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Leaf Gas Exchange of Eastern Redbud (*Cercis canadensis* L.) Grown Under Sun and Shade[1]

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Abstract

Leaf physiology of eastern redbud (*Cercis canadensis* L.) was assessed under natural photoperiod when grown in 100% sun or under polyethylene shade with a light transmittance of 69%, 47%, or 29% sun. Net CO_2 assimilation rate (A) was similar under 100%, 69%, and 47% sun; A was reduced under 29% sun. Adaptations to shade included a near perpendicular leaf orientation to the sun, reduction in specific leaf weight (SLW), and a decreased chlorophyll *a*: chlorophyll *b* ratio. Conversely, eastern redbud adapted to 100% sun by manifesting an increased SLW and a vertical orientation of leaves that curled inward toward the midrib. Light response curves were similar for sun- and shade-acclimatized plants. When all data were analyzed collectively, A was most closely related to photosynthetic photon flux (PPF) ($R^2 = 0.52$), whereas stomatal conductance to water vapor (gs) was primarily influenced by vapor pressure deficit (VPD) ($R^2 = 0.75$). Hence, A and gs were not well correlated ($R^2 = 0.41$). The lack of strong coupling between A and gs allowed the stomates to remain open under low PPF, resulting in an elevated intercellular CO_2 concentration. Thus, A was stimulated above what might have normally occurred under low PPF.

Index words: net CO_2 assimilation, transpiration, stomatal conductance, chlorophyll

Significance to the Nursery Industry

Eastern redbud (*Cercis canadensis* L.) typically is grown in full sun in nurseries throughout the country. Physiological evidence from our research suggests that eastern redbud performs equally well at moderate to high light intensities in the deep south. Net photosynthetic rate was reduced under heavy shade (29% sun). The only advantage of producing eastern redbud under less than full sun, especially in the south, is the improved foliage display resulting from darker green leaves with a less vertical orientation.

Introduction

Cercis canadensis, the eastern redbud, is widely grown and cultivated as a small tree. In the cooler northern limits of its natural distribution, eastern redbud is found in areas of high light such as open woodlands and along borders of woods, while it is more prevalent under shaded conditions in the warmer southern part of its range (12). Therefore, eastern redbud appears to be a shade-tolerant species (and possibly shade obligate) in the southern part of its range, and possibly farther north. No physiological analyses have demonstrated that these empirical observations are due to physiological responses to varied light availability.

Information regarding the shade tolerance of eastern redbud may prove beneficial to the nursery and landscape maintenance industries. The objective of this study was to determine the sun tolerance of containerized eastern redbud by assessing leaf gas exchange and chlorophyll levels under four light regimes—100%, 69%, 47%, and 29% sun.

Materials and Methods

1987 to 1989 experiments. Eastern redbud seedlings, derived from seeds collected in the southeast (specific location not identified), were obtained from a local nursery. In April 1987, plants were potted into 3.8 l (1 gal) containers with a medium of pine bark: Canadian sphagnum peat: sand (2:1:1 by vol). One cubic meter (1.3 yd^3) of medium was amended with 2.97 kg (6.6 lb) dolomite, 2.97 kg (6.6 lb) superphosphate, 0.89 kg (2.0 lb) Micromax (12S-0.1B-0.5Cu-12Fe-2.5Mn-0.05Mo-1Zn), and 5.9 kg (13.0 lb) Osmocote 18N-2.6P-10.0K (18-6-12). Plants were placed outdoors under shadecloth (69% sun transmittance) until the experiment was started on June 17, 1987.

The experiment, set up as a randomized complete block design, was conducted in an 24.4 × 17.1 × 2.0 m (80 × 56 × 6.6 ft) open-sided structure with the long axis oriented

[1]Received for publication June 3, 1991; in revised form August 9, 1991. Florida Agricultural Experiment Station Series Journal No. R-01363.
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in a north-south direction. The structure was subdivided into four rows (four blocks), each row consisting of four individual 6.1 × 4.3 m (20 × 14 ft) shade structures of four light intensities (100%, 69%, 47%, or 29% full sun). Light intensity was modified by commercially-obtained woven polypropylene shade material. On June 17, 1987, four plants were placed on 2.7 × 0.8 m (8.8 × 2.6 ft) benches that were 1 m (3.3 ft) high and centered under each of the 16 shade structures. Azimuth angle of the sun was used to determine shadecloth size and bench height to minimize plant exposure to full sunlight during early morning and late afternoon (2). Plants were top-dressed with 9.8 g (0.35 oz) Nutricote 16N-4.4P-8.3K (16-10-10) Type 180 at the start of the experiment, and then every 3 months afterward with 80 g (2.8 oz) Osmocote 18N-2.6P-10.0K. On September 9, 1987, plants were repotted in 19 l (5 gal) containers in the same medium. In April 1988, all plants were placed on the ground since the plant tops were touching the shadecloth. Two liters (2.1 qt) of water per container (4 liters [4.2 qt] per 19 l [5 gal] container) were supplied daily at 0800 and 1400 HR via trickle irrigation.

Photosynthetic photon flux (PPF), ambient and leaf chamber CO_2 and H_2O vapor concentration, air temperature, and relative humidity were measured with an Analytical Development Corporation Ltd. (ADC) Model LCA-2 infrared gas analyzer, an air supply unit (flow rate 400 $cm^3 \cdot min^{-1}$), and a Parkinson broadleaf chamber as described previously (10). Net CO_2 assimilation rate, gs, transpiration rate (E), leaf temperature (LT), VPD, and intercellular CO_2 concentration (Ci) were calculated using an ADC Model DL2 datalogger and the accompanying software. Water use efficiency (WUE) was estimated as the mole fraction of CO_2 uptake and H_2O vapor loss × 1000.

Gas exchange of fully expanded leaves oriented perpendicular to the sunlight and inserted into a leaf chamber was measured between 1000 and 1400 HR on selected days (1987–June 19, 28, and 29; July 10 and 28; September 15, 1987; 1988–September 21). Leaves fully expanded before treatment initiation were measured on all dates in 1987. Leaves fully expanded after treatment initiation were measured on July 10 and 28, 1987, and September 21, 1988. Leaf gas exchange was measured on one or two leaves per plant.

Data for the entire experiment were combined and subjected to a split plot analysis of variance by general linear model procedures (13). Day was the main plot with an error term of block × day. Percent sun was the subplot with an error term of block × percent sun + block × percent sun × day. LSD (5%) values for PPF, A, gs, E, WUE, and Ci were calculated using the subplot error term. Leaf gas exchange data were also subjected to nonlinear regression analysis (4). The relationship of A and gs to PPF, VPD, and LT was assessed, and the relationship of A to gs was noted.

Chlorophyll concentration was quantified on August 26, 1987 in leaves expanded before and after treatment initiation obtained from one plant per replicate. Three 1-cm (0.4-in) discs per leaf were immersed in N,N-dimethylformamide for 24 hr in the dark. Total chlorophyll, chlorophyll *a* (chl *a*), and chlorophyll *b* (chl *b*) were quantified from absorbance at 647 and 664 nm (5). Specific leaf weight, defined as:

$$SLW = \text{leaf dry weight/leaf area}$$

was measured on November 8, 1988 using two plants per replicate. No leaf data were recorded in 1987. Data were analyzed by general linear model procedures (13) and LSD (5%) values calculated.

1990 experiments. Time course characteristics (0800 to 2000 HR) of leaf gas exchange and light response curves were compiled using two-year-old seedlings obtained from a local nursery. The seedlings were potted into 12.3-l (3 gal) containers in a medium composed of pine bark: Canadian sphagnum peat: sand (3:1:1 by vol), and amended as described before. Four plants were placed in the 100% or 29% sun treatments on April 6, 1990. On May 30, leaf gas exchange was measured using recently expanded leaves. Photosynthetic photon flux was manipulated by shading leaves with various combinations of shadecloth. The relationship of A to PPF was analyzed by nonlinear regression (4). Dark respiration and light compensation points were calculated from regression equations at PPF = 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and A = 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. Apparent quantum yields were estimated from the slope of A/PPF at PPF < 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and light saturation points were estimated when values of A approached an asymptote (95% of maximum A). Time course characteristics of leaf gas exchange were compiled for 100% sun- and 29% sun-grown plants on May 31. Measurements were recorded every 2 hr from 0800 to 2000 HR. Mean ± 1 standard error of PPF, A, E, WUE, gs, and Ci were plotted as a function of time.

Results and Discussion

Shadecloth ratings (69%, 47%, and 29% sun transmittance) claimed by the manufacturer were generally accurate throughout the day, with ≈95% of the midday variation in PPF due to the shadecloth density (data not shown).

Midday values of A during 1987 and 1988 were similar for leaves of plants grown under 100%, 69%, and 47% sun (Table 1), despite some physiological and morphological adaptations (see below). Maximum A of eastern redbud

Table 1. Mean values of midday leaf gas exchange determined on leaves of *Cercis canadensis* during 1987 and 1988, chlorophyll levels[z], and specific leaf weight under 4 levels of light intensity induced by shadecloth. Treatments were initiated on June 17, 1987.

	Light level (% sun)				
Parameter[y]	100	69	47	29	LSD 5%
PPF ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	1744	1171	869	474	75
A ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	10.1	10.0	9.8	7.4	1.1
gs ($mmol \cdot m^{-2} \cdot s^{-1}$)	236	270	273	268	NS
E ($mmol \cdot m^{-2} \cdot s^{-1}$)	6.65	6.82	6.29	6.23	NS
Ci ($\mu mol \cdot mol^{-1}$)	222	232	246	257	9
WUE (mmol $CO_2 \cdot$ mol H_2O^{-1})	1.51	1.46	1.45	1.17	0.14
Total chl ($\mu g \cdot cm^{-2}$)	48.3	50.9	49.4	52.0	NS
chl a: chl b	2.8	2.5	2.5	2.6	0.1
SLW ($mg \cdot cm^{-2}$)	12.0	10.4	10.3	8.8	1.7

[z]Chlorophyll levels were measured using two leaves per plant, one developed before treatment initiation and one developed after treatment initiation.

[y]Abbreviations: Photosynthetic photon flux (PPF), net CO_2 assimilation (A), stomatal conductance to water vapor (gs), transpiration rate (E), leaf internal CO_2 concentration (Ci), water use efficiency (WUE), chlorophyll (chl), and specific leaf weight (SLW).

(≈10 μmol·m^{-2}·s^{-1}) was similar to A of other deciduous woody plants (6, 7, 8). Light response curves of 100% and 29% sun-preconditioned leaves were similar although A of 100% sun-preconditioned leaves was slightly higher at PPF > 400 μmol·m^{-2}·s^{-1} (Fig. 1). Light compensation point (PPF ≈80 μmol·m^{-2}·s^{-1}), dark respiration rate (≈2.5 μmol·m^{-2}·s^{-1}), and apparent quantum yield (≈0.027 mol CO_2·mol light^{-1}) were not affected by light preconditioning. The similar response of preconditioned to sun or shade for 54 days indicates that light acclimation was not complete (1, 7, 8).

Light-saturated A occurred at a PPF ≈1000 μmol·m^{-2}·s^{-1}. Most leaves of plants in 100% sun received sufficient light to be operating near maximum A for most of the day (Figs. 1, 2). Similarly, exterior canopy leaves of plants grown under 69% sun were exposed to light at or near saturating PPF for most of the day, although light levels were probably not sufficiently high for maximum A of the innermost leaves due to mutual leaf shading. Under 47% sun, light-saturating PPF only occurred during midday. The light saturation point was not achieved for any leaves of any plants under 29% sun.

Eastern redbud manifested several morphological and physiological adaptations to sun and shade. Leaves in 100% sun were curled inward and oriented vertically, which would tend to decrease light interception and leaf temperature. Also, leaves in 100% sun had an increased chl *a*: chl *b* ratio and SLW (Table 1). These adaptations to conditions of high light resulted in similar relative leaf water content and leaf water potential (data not shown), and similar values of leaf gas exchange among the 100%, 69%, and 47% sun treatments (Table 1).

Conversely, adaptation of leaves to reduced light intensity through orientation perpendicular to sunlight would tend to improve light harvesting capacity. Shade-grown leaves also had a reduced SLW (29% sun only) and chl *a*: chl *b* ratio,

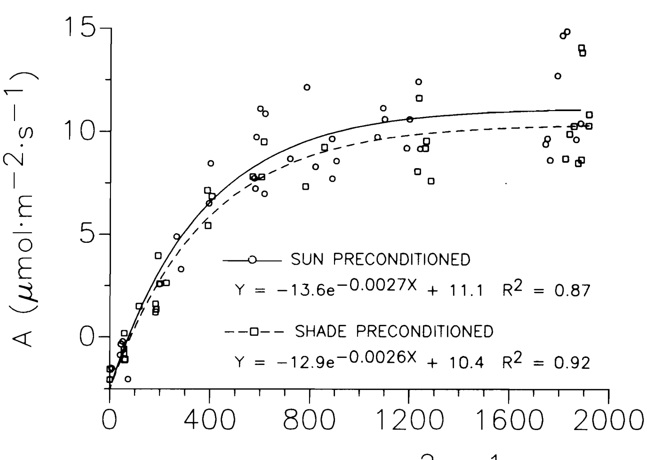

Fig. 1. Light response curve for eastern redbud leaves preconditioned to 100% sun (SNLV) or 29% sun (SHLV) from April 6 to May 30, 1990. Net CO_2 assimilation (A) was measured on May 30 from 1000 to 1400 HR. Maximum photosynthetic photon flux (PPF): SNLV = 1884 ± 117 μmol m^{-2} s^{-1}, SHLV = 1917 ± 122 μmol m^{-2} s^{-1}; air temperature: SNLV = 30.8 ± 0.1°C, SHLV = 31.7 ± 0.2°C; leaf temperature: SNLV = 29.3 ± 0.3°C, SHLV = 29.9 ± 0.4°C; vapor pressure deficit: SNLV = 2.8 ± 0.1 kPa, SHLV = 2.9 ± 0.1 kPa.

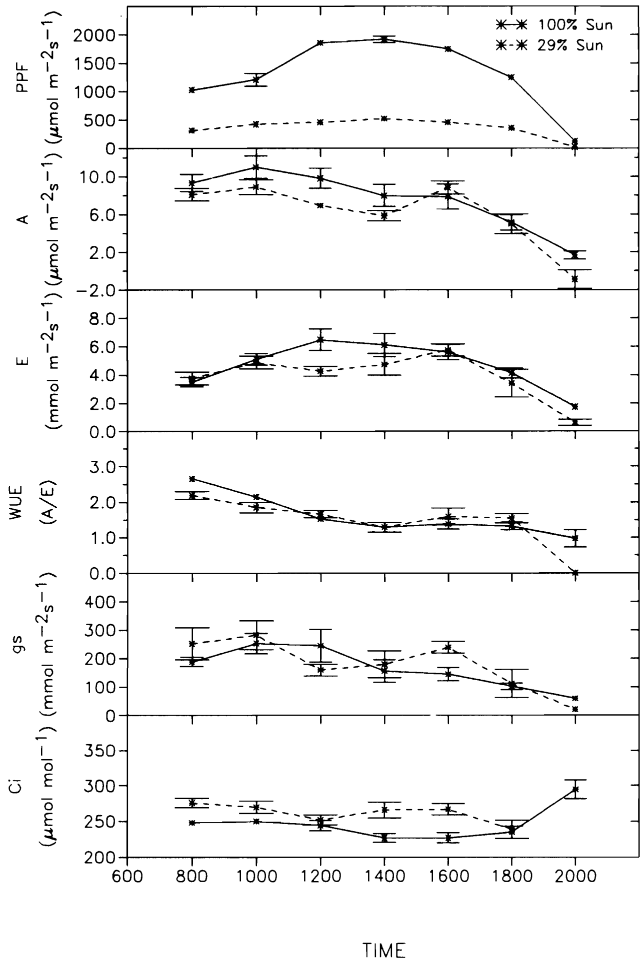

Fig. 2. Time course of leaf gas exchange of eastern redbud preconditioned to 100 or 29% sun from April 6 to May 31, 1990. Leaf gas exchange was measured on May 31. Points and error bars represent the mean and ± 1 SE, respectively; n = 4. Abbreviations: photosynthetic photon flux (PPF), net CO_2 assimilation (A), transpiration (E), water use efficiency (WUE), stomatal conductance to water vapor (gs), intercellular CO_2 concentration (Ci).

which are common features of shade-adapted plants (Table 1) (1). Net CO_2 assimilation rate and gs were weakly coupled under shade as evidenced by the rise in Ci under reduced light levels (Table 1; Fig. 2). Plants exposed to nonlimiting soil moisture have an advantage when A and gs are not strongly coupled (i.e., nonconstant Ci) since carbon gain is maximized at the expense of increased moisture loss (9). The weak coupling of A and gs (R^2 = 0.41) can be traced to the fact that CO_2 uptake and H_2O vapor loss were controlled predominantly by different environmental factors. Net CO_2 assimilation was principally dependent upon PPF (R^2 = 0.52), with other independent variables (VPD, gs, LT) being poorly correlated to A, e.g., A to VPD (R^2 = 0.04; results not shown). Conversely, gs was highly dependent upon VPD (R^2 = 0.75; Fig. 3) and poorly correlated with PPF (R^2 = 0.04; results not shown).

Despite the above-mentioned adaptations to shade, plants in 29% sun were unable to fully acclimate as evidenced by the lower A compared to other treatments (Table 1). Furthermore, the reduced A under 29% sun combined with the similar E among all light regimes resulted in a decreased WUE for plants under 29% sun.

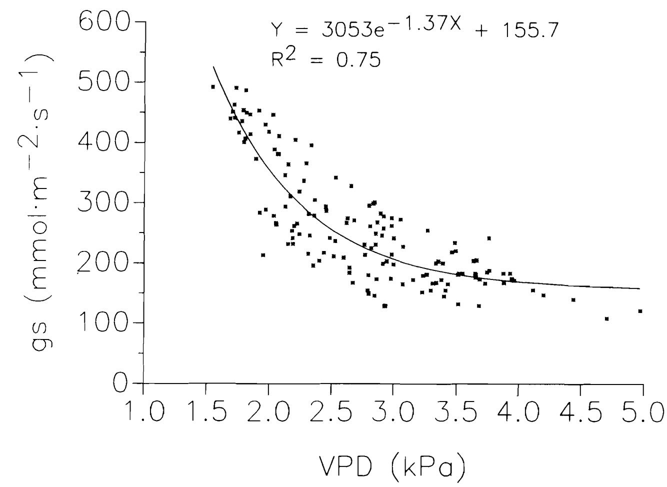

Fig. 3. Relationship of eastern redbud stomatal conductance to water vapor (gs) to leaf-to-air vapor pressure deficit (VPD). Measurements were performed during midday during 1987 and 1988. Treatments were initiated on June 17, 1987.

In conclusion, eastern redbud fully acclimated to 100% to 47% sun, and partially to 29% sun without detrimental effects on plant appearance. Our results are consistent with observations of horticulturists that state that eastern redbud grows equally well in full sun or shade (3, 11). There was no evidence that it prefers heavy shade here in the southern part of its range as has been suggested (12), at least under nonlimiting soil moisture. Also, because eastern redbud is seed propagated, there may be considerable intraspecific variation in its ability to acclimatize to sun and shade; thus ecotype differences must be considered.

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Asexual Propagation of *Shepherdia canadensis* and *S. rotundifolia*[1]

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Abstract

Shepherdia canadensis and *S. rotundifolia* were asexually propagated by hardwood cuttings and aseptic micropropagation. *S. canadensis* showed greatest rooting of 46.5% with 0.3% IBA. *S. rotundifolia* showed greater proliferation in woody plant media (WPM) with 0.89 µM BA and optimum rooting in WPM with 5.4 µM NAA.

Index Words. buffaloberries, Elaeagnaceae, *S. argentea*, russet buffaloberry, desert buffaloberry, IBA, BA, NAA

Significance to the Nursery Industry

Results from these experiments indicate that *S. canadensis* can be rooted from cuttings which might be an alternative to using seeds, especially given the low viability previously experienced by the authors. *S. rotundifolia*, on the other hand, can be successfully propagated in vitro. These asexual propagation methods would be valuable if a plant exhibiting unique characteristics was found. Cloning could reliably be accomplished by the procedures described.

[1]Received for publication May 6, 1991; in revised form August 12, 1991.
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