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HYDRAULIC, BIOMECHANICAL, AND ANATOMICAL INTERACTIONS OF XYLEM FROM FIVE SPECIES OF *ACER* (ACERACEAE)[1]

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Possible trade-offs between hydraulic conductivity and mechanical properties of woody stems from five species were assessed. *Acer negundo* is a ruderal tree, *A. saccharinum*, and *A. rubrum* are fast-growing and shade-intolerant soft maples, whereas *A. nigrum* and *A. saccharum* are slow-growing and shade-tolerant hard maples. It was hypothesized that the ruderal and soft maples would have lower modulus of elasticity (MOE) and modulus of rupture (MOR), but higher maximum specific conductivity ($K_{s\ max}$) than hard maples. Many anatomical and general morphological characteristics were measured in an attempt to correlate them to water transport and/or mechanical strength differences between species. No difference was found between species in vessel diameter, fiber wall thickness, initial hydraulic conductivity ($K_{h\ initial}$), specific conductivity ($K_{s\ max}$), native percent embolism, or Huber value. Similarly, no trade-off was found between $K_{s\ max}$ and MOE or MOR across the genus. However, fiber lumen diameter was inversely correlated to MOE and MOR. Surprisingly, percentage of ray parenchyma was positively related to MOE. The results suggest transport/mechanical trade-offs do not occur in *Acer* and differences in mechanical properties may be due to fiber lumen differences that do not influence the efficient transport of water.

Key words: Aceraceae; fiber lumen; maple; modulus of elasticity; modulus of rupture; ray parenchyma; specific conductivity; vessel lumen area.

Studies of possible trade-offs between hydraulic conductivity and mechanical strength of wood (secondary xylem) of plants are rare despite the possible ecological importance. It has been asserted that as water conduction is increased via greater vessel lumen area, mechanical strength of the wood may be reduced due to the reduced cross-sectional area available for fibers (Wagner et al., 1998). However, other anatomical variables may confound the influence of the number and diameter of conduits. These variables include pith diameter, ray width, and fiber cell wall thickness, to name a few.

Due to the complexity of the interactions between anatomy, hydraulic conductivity, and mechanical strength of wood, there have been few studies addressing all three variables. Early work focused on just two factors at a time.

Gartner (1991a, b) showed that in *Toxicodendron diversilobum*, Huber value (HV; conductive xylem per leaf area) was lower, but that maximum specific conductivity ($K_{s\ max}$) was greater for a vine (supported) growth habit than for freestanding shrubs. This resulted from the supported vines having similar vessel frequency but greater vessel lumen area than shrubs. It was concluded that structural stability of shrubs was a function of the second moment of area rather than material stiffness.

Ewers and Fisher (1991) found that vines in the genus *Bauhinia* had less xylem per distal leaf area than tree and shrub species of the same genus. Vines allocate fewer resources to xylem since they are not freestanding and instead depend on other plants or structures for support. To compensate hydraulically for the reduced xylem area, vines have long and wide vessels. However, that study used specimens from a botanical garden and not a natural habitat. In addition, the mechanical strength of the test specimens was not directly measured.

Wagner et al. (1998) compared two pairs of chaparral shrubs in a similar habitat. *Adenostoma sparsifolium* had significantly greater mean and maximum vessel diameters, corresponding to a 34% greater vessel lumen area and a twofold greater $K_{s\ max}$ than *A. fasciculatum*. As a result, *A. sparsifolium* had a 14% smaller stem wood density, 37% smaller modulus of elasticity (MOE), and 30% smaller modulus of rupture (MOR). Similar trade-offs occurred between *Ceanothus megacarpus* and *C. spinosus*. However, the hydraulic conductivity and mechanical strength tests of a given species were not performed on the same segments. In fact, the branches for each test came from different sites.

Acer negundo, *A. saccharinum*, and *A. rubrum* are included in section *Rubra* Pax (Gelderen et al., 1994). *Acer nigrum* Michx. f. and *A. saccharum* Marsh. are in section *Acer*, series *Saccharodendron* (Rafinesque) Murray (Gelderen et al., 1994). Of the five species, *A. negundo* has been reported as the most ruderal, the fastest growing, the shortest-lived, the least shade tolerant (Barnes and Wagner, 1981; Voss, 1985), and as having very weak wood (Preston, 1961). *Acer saccharinum* and *A. rubrum* are considered indistinguishable by the lumber industry and are known as ''soft maple.'' They both are rather fast growing, rather shade intolerant and moderately long-lived, and are most common at moist or swampy lowland sites. At the ecological extreme are the two ''hard maple'' species, *A. nigrum* and *A. saccharum*, which are slow-growing, highly shade-tolerant and long-lived members of beech–maple and other climax forests (Preston, 1961; Barnes and Wagner, 1981; Voss, 1985).

Previous work on four of these species was done on isolated

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wood segments in the green state (moisture content of 58–66%; U.S. Forest Products Laboratory, 1999). The specific gravity of *Acer saccharum*, *A. nigrum*, *A. rubrum*, and *A. saccharinum* was 0.56, 0.52, 0.49, and 0.44, respectively. Similarly, the MOE and MOR were greatest for *A. saccharum* and least for *A. saccharinum*.

The current study examined the five congeneric tree species that are native to the same site to determine if trade-offs occur in hydraulic properties and mechanical strength. Anatomical characteristics were examined to determine the structural basis for differences between species. It was hypothesized that there would be an inverse relationship between water conductive properties (especially $K_{s\ max}$) and stem mechanical strength (MOE and MOR) across the genus. It was further hypothesized that the faster-growing, more ruderal species would have greater water conductive abilities (*A. negundo* > soft maples > hard maples) but lower mechanical strength (hard maples > soft maples > *A. negundo*) when compared to the slower-growing, more shade-tolerant species. Various anatomical measurements were made to understand the basis for any differences in the physiological parameters.

MATERIALS AND METHODS

Branches from *Acer negundo*, *A. saccharinum* L., *A. rubrum* L, *A. nigrum* Michx. f., and *A. saccharum* Marsh. were collected from Lott woodlot (42°40′22″ N, 84°28′25″ W) located in Ingham County in central southern lower Michigan (elevation 283–296 m a.s.l.). All sampled trees were within 1 km of one another within an undeveloped natural area under the management of Michigan State University. The diversity of soil type, topography, and seed bank led Frye (1976) to divide the site into 10 distinct microhabitats. These range from dry upland beech–maple forest in the north, to the poorly drained floodplain around Felton Drain on the east.

A preliminary study of *A. nigrum* and *A. negundo*, in which six branches per individual were sampled, showed that variances between trees of a species, for the various parameters, were not statistically significant (Woodrum, 2002). Therefore, to detect differences between the five species, only one branch per individual was sampled. Ten individuals per species were sampled in late June or early July of 2000 and 10 were sampled in July or early August of 2001, for a total sample size of $N = 20$ individuals.

Branches were horizontal and from the lower crown. We cut all branches in the field several times longer than the mean maximum vessel length (36 cm), as determined by a preliminary study, to prevent introduction of embolism. At the time of collection branches were placed in opaque plastic bags with wet paper towels to prevent excessive transpiration. Bagged branches were returned to the laboratory within 1 h of collection. In the laboratory branches were recut under water, to prevent introduction of new embolism, to a final length of approximately 15 cm. Efforts were made to pick stem portions that were relatively straight, about 8 mm in diameter, unbranched, and without wounds.

Hydraulic conductivity—Measurements of conductivity and native embolism were made as described by Sperry et al. (1988). Degassed 10 mmol citric acid filtered through a 0.2-μm-mesh Gelman filter (Gelman Laboratory, Ann Arbor, Michigan, USA) was used for measurement of the flow rates onto a Sartorious ISO 9001 electronic balance (Sartorius Corporation, Edgewood, New York, USA).

Following conductivity measurements, conductive vessels were stained using 0.5% crystal violet to determine sapwood area. When crystal violet could be seen at the proximal end of the specimen, double distilled water was added to the tubing and allowed to flow through the branch segment to flush out any excess dye. Branch segments were then sealed in a plastic bag with a moist paper towel and refrigerated for up to 10 d until mechanical testing.

The mean xylem cross-sectional area and heartwood areas were measured for each segment using digital calipers. Since pith and nonconductive rings do not contribute to conductive tissue, this area was subtracted from the total cross-sectional area of the branch before conductivity calculations (Zimmermann, 1978). Hydraulic conductivity (initial and maximum) was calculated using the equation $K_h = F/(dP/dx)$ (Tyree and Ewers, 1991), where F is the water flux (in kilograms per second), and dP/dx (in megapascals per meter) is the pressure gradient causing the flow. Maximum specific conductivity was calculated as $K_s = K_{h\ max}/A_s$ (Tyree and Ewers, 1991), where A_s is the sapwood cross-section area (in square meters). The percentage of embolism was calculated via the equation % embolism $= \{(K_{h\ max} - K_{h\ initial})/K_{h\ max}\} \times 100\%$.

Leaf areas were measured using a LI-COR portable area meter model LI-3000 (LI-COR, Lincoln, Nebraska, USA). The leaf area of those leaves distal to the segment was added to one-half the leaf area of those leaves on the segment. The total distal leaf area was used to calculate leaf specific conductivity via the equation $LSC = K_h/A_l$ (Tyree and Ewers, 1991), where A_l is the total leaf area (in square meters). The Huber value, defined as $HV = A_s/A_l$ (Tyree and Ewers, 1991) was also calculated.

Biomechanics—Branch segments were kept in the cooler at a temperature of approximately 18°C during transport from refrigerator to the Instron Universal Machine (model 4202, serial # 537, Canton, Massachusetts, USA). Mechanical strength testing was conducted on the Instron using a four-point test with a compression load cell of 45.46 kg (Pruyn et al., 2000). Bark was retained during testing except for 1 cm at the ends of branch segment, where the Sperry apparatus had been attached during hydraulic conductivity measurements. The span length (L), the distance between the two supported ends, was 13.5 cm. The load was applied at two points along the span length. The distance between one supported end and the nearest loading point (a in the equations below) was 4.5 cm. The load cell was applied at a crosshead speed of 20 mm/min. Stress vs. strain data was collected every 0.1 mm using Cy4200 software on a computer networked with the Instron. Branches were stressed until the load reached a maximum value (asymptote of the curve).

Due to the size, water content (assumed to be saturated), and juvenility of the wood, the branches did not rupture. The point at which the bending moment reaches a maximum is the critical strain and is the limit of the elastic range (Spatz and Bruechert, 2000). Therefore, modulus of rupture was estimated using the load value at the asymptote of the curve and the equation $MOR = P_{max}ar_{major}/I$ (modified from Ugural, 1991), where P_{max} is the load at failure, r_{major} is the major radius of the branch segment minus the pith, and I is the second moment of the cross-sectional area for a hollow ellipse $I = \pi(r_{major} \times r_{minor}{}^3)/4$, as described in Gere and Timoshenko (1984). Flexural stiffness (EI) was calculated using the slope (P/V) of the linear portion (elastic portion) of the curve and the equation $EI = P/V\ (a^2/12)(3L - 4a)$ (Gere and Timoshenko, 1984). Flexural stiffness was divided by second moment of area to obtain the modulus of elasticity (E) of the wood.

In order to determine any correlation between estimated green MOR (MOR_G) and actual dried MOR (MOR_D) a subset of six branches from each species collected in 2000 was taken only through its elastic phase and then load was released, not compromising the property of the wood. These branches were then oven dried at 60°C in a Lipshaw incubator oven (model #249, Lipshaw Manufacturing Company, Detroit, Michigan, USA) until the mass of the segment was stable to one-hundredth of a gram from one day to the next. They were then fractured using a four-point test and MOR_D was calculated.

Anatomical study—*Macerations*—Shavings of xylem from bark to pith from eight segments of each species collected in 2000 and all samples from 2001 were placed in Jeffries solution (1 : 1 10% nitric acid : 10% chromic acid) in a 60°C oven for 4 d. Macerations were stained with safranin and analyzed using a light microscope interfaced with a CCD video camera and multi-scan analog monitor (model VE 1000 CCD, Dage-MTI, Michigan City, Indiana, USA). NIH Image 1.5 software was used to measure cell wall thickness and lumen diameters of 25 vessels, 10 fibers, and 10 axial parenchyma cells from each segment. Fiber cell wall thickness : lumen diameter ratios were calculated, and a random cell count of 300 was used to determine the relative abundance of each cell type.

TABLE 1. Hydraulic conductivity (means ± 1 SE). Units for $K_{h\ initial}$ (kg · m^{-1} · MPa^{-1} · s^{-1}) are 10^{-5}. Units for $K_{h\ max}$ (kg · m^{-1} · MPa^{-1} · s^{-1}), HV (m^2/m^2), and LSC (kg · MPa^{-1} · s^{-1} · m^{-1}) are 10^{-4}. $N = 20$ for $K_{h\ initial}$, $K_{h\ max}$, and percentage of embolism. $N = 18$ for $K_{s\ max}$ (kg · MPa^{-1} · s^{-1} · m^{-1}), HV, and LSC. Groups with letters in common are not significantly different at $P = 0.05$.

Group Species	$K_{h\ initial}$	$K_{h\ max}$	Percentage of embolism	$K_{s\ max}$	HV	LSC[a]
Ruderal						
Acer negundo	4.66 ± 0.793^A	3.36 ± 1.72^A	55.2 ± 7.58^A	8.56 ± 1.61^A	1.24 ± 0.158^A	7.80 ± 1.52
Soft maples						
Acer saccharinum	4.21 ± 0.751^A	0.919 ± 0.0692^B	55.0 ± 6.97^A	4.69 ± 0.476^A	1.70 ± 0.402^A	5.50 ± 1.66
Acer rubrum	4.36 ± 0.760	1.17 ± 0.155	54.7 ± 7.21^A	5.85 ± 1.03^A	1.21 ± 0.149^A	4.50 ± 0.813
Hard maples						
Acer nigrum	4.76 ± 0.766^A	1.00 ± 0.0683^A	54.1 ± 6.46^A	4.53 ± 0.467^A	1.14 ± 0.166^A	3.26 ± 0.695
Acer saccharum	4.91 ± 0.833	1.51 ± 0.154	61.1 ± 5.77^A	6.24 ± 0.860^A	1.13 ± 0.191^A	5.03 ± 0.937
P_{groups} value	0.9970	<0.0001	0.9182	0.2936	0.2972	0.0180

[a] Friedman's two-way nonparametric ANOVA.

Cross sections—Eight branches from each species collected in 2000 and all 10 branches per species collected in 2001 were used for further analysis of anatomical differences. Transverse sections approximately 40 μm thick were made from the middle of each branch segment using a sliding microtome (American Optical Company, Buffalo, New York, USA). Sections were taken through a dehydration series of ethanol and xylene (modified from Johansen [1940]) and mounted on slides using Permount.

Sections were analyzed using a light microscope interfaced with a CCD video camera and multi-scan analog monitor. NIH Image 1.5 analysis was performed on a pie-shaped wedge, bordered by rays, of a lateral side of each branch cross section, to measure vessel lumen areas, fibers per unit area, and ray parenchyma per unit area in the wood. In addition, two samples from each species were sectioned, stained with phloroglucinol, and analyzed under a compound light microscope to qualitatively determine the presence or absence of lignin in ray parenchyma cell walls.

General morphology—Green wood density was determined for all branch segments. Mass was determined using an electronic balance, and volume displacement was quantified in a graduated cylinder. The dry wood density of the six branches from 2000 that were oven dried was also calculated in order to access any correlation between green and dried wood density.

Stem diameter, xylem diameter, pith area, and cortex thickness were measured with a digital caliper. The number of growth rings and the percentage of rings that were conductive were determined with a compound light microscope.

Data analysis—All data were analyzed using SAS, version 8.1. ANOVAs were run to identify any differences between species for all variables tested, followed by contrasts. Friedman's two-way nonparametric ANOVA was used for LSC where data could not be normalized. In this case, contrasts were unavailable. Trendlines were plotted to attain R^2 values.

RESULTS

Hydraulic conductivity—$K_{h\ max}$ was different between groups ($P < 0.0001$). Contrasts showed the ruderal species, *A. negundo*, had the greatest $K_{h\ max}$ of the three groups. Surprisingly, $K_{h\ max}$ values of hard maples were significantly greater than in soft maples ($P = 0.0446$). Leaf specific conductivity was also significantly different between groups ($P = 0.0180$). Unfortunately, non-normal data required the use of Friedman's two-way ANOVA for which no contrasts are available. However, mean LSCs were in the order ruderal > soft maples > hard maples. Higher LSCs indicate greater hydraulic sufficiency of stems relative to leaf area. No significant differences were found between groups for most of the hydraulic parameters including $K_{h\ initial}$, percentage of embolism, $K_{s\ max}$ or HV (Table 1).

Biomechanics—Significant differences were found for all mechanical variables tested except for MOR_D. The EI for the ruderal species was the lowest, as expected, and the hard maples had a significantly greater EI than either the ruderal or soft maples ($P < 0.0001$) (Table 2).

Hard maples had a significantly greater MOE ($P = 0.0337$) and MOR_G ($P = 0.0362$) than the soft maples, as predicted. Also as expected, MOR_G was smaller in *A. negundo* than in

TABLE 2. Biomechanics (means ± 1 SE). Units for flexural stiffness (EI) (N/mm^2) and modulus of elasticity (MOE) (N/mm^2) are 10^5 and 10^4, respectively. $N = 20$ for EI, second moment of area (I) (N/mm^4), and MOE. $N = 14$ for green modulus of rupture (MOR_G) (N/mm^2). $N = 6$ for dry modulus of rupture (MOR_D) (N/mm^2). Groups with letters in common are not significantly different at $P = 0.05$.

Group Species	EI	I	MOE	MOR_G	MOR_D
Ruderal					
Acer negundo	6.69 ± 0.414^A	25.4 + 2.87^B	3.31 ± 0.523^{A,B}	505 ± 61.1^A	650 + 56.6^A
Soft maples					
Acer saccharinum	6.80 ± 0.532^A	30.3 ± 3.52^A	2.78 ± 0.346^A	473 ± 56.1^A	541 + 36.6^A
Acer rubrum	8.23 ± 0.787	34.6 ± 4.68	3.23 ± 0.481	606 ± 73.3	539 + 76.3
Hard maples					
Acer nigrum	9.06 ± 0.637^B	31.5 ± 4.13^{A,B}	3.72 ± 0.431^B	668 ± 69^B	832 + 140^A
Acer saccharum	11.2 ± 0.558	42.2 ± 6.31	4.32 ± 0.791	653 ± 85.1	807 + 256
P_{groups} value	<0.001	<0.0001	<0.0001	<0.0001	0.1370

TABLE 3. Anatomy (means ± 1 SE). $N = 18$ for percentage of ray parenchyma, mean vessel lumen diameter (VL), and mean fiber lumen diameter (FL). $N = 8$ for fiber cell wall thickness (FW). Groups with letters in common are not significantly different at $P = 0.05$.

Group Species	Ray parenchyma (%)	VL (μm)	FL (μm)	FW (μm)
Ruderal				
Acer negundo	5.28 ± 0.826^{A}	26.4 ± 0.646^{A}	10.2 ± 0.354^{A}	1.00 ± 0.051^{A}
Soft maples				
Acer saccharinum	5.40 ± 0.849^{A}	25.9 ± 0.564^{A}	10.7 ± 0.330^{A}	1.17 ± 0.155^{A}
Acer rubrum	6.46 ± 1.11	24.5 ± 0.530	9.74 ± 0.269	1.36 ± 0.127
Hard maples				
Acer nigrum	7.16 ± 1.36^{A}	23.6 ± 0.487^{A}	7.80 ± 0.312^{B}	1.22 ± 0.113^{A}
Acer saccharum	8.01 ± 1.52	24.4 ± 0.636	8.42 ± 0.351	1.33 ± 0.180
P_{groups} value	0.0642	0.8748	<0.0001	0.2736

the hard maples ($P = 0.0060$). Surprisingly, MOE of the ruderal maple was not significantly different from the hard maples. However, that result depends upon calculations of *I;* when cortex and pith were included in *I*, the MOE of *A. negundo* was significantly smaller than in the hard maples.

No significant difference between groups was found in MOR_D, that is, in stems that were oven dried. Nor was there a statistically significant correlation between MOR_G and MOR_D (Table 2).

Anatomical study—*Macerations*—Fiber lumen diameter was significantly different between groups ($P < 0.0001$). Hard maples produced fiber lumens that were much narrower in diameter than those of soft maples and the ruderal species ($P < 0.0001$). Although the ratio of fiber cell wall thickness : lumen diameter was smallest in the ruderal group (0.094 ± 0.009) and greatest in hard maples (0.153 ± 0.028) it was not significantly different at $P = 0.05$ due to statistically similar fiber cell wall thickness among groups (Table 3).

No significant difference was found between groups for vessel cell wall thickness, vessel lumen diameter, axial parenchyma lumen diameter, or axial parenchyma cell wall thickness. Vessel frequency ranged from 211 ± 11.9 mm^{-2} in *A. negundo* to 233 ± 11.8 mm^{-2} in soft maples, but was not significantly different between groups (data not shown).

Transverse sections—Although there was not a statistically significant difference between groups in percentage of cross sectional area composed of ray parenchyma, the *P* value was only 0.0642. The means for hard maples were greater than that of the other two groups and lowest in the ruderal species (Table 3).

No significant difference between groups was present for percentage of vessel lumen area, maximum vessel diameter, minimum vessel diameter, or hydraulic diameter. Values for percentage of vessel lumen area ranged from 10.9 ± 0.716% in hard maples to 13.0 ± 1.02% in *A. negundo*. Maximum vessel lumen diameter was greatest in *A. negundo* (47.6 ± 3.76 μm) and smallest in hard maples (44.3 ± 5.27 μm).

Percentage of fiber area was nearly identical in all groups. Hard maples had an average of 81% of cross-sectional area composed of fibers, while the ruderal group had 82%.

Qualitative analysis of lignin in ray parenchyma cell walls revealed that all five species were similar in having lignified ray cells. Furthermore, the relative amount of staining was similar for ray parenchyma and vessels of the same branch segment.

General morphology—As expected, both the green and dry wood densities were significantly different between groups, with hard maples > soft maples > ruderal. Hard maples had significantly greater distal leaf area than the soft maples (Table 4).

Both pith area and cortex thickness were significantly different between groups (Table 4). However, no significant differences between groups were found for stem or xylem diameter, number of xylem growth rings, number of conductive growth rings, and conductive xylem area (data not shown).

Trade-offs—Contrary to our hypothesis, there was no inverse relationship found between mechanical strength param-

TABLE 4. General morphology (means ± 1 SE). $N = 20$ for pith area, number of growth rings, and distal leaf area. $N = 18$ for $density_G$. $N = 6$ for $density_D$. $N = 10$ for cortex thickness. Groups with letters in common are not significantly different at $P = 0.05$.

Group Species	Pith area (mm^2)	No. growth rings	$Density_G$ (g/cm^3)	$Density_D$ (g/cm^3)	Distal leaf area (m^2)	Cortex thickness (mm)
Ruderal						
Acer negundo	5.23 ± 0.451^{A}	4.30 ± 0.341^{A}	0.962 ± 0.018^{A}	0.470 ± 0.020^{A}	25.6 ± 2.11^{A,B}	0.450 ± 0.026^{A,B}
Soft maples						
Acer saccharinum	4.12 ± 0.437^{B}	5.65 ± 0.357^{A}	1.03 ± 0.014^{B}	0.560 ± 0.029^{B}	21.6 ± 2.29^{A}	0.507 ± 0.038^{A}
Acer rubrum	3.07 ± 0.321	6.55 ± 0.713	1.07 ± 0.016	0.602 ± 0.026	26.1 ± 2.23	0.528 ± 0.044
Hard maples						
Acer nigrum	4.05 ± 0.275^{B}	6.95 ± 1.49^{A}	1.09 ± 0.014^{C}	0.723 ± 0.039^{C}	27.8 ± 2.54^{B}	0.400 ± 0.040^{B}
Acer saccharum	3.25 ± 0.299	5.70 ± 0.417	1.06 ± 0.013	0.692 ± 0.024	35.4 ± 3.10	0.340 ± 0.039
P_{groups} value	0.0010	0.0981	<0.0001	<0.0001	0.0012	0.0064

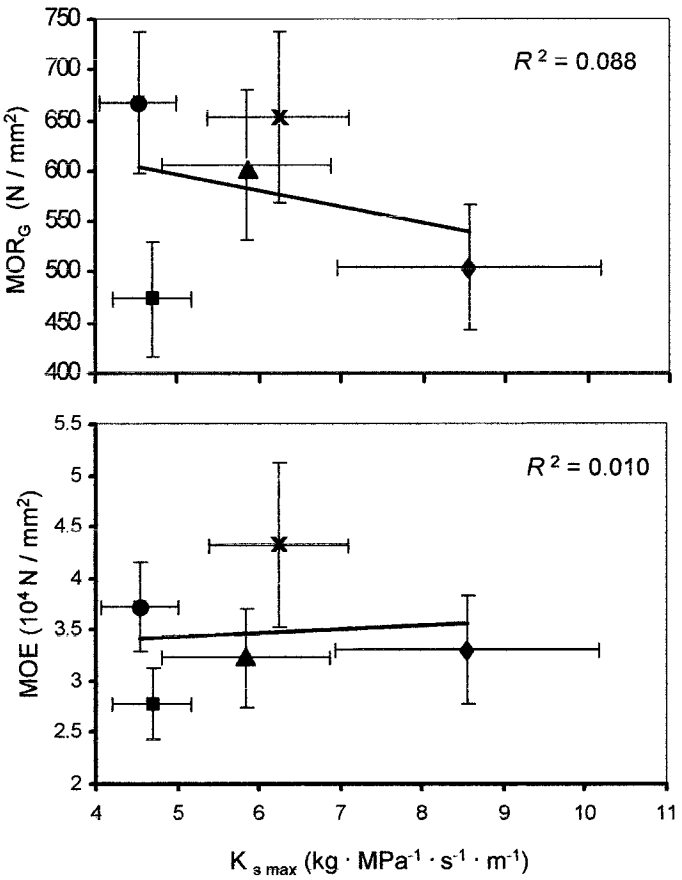

Fig. 1. Green modulus of rupture (MOR_G, top panel) and modulus of elasticity (MOE, bottom panel) as functions of maximum specific conductivity ($K_{s\ max}$). Vertical lines are + 1 SE, N = 18. ◆, *A. negundo*; ●, *A. nigrum*; ▲, *A. rubrum*; ■, *A. saccharinum*; and **x**, *A. saccharum*.

eters and conductive efficiency. For instance, MOE and $K_{s\ max}$ had an R^2 value 0.010 (Fig. 1, bottom panel). Similarly, there was no relationship between MOR_G and $K_{s\ max}$ (R^2 = 0.088) (Fig. 1, top panel).

Percentage of fiber area in a cross section was inversely correlated with differences in MOE_G (R^2 = 0.46) and MOR_G (R^2 = 0.456). However, fiber lumen diameter was a better predictor of MOE_G (R^2 = 0.681). Fiber cell wall thickness : lumen diameter was highly correlated with MOR_G (R^2 = 0.723), but fiber lumen diameter alone accounted for more variation in MOR_G, with an inverse relationship (R^2 = 0.875) (Fig. 2). Percentage of ray parenchyma in the cross-sectional area was also highly correlated with MOE_G (R^2 = 0.801) (Fig. 3).

DISCUSSION

In this study differences in mechanical properties were related to fiber anatomy. This differs from studies in which mechanical differences were related to vessel diameter (Ewers and Fisher, 1991; Gartner, 1991a, b; Chiu and Ewers, 1992; Wagner et al., 1998). Because the three groups were not significantly different in $K_{s\ max}$, the lack of a negative linear relationship between $K_{s\ max}$ and MOE_G is not surprising. It is important to realize that several of those studies compared contrasting growth habits within a genus, and Wagner et al.

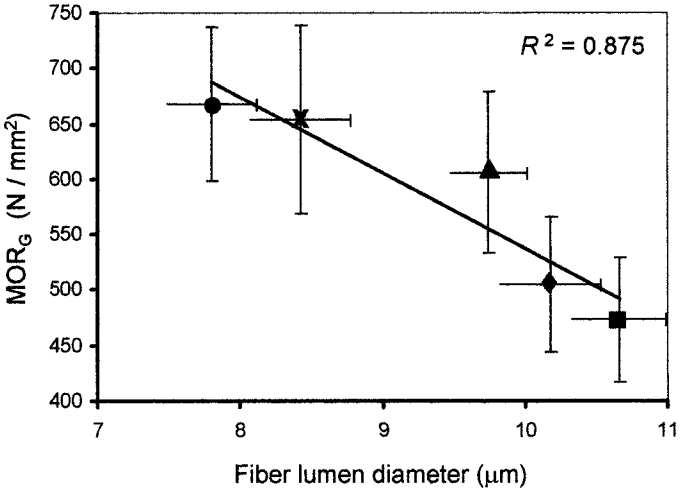

Fig. 2. Green modulus of rupture (MOR_G) vs. fiber lumen diameter in five species of *Acer*. Vertical lines are ± 1 SE, N = 18. Symbols as in Fig. 1.

(1998) contrasted deep rooted vs. shallow rooted species that varied in many water use characteristics. In contrast, all the maple species in the present study were shallow-rooted trees in a fairly mesic environment.

The relative trends in biomechanical data for green branch tips from this experiment were consistent with data for dried lumber published by the U.S. Forest Products Laboratory (1999). *Acer saccharum* had the highest EI, MOE, and MOR followed by *A. nigrum*, *A. rubrum*, and *A. saccharinum*, respectively. However, as a statistically significant linear relationship between MOR_G and MOR_D was not found in the current research, it is not recommended that strength values of dried wood be used as predictors for strength in the green state.

It was surprising that MOE of *A. negundo* was not significantly smaller than soft and hard maples. However, the calculation of MOE is dependent on the measurement of *I*, since MOE was derived by EI divided by *I*. Although *I* was controlled for in the field by collecting branches approximately 8 mm in diameter, only the xylem area was used in calculating

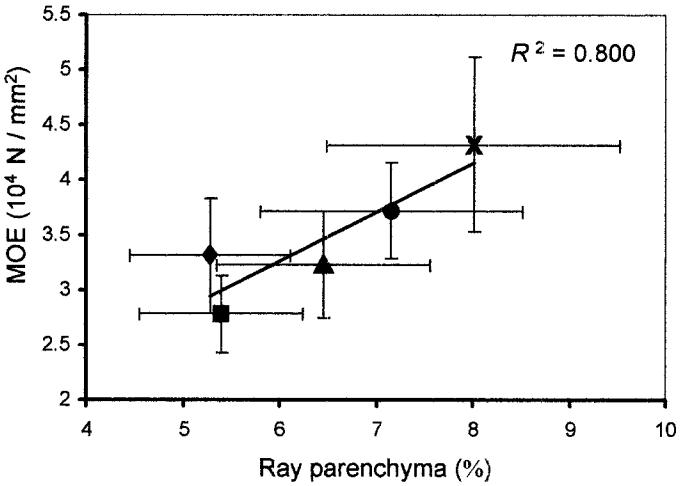

Fig. 3. Modulus of elasticity (MOE) vs. percentage of cross-sectional area of ray parenchyma in five species of *Acer*. Vertical lines are ± 1 SE, N = 18. Symbols as in Fig. 1.

branch second moment of area in this study based on findings by Wagner et al. (1998). This could easily explain differences in EI between soft and hard maples found here, as the soft maples had significantly thicker cortex. It might also explain why MOE for *A. negundo* was greater than expected. Pith area in that species was significantly larger and thus second moment of area was significantly smaller than for soft and hard maples. When MOE of the branch segments from 2001 were determined using an *I* value that included both pith and cortex, the MOE of *A. negundo* was smaller than the other four species, as hypothesized. Even so, the expected trade-off was not seen when $K_{s\ max}$ was regressed with the revised MOE.

Significant differences in LSC can be attributed to differences in distal leaf area as $K_{s\ max}$ was not statistically different between species. Greater distal leaf areas were found in the shade-tolerant hard maples, lowering their LSC values. Additionally, shaded environments require less water use by leaves and so the relationship between leaf area and xylem area may be altered.

There was no difference between groups in percentage of area composed of fibers, but the number of cells within that area was not determined. Although cell wall thickness was not significantly different between species, fiber lumen diameter was significantly smaller in hard maples. It might be expected then that hard maples would have a greater density of fibers.

This is the first time that a high correlation between percentage of ray parenchyma and four-point bending MOE has been shown. In contrast, a positive correlation between volume fraction of rays and transverse or radial tensile strength is well established (Schniewind, 1959; Beery et al., 1983; Burgert et al., 2000). However, these relationships may be coincidental. Hard maples are slow-growing, long-lived trees. This life history may require a greater volume of ray parenchyma in order to store adequate amounts of starch for reserve in case of prolonged environmental stresses. The narrower fiber lumens may more than compensate for the potential loss in structural support from high amounts of parenchyma.

Although a qualitative study was conducted on the presence of lignin in the ray parenchyma, a quantitative study would be more useful. Chafe (1974) and Murakami et al. (1999) differentiated between two types of ray parenchyma cells: those that are adjacent to vessels, contact cells, and those that are not in contact with vessels. Both studies showed that complete lignification of the contact cells was delayed until heartwood formation. Conversely, ray parenchyma not associated with vessels differentiated during the same year as their formation. Thus, the trend of increasing ray parenchyma area and mechanical strength from soft to hard maples may be explained, for instance, by a greater amount of non-vessel-associated ray parenchyma cells in hard maples.

One important factor to consider in this study is microhabitat. All the specimens were from the same 108.7-ha woodlot, where general climate and photoperiod are similar. However, there exist many microhabitats in the area as categorized by Frye (1976). Wood density is correlated to a tree's ability to tolerate shade and its demographic habitat (Lawton, 1984). Shade-tolerant species have more dense wood than shade-intolerant species. This correlation was supported by the distribution of the five species within the woodlot. *Acer saccharinum* and *A. negundo* were found in greater light microenvironments than *A. saccharum* and *A. nigrum*. Thus, environmental factors such as soil moisture, light intensity, and extent of disturbance differed somewhat for each species. In order to reduce possible effects from microhabitat differences, samples collected in summer 2001 were all sun branches.

This study shows that there is not a direct trade-off between conductivity and mechanical strength, at least in the genus *Acer*. This could happen if water transport is not limiting, and subsequently there is no selection for wider vessel lumen diameters and thus, greater $K_{s\ max}$. It is also possible that the division of functional roles into separate cell types, namely, vessels and fibers, facilitates the decoupling of the water transport and mechanical roles.

LITERATURE CITED

BARNES, B. V., AND W. H. WAGNER, JR. 1981. Michigan trees. University of Michigan Press, Ann Arbor, Michigan, USA.

BEERY, W. H., G. IFJU, AND E. MCLAIN. 1983. Quantitative wood anatomy: relating anatomy to transverse tensile strength. *Wood Fiber Science* 15: 83–86.

BURGERT, I., D. ECKSTEIN, AND A. BERNASCONI. 2000. The strength and volume fraction of rays in trees subjected to radial tensile stresses. *In* H.-C. Spatz and T. Speck [eds.], Plant biomechanics 2000. Proceedings of the third plant biomechanics conference, 413–419. Georg Thieme Verlag Stuttgart, New York, New York, USA.

CHAFE, S. C. 1974. Cell wall formation and ''protective layer'' development in the xylem parenchyma of trembling aspen. *Protoplasma* 80: 335–354.

CHIU, S.-T., AND F. W. EWERS. 1992. Xylem structure and water transport in a twiner, a scrambler, and a shrub of *Lonicera* (Caprifoliaceae). *Trees: Structure and Function* 6: 216–224.

EWERS, F. W., AND J. B. FISHER. 1991. Why vines have narrow stems: histological trends in *Bauhinia* (Fabaceae). *Oecologia* 88: 233–237.

FRYE, D. M. 1976. A botanical inventory of sandhill woodlot, Ingham county, Michigan. I. The vegetation. *Michigan Botanist* 15: 131–140.

GARTNER, B. L. 1991a. Stem hydraulic properties of vines vs. shrubs of western poison oak, *Toxicodendron diversilobum*. *Oecologia* 87: 180–189.

GARTNER, B. L. 1991b. Structural stability and architecture of vines vs. shrubs of poison oak, *Toxicodendron diversilobum*. *Ecology* 72: 2005–2015.

GELDEREN, D. M., P. C. DE JONG, AND H. J. OTERDOOM. 1994. Maples of the world. Timber Press, Portland, Oregon, USA.

GERE, J. M., AND S. P. TIMOSHENKO. 1984. Mechanics of materials, 2nd ed. Pridle, Weber & Schmidt, Belmont, California, USA.

JOHANSEN, D. A. 1940. Plant microtechnique. McGraw-Hill, New York, New York, USA.

LAWTON, R. O. 1984. Ecological constraints on wood density in a tropical montane rain forest. *American Journal of Botany* 71: 261–267.

MURAKAMI, Y., R. FUNADA, Y. SANO, AND J. OHTANI. 1999. The differentiation of contact cells in the xylem ray parenchyma of *Populus maximowczii*. *Annals of Botany* 84: 429–435.

PRESTON, R. J. 1961. North American trees, 2nd ed. Iowa State University Press, Ames, Iowa, USA.

PRUYN, M. L., D. J. EWERS, AND F. W. TELEWSKI. 2000. Thigmomorphogenesis: changes in the morphology and mechanical properties of two *Populus* hybrids in response to mechanical perturbation. *Tree Physiology* 20: 535–540.

SCHNIEWIND, A. P. 1959. Transverse anisotropy of wood: a function of gross anatomic structure. *Forest Products Journal* 9: 350–359.

SPATZ, H.-C., AND F. BRUECHERT. 2000. Basic biomechanics of self-supporting plants: wind loads and gravitational loads on a Norway spruce tree. *Forest Ecology and Management* 135: 33–44.

SPERRY, J. S., J. R. DONNELLY, AND M. T. TYREE. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* 11: 35–40.

TYREE, M. T., AND F. W. EWERS. 1991. The hydraulic architecture of trees and other woody plants. *New Phytologist* 119: 345–360.

UGURAL, A. C. 1991. Mechanics of materials. McGaw-Hill, New York, New York, USA.

U.S. FOREST PRODUCTS LABORATORY. 1999. Wood handbook: wood as an engineering material. General Technical Report FPL-GTR-113. U.S. Forest Products Laboratory, Madison, Wisconsin, USA.

VOSS, E. G. 1985. Michigan flora. Part II. Dicots (Saururaceae-Cornaceae). Cranbrook Institute of Science, Bloomfield Hills, Michigan, USA.

WAGNER, K. R., F. W. EWERS, AND S. D. DAVIS. 1998. Tradeoffs between hydraulic efficiency and mechanical strength in the stems of four co-occurring species of chaparral shrubs. *Oecologia* 117: 53–62.

WOODRUM, C. L. 2002. Hydraulic, biomechanical, and anatomical study of five tree species of *Acer*. M.S. thesis, Michigan State University, East Lansing, Michigan, USA.

ZIMMERMANN, M. H. 1978. Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany* 56: 2286–2295.