Effects of drought stress on hydraulic architecture of seedlings from five populations of green ash

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Two-year-old seedlings of green ash, Fraxinus pennsylvanica Marsh., representing five native populations from an east to west precipitation gradient, were grown under contrasting moisture regimes in the greenhouse. At midsummer and the end of the growing season, leaf areas, earlywood and latewood transverse areas, and several structural attributes of the xylem hydraulic system were compared between well-watered and drought-stressed seedlings. Xylem hydraulic capacity was essentially fixed by midsummer. Drought significantly reduced both earlywood and latewood production but had no significant effect on potentially functional xylem area (Aₚ) or flow velocity (v). The principal effect of drought on hydraulic architecture was a significant reduction in leaf area and therefore the ratio of potentially functional xylem area to unit leaf area (Aₚ/A) and leaf specific conductivity (LSC). In contrast, populations differed significantly in all measured parameters, especially under drought conditions. Path analysis of LSC and its component variables revealed that treatment differences in LSC arose primarily through differences in Aₚ contributions from variation in Aᵣ and especially flow velocity were relatively minor. In contrast, population variation in LSC could be attributed in roughly equal measure to variation in Aᵣ and Aₛ and to a lesser degree to variation in flow velocity. The covariance between Aᵣ and Aₛ was important for both treatment and population variation in LSC, suggesting a fundamental physiological linkage between these two aspects of plant hydraulic architecture. Among populations, high flow velocity tended to be associated with low Aᵣ and Aₛ values, thereby minimizing population differences in the composite character LSC. Populations differed significantly in all attributes studied, in one environment or another, but those at either end of the precipitation gradient did not differ in several presumably important structural attributes. Although plant hydraulic architecture is genetically controlled and variable in green ash seedlings, its adaptive significance cannot be considered in isolation from other factors that control plant response to water stress.

Key words: leaf specific conductivity, ecotypic variation, xylem structure.

SHUMWAY, D. L., STEINER, K. C., and ABRAMS, M. D. 1991. Effets de la sècheresse sur l’architecture hydraulique des plants d’âge de deux ans du Fraxinus pennsylvanica Marsh., représentant cinq populations indigènes recueillies le long d’un gradient de précipitation en direction est-ouest. Au milieu de l’été et à la fin de la saison de croissance, ils ont comparé les surfaces foliaires, les surfaces transverses du bois primevère et plusieurs propriétés structurales du système hydraulique du xylème chez des plantes qui ont été bien arrosées et des plantes soumises à des stress hydriques. La capacité hydraulique du xylème est essentiellement fixée vers le milieu de l’été. La sècheresse réduit significativement aussi bien la production de jeune bois que celle du bois âgé, mais reste sans effet significatif sur la surface du xylème potentiellement fonctionnelle (Aₚ) ou la vitesse du flux (v). La principale cause de la sècheresse sur l’architecture hydraulique se manifeste par une réduction significative de la surface foliaire et, par conséquent, des rapports entre les surfaces du xylème potentiellement fonctionnel par unité de surface foliaire (Aᵣ/Aₛ) et de la conductivité foliaire spécifique (LSC). Au contraire, les populations diffèrent significativement pour tous les paramètres mesurés, surtout sous les conditions de sècheresse. L’analyse du parcours du LSC et de ses variables constitutantes révèle que les différences de LSC entre les traitements proviennent de différences de Aᵣ. Les contributions venant des variations en Aᵣ et surtout de la vitesse du flux sont relativement mineures. Au contraire, les variations du LSC dans les populations peuvent être attribuées en parties à peu près égales à la variation en Aᵣ et en Aₛ, et à un moindre degré à la variation dans la vitesse du flux. La covariance entre Aᵣ et Aₛ est importante pour les deux traitements et pour la variation du LSC des populations, ce qui suggère une relation physiologique fondamentale entre ces deux aspects de l’architecture hydraulique de la plante. Parmi les populations, la vitesse du flux élevée a tendance à être associée avec de faibles valeurs de Aᵣ à Aₛ, minimisant ainsi les différences dans les populations du caractère composite LSC. Les populations diffèrent significativement pour tous les caractères étudiés dans un environnement où dans un autre, mais ceux qui sont situés à une extrémité où l’autre du gradient de précipitation ne montrent pas de différences pour plusieurs caractéristiques importantes. Bien que l’architecture hydraulique de la plante soit génétiquement contrôlée et variable chez les jeunes plants de frêne, cette expression adaptative ne peut pas être considérée de façon isolée par rapport aux autres facteurs qui contrôlent la réaction de la plante aux stress hydriques.

Mots clés : conductivité foliaire spécifique, variation écotypique, structure de xylème.

[Traduit par la rédaction]

Introduction

Transpirational water loss from woody plants depends in part upon xylem hydraulic capability and, therefore, stem anat-

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omy and morphology. For example, Tyree and Sperry (1988) have presented evidence that woody plants may normally transpire near-maximal rates determined by the water supply capacity of the stem. In their models, higher rates of transpiration could cause "catastrophic" loss of xylem function.
through cavitation, leading to drought-induced leaf loss and consequent restoration of the balance between transpiration demand and water supply capability. Thus, stem structure, by limiting the maximal "safe" level of transpiration (and indirectly photosynthesis) under a given water potential gradient, may impose constraints on processes that affect a plant’s ecological status. Even across distinct relations taxa, which presumably differ in many ecologically important respects, xylem structure may account for some of the variation in species relative dominance along a moisture gradient (Guthrie 1989).

The relative efficiency with which xylem can provide water to the foliage is conventionally expressed with leaf specific conductivity (LSC), defined as the water flow rate through a stem section per unit potential gradient per unit leaf area supported (Zimmermann 1978). Alternatively, LSC can be viewed as the inverse of foliar display per unit water supply capacity. The critical importance of a balance between a plant’s capacities to transport and lose water suggests a close physiological link between xylem and leaf development. This may involve foliar regulation of the production of vascular cambium and its earlywood derivatives (Larson 1976) or a somewhat more complex reciprocal feedback relationship, as suggested by Kauffmann and Troendle (1981). LSC displays considerable variability within individual species and plants (Ewers and Zimmermann 1984; Salleo et al. 1985; Sellin 1987; Tyree et al. 1983), but we know of no study in which specific environmental or genetic control of LSC has been demonstrated experimentally.

Since a tree can transpire no more water than its xylem is capable of supplying, a high LSC would seem at first to have obvious selective advantages. LSC can be enhanced through the production or maintenance of greater sapwood cross-sectional area, or the production of sapwood with greater porosity. But each alternative represents an adaptive cost to the plant, the former in growth or maintenance respiration and the latter as risk of mechanical failure of the stem. Thus, it would appear to be most advantageous for a tree to have neither more nor less water supply capacity than is needed by the transpirational demands of its foliage within a particular environment. This leads to the hypothesis that plant hydraulic architecture should vary ecologically within a species whose natural occurrence spans a significant precipitation gradient.

We observed that hypothesis by examining variability in the relationship between xylem hydraulic conductivity and supported leaf area for 2-year-old seedlings of green ash, Fraxinus pennsylvanica Marsh., grown in contrasting moisture regimes. The seedlings were progenies from natural stands located along a precipitation gradient across the rather large east–west distribution of the species in North America. We hypothesized that plants would adjust to water stress to maximize the capability of the xylem to supply water to the foliage and that the nature and degree of this adjustment would differ by population in accordance with the moisture regimes of their original habitats.

### Materials and methods

Progenies from five wild populations of green ash, representing an east to west transect through the natural distribution of the species, were grown from seed for 2 years in 8-L containers. In each population, seed had been collected from three or four female trees that presumably had been pollinated by a representative sample of surrounding males (the species is dioecious). Population designations and geographic locations are NY (New York), OH (Ohio), IL (Illinois), NE (Nebraska), and SD (South Dakota). These populations lie within a narrow band of latitude from 40 to 43° N but over a longitudinal range of 76 to 103° W (Table 1).

Seedlings were grown in the greenhouse under well-watered conditions during 1989, except for a 17-day drought at the end of the growing season (Abrams et al. 1990). Beginning April 15, 1990, following winter dormancy but before bud burst, six to eight seedlings from each population were randomly assigned to one of two watering regimes administered on a greenhouse bench. Predawn leaf water potential was measured for a random sample of one leaf per tree from five trees per treatment at two times when soil began to dry. Only two determinations of predawn leaf water potential were made to minimize leaf area removal. Plants were watered to container capacity to maintain a predawn water potential above −0.40 MPa in well-watered seedlings and above −0.60 MPa in droughted seedlings. The drying cycles were approximately 1 week in length for droughted plants. The first drying cycle began at bud swell (the week of April 25, 1989) and continued throughout the duration of the experiment.

Trees were harvested at the end of 6 weeks (midsummer) and then at 16 weeks (end-of-season). Because of the limited number of seedlings, only trees representing the IL (n = 6), NE (n = 8), and SD (n = 7) populations were sampled at midsummer. All populations were represented in the end-of-season harvest. After measuring tree heights, the leaves were removed and measured for area to the nearest 0.1 cm² (Li-Cor 3000 leaf area meter). Stem sections were prepared for hydraulic measurements by removing basal stem section of 150 mm in length with the entire seedling under water to reduce the risk of introducing air into the xylem. Stem sections were then fitted with plastic tubing and neoprene rubber seals, and a pressure gradient of 0.14 MPa/m was used to establish steady-state flow in the stem segments. Distilled water was filtered and then deaerated in-line with an apparatus similar in design to that described by Kelso et al. (1963). In contrast to Zimmermann (1978), we found no need to use a dilute solution of KCl to sustain constant flow rate in green ash stem segments over time periods used in this study. Steady-state volume flow rate (q) was measured by collection in graduated cylinders over a 10-min time interval, and the flow rate (mm²·s⁻¹) was calculated.

An electrolyte (KCl) was then injected with a syringe into the water stream and its passage timed by the change in electrical resistance of the output water stream to calculate the flow velocity (mm·s⁻¹). Care was taken to minimize the increase in pressure in the upstream water

Table 1. Geographic origin and normal annual precipitation and pan evaporation for populations whose seedling progenies were studied in this experiment

<table>
<thead>
<tr>
<th>Pop. No.</th>
<th>State</th>
<th>County</th>
<th>Lat. N</th>
<th>Long. W</th>
<th>Precipitation</th>
<th>Pan evaporation</th>
</tr>
</thead>
<tbody>
<tr>
<td>201</td>
<td>NY</td>
<td>Dutchess</td>
<td>41.80</td>
<td>75.53</td>
<td>115.6</td>
<td>75</td>
</tr>
<tr>
<td>249</td>
<td>OH</td>
<td>Licking</td>
<td>39.92</td>
<td>82.42</td>
<td>105.2</td>
<td>82</td>
</tr>
<tr>
<td>161</td>
<td>IL</td>
<td>Mason</td>
<td>40.50</td>
<td>90.00</td>
<td>85.2</td>
<td>89</td>
</tr>
<tr>
<td>405</td>
<td>NE</td>
<td>Stanton</td>
<td>42.00</td>
<td>97.08</td>
<td>66.8</td>
<td>100</td>
</tr>
<tr>
<td>273</td>
<td>SD</td>
<td>Full River</td>
<td>43.47</td>
<td>103.35</td>
<td>47.8</td>
<td>110</td>
</tr>
</tbody>
</table>

*Compare Steiner et al. (1988).*
TABLE 2. Treatment means on a per plant basis for foliage and xylem characteristics at midsummer and end-of-season harvests

<table>
<thead>
<tr>
<th>Variable</th>
<th>Midsummer</th>
<th>End-of-Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Well watered</td>
<td>Droughted</td>
</tr>
<tr>
<td></td>
<td>(n = 12)</td>
<td>(n = 9)</td>
</tr>
<tr>
<td>A_L</td>
<td>2732b</td>
<td>2174b</td>
</tr>
<tr>
<td>A_w</td>
<td>3.54b</td>
<td>3.11b</td>
</tr>
<tr>
<td>A_s</td>
<td>12.39b</td>
<td>2.68c</td>
</tr>
<tr>
<td>A_v</td>
<td>0.47c</td>
<td>0.55a</td>
</tr>
<tr>
<td>LSC</td>
<td>3.05ab</td>
<td>4.13a</td>
</tr>
<tr>
<td>A_v to A_s</td>
<td>1.79bc</td>
<td>2.76a</td>
</tr>
<tr>
<td>v</td>
<td>23.69a</td>
<td>21.44a</td>
</tr>
</tbody>
</table>

Note: Means in each row followed by the same letter were not significantly different using Fisher's LSD. A_L, leaf area (cm²); A_w, xylem area (mm²); A_s, water area (mm²); A_v, potentially functional xylem area (mm²); LSC, leaf specific conductivity × 10⁶ (µS/m); A_v to A_s, potentially functional xylem to leaf area ratio × 10⁶; v, flow velocity (mm·s⁻¹). Variables and units are explained in the text.

due to this injection and increases were observed to be less than 0.0007 MPa. The potential functional cross-sectional area of xylem (A_w) was calculated using the relationship between volume flow rate (q) and velocity (v), as described by Heine (1970)

\[ A_w = \frac{q (\text{mm}³·\text{s}⁻¹)}{v (\text{mm}·\text{s}⁻¹)} = \frac{\text{mm}²}{\text{mm}³·\text{s}⁻¹} \]

Leaf specific conductivity was calculated from the following:

\[ LSC = \frac{q L \cdot \eta}{A_w \cdot p} \text{[mm}] \]

where q is volume flow rate in mm³·s⁻¹, L is stem segment length in mm, \( \eta \) is viscosity of water at 20°C, 1000 × 10⁻¹³ µN s·mm⁻², µN·p is water pressure in mm², and A_L is leaf area in mm². Therefore, the units of LSC are

\[ \text{LSC} = \frac{(\text{mm}³·\text{s}⁻¹) (\text{mm}) (\text{s} \mu\text{N}·\text{s}·\text{mm}⁻²)}{(\text{mm}²) (\mu\text{N}·\text{mm}⁻²)} = \frac{\text{mm}}{\text{mm}²·\text{s}} \]

For convenience, the values of LSC are expressed in 1 × 10⁻¹⁰ mm².

An extension of path analysis (Wright 1934) was used to determine the relative contribution of the components A_w, A_s, and v to the variance observed in LSC for the experiment. Path analysis may be used to identify the correlations of correlated components by determining the fraction of the complete determination of a response variable that is due to each component through all paths of influence (Wright 1934; Li 1975). For the factorial design used in each experiment, source of variation contributing to the total variance in LSC was computed, and the relative contributions of the component variables were compared.

The contribution of the components A_w, A_s, and v to the observed variance in LSC was quantified using a logarithmic transformation of [3].

\[ \log (LSC) = \log(A_w) - \log(A_s) + \log(v) + \log(L \cdot \eta / p) \]

Since the term \( L \cdot \eta / p \) was constant for the experiment, the variance of log (LSC) is determined by the variance in log (A_w), log (A_s), log (v), and the covariance of the three components

\[ \sigma²(LSC) = \sigma²(A_w) + \sigma²(A_s) + \sigma²(v) - 2 \text{cov}(A_w, A_s) - 2 \text{cov}(A_w, v) - 2 \text{cov}(A_s, v) \]

where prime indicates logarithmic transformed variables. Thus the sum of squared deviations for each of the components and twice the sum of deviation products for each pair of components add to the sum of squared deviations for log (LSC) following [5].

A procedure similar to that described by Sperry et al. (1988) was used to quantify the effect of embolism on xylem hydraulic function in a small subset of end-of-season samples (n = 12; composed of at least one tree per population per treatment). For this subset of seedlings, stem segments were pressurized at a low pressure gradient of 0.02 MPa m⁻¹, water exude was collected on filter paper, and volume flow rate determined gravimetrically. Flow velocity was determined in the same way as described for the higher pressure gradient. As pressure was increased slowly on the submerged twig, bubbles appearing as embolisms in the xylem were dislodged and removed. In all stem sections examined, apparent embolism removal began at a pressure gradient greater than 0.03 MPa m⁻¹ and apparent embolism removal was complete at a pressure gradient less than 0.11 MPa m⁻¹. In this study we express the degree of embolism as the difference in potentially functional cross-sectional area (A_w) before and after the removal of embolisms.

The earlywood to latewood transition in the ring-porous green ash was very distinct and allowed determination of the relative proportions of cross-sections using a dissecting microscope and a micrometer. In addition, thin transverse sections of eight trees were prepared for determination of vessel size and number. Intrusive growth of libriform fibers was assessed by the presence of small fiber apical tips in transverse section (Esau 1977). Vessel number and diameter were determined for three microscopic fields, each of which encompassed an area defined by a 500-µm width along the boundary with 1-year xylem and a length extending from the boundary of the 1-year xylem to the cambium. The number of vessels in the earlywood and latewood portions of each tree was then calculated from the product of average vessel density and the transverse area under consideration. A total of 124 earlywood vessels and a total of 130 latewood vessels were measured in trees from the well-watered regime. A total of 87 earlywood vessels and 87 latewood vessels were measured in droughted trees. Vessel diameters (tangential direction) were measured to the nearest 10 µm with an eyepiece scale.

Results

Midsummer

At midsummer, well-watered seedlings had somewhat greater leaf area and earlywood area than drought-stressed seedlings, but the differences were not statistically significant (Table 2). On the other hand, latewood production was several-fold higher by midsummer in well-watered seedlings than in drought-stressed seedlings (P < 0.05). Although functional area (A_w) was not significantly different between well-watered
Table 3. End-of-season population means for leaf area (A_L), earlywood transverse area (A_E), latewood transverse area (A_L), and potentially functional cross-sectional area (A_P) after growth in well-watered (W-W) and droughted (DRT) conditions

<table>
<thead>
<tr>
<th>Pop.</th>
<th>W-W</th>
<th>DRT</th>
<th>W-W</th>
<th>DRT</th>
<th>W-W</th>
<th>DRT</th>
</tr>
</thead>
<tbody>
<tr>
<td>NY</td>
<td>2573</td>
<td>6.2a</td>
<td>3.9bcd</td>
<td>35.2</td>
<td>12.7d</td>
<td>0.60ab</td>
</tr>
<tr>
<td>OH</td>
<td>3882</td>
<td>5.8ab</td>
<td>4.6b</td>
<td>33.5bc</td>
<td>14.9d</td>
<td>0.81a</td>
</tr>
<tr>
<td>IL</td>
<td>4963</td>
<td>5.0bcd</td>
<td>4.4ab</td>
<td>57.5a</td>
<td>19.5cd</td>
<td>0.69ab</td>
</tr>
<tr>
<td>NE</td>
<td>4324</td>
<td>5.2abc</td>
<td>4.1abc</td>
<td>32.3bc</td>
<td>11.9d</td>
<td>0.61ab</td>
</tr>
<tr>
<td>SD</td>
<td>2543</td>
<td>3.5cd</td>
<td>3.1d</td>
<td>36.1b</td>
<td>9.4d</td>
<td>0.41b</td>
</tr>
</tbody>
</table>

Note: Means for each variable followed by the same letter are not significantly different from each other based on Fisher’s LSD, using experiment-wise error rate and pooled sample sizes where sample sizes differed. Units are same as in Table 2.

Table 4. End-of-season population means for leaf specific conductivity (LSC), functional xylem to leaf area ratio (A_E to A_L), and flow velocity after growth under well-watered (W-W) and droughted (DRT) conditions

<table>
<thead>
<tr>
<th>LSC</th>
<th>A_E to A_L</th>
<th>Velocity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pop.</td>
<td>W-W</td>
<td>DRT</td>
</tr>
<tr>
<td>NY</td>
<td>2.95abc</td>
<td>2.63bc</td>
</tr>
<tr>
<td>OH</td>
<td>2.74abc</td>
<td>5.10a</td>
</tr>
<tr>
<td>IL</td>
<td>1.67c</td>
<td>2.88abc</td>
</tr>
<tr>
<td>NE</td>
<td>2.61bc</td>
<td>4.37ab</td>
</tr>
<tr>
<td>SD</td>
<td>2.41bc</td>
<td>3.13abc</td>
</tr>
</tbody>
</table>

Note: Means for each variable followed by the same letter are not significantly different from each other based on Fisher’s LSD, using experiment-wise error rate and pooled sample sizes where sample sizes differed. Units are same as in Table 2.

and drought-stressed plants at midsummer, the ratio A_E to A_L was significantly higher in drought-stressed seedlings. Correspondingly, LSC was also higher in drought-stressed versus well-watered plants, though the difference was not statistically significant. The difference in flow velocity between well-watered and drought-stressed plants at midsummer was negligible.

End-of-season

Table 2 reports end-of-season means based upon measurements of all five populations rather than the reduced sample of three populations measured at midsummer. However, the developmental changes described below are valid for either sampling base.

Leaf area (A_L) production between midsummer and end-of-season differed by moisture treatment. Well-watered seedlings increased in leaf area by 37% (P < 0.05) from midsummer to the end of the season, while drought-stressed plants showed a negligible change (Table 2). Although latewood was present in all but one of the seedlings sampled at midsummer, earlywood transverse area (A_E) continued to increase in both moisture treatments by an average overall of 35% (P < 0.05) between midsummer and the end of the season. Not surprisingly, there were large and significant increases in A_P, in the latter portion of the growing season. LSC decreased modestly (ca. 17%) in both treatments between midsummer and end-of-season, but the apparent change was not quite statistically significant. There were no significant changes in A_E, the ratio A_E to A_L, or flow velocity (v) between the first and second harvests in either treatment considered alone or together.

At the final harvest, well-watered plants averaged 78% greater leaf area than drought-stressed plants, 31% greater earlywood area, and 188% greater latewood area (P < 0.05) (Table 2). Neither A_E nor flow velocity (v) differed significantly between treatments at the final harvest (Table 2). However, LSC was significantly greater in drought-stressed versus well-watered seedlings, primarily owing to a significantly higher ratio of A_E to A_L in drought-stressed plants.

Average tangential diameter of vessels at end-of-season was apparently unaffected by moisture regime, averaging 56.3 and 59.0 μm for earlywood and 19.9 and 22.1 for latewood. We observed no apparent differences between the treatments in the shape of vessels. On the other hand, drought-stressed seedlings showed a significant 37% reduction in number of earlywood vessels and a significant 69% reduction in number of latewood vessels. At the final harvest the total functional xylem area (A_L) occluded by embolism was 22% for well-watered plants and 80% for drought-stressed plants.

Results of population comparisons

Leaf area of well-watered plants was greater in midrange IL, NE, and OH plants than in plants from both longitudinal extremes (NY and SD) (Table 3). However, populations did not differ significantly in A_L under drought conditions. Drought-stressed seedlings from each population had less A_L than well-watered seedlings, but differences were significant (P < 0.05) only in the IL and NE seedlings.

SD seedlings had significantly less earlywood production than NY and OH seedlings under well-watered conditions. No populations differed significantly in this characteristic under drought conditions. All populations exhibited a decrease in earlywood production associated with drought (Table 3), but the effect was significant only in the case of NY plants. IL plants produced more latewood than others in both moisture treatments, though the difference was significant only under well-watered conditions. OH plants had the largest potentially functional xylem area (A_E) and SD plants the smallest, in both drought-stressed and well-watered treatments, and the differ-
ence between these populations was statistically significant in both cases.

Populations did not differ significantly in LSC or in either of its component variables, $A_{ps}$ to $A_{l}$ and velocity, under well-watered conditions (Table 4). Differences in LSC between well-watered and drought-stressed treatments were not statistically significant for any of the populations, although in all cases except NY mean LSC was higher in drought-stressed results (Table 4). Under drought conditions, OH seedlings had significantly greater LSC than NY seedlings, and this is attributable to the fact that OH seedlings had significantly greater $A_{ps}$ to $A_{l}$ than seedlings of all other populations in the drought-stressed treatment. On the other hand, OH seedlings had exceptionally low (and NE exceptionally high) flow velocities in the drought-stressed treatment.

Results of path analysis
Table 5 shows the relative contributions of moisture treat- ment (environmental), population (genetic), and treatment × population interaction effects on observed variation in hydraulic parameters that compose LSC’. Note that LSC’ represents the sum of the remaining columns using the coefficients presented in [5]. Treatment and population were equally important influences on variation in $A_{ps}$ and $A_{l}$, while $A_{l}$ was influenced principally by treatment and velocity was influenced principally by population. In the latter case, for example, the contribution of population differences to variation in velocity was about 50 times more important than the contribution of moisture treatment differences. interaction effects were relatively small for all parameters. Three covariance terms were relatively large compared with others: the one between $A_{ps}$ and $A_{l}$ over moisture treatments, and those between $A_{ps}$ and $A_{l}$ and between $A_{l}$ and velocity over populations (Table 5). All of these covariances were statistically significant.

Discussion
Seedlings were kept well watered or drought stressed from the very beginning of the growing season, and the pattern of developmental responses in hydraulic architecture apparently was set before the midsummer harvest. That is, in the case of every pertinent variable, significant differences at end-of-season between moisture treatments were consistent with midsummer values. The principal revelations of the midsummer results (i) seasonal leaf production was completed by the time in drought-stressed seedlings, (ii) earlywood production was not necessarily complete by midsummer despite that fact that latewood production had already begun in virtually every seedling, and (iii) xylem production continued from midsummer to end-of-season in both treatments but $A_{ps}$ did not increase significantly.

The fact that earlywood areas apparently continued to increase after midsummer appears paradoxical at first, considering that measurable latewood production had already begun at that time. However, $A_{ps}$ did not increase significantly after midsummer, suggesting that vessel production must have virtually ceased by that point. We believe that the increase in earlywood after midsummer was probably caused by intrusive growth of xylel fibers and perhaps some continued expansion of vessel elements as described by Esau (1977). We found evidence of intrusive fiber growth in all samples examined microscopically.

Seedlings responded to drought primarily by producing less "latewood," and less latewood. Moisture treatment affected LSC primarily through leaf area. Neither flow velocity nor $A_{ps}$ were significantly affected by the treatments, although the observed reduction in $A_{ps}$ associated with drought was rather large (18%) and nearly significant ($P = 0.10$). The effect of drought on xylem structure was evident in a reduction in the number of vessels produced, but there was no appreciable change in average vessel size. This is evident not only from direct measurements of vessel size on a sample of seedlings but also from the fact that flow velocity (primarily a function of vessel diameter) was not diminished by the drought conditions.

The reduction in number of vessels caused by drought would seem to suggest a larger reduction in $A_{ps}$ (50%) than was actually observed (18%). However, the potentially functional xylem area ($A_{ps}$) is determined by the number of vessels, the diameter of the vessels, and in particular, vessel diameter distribution (Heine 1971). Thus, a potentially functional area calculated from average vessel diameter and average number of vessels is not necessarily expected to agree with that obtained experimentally from flow rate and velocity. Furthermore, an accurate calculation of $A_{ps}$ depends upon an accurate determination of average flow velocity. Our apparatus is more sensitive to differences in peak velocity than to differences in average velocity. Despite our attempts to compensate, it is possible that this fact introduced an upward bias in estimates of average velocity for samples with a high proportion of inefficient latewood.

The presence of embolism in both treatments and the higher degree of embolism observed in drought-stressed plants indicates that not all of the potentially functional xylem had been active in water conduction by the end-of-season. However, our method of determining embolism blockage may have underestimated the actual degree of blockage because we cannot rule out the possibility that some emboli re-solution occurred during measurement. Although embolism blockage of xylem has been suggested to result from stresses associated with high drought-induced tensions in xylem (Tyree and Sperry 1988), the risk of embolism blockage is related to xylem architecture and this suggests that there may be cavitation avoidance in some species (Salleo and Lo Gullo 1989). We found no evidence of xylem structural changes ($A_{ps}$ or $v$) in response to drought stress that would suggest a developmental mechanism of cavitation avoidance in the xylem of green ash seedlings. Instead, we found that drought-stressed seedlings produced less $A_{l}$ relative
to $A_{tu}$ compared with well-watered seedlings and as a result LSC was higher in drought-stressed seedlings. However, this contrast does not take into account the fact that $A_{tu}$ of droughted plants was at least 80% included by embolism, so that in fact the actual ability of the xylem in droughted plants to supply their foliage with water was considerably less (by nearly two-thirds) than that of well-watered plants.

Under equal water potential gradients, xylem with low LSC will supply less water than xylem with high LSC (Tyree 1988). When evapotranspiration is high, the water potential gradients that $A_{tu}$ xylem are inversely proportional to LSC, at least in xylem segments proximal to the leaves supported (Salleo and La Gullo 1989; Tyree and Dixon 1986; Zimmermann 1978). Sellin (1987) found that the shaded conditions of a spruce overstory resulted in a lower LSC and suggested that the inability of xylem to match the increased demand for water upon sudden exposure to full sun contributed to the desiccation of most of the young trees growing at the edge of forest cuttings. Our study was concerned with the structural aspects of the hydraulic system rather than its functioning at a given point in time. The important result is that significant developmental adjustments in the components of LSC, in response to moisture regime, took place only in the foliar surface area. Furthermore, the inhibition in leaf area production on droughted plants was insufficient to offset the occlusion of $A_{tu}$ by embolism in those plants.

Recalling that component covariances make two-fold contributions to the total variance in LSC, some of the covariance sources of variation in LSC are large and rather of course some are small. They suggest the presence or absence of physiological relationships among component variables. For example, for all sources of variation (treatment, population, genetic and developmental) tended to the droughted plants was more influential than the influence of the other covariances. This implies the presence of both genetic and physiological independence between the production of leaf area and the production of potentially functional xylem area. In other words, whether a seedling exhibited greater leaf area as a result of favorable environmental conditions or as a result of a genetic propensity for greater leaf area production, the net effect of greater potential functionally xylem area. More or less the same can be said of $A_{tu}$ and velocity, whose covariance over populations was smaller than that for $A_{tu}$ and $A_{tu}$', but still statistically significant. In contrast, small (and nonsignificant) covariances between $A_{tu}$ and velocity suggest that both genetic and physiological independence between these components in LSC. In the case of treatment effects, large increases in leaf area under well-watered conditions were not accompanied by commensurate increases in xylem functional area ($A_{tu}$ to $A_{tu}$ varied significantly both in response to drought. Earlywood production in well-watered plants decreased with an east to west pattern among the populations studied, but this pattern was not seen in seedlings grown under drought conditions. A different but consistent pattern among the populations emerged for both leaf area and latewood production. When grown under well-watered conditions, seedlings representing populations in the middle of the range (particularly IL) had the greatest leaf area and latewood production. When grown in drought conditions, both leaf area and latewood production were less than in well-watered plants, and neither were different between the populations. This suggests a greater capacity in plants from populations in the middle of the range to develop latewood areas under favorable conditions. Its capacity to develop relatively large leaf areas under favorable conditions may explain in part why IL population 161, and geographically adjacent populations, are among the fastest growing trees in provenance test plantations of green ash (Steiner et al. 1988).

Populations differed significantly in all attributes studied, at least in one treatment or another, but population differences and population response to drought appeared to reflect environmental conditions at the origin in only one respect, i.e., NY compared with other populations. NY had the smallest reduction in $A_{tu}$ with the result that NY was the only population that responded to drought in a manner that diminished its capability of supplying water to the foliage (reduced LSC). Thus, the least adaptive response to drought occurred in the population from the most humid locality.

However, differences among all populations considered together did not parallel the precipitation pattern in the environment described in Table 1. Indeed, NY and SD seedlings differed significantly in only one characteristic, earlywood area in the well-watered environment. These apparent similarities in structural aspects of the hydraulic system contrast with differences at the leaf physiological level demonstrated for the same populations by Abrams et al. (1990). As severity of drought increased in their study, SD plants generally maintained the highest rates of net photosynthesis and leaf conductance to water vapor diffusion, whereas NY plants had the lowest gas exchange rates and the highest osmotic potentials of any of the populations. Moreover, SD plants had smaller and thicker leaves and lower stomatal density than did NY plants when grown under well-watered conditions. Since NY and SD plants in this study did not differ in $A_{tu}$, $A_{tu}$ to $A_{tu}$, flow velocity, or LSC in either environment, it appears that hydraulic architecture does not further explain differences among the populations in leaf photosynthesis and water relations during drought.

The magnitude and sign of differences between the contributions of $A_{tu}$ and $A_{tu}$ to the treatment and population mean squares for LSC suggests the occurrence of compensatory changes for these two components. The genetic (ecotypic) source of variation was most influenced by the environmental source was manifested primarily in $A_{tu}$'. Our results suggest that a balance between leaf area and xylem hydraulic structure in 2-year-old green ash seedlings is perturbed by drought and this perturbation occurs primarily by changes in leaf area production and less so in xylem structure. In fact, flow velocity was virtually unaffected by drought treatment. Although statistically significant, population differences in LSC tended to be diminished by an apparent compensation between the ratio of $A_{tu}$ to $A_{tu}$ and flow velocity. In general, high velocity of flow was associated with low $A_{tu}$ to $A_{tu}$ values. In particular, the highest $A_{tu}$ to $A_{tu}$ and the lowest velocity were observed in plants of the same treatment combination (drought-stressed OH).

The drought conditions imposed during this experiment resulted in deviations from well-watered trees for a suite of response variables. Furthermore, populations along a major
precipitation gradient differ significantly in many of these variables but not necessarily in parallel with the environmental gradient. When the correlations between the variables are taken into account, it is apparent that the components of balance between foliar surface and xylem hydraulic capability compensated to some extent but insufficiency to result in a constant LSC for all factor combinations. It is apparent from this investigation that whole-plant responses to drought are not well reflected in a single component of hydraulic architecture but involve coordinated changes in many variables. Although plant hydraulic architecture is genetically controlled and variable in green ash seedlings, its adaptive significance cannot be considered in isolation from other factors that control plant response to water stress.


