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**Ecophysiological analysis of woody species in contrasting temperate communities during wet and dry years**

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**Abstract** This study employed an intensive sampling regime in which leaf gas exchange and tissue-water relations were measured simultaneously on the same leaf at midday on 19 tree species from three distinct forest communities during wet (1990) and dry (1991) growing seasons. The study sites were located on a xeric barrens, a mesic valley floor, and a wet-mesic floodplain in central Pennsylvania, United States. The xeric, mesic, and wet-mesic sites had drought-related decreases in gravimetric soil moisture of 53, 34, and 27%, respectively. During the wet year, xeric and mesic communities had high seasonal mean photosynthetic rates (A) and stomatal conductance of water vapor (g_w) and low midday leaf water potential (Ψ), whereas the wet-mesic community had low A and g_w and high midday Ψ. The mesic and wet-mesic communities had dry year decreases in predawn Ψ, Ψ_m, and Ψ_v with the greatest drought effect occurring in the mesic community. Regression analysis indicated that species from each site that exhibited high wet-year A and g_w tended to have low midday Ψ. This trend was reversed only in the mesic community in the drought year. Despite differences in midday Ψ, all three communities had similar midday leaf turgor pressure (Ψ_t) in the wet year attributable to lower osmotic potential at zero turgor (Ψ^0) with increasing site droughtiness. Lower wet year Ψ^0 in the xeric community was due to low symplast volume rather than high solute content. Species with the lowest Ψ^0 in the wet year often did not have the lowest Ψ^0 possibly related to differences in tissue elasticity. Moreover, increased elasticity during drought may have masked osmotic adjustment in Ψ^0 (Ψ) but not in Ψ^0, via dilution of solutes at full hydration in some species. Despite the sampling regime used, there were no relationships between gas exchange and osmotic and elastic parameters that were consistently significant among communities or years. This result questions the universal, direct effect of osmotic and elastic adjustments in the maintenance of photosynthesis during drought. By including a large number of species, this study provided new insight to the ecophysiology of contrasting forest communities, and the community-wide impact of drought on contrasting sites.

**Key words** Drought · Tissue-water relations · Gas exchange · Microenvironment · Pennsylvania

**Introduction**

Ecophysiological differences have been reported between ecotypes of the same species (Parker and Pallardy 1985; Abrams et al. 1990a) and between species of the same genus (Yoon and Richter 1990; Ranney et al. 1991), and community (Hinckley et al. 1979; Bahari et al. 1985; Abrams et al. 1990b; Kloepel et al. 1993). Despite the abundance of such information, few studies have addressed ecophysiological differences among forest communities (Bunce 1977; Hull and Wood 1984; Jurik et al. 1988) or for more than one growing season (Bahari et al. 1985; Ellsworth and Reich 1992). In addition, the partitioning of ecophysiological variation among communities, species and trees has not been the subject of formal investigation. Thus, with increasing focus on ecosystem and landscape level processes, a better understanding of broad scale ecophysiology over consecutive growing seasons and of the relative influence of site moisture conditions versus intrinsic characteristics of species is warranted.

Gas exchange and tissue-water relations parameters are often weakly correlated, particularly in field studies (but see Ranney et al. 1991). Typically, tissue-water relations (as with pressure-volume analysis) are examined on different leaves and/or at different times from gas ex-
change, and results may be strongly influenced by temporal and micro-environmental variation.

Consequently, a universal transducer between some measure of leaf water status and photosynthesis has eluded even the most thorough investigations (Ludlow 1987). In the absence of such findings, it is unclear which aspect of leaf water status plays a greater role in leaf carbon assimilation: the thermodynamic properties of tissue water, i.e., water potential and its components, or the actual volume of water contained within the leaf symplast (Schulte 1992). Thus, a sampling regime which minimizes diurnal or micro-environmental effects between gas exchange and tissue-water relations measurements may be necessary to elucidate stronger, more meaningful, and perhaps unique relationships among these properties in field plants.

Site moisture conditions are strongly influenced by topographic position, land form and soil type, while species adaptations to moisture availability are major determinants in their geographic distribution. In the Ridge and Valley province of central Pennsylvania, United States, valley floors are predominantly mesic in site moisture status. Nevertheless, they are composed of several distinct soils and topographic features in which site moisture relations range from xeric, sandy barrens to wet-mesic flood plains along indented stream beds (Braker 1981). Such land forms and soil types support a wide array of species within valley ecosystems, and provide a rare opportunity to study the contrasting ecophysiology of xerophytes, but distinct communities (Keever 1973; Nowacki and Abrams 1992).

In this study, ecophysiological differences among three forest communities were examined over two consecutive growing seasons. The first objective of this study was to examine the variation in drought tolerance of representative tree species from valley sites of contrasting moisture availability, and to partition the variation in ecophysiological parameters by site conditions and species. The second objective was to investigate the relationships of gas exchange, tissue-water relations and microenvironment using a sampling regime in which these parameters were measured on the same leaf and at the same time of day. The study was enhanced by a moderate drought in the second growing season that allowed us to better describe contrasting ecophysiological adaptations and responses at the community level over a broad range of soil moisture conditions.

### Methods

#### Study site description

Xeric, mesic and wet-mesic sites located within 10 km of State College, Pennsylvania, United States (47°48' 47'' N, 71°18' 33'' W), were selected for study on the basis of site-water relations, species composition, and exposure of study plants to full sun. Six or seven species typical of each site were selected for study (Table 1). Six, sapling-size (2-3 m in height) individuals in large gaps and exposed to full sun for at least 50% of daylight hours were selected from each species.

The xeric site was a barrens community consisting primarily of a *Quercus prinus* overstory and a *Vaccinium* understory growing on sandy soil with less than 10% coarse fragments and rapid permeability (Braker 1981). The mesic and wet-mesic sites were a valley forest floor and floodplain, respectively, and had mixed overstories similar in composition to the study species listed in Table 1 for each site. Soil on the mesic site was a sandy loam with less than 10% coarse fragments and moderate to slow permeability. The wet-mesic site was a floodplain located along an indented stream bed and had a herbaceous understory dominated by *Impatiens* and *Carex*. The soil was a loam alluvium of moderate permeability, frequently subjected to spring flooding and mottled at 1 m indicating frequent saturation at that depth.

The region moderates between a dry continental and a maritime climate with warm, humid summers (Braker 1981). Average monthly growing season (May–September) precipitation is 9.2 cm and the average maximum summer temperatures range from 26 to 28°C.

### Data collection

Ecophysiological measurements were made at each site four times during the 1990 growing season and twice during 1991, on relatively cloud-free days (Table 1). Predawn (0600 hours solar time) leaf water potential (ψ) was measured on a fully expanded leaf of three to six study plants of each species using a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, OR, USA) on each sampling date. At midday (1100–1300 hours solar time) on these same days, leaf CO₂ and H₂O vapor exchange and photosynthetic photon flux density (PPFD) were measured with a portable, open

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Study species from contrasting sites in central Pennsylvania and sampling dates of ecophysiological measurements during wet (1990) and dry (1991) growing seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xeric</td>
<td>Mesic</td>
</tr>
<tr>
<td>sandy barrens</td>
<td>sandy loam valley floor</td>
</tr>
<tr>
<td><em>Acer rubrum</em> L.</td>
<td><em>Celtis tenuifolia</em> Nuttall.</td>
</tr>
<tr>
<td><em>Betula lenta</em> L.</td>
<td><em>Cornus alternifolia</em> L.</td>
</tr>
<tr>
<td><em>Carpinus dentata</em> (Marsh.) Borkh.</td>
<td><em>Fraxinus americana</em> L.</td>
</tr>
<tr>
<td><em>Sassafras albidum</em> (Nutt.) Nees</td>
<td><em>Ulmus rubra</em> Muhl.</td>
</tr>
</tbody>
</table>

12 June 1990 | 20 June 1990 | 14 June 1990 |
28 August 1990 | 1 September 1990 | 10 September 1990 |
flow, infrared gas analyzer (Model LCA-2, Analytical Development Co., Ltd., Hertz, England) on a sunlit (PPFD) > 1000 μmol m⁻² s⁻¹ leaf from four to six of the study plants of each species in random order. Immediately following gas exchange measurement, the leaf was harvested for midday Δv determination and then sealed in a plastic bag with a moist paper towel in a darkened container for later (within 4 h of harvest) pressure-volume analysis at the laboratory.

On each measurement day, three midday soil samples at 15 to 20 cm depth were collected from each site for gravimetric moisture analysis (soil dried at 100°C for 48 h). Micro-environmental conditions (air temperature and relative humidity) at each site were measured three to four times during the midday period of each sampling date with the LCA-2 system. Daily growing season precipitation was monitored by The Pennsylvania State University Weather Station at University Park, PA.

Pressure-volume (PV) analysis was performed using the bench-drying technique on four to six of the leaves used for gas exchange measurements. With few exceptions, no rehydration period was used to avoid potential rehydration-induced shifts in tissue-water relations parameters (Parker and Pallardy 1987; Kubiske and Abrams 1991). Because some leaves had very low midday Δv, particularly those from the mesic site during 1991, they required a brief rehydration period (1-2 h) with the petiole placed in a beaker of distilled water in the dark. This was necessary to ensure a sufficient amount of data above the wilting point for extrapolation of leaf saturated weight (see below).

Data analysis

Net photosynthetic rate (A), stomatal conductance of water vapor (gₑ) and leaf temperature (Tₑ) were calculated according to von Caemmerer and Farquhar (1981). Leaf to air vapor pressure deficit (VPD) was determined by assuming that vapor pressure in the substomatal cavities was at the saturated vapor pressure for Tₑ.

From moisture release curves of PV data (X vs. Y = fresh weight), leaf saturated weight was determined by extrapolating to y = 0.1 MPa using linear regression on data above the wilting point (Kubiske and Abrams 1990). Leaf relative water content (RCW) at each measurement was calculated from the extrapolated saturated weight and used to construct PV curves (X = RCW versus Y = 1 − Y).

Osmotic potential at full turgor (φw0) was the inverse of the Y intercept of the straight line portion of the PV curve, determined using linear regression for each leaf. Relative water content and osmotic potential at zero turgor (RCWo and φw0, respectively) were the X and Y intercepts of the straight line portion of the curve. Tissue elastic modulus (ε) was estimated as the change in turgor pressure over the change in RCW for the entire range from full to zero turgor, which provides a concise measure of the turgor maintenance capacity of cell walls (Colombo and Teng 1992). Relative symplast volume at full hydration (R₁) was calculated as 100% minus the X-intercept, determined by linear regression of the straight-line portion of the PV curve. Symplast solute content per gram of dry weight (RN) was calculated from φw0 according to Tyree et al. (1978).

Data were analyzed using a crossed-nested ANOVA model (Neter et al. 1985). In this model, where all levels of one factor were present in all levels of another factor, the two factors were crossed (e.g., year and community). Where different levels of a factor were present in levels of another factor, the first was nested within the second (e.g., species within community):

\[ y_{ijkl} = \mu + a_i + b_j + (a_b)_{ij} + \delta_k + (a\delta)_{ijk} + e_{ijkl} \]

where μ is the overall mean, aᵢ is the year effect, bⱼ is the community effect, (a_b)ᵢⱼ is the year by community interaction, δₖ is the species effect, (aδ)ᵢⱼₖ is the year by species effect, Sᵢⱼ is the sampling date within year and community effect, (aδ)ᵢⱼₖ is the year by species (within community) interaction, (δ)ₖ is the sampling day be species (within year and community) interaction and eᵢⱼₖᵢⱼₖ is the sampling error or variation due to species, within community, species, and sampling date. All factors were treated as fixed except for eᵢⱼₖᵢⱼₖᵢⱼₖ which was random. Means were compared using Fisher’s protected least significant difference procedure. Relationships among ecophysiological parameters were examined using Pearson’s product-moment correlation and least-squares linear regression. All statistical procedures were performed at P < 0.05 level of significance using SAS (SAS Institute 1985).

Results

Microenvironment

Precipitation during May to August in 1990 and 1991 averaged 24% above and 29% below the 100-year mean, respectively (referenced to as wet and dry years, respectively). As a result, soil moisture decreased with increasing site droughtiness in both years and with climatic drought between 1990 and 1991 (Table 2). Site characteristics had more than twice the effect on soil moisture in the upper 20 cm (15% of the total variation) as did annual rainfall (7% of the total variation, data not shown). Sampling date accounted for 61% of the total variation in soil moisture, entirely because of the saturated conditions on the wet-mesic site on 14 June 1990. Omission of these 14 June 1990 data from the ANOVA resulted in no significant sampling date effect (P = 0.36). Predawn Δv of the xeric community was significantly lower than that of the mesic and wet-mesic communities in 1990 and it was significantly lower in 1991 than in 1990 in the mesic and wet-mesic communities. Leaf-to-air VPD was highest (P = 0.05) on the xeric site and lowest on the wet-mesic site in 1990, and higher on the mesic and wet-mesic sites in 1991 than in 1990. Leaf temperature (Tₑ) was highest in the mesic community in both years. In the dry compared to wet year, Tₑ was higher in the mesic and lower in the wet-mesic communities.

Partitioning variation of ecophysiological parameters

In the crossed-nested ANOVA model, the error term represented variation among study trees within species and

<table>
<thead>
<tr>
<th>Year</th>
<th>Xeric</th>
<th>Mesic</th>
<th>Wet-mesic</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>13.5 ± 2.6a</td>
<td>34.3 ± 2.5c</td>
<td>40.9 ± 0.7a</td>
</tr>
<tr>
<td>1991</td>
<td>6.4 ± 0.7b</td>
<td>22.6 ± 1.4d</td>
<td>29.7 ± 0.9f</td>
</tr>
<tr>
<td>1990</td>
<td>0.26 ± 0.02a</td>
<td>0.12 ± 0.01c</td>
<td>0.12 ± 0.01c</td>
</tr>
<tr>
<td>1991</td>
<td>0.26 ± 0.02a</td>
<td>0.25 ± 0.02a</td>
<td>0.25 ± 0.02a</td>
</tr>
<tr>
<td>1990</td>
<td>1.68 ± 0.05a</td>
<td>1.16 ± 0.04b</td>
<td>0.97 ± 0.04c</td>
</tr>
<tr>
<td>1991</td>
<td>2.76 ± 0.05c</td>
<td>2.76 ± 0.05c</td>
<td>1.81 ± 0.02a</td>
</tr>
<tr>
<td>1990</td>
<td>26.6 ± 0.2a</td>
<td>27.4 ± 0.2b</td>
<td>26.4 ± 0.2a</td>
</tr>
<tr>
<td>1991</td>
<td>25.9 ± 0.3a</td>
<td>29.0 ± 0.3c</td>
<td>23.7 ± 0.9d</td>
</tr>
</tbody>
</table>

1 Mean does not include an early June 1990 sample date, which was 259.4 ± 76.3%
Table 3 Analysis of variance (MS=mean square; $s^2$=variance component; %=$\%$ of total variation) for net photosynthesis rate (A, $\mu$mol m$^{-2}$s$^{-1}$), stomatal conductance to water vapor ($g_{svw}$, mmol m$^{-2}$ s$^{-1}$) and midday leaf water potential (md $\psi$; MPa) of 19 woody species on three contrasting sites measured on four dates during a wet (1990) growing season and measured on two dates during a dry (1991) growing season in central Pennsylvania, USA. The factor 'comm' represents the community effect.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>A</th>
<th>$g_{svw}$</th>
<th>Midday $\psi$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>$s^2$</td>
<td>P</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>146.4 0.0001</td>
<td>0.44 6</td>
<td>5952241</td>
</tr>
<tr>
<td>Comm</td>
<td>2</td>
<td>122.2 0.0001</td>
<td>0.55 7</td>
<td>2069328</td>
</tr>
<tr>
<td>Year*comm</td>
<td>2</td>
<td>52.8 0.0001</td>
<td>0.46 6</td>
<td>490702</td>
</tr>
<tr>
<td>Species (comm)</td>
<td>16</td>
<td>53.7 0.0001</td>
<td>1.32 17</td>
<td>626058</td>
</tr>
<tr>
<td>Species<em>year</em>comm</td>
<td>16</td>
<td>6.2 0.0206</td>
<td>0.16 2</td>
<td>172854</td>
</tr>
<tr>
<td>Date</td>
<td>12</td>
<td>44.9 0.0001</td>
<td>1.16 15</td>
<td>944690</td>
</tr>
<tr>
<td>Species<em>year</em>comm</td>
<td>62</td>
<td>4.6 0.0290</td>
<td>0.22 3</td>
<td>259284</td>
</tr>
<tr>
<td>Error</td>
<td>454</td>
<td>3.3</td>
<td>3.3</td>
<td>69579</td>
</tr>
</tbody>
</table>

Table 4 Analysis of variance (MS=mean square; $s^2$=variance component; %=$\%$ of total variation) for osmotic potential at full and zero turgor ($\psi^{100}$ and $\psi^{0}$, respectively, MPa), relative water content at zero turgor (RWC$_{0}$, %) and elastic modulus ($e$, MPa) of 19 woody species on three contrasting sites measured on four dates during a wet (1990) growing season and measured on two dates during a dry (1991) growing season in central Pennsylvania, USA. The factor 'comm' represents the community effect.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>$\psi^{100}$</th>
<th>$\psi^{0}$</th>
<th>RWC$_{0}$</th>
<th>$e$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>$s^2$</td>
<td>P</td>
<td>%</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>0.15 0.1173</td>
<td>0.0003</td>
<td>0</td>
<td>1.25 0.0001</td>
</tr>
<tr>
<td>Comm</td>
<td>2</td>
<td>1.81 0.0001</td>
<td>0.0081</td>
<td>5</td>
<td>8.14 0.0001</td>
</tr>
<tr>
<td>Year*comm</td>
<td>2</td>
<td>0.15 0.0876</td>
<td>0.0008</td>
<td>0</td>
<td>0.89 0.0001</td>
</tr>
<tr>
<td>Species (comm)</td>
<td>16</td>
<td>1.17 0.0001</td>
<td>0.0309</td>
<td>17</td>
<td>1.66 0.0001</td>
</tr>
<tr>
<td>Species<em>year</em>comm</td>
<td>16</td>
<td>0.15 0.0015</td>
<td>0.0049</td>
<td>4</td>
<td>0.24 0.0001</td>
</tr>
<tr>
<td>Date</td>
<td>12</td>
<td>1.24 0.0001</td>
<td>0.0327</td>
<td>19</td>
<td>1.51 0.0001</td>
</tr>
<tr>
<td>Species<em>year</em>comm</td>
<td>59</td>
<td>0.26 0.0001</td>
<td>0.0340</td>
<td>20</td>
<td>0.39 0.0001</td>
</tr>
<tr>
<td>Error</td>
<td>453</td>
<td>0.06</td>
<td>0.0608</td>
<td>35</td>
<td>0.07</td>
</tr>
</tbody>
</table>

sample dates, which was the largest single variance component in all ecophysiological parameters (Tables 3 and 4). Also of major importance in all parameters was variation due to sampling date and/or the species by sampling date interaction within years and communities. Variation among species within communities accounted for a greater proportion of the total variance in A, midday $\psi$, $\psi^{100}$, $\psi^{0}$ and RWC$_{0}$ than did variation among communities or years. This was unexpected because among community variation includes both genetic and environmental effects since different species were present in each community. Year effects in A and $g_{svw}$ were greater than in tissue-water relations parameters and they were not significant in $\psi^{100}$. Community effects were greatest in $\psi^{0}$ and lowest in $e$.

Gas exchange and plant-water relations

Compared to the xeric and mesic communities, the wet-mesic community had the highest (P<0.05) midday $\psi$ in both years (Fig. 1). Both the wet-mesic and mesic communities had significantly lower midday $\psi$ in the dry year than in the wet year. The wet-mesic community had the lowest mean A and $g_{svw}$ in the wet year despite having the highest soil moisture and lowest VPD. Although all seasonal variation in soil moisture was due to saturated conditions on the wet-mesic site on 14 June 1990, omission of those data from the community means for A, $g_{svw}$, and midday $\psi$ did not result in significantly different means from those of the complete data set (not shown). The xeric and mesic communities had similar A and $g_{svw}$ in the wet year, although the mesic community had the highest maximum A ($10.94 \pm 0.18 \mu$mol m$^{-2}$ s$^{-1}$) compared with the xeric and wet-mesic communities ($9.03 \pm$
Table 5 Significant \((P<0.05)\) least squares linear regression functions for net photosynthetic rate \((A, \mu mol \ m^{-2} \ s^{-1})\) and conductance to water vapor \((g_{wv}, \mu mol \ m^{-2} \ s^{-1})\) versus midday bulk leaf water potential \((\psi, MPa)\) for 19 tree species on three contrasting sites in Pennsylvania. Regressions were performed on the mean of each species from four sampling days in a wet growing season (1990) and two sampling days in a dry growing season (1991). Regression lines are presented in Fig. 2.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Regression equation</th>
<th>(r^2)</th>
<th>(n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xeric</td>
<td>wet</td>
<td>(A=2.15-2.13 (\psi))</td>
<td>0.54</td>
<td>26</td>
</tr>
<tr>
<td>Xeric</td>
<td>dry</td>
<td>(A=0.57-3.04 (\psi))</td>
<td>0.46</td>
<td>13</td>
</tr>
<tr>
<td>Mesic</td>
<td>wet</td>
<td>(A=1.27-3.08 (\psi))</td>
<td>0.20</td>
<td>21</td>
</tr>
<tr>
<td>Mesic</td>
<td>dry</td>
<td>(A=5.94+1.77 (\psi))</td>
<td>0.33</td>
<td>12</td>
</tr>
<tr>
<td>Wet-mesic</td>
<td>wet</td>
<td>(A=1.62-2.92 (\psi))</td>
<td>0.42</td>
<td>21</td>
</tr>
<tr>
<td>Wet-mesic</td>
<td>dry</td>
<td>(A=1.66-1.30 (\psi))</td>
<td>0.33</td>
<td>12</td>
</tr>
<tr>
<td>Xeric</td>
<td>wet</td>
<td>(g_{wv}=63.7-239.7 (\psi))</td>
<td>0.25</td>
<td>26</td>
</tr>
<tr>
<td>Xeric</td>
<td>dry</td>
<td>(g_{wv}=8.28-166.4 (\psi))</td>
<td>0.52</td>
<td>13</td>
</tr>
<tr>
<td>Mesic</td>
<td>wet</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesic</td>
<td>dry</td>
<td>(g_{wv}=240.8-40.4 (\psi))</td>
<td>0.36</td>
<td>12</td>
</tr>
<tr>
<td>Wet-mesic</td>
<td>wet</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wet-mesic</td>
<td>dry</td>
<td>(g_{wv}=79.0-43.8 (\psi))</td>
<td>0.43</td>
<td>12</td>
</tr>
</tbody>
</table>

Fig. 1 Seasonal mean (SE) midday water potential (midday \(\psi\)), net photosynthetic rate \((A)\) and stomatal conductance to water vapor \((g_{wv})\) of eastern deciduous communities during wet (1990, solid bars) and dry (1991, shaded bars) growing seasons. Bars with the same letters are not significantly different \((P<0.05)\). 0.24 and 8.90±0.31 \(\mu mol \ m^{-2} \ s^{-1}\), respectively, data not shown). In the dry year, the mesic and wet-mesic communities had significantly lower mean \(A\) and \(g_{wv}\) than in the wet year whereas the xeric community had lower \(g_{wv}\) but not \(A\). Consequently, the xeric community had the highest \(A\) and \(g_{wv}\) in the dry year. The mesic community had the greatest decrease in \(A\) and \(g_{wv}\) of all from wet to dry years.

In general, species of a community that had low mean midday \(\psi\) also had high \(A\) and \(g_{wv}\) (Fig. 2). An exception was the mesic community in the dry year in which species with the lowest mean midday \(\psi\) also had the lowest \(A\) and \(g_{wv}\). There were no significant differences in the \(A/\psi\) relationship among the three communities in the wet year. The slopes of \(A\) and \(g_{wv}\) versus midday \(\psi\) were not significantly different among years in the xeric community, but in the wet-mesic community \(A\) versus midday \(\psi\) was shallower in the dry year than in the wet year. In the mesic community, the \(A/\psi\) slope was negative and in the dry year it was positive.

Gas exchange rates of individual species generally reflected the site and year differences in the community means. Nevertheless, several exceptions to these trends were evident. *Acer rubrum* and *Betula lenta* on the xeric site had among the lowest \(A\) and \(g_{wv}\) of the study in both years whereas *Tilia americana* on the wet-mesic site had one of the highest \(A\) of the study in 1990 (Fig. 3). *Ulmus rubra* on the mesic site had the lowest \(A\) of all study species in 1991 and had mean net \(A\) less than zero for the later (2 August) sampling date in 1991. *Populus grandidentata* had the highest \(g_{wv}\) of the study, but *Juglans nigra* and *Quercus macrocarpa* of the mesic site also had among the highest \(g_{wv}\). In addition, there were exceptions to the negative \(A/\psi\) and \(g_{wv}/\psi\) relationships of Fig. 2 in the wet year. *Acer negundo* and *J. nigra* had the
highest \((P<0.05)\) \(g_{wv}\) on their respective sites, but they also had among the highest \(\psi\) (Fig. 3). Similarly, *S. albidum* had among the highest \(A\) and \(g_{wv}\) of the study, but also had among the highest \(\psi\).

**Tissue-water relations**

In both growing seasons, mean \(\psi_{s100}\), \(\psi_{m100}\), RN, and \(R_{w}\) decreased \((P<0.05)\) with increasing site aridity (Fig. 4). In the dry compared to wet year, the xeric and mesic communities had significantly lower mean \(\psi_{s100}\), \(\psi_{m100}\) and RWC, and the xeric community had significantly higher RN. In all three communities, RN, was positively correlated \((P<0.05)\) with \(R_{w}\) \((r=0.59–0.88)\), and negatively correlated with \(\psi_{m100}\) and \(\psi_{s100}\) \((r=-0.56 to -0.79)\). The xeric and mesic communities had lower \(\psi\) and RWC, but not midday \(\psi_{s}\), from 1990 to 1991. Consequently, RWC in 1991 was well below the midday RWC in the xeric and mesic communities. Lack of osmotic adjustment in the wet-mesic community contributed to lower \(\psi_{m}\) in 1991 than in 1990 and in midday RWC that was very close to wilting in 1991. Species of a community that had low mean midday \(\psi\) also had low mean \(\psi_{s}\) (Fig. 5). This relationship was significant in the dry year, but not in the wet year. There were no significant differences among slopes, but \(Y\)-intercepts decreased with increasing site droughtiness.

*Populus grandidentata* had the lowest \((P<0.05)\) \(\psi_{m100}\) in 1990 (Fig. 6). Species ranking of \(\psi_{s100}\) was different from that of \(\psi_{m100}\) in that only three species with the lowest \(\psi_{s100}\) \(*P. grandidentata, F. americana, P. serotina, C. alternifolia\) and *A. rubrum* also had the lowest \(\psi_{m100}\). Species with the highest \((P<0.05)\) \(\psi_{m100}\) in 1990 occurred on the mesic and wet-mesic sites (A. negundo, P. serotina, F. americana, C. tenuifolia, Pop. grandidentata and Co. alternifolia). All three sites were represented among species with the lowest \(\psi_{s}\) (Carya cordiformis, Castanea dentata, Ulmus rubra, B. lenta, and A. saccharum). The percent change in \(\psi_{s}\) from full to zero turgor was negatively correlated \((P<0.05)\) with \(\psi\) across the study species \((r=0.46)\), such that species with the greatest change in \(\psi_{s}\)
had the lowest ε. Significantly lower RWC₀ in 1991 than in 1990 generally occurred in species with decreased ε, irrespective of year-to-year decreases in Ψₑ.

Despite nearly concurrent measurements of gas exchange and tissue-water relations measurements on the same leaf for each study sapling, there were no relationships between gas exchange and tissue-water relations parameters that were consistently significant for all three communities and/or both years (not shown). Due in part to high intraspecific variation ('error' variance of Tables 3 and 4), relationships between gas exchange and tissue-water relations parameters that were statistically significant at the community level generally accounted for less than 20% of the variation in the dependent variable. Thus, while gas exchange and tissue water relations may have been related within some species, these relationships were not consistent at the community level.

**Discussion**

Partitioning variation of ecophysiological parameters

While numerous studies have reported dramatic differences in the ecophysiology of co-occurring tree species, detailed comparison of intra- and inter-community varia-

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Fig. 5 Relationship of osmotic potential at zero turgor (Ψₑ) versus midday leaf water potential (midday Ψₑ) of 19 eastern woody species on contrasting sites during wet (1990, closed symbols) and dry (1991, open symbols and dashed lines) growing seasons. Individual points represent species × sampling date means.

Fig. 6 Seasonal mean (±SE) osmotic potential at full (Ψₑ₂₀) and zero turgor (Ψₑ), relative water content at zero turgor (RWC₀) and leaf elastic modulus (ε) of 19 deciduous tree species from three contrasting sites during wet (1990; solid bars) and dry (1991; shaded bars) growing seasons. Parameters that are significantly different between the two years are indicated by *P<0.05*. The seasonal variation is unprecedented in the ecophysiological literature. Sampling date (within year) was of greater importance than year, community or species effects in ecophysiological variation. This well-recognized effect has been related to plant ontogeny and seasonal changes in water and nutrient availability and temperature (Tyree et al. 1978; Parker et al. 1982; Jurik et al. 1988; Kloeppel et al. 1993). In this study, seasonal variation in soil moisture had negligible effect on plant ecophysiology, including saturated soil conditions on the wet-mesic site early in 1990. Ecophysiological variation was greater within the forest communities than among them. Similarly, differences in simulated canopy A and leaf area index among co-occurring tree species were greater than differences among three forest stands (Reich et al. 1990). It has been reported that ecological differences among co-oc-
occurring species may be largely due to intrinsic characteristics. For example, *Quercus* species often rank among the highest A and $g_{sv}$ in field studies (Bahari et al. 1985; Abrams et al. 1990b; Ni and Pallardy 1991), whereas *Acer* and *Betula* species consistently rank among the lowest (Abrams 1988; Ranney et al. 1990; Ni and Pallardy 1991), a trend also evident in this study regardless of site conditions. Numerous, uncontrollable factors inherent in field studies likely contributed to the large intraspecific variation in ecophysiology, such as within-canopy variation in microenvironment, sapling and leaf age, and possible localized root restrictions. Community effects were greatest in $g_{sv}$, and were generally greater than year effects in tissue water parameters. This may reflect the greater influence that site conditions had on soil moisture than did growing season precipitation. In contrast, year effects accounted for a greater proportion of total variation in gas exchange parameters than in tissue-water parameters, possibly due to the combined influence of atmospheric conditions (i.e., VPD and temperature) and soil moisture on leaf CO$_2$ and H$_2$O vapor conductance (Osmundi and Davies 1980).

Gas exchange and plant-water relations

Species on xeric sites tend to be less shade-tolerant than those of more mesic sites (Wuenschner and Kozlowski 1971) and shade intolerant species tend to have higher light-saturated $A$ and $g_{sv}$ than shade tolerant species (Bazzaz and Carlson 1982). This generalization was met by the shade tolerance rank of species in this study, and by the gas exchange rates of the three communities. In addition to species characteristics, site water availability often has a profound impact on photosynthetic rate (Davies and Kozlowski 1977; Bahari et al. 1985; Abrams et al. 1990b). For example, higher water holding capacity on the mesic site probably contributed to the highest maximum $A$ in the mesic community. Although the xeric site had the lowest surface soil moisture in both years, deep rooting in the xeric species may have facilitated high mean $A$ (Parker et al. 1982; Bahari et al. 1985; Abrams and Knapp 1986). This was supported by no significant decrease in predawn $\psi$ in the xeric community, as seen in the other two communities, despite the xeric site having the greatest drought-year decrease in surface soil moisture.

High gas exchange rates were associated with low mean midday $\psi$ among communities and among species within communities in 1990. In individual species, it is well understood that increasing gas exchange rates tend to lower $\psi$ until a $\psi$ threshold is reached for stomatal closure (Bazzaz 1979). In this study, the lower midday $\psi$ was a reflection of high gas exchange rates in some species rather than an indication of leaf water stress (cf. Ludlow 1987). Drought had the greatest impact on the mesic community as evidenced by the large decrease in mean $A$, $g_{sv}$, and midday $\psi$ from 1990 to 1991, and by low A with the development of low midday $\psi$ in several of the mesic species, in contrast to the other communities. Decreases in $A$ during drought may be related to stomatal closure induced by decreased leaf $\psi$ (Bazzaz 1979) or chemical signals produced by roots in drying soil (Ludlow 1987; Schulte 1992), or to nonstomatal interruption of the photosynthetic apparatus (Ni and Pallardy 1992; Kubiske and Abrams 1993). It was previously shown that nonstomatal limitations to $A$ were more important in these wet-mesic than mesic species during drought (Kubiske and Abrams 1993).

Although species that had the highest gas exchange rates in the wet year also generally had the lowest midday $\psi$, exceptions included *A. negundo*, *J. nigra* and *Sassafras albidum*, which had among the highest $g_{sv}$ and midday $\psi$ on their respective sites. Transpirational water loss was apparently replenished more rapidly in *A. negundo* and *J. nigra* than in co-occurring species, and in *S. albidum* even more so than in the mesic and xeric mesic sites (cf. Ni and Pallardy 1991; Foster 1992; Kloeppel et al. 1993). Maintaining high midday $\psi$ via extensive rooting or effective water transport may be necessary in these species to prevent early stomatal closure or leaf senescence as has been reported for *J. nigra* (Davies and Kozlowski 1977; Hinckley et al. 1979; Ni and Pallardy 1991).

Drought-related differences in gas exchange among the study species were generally consistent with other studies (Hinckley et al. 1979; Bahari et al. 1985; Abrams et al. 1990b). *Ulmus rubra* had similar $g_{sv}$ from 1990 to 1991, but had one of the largest decreases in $A$, which implies a large increase in the non-stomatal limitation of $A$. Increased non-stomatal limitation of $A$ is not uncommon in eastern deciduous species during severe drought (Bunee 1977; Ni and Pallardy 1992; Kubiske and Abrams 1993). However, the magnitude of nonstomatal limitations to $A$ evident in *U. rubra* during this moderate drought appears to be much larger than reported in other temperate trees. In contrast, *Populus grandidentata*, *S. albidum*, *J. nigra* and *A. negundo* had among the greatest decreases in $g_{sv}$ from 1990 to 1991 with no decrease in mean $A$. Interestingly, three of these species were noted above to have maintained high $\psi$ despite high $g_{sv}$.

Tissue-water relations

Despite statistically lower midday $\psi$, the xeric and mesic communities had midday $\psi$ similar to the wet-mesic community in the 1990 growing season, which was probably the result of lower $g_{sv}$ (Turner and Jones 1980, Abrams 1988). Similarly, significant decreases in $g_{sv}$ and $e$ from 1990 to 1991 in the xeric and mesic communities extended the range of positive $g_{sv}$. In addition, $R_n$ and RN, both increased with site droughtiness. Plants of xeric habitats often have lower sympatric volume than more mesic species. This has been attributed to smaller cell sizes (Cutler et al. 1977; Tyree and Jarvis 1982) which would enable species on drought-prone sites to attain lower $\psi_{x}$ with a given solute content (Wilson et al. 1980;
Conclusion

There were significant differences in drought adaptation and response of gas exchange and water relations among the three forest communities in this study. Previous studies have demonstrated that xeric species often have higher gas exchange rates during both well-watered and drought conditions than mesic or wet-mesic species in the same soil. However, the relative impact of drought on the ecophysiology of xeric, mesic and wet-mesic species in their respective environments has not been well understood. By including a broad sample of species from each community, this study has provided new insight into the impact of drought on contrasting sites. These results indicate that xeric species are best suited to tolerate moderate drought despite the most limiting soil moisture conditions. In contrast, species of mesic sites may be most affected by drought, being less tolerant of drought than are xeric species, and having less available moisture than species on wet-mesic sites. Although wet-mesic species have the greatest water availability, they lack the drought tolerance mechanisms of xeric and even mesic species, and thus are adversely affected by slight decreases in soil moisture.

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