Shading Affects Morphology, Dry-matter Partitioning, and Photosynthetic Response of Greenhouse-grown 'Chardonnay' Grapevines

Justine E. Vanden Heuvel¹, John T.A. Proctor, K. Helen Fisher, and J. Alan Sullivan²

Department of Plant Agriculture, University of Guelph, Guelph, ON, Canada N1G 2W1

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Abstract. In order to gain an understanding of the capacity of severely shaded leaves to be productive in dense canopies, the effects of increased shading on morphology, dry-matter partitioning, and whole-plant net carbon exchange rate (NCER) were investigated on greenhouse-grown *Vitis vinifera* L. 'Chardonnay' grapevines. Vines were subjected to whole-plant shading levels of 0%, 54%, 90%, and 99% of direct sun 3 weeks after potting. Data were collected 8 to 10 weeks after potting. Nonlinear regression was used to investigate the relationship of leaf morphological traits and organ dry weights to increased shading. Leaf size was maintained with increased shading to approximately the 90% shading level, while leaf fresh weight, volume, density, and thickness were immediately reduced with increased shading. Root dry weight was most affected by increased shading, and root to shoot ratio was reduced. When nonlinear regressions were produced for light response curves, light compensation point was reduced by approximately 49% by moderate shading, and 61% by severe shading. Shaded leaves approached the asymptote of the light response curve more quickly, and had reduced dark respiration rates, indicating that the morphological compensation responses by the vine allow shaded leaves to use available light more efficiently. However, the long-term ramifications of reduced root growth in the current year on vines with shaded leaves may be significant.

The interior of a grapevine canopy has been characterized as a dark environment with as little as 1% of ambient photosynthetic photon flux (PPF) (Smart, 1985), and a red : far-red ratio (R:FR) of 0.1 or lower (Dokoozlian and Kliewer, 1995), requiring interior leaves to acclimate to a low light stress. The percentage of leaves located on the interior of the canopies vs. the canopy surface area differs between growing systems (Smart et al., 1990).

Both short-term physiological responses and long-term physiological, structural, and morphological modifications are used by plants to acclimate to stress. Increases in whole-plant or leaf photosynthetic rate do not necessarily increase yield, as the carbon must not only be produced by the plant, but must also be efficiently partitioned (Flore and Lakso, 1989). The response of a vine to low light stress in the interior of the canopy likely involves a series of compensation responses to minimize stress in the plant and maximize the use of resources. The ratio of dry-matter partitioning to roots vs.

stems and leaves is a revealing stress indicator (Mooney and Winner, 1991).

Cartechini and Palliotti (1995) concluded that grapevines acclimate to modified light intensity and produce a given amount of carbohydrate. Their data indicated differences in photoassimilate utilization between sun- and shade-grown plants, at both structural and accumulation levels. Shade-grown vines (30% PPF) had lower total leaf area per vine, specific leaf weight, alcohol-soluble carbohydrates and starch content in the leaves, as well as lower soluble solids in the berries compared to light-adapted vines. These differences indicated that light- and shade-adapted plants utilize photoassimilates differently at both structural and storage levels.

While the effect of a semi-darkened environment (30% PPF) on anatomy and morphology of leaves (Cartechini and Palliotti, 1995) has been measured, little is understood about acclimation of grape leaves to dark environments (i.e., canopy interiors of <10% PPF). Estimates have been made of the contribution of interior grapevine leaves to vine carbon balance (Smart 1974; Williams, 1996), although the compensation responses of grape leaves and vines subjected to increased shading have not been thoroughly studied. The capacity of these shaded leaves to be productive may have a large effect on carbon balance of the vine within the current year. In an experiment using potted vegetative vines in a phytotron room, leaves fed with ¹⁴CO₂ on a light-adapted

shoot translocated 26.1% and 12.7% more radioactivity to the roots and trunk, respectively, than leaves from shade-adapted shoots (Vanden Heuvel et al., 2002). Therefore some trellising systems with multiple leaf layers, or a high ratio of shaded to exposed leaves, may be inefficient due to the effect of interior leaves on overall carbon balance. Therefore, our objectives were to quantify: 1) the effect of increased shading on the leaf morphology of greenhouse-grown 'Chardonnay' leaves; and 2) the effect of these modifications on dry-matter partitioning and photosynthetic characteristics of whole plants.

Materials and Methods

Plant material. Dormant *Vitis vinifera* 'Chardonnay' clone 96 vines on Couderc 3309 (C3309) rootstock were potted into 12-L nursery pots with PRO-MIX® on 17 Mar. 2000. Vine sizes were consistent at potting, so data on initial vine size were not collected. The potted vines were placed on the floor in an acrylic greenhouse and were exposed to a 15-h photoperiod with supplemental irradiance provided by overhead 1000-W high-pressure sodium (HPS) lamps. Vines were maintained with two shoots, and further shoot extension was prevented by pinching when plants attained 10 leaves. All developing axillary shoots were removed to reduce within-plant shading. Vines were watered and fertilized on a regular basis (20N–20P–20K at 2 g·L⁻¹).

Greenhouse experimental design. The experiment was designed as a randomized complete block with two replications (under separate shade panels) in the greenhouse. Three weeks following planting the vines were placed under one of four shading treatments. Most shoots contained five to seven leaves at this time. Shading was applied using combinations of two shade cloths (PH 44 and ULS 17, VRE, Grassie, Ont., Canada). PH 44 provided 54% shade, while ULS 17 provided 78% shade. Treatments consisted of a control (nonshaded treatment) and combinations of shade cloth providing 46%, 10%, and 1% of direct light (shading levels equivalent to 0%, 54%, 90%, and 99%, respectively) transmitted through the acrylic greenhouse. The treatment replications were randomly distributed in the greenhouse. Air temperature under the shades did not vary between treatments (data not shown).

Shade cloths of 4 × 4 m were suspended at a height of ≈1.3 m above ground level. The shades hung down to ≈0.5 m above ground level in order to block early morning/late afternoon sun while allowing for air circulation below the shades. This allowed a small amount of diffuse light to reach the plants in all treatments. Values of PPF measured at the top of the vines deviated from calculated PPF due to distance between the top of the vine and the shade, and averaged 1200, 350, 105, and 15 μmol·m⁻²·s⁻¹ at approximately solar noon for the 0%, 54%, 90%, and 99% shading treatments, respectively.

Plants from the two replications of each treatment were randomly selected between 8 to 10 weeks after potting for either analysis of

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¹Current address: Univ. of Massachusetts Cranberry Station, East Wareham, MA 02538.

²To whom reprint requests should be addressed. E-mail: asulliva@uoguelph.ca

leaf morphological traits or for determination of light response curves. Single plants were considered the experimental unit.

Whole-plant photosynthesis. A computer-controlled whole-plant gas analysis system designed by Dutton et al. (1988) was used to monitor whole-plant net CO_2 exchange (NCER). Briefly, the system consisted of plexiglass chambers operating in a semi-closed mode. Carbon dioxide concentration was monitored in open mode using an infrared gas analyzer (IRGA) (Model 200; Analytical Development Co., Hoddeson, England). Carbon dioxide concentration inside the chambers was maintained at $\approx 350 \text{ mg} \cdot \text{L}^{-1}$ by adding pure CO_2 with a mass flow controller (MKS Instruments, Nepean, Ont.). Net carbon exchange rate was estimated while the chamber was in semi-closed mode, and CO_2 was monitored with an IRGA (LI-6262; Li-Cor, Lincoln, Nebr.). To compensate for depletion due to plant metabolic activity, pure CO_2 was injected into the chambers with a second mass flow controller (MKS Instruments).

Plants were randomly selected from the two replications per treatment in the greenhouse to be used in the gas analysis chambers; therefore, variation due to location in the greenhouse was incorporated into the error term of the model. The experimental design within the chamber experiment was an incomplete block with 10 blocks (blocked by chamber and time), resulting in either seven or eight replications over time of each greenhouse treatment.

Influence of irradiation. Light was supplied to the chambers by high-pressure sodium lights (Lumalux LU1000; GTE Sylvania Canada Ltd.), which provided a maximum *PPF* of $\approx 1400 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

Plants were sealed in the chambers for 15 h (overnight) in darkness to allow equilibration to air movement within the chambers before the light treatments began. Shoots were positioned as horizontally as possible in the chambers in order to maximize light interception; however, inter-leaf shading was not completely eliminated.

The influence of irradiance on whole-plant net carbon exchange rate (NCER) was studied by subjecting the vines to eight increasing irradiance levels (i.e., 0, 100, 300, 500, 700, 900, 1100, and $1300 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for a duration of 1 h per irradiance level while all other environmental variables were held constant ($\text{CO}_2 \approx 350 \pm 25 \text{ mg} \cdot \text{L}^{-1}$; temperature $\approx 22 \pm 1^\circ\text{C}$; relative humidity $\approx 30\% \pm 3\%$; saturated vapor pressure deficit $\approx 1.76 \pm 0.03 \text{ kPa}$). Irradiance levels were monitored in the chambers with quantum sensors located at the top of the plant canopy (LI-Q3991-4; Li-Cor).

Net carbon exchange rate was calculated as both a function of leaf area and dry weight. Carbon dioxide concentration inside the chambers was divided by leaf area or total plant dry weight to determine NCER.

Prior to the experiment, two vines from each shading treatment were placed in the chambers for the 15-h overnight period. Beginning at 0700 EST, the plants were subjected to an irradiance level of $700 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for a 10-h period in order to determine the role

of circadian rhythms in the experiment. Following a period of ≈ 20 –30 min, the NCER of the vines remained relatively constant for the duration of the irradiance treatment, indicating that circadian rhythms were not an issue.

Leaf morphology. Analysis of leaf morphology was performed on eight leaves from each of three nodes (i.e., nodes four, seven, and 10 from base of shoot) from a total of four plants (each vine containing two shoots) per treatment (two from each greenhouse rep) that had not been subjected to light treatments. Leaves were removed from plants and analyzed within 1 h. Leaf areas were determined using a leaf area meter (LI-3100; Li-Cor). Leaf fresh weight in both air and water (following dipping in a surfactant solution to remove air bubbles from the surface) was determined using a balance (Mettler, Zurich, Switzerland) sensitive to $\pm 1 \text{ mg}$. Leaves were then placed in a desiccator containing a 0.1% solution of Triton-X surfactant. A vacuum of 500 mm Hg was applied 3 times for 30 s each and released to allow replacement of internal gases with surfactant solution. Leaf weight in water was measured again. Leaf volume, density, and thickness were then calculated based on Archimedes' principle according to Raskin (1983).

Dry-matter partitioning. Plants that had previously been subjected to light response curves were destructively harvested. Leaves and shoots were removed from each vine. Roots were then carefully washed and cut from the trunk at the crown. All organs were placed in separate paper bags and dried for 5 d at 80°C , after which dry weights were recorded.

Data analysis. All statistical computations were performed in SAS ver 6.12 (SAS Institute, Cary, N.C.). Proc NLIN was used to generate equations for the leaf character and organ dry weight data in the form of:

$$Y = a - be^{cx} \quad [\text{Eq. 1}]$$

where a = asymptote; b = intercept; c = rate of approach to asymptote; and x = the x -axis value. Leaf density, however, would not converge as a nonlinear equation and was fit to the model:

$$Y = a + bx \quad [\text{Eq. 2}]$$

Photosynthetic data were fitted to the model:

$$Y = a - be^{cx} \quad [\text{Eq. 3}]$$

following Proctor et al. (1976), where a = asymptote; b = intercept; c = rate of approach to asymptote; and x = the x -axis value. Respiration rate was calculated using Equation 3 by setting $X = 0$, and light compensation point was calculated by setting $Y = 0$ and solving for X based on Equation 3, so that:

$$X = -1/c \cdot \ln[(a - y)/b] \quad [\text{Eq. 4}]$$

where a = asymptote; b = intercept; c = rate of approach to asymptote; and x = the x -axis value. Model assumptions were tested through residual analysis and were determined to have been met. The Type I error rate (%) was set at 0.05 for all statistical tests.

Results and Discussion

Leaf morphology. The changes in the physical characteristics of grape leaves in response to

light levels during growth illustrate the ability of the leaf to acclimate to different conditions within the canopy. Leaf fresh weight, volume, density, and thickness all decreased with increased shading level (Fig. 1B–E). Contrary to published reports (Kappel and Flore, 1983; Morgan et al., 1985), leaf size did not increase with increased shading in this study (Fig. 1A); however, it was not reduced until a shading level beyond 90%, while other leaf traits (Fig. 1B–E) were increasingly reduced with minimal shading. An increase in leaf size by a plant generally results in improved light interception (Kappel and Flore, 1983; Morgan et al., 1985). Shaded vines in this study, due to the decrease in leaf size in the severely shaded treatments, were likely unable to improve light interception.

While light intercepting surfaces of the vine were not enlarged, morphology of the leaves was altered during growth, likely resulting in improved photosynthetic abilities of leaves in the shaded treatments. Increased shading resulted in leaves with reduced volume, density, and thickness (Fig. 1C–E), all of which should result in improved ability by the vine to efficiently use available light and CO_2 (Boardman, 1977; Cartechini and Palliotti, 1995; Pearcy, 2000).

Dry-matter partitioning in the vine. Leaf, shoot, trunk, root, and total plant dry weight were reduced by increased shading (Fig. 2A–E). Dry-matter accumulation in the trunk was less affected by moderate shading than other organs (Fig. 2). Total vine dry weight was also not significantly affected by moderate shading, indicating a change in resource partitioning in the vine as shading increased, as leaf, shoot, and root dry weights were all affected by moderate shading.

Plants grown under increased shade usually have increased light-intercepting surfaces (Kappel and Flore, 1983; Morgan et al., 1985), and although the root to shoot ratio decreased with increased shading in this study, leaf size decreased (Fig. 1; Fig. 2F). Increased dry-matter partitioning to the aboveground organs (as evidenced by the reduced root to shoot ratio), particularly the trunk, appears to be at the cost of root growth, as root dry weight was reduced by $\approx 28\%$ in this experiment when shading level was increased from 0% to 99%. Decreases in root growth of 84% were observed by Vanden Heuvel (2002) in vines that had been shaded for 16 weeks at the 99% shading level. McCartney and Ferree (1999) shaded vines with 80% shade cloth and found that root dry weight was reduced by 47% in 'Sevval' and 51% in 'DeChaunac' in the following year. Root dry weight declined in the first 3 weeks after budbreak, indicating the importance of roots as a storage pool for reserves, and suggesting that root tissues are the largest pool from which reserves are drawn. Our data suggest that roots are the first major organ to suffer from reduced growth when greenhouse-grown vegetative vines are subjected to low light stress. In a study tracing translocation of ^{14}C photoassimilate, leaves on light-adapted shoots fed with $^{14}\text{CO}_2$ translocated 26.1% more of total plant ^{14}C to the root system than

Fig. 1. The influence of shading level on leaf morphological traits of *Vitis vinifera* 'Chardonnay' grapevines as fitted to Equation 1, with the exception of leaf density, which was fitted to Equation 2. Level of significance of F-test for regression follows the regression equation in brackets. (A) Size: ($Y = 115.1 - 1.817 \times 10^{-8} e^{0.2171x}$) ($P = 0.0004$); (B) fresh weight: ($Y = 2093.1 - 338.3 e^{0.0136x}$) ($P = <0.0001$); (C) volume: ($Y = 2151.6 - 221.5 e^{0.0174x}$) ($P = <0.0001$); (D) density: ($Y = 0.9069 - 0.00032x$) ($P = 0.0007$); (E) thickness: ($Y = 2.5736 - 0.991e^{0.00039x}$) ($P = <0.0001$). Least square means of treatments have been plotted (•).

did leaves on a shade-adapted shoot (Vanden Heuvel et al., 2002).

While carbon partitioning within the vine is altered by growth in a low-light environment, it is unlikely that assimilates stored in roots are being retranslocated to interior shoots in the current season. This was illustrated in a study where container-grown plants with the six lower leaves shaded produced greater root dry weight than plants with the same leaves removed (Kaps and Cahoon, 1992). It is possible that, even though interior leaves are photosynthesizing at low levels, sucrose is exported from exterior leaves in order to assist this function (Vanden Heuvel et al., 2002).

Photosynthetic performance. Whole-plant shading reduced maximum NCER (Table 1; Fig. 3). Maximum NCER (i.e., asymptote of curve) decreased with increased shading level.

When NCER was expressed as a function of total plant dry weight (Table 1; Fig. 3A), maximum NCER did not differ between the 0% and 54% shading treatments. Maximum NCER decreased by 61% between the 0% and 99% shading treatments. When NCER was expressed as a function of leaf area (Table 1; Fig. 3B), the asymptote decreased by 58% between the 0% and 99% shading treatments.

The intercept (i.e., dark respiration rate) did not differ when NCER was expressed as a function of leaf area, but did differ between the 0% and 99% shading treatments when expressed as a function of total plant dry weight (Table 1). The dark respiration rate (i.e., intercept) of severely shaded vines was less than that of the 0% shading treatment (Table 1), possibly due to lower carbohydrate levels in shade leaves (Schultz, 1991), or lower protein concentra-

tions (Percy, 2000). This same trend was also seen when NCER was expressed as a function of leaf area.

Rate of approach of the curves to the asymptote differed, with the 0% and 54% treatments having similar rates of approach, and the 90% and 99% treatments having similar, but faster rates of approach to the asymptote when compared to the 0% and 54% shading treatments (Table 1), suggesting that the severely shaded leaves are likely able to capitalize on the existing light microclimates in the vine interior. Although the 90% and 99% treatments approached the asymptote of the light response curve more quickly than the other treatments, the arguments of Givnish (1988) suggest that, in order for leaves to have acclimated to a given irradiance level, the net carbon exchange rate of the acclimated vines at the low-light levels

Fig. 2. The influence of shading level on organ dry weight, total vine dry weight, and root to shoot ratio of *Vitis vinifera* 'Chardonnay' grapevines as fitted to Equation 1. Level of significance of F-test for regression follows the regression equation in brackets. (A) Leaf: ($Y = 23.5156 - 0.1555 e^{0.0346x}$) ($P = <0.0001$); (B) shoot: ($Y = 21.8509 - 0.1233 e^{0.0361x}$) ($P = <0.0001$); (C) trunk: ($Y = 30.0787 - 8.1 \times 10^{-8} e^{0.1802x}$) ($P = 0.050$); (D) root: ($Y = 28.8758 - 0.4932 e^{0.0298x}$) ($P = <0.0001$); (E) total: ($Y = 102.9000 - 0.1158 e^{0.0528x}$) ($P = <0.0001$); (F) root to shoot ratio: ($Y = 0.4775 - 0.0943 e^{0.0055x}$) ($P = 0.0002$). Least square means of treatments have been plotted (•).

Table 1. Parameter estimates ($\pm$ SE) for nonlinear regressions for light response curves of *Vitis vinifera* L. cv. Chardonnay vines in four shading treatments. $Y = a - be^{-cx}$ where: a = asymptote; b = intercept; and c = rate of approach to asymptote.

Shading treatment (%)	Asymptote	Intercept	Rate of approach
<i>NCER as a function of total plant dry weight ($\mu\text{mol}\cdot\text{g}^{-1}\text{CO}_2$)²</i>			
0%	0.0200 ± 0.00110 a ³	-0.0018 ± 0.00028 a	0.0024 ± 0.00041 a
54%	0.0171 ± 0.00117 a	-0.0010 ± 0.00030 ab	0.0031 ± 0.00043 a
90%	0.0101 ± 0.00110 b	-0.0010 ± 0.00028 ab	0.0046 ± 0.00041 b
99%	0.0077 ± 0.00110 b	-0.0006 ± 0.00028 b	0.0047 ± 0.00041 b
P-value	<0.0001	0.0394	0.0006
<i>NCER as a function of leaf area ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\text{CO}_2$)</i>			
0%	11.45 ± 0.362 a	-1.00 ± 0.154 a	0.002 ± 0.0004 a
54%	9.34 ± 0.387 b	-0.61 ± 0.165 a	0.003 ± 0.0004 a
90%	5.70 ± 0.362 c	-0.58 ± 0.154 a	0.005 ± 0.0004 b
99%	4.85 ± 0.362 c	-0.41 ± 0.154 a	0.005 ± 0.0004 b
P-value	<0.0001	0.0703	0.0002

²NCER = Net carbon exchange rate.

³Means within columns separated by *t* tests. Means followed by the same letter are not statistically different at $P < 0.05$.

must be higher than that of the nonshaded treatments. However, net carbon exchange rate of vines in the 90% shading treatment at the 90% shading level (i.e., $\approx 100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) is lower than those in the 0% and 54% shading treatments, which suggests that severely shaded leaves may not be able to truly acclimate [according to the definition of Givnish (1988)] to the shaded conditions. Increased quantum yield of shade leaves (Syvertsen, 1984) was likely not seen in this experiment due to the use of whole vines as opposed to single leaves in the NCER measurement, which resulted in some intra-leaf shading.

Light compensation point (as determined using Equation 3) was reduced by both moderate and severe shading. When NCER was expressed as a function of total plant dry weight, compensation points for the 0%, 54%, 90%, and 99% shading treatments were 35.9, 18.3, 20.5, and $16.0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively, a reduction of 55% between the 0% and 99% shading treatments. When NCER was expressed as a function of leaf area, compensation points for the same treatments were 41.9, 21.2, 19.4, and $16.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (reduction of 61%), respectively. Palliotti et al. (2000) reported that shade leaves reached their compensation point at $\approx 25 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared to sun leaves at $59 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, with Cartechini and Palliotti (1995) reporting similar values for shade (i.e., 30% PPF) leaves. This experiment suggests that light compensation point of severely shaded (i.e., 1% PPF) grape leaves can be lower than reported for moderately shaded (i.e., 30% PPF) leaves (Cartechini and Palliotti, 1995; Palliotti et al., 2000).

Although a comparative analysis of photosynthetic abilities of vines acclimated to differing but constant irradiance levels reveals useful information, the approach does simplify the factors affecting gas exchange (Givnish, 1988). Natural light regimes in the canopy interior are variable (Dokoozlian and Kliewer, 1995), allowing grape leaves to improve their carbon balance through the use of sunflecks (Poni et al., 1993).

The morphological modifications of interior leaves observed here and by other researchers (Boardman, 1977; Kappel and Flore, 1983; Syvertsen and Smith, 1984) are common responses that serve to maximize carbon fixation while minimizing respiration. The maintenance of leaf size until approximately the 90% shade level results in static light interception with increased shading, although morphological adaptations of the leaves likely result in improved efficiency to photosynthesize in the low light environment, as evidenced from the faster rate of approach of shaded leaves to the asymptote of the light response curve. Shaded leaves also respired at slower rates. Dry-matter partitioning patterns observed in this experiment, particularly the reduction in root to shoot ratio with increased shading, suggest that shaded leaves may reduce partitioning of photoassimilate to permanent vine structures, such as the roots in the current season. The long-term effect of reduced dry-matter partitioning to the root system could result in significant ramifications for the vine, such as a reduced ability to withstand

Fig. 3. The influence of irradiation on net carbon exchange rate (NCER) of four treatments of shaded *Vitis vinifera* 'Chardonnay' grapevines as fitted to Equation 3. Level of significance of F-test for regression follows the regression equation in brackets. (A) Regression of NCER as a function of total plant dry weight on irradiance level: 0% ($Y = 0.0199 - 0.0217e^{-0.00238x}$) ($P < 0.0001$); 54% ($Y = 0.0168 - 0.0183e^{-0.00310x}$) ($P < 0.0001$); 90% ($Y = 0.0100 - 0.0107e^{-0.00389x}$) ($P < 0.0001$); 99% ($Y = 0.0076 - 0.00818e^{-0.00420x}$) ($P < 0.0001$); (B) regression of NCER as a function of leaf area on irradiance level: 0% ($Y = 11.3306 - 12.3851e^{-0.00240x}$) ($P < 0.0001$); 54% ($Y = 9.1899 - 10.0364e^{-0.00325x}$) ($P < 0.0001$); 90% ($Y = 5.6706 - 6.1195e^{-0.00445x}$) ($P < 0.0001$); 99% ($Y = 4.7776 - 5.2413e^{-0.00474x}$) ($P < 0.0001$). SES of parameter estimates are given in Table 1.

freezing temperatures in more northerly temperate regions, and fewer resources available for spring growth (McArtney and Ferree, 1999). This experiment provides new quantifications of the capacity of grapevine leaves to acclimate to severely darkened environments and contribute to overall vine carbon balance.

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