Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understory sites during a drought

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Summary  Seasonal ecophysiology, leaf structure and nitrogen were measured in saplings of early (Populus grandidentata Michx. and Prunus serotina J.F. Ehrh.), middle (Fraxinus americana L. and Carya tomentosa Nutt.) and late (Acer rubrum L. and Cornus florida L.) successional tree species during severe drought on adjacent open and understory sites in central Pennsylvania, USA. Area-based net photosynthesis (A) and leaf conductance to water vapor diffusion (g_{vw}) varied by site and species and were highest in open growing plants and early successional species at both the open and understory sites. In response to the period of maximum drought, both sunfleck and sun leaves of the early successional species exhibited smaller decreases in A than leaves of the other species. Shaded understory leaves of all species were more susceptible to drought than sun leaves and had negative midday A values during the middle and later growing season. Shaded understory leaves also displayed a reduced photosynthetic light response during the peak drought period. Sun leaves were thicker and had a greater mass per area (LMA) and nitrogen (N) content than shaded leaves, and early and middle successional species had higher N contents and concentrations than late successional species. In both sunfleck and sun leaves, seasonal A was positively related to predawn leaf Ψ, g_{vw}, LMA and N, and was negatively related to vapor pressure deficit, midday leaf Ψ and internal CO₂. Although a significant amount of plasticity occurred in all species for most gas exchange and leaf structural parameters, middle successional species exhibited the largest degree of phenotypic plasticity between open and understory plants.

Keywords: net photosynthesis, phenotypic plasticity, shading, sunflecks, understory, water potential.

Introduction

Plants display nongenetic variation in morphology and physiology in response to environmental variation; a phenomenon known as phenotypic plasticity (Bradshaw 1965, Schlichting 1986, Abrams 1994). Although many ecophysiological studies have focused on phenotypic response to a single environmental factor, such as temperature, light or water (Fryer and Ledig 1972, Bazzaz and Carlson 1982, Abrams and Kubiske 1990, Walters et al. 1993, Kloppel et al. 1993), there have been few studies of phenotypic variation in relation to multiple stress interactions (Osmond 1983, Vance and Zaerr 1991).

Tree species of varying successional status exhibit differences in ecophysiological responses and leaf structural characteristics. For example, early successional species often have higher light-saturated gas exchange rates, less non-stomatal inhibition of photosynthesis, lower osmotic potentials and more xerophytic leaves than late successional species (Bazzaz and Carlson 1982, Abrams and Kubiske 1990, Abrams et al. 1994, Kubiske and Abrams 1993, 1994). High gas exchange rates in many species are associated with high leaf nitrogen concentrations, although few studies have compared N concentrations in early versus late successional tree species or in high- versus low-light phenotypes in relation to gas exchange rates (Reich et al. 1990, Ellsworth and Reich 1992). Early successional species may be capable of a wider range of phenotypic responses than middle or late successional species (Bazzaz 1979); however, there is little empirical evidence of this phenomenon in tree species (Bazzaz and Carlson 1982, Teskey and Shrestha 1985).

We measured seasonal gas exchange, water potential, leaf structure, leaf nitrogen and the microenvironment during a seasonal drought in six early, middle and late successional broadleaf tree species in adjacent open and understory sites in central Pennsylvania, USA. We used the data to test four hypotheses: (1) understory plants are more susceptible to drought from multiple stress interactions than open-growing plants, (2) early successional plants have higher gas exchange rates during well-watered and drought conditions in both open and understory sites than middle and late successional species, (3) physiological and morphological plasticity to open and understory environments vary among early, middle and late successional species, and (4) seasonal variations in ecophysiology among the contrasting species is related to variations in microenvironment, leaf structure and nitrogen in the open and understory environments.

Materials and methods

Study site

The study site is located approximately 4 km north of State College, in central Pennsylvania (40°48'52" N, 77°55'50" W).
Average monthly minimum winter temperatures (December--February) range from −5 to −7 °C, and average maximum summer temperatures (June--August) range from 26 to 28 °C. Average monthly precipitation varies from 6.5 to 10.3 cm, with a total average annual precipitation of 97.9 cm. Braker (1981) characterized the soil as a deep, well-drained cherty limestone derivative with moderate permeability and high available water capacity. Soil texture is silt loam on the surface horizon and clay loam at 50 cm.

The study site included a 100-year-old relatively undisturbed valley floor forest dominated by oak (*Quercus alba* L.) and *Q. velutina* Lamb.) in the overstory and by mixed moso-phytic species, including *Acer rubrum* L., *Praunus serotina* J.F. Ehrh. and *Fraxinus americana* L., in the understory. A portion of this forest was clear-cut in 1986, and presently supports a diverse mixture of sapling-sized tree species. We selected saplings (between 1.4 and 3.0 m in height) from six species of contrasting successional status that occurred in both the mature forest understory and the adjacent clear-cut: *A. rubrum* and *Cornus florida* L. for the late successional group, *F. americana* and *Carya tomentosa* Nutt. for the middle successional group, and *Populus grandidentata* Michx. and *P. serotina* for the early successional group (cf. Burns and Honkala 1990). We studied five saplings per species.

### Data collection

During the 1993 growing season, midday (1100–1300 h solar time) microenvironmental and plant ecophysiological measurements were made at the open and understory sites at 6–15-day intervals (n = 9) between May 27 and August 31 on relatively cloud-free days. All ecophysiological measurements were conducted on first flush or early season leaves. Predawn (0600 h solar time) leaf water potential (Ψ) was measured on each sampling date on one leaf from each sapling with a pressure chamber (PMS Instrument Co., Corvallis, OR). Midday gas exchange, photosynthetic photon flux density (PPFD), and Ψ were measured on one mid-canopy leaf from each sapling. For the compound-leaf species, *F. americana* and *C. tomentosa*, gas exchange measurements were made on the terminal leaflet. Gas exchange, leaf temperature and PPFD measurements were made with an open-flow infrared gas analysis system (LCA-3, Analytical Development Co., Herts, U.K.). On the open site, only leaves that were in full sunlight were measured. In the understory, two types of leaves were measured, leaves growing in shade and leaves exposed to occasional sunflecks. Leaves were allowed to acclimate to sunflecks for a minimum of 15 min before measurement. Net photosynthesis (A), leaf conductance to water vapor diffusion (g<sub>sv</sub>) transpiration (J), leaf temperature, and vapor pressure deficit (VPD) were calculated according to von Caemmerer and Farquhar (1981). Gravimetric soil water of the upper 25 cm of soil was measured on four replicate samples from each site at each date.

On June 23, 1993, midcanopy leaves from each sapling in each species × site combination were collected for structural and nitrogen (N) analyses. Leaf thickness was measured in three places on each leaf at the approximate midpoint between major veins by means of an ocular micrometer and light microscope. Three measurements of guard cell length were made and stomatal density was measured by means of acetate impressions of the abaxial surface of each leaf (Payne 1968). Leaf mass per area was calculated by dividing total area, measured with an LI3100 leaf area meter (Li-Cor Inc., Lincoln, NE), by dry weight (48 h at 80 °C). For the compound-leaf species, leaf area and mass per area were measured using the entire leaf, whereas leaf thickness, guard cell length and stomatal density were measured on the terminal leaflet. Leaf N was analyzed by the Agricultural Analytical Services Laboratory at Penn State University using a micro-Kjeldahl digest and an auto-analyzer. Additional measurements of leaf N and mass per area were made on each sapling on August 5, 1993, to evaluate temporal variation in these parameters (cf. Kloeppe et al. 1993).

Statistical analyses for microenvironmental, leaf ecophysiological, structural and chemical parameters included one-way, two-way and repeated measures analysis of variance (ANOVA) with general linear models, with time as a repeated measures factor and site as the whole plot factor (SAS Institute Inc., Cary, NC). Three-way ANOVA models with fixed effects were used to partition the variation of A, g<sub>sv</sub>, and Ψ among sampling date, site, and species. Tukey’s multiple-range test (P < 0.05) was used for all multiple comparisons. The interrelations between parameters were evaluated with Pearson product-moment correlation and least squares linear and nonlinear regression analyses.

### Results

#### Microenvironment

Daily average maximum and minimum monthly temperatures from May through August 1993 were within 0.3–1.0 °C of the 30-year means (Figure 1). However, mean monthly precipitation was 52 and 41% below the 30-year mean for May and June, respectively, and 16 and 18% below average for July and August, respectively. Soil water decreased (P < 0.05) at both the open and the understory study sites from a high of about 20% in late May and early June to about 10% in July and August, but was generally not significantly different between sites.

Seasonal mean photosynthetic photon flux density (PPFD) differed significantly between sites, being highest in the open site (1328 ± 23 µmol m<sup>−2</sup> s<sup>−1</sup>) and lowest in the shaded understory site (47 ± 3 µmol m<sup>−2</sup> s<sup>−1</sup>) (Figure 2). Leaves in understory sunflecks generally experienced decreasing PPFD as the season progressed, ranging from 1000 to 350 µmol m<sup>−2</sup> s<sup>−1</sup> and averaging 743 ± 33 µmol m<sup>−2</sup> s<sup>−1</sup> for the season. Leaf temperature increased during the season in all three light regimes, and was generally highest (P < 0.05) in leaves at the open site and lowest in understory leaves. Vapor pressure deficit (VPD) varied with sampling dates, but was highest in the open during the peak drought period and lowest in the understory across all dates.
Gas exchange and leaf water potential

In general, for each species, midday net photosynthesis ($A$) was high, intermediate and low in sun, sunfleck and shaded leaves, respectively (Figure 3), except for *P. grandidentata* and *A. rubrum*, where $A$ in sun and sunfleck leaves was generally not significantly different until later in the season when drought effects were pronounced. Although $A$ was low in all understory leaves, it was positive for all species in late May and June (overall mean = 0.05 to 0.45 µmol m$^{-2}$ s$^{-1}$), and consistently near or below zero ($P < 0.05$) in July and August (overall mean = −0.05 to −0.44 µmol m$^{-2}$ s$^{-1}$). Among species, *Prunus serotina* had the highest seasonal understory $A$, whereas *P. grandidentata* had the lowest understory $A$. For sunfleck leaves, $A$ was generally highest early in the season and decreased ($P < 0.05$) during the season in most species, with the exception of *F. americana*. In contrast, species at the open site had more variable seasonal patterns of $A$, although, in most species, it was lowest on July 24 at the peak of the drought. From early to mid-season, $A$ decreased across all species by an average of 11, 36 and 193% in sun, sunfleck and shaded leaves, respectively, ($P < 0.05$). Among the open-site species, *A. rubrum* and *C. florida* had the largest relative decreases in $A$ (50 and 21%, respectively) from early to mid-season.

Differences in $g_{wv}$ among species and light regimes were less pronounced than those observed for $A$ (Figure 4). Although most species had higher ($P < 0.05$) $g_{wv}$ in sun than in understory leaves, $g_{wv}$ in sunfleck and understory leaves was often not statistically different. Drought had little effect on $g_{wv}$ on any sampling date, although $g_{wv}$ was slightly lower on July 24 than on other dates.

Predawn leaf water potential (Ψ) remained at −0.2 MPa from late May to early July, declined to −0.6 and −0.8 MPa in the open and understory sites, respectively, by late July, then increased during August at both sites (Figure 1). Predawn Ψ was usually lower ($P < 0.05$) in shaded leaves than in sun leaves, with seasonal means (± SE) of −0.41 ± 0.02 and −0.33 ± 0.01 MPa, respectively, but it did not differ significantly among species within each site.

For all species, midday Ψ was significantly lower in sun than in shaded leaves (Figure 5). At both sites, there was a seasonal decline ($P < 0.05$) in Ψ in all species except in *A. rubrum*. In most species, there was a significant drop in midday Ψ during the period of maximum drought (July 18–24).

For plants at the open site, seasonal mean $A$ was highest ($P < 0.05$) in the early successional species, *P. grandidentata,*
P. serotina and middle successional species C. tomentosa, and intermediate in F. americana (Figure 6). In shaded leaves, seasonal A was not significantly different from zero for any species. In sunfleck leaves, seasonal mean A was highest for P. grandidentata, intermediate in P. serotina, and not significantly different among the other species. Mean gₚᵥ of sun leaves followed the same ranking as A, except that the highest value was observed in C. tomentosa. Mean gₚᵥ in shaded and sunfleck leaves was highest in P. grandidentata and intermediate in P. serotina. Midday Ψ was lowest in P. grandidentata and P. serotina at the open site and lowest in these species plus F. americana in the understory. Measurements of Ψ were not made on sunfleck leaves.

Partitioning of variances among sampling date, site, species and the interaction terms indicated that 94% of the variance in A was due to site. Although site was also the major source of variation for gₚᵥ (57%) and Ψ (68%), sampling date (i.e., drought effects) and species differences combined explained 30–32% of the variation, and interactions among these factors represented 1% of the variance.

There was a significant relationship between A and PPFD for late May–June, but not for July (Figure 7). Only about 20% of understory leaves had positive A values in July (mean A of −0.16 ± 0.06 µmol m⁻² s⁻¹) compared to 90% in late May–June (mean A of 0.23 ± 0.15 µmol m⁻² s⁻¹), indicating that drought decreased the photosynthetic light response in these species.

Figure 2. Mean (± SE) midday photosynthetic photon flux density (PPFD), leaf temperature and vapor pressure deficit for sun (⧫), sunfleck (◇) and shaded (■) leaves for six successional tree species at nine sampling dates.

Figure 3. Mean (± SE) midday net photosynthesis (A) at nine sampling dates for sun (⧫), sunfleck (◇) and shaded (■) leaves of six tree species. Pogr = Populus grandidentata, Prse = Prunus serotina, Cato = Carya tomentosa, Fram = Fraxinus americana, Acru = Acer rubrum, Cofl = Cornus florida.
Figure 4. Mean (± SE) midday leaf conductance to water vapor diffusion ($g_{wv}$) at nine sampling dates for sun (□), sunfleck (♦) and shaded (■) leaves of six tree species: Pogr = Populus grandidentata, Prse = Prunus serotina, Cato = Carya tomentosa, Fram = Fraxinus americana, Acru = Acer rubrum, Cofl = Cornus florida.

Figure 5. Mean (± SE) midday leaf water potential ($\Psi$) at nine sampling dates for sun (□) and shaded (♦) leaves of six tree species: Pogr = Populus grandidentata, Prse = Prunus serotina, Cato = Carya tomentosa, Fram = Fraxinus americana, Acru = Acer rubrum, Cofl = Cornus florida.
Leaf structure and nitrogen

Sun leaves were thicker (with the exception of *P. serotina*) and had higher mass per area (LMA) than shaded leaves (Table 1). Leaf thickness was highest in *F. americana*, *C. tomentosa* and *P. serotina* at the open sites and highest in *P. serotina* in the understory, whereas LMA was generally highest for *F. americana* at the open sites and highest for *P. grandidentata* in the understory. In all species, leaf areas of sun leaves were similar to those of shaded leaves. At both sites, leaf area was highest in the compound-leaf species, *F. americana* and *C. tomentosa*, and lowest in *P. serotina*. These three species also had longer guard cells than the other species at both sites. In some species, guard cells were larger and stomatal densities higher in sun leaves than in shaded leaves.

Foliar nitrogen content (expressed as mass per area) was higher in sun leaves than in shaded leaves of all species, even though percent N was generally not significantly different between sites (Table 2). Percent N varied among species, it was lowest in the late successional species, *A. rubrum* and *C. floridana*. Both sun and shaded leaves of these species also had low N contents, as did shaded leaves of *F. americana*. Percent N tended to decrease between June 23 and August 5, as LMA increased in both shaded and sun leaves. Nitrogen content of sun leaves tended to increase as the season progressed, whereas N content of shaded leaves remained constant, except for increases (*P < 0.05*) in *C. tomentosa* and *P. grandidentata*.

Interrelating gas exchange

Seasonal mean $A$ in sun and sunfleck leaves was negatively related to midday $\Psi$, VPD and internal CO$_2$ ($C_i$), and was positively related to early and late season leaf mass per area.
Table 1. Leaf structural characteristics (mean ± SE) for six hardwood tree species in understory and open locations in central Pennsylvania. Leaves collected on June 23 were measured for all five structural parameters, leaves collected on August 5 were only measured for leaf mass per area.

<table>
<thead>
<tr>
<th>Location</th>
<th>Leaf thickness (µm)</th>
<th>Guard-cell length (µm)</th>
<th>Stomatal density (no. mm⁻²)</th>
<th>Leaf mass per area 1 (mg cm⁻²)</th>
<th>Leaf mass per area 2 (mg cm⁻²)</th>
<th>Leaf area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acer rubrum</em></td>
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<td></td>
</tr>
<tr>
<td>Open</td>
<td>115.8 ± 4.9 c¹</td>
<td>13.35 ± 0.44 a</td>
<td>371 ± 9 d</td>
<td>5.24 ± 0.41 de</td>
<td>7.03 ± 0.48 f</td>
<td>61.8 ± 7.2 bc</td>
</tr>
<tr>
<td>Under</td>
<td>88.8 ± 5.9 ab</td>
<td>12.45 ± 0.38 a</td>
<td>206 ± 16 c</td>
<td>3.55 ± 0.17 bc</td>
<td>3.98 ± 0.21 c</td>
<td>72.4 ± 6.0 c</td>
</tr>
<tr>
<td><em>Cornus florida</em></td>
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</tr>
<tr>
<td>Open</td>
<td>124.2 ± 2.4 cd</td>
<td>18.45 ± 0.91 bc</td>
<td>56 ± 6 a</td>
<td>4.10 ± 0.26 cd</td>
<td>6.95 ± 0.72 ef</td>
<td>58.5 ± 6.3 bc</td>
</tr>
<tr>
<td>Under</td>
<td>96.9 ± 1.5 b</td>
<td>17.55 ± 0.77 b</td>
<td>44 ± 3 a</td>
<td>2.66 ± 0.15 a</td>
<td>2.30 ± 0.19 b</td>
<td>49.0 ± 5.0 c</td>
</tr>
<tr>
<td><em>Fraxinus americana</em></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Open</td>
<td>151.5 ± 6.9 e</td>
<td>24.15 ± 0.96 ef</td>
<td>79 ± 10 b</td>
<td>6.49 ± 0.22 ef</td>
<td>9.02 ± 0.34 g</td>
<td>218.2 ± 44.7 d</td>
</tr>
<tr>
<td>Under</td>
<td>85.8 ± 3.1 a</td>
<td>19.95 ± 0.18 c</td>
<td>93 ± 16 b</td>
<td>2.86 ± 0.21 a</td>
<td>3.92 ± 0.18 c</td>
<td>266.9 ± 30.7 dc</td>
</tr>
<tr>
<td><em>Carya tomentosa</em></td>
<td></td>
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</tr>
<tr>
<td>Open</td>
<td>141.3 ± 15.4 de</td>
<td>26.55 ± 0.97 f</td>
<td>240 ± 5 c</td>
<td>5.32 ± 0.92 de</td>
<td>8.73 ± 1.14 fg</td>
<td>312.5 ± 41.3 ef</td>
</tr>
<tr>
<td>Under</td>
<td>79.5 ± 2.4 a</td>
<td>21.75 ± 0.53 d</td>
<td>231 ± 6 c</td>
<td>3.05 ± 0.06 ab</td>
<td>3.94 ± 0.09 c</td>
<td>296.1 ± 53.8 ef</td>
</tr>
<tr>
<td><em>Prunus serotina</em></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Open</td>
<td>154.5 ± 8.2 e</td>
<td>23.70 ± 0.97 de</td>
<td>232 ± 3 c</td>
<td>5.24 ± 0.37 de</td>
<td>8.55 ± 0.55 fg</td>
<td>22.3 ± 1.8 a</td>
</tr>
<tr>
<td>Under</td>
<td>144.9 ± 5.0 e</td>
<td>23.85 ± 0.37 e</td>
<td>100 ± 3 b</td>
<td>3.66 ± 0.11 bd</td>
<td>4.12 ± 0.08 c</td>
<td>26.8 ± 3.8 a</td>
</tr>
<tr>
<td><em>Populus grandidentata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>118.8 ± 5.0 cd</td>
<td>12.30 ± 0.18 a</td>
<td>354 ± 3 d</td>
<td>5.77 ± 0.13 de</td>
<td>7.63 ± 0.35 fg</td>
<td>45.0 ± 6.9 b</td>
</tr>
<tr>
<td>Under</td>
<td>96.6 ± 1.0 b</td>
<td>12.75 ± 0.41 a</td>
<td>206 ± 3 c</td>
<td>3.84 ± 0.08 bc</td>
<td>5.34 ± 0.26 d</td>
<td>42.0 ± 6.2 b</td>
</tr>
</tbody>
</table>

1 Means within a column followed by the same letter are not significantly different at P < 0.05. When comparing leaf mass per area, means in both columns followed by the same letter are not significantly different at P < 0.05.

Table 2. Mean (± SE) foliar nitrogen content (g m⁻²) and % N for six hardwood tree species in understory versus open locations in central Pennsylvania. Samples were collected on two dates during the 1993 growing season.

<table>
<thead>
<tr>
<th>Location</th>
<th>June 23</th>
<th>August 5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g m⁻²</td>
<td>% N</td>
</tr>
<tr>
<td><em>Acer rubrum</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>0.98 ± 0.14 cd¹</td>
<td>1.89 ± 0.25 ab</td>
</tr>
<tr>
<td>Under</td>
<td>0.61 ± 0.05 e</td>
<td>1.70 ± 0.07 b</td>
</tr>
<tr>
<td><em>Cornus florida</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>0.79 ± 0.05 d</td>
<td>1.92 ± 0.05 bc</td>
</tr>
<tr>
<td>Under</td>
<td>0.52 ± 0.02 e</td>
<td>1.97 ± 0.09 c</td>
</tr>
<tr>
<td><em>Fraxinus americana</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>1.31 ± 0.10 ab</td>
<td>2.01 ± 0.13 bc</td>
</tr>
<tr>
<td>Under</td>
<td>0.57 ± 0.06 e</td>
<td>1.98 ± 0.09 c</td>
</tr>
<tr>
<td><em>Carya tomentosa</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>1.17 ± 0.16 bc</td>
<td>2.26 ± 0.14 cd</td>
</tr>
<tr>
<td>Under</td>
<td>0.70 ± 0.02 d</td>
<td>2.28 ± 0.04 d</td>
</tr>
<tr>
<td><em>Prunus serotina</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>1.05 ± 0.08 eb</td>
<td>2.05 ± 0.21 bc</td>
</tr>
<tr>
<td>Under</td>
<td>0.94 ± 0.07 b</td>
<td>2.57 ± 0.07 c</td>
</tr>
<tr>
<td><em>Populus grandidentata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>1.42 ± 0.09 a</td>
<td>2.46 ± 0.16 de</td>
</tr>
<tr>
<td>Under</td>
<td>0.96 ± 0.12 b</td>
<td>2.51 ± 0.12 e</td>
</tr>
</tbody>
</table>

1 Means of the same N parameter within a column or row followed by the same letter are not significantly different at P < 0.05.

(Figure 8). Seasonal A was positively correlated (r = 0.30) with predawn Ψ. Both mean and maximum A per plant were positively related to early and late season N content.

Phenotypic plasticity

We compared phenotypic plasticity in light-saturated mean gas exchange rates of sun and sunfleck leaves across the first three sampling periods (May 27, June 11 and June 23) when PAR values between sites were most similar (Figures 2 and 3). The middle successional species, F. americana and C. tomentosa, exhibited the largest relative differences in A and gₛᵥ between sun and sunfleck leaves (81 to 114%), whereas P. grandidenta-
tata exhibited the smallest differences (−14 to 4%). Fraxinus americana and C. tomentosa also exhibited the highest degree of phenotypic expression for leaf thickness (77–78%), guard cell length (21–22%) and (LMA 122–130%), although C. florinda and P. serotina also showed high plasticity for LMA (107–117%) (Table 1).

**Discussion**

Saplings in the open site experienced higher PPFD, leaf temperatures, and VPD than saplings in the understory. Saplings in the open also had higher predawn Ψ than understory saplings, indicating less competition for soil water (cf. Abrams 1986, Kloeppel et al. 1993). This difference was most pronounced during the peak drought on July 24 when predawn Ψ in open and understory study species varied by an average of 0.2 MPa. The increased opportunity for open-grown plants to rehydrate overnight might be partially responsible for their ability to maintain higher relative gas exchange rates than understory plants during the drought (cf. Hinckley et al. 1978a).

During the drought period, gas exchange decreased more in shaded leaves than in sun leaves of all species, resulting in A values significantly less than zero in the shaded leaves. Decreased A coupled with decreased photosynthetic light response suggest that shaded leaves were more sensitive to drought than sun leaves (cf. Abrams 1986, Abrams and Knapp 1986). Sunfleck leaves also exhibited a greater decrease in A in response to the drought than sun leaves, indicating that understory leaves have morphological and physiological limitations to high PPFD and drought compared with sun leaves. However, A was positive in understory sunfleck leaves during July and August, indicating that any potential carbon gain in droughted understory plants at midday was derived from the photosynthetic activity of sunfleck leaves. The large differences in seasonal A among shaded, sunfleck and sun leaves accounted for almost all of the variance in A.

Despite large differences in A between sites, variation in gas...
exchange in sun leaves was distinct along successional lines, and there were smaller decreases in gas exchange in response to the drought in early than in later successional species (cf. Hinckley et al. 1978b, Bazzaz 1979, Bazzaz and Carlson 1982, Bahari et al. 1985, Abrams and Knapp 1986, Abrams et al. 1994). Both mean and minimum midday $\Psi$ values were lower in the early successional species than in the later successional species. There were also differences between shaded and sunfleck leaves in $A$, $g_{sv}$, and $\Psi$, indicating that the intrinsic ecophysiological variation between early and late successional species occurred, at least in the short-term, in both high and low irradiance environments (cf. Bazzaz and Carlson 1982, Abrams 1988, Kloeppe et al. 1993, Walters et al. 1993). In the case of understory P. serotina, relatively high $A$ values probably contributed to the success of this reputed early successional species in the understory of many forests in eastern North America (Abrams 1992, Abrams et al. 1992, Horsley and Gottschalk 1993).

Plants grown at high irradiances typically produce leaves with greater thickness, mass per area, and stomatal density and smaller area per leaf than plants grown at low irradiances (Salisbury 1927, Jackson 1967, Carpenter and Smith 1981, Abrams and Kubiske 1990). Similar differences are also apparent in early versus late successional and xeric versus mesic species (Abrams and Kubiske 1990, Abrams et al. 1994). Leaf thickness and mass per area were higher in open than in understory plants and higher in early and middle successional species than in late successional species, which may have contributed to the increased drought tolerance in these plants (cf. Abrams 1986, Abrams and Kubiske 1990, Abrams et al. 1994). The seasonal increase in leaf mass per area and its positive relationship with $A$ and $g_{sv}$ in sun and understory sunfleck leaves are typical of many temperate hardwood species (Jurik 1986, Reich et al. 1991a, Kloeppe et al. 1993, Abrams et al. 1994).

Leaf $N$ content was highest in open growing, early and middle successional species and increased during the growing season. Similarly, Reich et al. (1990, 1991) reported higher seasonal $N$ content in early successional Rubus, Quercus and Prunus species than in later successional Acer species. Higher leaf $N$ in early than in late successional species is consistent with the physiological and morphological adaptations of early successional species that result in high rates of photosynthesis and growth in post-disturbance, high-resource environments (cf. Bazzaz 1979). Mean area-based $A$ was positively related to leaf $N$ content or percent $N$, or both, in the open and understory sunfleck leaves (cf. Field and Mooney 1986, Evans 1989, Reich et al. 1990, 1991). Higher $N$ content in sun leaves than in shaded leaves is consistent with the idea that $N$ acquisition and allocation between plants and within canopies parallel gradients of light availability (Björkman and Holmgren 1963, Evans 1989, Ackerly 1992). However, percent $N$ was generally not significantly different between shaded and sun leaves of the same species, indicating that higher $N$ content of sun leaves was predominantly a function of increased LMA (cf. Björkman and Holmgren 1963, Ackerly 1992). The finding that percent $N$ did not vary between plants in the open and understory sites may reflect differential $N$ partitioning. In the understory, greater amounts of $N$ may be partitioned into chlorophyll, whereas in the open more $N$ may be partitioned into Rubisco, resulting in similar percent $N$ values between sites (Evans 1989).

It has been suggested that early successional plants may have greater acclimation potential than later successional plants (Bazzaz 1979, Bazzaz and Carlson 1982). However, our results indicate that middle successional tree species may have greater phenotypic plasticity than early or late successional tree species. Middle successional species may have evolved adaptations to a broader range of ecosystem conditions than strictly early or late successional species, and therefore may be capable of greater phenotypic plasticity (T.J. Givnish, personal communication). Alternatively, successional status may not be closely associated with phenotypic plasticity. For example, the phenotypic plasticity exhibited by all our study species may be a dominant mechanism by which trees respond to contrasting microenvironmental conditions. Moreover, our study provides an example of function following form, in which open growing plants produced thicker leaves with higher mass per area and $N$ content than understory plants, which, in turn, permitted higher gas exchange rates, lower leaf $\Psi$ and greater tolerance to drought. On the other hand, understory plants of all species were able to maintain positive $A$ at very low PAR early in the season and $A$ of sunfleck leaves often approached $A$ of sun leaves. Similar differences were apparent among the species, with early and mid-successional species having higher leaf $N$, $A$ and mass per area and potentially greater tolerance to drought than the late successional species.

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References


