

Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments

BRIAN D. KLOEPPPEL,¹ MARC D. ABRAMS, AND MARK E. KUBISKE

School of Forest Resources, Ferguson Building, Pennsylvania State University, University Park, PA 16802, U.S.A.

Received December 30, 1991

Accepted June 29, 1992

KLOEPPPEL, B.D., ABRAMS, M.D., and KUBISKE, M.E. 1993. Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. *Can. J. For. Res.* **23**: 181–189.

Seasonal net photosynthesis, water relations, and leaf structure were measured in co-occurring saplings of *Quercus velutina* Lam., *Quercus prinus* L., *Sassafras albidum* (Nutt.) Nees, and *Acer rubrum* L. from adjacent open and understory sites in the central Pennsylvania barrens, United States. Saplings of all species exhibited significant physiological and morphological plasticity, which included greater area-based photosynthesis, leaf conductance, water-use efficiency, stomatal density, specific leaf mass, and leaf thickness on the open site. However, only *Q. velutina* had greater net photosynthesis in the open versus understory when photosynthesis was expressed on a mass basis. The earlier successional *Quercus* spp. and *S. albidum* exhibited higher diurnal and seasonal gas exchange in the open than the later successional *A. rubrum*, although all species exhibited significant diurnal declines in photosynthesis. *Quercus* spp. exhibited a 56–62% greater decrease in diurnal water potential compared with *S. albidum* and *A. rubrum* in both the open and understory. *Sassafras* maintained high gas-exchange rates in the open without experiencing large diurnal tissue water deficits. Seasonal variations in net photosynthesis and leaf conductance were significantly correlated with each other and with specific leaf mass. Light-response curves predicted greater saturating light levels and greater rates of maximum photosynthesis in the early successional species versus *A. rubrum*, but similar light compensation values in all species. The results of this study suggest that each species displayed many similar and unique adaptations and responses to varying light and water availability in the barrens environment.

KLOEPPPEL, B.D., ABRAMS, M.D., et KUBISKE, M.E. 1993. Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. *Can. J. For. Res.* **23** : 181–189.

Nous avons mesuré la photosynthèse nette saisonnière, les relations hydriques et la structure foliaire chez des gaulis voisins de *Quercus velutina* Lam., *Quercus prinus* L., *Sassafras albidum* (Nutt.) Nees et *Acer rubrum* L. sur des sites adjacents en milieux ouverts et de sous-bois, sur les terres dénudées du centre de la Pennsylvanie, États-Unis. Les gaulis de toutes les essences ont démontré une plasticité physiologique et morphologique significative, avec de plus fortes valeurs de photosynthèse par unité de surface foliaire, de conductance foliaire, d'efficacité d'utilisation de l'eau, de densité stomatique, de masse foliaire spécifique et d'épaisseur foliaire en milieu ouvert qu'en sous-bois. Cependant, seul *Q. velutina* a conservé une photosynthèse plus élevée en milieu ouvert qu'en sous-bois lorsque celle-ci était exprimée par unité de masse. En milieu ouvert, les taux journaliers et saisonniers d'échanges gazeux étaient plus élevés chez *Quercus* spp. et *S. albidum*, des essences plus hâtives dans la succession, que chez *A. rubrum*, une essence plus tardive, et ce malgré un déclin de la photosynthèse diurne chez toutes les essences. Le potentiel hydrique diurne de *Quercus* spp. a chuté de 56 à 62% de plus que celui de *S. albidum* et de *A. rubrum* dans les milieux ouverts et de sous-bois. En milieu ouvert, le taux d'échanges gazeux de *Sassafras* est demeuré élevé, sans entraîner de fluctuations importantes de déficit hydrique des tissus. Les variations saisonnières de la photosynthèse et de la conductance étaient corrélées entre elles, ainsi qu'avec la masse foliaire spécifique. Les taux de saturation lumineuse et de photosynthèse nette prédits par les courbes de réaction à la lumière étaient plus élevés chez les essences hâtives dans la succession que chez *A. rubrum*, et ce malgré des valeurs prédites de point de compensation similaires chez toutes les essences. Ces résultats suggèrent que chaque essence possède certains traits communs aux autres essences, et certains traits uniques dans son adaptation et ses réponses à la disponibilité variable en eau et en lumière dans l'environnement des terres dénudées.

[Traduit par la rédaction]

Introduction

Water and light availability are dominant influences on the seasonal ecophysiology of plants. Though water is the most abundant compound on the planet, it frequently is limiting to plants because of prevailing weather patterns, low soil-holding capacity, and competition from other vegetation (Schulze *et al.* 1987). Also, diurnal water deficits may occur because of high transpiration and simultaneous low hydraulic conductivity (Robichaux 1984). Light, on the other hand, is most limited by atmospheric conditions and overtopping from neighboring vegetation (Kuuluvainen and Pukkala 1989; Reich *et al.* 1990b; Whitehead *et al.* 1990). These two variables commonly act in concert to create a wide range of

growth environments, even in a small geographic area. Nonetheless, the effects of water and light have typically been studied independently, an approach that does not effectively simulate the array of conditions that plants normally experience. For example, little is known about drought responses in plants adapted to high-light versus low-light conditions (Vance and Zaerr 1991; Abrams *et al.* 1992; Ellsworth and Reich 1992). Therefore, a more valuable approach is to study the effects and interrelationships of these two resources to better understand their impact on plant ecophysiology.

The successional status of a species is often associated with its ability to compete for varying levels of water and light (Hinckley *et al.* 1978; Bazzaz 1979). It is generally assumed that early successional species growing in open areas are exposed to greater fluctuations in temperature and soil moisture and are more drought tolerant than later successional species found in mature forests. Ecophysiological adaptations

¹Author to whom all correspondence should be addressed. Present address: Department of Forestry, 1630 Linden Drive, University of Wisconsin – Madison, Madison, WI 53706, U.S.A.

of early versus late successional species include higher maximum gas-exchange rates, more xerophytic leaves, and deeper rooting (Bazzaz 1979; Lyford 1980; Koike 1988; Abrams 1990). However, both early and late successional tree species may exhibit plasticity in leaf morphology to open and understory environments (Abrams and Kubiske 1990).

Despite the mesic environmental conditions in the north-eastern United States, areas of xeric, barrens soils occur throughout the region. These sites are characterized by sandy soils of low nutrient and water-holding capacity, seasonal drought, and typically a long history of logging and fire (Harshberger 1916). Because of their disturbed nature, a wide variety of plants can be found growing in both open and understory barrens sites. Despite the long-term interest in studying the ecophysiology of plants in stressed environments, few studies have focused on the barrens vegetation in North America (Reich and Hinckley 1980; Hull and Wood 1984). In this study, we located adjacent open and understory barrens sites supporting saplings of the same early and late successional species. Our objective was to monitor diurnal and seasonal gas-exchange and water relations and leaf structure in high- and low-light phenotypes of species during well-watered and droughty periods of a growing season. We were particularly interested in identifying ecophysiological attributes in species of varying successional rank to high and low-light environments in the barrens habitat.

Materials and methods

Study site

The barrens ecosystem used for study is located approximately 2 km northwest 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 sandstone derivative with rapid permeability and very low available water capacity. Soil texture is sand, loamy sand, and sandy loam on the surface horizon and at depths of 25 and 50 cm, respectively (Day 1965).

From the late 18th to the early 20th century, barrens' forests were frequently disturbed by clear-cutting and burning associated with the charcoal iron industry (Abrams and Nowacki 1992). The current stand was established in approximately 1934. The site is dominated by chestnut oak (*Quercus prinus* L.), with an understory of mostly red maple (*Acer rubrum* L.) (Nowacki and Abrams 1991).

Four species of differing successional status were selected for study from juxtaposed open and understory sites. Included were red maple, considered to be the climax species for the site, and three early to midsuccessional species, black oak (*Quercus velutina* Lam.), chestnut oak, and sassafras (*Sassafras albidum* (Nutt.) Nees) (Burns and Honkala 1990; Nowacki and Abrams 1991). Since all four species were present as saplings in both light regimes, we formulated a two-factorial design with four species and two microenvironments with six to seven individuals in each species–treatment combination. The sassafras saplings were widely distributed and did not appear to be clonal in nature.

Data collection

During the 1990 growing season, diurnal microenvironmental and plant ecophysiological measurements were conducted in the open and understory sites on 5 June, 22 June, 18 July, 3 August, and 31 August. All ecophysiological measurements were conducted on first flush or early season leaves. Predawn (06:00 solar time) leaf water potential (Ψ) was measured on one leaf from each study plant with a pressure chamber (PMS Instrument Co., Corvallis, Oreg.). Gas

exchange, photosynthetically active radiation (PAR), and Ψ were measured every 2.5 h from 07:30 to 15:00 solar time on one leaf from each study sapling. Gas-exchange and PAR measurements were made with an open-flow infrared gas analysis system (LCA-2, Analytical Development Co., Herts, England). Leaves that were measured during the second round of each sampling date were collected for specific leaf mass (see below) analysis to allow for a simultaneous comparison of photosynthesis on both an area and a mass basis. On the open site only leaves that were in full sunlight were measured. Understory leaves were sampled under the range of available diffuse light and occasional sunflecks to characterize the wide range of physiological activity present in a forest understory (Percy 1990). Net photosynthesis (A), leaf conductance to water vapor (g_{wv}), transpiration (J), leaf temperature, and vapor-pressure deficit (vpd) were calculated according to von Caemmerer and Farquhar (1981). Instantaneous water-use efficiency (WUE) was calculated as $A \cdot J^{-1}$. Gravimetric soil moisture of the upper 25 cm was measured on four replicate samples in both sites at each date.

Within 2 days of each diurnal measurement one midcanopy leaf from four of the study plants in each species–site combination was brought to the laboratory for structural analysis. Leaf thickness was measured in three places on each leaf at the approximate midpoint between major veins with a light microscope and ocular micrometer. Three measurements of guard-cell length and stomatal density were measured with acetate impressions of the abaxial surface of each leaf (Payne 1968). Specific leaf mass (SLM) was calculated by dividing total leaf area without petiole, measured with a leaf area meter (Li-Cor, Lincoln, Nebr.), by the dry weight (48 h at 70°C).

Light-response curves of the four species in the understory were compiled from data on the five measurement dates. A Michaelis–Menten model (Sheve 1984; Givnish 1988) was fitted with PROC NLIN (procedure nonlinear regression) in SAS:

$$[1] \quad A = \frac{A_{\max} \text{PAR}}{\text{PAR} + K} - R_s$$

where

A is net photosynthesis ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)

A_{\max} is maximum asymptotic photosynthesis ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)

PAR is photosynthetically active radiation ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)

K is saturation constant ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)

R_s is dark respiration ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)

Light-compensation points (LCP) were determined by solving the fitted model for $A = 0$. Since all measurements made in the open had light levels above 500 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, similar modeling could not be done on open-grown plants.

Statistical analyses for microenvironmental and plant ecophysiological parameters were carried out using one-way and two-way general linear models for a completely randomized design and Pearson product-moment correlation (SAS Institute Inc. 1985). Tukey's multiple-range test ($P < 0.05$) was used for all multiple comparisons, including light-response parameters.

Results

Seasonal site conditions and microenvironment

The monthly averages of daily maximum and minimum temperatures from June to August were within 1.0°C of 30-year means, and daily precipitation during the measurement period was 5.05 cm above the 100-year mean (Fig. 1). However, a 10-day drought from 25 July to 4 August resulted in significantly lower soil moisture (0–25 cm) in both the understory and open sites on the 3 August sampling date. Soil moisture was not significantly different between sites on any sampling date. Mean predawn leaf Ψ was greater than –0.25 MPa on both sites across all sampling dates; however, values were generally lower in understory plants. PAR was significantly higher in the open on all sampling dates (Fig. 2).

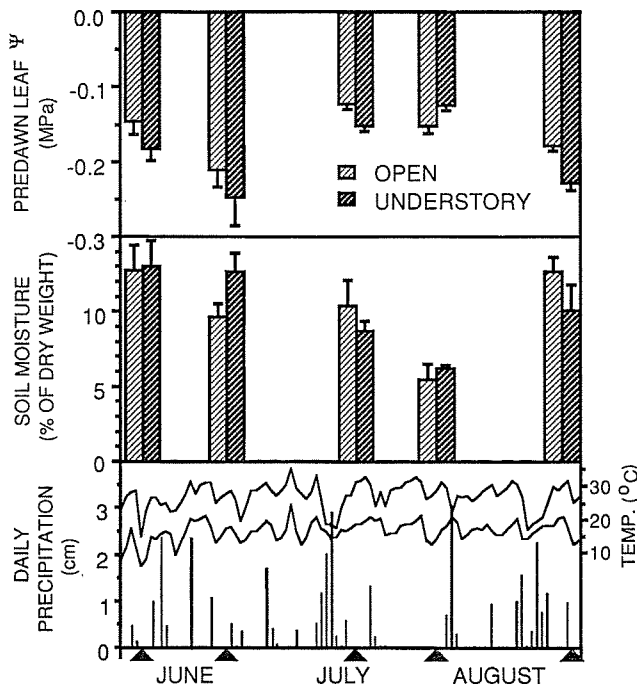


FIG. 1. Open and understory site gravimetric soil moisture and mean (± 1 SE) predawn leaf water potential (Ψ) of four tree species in a barrens ecosystem of central Pennsylvania. Daily ambient maximum and minimum temperature (lines) and precipitation (vertical bars) are also presented. \blacktriangle , sampling dates.

Leaf temperature was only slightly but significantly higher in the open than in the understory on all sampling dates and times. Daily average leaf temperatures were greatest on the three middle sampling dates. Vapor-pressure deficit (VPD) did not exhibit clear differences between sites, but it was significantly higher ($P < 0.05$) on 3 August than the other sampling dates. Significant diurnal increases in both leaf temperature and vpd were apparent throughout the study.

Leaf structure

Leaf area and thickness, stomatal density, and guard-cell length exhibited no significant seasonal changes across the five sampling dates; therefore, overall seasonal means were calculated for site and species comparisons (Fig. 3). Understory plants generally had significantly greater area and lower thickness and stomatal density than open plants. One exception was red maple, which had similar leaf area between open and understory sites. Black oak had the largest leaves, whereas red maple had the smallest and thinnest leaves, in the understory. There were no significant species differences in leaf area or thickness in the open site. Sassafras had the lowest stomatal density in both sites, and chestnut oak had the greatest stomatal density of the open-site plants. Guard-cell length was greater in open than understory for sassafras and black oak, whereas the reverse occurred in red maple and chestnut oak. Red maple had the smallest guard cells in both sites. The greatest guard cell length occurred in sassafras in the open and in chestnut oak in the understory.

SLM exhibited a significant seasonal increase in all four species at both sites (Fig. 4). The highest increase in SLM in the open site occurred early in the season. Open plants had significantly greater values of SLM than the understory plants for all species and sampling dates. Specific leaf mass was

greatest in black and chestnut oak and lowest in sassafras, despite its relatively thick leaves ($P < 0.05$).

Gas exchange and leaf water potential

Diurnal gas exchange and leaf water potential (Ψ) data are presented for 18 July, which exhibited trends typical of all five sampling dates (Fig. 5). Net photosynthesis (A) and leaf conductance to water vapor (g_{wv}) were significantly higher in open than in understory plants throughout the day, although open plants exhibited significant diurnal decreases in A . Red maple consistently had the lowest A and g_{wv} of all open-grown plants. Leaf water potential was generally lower ($P < 0.05$) in the open site. The oak species experienced much greater diurnal decreases in Ψ compared with sassafras and red maple. Diurnal Ψ was negatively correlated ($P < 0.05$) with g_{wv} in all species in the open and understory ($r = -0.41$ and -0.22), but not with A .

Daily mean A and g_{wv} were consistently higher ($P < 0.05$) in open than in understory plants, particularly when gas-exchange rates peaked during midseason in the open site (Fig. 6). In contrast, g_{wv} had decreased significantly by 3 August, possibly in response to higher VPD and lower soil moisture on that date (Figs. 2 and 6). This relationship was also seen to a lesser degree in the understory plants. Nonetheless, daily mean A was significantly correlated with g_{wv} and SLM in both the open and understory sites ($r = 0.40$ – 0.59). Black oak and sassafras exhibited significantly greater A than chestnut oak and red maple in the open during midseason. There were few significant species differences in A in the understory. In the open, black oak had the highest g_{wv} on all dates and red maple the lowest. Red maple also had the lowest g_{wv} in the understory. Daily mean leaf Ψ was significantly lower in the open than understory on all dates except 5 June, when species on both sites had their least negative values of Ψ (Fig. 6). The oaks had the lowest ($P < 0.05$) Ψ values of all species on both sites. Daily mean Ψ and g_{wv} were negatively correlated in both open and understory plants ($r = -0.20$ and -0.22).

Photosynthetic rates in the open were also compared with those in the understory at $PAR > 500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. In all species, open plants had significantly greater area-based A (Fig. 7). However, when A was expressed on a leaf-mass basis, only black oak exhibited significantly greater values in the open. This suggests that in the other three species, the difference in SLM between the two sites accounted for much of the difference in A at light saturation. In contrast, black oak seemed to exhibit a higher biochemical capacity for photosynthesis in the open, in addition to the increased SLM exhibited by the other species.

Daily mean instantaneous water-use efficiency (WUE) for each species–site combination was compared for each sampling date. When all species were grouped, WUE was significantly higher in the open on all dates except 5 July (Fig. 8). Both sites exhibited significant increases in WUE from 22 June to 31 August after initially higher values on 5 June. In the open, black oak generally exhibited low WUE values as a result of higher rates of transpiration (data not shown). No species consistently exhibited the highest WUE throughout the season on either site.

Light-response curves

A Michaelis–Menten saturation kinetics model was fitted to the A and PAR data for each species in the understory (Fig. 9). Fitted model parameters indicated that A_{max} was

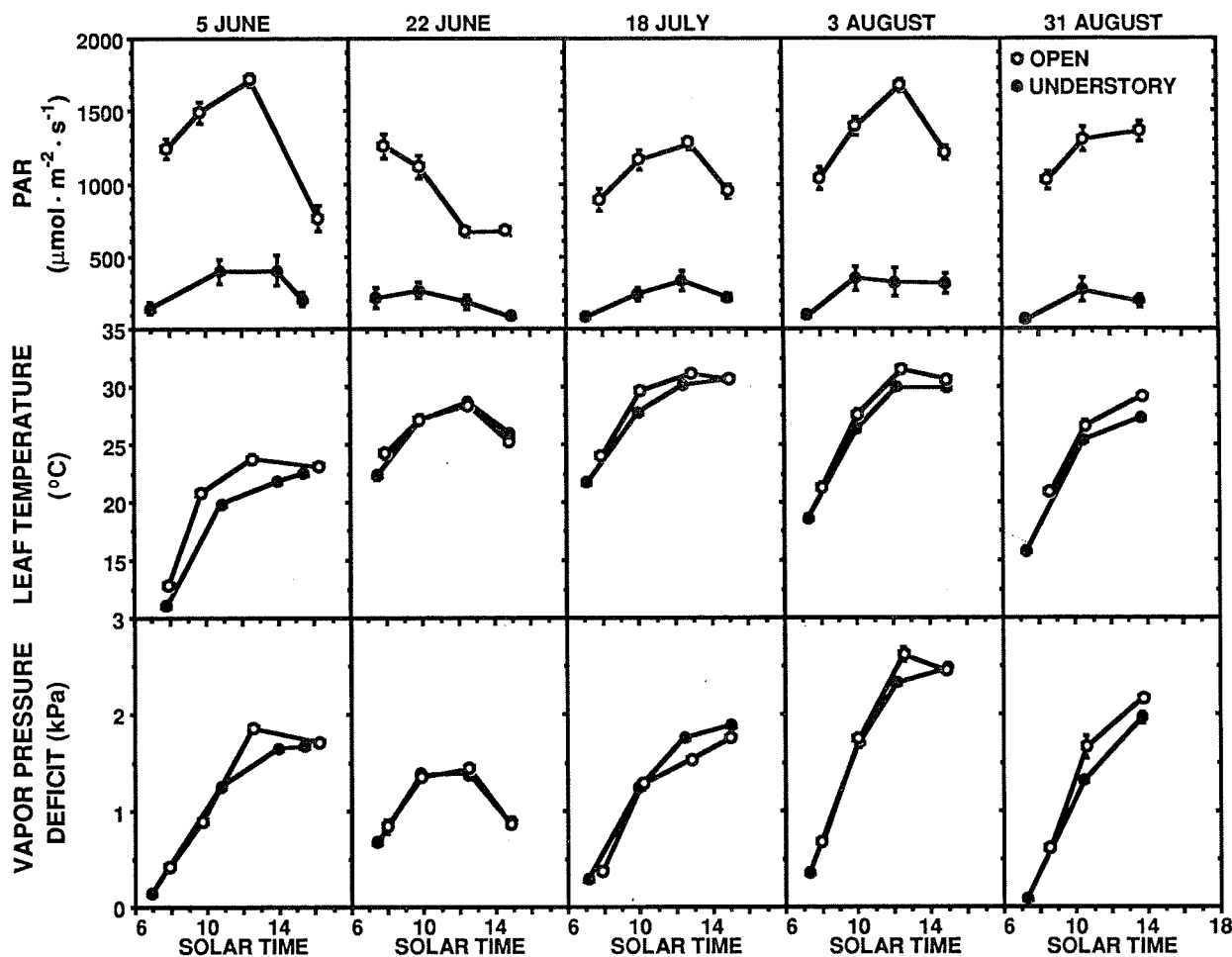


FIG. 2. Diurnal photosynthetically active radiation (PAR), leaf temperature, and vapor-pressure deficit for open and understory sites during the 1990 growing season in a barrens ecosystem of central Pennsylvania.

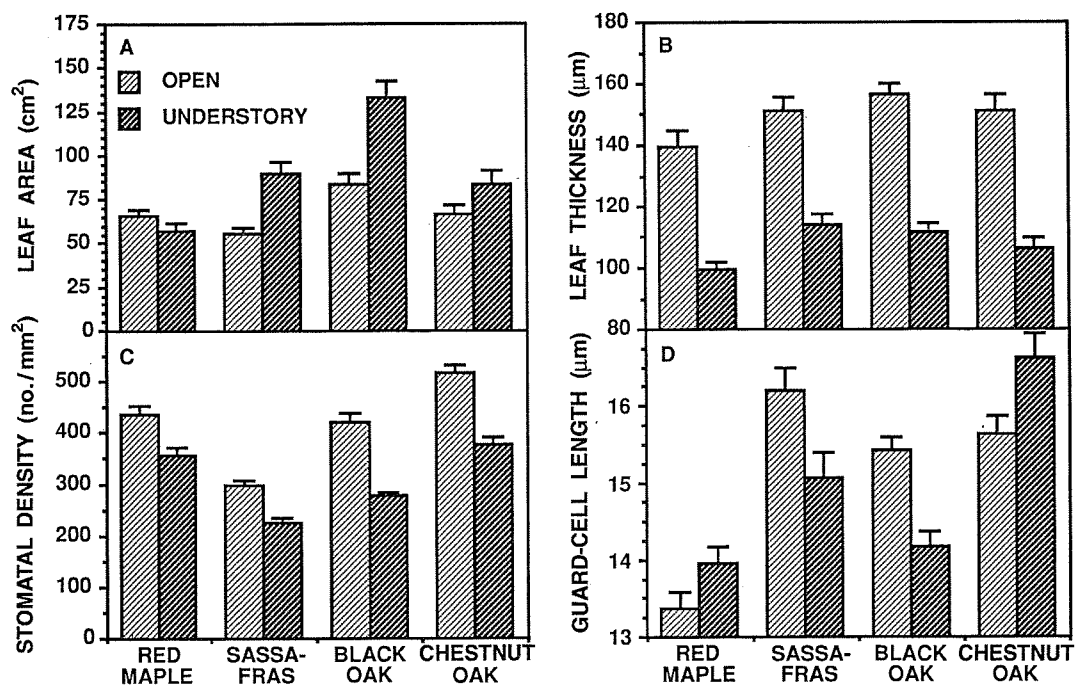


FIG. 3. Leaf structure parameters during the 1990 growing season in four Pennsylvania barrens species growing in open and understory environments. Values represent an overall seasonal mean (± 1 SE) from five sampling dates.

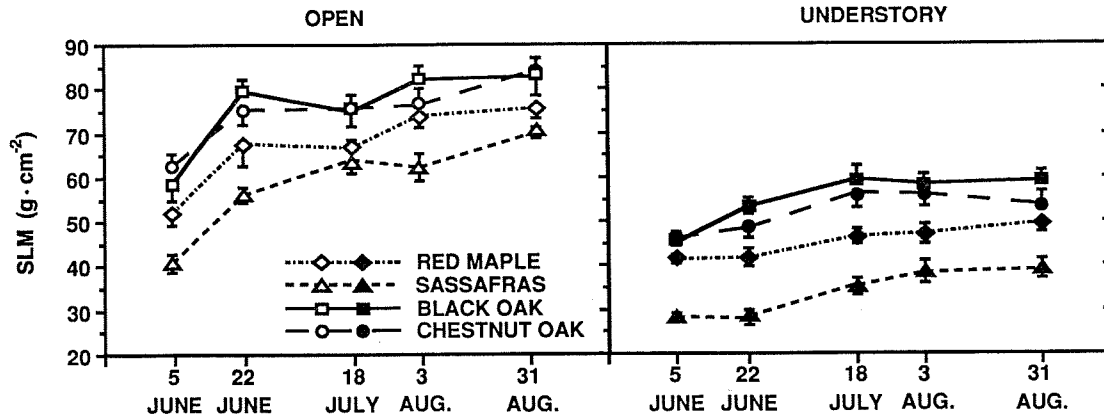


FIG. 4. Specific leaf mass (SLM) (mean \pm 1 SE) of four Pennsylvania barrens species in contrasting environments during the 1990 growing season.

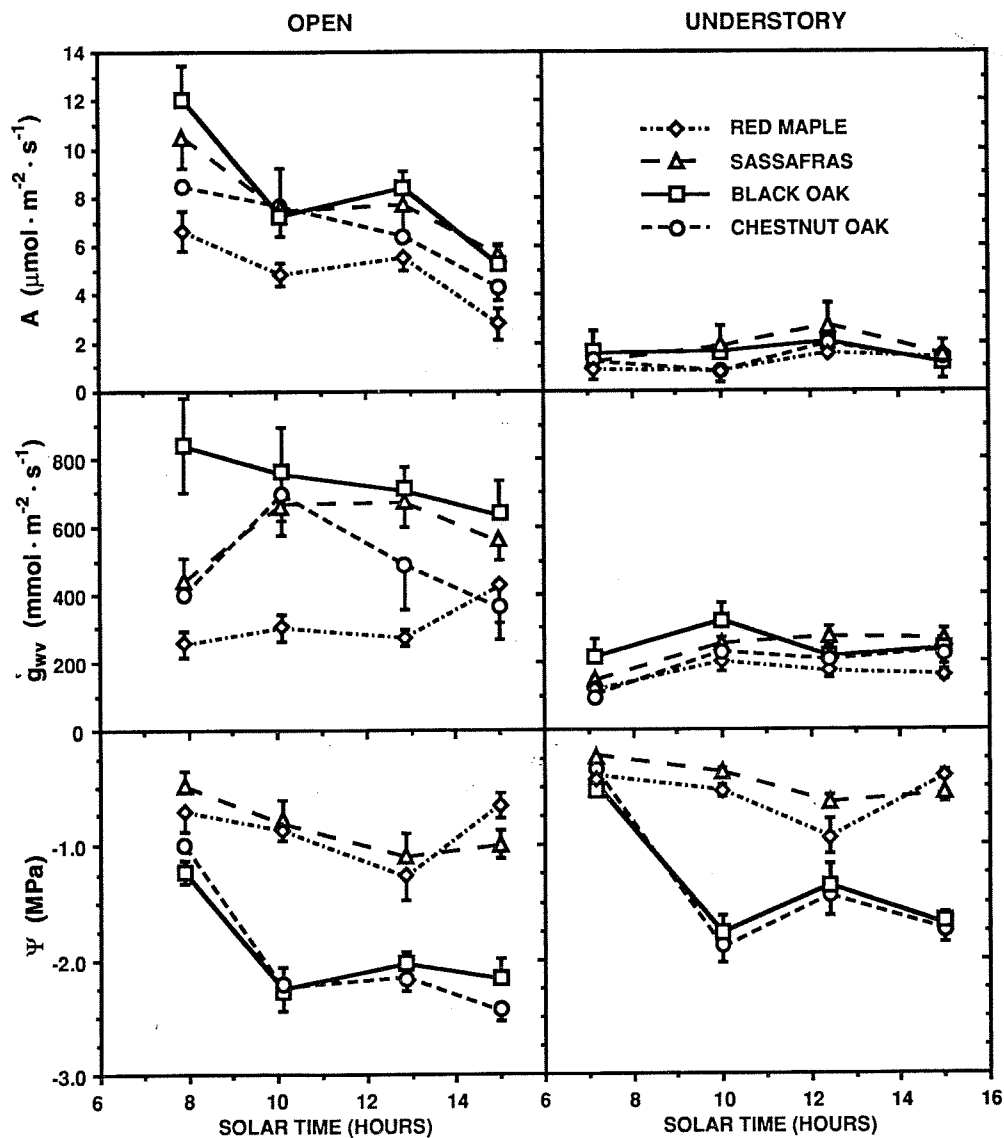


FIG. 5. Diurnal (mean \pm 1 SE) course of net photosynthesis (A), leaf conductance to water vapor (g_{wv}), and bulk leaf water potential (Ψ) of four Pennsylvania barrens species in the open and understory on 18 July 1990.

greatest in sassafras and black oak, whereas in red maple it was significantly lower (Table 1). Chestnut oak has intermediate A_{max} but significantly greater R_s than all other species,

indicated by the x-intercept of the fitted curve. The saturation constant K, an indication of the relative level of PAR at which A becomes saturated, was highest in sassafras followed by

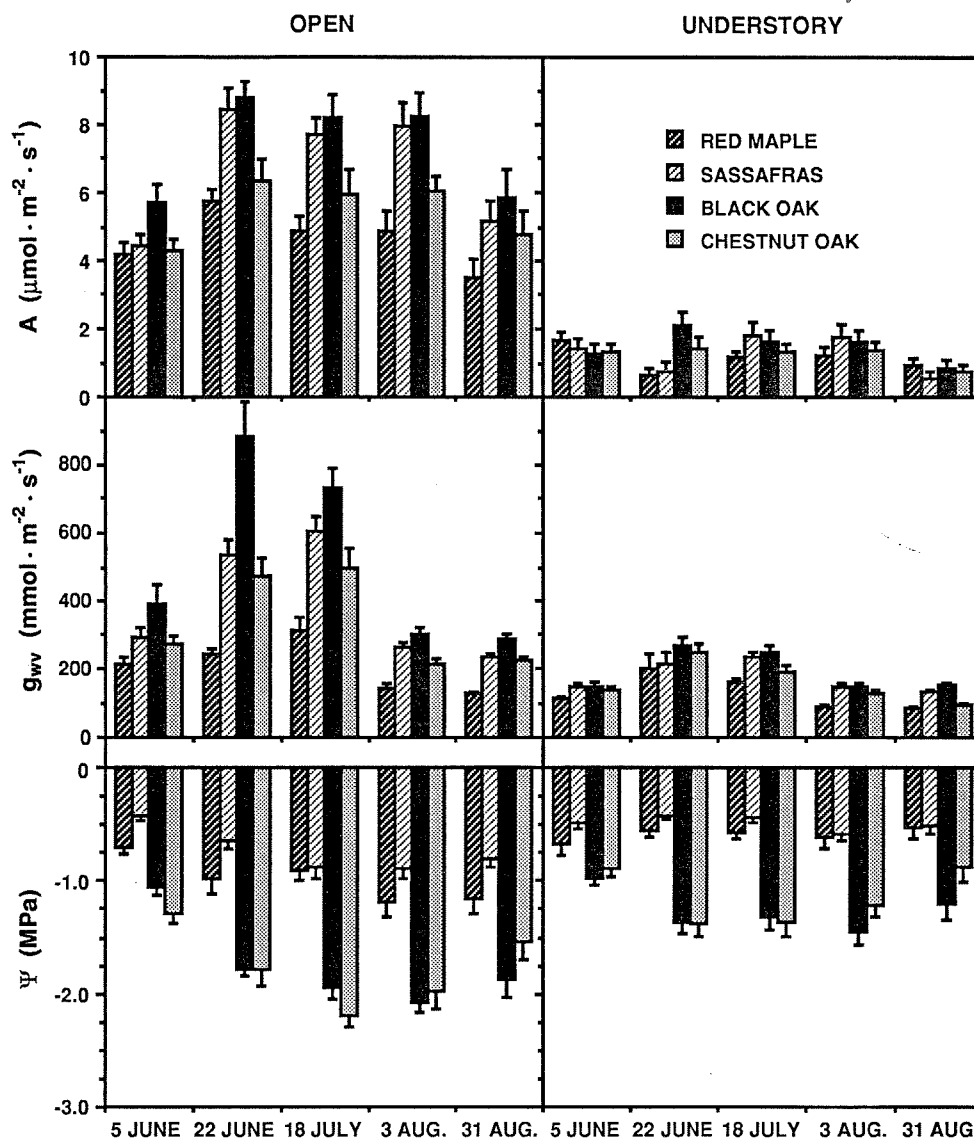


FIG. 6. Daily mean (± 1 SE) net photosynthesis (A), leaf conductance to water vapor diffusion (g_{wv}), and bulk leaf water potential (Ψ) of four Pennsylvania barrens species in the open and understory during the 1990 growing season.

black oak, while chestnut oak and red maple had similarly lower values. The LCP showed little variation between species, with a range of only 23.3–33.4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Discussion

The open microenvironment stimulated much greater A and g_{wv} than the understory for all species (cf. Reich 1984; Abrams 1986; Nonami *et al.* 1990; Turnbull 1991). Higher g_{wv} and J resulted in significantly greater diurnal declines in leaf Ψ in the open, particularly for the oak species. However, large diurnal decreases in Ψ are not typical of oaks, especially in understory conditions (Abrams 1988, 1990), although large diurnal decreases in Ψ were reported for open-growing oak species in a xeric ridge community during moist periods (Abrams *et al.* 1990). Sassafras maintained high rates of A and g_{wv} in the open and did not experience large diurnal tissue water deficits at either site. This relationship may be due to sassafras having higher hydraulic conductivity, stem capacitance, or a more extensive root system, although these eco-

physiological features have been also associated with oak species (Abrams 1990). Nonetheless, the diurnal decline in Ψ averaged only 0.48 MPa across all species and sampling dates, representing a 34% greater decrease in the open than the understory compared with a 79% increase in A . Thus, WUE was often greater in open than in understory plants. Seasonal A and g_{wv} values for the oaks and sassafras were greater than those of red maple, a typical difference found in early versus later successional tree species (Bazzaz 1979; Bazzaz and Carlson 1982; Koike 1987, 1988; Abrams 1988; Reich *et al.* 1990a). Among the early successional species, chestnut oak displayed the lowest values of A and g_{wv} , a response that may reflect this species' adaptation to stressful, resource-limited environments (Chapin *et al.* 1987). Intrinsically low g_{wv} and J in red maple and chestnut oak may retard desiccation in this drought-prone environment.

Light-response curves indicated similar species relationships to that of the diurnal and seasonal patterns of A . Thus, A_{max} was highest for black oak and sassafras and much lower

TABLE 1. Understory light saturation curve parameter estimates ($\bar{x} \pm$ asymptotic standard error) for four species in the Pennsylvania barrens, U.S.A.

	A_{\max}	R_s	K	LCP	Residual df	RMS
Sassafras	$7.59 \pm 1.42a$	$0.29 \pm 0.25b$	561	22.3	111	1.01
Black oak	$6.34 \pm 0.55ab$	$0.47 \pm 0.27b$	361	28.9	128	0.99
Chestnut oak	$4.83 \pm 0.37bc$	$0.87 \pm 0.37a$	152	33.4	129	0.86
Red maple	$3.58 \pm 0.33c$	$0.50 \pm 0.35b$	139	22.5	111	0.59

NOTE: Maximum photosynthesis (A_{\max}), dark respiration (R_s), saturation constant (K), residual degrees of freedom, and residual mean squares (RMS) were estimated with PROC NLIN in SAS, while the light-compensation point (LCP) was determined by solving the overall net photosynthesis equation for $A = 0$. Means in a column followed by the same letter are not significantly different utilizing Tukey's mean separation test at $\alpha = 0.05$. Units for A_{\max} , R_s , K , and LCP are all $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

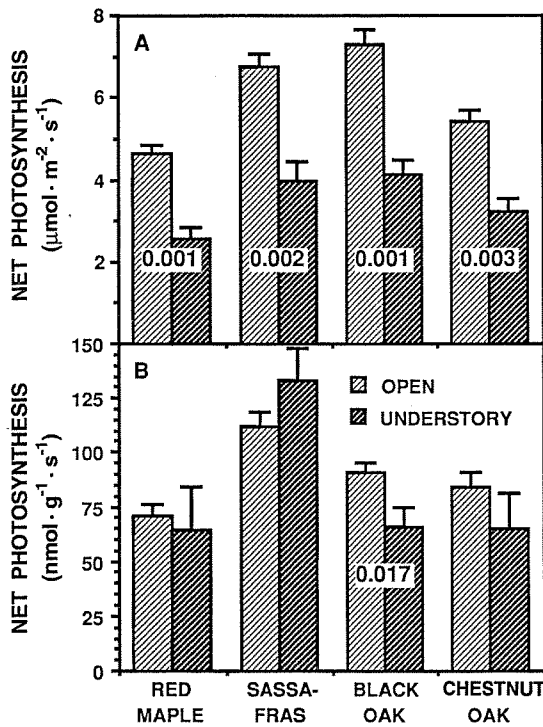


FIG. 7. Open and understory rates of net photosynthesis in high-light conditions on both a leaf-area (A) and mass (B) basis of four Pennsylvania barrens species. Vertical lines represent 1 SE, and P -values are given for significant differences ($P < 0.05$).

for chestnut oak and red maple. Even though these species were growing in a suboptimal barrens site, their gas-exchange rates were comparable to those of hardwood tree species on more favorable sites in other regions of eastern North America (Loach 1967; Bazzaz *et al.* 1972; Turner and Heichel 1977; DeSoyza and Kincaid 1991). In contrast, Reich and Hinckley (1980) studied a pygmy oak ecosystem where they observed low rates of gas exchange, even during moist periods of the growing season, due to low tissue nutrient content. This pattern was not observed in this study, despite low soil pH and N, P, K, and Ca availability in the barrens ecosystem (K.W. Kleiner and M.D. Abrams, unpublished data).

Despite species differences in A_{\max} , there was little variation in their LCP. This was unexpected, since shade-tolerant, understory species such as red maple usually have a lower LCP (Bazzaz 1979). However, oak and sassafras saplings used in this study may have exhibited a lower than expected LCP

as a plastic response to an understory environment or simply because of their young age. It is known that plants may develop a high degree of shade tolerance at an early age, which may decrease as they mature (Spurr and Barnes 1980). Nevertheless, black oak and sassafras had greater saturating light levels for A and greater A_{\max} during sunflecks, which may facilitate the survival of these early or midsuccessional species in a shaded understory.

All four study species exhibited morphological plasticity and produced leaves that should have a functional advantage in either open or understory environments. Stomatal density, leaf thickness, and specific leaf mass were highest in the open species (cf. Abrams 1986; Abrams and Kubiske 1990). Although leaf area was greater in the understory for three of the species, red maple did not exhibit this difference (cf. Goulet and Bellefleur 1986). Abrams and Kubiske (1990) noted that there were no consistent differences in guard-cell length between sun and shade leaves of 26 hardwood tree species, which supports our finding that red maple and chestnut oak exhibited longer guard cells in the understory, whereas sassafras and black oak exhibited the opposite trend.

Net photosynthesis and g_{wv} were significantly lower on 5 June than the middle sampling dates, which may be related to lower leaf and air temperatures early in the season. However, SLM also increased during this time, resulting in significant correlations between SLM and A and g_{wv} across both sites. Thus, fully expanded foliage sampled at the beginning of the growing season may not have reached its full morphological or physiological potential for maximum gas-exchange values, as previously reported in other oak species (Turner and Heichel 1977; Abrams 1988; Abrams and Menges 1992). Reich *et al.* (1991) observed a similar pattern with gas exchange and SLM as well as seasonal fluctuations in leaf nitrogen content in maple and oak trees. It appears that increased SLM could integrate the effects of greater leaf thickness, chlorophyll content, and mesophyll cell wall exposure to intercellular air spaces, thereby resulting in greater carbon assimilation (cf. Nobel 1983). Other leaf structural parameters measured in this study were not correlated with gas-exchange parameters.

This study detected peak gas-exchange rates early in the morning when ambient conditions included lower leaf temperature, VPD, and plant water deficit. This pattern has been recorded in other xeric habitats and in mesic habitats during droughty conditions (Hinckley *et al.* 1979; Williams 1983; Abrams *et al.* 1990; Reich *et al.* 1990a). Both the early and late successional study species adjusted to open and understory environments via morphological and physiological

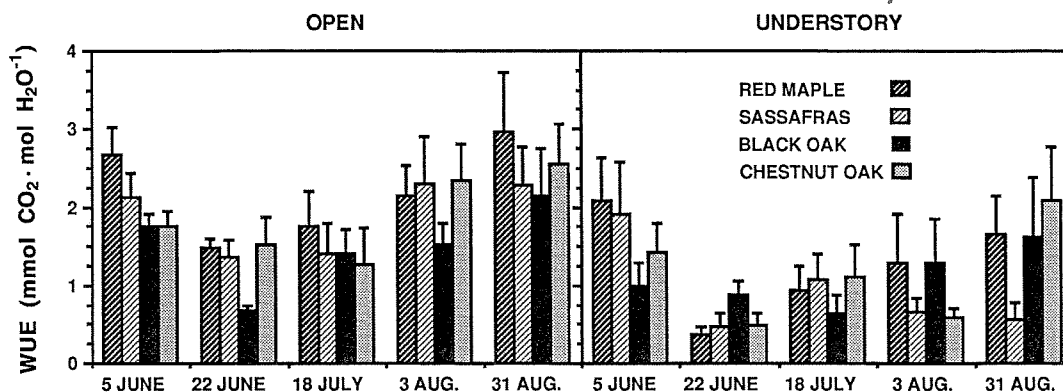


FIG. 8. Seasonal comparison of daily instantaneous water-use efficiency (WUE) (mean \pm 1 SE) of four Pennsylvania barrens species growing in understory and open conditions.

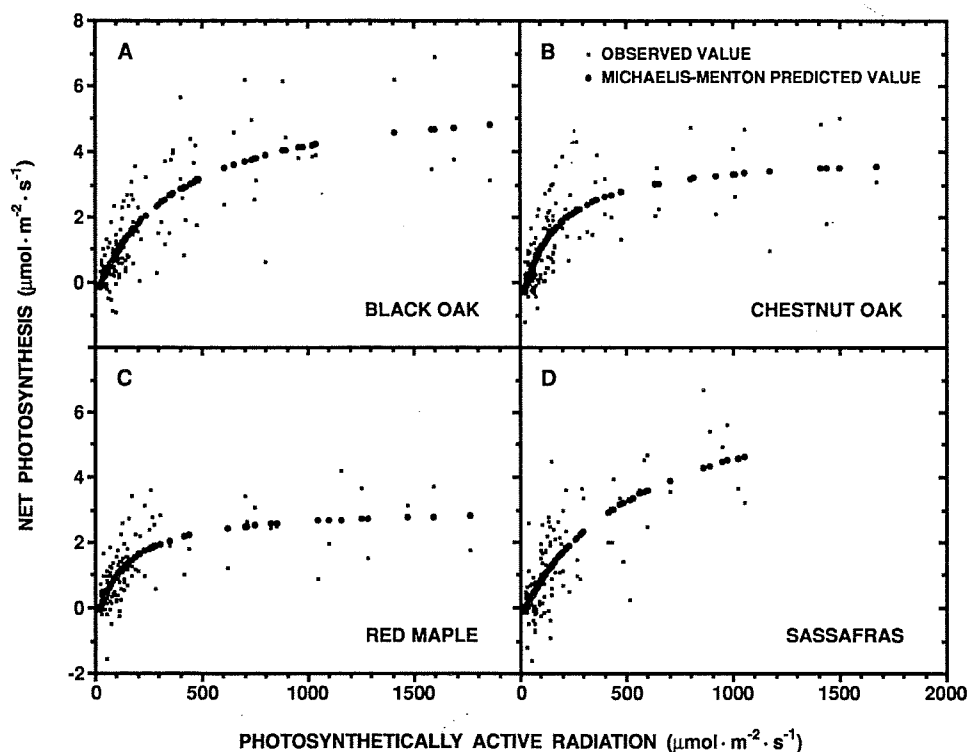


FIG. 9. Light saturation curves of four Pennsylvania barrens species growing in the forest understory. All seasonal observations are presented, while corresponding Michaelis-Menten predicted values make up the curve (cf. Table 1).

plasticity. Saplings in the open site were characterized by having more xerophytic leaves, high gas-exchange rates and WUE, and lower leaf Ψ . Species differences included higher diurnal and seasonal gas exchange and greater saturating light levels for A in early successional *S. albidum* and *Quercus* spp. than in *A. rubrum*. Thus, the four study species displayed many similar as well as unique adaptations and responses to varying levels of light and water availability, and potential nutrient limitations, associated with the barrens environment.

Acknowledgement

The authors thank David Harrison, who assisted with field data collection.

- Abrams, M.D. 1986. Physiological plasticity in water relations and leaf structure of understory versus open-grown *Cercis canadensis* in northeastern Kansas. *Can. J. For. Res.* **16**: 1170–1174.
- Abrams, M.D. 1988. Comparative water relations of three successional hardwood species in central Wisconsin. *Tree Physiol.* **4**: 263–273.
- Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiol.* **7**: 227–238.
- Abrams, M.D., and Kubiske, M.E. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. *For. Ecol. Manage.* **31**: 245–253.
- Abrams, M.D., and Menges, E.S. 1992. Leaf aging and plateau effects on seasonal pressure-volume relationships in three sclerophyllous *Quercus* species in southeastern U.S. *Funct. Ecol.* **6**: 353–360.

- Abrams, M.D., and Nowacki, G.J. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bull. Torrey Bot. Club*, **119**: 19–28.
- Abrams, M.D., Schultz, J.C., and Kleiner, K.W. 1990. Ecophysiological responses in mesic versus xeric hardwood species to an early-season drought in central Pennsylvania. *For. Sci.* **36**: 970–981.
- Abrams, M.D., Kloeppel, B.D., and Kubiske, M.E. 1992. Ecophysiological and morphological responses to shade and drought in two contrasting genotypes of *Prunus serotina*. *Tree Physiol.* **10**: 343–355.
- Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* **10**: 351–371.
- Bazzaz, F.A., and Carlson, R.W. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia*, **54**: 313–316.
- Bazzaz, F.A., Paape, V., and Boggess, W.R. 1972. Photosynthetic and respiratory rates of *Sassafras albidum*. *For. Sci.* **18**: 218–222.
- Braker, W.L. 1981. Soil survey of Centre County, Pennsylvania. USDA Soil Conservation Service, Washington, D.C.
- Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Vol. 2. Hardwoods. U.S. Dep. Agric. Agric. Handb. 654.
- Chapin, F.S., III, Bloom, A.J., Field, C.B., and Waring, R.H. 1987. Plant response to multiple environmental factors. *BioScience*, **37**: 49–57.
- Day, P.R. 1965. Particle fractionation and particle-size analysis. In *Methods of soil analysis*. Edited by C.A. Black. American Society of Agronomy, Madison, Wis. pp. 545–563.
- DeSoyza, A.G., and Kincaid, D.T., 1991. Patterns in leaf morphology and photosynthesis in shoots of *Sassafras albidum* (Lauraceae). *Am. J. Bot.* **78**: 89–98.
- Ellsworth, D.S., and Reich, P.B. 1992. Water relations and gas exchange of *Acer saccharum* seedlings in contrasting natural light and moisture regimes. *Tree Physiol.* **10**: 1–20.
- Givnish, T.J. 1988. Adaptation to sun and shade: a whole-plant perspective. *Aust. J. Plant. Physiol.* **15**: 63–92.
- Goulet, F., and Bellefleur, P. 1986. Leaf morphology plasticity in response to light environment in deciduous tree species and its implication on forest succession. *Can. J. For. Res.* **16**: 1192–1195.
- Harshberger, J.W. 1916. The vegetation of the New Jersey pine barrens: an ecological investigation. Christopher Sower Company, Philadelphia, Penn.
- Hinckley, T.M., Aslin, R.G., Aubuchon, R.R., Metcalf, C.L., Metcalf, J.E., and Roberts, J.E. 1978. Leaf conductance and photosynthesis in four species of the oak-hickory forest type. *For. Sci.* **24**: 73–84.
- Hinckley, T.M., Dougherty, P.M., and Lassoie, J.P., Roberts, J.E., and Teskey, R.O. 1979. A severe drought: impact on tree growth, phenology, net photosynthetic rate, and water relations. *Am. Midl. Nat.* **102**: 307–316.
- Hull, J.C., and Wood, S.G. 1984. Water relations of oak species on and adjacent to a Maryland serpentine soil. *Am. Midl. Nat.* **112**: 224–234.
- Koike, T. 1987. Photosynthesis and expansion in leaves of early, mid, and late successional tree species of birch, ash, and maple. *Photosynthetica*, **21**: 503–508.
- Koike, T. 1988. Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. *Plant Species Biol.* **3**: 77–87.
- Kuuluvainen, T., and Pukkala, T. 1989. Simulation of within-tree and between-tree shading of direct radiation in a forest canopy: effect of crown shape and sun elevation. *Ecol. Modell.* **49**: 89–100.
- Loach, K. 1967. Shade tolerance in tree seedlings 1. Leaf photosynthesis and respiration in plants raised under artificial shade. *New Phytol.* **66**: 607–621.
- Lyford, W.H. 1980. Development of the root system of northern red oak (*Quercus rubra* L.). *Harv. For. Pap.* 21.
- Nobel, P.S. 1983. Biophysical plant physiology and ecology. W.H. Freeman and Co., New York.
- Nonami, H., Schulze, E.D., and Ziegler, H. 1990. Mechanisms of stomatal movement in response to air humidity, irradiance, and xylem water potential. *Planta*, **183**: 57–64.
- Nowacki, G.J., and Abrams, M.D. 1991. Community and edaphic analysis of mixed oak forests in the ridge and valley province of central Pennsylvania. In *Proceedings of the 8th Central Hardwoods Forest Conference*. Edited by L.H. McCormick and K.W. Gottschalk. U.S. For. Serv. Gen. Tech. Rep. NE-148. pp. 247–260.
- Payne, W.W. 1968. The use of cellulose acetate film for the production of epidermal casts. *Ward's Bull.* **7**: 6–7.
- Pearcy, R.W. 1990. Sunflecks and photosynthesis in plant canopies. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **41**: 421–453.
- Reich, P.B. 1984. Relationships between leaf age, irradiance, leaf conductance, CO₂ exchange, and water use efficiency in hybrid poplar. *Photosynthetica*, **18**: 445–453.
- Reich, P.B., and Hinckley, T.M. 1980. Water relations, soil fertility, and plant nutrient composition of a pygmy oak ecosystem. *Ecology*, **61**: 400–416.
- Reich, P.B., Abrams, M.D., Ellsworth, D.S., Kruger, E.L., and Tabone, T.J. 1990a. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. *Ecology*, **71**: 2179–2190.
- Reich, P.B., Ellsworth, D.S., Kloeppel, B.D., Fownes, J.H., and Gower, S.T. 1990b. Vertical variation in canopy structure and CO₂ exchange of oak-maple forests: influence of ozone, nitrogen, and other factors on simulated canopy carbon gain. *Tree Physiol.* **7**: 329–345.
- Reich, P.B., Walters, M.B., and Ellsworth, D.S. 1991. Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area, and photosynthesis in maple and oak trees. *Plant Cell Environ.* **14**: 251–259.
- Robichaux, R.H. 1984. Variation in the tissue water relations of two sympatric Hawaiian *Dubautia* species and their natural hybrid. *Oecologia*, **65**: 75–81.
- SAS Institute, Inc. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, N.C.
- Schulze, E.D., Robichaux, R.H., Grace, J., Rundel, P.W., and Ehleringer, J.R. 1987. Plant water balance. *BioScience*, **37**: 30–37.
- Sheve, L.G. 1984. Elements of biochemistry. Allan and Bacon, Inc., Newton, Mass.
- Spurr, S.H., and Barnes, B.V. 1980. Forest ecology. John Wiley & Sons, New York.
- Turnbull, M.H. 1991. The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. *Oecologia*, **87**: 110–117.
- Turner, N.C., and Heichel, G.H. 1977. Stomatal development and seasonal changes in diffusive resistance of primary and regrowth foliage of red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.). *New Phytol.* **78**: 71–81.
- Vance, N.C., and Zaerr, J.B. 1991. Influence of drought stress and low irradiance on plant water relations and structural constituents in needles of *Pinus ponderosa* seedlings. *Tree Physiol.* **8**: 175–184.
- von Caemmerer, S., and Farquhar, G.D. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, **153**: 376–387.
- Whitehead, D., Grace, J.C., and Godfrey, M.J.S. 1990. Architectural distribution of foliage in individual *Pinus radiata* D. Don crowns and the effects of clumping on radiation interception. *Tree Physiol.* **7**: 135–155.
- Williams, W.E. 1983. Optimal water-use efficiency in a California shrub. *Plant Cell Environ.* **6**: 145–151.