

Ecophysiological and morphological responses to shade and drought in two contrasting ecotypes of *Prunus serotina*

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Summary

Photosynthesis (A), water relations and stomatal reactivity during drought, and leaf morphology were evaluated on 2-year-old, sun- and shade-grown *Prunus serotina* Ehrh. seedlings of a mesic Pennsylvania seed source and a more xeric Wisconsin source. Wisconsin plants maintained higher A and leaf conductance (g_{wv}) than Pennsylvania plants during the entire drought under sun conditions, and during the mid stages of drought under shade conditions. Compared to shade plants, sun plants of both sources exhibited a more rapid decrease in A or % A_{max} with decreasing leaf water potential (Ψ). Tissue water relations parameters were generally not significantly different between seed sources. However, osmotic potentials were lower in sun than shade plants under well-watered conditions. Following drought, shade plants, but not sun plants, exhibited significant osmotic adjustment. Sun leaves had greater thickness, specific mass, area and stomatal density and lower guard cell length than shade leaves in one or both sources. Wisconsin sun leaves were seemingly more xerophytic with greater thickness, specific mass, and guard cell length than Pennsylvania sun leaves. No source differences in leaf structure were exhibited in shade plants. Stomatal reactivity to sun–shade cycles was similar between ecotypes. However, well-watered and droughted plants differed in stomatal reactivity within and between multiple sun–shade cycles. The observed ecotypic and phenotypic variations in ecophysiology and morphology are consistent with the ability of *Prunus serotina* to survive in greatly contrasting environments.

Introduction

Adaptation of species to macro- and micro-climatic variation may depend on genetic differentiation among populations (Mooney and Billings 1961, Schlichting 1986, Abrams 1986, 1988a). Several studies have investigated either genetic variation or phenotypic response in ecophysiological and morphological parameters to a single environmental factor, such as temperature, light or water (Fryer and Ledig 1972, Boardman 1977, Berry and Björkman 1980, Abrams and Kubiske 1990a, 1990b). However, few studies have investigated both genotypic and phenotypic responses to multiple resource limitations (Gauhl 1979, Osmond 1983), especially with tree species. This approach is particularly relevant to ecophysiological studies because plants in the field are often exposed to several concurrent stresses (Mooney et al. 1987).

We are interested in the ecophysiology of *Prunus serotina* Ehrh. (black cherry) because of its widespread importance in oak forest understories in eastern North America. In the Lake States, for example, black cherry regeneration is abundant on dry-mesic and xeric sites, whereas in southern and central Pennsylvania this species is best developed on mesic sites (McCune and Cottam 1985, Host et al. 1987, Abrams

and Downs 1990, Nowacki and Abrams 1991). Moreover, in Wisconsin, black cherry is considered intolerant of shade (Spurr and Barnes 1980), and is dependent on gaps for canopy recruitment in closed forests (Auclair and Cottam 1971, McCune and Cottam 1985). In contrast, canopy recruitment of black cherry on mesic oak forests in central Pennsylvania does not appear to be gap dependent, suggesting a higher degree of shade tolerance (Nowacki and Abrams 1991). Thus, distinct ecotypes for black cherry may exist in different regions of eastern North America.

The purpose of this study was to evaluate photosynthesis, plant and tissue water relations, and stomatal reactivity during drought and leaf morphology in Wisconsin and Pennsylvania ecotypes of black cherry grown in full sun or partial shade. We tested the hypothesis that the Wisconsin ecotype is more drought tolerant and less shade tolerant than the Pennsylvania ecotype. We also compared the ecophysiological responses to drought in plants grown in full sun or partial shade.

Material and methods

Study site description

Black cherry seeds were collected from natural populations on valley-floor sites near State College in central Pennsylvania and near Rhinelander in north-central Wisconsin (Table 1). Each collection included seeds of a representative sample of five or six parents. Annual precipitation and the ratio of annual precipitation to annual pan water evaporation are substantially higher and the percent of months with severe or extreme drought are lower in Pennsylvania than in Wisconsin (Court 1974). Soils of north-central Wisconsin are predominantly coarse-textured sands with low water holding capacity and fertility, whereas valley-floor soils in central Pennsylvania are fine-textured clays with high water holding capacity and fertility.

Seedling establishment

Seeds from both locations were collected between August and September 1989, stratified for 120 days, and then planted in flats in January 1990. One month later, seedlings were transplanted to individual pots (8.4 dm³) containing a mixture of peat, loam, vermiculite and perlite (3/1/1/1, v/v). Seedlings were grown in a naturally lighted greenhouse supplemented with artificial light from fluorescent lamps to provide a 16-h photoperiod. On May 3, 1990, 24 seedlings of similar size and vigor within each source were selected for further treatment.

Table 1. Black cherry sources and climate.

State	Latitude	Longitude	Mean annual precipitation (cm)	Mean annual evaporation (cm)	Precip/evap. (%)	Months with \geq severe drought (%)
Pennsylvania	40°47' N	77°51' W	103	75	1.37	5
Wisconsin	45°38' N	89°24' W	76	70	1.09	10

Half of the seedlings from each source were retained in full sun, whereas the other half were placed on the same greenhouse bench under 80% shade cloth. Seedlings were randomly arranged in their respective light regimes, kept well-watered and fertilized, and periodically rotated to minimize positional effects in the greenhouse. Heat and artificial light in the greenhouse were turned off in November 1990 and resumed in early March 1991.

Photosynthesis and plant water relations

Eight similar seedlings from each source and light treatment were watered to soil capacity on April 15, 1991. Thereafter, water was withheld and the plants were observed over a 12- and a 25-day period for the sun and shade treatments, respectively, during which time all plants reached incipient wilting (defined as $A \leq 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$). At 1–2 day intervals in the sun and 1–7 day intervals in the shade treatment, late morning (1000–1200 h. solar time) measurements of net photosynthesis (A), transpiration and leaf conductance to water vapor diffusion (g_{wv}) were made on a fully expanded leaf on all eight seedlings from each treatment combination. Gas exchange measurements were made during relatively cloud-free conditions with a portable photosynthesis unit (LCA-2, ADC Ltd., Herts, England), which utilizes the mass balance technique to estimate leaf CO_2 exchange. During each gas exchange measurement, the ADC system also measured photosynthetic photon flux density (PPFD) and calculated leaf temperature (T_{leaf}). Three to eight leaves from each population were harvested immediately after the gas exchange measurements and their water potentials (Ψ) were determined with a pressure chamber (Model 600, PMS Instruments Co., Corvallis, Oregon). In addition, predawn leaf Ψ (0600 h) was periodically monitored during the experiment; measurements were concentrated when plants were fully hydrated and when many approached incipient wilting in each treatment combination.

During the measurement period, mean (\pm SE) PPFD was 966 ± 76 and $211 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ and mean T_{leaf} was 29.1 ± 0.5 and 26.5 ± 0.5 °C for the sun and shade treatments, respectively. Differences in PPFD and T_{leaf} were statistically significant ($P < 0.05$) between light regimes but not between seedling sources.

Tissue water relations

On the first day after cessation of watering, a fully expanded leaf from 4–5 plants in each source and light treatment was collected before dawn and subjected to pressure-volume (P-V) analysis. Samples were not artificially rehydrated to avoid potential shifts in P-V relationships (Kubiske and Abrams 1990). To construct P-V curves ($1/\Psi$ versus relative water content, RWC), the weight and Ψ of leaves were periodically measured as they dried by free transpiration under ambient conditions on the laboratory bench (cf. Abrams and Kubiske 1990b). At the later stages of drought, when a plant reached incipient wilting it was moved to a dark chamber to minimize additional water loss. The following morning a leaf was harvested and used in P-V analysis. Thus, the timing of P-V analysis during peak drought varied among the plants. Predawn Ψ in the drought plants was generally -0.8 to -1.0 MPa, which

allowed us to collect sufficient P-V data iterations before the turgor loss point. In addition, parallel leaf samples were collected from each plant on the respective dates and rehydrated for 12 h in darkness in sealed beakers solely to determine Ψ for tissue near full hydration.

Tissue weights at saturated Ψ were estimated by linear regression of P-V data above and including the turgor loss point (cf. Kubiske and Abrams 1990, 1991). Estimated saturated sample weights were then used to calculate RWC and the standard P-V parameters: the osmotic potential at full turgor (Ψ_{π}^{100}) and zero turgor (Ψ_{π}^0), relative water content at zero turgor (RWC_0) and the bulk modulus of elasticity from full to zero turgor (ϵ , calculated according to Robichaux and Canfield (1985)).

Leaf morphology

Leaf area, specific leaf mass, leaf thickness, stomatal density and guard cell length were measured on fully expanded leaves from the mid-canopy of 10 seedlings from each source and light treatment. Three measurements of stomatal density and guard cell length were made on each leaf with cellulose acetate impressions of the lower leaf surface (Payne 1970). Free-hand transverse sections of leaves taken at an approximate mid-point between the mid-rib vein and leaf margin were measured under a light microscope for leaf thickness. Specific leaf mass was determined by weighing oven-dried (70 °C, 48 h) sections of fresh material of known area. Leaf area was measured with a Li-Cor 3100 leaf area meter.

Stomatal reactivity

Stomatal reactivity to alternating shade (50 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and sun (600 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured in three black cherry plants for each source and light treatment combination under both well-watered and droughted conditions. Each plant was acclimated to low light and then subjected to three 10-min cycles of sun and shade (5 min each), which allowed the stomata to equilibrate to the respective light regime (cf. Knapp and Smith 1989). Two adjacent leaves on each of the three plants were selected for measurement, one for the sun and one for the shade cycle, to minimize cuvette effects on gas exchange. Using the ADC LCA-2 system, stomatal conductance values were recorded at 1-min intervals after stable readings were observed, approximately 30 seconds, after which the cuvette was removed for 30 seconds to allow the leaf to adjust to ambient conditions.

Gas exchange, stomatal reactivity, tissue water relations and leaf morphology data were analyzed by one- and two-way analysis of variance, Fisher's LSD test, and least squares regression analysis at $P < 0.05$.

Results

Gas exchange and leaf water potential

Maximum values of net photosynthesis (A) and leaf conductance (g_{wv}) for both Pennsylvania and Wisconsin seedlings were obtained in the sun treatment on Day 1

after cessation of watering (Figure 1). Low values of A in the sun for both sources on Day 3 were associated with maximum T_{leaf} (32.6°C) recorded on that date. Significantly higher A and g_{wv} were maintained in the sun than shade plants during the early stages of drought. With increasing drought, plants of both seed sources exhibited decreasing A and g_{wv} , but values were consistently higher ($P < 0.05$) in Wisconsin than in Pennsylvania seedlings in the sun treatment. In contrast, source differences in A and g_{wv} across all sample dates were not significant in the shade treatment, although Wisconsin seedlings generally maintained higher gas exchange rates than Pennsylvania seedlings during the mid-stages (Days 14–19) of drought.

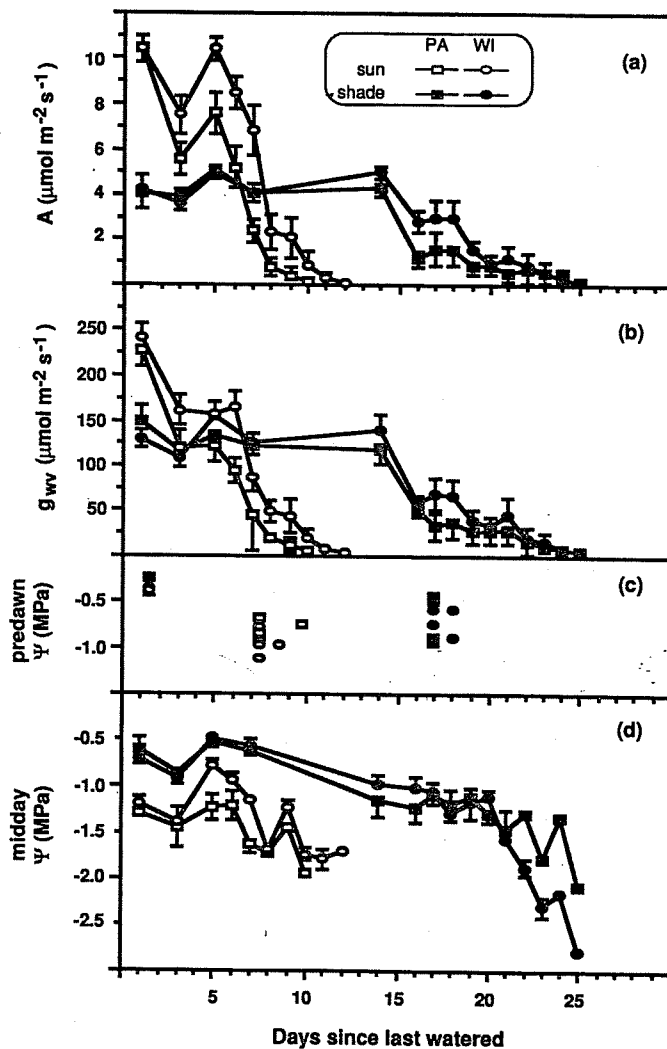


Figure 1. Changes in net photosynthesis (A), leaf conductance to water vapor diffusion (g_{wv}) and leaf water potential (Ψ) (mean \pm SE) during drought in sun and shade plants of Pennsylvania (PA) and Wisconsin (WI) ecotypes of *Prunus serotina*.

Across all dates, source differences in predawn and midday leaf water potential (Ψ) were not significant in either light treatment, although midday Ψ values tended to be higher (less negative) in Wisconsin seedlings in the sun treatment. Relatively low midday Ψ in sun plants on Days 1 and 3 of drought apparently reflected high g_{wv} and high T_{leaf} , respectively.

After pooling seed source data, a significant linear relationship between A or $\%A_{max}$ ($A/A_{maximum}$) and Ψ existed for both sun and shade plants, with significantly different Y -intercepts and slopes (Figure 2). Sun plants exhibited a much greater decline in A or $\%A_{max}$ with decreasing Ψ , whereas shade plants maintained positive A at lower Ψ . Shaded Wisconsin plants maintained positive A at lower Ψ relative to Pennsylvania plants at the later stages of drought, and they obtained the two lowest Ψ values at incipient wilting (-2.45 and -2.78 MPa) (Figure 1).

Tissue water relations

Under well-watered conditions, both seed sources had lower osmotic potentials at full (Ψ_{π}^{100}), or zero (Ψ_{π}^0) turgor, or both in the sun versus shade treatment, which was consistent with lower bulk leaf Ψ at that time (Table 2). There were no light treatment or source differences in elastic modulus (ϵ) and RWC_0 at predrought conditions. No osmotic adjustment to drought was detected in the sun plants for either source, whereas shaded plants of both sources exhibited significant osmotic adjustment.

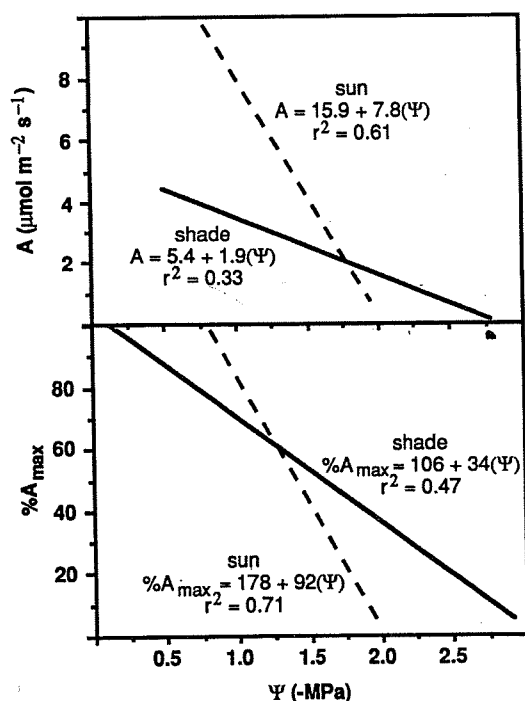


Figure 2. Linear regression of net photosynthesis (A) and $A/A_{maximum}$ ($\%A_{max}$) versus midday leaf water potential in sun and shade *Prunus serotina* plants, after pooling seed source data.

Table 2. Tissue water relations parameters derived from pressure-volume analysis of the Wisconsin (WI) and Pennsylvania (PA) black cherry sources in sun and shade treatments during pre- and peak-drought. Means (\pm SE) in a column followed by the same letter are not significantly different. Ψ_{π}^{100} = osmotic potential at full turgor; Ψ_{π}^0 = osmotic potential at zero turgor; RWC_0 = relative water content at zero turgor; ϵ = bulk modulus of elasticity.

Light regime	Seed source	Drought status	Ψ_{π}^0 (MPa)	Ψ_{π}^{100} (MPa)	ϵ (MPa)	RWC_0 (%)
Sun	WI	Pre	$-1.39 \pm 0.03bc$	$-1.11 \pm 0.08a$	$10.3 \pm 1.6ab$	$89.8 \pm 1.5ab$
Sun	WI	Peak	$-1.49 \pm 0.08cd$	$-1.22 \pm 0.12a$	$9.0 \pm 0.5a$	$87.4 \pm 1.5a$
Sun	PA	Pre	$-1.44 \pm 0.05cd$	$-1.17 \pm 0.08a$	$11.0 \pm 1.0ab$	$90.2 \pm 0.4ab$
Sun	PA	Peak	$-1.43 \pm 0.14bd$	$-1.10 \pm 0.09ab$	$9.3 \pm 0.3a$	$89.2 \pm 1.2a$
Shade	WI	Pre	$-1.13 \pm 0.11a$	$-0.90 \pm 0.04b$	$12.4 \pm 1.0bc$	$92.5 \pm 1.1b$
Shade	WI	Peak	$-1.54 \pm 0.08cd$	$-1.15 \pm 0.09a$	$11.1 \pm 1.8ab$	$89.8 \pm 1.3ab$
Shade	PA	Pre	$-1.21 \pm 0.09ab$	$-1.04 \pm 0.07ab$	$10.0 \pm 1.4ab$	$90.0 \pm 0.9ab$
Shade	PA	Peak	$-1.64 \pm 0.08d$	$-1.19 \pm 0.11a$	$9.2 \pm 0.1a$	$88.1 \pm 1.1a$

Drought-induced adjustments in ϵ and RWC_0 within a light treatment did not occur. However, when comparing shaded plants at predrought to sun plants at peak drought, Wisconsin sun plants had lower Ψ_{π}^{100} , Ψ_{π}^0 , ϵ and RWC_0 ; these differences were not seen in Pennsylvania plants.

Leaf structural characteristics

Seed source and light treatment differences were apparent in the five measured leaf variables (Table 3). Sun leaves of both sources were larger than shade leaves, and Wisconsin plants produced larger leaves than Pennsylvania plants in the sun. Leaves of Wisconsin sun plants were thicker and had higher specific leaf mass than Pennsylvania sun leaves and the shaded leaves of either source. Stomatal density of both sources was higher in sun than shade plants, but not significantly different between

Table 3. Leaf structural characteristics of the Pennsylvania (PA) and Wisconsin (WI) black cherry sources in sun and shade treatments. Parameter means (\pm SE) in a row or column followed by the same letter are not significantly different.

Leaf characteristics	Pennsylvania source		Wisconsin source	
	Sun	Shade	Sun	Shade
Leaf area (cm ²)	$40.6 \pm 2.7a$	$31.0 \pm 3.4c$	$53.7 \pm 4.0b$	$30.6 \pm 3.0c$
Leaf thickness (μ m)	$290.4 \pm 15.7a$	$280.3 \pm 9.2a$	$372.0 \pm 15.3b$	$293.6 \pm 5.5a$
Specific leaf mass (mg cm ⁻²)	$3.93 \pm 0.14a$	$2.69 \pm 0.06c$	$4.48 \pm 0.20b$	$2.57 \pm 0.04c$
Stomatal density (mm ⁻²)	$545.4 \pm 41.2a$	$402.3 \pm 23.1b$	$520.4 \pm 24.8a$	$399.9 \pm 37.2b$
Guard cell length (μ m)	$53.6 \pm 1.2a$	$57.2 \pm 1.5b$	$57.3 \pm 1.2b$	$59.3 \pm 1.3b$

sources in either light regime. Guard cell length was lower in Pennsylvania sun plants than in the three other ecotype \times light combinations.

Stomatal reactivity

Leaf stomata of both sources typically opened faster ($P < 0.05$) in the first sun cycle (2.25 min) than they closed in the first shade cycle (3.17 min) under well-watered, but not droughted, conditions (Figures 3A, B and D). Stomatal conductance in well-watered plants decreased with subsequent sun-shade cycles (Figures 3A-D), which may explain why differences in sun-shade response time was only significant in the first cycle. In contrast, shade plants exhibited higher g_{wv} with subsequent cycling (Figures 3G and H), possibly because of a priming effect of the first light cycle (cf. Pearcy 1990). Under well-watered conditions, g_{wv} in sun leaves ($\bar{x} = 108.2 \text{ mmol m}^{-2} \text{ s}^{-1}$) was higher than in shade leaves ($\bar{x} = 64.4 \text{ mmol m}^{-2} \text{ s}^{-1}$) in both the sun and shade cycles (Figures 3A and B versus 3C and D). However, differences in g_{wv} between sun and shade cycles decreased over time in well-watered plants

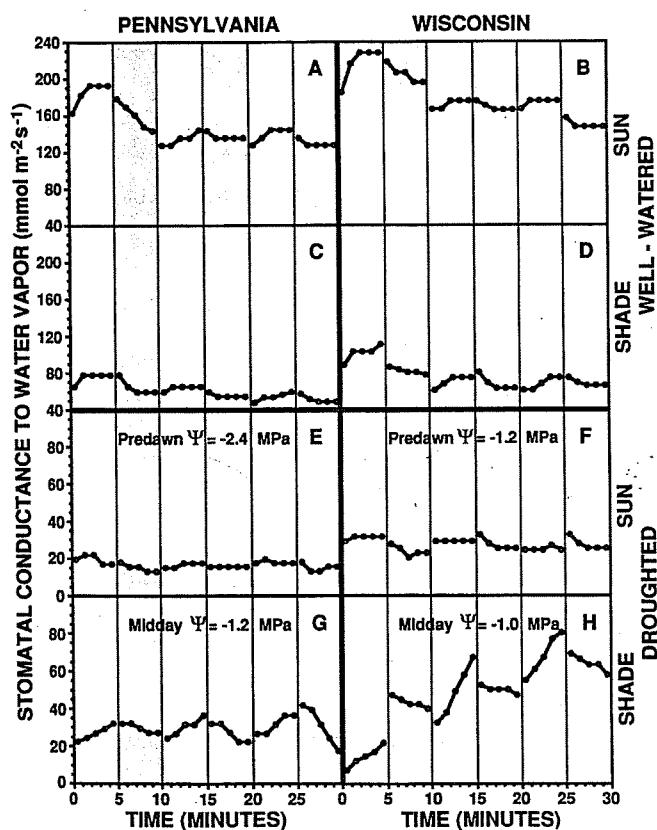


Figure 3. Selected stomatal reactivity curves for *Prunus serotina* from the eight combinations of seed source, water status, and light treatment. Points in the stippled area indicate observations made in the shade, whereas those in the clear area indicate sun measurements. Water potentials are noted for those plants studied in the droughted condition.

because of stabilization of stomatal aperture. The most severely droughted sun plants exhibited low g_{wv} and negligible stomatal reactivity in both sun and shade cycles (Figures 3E and F).

Discussion

Regional climatic data and soil features indicate that black cherry is subjected to more xeric conditions in Wisconsin than in Pennsylvania. Our results suggest considerable variation between the sources that is consistent with regional differences in water availability. Wisconsin plants maintained higher rates of gas exchange during the entire or mid-stages of drought in sun and shade conditions, respectively. Maximum net photosynthetic rates of 10.4 and 4.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the sun and shade, respectively, are within the range of daily maximum A reported for this species in sunlit and shaded field conditions in Wisconsin (Harrington et al. 1989, Reich et al. 1990).

Sun plants from both sources exhibited a more rapid reduction in A or % A_{max} with decreasing Ψ than did shade plants. Shaded plants, particularly of the Wisconsin source, maintained positive A at lower Ψ than sun plants of either source. These results are consistent with sun and drought effects on gas exchange in *Vitis californica* (Gamon and Pearcy 1990), and on growth in *Quercus rubra* and *Liriodendron tulipifera* in which the inhibitory effects of low water availability and low fertility were more pronounced in full sun than in shade (Kolb et al. 1990). Similarly, water stress predisposed leaves of *Nerium oleander* (an evergreen shrub) to photo-inhibition, and reduced the tolerance of shade ecotypes of *Solanum dulcamara* to high light (Gauhl 1979, Björkman and Powles 1984). In contrast, drought effects on A were similar in sun and shade leaves of *Salix* sp. (Ogren and Oquist 1985), and shaded seedlings of *Pinus ponderosa* were killed at less severe water deficits than unshaded seedlings (Vance and Zaerr 1991).

Osmotic potentials for black cherry have not been previously reported, but the results of this study indicate that this species has high (less negative) Ψ_{π} relative to other North American tree species and to *Prunus avium* and *P. domestica* in Austria under well-watered and droughted conditions (Abrams 1988b, 1990, Yoon and Richter 1990). Both ecotypes in this study exhibited lower Ψ_{π} in sun than in shade under well-watered conditions. Leaves in high light typically develop lower bulk Ψ and Ψ_{π} relative to shaded leaves (Myers et al. 1987, Pothier and Margolis 1990, Auge et al. 1990, Ellsworth and Reich 1992). Osmotic adjustment to drought was detected in shade plants but not sun plants, which reached incipient wilting in 10–12 and 25 days, respectively. In contrast, other studies have reported greater plant osmotic adjustment in high than in low irradiance (Auge et al. 1990). However, the rapid imposition of drought in sun plants in this study may have prevented osmotic adjustment from occurring (cf. Turner and Jones 1980, Abrams 1988b). Moreover, less osmotic adjustment is generally detected in greenhouse than in field studies (Abrams 1990).

The black cherry ecotypes had similar tissue water relations in the sun and shade

and during pre- and peak-drought conditions. Several studies have reported genotypic variation in tissue water relations that were consistent with habitat, such as xeric genotypes with lower Ψ_{π} and RWC_0 and higher or lower ϵ than mesic genotypes (Abrams 1988a, Abrams et al. 1990), whereas other studies have found a weak relationship between genotype habitat and tissue water relations (Parker and Pallardy 1985, Bongarten and Teskey 1986, Abrams and Kubiske 1990b). One genotypic difference in this study was the greater ability of Wisconsin plants to lower Ψ_{π} , ϵ and RWC_0 under water limiting conditions (cf. well-watered shade plants versus droughted sun plants). Nonetheless, small genotypic differences in Ψ_{π} and ϵ in the various light-water treatments used in this study do not seem to explain the significant gas exchange differences between the sources.

Plants from xeric or high light environments generally develop smaller and thicker leaves, with higher specific mass, stomatal density and lower guard cell length than plants on mesic or low light sites (Jackson 1967, Carpenter and Smith 1975, 1981, Abrams and Kubiske 1990a, 1990b). These features are thought to minimize the potential for excessive water loss and wilting, and increase water use efficiency during drought. Many of these leaf structural differences were apparent in this study. For example, sun plants had thicker leaves with greater specific mass and stomatal density and lower guard cell length than shade plants in one or both sources. In contrast, however, sun plants of both sources had higher leaf areas than shade plants. No ecotypic differences in leaf structure were exhibited in shade plants. However, Wisconsin sun leaves were thicker and had greater specific mass than Pennsylvania sun leaves, whereas Pennsylvania sun leaves were smaller and had shorter guard cells than Wisconsin sun leaves. Thus, each source produced leaves with different characteristics that are thought to confer an advantage in high light or droughty environments. However, thicker leaves in the Wisconsin plants could provide a greater total area of mesophyll cell walls exposed to intercellular air spaces, which may contribute to higher A at high and low Ψ (Nobel 1983).

Shade-tolerant plants are thought to have more rapid stomatal opening in sunflecks relative to shade intolerant plants, which should promote rapid carbon assimilation in understory conditions (Woods and Turner 1971, Davies and Kozlowski 1974). In this study, however, no source difference in stomatal reactivity was detected. We found that stomata generally opened faster than they closed in the first sun-shade cycle (cf. Woods and Turner 1971), however this was not apparent in droughted plants. Stomatal conductance in well-watered plants decreased, as did Δg_{wv} between sun-shade cycles, with subsequent cycling. This response was also reported for several subalpine plants in which water use efficiency increased during sun intervals (Knapp and Smith 1989). Our most severely droughted plants exhibited greatly reduced stomatal reactivity to sun-shade cycles, as was also reported by Knapp and Smith (1989).

In conclusion, our hypothesis that the Wisconsin black cherry was more drought tolerant but less shade tolerant than the Pennsylvania ecotype was only partially supported by the results of this study. The photosynthesis and stomatal reactivity data provided no evidence that the Pennsylvania source was more shade tolerant than the

Wisconsin source. However, the data indicated that Wisconsin plants were more drought tolerant. We observed higher rates of gas exchange during drought and thicker leaves in Wisconsin sun plants than in Pennsylvania sun plants. Both ecotypes exhibited phenotypic responses to light treatment, but most of the source differences exhibited in high light were not evident in shade. Drought responses in both ecotypes differed markedly between sun versus shade treatments, including variation in A/Ψ relationships and stomatal reactivity. In general, the effects of drought on ecophysiological responses were more inhibitory in sunlight than in shade. Nonetheless, considerable ecotypic and phenotypic variation between the two black cherry sources is consistent with their ability to survive in greatly contrasting environments.

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