Full Length Research Paper

Variation in anatomical features along *Acer platanoides* (Sapindaceae) branches

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This paper investigates the balance between hydraulics and mechanics in tree branches by analyzing changes in the percentage of area composed of four cell types along *Acer platanoides* L. branches. Percent area composed of vessels members, fibers, ray parenchyma, and axial parenchyma were compared at five locations along each branch from the stem towards the branch tips. The percentage of each cell type was not found to be correlated with the angleof branch attachment to the trunk, nor the top versus bottom of each branch location. In general vessel radii decreased in the distal direction along each branch. Percent area comprised of vessels was highest in the middle of the branches and lowest at both ends, while the percent area for fibers did not differ in the secondary (radial) growth. Vessel to fiber ratios were found to vary in the same pattern as percent area vessel, which suggests that water movement is governing the balance between hydraulics and mechanics in these branches.

Key words: Anatomy, vessel, fiber, branches, hydraulics, mechanics.

INTRODUCTION

Water transportation, storage of water and sugars, mechanical support, and defense are considered to be principle functions for xylem (Niklas, 1992; Tyree and Zimmermann, 2002; Gartneret al., 2003). Niklas (1992) used a four-legged diamond to describe a balance between plant functions throughout their lives anchored by photosynthesis, hydraulic support, mechanical support and reproduction. Two of these functions are filled exclusively by primary tissues; photosynthesis and reproduction. Primary tissues also play an important role in both hydraulic and mechanical functions.

One of the principal functions of secondary tissues is hydraulic support (Tyree and Zimmermann, 2002;Sperry et al., 2006; Dahle and Grabosky, 2009). The ability to supply an adequate amount of water to drive the transportation stream necessary for photosynthesis is of great importance for trees. Yet the importance of hydraulics should not diminish the significance of mechanical support, the other principal function of secon-

dary tissue. In order to survive decades or even hundreds of years, a tree must be capable of resisting the load placed on the woody tissues by the constant force of gravity (self-loading) and resist loads applied externally by the elements such as wind, ice and snow.

Angiosperm xylem is heavily comprised of vessel elements and fibers, and separates the principal function of secondary wood between these two cells types (Esau, 1977; Niklas, 1992; Sperry et al., 2006). Vessels are the conduits for water and nutrients and they have large lumens and relatively thin cell walls. While the walls resist cavitations (Sperry et al., 2006), they provide little structural support to the stem or branch. Additionally, the open void of the vessel lumen is an inherent weak location in the wood. Fibers, on the other hand, have relatively small lumens and thick cell walls and provide the bulk of the mechanical support in angiosperm xylem (Niklas, 1992; Woodrum et al., 2003;Sperry et al., 2006; Dahle and Grabosky, 2010).

The tree must balance hydraulics and mechanics, yet the literature does not comprehensively address the potential tradeoff between hydraulics and mechanics (Gartner et al., 2003; Woodrum et al., 2003; Dahle and Grabosky, 2009, 2010). Indeed, the knowledge of wood anatomy far outweighs our knowledge of function and it has been sug-

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gested that research should concentrate on biomechanical and physiological studies (Sperry et al., 2006). One way to measure this trade-off would be a comparison of the percentage of area comprised of vessels to that of fibers. An increase in the percentage of area containing vessels may suggest an investment in hydraulic capacity potentially at the expense of mechanical support, while an increase in the percentage of area with fibers may suggest added investment in mechanics or a change in the pattern of hydraulics.

The Hagen-Poiseuille equation shows that flow in pipes is governed by r^4; see Tyree and Zimmermann (2002) for detailed equation and discussion. Vessel size is constrained by cavitation pressure and minimally by structural support (Tyree and Zimmermann, 2002; Sperry et al., 2006). Research has shown that conduit diameter (vessel and tracheids) is smaller in juvenile wood than adult wood and tends to taper in the distal direction in stems and branches (Bannan, 1943; Gartner, 1995; Domec and Gartner, 2002; Anfodillo et al., 2006). The WBE model utilized conduit tapering (narrowing distally) to explain vertical hydraulic supply in xylem as a function of tree height (West et al., 1999). As vessels become larger, flow efficiency increases and fewer vessels are required, potentially making more room for fibers and mechanical support.

The literature suggests that hydraulics can be modified in response to mechanical need. Conifers have been shown to reduce specific conductivity in favor of increased mechanical support in leaning stems (Spicer and Gartner,1998a, 1998b, 2002). Angiosperm vines and lianas were found to have higher specific conductivity than self-supporting angiosperms like trees and shrubs (Ewers, 1985; Gartner et al., 1990). Vessel diameter and the percent area of vessels in *Toxicodendron diversilobum* (T&G) Green (Anacardiaceae) were found to be lower inself-supported than staked plants, leading to a reduction in specific conductivity and more cross-sectional space for mechanics (Gartner, 1991). This loss in hydraulic capability was compensated by a decrease in leaf specific conductivity and therefore a similar pressure gradient was expected. Chiu and Ewers (1992) found that *Lonicerajaponica* Thunb. (Caprifoliaceae), atwiner vine, had smaller stems and larger vessels than self supported stems in *L. maackii* (Rupr.) Maxim or scrambling *L. sempervirens* L. (initially a self-supported plant, then leaning against other plants or the ground). This suggests that mechanics, not hydraulics, is the governing factor in the differences between the self-supported and staked plants. Much of this work concentrated on shrubs, vines or lianas rather than larger trees which may lead to greater water demands at the distal leaves as well a more investment in mechanics to survive during their longer lives. Woodrum et al. (2003) found that wood strength was negatively related to fiber lumen diameter and reported that no trade-off was found between hydraulics and mechanics in five species of trees of the genus *Acer* (Aceraceae). A trade-off implies that an increase in investment in one function is a direct cost to the other, so it may be better to consider that hydraulics and mechanics are balanced in trees.

This project was aimed at determining if vessel element tapering is found in Norway maple (*Acer platanoides* L.) branches. Investigation also examined if the percentage of area of the four principle cell types (vessel elements, fibers, ray files and axial parenchyma) changed along the top versus bottom oraxially along a branch, or due to variation in the angle of branch attachment to the stem.

MATERIALS AND METHODS

Twelve first order *Acer platanoides* L. (Aceraceae) (Norway maple) branches, four each from three trees, were harvested between March 19 and April 2, 2007 from Norway maple trees at Rutgers University Horticultural Farm III in East Brunswick, NJ. The trees were located along the perimeter of a mixed plantation with bare ground and mixed grass beginning approximately half way the trunk and canopy drip line. All sample branches were growing to the exterior of the plot and considered dormant as the terminal buds had not begun to swell. Branch diameter and branch angle, zero being parallel to the ground, were measured and the upper side of the branch was marked at the point of attachment to the central trunk. Branch slenderness was calculated as branch length / branch radius. Each branch was removed and divided into 5 sections (P_1, S_1, S_2, S_3, S_4) with a top and bottom sample at each section (Figure 1). P_1 was harvested approximately 5 cm distally to the most recent bud scale scar and consisted solely of primary elongation. $S_1$was obtained 5 cm proximal to the most recent bud scale scar and thus the outer growth ring consisted of elongation and one year of secondary (radial) growth. S_2 was at the middle of the branch and S_3 was harvested from the midpoint between S_2 and S_4. Finally S_4 was collected from the base of the branch, 5 cm distal to the branch collar. The sections were placed in bags, containing wet paper towels and stored in a refrigerator for up to seven days until milling and slide preparation.

A band saw was used to cut sections S2 – S4 in half through the pith, and the top and bottom sections were milled to approximately 1 cm wide and 2 – 3 cm long (Figure 2). Sections P1 and S1 were cut to 2 – 3 cm longand split in half using a razor knife to create the top and bottom sections. A Reichert sliding microtome was used to cut three transverse sections approximately30 µm thick for sample S2 – S4 and 40 µm for P1 and S1. Each sample was stained in a solution of 67% alcian blue and 33% safranin, rinsed two times in distilled water baths, dehydrated in series of ethanol baths (50%, 70%, 95%, 100%) and finally into Histoclear (Jansen et al., 1998).
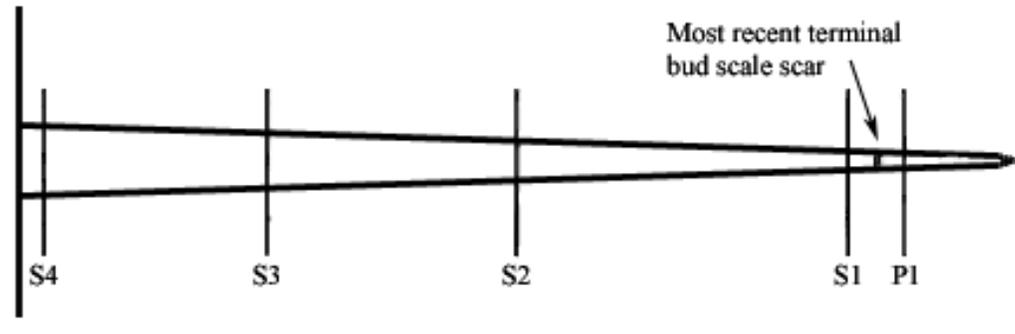
Figure 1. Sampling locations for anatomical study of *Acer platanoides* L. Sections S1 – S4 were taken from secondary (radial) growth, while P1 was obtained from primary elongation.
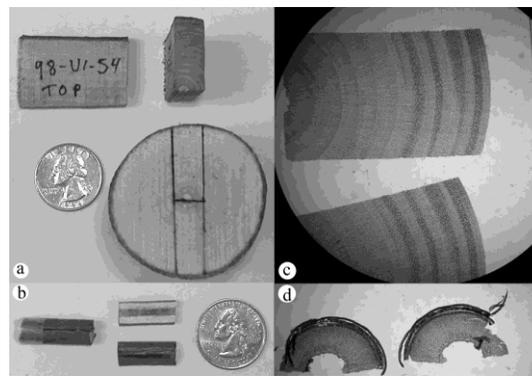

Figure 2. *Acer platanoides* L. milled sections S4 (a) and P1 (b). Prepared slide mounts of transverse sections for S4 (c) and P1 (d).
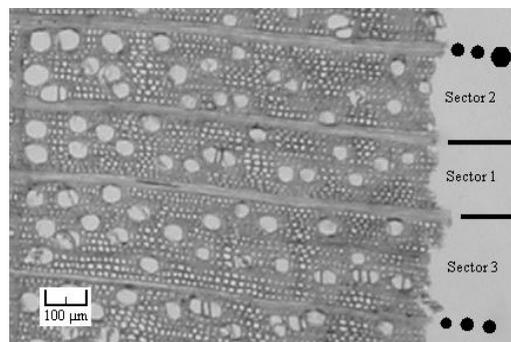

Figure 3. Prepared slide mounts of *Acer platanoides* L. tissue detailing the three sectors utilized during cell measurements.

The tissues were submersed in all baths (stain, ethanol, Histoclear) for two minutes. The sections were permanently mounted on slides using Permount. Samples were photographed under a microscope (Nikon SMZ1500) using a digital camera (Nikon Coolpix 5000). Photographs were processed in Adobe Photoshop version 7.0 (Adobe Systems Inc) and the center-most sectorbordered by contiguous ray parenchyma cells and two adjoining sectors were located for each sample (Figure 3). The photos were cropped to contain the three sectors and saved as grayscale TIFF files without compression to minimize distortion. All anatomical analyses were conducted on the outermost growth ring using WinCELL Pro version 2007a (Regent Instruments Inc.).

A preliminary study was conducted to determine the minimum area for classification of vessels. Photographs were analyzed from thirty randomly selected slides, five

Table 1. Mean branch radius (± SE) for each location along 12 first order *Acer platanoides* L. branches. Values with the same letter were not found to be significantly different using a Tukey HSD comparison (p<0.0001).

Branch Location	Mean Branch Radius (mm)
S4	29.2a ±1.1
S3	22.4b ±0.9
S2	16.0c ±0.7
S1	3.4d ±0.3
P1	2.9d ±0.3

each from top and bottom from positions P1, S2, and S3. The minimum vessel lumen area was found to be 153.3 μm^2 and a minimum threshold of 150 μm^2 was therefore used to classify cells as vessels in the image analytical part of this study.

Two image analyses, using WinCELL, were conducted for each slide photograph. The first analysis determined the total area measured, and number of vessels and the luman area for each vessel. The second analysis determined the area of the four ray parenchyma, two interior (sector 1, see Figure. 3) and two exterior border ray (sectors 2 and3). Data files were summarized into an Excel spreadsheet(Microsoft Corporation). Vessel radius ($[$measured lumen area/$\pi]^{0.5}$), percent area containing vessels, rays, and fiber [(total area – (area vessels + area ray files+ mean area axial parenchyma))/total area] were calculated.Vessel density (# vessels / mm^2) was derived, as was the vessel to fiber (V:F) (percent area vessel / percent area fiber). .Theoretical % cumulative mean flowcapacity was calculated using aweighted percentage equation:

$$Theoretical\%MeanFlowCapacity = \frac{r_{ij}^{4} * n_{ij}}{\sum \left(r_{ij}^{4} * n_{ij} \right)}$$

with r_{ij}^{4} being mean vessel radius^4, i the 5 µm vessel size class, j was branch location, and n was vessel count.

Estimated mean area for axial parenchyma was determined in a follow up study of twenty randomly selected slides, four from each branch location. Slides were photographed under a microscope (Zeiss Axioskop 40)with a digital camera (Insight Spot Firewise 4, model 18.2). *Acer* is considered to have scanty paratracheal parenchyma with axial parenchyma cells,which are usually found only surrounding the vessels (Panshin and de Zeeuw 1980). One photograph, centered on a randomly select vessel element, was taken from each of the three sectors per slide. Axial parenchyma cells were identified, measured for area, and percentage of area calculated for each branch location. The mean area for each branch location was subtracted during the determination of percentage ofarea for fiber in the whole population.

All data was analyzed using SAS 9.1 (SAS Institute). Mean and standard deviations (s) were run with Proc Means. Proc Univariate was used to verify normality of the residuals. ANOVA were run with Proc GLM and means separations were analyzed using Tukey HSD. All statistics used alpha = 0.05.Data was determined to be normally distributed and residuals were normally distributed.

RESULTS

Mean branch length was 5,716.4 mm (4,705 – 7,915, s=933.7), mean branch diameter (at branch base) was 62.1 mm (48 – 75, s=8.2). A significant difference was found between branch radii at the five locations along the branches (Table 1). Mean radius decreased significantly distally in secondary (radial) growth along the branches (S4 to S1), and P1 was not significantly different than S1. Branches had a mean slenderness ratio of 184.3 (165 – 216, s=18.2). Mean branch angle was 61.3 degrees (40 – 78, s=10.9). No significant relationship was found between branch angle and the following variables; mean vessel radius (p=0.1465), vessel area density (p=0.2173), percent area vessel (p=0.8021), percent area fiber (p=0.9683), percent area ray (p=0.7970), nor V:F (p=0.8467).

No significant differences were found between top and bottom samples at each branch location for mean vessel radius, vessel density, % area vessel, % area fiber, % area ray, and V: F (Table2). One exception was mean vessel radius at branch location S3 (p=0.0262) where the top averaged a vessel radius of 18.01 µm and the bottom

Table 2. ANOVA p-values for of top versus bottom sample at each location first order *Acer platanoides* L. branches. Significant value, α=0.05, is noted with an asterisk. Sample size was 24 at each location, 12 top and 12 bottom.

Variable	p-value for Branch Location				
	S4	S3	S2	S1	P1
Mean vessel radius (µm)	0.7830	0.0262*	0.6928	0.9870	0.5114
Vessel Density (#/mm^2)	0.2354	0.0967	0.1853	0.3803	0.7259
% Area Vessel	0.3028	0.5972	0.1949	0.2975	0.6894
% Area Fiber	0.6579	0.5605	0.0511	0.4336	0.7368
% Area Ray Parenchyma	0.8511	0.7169	0.1418	0.8792	0.8892
Vessel to Fiber ratio	0.3376	0.5962	0.1161	0.2064	0.7263

Table 3. Mean values (± SE) at each location along first order *Acer platanoides* L. branches. Values with the same letter were not found to be significantly different using a Tukey HSD comparison (α=0.05). Sample size was 120 for all samples, except % area axial parenchyma where n=20.

Variable	Branch Location					p-value
	S4	S3	S2	S1	P1	
Mean Vessel Radius (µm)	16.22a ±0.22	16.98a ±0.21	16.88a ±0.21	13.18b ±0.13	11.49c ±0.14	<.0001
Vessel Density (#/mm^2)	107.20d ±3.24	148.51cd ±4.91	150.51c ±4.31	240.32a ±6.53	197.35b ±4.27	<.0001
% Area Vessel	0.101b ±0.0026	0.150a ±0.0036	0.147a ±0.0031	0.139a ±0.0027	0.089b ±0.0026	<.0001
% Area Fiber	0.730ab ±0.0045	0.703b ±0.0057	0.711b ±0.0048	0.715ab ±0.0046	0.757a ±0.0055	0.0083
% Area Ray Parenchyma	0.161a ±0.0039	0.139a ±0.0039	0.137a ±0.0036	0.135a ±0.0048	0.140a ±0.0056	0.3654
% Area Axial Parenchyma	0.009a ±0.0009	0.007a ±0.0004	0.005a ±0.0004	0.012a ±0.0007	0.014a ±0.0018	0.0640
Vessel to fiber ratio	0.140b ±0.0037	0.219a ±0.0043	0.209a ±0.0056	0.195a ±0.0066	0.118b ±0.0042	<.0001

15.95 µm. Although mean vessel radius was significantly different at this single location, a difference was not identified at any of the other four locations and it was deemed acceptable to group the top and bottom samples for all six variables in the subsequent analyses.

Mean vessel radius was larger in the proximal half (S2 – S4) of the branch than at the tip (S1 and P1; Table 3). Vessel density was highest at location S1, significant lower at P1 and further reduced from S2 to S4. Locations S1 – S3 were found to have higher percentages of area comprised of vessels than either end of the branches (P1 and S4). No significant differences were found in percent area fiber in locations with secondary growth (S1 – S4), yet S2 and S3 were found to be different from P1, while S1 and S4 were not. Vessel to fiber ratio was highest in the middle of the branches (S1 – S3) and significantly lower at the ends (S4 and P1). The Percent areas for ray parenchyma and axial parenchyma were not found to differ along the branches. Figure 4 shows the theoretical percent cumulative mean flow capacity (r^4)along the

branches, mean radius at each location was: S4=15.90 (6.99 – 83.39, n=4130, s=6.87), S3=16.57 (6.99 – 62.45, n=3833, s=7.39), S2=16.10 (6.99 – 55.94, n=4433, s=6.85), S1=13.47 (6.99 – 37.11, n=2555, s=4.23), and P1=12.20 (6.99 – 26.37, n=2105, s=3.74).

DISCUSSION

One of the goals of this study was to determine if branch angle had an effect on the basic anatomical features along branches. It was anticipated that a decrease in branch angle would lead to a change in vessel size or the proportion of vessels and fibers from the top versus bottom. The only location where the vessel radius differed was at S3 (Table 2) where the top was found to have larger vessel radii. This is contrary to findings by radius decreased in tension wood (Kaeiser and Boyce, 1965; Aloni et al., 1997; Jourez et al., 2001).The percentages of area for the four cell types were not found
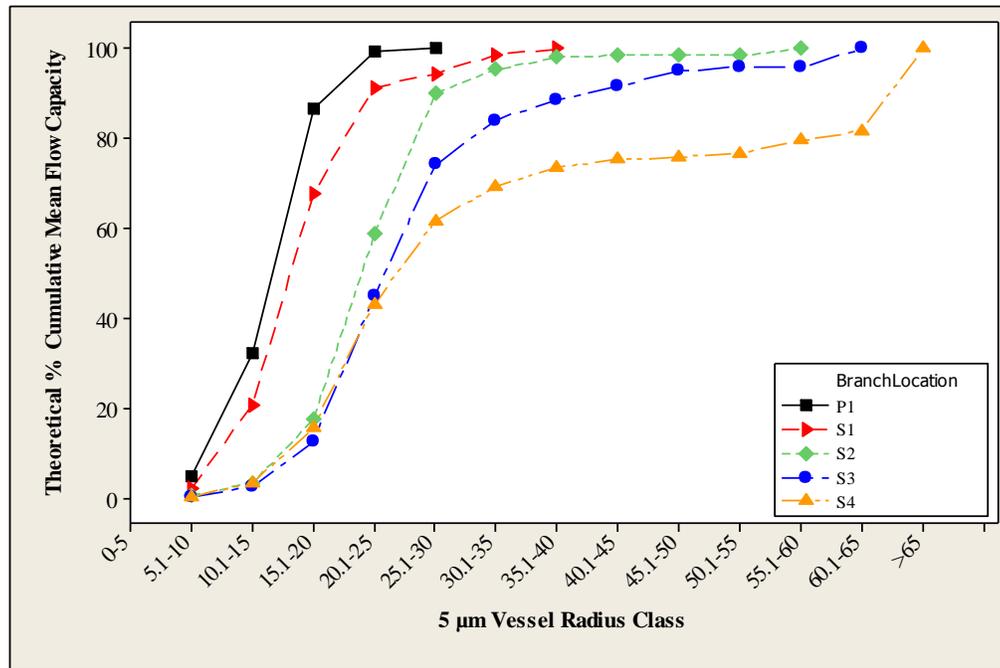
Figure 4. Theoretical % cumulative mean flow capacity (radius[4]) per 5 μm radius size class for each location along first order *Acer platanoides* L. branches.

to vary with angle, nor were there any differences between the top and bottom sections along the branches. This suggests that that angle of branches may not influence the tissue composition in trees.

It is likely that any compensation due to branch angle and/or radial location is at the microcellular level. Reaction wood in angiosperms is typically found on the upper side of a leaning stem or branch and labeled as tension wood. While tension wood was not measured in this study, Dahle and Grabosky (2010), did not find the presence of tension wood to influence overall wood strength.

Vessel size has been reported to decrease in the distal direction in both trunks and branches (Bannan, 1943; Gartner, 1995; Domec and Gartner, 2002; Tyree and Zimmerman, 2002; Anfodillo et al., 2006). Our branches showed similar patterns in that larger vessels were found in the proximal half of the branches (S2 – S4), reduced at S1 and smallest at P1 (Table 3). The tapering of the vessels in the distal direction helps to maintain the flow of water in the parent branch as a portion of the water is diverted into the lateral branches. Indeed the Hagen-Poiseuille equation and WBE model suggests this occurs to maintain a constant flow along a branch and the theoretical hydraulic flow in our branches fit the expected pattern (Figure 4). Vessel density increased in the proximal direction, except at the tip where P1 was lower than S1 despite being only 10 cm apart. Tyree and Zimmerman (2002) suggested that it is common for

vessels to end at nodes. Indeed S1 is 5 cm from the previous years' terminal bud and vessels formed at this location during the current year supply three points of growth; the continuation of the branch axis and two new lateral branches. Additionally, hydraulic constrictions have been found through the branch protection zone (Tyree and Ewers, 1991; Aloni et al., 1997; Eisner et al., 2002), and it is likely that the increase in vessel density at S1 is associated with this potential hydraulic constriction, yet future research is determining this.

The percent area of vessels should be a function of size and density, and therefore it is not surprising to see a sharp drop between locations S1 and P1. Vessels at P1 are smaller and less dense as they most likely supply less leaf area. Moving toward the base S2 and S3 had the same percent area of vessels due lower densities and high vessel size. Furthermore, percent area vessel was lower at the base of the branches which corresponds to larger flow capacity. Using the Hagen-Poiseuille equation, the estimate of flow capacity shows the influence of a few large vessels; a single 35 μm vessel is approximately as efficient astwo25 μm vessels. The estimated cumulative flow lines are similar for S2 – S4 until around 25 – 30 μm where S4 is only at 64% of total capacity, S3 at 74%, and S2 at 90%, while S1 and P1 begin to peak around 15 – 20 μm and by 20 – 25 μm are essentially at full capacity (95% and 100%, respectively). As the percentage of area vessels decrease, one should expect to see a corresponding increase in the percent area

with fibers. The pattern for variation in percent area of fiber was not as clear as with the vessels; all the secondary wood had the same percentages of area as fiber but S2 and S4 did not differ from primary wood (P1). Woodrum et al. (2003) did not observe a difference in the percentage of area of fibers at the branch midpoint on five species of *Acer*, yet their values were slight higher (0.81 – 0.82) than this study (S2=0.711). It appears that the percent area of fibers does not vary greatly in branches, again suggesting that variation to compensate for mechanics in fibers might be at the microcellular level.

Vessel to fiber ratios (V:F) were found to vary along the branches with the base (S4) and tip (P1) having a smaller mean V:Fratio (Table 3). The lower V: F is driven by the reduction in the area of vessels, especially since the area of fibers was mostly consistent in the branches. This would suggest that the ability to move water is governing the balance between hydraulics and mechanics at the cellular level. Yet previous research determined that the fiber cell walls were thicker at the base that at the branch tips (Dahle and Grabosky, 2010) which suggest that one must consider the microcellular level to fully explain the balance. We believe that additional research is warranted to determine the importance of the V: F.

It appears that trees balance the important functions of hydraulics and mechanics along branches. While no differences between four cell types were found between the top and bottom location, differences were found in vessels and fibers along the branches. Variation in the area composed of fibers was not different in the secondary growth, yet slightly higher in the primary wood compared to the middle portion of branches. Future research should investigate the influence of fiber cell wall and lumen size on mechanical properties along branches. It seems that hydraulic may be the principle function in branches as a more distinct pattern was found in the percent area of vessels and the ratio of vessel to fiber where the branch ends were lower than the middle locations and research should determine if V:F can be used to predict mechanical properties along branches. Additionally vessel radius decreased in the distal direction while density generally increased following patterns that maintain constant hydraulic flow. Vessel density decreased in the primary growth compared to the most recent secondary growth and future researcher should investigate if the difference is due to hydraulic constriction in the internode and lateral branch attachment zone.

ACKNOWLEDGEMENTS

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