Leaf Color Retention, Dark Respiration, and Growth of Red-leafed Japanese Maples Under High Night Temperatures

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Abstract. Red- and purple-leafed seedlings and clonal material selected for superior color and growth under northern climatic conditions may exhibit progressive color loss and reduced growth rates when exposed to the hot summers and high night temperatures of more southern climates. Studies were conducted to characterize the color loss associated with red-leafed seedlings of *Acer palmatum* Thunb. (Japanese maple), and to determine to what extent night temperatures affect the dark respiration, growth, and anthocyanin expression of *A. palmatum* 'Bloodgood'. The percentage of seedlings within each of five color classes was determined for five dates from spring to early fall. Significant shifts in class distribution occurred on every evaluation date tested. The class changes contributing the most to these shifts varied with age of leaf material and date. Dark respiration rates increased by 0.09 mg CO₂/g leaf dry weight per hour for every 1C rise in temperature, regardless of exposure duration. Dark respiration rates of 0.69 and 1.73 mg CO₂/g per hour were found at 14 and 26C, respectively. The greatest amount of growth occurred during weeks 6 through 8 at a night temperature of 14C. Plant growth during this period increased by an average 51%, compared to that at warmer night temperatures. Ultimately, total plant growth at 14C decreased 7%, 19%, and 32% as night temperatures increased from 18 to 22 to 26C. Leaf redness index values at 14 or 18C were from two to seven times greater than those at warmer night temperatures.

Red- and purple-leafed seedlings and clonal material [e.g., European beech (*Fagus sylvatica* L. 'Cuprea') eastern redbud (*Cercis canadensis* L. 'Forest Pansy'); 'Bloodgood' Japanese

maple; and European filbert (*Corylus avellana* L. 'Rode Zeller')] selected for superior color and growth under northern climatic conditions exhibit progressive color loss and reduced growth rates when exposed to the hot summers of more southern climates—especially those of the southeastern United States (Dirr, 1983; Jeong et al., 1988). Many of these plants maintain dark foliage color and grow well in certain geographic areas of the western United States, even though maximum temperatures are comparable to or greater than those in much of the southern United States. However, local climatic factors and high elevations cause rapid radiational cooling at night, producing night temperatures typical of more northern climates (Richard and Nicholson, 1978; American Society of Heating, Refrigerating and Air-Conditioning Engineers, 1977).

Temperature is the most important external factor influencing dark respiration (Levitt, 1972). Plants exposed to supraoptimal

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night temperatures in many cases may operate at low net photosynthesis : dark respiration ratios ($P_n:R_n$) or reduced energy budgets. Growth respiration normally represents the majority of daily carbon loss (Pearcy et al., 1987). However, maintenance respiration is also environmentally sensitive, and can play an important role in net carbon gain (Mooney and Gulmon, 1979). The correlation between a high respiration rate and reduced crop productivity is often greater than that of photosynthetic rate and yield (Lambers, 1985). High dark respiration rates can be associated with increases in the proportion of assimilates respired for maintenance and higher rates of uncoupled respiration (Beevers, 1970). This condition may limit the successful introduction of many northern species into southern areas of the United States that have high night temperatures. Cooler nights should minimize the loss of carbohydrates associated with maintenance and uncoupled respiration, leaving more for growth, storage, and pigment production (Lambers, 1985).

Red and purple pigmentation in leaves is due to glycosidic flavonoid compounds called anthocyanins (Goodwin, 1976). These water-soluble pigments are found in the vacuole of leaf cells primarily as the anthocyanin cyanidin 3-glycoside. While common in young leaves, permanent anthocyanin pigmentation is a relatively uncommon and highly desirable ornamental characteristic. Anthocyanins usually accumulate when sugars in leaf tissue occur in amounts exceeding that required for immediate growth, and their presence is related to the rate of carbohydrate metabolism (Goodwin, 1976). Cool night temperatures reduce dark respiration rates, favor a higher sugar content in leaves, and increase development and retention of anthocyanins (Levitt, 1972). Through simple hydrolysis of the glycosidic linkage, these sugar derivatives can potentially be used as a source of energy during periods of low carbohydrate reserves. During periods of high night temperatures, these leaves may gradually fade as their anthocyanin pool is depleted.

The objectives of this study were to: a) characterize the color loss during the summer associated with red-leafed Japanese maple seedlings grown in a southern climate, and b) determine to what extent "elevated night temperatures affect the dark respiration, subsequent growth, and anthocyanin expression of clonal material of this species.

Materials and Methods

Field study: Characterization of color loss

This study was conducted from 16 May to 30 Sept. 1985 and 1986 in Raleigh, N.C. (lat. 36°N, long. 79°W). Sixty Japanese maple seedlings exhibiting dark red to red foliage (1:1 by type, Munsell color 2.5R 2/8 to 2/10; Macbeth Color and Photometry Division, 1977) during mid-May were randomly chosen from ≈ 3000 seedlings at a local nursery. Well-rooted liners 20 cm high were potted into 1.7-liter black plastic containers 15.2 cm in diameter, pruned to one dominant leader, and all subterminal pinched to one leaf pair. The growing medium was 1 composted pine bark : 1 Canadian peat : 1 sand (by volume) amended with dolomite at 5.9 kg·m⁻³. The initial pH was 6.3.

Because leaf scorch and foliar damage commonly occur when using intermittent overhead irrigation on containerized Japanese maples, subirrigation was provided as a watering system (Moles, 1979). Containers were placed randomly (38-cm centers) on a sloped, plastic-lined capillary sand bed 7.5 cm in depth (Stanley and Baldwin, 1980). The sand was saturated by periodic hand-irrigation and excess water siphoned-off using a stand pipe lo-

cated at the lower end of the bed. Prior to placement, 3-[2,4-dichloro-5-(1-methylethoxy)phenyl] -5-(1,1-dimethylethyl)-1,3,4-oxadiazol-2(3H)-one (oxadiazon) at 3.9 kg·ha⁻¹ was applied to the capillary sand bed to prevent weed seed germination and rooting of plants into the sand. Plants were fertilized using Peters (W.R. Grace, Fogelsville, Pa.) water-soluble fertilizer supplying N, P, and K at 14.3, 1.4, and 4.2 mmol·liter⁻¹, respectively, by application of 0.8 liter of this solution to each container every 3 weeks. Plants were grown in full sun. Average day (0500 to 2000 HR) and night (2000 to 0500 HR) temperatures and relative daily ranges during this study are shown in Fig. 1. These values were calculated using hourly data and are not the means of the maximum and minimum values recorded during each period.

Seedlings were periodically graded into one of five relative color classes based on the amount of red pigmentation visible, or leaf drop category based on the occurrence of foliar loss. The classes dark red, red, red-mottled-green, green-mottled-red, and green denote decreased redness, respectively. Top and bottom portions (1:1, by height) of each seedling were graded separately. Following new flushes of growth, ratings of the top (the new growth), middle (previously the top), and bottom portion were taken, indicating the color of progressively older foliage. The mean percentage of individuals in each color class and leaf drop category is reported for five dates for each position. These values were evaluated using χ^2 with 5 df. Expected distribution values were obtained by using the appropriate percentages observed previously in each class and category, assuming no further changes in distribution occurred with time.

Phytotron study

Materials, conditions, and growth characteristics. Well-rooted liners of 'Bloodgood' Japanese maple 20 cm high were potted into 0.6-liter black plastic containers, 11.4 cm in diameter. Leaf

Fig. 1. Relationship between the average day (0500 to 2000 HR) and night (2000 to 0500 HR) temperatures for Raleigh, N. C., from May through Sept. 1985 and 1986.

color was black-red to deep red (Munsell color 2.5R 2/2 to 2/4). Foliage color of this cultivar is retained into late summer, longer than most red-leafed forms (Vertrees, 1978). Plants were pruned and pinched as described previously. The growing medium was 2 composted pine bark :1 Canadian peat :1 coarse sand (by volume) amended with dolomite at 5.9 kg·m⁻³. The initial pH was 6.1.

Plants were placed in growth chambers (3.7 × 2.4 m) in the Southeastern Plant Environment Laboratory (phytotron), Raleigh, N.C. Day temperatures of 30 and 26°C were combined factorially with night temperatures of 14, 18, 22, and 26°C. Chamber temperatures were maintained within ± 0.25°C. Four chambers were used and plants were moved between chambers at 0800 and 1700 HR daily to maintain proper day/night temperature regimes. Plants were relocated randomly each week within each chamber to minimize positional effects.

Cool-white fluorescent and incandescent lamps provided a photosynthetic photon flux of ≈640 to 650 μmol·s⁻¹·m⁻² at wavelengths of 400 to 700 nm for 9 hr per day (0800 to 1700 HR) plus 9 to 11 W·m⁻² of photomorphogenic radiation between 700 to 850 nm measured at 33 cm above the surface on which the pots were standing. Plants were exposed to a 3-hr night interruption (2300 to 0200 HR) of 11 to 12 μmol·s⁻¹·m⁻² at wavelengths of 400 to 700 nm with incandescent lamps to simulate a long-day photoperiod. Relative humidity was ≥ 70%, CO₂ concentration 1.3 to 1.8 mmol·m⁻³, and chamber top-to-bottom airflow 0.3 m·s⁻¹. Plants were irrigated three times weekly with a modified Hoagland's solution supplying 7.6, 0.3, and 2.8 mmol·liter⁻¹ of N, P, and K, respectively, and reverse osmosis purified water at least once daily.

Height measurements were taken at the end of 5, 8, and 13 weeks. Projected (one-sided) leaf area, dry weight (mg·cm⁻²), and redness were determined after 13 weeks using the first, second, third, and fifth fully expanded leaf pair produced by the central leader. Leaf area was measured with a LI-3100 (LI-COR, Lincoln, Neb.) area meter. Leaf dry weight was determined after drying at 45°C for 48 hr. Leaf redness index values were determined for the upper surface of each leaf pair using a model D25A-2 Hunterlab Calorimeter (Conrad et al., 1987). A tomato red reference plate was used as a standard ($L = 25.4$, $a_L = 28.2$, $b_L = 12.2$). Data were analyzed from a 2 × 4 factorial (day × night temperature) in a randomized complete block design with two replicates (years) and four plants per treatment per replicate.

Comparative dark respiration measurements. Two closed-system respiration chambers were constructed from 6.4-mm plexiglass. Each chamber measured 13.9 × 13.9 × 50.8 cm for a total volume of 9.8 liters (Fig. 2). Removable tops and bottoms were fitted with 3.2-mm high-grade rubber gaskets, allowing easy plant introduction and chamber closure. Chambers were equipped with an inlet and outlet port to which a modified oilless diaphragm air pump (Optima model; Rolf C. Hagen, United States, Corp., Mansfield, Mass.) was attached. The pump was sealed with clear silicon so as to only draw air from a tygon outlet hose (6.4 mm id.) attached to the chamber. This air was delivered through a tygon tube (3.2 mm id.) T-shaped manifold designed to reintroduce and mix this air within the chamber at the rate of 6 liters·min⁻¹, ±5%.

Plants were sealed into respiration chambers just before the end of the high-intensity light period. Phytotron, and respiration chamber temperatures were allowed to equilibrate for 15 min during the beginning of the dark period, then various bleeder clamps were secured to provide a recirculating closed system.

Fig. 2. Recirculating closed-system respiration chamber used to measure the efflux of carbon dioxide. 1) Oilless diaphragm air pump; 2) air inlet; 3) T-shaped manifold; 4) sampling port and rubber septum; 5) air outlet; 6) bleeder clamp; 7) bored, slitted rubber stopper.

Night temperatures within phytotron and respiration chambers stabilized within 8 to 12 min.

A Fisher model 1200 gas partitioned (helium carrier gas, Porapak Q column at 50°C) and Spectra-Physics SP4270 integrator were used to quantify the efflux of CO₂. Preliminary experiments indicated no difference between 30 and 26°C day temperatures on subsequent dark respiration (data not shown). Two temperatures were tested nightly for plants grown as described previously for ≈ 11 weeks with days at 30°C. Three replicates were achieved by repeating this process on three consecutive nights. Night temperature and plant selection were done on a random basis. Carbon dioxide standards of 343 and 5000 ppm were used to calibrate the partitioned prior to each nightly run. Five air samples were taken from each chamber using a 1.0-cm³ disposable tuberculin needle. Standard deviations of these five samples varied on a mean basis 6.9% over the range of night temperatures and CO₂ concentrations measured. Initial and hourly air samples were taken up to 4 hr after enclosure and the mean CO₂ efflux calculated according to Sesták et al. (1971) for a closed gas exchange system. Cumulative CO₂ totals were then fitted to the following response surface model and the significant components determined (Hicks, 1982): $Z = (B_0 + B_1H + B_{11}H^2 + B_2T + B_{22}T^2 + B_{12}H \cdot T)$, where Z = cumulative flux of CO₂ at the end of a 1- to 4-hr period (mg CO₂/g leaf

dry weight); H = dark exposure period (hr), and T = night temperature (C).

Data were fitted to a reduced model when the terms for one variable, and/or the quadratic terms, and/or the interaction term were not significant. This procedure was repeated until all remaining terms in the model were significant at the 0.05 level (Hicks, 1982). Additionally, when a quadratic term was significant and its linear term was not, both terms were retained. When the interaction term was significant, linear terms of both variables were retained.

Results and Discussion

Field study

Characterization of color loss. Shifts in class distribution occurred on every evaluation date and positional combination tested (Fig. 3). The probability of a greater X^2 was <0.001 for all but one combination (data not shown). The class changes contributing the most to these shifts varied with leaf position and date.

All plants had dark-red or red foliage in the upper crown on 16 May (Fig. 3 top). During the next month, color in the upper crown faded such that 53% of the plants were in the red-mottled green color class by 14 June. Following a flush of growth in late June, the proportion of plants with dark-red or red foliage in the upper crown increased to $\approx 65\%$ by 10 July, indicating that these seedlings retained the ability to produce anthocyanins in new foliage, while concurrently losing the ability to express anthocyanin production and/or retention in older tissue. This phenomenon might be linked to changing source-sink relationships within the canopy during growth. Not all seedlings flushed,

and no plant flushed more than once. One-third of the population experienced substantial leaf drop and no height growth. Night temperatures 2 weeks before 10 July averaged 22C in 1985 and 23C during 1986 (Fig. 1). Day temperatures during this period averaged 26 and 29C during 1985 and 1986, respectively. Seedlings grown in areas where night temperatures remain relatively cool throughout the summer often have recurrent flushes of red foliage (Vertrees, 1978). Fading of new foliage occurred from 10 July to 30 Sept., but 75% of the plants retained enough red coloration to be classified as either red or red-mottled-green.

Fading of foliage intermediate in age was more evident and occurred more rapidly than that found with younger foliage, with 73% green-mottled-red and 15% green by 19 Aug. (Fig. 3 middle). Forty-five percent of the plants lost all red coloration in the middle crown by 30 Sept. Foliage intermediate in age and position also had the lowest percentage (10%) of leaf drop in late summer.

Color loss occurred most rapidly in the lower crown, which contained the oldest leaves (Fig. 3 bottom). As early as 14 June, only 5% of the seedlings had dark red or red foliage in this area. Two-thirds of the plants had totally green foliage in the lower crown by 19 Aug. Leaf drop was also greatest from this area, with 43% of the seedlings affected by 30 Sept.

Superior red and purple phenotypes are commonly selected in early spring with the hope that appreciable fading will not occur before mid- to late summer. Plants having greater esthetic and commercial appeal could be obtained if evaluation were delayed until late summer, when plants with superior color retention—of older foliage, especially—could be chosen. These plants would not fade as quickly, and should retain darker coloration throughout the growing season in areas with high night temperatures.

Phytotron study

Comparative dark respiration measurements. The treatment design dealt with minima of 14C and 1 hr, and maxima of 26C and 4 hr, for night temperature and exposure to darkness, respectively. Time zero occurred at the initial dark sampling. These initial values were used as a baseline for calculating the amount of CO_2 evolved (Fig. 4). The "H.T" term (dark exposure period by night temperature) of the response surface model results in a different "H linear" for each temperature. The quadratic term " T^2 " is associated with a nonlinear response or lack of fit to a linear response due to temperature on the amount of CO_2 evolved. However, dark respiration rates increased by $\approx 0.09 \text{ mg CO}_2/\text{g}$ per hr for every 1C rise in temperature, regardless of exposure duration. Dark respiration rates of 0.69 and 1.73 $\text{mg CO}_2/\text{g}$ per hr occurred at 14 and 26C, respectively. Relative Q_{10} values across this surface ranged from 2.3 to 2.0 over the interpolable ranges of 14 to 24C and 16 to 26C, respectively.

Plants grown under cooler night temperatures of more northern latitudes would not only experience lower respiration rates, but would also exhibit these rates during the summer over a shorter dark period, compared to plants in lower latitudes. To illustrate, the length of the dark period for 22 June was determined as a function of Julian date and latitude over the range of 45° to 25°N (Parton and Logan, 1981; Sellers, 1965). This range represents a north-south movement from mid-Maine to the Florida Keys. Total CO_2 evolution was calculated as a function of night temperature and length (Fig. 5). Absolute differences increased as the length of the dark period increased, accounting for $\approx 20\%$ of the variation in CO_2 evolution when

Fig. 3. Changes in the foliar color of red-leaved Japanese maple seedlings from spring to early fall. Values shown are the mean percentage of individuals in each of five color classes for three spatiotemporal positions; leaf drop indicates the frequency of foliar loss.

Fig. 4. Dark respiration of 'Bloodgood' Japanese maple under various night temperatures (T) and dark exposure periods (H). Response (Z) is cumulative flux CO_2 totals in $\text{mg CO}_2/\text{g}$ leaf dry weight over a 4-hr period: $Z = 8.3773 - 0.5232H - 0.8628T + 0.0220T^2 + 0.0868H \cdot T$, $R^2 = 0.97$.

Fig. 5. Dark respiration of 'Bloodgood' Japanese maple under various night temperatures and dark periods determined for lat. 45°N to 25°N on 22 June. Response Z, $\text{mg CO}_2/\text{g}$ leaf dry weight, was calculated using the equation given in the legend of Fig. 4.

calculated for 25° and 45°N and equal temperatures. Additionally, the total amount of CO_2 evolved at 26°C was 2.4 times greater than at 14°C when calculated for equal latitudes.

Effect of day and night temperatures on vertical growth. Growth was similar for plants grown either in 30 or 26C days (data not shown). Both day temperatures are greater than the average day temperatures expected in Raleigh, N.C. during a typical growing season (Fig. 1). However, vertical growth of this red-leaved cultivar during the first 5 weeks generally decreased as night temperatures increased (Fig. 6). Growth during weeks 6 through 8 was $\approx 50\%$ greater with 14°C nights than with warmer nights. Growth during weeks 9 through 13 was similar for nights at 14, 18, or 22°C , but decreased at higher temperatures. Plants exposed to nights of 22 and 26°C increased in height 25.3 and 16.5 cm, respectively, during weeks 9 through 13. Nights of 18, 22, and 26°C decreased total vertical plant growth 7%, 19%, and 32%, respectively, compared to 14°C .

Effect of day and night temperatures on leaf size. Day/night temperatures did not affect leaf dry weight (data not shown). There were no differences in individual leaf area between 30 or 26°C days (data not shown). Leaf area was affected by night temperature, with this effect varying according to leaf age (Fig.

Fig. 6. Vertical growth of 'Bloodgood' Japanese maple under various night temperatures. Weeks denoted are inclusive. Values are means and SE.

Fig. 7. Mean area (one-sided) of 'Bloodgood' Japanese maple leaves grown under various night temperatures. Values are means and SE.

7). The first and second leaf pairs decreased linearly in size with increasing night temperature, and were 26% smaller with 26°C than with 14°C nights. As plant growth continued (i.e., pair 3), a shift towards a warmer optimum night temperature occurred. Nights of either 14 or 26°C produced smaller leaves than intermediate temperatures. The largest leaves for pairs 3 and 5 were produced by plants grown in 18°C nights. Mean leaf size decreased with each new pair produced.

Effect of day and night temperatures on leaf color retention.

Leaf redness was similar after 13 weeks for plants grown in 30 or 26°C days (data not shown). However, color retention was best for those plants exposed to 14 to 18°C nights (Fig. 8). Leaf redness index values of these plants were from 2 to 8 times greater than those grown at warmer night temperatures. Leaf color index values were generally lower for older leaves. Greatest color loss occurred in nights at 26°C . High night temperatures increased dark respiration (Fig. 4), perhaps decreasing the carbon pool available for growth and anthocyanin production and/or retention.

Perry (1962), using six geographic sources of red maple (*A. rubrum* L.) seedlings, found that a Canadian source grew best in nights of 14°C , Vermont and Minnesota sources at 17°C , and a North Carolina and Florida source best at 20°C . Anthocyanin production was noted visually for plants from northern provenances grown with 7 and 10°C nights but not at higher temperatures. Optimum day/night temperatures for growth were different for each source and corresponded well with the day/night temperatures where the collections were made. Mooney et al. (1964) found that, for various tree species in the White Mountains, California, the higher their altitude of origin the higher their

Fig. 8. Hunter a:b ratio or leaf redness index values of 'Bloodgood' Japanese maple leaves exposed to various night temperatures. An increase in this ratio indicates increased redness. Values are means and s.e.

rate of dark respiration at 20C. The ratio of $P_N:R_d$ decreased with altitude, primarily as the result of increased dark respiration. They proposed that the downward elevational range of a species could be restricted by an unfavorable carbohydrate balance due to relatively high night temperatures at lower elevations.

When exposed to the same night temperatures, dark respiration rates for various plant species are greater for those from cooler regions than those from warmer regions (Larcher, 1961). Increased dark respiration could be a physiological adaptation allowing adequate respiration for synthetic and maintenance events under unfavorably cool conditions. However, this mechanism might result in increased respiratory sensitivity in many northern species upon exposure to supraoptimal night temperatures. In many cases, increased respiratory sensitivity may predispose these species to other environmental stresses. Historically, plant cold tolerance has been the major criterion for evaluating the adaptive range of woody ornamental species. Many commercial cultivars of Japanese maple and other species are selected for superior growth, color, flower, and fruiting characteristics in the relatively cool climates of Oregon, New England, Netherlands, New Zealand, and England—climates with relatively cool night temperatures. Expression of these traits over a larger geographic area would occur if selection took place within peak stress environments characteristic of both day and night maximum and minimum temperatures.

Differences between day/night temperatures generally become larger and are attained more rapidly as the amount of water vapor in the air decreases. On average, less water vapor is present at elevated locations than near sea level. Consequently, seasonal and daily ranges in temperatures increase with altitude. The greatest daily temperature fluctuations occur in the United States over the dry interior western plateaus and mountainous regions of high elevations (Sellers, 1965). Latitudinal differences in locations are commonly related to altitude and temperature by a conversion factor of 305 m of elevation (American Society of Heating, Refrigerating and Air-Conditioning Engineers, 1977) or 2.8C (Mergen et al., 1974), respectively, for every 3° difference in latitude. These relationships might explain why many northern species tend to be introduced more easily into southern areas of greater elevation having cooler night temperatures.

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