X + 1.065X^2 - 0.152X^3$, $R^2 = 87.8\%$, $N = 1,735$. An inflection point was identified at log length 3.51 (3,245 mm), which is similar to the 3,000 mm used to split branches into sun versus structural branches

identified between log slenderness ratio and log branch length for all first, second and third order branches used in the elastic similarity test, ($P < 0.0001$, $MSE = 0.007$, Fig. 7). The third order polynomial equation has a zero slope at branch length 3,254 mm (log 3.51), which suggests that 3,000 mm is a reasonable location for splitting the data set in the allometric analysis between log length and log radius.

Discussion

Branches are of two types, with different roles: sun branches that place the leaves in position to intercept solar radiation to drive photosynthesis, and structural branches, upon which subordinated sun branches grow. The literature suggests that the allometric log–log relationship between branch length and radius is curvilinear for sun branches and linear for structural branches (McMahon and Kronauer 1976; Bertram 1989; Niklas 1992; Suzuki and Hiura 2000; Niklas and Spatz 2004). This study was designed to determine if the shift in growth form is applicable to open-grown urban trees. Our data confirms that the log–log relationship between branch length and radius appears to follow a curvilinear pattern (Fig. 1) until about 3,000 mm in length, after which they converge towards a linear relationship scaling to the 0.67 power labeled the elastic similarity model by McMahon (1975). It appears that larger structural branches on open-grown urban trees can be modeled as cantilevered beams using the elastic similarity model as our findings are consistent with findings for *Q. alba* and *A. saccharinum* branches (McMahon and Kronauer 1976; Bertram 1989).

This change in form suggests that the ratio of the relative growth rate of length to the relative growth rate of radius is changing. While this study did not measure annual growth, we can turn to the number of lateral branches as a variable that provides some explanation for the shift in allometry. If annual branch elongation reduces as branches grow beyond 3,000 mm, it is likely that a branch has assumed the role of permanent structural branch, while subordinate branches support the bulk of photosynthetic processes. Figure 3 shows that the number of second order branches begins to increase rapidly as branches approach 3,000 mm in length, at least in relatively large shade trees displaying a more decurrent growth form. The quadratic regression in Fig. 5 shows that the number of second order branches arising axially along a first order branch in our *A. platanoides* increased from 4–5 (at 2,000 mm length) to 5–6 (at 3,000 mm length) and then jumped to 9–10 (by 4,000 mm in length). A corresponding decrease in slenderness with branch size suggested a reduced investment in elongation along the primary axis of growth, while the

subordinate lateral branches fill the role of sun branches. Mäkelä (2002) used foliage growth as an input in branch modeling; the present study did not examine photosynthetic capacity of the branches, future work should explore the relationship between leaf area and shifts in allometry.

The initial portion of curvilinear relationship in Fig. 1 suggests that the relative growth rate of length is growing more than the relative growth rate of radius which would lead to more slender branches. By the time the branches fit the elastic similarity model, slenderness (branch length/branch basal radius) should be decreasing. Bertram (1989) plotted slenderness in relationship to branch radius and found that slenderness peaked around 260 (a unitless number). Our *A. platanoides* branches peaked near 300 and it appears that branch length of 3,000 mm is a reasonable point at which branch form shifts (Fig. 7). Modification of form when branches approach potential instability makes sense if the branches are transitioning from a primary role of flexible sun branch to that of a stiffer structural branch (Dahle and Grabosky 2009). Indeed, slenderness begins to decline at lengths around 3,000 mm. Although we did not test for mechanical stability in this study, Dahle and Grabosky (unpublished) report a fourfold increase in the branch modulus of elasticity along the first order branch axis between the terminal bud scale scar and the midpoint of *A. platanoides* branches that averaged 5.9 m in length. Future research should investigate if variations in modulus of elasticity correspond to a shift in branch allometry, especially as branches increase in length from 2,000 to 4,000 mm. Additionally, slenderness values may provide a useful tool in predicting branch instability. Arborists and managers of amenity trees may wish to explore this potential important relationship across different species and genera.

This study suggests that the use of the elastic similarity model is appropriate for open-grown urban trees with larger branches (>3,000 mm). As branch length approaches 3,000 mm, the function of branches transition from that of a flexible sun branch to a stiffer structural support branch and slenderness begins to decline. The variation in slenderness ratio in this study is associated with branch length rather than radius and corresponds to an increase in the number of subordinate lateral branches along the principle axis of growth. It is these lateral branches that assume an increased role in placing the leaves in the sun until they approach the 3,000-mm threshold. This knowledge can help managers of amenity trees understand how normal tree development leads to a stable canopy form.

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