Int. J. Plant Sci. 155(1):73–79. 1994.

1058-5893/94/5501-0009$02.00

SEASONAL TISSUE WATER RELATIONS OF FOUR SUCCESSIONAL PENNSYLVANIA BARRENS SPECIES IN OPEN AND UNDERSTORY ENVIRONMENTS

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Seasonal tissue water relations 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. Open-growing plants exhibited greater and earlier phenological shifts in osmotic potentials under moist conditions, whereas understory plants had greater osmotic adjustment during a mild, late-season drought. *Sassafras albidum* was an exception, exhibiting steadily declining osmotic potentials at full and zero turgor over the course of the season on both sites. Elastic modulus (ϵ) steadily increased for all species on the open site, while *A. rubrum* showed a decrease and *S. albidum* and *Q. velutina* showed an increase in ϵ in the understory. Relative water content at zero turgor (RWC_0) was similar in the understory and open sites except during the drought period when understory plants had lower values. *Quercus prinus* generally exhibited the lowest RWC_0 values, although *A. rubrum,* a later successional species, had a seasonal decrease in RWC_0 at both sites. Thus, each species exhibited somewhat unique combinations of seasonal osmotic and elastic adjustment, which acted in concert to balance tissue water loss with turgor maintenance under changing environmental conditions. These results indicate that a variety of ecophysiological mechanisms operate to allow species of different successional rank to tolerate open and understory barrens environments.

Introduction

The northeastern United States is influenced by maritime climates resulting in humid conditions and relatively stable seasonal precipitation. Despite this relatively mesic environment, atypical soil and topographic features have resulted in the formation of some xeric sites in the region. One such example is the sandy barrens of central Pennsylvania. Because of the high iron content in the sandstone parent material of the barrens, these sites have a long history of mining, logging, and fire disturbance associated with the charcoal-iron industry (Harshberger 1916; Nowacki and Abrams 1992). The plant communities on these barrens are a mosaic of open and forested sites within a geographically small area representing a unique opportunity to study seasonal light and water interactions on a diverse group of woody plants.

Despite the long-term interest in studying the ecophysiology of plants in stressful environments (Loustalot 1945), only a few studies have focused on hardwood vegetation restricted to atypically xeric sites in eastern North America (Reich and Hinckley 1980; Hull and Wood 1984). This study is unique since it focuses on the importance of seasonal tissue water relations in the xeric barrens environment. Tissue water relations include osmotic and cell wall elasticity adjustments that can effectively moderate the water balance of plants in response to dry conditions (Turner 1986; Schulze et al. 1987; Nunes et al. 1989; Richter and Kikuta 1989). Though tissue water relations may be most important to survival during seedling establishment, Zobel (1974) documented the death of large saplings during a summer drought, indicating the need for physiological adjustment long after seedling establishment.

Osmotic and elastic adjustment during drought has been observed in a variety of plant species worldwide, but the effect of high and low light exposure on seasonal tissue water relations is less understood (Vance and Zaerr 1991; Abrams et al. 1992; Ellsworth and Reich 1992). Overstory trees provide a stable and buffered environment to understory saplings relative to those in the open, including relief from high vapor pressure deficit, but they may also impinge on soil water supplies available to both growth classes. Thus, late-season water availability may be more limited to understory saplings than to those growing in the open. Therefore, osmotic and elastic adjustment may be more likely to occur later in the season in the understory saplings, while earlier season adjustments may be more necessary in the warmer, open, sunlit environments. Our objective was to monitor tissue water relations in open and understory phenotypes of four species during moist and droughty periods of a growing season. This will provide a solid framework on which to elucidate the impacts of seasonal water availability on tissue water parameter adjustments. We were particularly interested in identifying drought avoidance or tolerance mechanisms in species of varying successional rank.

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Manuscript received September 1992; revised manuscript received August 1993.

Material and methods

STUDY SITE

The central Pennsylvania barrens are located approximately 2 km northwest of State College, Pennsylvania (40°48′52″N, 77°55′50″W). Average monthly temperatures range from a winter minimum of -7°C to a summer maximum of 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 high permeability and very low available water capacity. Soil texture is sand, loamy sand, and sandy loam in the surface horizon and at depths of 25 and 50 cm, respectively, as determined by the soil hydrometer technique (Day 1965).

The current dominant overstory of chestnut oak (*Quercus prinus* L.) was established in approximately 1934, with lesser amounts of black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), and sassafras (*Sassafras albidum* [Nutt.] Nees). These same species dominate the sapling class with the inclusion of red maple (*Acer rubrum* L.) (Nowacki and Abrams 1992).

Six or seven individuals with a diameter at 1.37 m of 0.5–4.0 cm of four species were selected for study from juxtaposed open and understory sites. *Acer rubrum,* considered to be the climax species for the site, and three earlier successional species of low to intermediate shade tolerance: *Q. velutina, Q. prinus,* and *S. albidum* (Burns and Honkala 1990; Nowacki and Abrams 1992) were located and permanently tagged in the approximately 400 m^2 plot. Special care was taken to include only true saplings and to avoid stump and clonal sprouts. Since all four species were present as saplings in both light regimes, we were able to formulate an unreplicated factorial design with four species and two light environments.

DATA COLLECTION

On each sampling date during the 1990 growing season (June 5, June 22, July 18, August 3, and August 31), a single midcrown leaf was collected from five replicate saplings of each species on each site before dawn (0600 hours solar time) for pressure-volume (P-V) analysis. Samples were sealed in a plastic bag with a damp paper towel, stored in a dark container, and transported to the laboratory. Samples were not rehydrated to avoid potential shifts in P-V relationships (Parker and Pallardy 1987; Kubiske and Abrams 1990). The methods for constructing the P-V curves (1/Ψ vs. relative water content [RWC]) were similar to those employed by Robichaux (1984) and Turner (1988), in which mass and bulk leaf water potential (Ψ) were periodically measured as leaf samples dried by free transpiration on a laboratory bench. Tissue mass at saturated Ψ was estimated via linear regression of P-V data above and including the turgor loss point for each sample (Ladiges 1975; Kubiske and Abrams 1990). An initial region of phloem exudate in some of the *A. rubrum* samples was excluded from this regression procedure (Abrams and Kubiske 1990), while plateaus present in some of the *Quercus* spp. samples were also excluded (Bahari et al. 1985; Kubiske and Abrams 1990, 1991*a*). Estimated saturated sample mass was then used to calculate RWC. Least squares linear regression was used to calculate the P-V parameters (SAS Institute 1985): osmotic potential at full turgor ($\Psi_\pi{}^{100}$) and zero turgor ($\Psi_\pi{}^0$) and RWC at zero turgor (RWC$_0$). The bulk modulus of elasticity between full and zero turgor (ϵ) was calculated according to Robichaux and Canfield (1985). Also during each sampling date, gravimetric soil moisture analysis of the upper 25 cm was conducted using four replicate soil samples in the open and understory sites. In addition, available soil moisture was evaluated by measuring predawn bulk leaf Ψ (predawn leaf Ψ) with a pressure chamber (PMS Instrument Co., Corvallis, Oreg.) on one leaf from each study plant ($N = 6$ or 7 for each species-treatment combination).

Statistical analyses for soil moisture, predawn leaf Ψ, and P-V parameters were carried out using a one-way ANOVA model for a completely randomized design, Tukey's multiple range test ($P < .05$), and Pearson product moment correlation ($P < .05$) (SAS Institute 1985).

Results and discussion

The monthly averages of daily maximum and minimum temperatures from June to August 1990 were within 1.0°C of the 30-yr mean and precipitation was 5.05 cm above the 100-year mean, indicating normal to moist weather patterns (fig. 1). However, a 10-d drought occurred from July 25 to August 4, resulting in significantly lower soil moisture (0–25 cm) on August 3 compared with the other four sampling dates. According to Broadfoot and Burke (1958), a soil moisture content of 6% in loamy sand, such as the value on August 3, equals a soil Ψ of -1.5 MPa, indicating a severe water deficit in the upper 25 cm. Over the 1990 growing season the barrens had consistently lower soil moisture (13.5 ± 0.4%) contents (0–25 cm) than mesic slope forests (34.3 ± 2.6%) and lowland hardwood forests (40.9 ± 0.7%) (Abrams et al. 1993). This 255%–304% lower soil moisture content illustrates the extremely xeric barrens conditions relative to other forest types in the State College, Pennsylvania, vicinity. Soil moisture was not significantly different between the open and understory sites on any sampling date. Predawn leaf Ψ was greater than -0.25 MPa

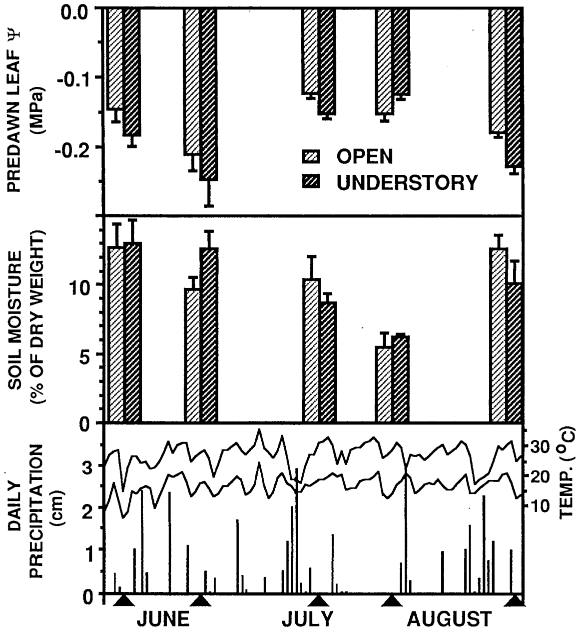

Fig. 1 Predawn leaf water potential (Ψ) and gravitational soil moisture at five sampling dates during the 1990 growing season for open and understory sites in the barrens ecosystem in central Pennsylvania. The values of four species were used to compute the open and understory means for predawn leaf Ψ, while the bars represent 1 SE. Daily ambient maximum and minimum temperature curves as well as daily precipitation bars are presented in the lower box. Sampling dates are indicated by triangles on the horizontal axis.

on both sites across all sampling dates. However, lower values were detected in understory plants, possibly indicating greater competition for water with overstory vegetation.

Osmotic potentials at full ($\Psi_\pi{}^{100}$) and zero turgor ($\Psi_\pi{}^{0}$) were similar between open and understory plants on all dates except June 22, when open plants had significantly lower values ($P < .05$) (fig. 2). Species occupying the barrens also had lower Ψ_π than other more mesic species within the same region, reflecting the ability of these species to adjust to the barrens environment (Kubiske and Abrams 1991*a*). However, mean osmotic potentials (MPa) in this study were higher (less negative) when compared with the same species in more xeric, western locations (−1.18 and −1.58 vs. −1.85 and −2.74, $\Psi_\pi{}^{100}$ and $\Psi_\pi{}^{0}$, respectively) of the eastern deciduous biome (Abrams 1988, 1990).

Seasonal comparisons of plants on both sites, averaged across all species, showed a significant decline in both $\Psi_\pi{}^{100}$ and $\Psi_\pi{}^{0}$ from June 5 to August 3, which included the 10-d drought in late July. However, open plants exhibited an earlier decline in Ψ_π (by June 22) than understory plants (by July 18) (fig. 2). Seasonal decreases in these parameters have been attributed to phenological shifts that occur in many species during leaf maturation, despite well-watered conditions (Parker et al. 1982; Abrams 1988; Kwon and Pallardy 1989), and to osmotic adjustment during drought (Hinckley et al. 1978; Schulze et al. 1987). In addition, recent studies have documented lower Ψ_π in sun than in shade plants, possibly related to lower diurnal Ψ resulting from greater transpirational losses (Abrams et al. 1992; Ellsworth and Reich 1992). This is supported by the development of lower midday Ψ and greater diurnal stomatal conductance of the plants (Kloeppel et al. 1993). Average midday Ψ (MPa) for the four species were: *Quercus prinus* (−2.13, −1.54), *Quercus velutina* (−2.02, −1.64), *Acer rubrum* (−1.35, −0.95), and *Sassafras albidum* (−1.04, 0.64), in the open and understory, respectively. Thus, greater and earlier decreases in osmotic potentials in the open site may be important in maintaining turgor pressure in the face of larger diurnal water deficits. Following the relief of a mild, late-July drought, all species in the understory and *Q. velutina* in the open had higher osmotic potentials. There were no consistent species differences among osmotic potentials within sampling dates at either site, although *S. albidum* generally had the highest values in both treatments (fig. 2). In contrast, previous studies from this and other regions have documented lower Ψ_π in *Quercus* spp. relative to other co-occurring species on upland sites (Osonubi and Davies 1978; Hinckley et al. 1983; Bahari et al. 1985; Abrams 1990). *Acer rubrum* did not exhibit higher Ψ_π than the earlier successional species in this study, whereas others have documented higher Ψ_π in later successional species, possibly because of lower gas exchange rates and lower diurnal water deficits (Roberts et al. 1980; Bahari et al. 1985).

In the open, *A. rubrum* generally exhibited the highest tissue elastic modulus (ϵ), followed by *S. albidum* and the *Quercus* spp. (fig. 3). Though several species differences were detected, values of ϵ in this study were similar to those of *Quercus* spp. in the eastern deciduous biome, 14.73 vs. 15.81 MPa, respectively (Abrams 1990). On August 3, ϵ was generally higher ($P < .06$) in open than in understory plants since ϵ increased in open plants and decreased simultaneously in understory plants during a late July drought. The understory shift in ϵ may have been stimulated by the sustained water use by overstory trees with deep root systems. Seasonal increases in ϵ similar to those seen here in the open plants have been documented for several oak and other eastern tree species and are likely to be related to tissue maturation and development (Parker et al. 1982; Bowman and Roberts 1985; Abrams and Menges 1992). In both sites, *S. albidum* and *Q. velutina* exhibited seasonal increases in ϵ, whereas understory *A. rubrum* had decreased ϵ ($P < .05$). Similarly, *Acer saccharum* developed higher ϵ during drought in a forest opening than in an

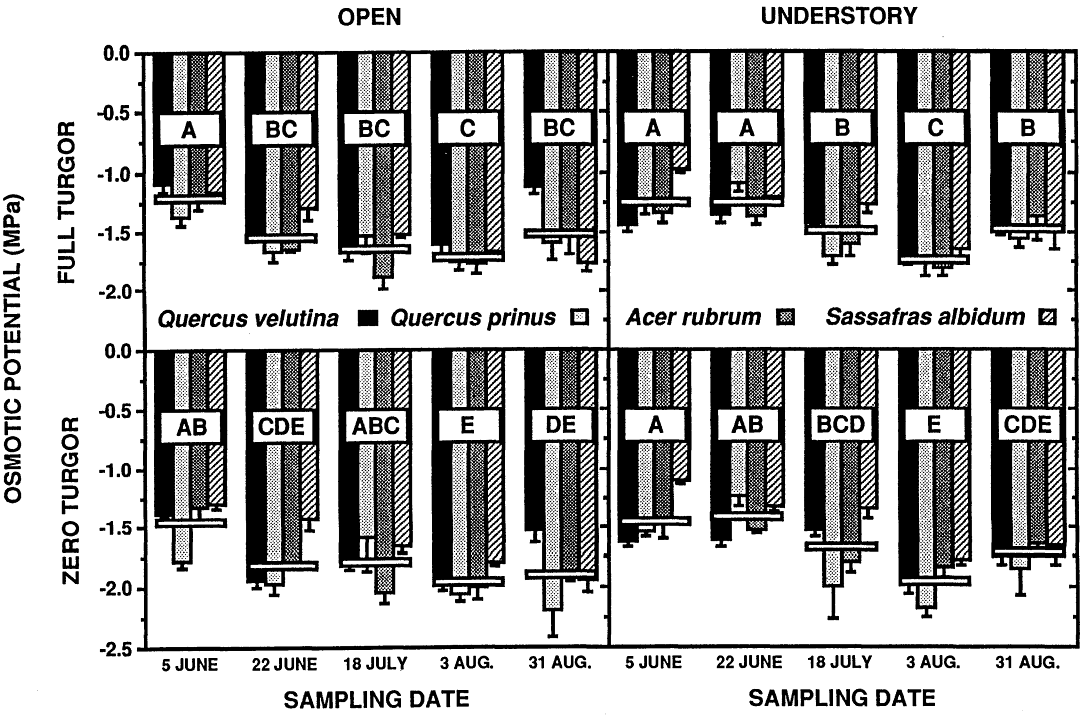

Fig. 2 Osmotic potentials at full and zero turgor (mean ± SE) from pressure-volume analysis of saplings of four species in open and understory environments in the barrens ecosystem in central Pennsylvania. The overall mean of each 1990 sampling date in each light regime is indicated by a horizontal bar. Means with the same letter within a row are not significantly different using Tukey's mean separation test at the $\alpha = .05$ level.

understory (Ellsworth and Reich 1992). It is generally accepted that low tissue elasticity (indicated by high ϵ) will result in relatively large decreases in Ψ during dehydration and maintain a favorable Ψ gradient for water uptake from drying soils (Robichaux 1984). A possible addition to the function of high ϵ, and the accompanying rapid decrease in turgor, is a mechanism promoting stomatal closure prior to the development of large leaf water deficits that become more difficult to replenish during drought. This is supported by the relatively low diurnal leaf conductance reported for these *A. rubrum* saplings (Kloeppel et al. 1993). The later successional un-

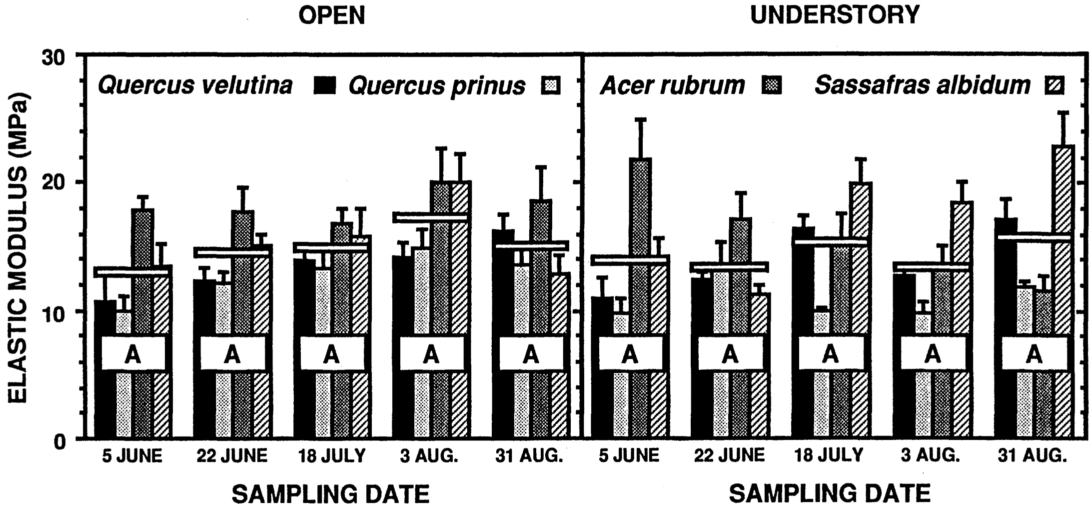

Fig. 3 Elastic modulus (mean ± SE) from pressure-volume analysis of saplings of four species in open and understory environments in the barrens ecosystem in central Pennsylvania. The overall mean of each 1990 sampling date in each light regime is indicated by a horizontal bar. Means with the same letter within a row are not significantly different using Tukey's mean separation test at the $\alpha = .05$ level.

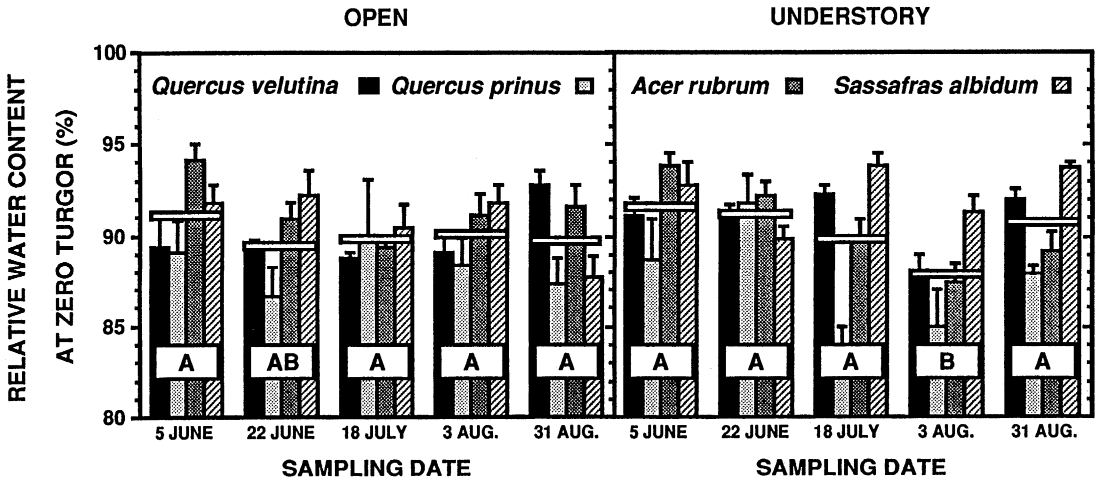

Fig. 4 Relative water content at zero turgor (mean ± SE) from pressure-volume analysis of saplings of four species in open and understory environments in the barrens ecosystem in central Pennsylvania. The overall mean of each 1990 sampling date in each light regime is indicated by a horizontal bar. Means with the same letter within a row are not significantly different using Tukey's mean separation test at the $\alpha = .05$ level.

derstory *A. rubrum* developed more elastic tissue, possibly because it exists under conditions of lower transpiration demand and can therefore undergo greater changes in cell volume to maintain higher turgor pressure during drought. Thus, either an increase or a decrease in tissue elasticity may contribute to the drought tolerance of a species.

Relative water content at zero turgor was similar in both light environments except for the August 3 sampling date, when understory saplings exhibited significantly lower values than those in the open (fig. 4). This coincides with a mild drought and indicates a greater net adjustment of elastic and osmotic properties in understory saplings, possibly because of increased competition for water with overstory vegetation. *Acer rubrum* exhibited a significant decline in RWC$_0$ ($P < .05$) from June 5 to July 18 or August 3 at the open and understory sites, respectively, whereas *Q. velutina* had its lowest RWC$_0$ values in the understory on August 3. *Sassafras albidum* exhibited decreased RWC$_0$ in the open by August 31 but no adjustments in the understory. *Quercus prinus* often exhibited the lowest RWC$_0$ in both treatments. This net result of low osmotic potentials and ϵ may contribute to the ability of this early successional species to tolerate xeric barrens and ridgetop environments (Nowacki and Abrams 1992).

The diurnal course of bulk leaf Ψ of these saplings (Kloeppel et al. 1993) along with P-V curve data allowed estimation of the value of minimal diurnal field RWC. However, this technique did not account for diurnal osmotic adjustment (Kubiske and Abrams 1991b) since the P-V tissue was collected under predawn conditions. Nonetheless, minimal diurnal RWC was near or slightly below the RWC$_0$ in both *Quercus* spp. across all sampling dates. However, RWC was 2%–6% higher than RWC$_0$ at its lowest point for both *A. rubrum* and *S. albidum*, indicating much less severe water shortage than in the early successional *Quercus* spp. Nonetheless, cell turgor and photosynthesis was maintained in all species, thereby allowing continued carbon assimilation and growth despite several different species patterns in RWC. Interestingly, *Q. velutina* reached its RWC diurnal minima on average 2 h earlier than all other species. However, all species did experience 1%–4% greater RWC in the understory compared with the open saplings since Ψ was never as low in the understory as in the open (Kloeppel et al. 1993).

Relative water content at zero turgor was positively correlated with $\Psi_\pi{}^0$ ($R = .60$) and ϵ ($R = .73$) across all species, dates, and sites (fig. 5). In this study Ψ_π generally decreased and ϵ increased during the season, thereby balancing the effect on RWC$_0$ over the growing season. Various combinations of ϵ and $\Psi_\pi{}^0$ will result in similar RWC$_0$, thus providing multiple pathways for plants to adjust to water-limiting environments (fig. 5). Interestingly, incremental changes in $\Psi_\pi{}^0$ at low values of ϵ (e.g., 8.8 MPa) result in greater relative changes in RWC$_0$ than at higher ϵ. Nonetheless, it is quite apparent from figure 5 that a reduction in both ϵ and $\Psi_\pi{}^0$ could potentially provide the greatest degree of turgor maintenance for plants experiencing drought conditions. However, only *Q. velutina* in the understory showed decreased ϵ during drought.

The coarse-textured soils of the barrens have inherently low water-holding capacity and nutrient content, necessitating certain ecophysiological adaptations in barrens plants (Forman 1979).

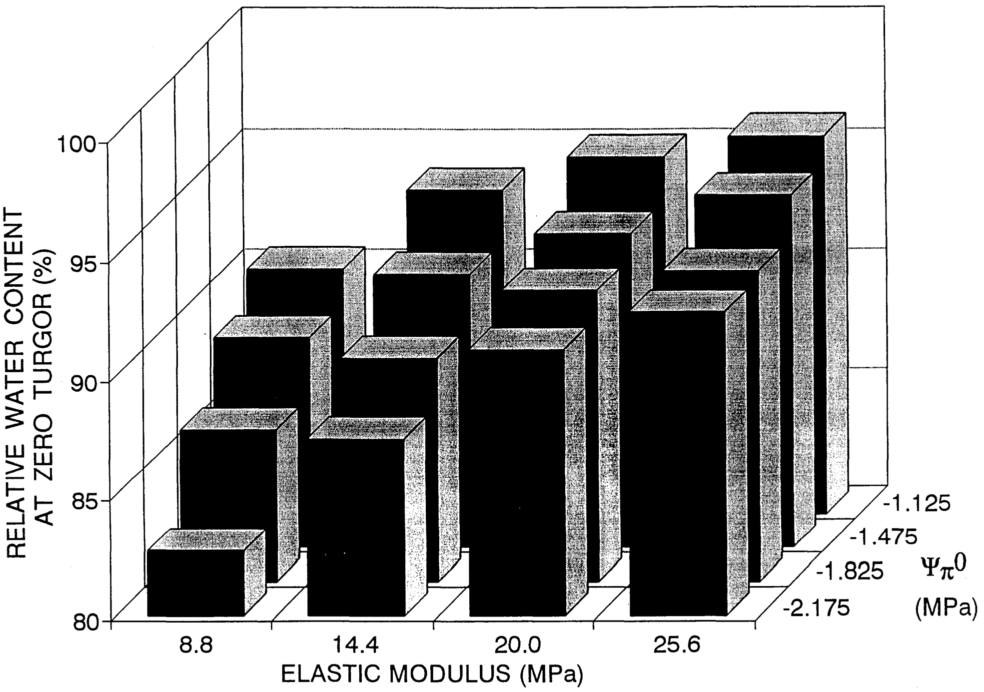

Fig. 5 Tissue elastic modulus and osmotic potential at zero turgor ($\Psi_\pi{}^0$) versus relative water content at zero turgor in a Pennsylvania barrens ecosystem. Data are pooled from five 1990 sampling dates for four species located in both open and understory environments.

These adaptations often include lower seasonal $\Psi_\pi$than in plants on mesic sites. Each study species exhibited significant seasonal changes in tissue water relations in the open and understory sites, including phenological shifts and adjustment to a mild drought. Moreover, seasonal shifts in Ψ_π under moist conditions may be most dramatic in open plants because of lower diurnal leaf Ψ and more rapid increases in specific leaf mass (Kloeppel et al. 1993). Nonetheless, increased competition for soil moisture in closed-forest environments may intensify the effect of drought. The study species in the open tended to decrease Ψ_π and increase ϵ, thereby maintaining a soil-to-leaf Ψ gradient while avoiding a severe tissue water deficit. In contrast, understory *A. rubrum* had decreasing Ψ_π and ϵ, while *S. albidum* had increasing ϵ; arguably, these species represent opposite ends of successional development. Though various adaptations have been noted for each species in this study, the differences observed would likely have been more accentuated during a year with a more severe drought. Nonetheless, these species of varying successional rank exhibited different ecophysiological responses in open versus understory barrens sites.

Acknowledgments

We would like to thank David Harrison, who assisted with field data collection, and Eric L. Kruger, who reviewed an earlier version of the manuscript.

Literature cited

Abrams MD 1988 Sources of variation in osmotic potentials with special reference to North American tree species. For Sci 34:1030–1046.

——— 1990 Adaptations and responses to drought in *Quercus* species of North America. Tree Physiol 7:227–238.

Abrams MD, BD Kloeppel, ME Kubiske 1992 Ecophysiological and morphological responses to shade and drought in two contrasting genotypes of *Prunus serotina*. Tree Physiol 10:343–355.

Abrams MD, ME Kubiske 1990 Photosynthesis and water relations during drought in *Acer rubrum* L. genotypes from contrasting sites in central Pennsylvania. Funct Ecol 4:727–733.

Abrams MD, ME Kubiske, SA Mostoller 1993 Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. Ecology (in press).

Abrams MD, ES Menges 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.

Bahari ZA, SG Pallardy, WC Parker 1985 Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. For Sci 31: 557–569.

Bowman WD, SW Roberts 1985 Seasonal changes in tissue elasticity in chaparral shrubs. Physiol Plant 65:233–236.

Braker WL 1981 Soil survey of Centre County, Pennsylvania. USDA Soil Conservation Service, Washington, D.C. 232 pp.

Broadfoot WM, HD Burke 1958 Soil-moisture contents and their variation. USDA Southern Forest Experiment Station occasional paper 166. 27 pp.

Burns RM, BH Honkala 1990 Silvics of North America. Vol. 2. Hardwoods. USDA Handbook 654, Washington, D.C. 877 pp.

Day PR 1965 Particle fractionation and particle-size analysis. Pages 545–563 *in* CA Black, ed. Methods of soil analysis. American Society of Agronomy, Madison, Wisc.

Ellsworth DS, PB Reich 1992 Water relations and gas exchange of *Acer saccharum* seedlings in contrasting natural light and moisture regimes. Tree Physiol 10:1–20.

Forman RTT 1979 The pine barrens of New Jersey: an ecological mosaic. Pages 569–585 *in* RTT Forman, ed. Pine barrens: ecosystem and landscape. Academic Press, New York.

Harshberger JW 1916 The vegetation of the New Jersey pine barrens: an ecological investigation. Christopher Sower, Philadelphia. 329 pp.

Hinckley TM, RG Aslin, RR Aubuchon, CL Metcalf, JE Roberts 1978 Leaf conductance and photosynthesis in four species of the oak-hickory forest type. For Sci 24:73–84.

Hinckley TM, F Duhme, AR Hinckley, H Richter 1983 Drought relations of shrub species: assessment of the mechanisms of drought resistance. Oecologia 59:344–350.

Hull JC, SG Wood 1984 Water relations of oak species on and adjacent to a Maryland serpentine soil. Am Midl Nat 112:224–234.

Kloeppel BD, MD Abrams, ME Kubiske 1993 Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. Can J For Res 23:181–189.

Kubiske ME, MD Abrams 1990 Pressure-volume relationships in non-rehydrated tissue at various water deficits. Plant Cell Environ 13:995–1000.

——— 1991*a* Rehydration effects on pressure-volume relationships in four temperate woody species: variability with site, time of season, and drought conditions. Oecologia 85: 537–542.

——— 1991*b* Seasonal, diurnal and rehydration-induced variation of pressure-volume relationships in *Pseudotsuga menziesii.* Physiol Plant 83:107–116.

Kwon KW, SG Pallardy 1989 Temporal changes in tissue water relations of seedlings of *Quercus acutissima, Q. alba,* and *Q. stellata* subjected to chronic water stress. Can J For Res 19:622–626.

Ladiges PY 1975 Some aspects of tissue water relations in three populations of *Eucalyptus viminalis* Labill. New Phytol 75:53–62.

Loustalot AJ 1945 Influence of soil moisture conditions on apparent photosynthesis and transpiration of pecan leaves. J Agric Res 71:519–532.

Nowacki GJ, MD Abrams 1992 Community, edaphic, and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. Can J For Res 22: 790–800.

Nunes MA, F Catarino, E Pinto 1989 Strategies for acclimation to seasonal drought in *Ceratonia siliqua* leaves. Physiol Plant 77:150–156.

Osonubi O, WJ Davies 1978 Solute accumulation in leaves and roots of woody plants subjected to water stress. Oecologia 32:323–332.

Parker WC, SG Pallardy 1987 The influence of resaturation method and tissue type on pressure-volume analysis of *Quercus alba* L. seedlings. J Exp Bot 38:535–549.

Parker WC, SG Pallardy, TM Hinckley, RO Teskey 1982 Seasonal changes in tissue water relations of three species of the *Quercus-Carya* forest type. Ecology 63:1259–1267.

Reich PB, TM Hinckley 1980 Water relations, soil fertility, and plant nutrient composition of a pygmy oak ecosystem. Ecology 61:400–416.

Richter H, SB Kikuta 1989 Osmotic and elastic components of turgor adjustment in leaves under stress. Pages 129–137 *in* KH Kreeb, H Richter, TM Hinckley, eds. Structural and functional responses to environmental stresses. Academic, The Hague.

Roberts SW, BR Strain, KR Knoerr 1980 Seasonal patterns of leaf water relations in four co-occurring forest tree species: parameters from pressure-volume curves. Oecologia 46:330–337.

Robichaux RH 1984 Variation in the tissue water relations of two sympatric Hawaiian *Dubautia* species and their natural hybrid. Oecologia 65:75–81.

Robichaux RH, JE Canfield 1985 Tissue elastic properties of eight Hawaiian *Dubautia* species that differ in habitat and diploid chromosome number. Oecologia 66:77–80.

SAS Institute 1985 SAS user's guide: statistics, version 5 ed. SAS Institute, Cary, N.C. 956 pp.

Schulze ED, RH Robichaux, J Grace, PW Rundel, JR Ehleringer 1987 Plant water balance. BioScience 37:30–37.

Turner NC 1986 Adaptation to water deficits: a changing perspective. Aust J Plant Physiol 13:175–190.

——— 1988 Measurement of plant water status by the pressure chamber technique. Irrigation Sci 9:289–308.

Vance NC, JB Zaerr 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.

Zobel DB 1974 Local variation in intergrading *Abies grandis-A. concolor* populations in the central Oregon Cascades. II. Stomatal reaction to moisture stress. Bot Gaz 135:200–210.