Leaf morphological and physiological adjustments to the spectrally selective shade imposed by anthocyanins in *Prunus cerasifera*

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Summary *Prunus domestica* L. has green leaves, whereas *Prunus cerasifera* Ehrh. var. atropurpurea has red leaves due to the presence of mesophyll anthocyanins. We compared morphological and photosynthetic characteristics of leaves of these species, which were sampled from shoots grafted in pairs on *P. domestica* rootstocks, each pair comprising one shoot of each species. Two hypotheses were tested: (1) anthocyanins protect red leaves against photoinhibition; and (2) red leaves display shade characteristics because of light attenuation by anthocyanins. Parameters were measured seasonally, during a period of increasing water stress, which caused a similar drop in shoot water potential in each species. As judged by predawn measurements of maximum PSII yield, chronic photoinhibition did not develop in either species and, despite the anthocyanins, the red leaves of *P. cerasifera* displayed lower light-adapted PSII yields and higher non-photochemical quenching than the green leaves of *P. domestica*. Thus, it appears that, in this system, anthocyanins afford little protection.

As predicted by the shade acclimation hypothesis, red leaves were thinner and had a lower stomatal frequency, area-based CO2 assimilation rate, apparent carboxylation efficiency and chlorophyll a:b ratio than green leaves. However, red leaves were similar to green leaves in conductivity to water vapor diffusion, dry-mass-based chlorophyll concentrations and carotenoid:chlorophyll ratios. The data for red leaves indicate adaptations to a green-depleted, red-enriched shade, rather than a neutral or canopy-like shade. Thus, green light attenuation by anthocyanins may impose a limitation on leaf thickness. Moreover, the selective depletion of light at wavelengths that are preferentially absorbed by PSII and chlorophyll b may lead to adjustments in chlorophyll pigment ratios to compensate for the uneven spectral distribution of internal light. The apparent photosynthetic cost associated with lost photons and reduced leaf thickness, and the absence of a photoprotective advantage, suggest that there are other, yet to be identified, benefits for permanently anthocyanic leaves of *P. cerasifera*.

Keywords: chlorophyll fluorescence, CO2 assimilation, internal light environment, non-photochemical quenching, photoprotection, pigments, PSII yield, red leaves.

Introduction

Leaves in some plants appear red because of the accumulation of anthocyanins that mask the green chlorophyll reflectance. Although in some species the anthocyanic character is permanent, in most cases reddening is transient. Transient redness may be developmentally or environmentally determined. In the former case, redness appears in young or senescing leaves, or both, of some species. Environmentally determined redness occurs when anthocyanins accumulate in mature leaves as a response to wounding (Stone et al. 2001), pathogen attack (Hipkind et al. 1996), nutrient deficiencies (Hodges and Nozzolillo 1996, Kumar and Sharma 1999), UV-B radiation (Lindoo and Caldwell 1978, Mendez et al. 1999) or high light in combination with low temperatures (Krol et al. 1995, Close and Beadle 2003, Pietrini et al. 2002).

Because anthocyanins absorb light, they should restrict photosynthesis. Although this appears to be disadvantageous to a healthy leaf under optimal conditions, it may be advantageous under stressful conditions during specific phases of leaf development because the abiotic stresses that induce the synthesis of anthocyanins predispose leaves to photoinhibition of photosynthesis (Long and Humphries 1994), it is reasonable to assume that anthocyanins have a photoprotective function, either as passive light filters (Krol et al. 1995, Manetas et al. 2002, Pietrini et al. 2002) or as antioxidants (Gould et al. 2002a, Steyn et al. 2002). Additional hypotheses on the role of anthocyanins include an osmotic effect and a protective function against UV-B radiation or herbivory (for recent reviews on possible functions of leaf anthocyanins see Chalker-Scott 1999, Gould et al. 2002b, Steyn et al. 2002, Close and Beadle 2003 and Manetas 2006).

Regardless of function, anthocyanin accumulation may impose a double cost on the leaf: the cost of carbon skeletons diverted to pigment biosynthesis; and the photosynthetic cost resulting from competition between anthocyanins and chlorophylls for light capture. In addition, the shade imposed on mesophyll chloroplasts by anthocyanins could alter their function and composition. For example, it has been reported that red leaves have lower maximum CO2 assimilation rates (Gould et al. 2002c), lower chl a:b ratios and a smaller pool of...
xanthophyll cycle components than green leaves (Manetas et al. 2003). These characteristics form part of a large array of traits that constitute the shade acclimation syndrome (Anderson 1986, Lambers et al. 1998). However, the magnitude of imposed shade in anthocyanic leaves cannot be easily defined.

Based on an indirect method, Pietrini and Massacci (1998) calculated that anthocyanins in red leaves reduce the photosynthetically active radiation reaching the chloroplasts by as much as 40%. Gould et al. (2002c), who studied chlorophyll fluorescence profiles in red leaf sections, concluded that it is mainly green light that is absorbed by anthocyanins, rendering it available for photosynthesis only in the uppermost cell layers. Thus, there are considerable quantitative and qualitative differences between natural canopy shade and light attenuation by anthocyanic leaves. Understory leaves are subjected to photon fluence rates at least an order of magnitude lower than those to which sun leaves are exposed, with only brief exposure to direct sunlight due to sunflecks. Moreover, natural shade is green and far-red enriched, whereas the mesophyll of a red leaf is exposed to light severely depleted in the green portion of the visible spectrum (Karabourniotis et al. 1999, Gould et al. 2002c).

With this background, we undertook a comparative study of Prunus domestica, possessing green leaves, and Prunus cerasifera, possessing red leaves. These species form compatible grafts producing chimeric trees bearing green- and red-leaved shoots on the same rootstock. We measured an array of morphological and photosynthetic parameters, during the Mediterranean summer, to investigate whether the presence of anthocyanins: (1) reduces the photo-inhibitory risk during the seasonal increase in water stress; and (2) is related to leaf structural and photosynthetic traits.

Materials and methods

Plant material and experimental design

Three specimens of Prunus cerasifera Ehrh. (var. atropurpurea) grafted on Prunus domestica L. rootstock (both Rosaceae) growing as ornamentals at the Patras University campus were used. Grafting was performed at the base of young P. domestica rootstocks about 10 years before the present study, producing 2-4-m-tall two-stemmed trees, one stem bearing green leaves (P. domestica), the other stem bearing red (P. cerasifera) leaves. Both stems are winter deciduous. Developing leaves of atropurpurea variety are bright red and mature leaves are dark red, with redness being apparent on both sides of the leaf. All measurements were made on mature leaves. Free-hand leaf cross sections viewed with the aid of a microscope revealed that anthocyanins were located in the mesophyll cells. Sampling was performed at 1-month intervals. During this period the plants received only natural precipitation. The canopies of both stems were relatively open and not mutually shaded. All measurements were made on clear days. Gas exchange and related parameters, as well as chlorophyll fluorescence measurements in the light-adapted state, were performed at various times during the day, on intact leaves in the field, in natural light. Dark-adapted chlorophyll fluorescence parameters were obtained on intact leaves at predawn. For destructive measurements (shoot water potential, leaf thickness, leaf mass per area and leaf pigment analyses), samples were collected at midday, placed in sealed plastic bags and taken to the laboratory for immediate analysis.

Measurements

To determine shoot water potential ($\Psi$), shoots were re-cut under water with a razor blade and $\Psi$ measured within 2–3 min with a SKPM 1400 (Skye Instruments, Ltd., Llandrindod Wells, U.K.) pressure chamber.

The thickness of veinless leaf areas was measured with a friction-stop caliper (Mitutoyo, Japan). Leaf discs of known areas were subsequently cut, dried in an oven at 80 °C and weighed to determine dry mass. Leaf mass per area (LMA) was then calculated.

Stomatal frequencies were determined by viewing free-hand paradermal sections with the aid of an Axioplan microscope (Zeiss, Oberkochen, Germany).

Leaf pigments were extracted by grinding leaf tissue with a mortar and pestle with pure methanol, a small amount of washed sand and about 0.05 g of CaCO3. The extract was centrifuged and the chlorophylls and carotenoids in the supernatant determined spectrophotometrically based on the equations of Lichtenthaler and Wellburn (1983). Anthocyanins were assessed by their peak absorbance ($\lambda = 529$ nm) after acidification of the medium and correction for pheophytin absorbance according to Lindoo and Caldwell (1978).

Leaf gas exchange was measured with a portable photosynthesis system (LC2000, Analytical Development Company, Hoddeston, U.K.) functioning in open flow mode. Attached leaves of various inclinations (i.e., different incident PPFs) were measured in the field between 0900 and 1500 h, permitting the construction of net photosynthesis ($A_d$), stomatal conductance ($g_s$) and internal CO2 concentration ($C_i$) versus incident PPF curves. Apparent carboxylation efficiency was calculated as $A_d/C_i$ based on measurements made at saturating PPF (> 1400 mmol m$^{-2}$ s$^{-1}$).

Chlorophyll fluorescence in the field was measured in leaves similar to those sampled for gas exchange with a portable pulse-amplitude-modulated fluorometer (MINI-PAM, Walz, Effeltrich, Germany) connected to a leaf clip (Leaf-Clip Holder 2030-B). The PSII photochemical efficiency in the light-adapted state was calculated according to Genty et al. (1989) as:

$$\Delta F/F_m = (F_m' - F)/F_m'$$

where $F$ is the initial fluorescence yield of a light-adapted sample before the application of a saturating light pulse, and $F_m'$ is the maximum fluorescence yield of a light-adapted sample during the application of a saturating light pulse. Maximum (dark-adapted) PSII photochemical efficiency ($F_v/F_m = (F_m - F_v)/F_m$) was measured at predawn, where $F_v$ is the initial fluorescence yield of a dark-adapted sample before the application of a saturating light pulse, and $F_m$ is the maximum fluorescence yield of a dark-adapted sample during the appli-
cation of a saturating light pulse. Non-photochemical quenching (NPQ) was calculated from predawn $F_{m}$ and light-adapted $F_{m}^{'}$ according to the formula (Maxwell and Johnson 2000):

$$\text{NPQ} = (F_{m} - F_{m}^{'} ) / F_{m}^{'}$$

During the photosynthetic measurements (both gas analysis and fluorometry), leaf temperatures were monitored by thermocouples.

Leaf optical properties were measured with an Optronic (Orlando, FL) spectroradiometer equipped with a Taylor-type integrating sphere and a stabilized quartz halogen source. For reflectance ($R$), the leaves covered the exit port of the sphere. For transmittance ($T$), the leaves covered the entrance port. Absorptance ($A$) was calculated as $A = 1 - R - T$. A Spectralon standard (reflectance > 0.97) was used for calibration.

**Statistics**

Significance of differences in the measured parameters between green and red leaves was tested by a two-tailed Mann-Whitney test. For best fit lines, the PSII yield versus PPF and the $C_{i}$ versus PPF curves were treated as double exponential decays, the $A_{n}$ versus PPF and the $g_{s}$ versus PPF as hyperbolas and the NPQ versus PPF as straight lines. An $F$-test assessing the null hypothesis for one curve fitting both green and red datasets was used. All statistical analyses were performed with SPSS 9.0 statistical software (SPSS Inc., Chicago, IL).

**Results**

The green leaves of *P. domestica* and the red leaves of *P. cerasifera* had characteristic optical properties. The characteristic green peak in reflectance and transmittance and the corresponding valley in absorptance of green leaves were absent in red leaves. The spectral profiles in the red band were similar in both leaf types (data not shown).

Red leaves were thinner and had lower LMA than green leaves (Table 1). Stomata were observed only on lower leaf surfaces, and their frequency was lower in red leaves than in green leaves (Table 1). Compared with green leaves, red leaves had reduced area-based chlorophyll and total carotenoid concentrations (Table 2). However, there were no differences between leaf types when pigment concentrations were expressed on a dry mass basis (Table 2). The chlorophyll $a:b$ ratio was considerably lower in red leaves than in green leaves, whereas the carotenoid:chlorophyll ratio was similar in red and green leaves. As expected, anthocyanin concentrations were much higher in red leaves than in green leaves (1.74 versus 0.06 absorbance units, normalized for 1 cm$^{2}$ of extract from 1 cm$^{2}$ of leaf surface). Absorbance spectra of extracted anthocyanins displayed a peak in the green band (529 nm) and negligible absorbance in the red band of the spectrum (above about 620 nm, results not shown).

Table 3 shows that, although shoot water potential declined from early to late summer, the values for both red and green stems were similar, except in early August, when red shoots had a lower $\Psi_{w}$.

<table>
<thead>
<tr>
<th>Leaf thickness (mm)</th>
<th>LMA (g dm$^{-2}$)</th>
<th>Stomatal frequency (no. mm$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Green</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.245 ± 0.022</td>
<td>0.921 ± 0.128</td>
<td>141 ± 19</td>
</tr>
<tr>
<td><strong>Red</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.191 ± 0.027</td>
<td>0.685 ± 0.064</td>
<td>95 ± 14</td>
</tr>
</tbody>
</table>

Maximum (predawn) PSII photochemical efficiency was always within the range for healthy leaves (about 0.8), indicating that water stress did not cause chronic photoinhibition in either red or green leaves. Compared with green leaves, slightly, but significantly, lower values (2–3%) of $F_{v} / F_{m}$ were observed in red leaves towards the end of the dry summer (Table 4).

Measurements of the effective PSII yield made during the day on various dates and plotted against incident PPF are shown in Figures 1A–D. Datasets of both leaf types followed the same curve in early June and early July. Later on, however, the effective PSII yield of red leaves progressively declined. We expected higher $\Delta F/F_{m}^{'}$ values in red leaves than in green leaves because part of the incident light is lost to anthocyanin absorption. Non-photochemical quenching was similar for green and red leaves in early June (Figures 1E–H). With progressive water stress, NPQ increased gradually in both leaf types. The increase, however, was more pronounced in red leaves and the best fit lines for green and red leaves departed considerably in late summer.

Net photosynthesis ($A_{n}$) was higher in green leaves than in red leaves at all PPFs (Figures 2A–D). Yet, stomatal conductance was slightly higher in green leaves only in early August (Figures 2E–H), probably because of the higher $\Psi_{w}$ of green-leaved shoots observed on this date, although transpiration rates were similar to those of red leaves (data not shown). Accordingly, the observed differences in $A_{n}$ were not due to stomatal limitations. As a result, internal CO$_{2}$ concentrations ($C_{i}$) were always higher in red leaves than in green leaves (Figures 2I–L). The combination of lower $A_{n}$ and higher $C_{i}$ in red leaves resulted in a large reduction in apparent carboxylation efficiency (Table 5). When $A_{n}$ was expressed on a dry mass basis, the differences between green and red leaves were smaller (Table 5). No temperature differences between the leaf types were found during the experiment.

**Discussion**

**Photoinhibitory risk and photoprotection**

Both green and red shoots experienced progressive water stress during the study, and the magnitude of stress, based on midday shoot water potentials, was similar (Table 3). In addi-
NPQ was higher at the end of the summer in red leaves than in our test system, however, PSII effective yield was lower and stress by accumulating anthocyanin (Pietrini et al. 2002). In leaf. This was found in genotypes of corn responding to cold leaf will maintain a higher PSII yield and lower NPQ for a evaluated by anthocyanins and not used photosynthetically, a red leaf will maintain a higher PSII yield and lower NPQ for a evaluated by anthocyanins and not used photosynthetically, a red experiment (Woodall and Stewart 1998, Dodd et al. 1998, risk of photoinhibition was obtained in field and greenhouse exclusion). However, no evidence that anthocyanins reduce the positive correlation between anthocyanins and high light tolerance (but see Burger and Edwards (1996) for a different conclusion). However, no evidence that anthocyanins reduce the risk of photoinhibition was obtained in field and greenhouse experiments (Woodall and Stewart 1998, Dodd et al. 1998, Lee et al. 2003, Karageorgou and Manetas 2006).

We predicted that, because part of the incident PPF is attenuated by anthocyanins and not used photosynthetically, a red leaf will maintain a higher PSII yield and lower NPQ for a given incident photon fluence rate of white light than a green leaf. This was found in genotypes of corn responding to cold stress by accumulating anthocyanin (Pietrini et al. 2002). In our test system, however, PSII effective yield was lower and NPQ was higher at the end of the summer in red leaves than in green leaves, whereas similar values were obtained earlier in the season for both leaf types (Figure 1). We conclude, therefore, that red leaves of P. cerasifera, despite their anthocyanic screen, require a higher photoprotective potential than those of the green-leaved P. domestica.

Properties of red leaves are partly compatible with the classical shade acclimation syndrome

Some of our results indicated shade adaptation in red leaves (see reviews by Anderson 1986, Lambers et al. 1998 and Lichtenthaler et al. 2000). For example, red leaves of P. cerasifera were thinner and had a lower LMA, stomatal frequency, chl a:b ratio and area-based net photosynthetic rate, and a considerably reduced apparent carboxylation efficiency compared with green leaves (Tables 1, 2 and 5 and Figure 2). It is generally accepted that a thick leaf is less well adapted to shade because the attenuation of light as it passes through a thick leaf may result in the irradiance impinging on some mesophyll cells falling below the light compensation point. The need to increase the probability of light capture in shade leaves results in an increased ratio of light harvesting antennae per reaction center, and, in turn, lower chl a:b ratios. The redistribution of tasks between light capture and electron flow leads to low enzymatic activities in the reducing pentose phosphate cycle, with the result that shade-adapted leaves display low area-based CO2 assimilation rates and low apparent carboxylation efficiencies.

Although these components of the shade acclimation syndrome were found in red leaves, others were absent. For exam-

Table 2. Photosynthetic pigments expressed per leaf area or leaf dry mass and their ratios in green and red leaves. Data are means ± SD of eight independent measurements, with three leaves per measurement. Abbreviation: Chl = chlorophyll. Within a column, different letters indicate significant differences between green and red leaves (P < 0.05). Because no differences were observed between sampling dates, results from all dates were pooled.

<table>
<thead>
<tr>
<th></th>
<th>Green leaves</th>
<th>Red leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chl a+b (µg cm⁻²)</td>
<td>Chl a+b (mg g⁻¹)</td>
</tr>
<tr>
<td>Green</td>
<td>43.62 ± 4.23 a</td>
<td>4.736 ± 0.440 a</td>
</tr>
<tr>
<td>Red</td>
<td>31.58 ± 2.47 b</td>
<td>4.610 ± 0.288 a</td>
</tr>
</tbody>
</table>

Table 3. Midday water potentials of green- and red-leaved shoots on the indicated dates. Data are means ± SD of 4–5 shoots. Within a row, different letters indicate significant differences (P < 0.05).

<table>
<thead>
<tr>
<th>Date</th>
<th>Predawn Fv/Fm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green leaves</td>
<td>Red leaves</td>
</tr>
<tr>
<td>June 5</td>
<td>0.816 ± 0.007 a</td>
</tr>
<tr>
<td>July 1</td>
<td>0.834 ± 0.008 a</td>
</tr>
<tr>
<td>August 1</td>
<td>0.818 ± 0.016 a</td>
</tr>
<tr>
<td>September 2</td>
<td>0.819 ± 0.019 a</td>
</tr>
</tbody>
</table>
LEAF ADJUSTMENTS TO A PERMANENT ANTHOCYANIC SHADE

Figure 1. The PSII effective yield ($\Delta F / F_{m}'$; A–D) and non-photochemical quenching (NPQ; E–H) of green (○) and red (●) attached leaves plotted against incident photosynthetic photon flux (PPF). Measurements were performed between 0800 and 1200 h on leaves of various inclinations and exposures.
ple, shade leaves usually have similar area-based, but higher dry-mass-based, total chlorophyll concentrations compared with sun leaves, whereas the red leaves we studied had a total chlorophyll concentration that was about 25% lower on a leaf area basis, but similar on a dry mass basis, to that of green leaves (Table 2). Because shade leaves require little photo-
LEAF ADJUSTMENTS TO A PERMANENT ANTHERCYANIC SHADE

Table 5. Net photosynthetic rates expressed per unit leaf dry mass (A_a) and apparent carboxylation efficiency (A/C_i) for measurements made at a saturating photosynthetic photon flux (PPF > 1400 µmol m⁻² s⁻¹) in green and red leaves. Data are means ± SD of 10–20 leaves. For A_a, different letters within a row indicate significant differences between green and red leaves (P < 0.05). For A/C_i, all differences are significant (P < 0.0013).

<table>
<thead>
<tr>
<th>Date</th>
<th>A_a (µmol g⁻¹ s⁻¹)</th>
<th>A/C_i (mol m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Green leaves</td>
<td>Red leaves</td>
</tr>
<tr>
<td></td>
<td>A_a</td>
<td>A/C_i</td>
</tr>
<tr>
<td>June 5</td>
<td>0.166 ± 0.039 a</td>
<td>0.128 ± 0.033 b</td>
</tr>
<tr>
<td>July 1</td>
<td>0.113 ± 0.020 a</td>
<td>0.087 ± 0.029 b</td>
</tr>
<tr>
<td>August 1</td>
<td>0.171 ± 0.060 a</td>
<td>0.132 ± 0.062 a</td>
</tr>
<tr>
<td>September 2</td>
<td>0.095 ± 0.030 a</td>
<td>0.093 ± 0.024 a</td>
</tr>
</tbody>
</table>

Effects of red-enriched, green-depleted shade

To explain the observed differences between the effects of anthocyanin pigmentation and those attributed to the shade acclimation syndrome, we considered the kind of shade imposed on the mesophyll of an anthocyanic leaf. Red anthocyanins absorb mainly in the green and less in the blue and yellow parts of the spectrum, and they are transparent in the red and near infrared region; i.e., anthocyanins essentially eliminate the green window of chlorophyll absorption. Anthocyanins thus appear to provide only limited protection against photohinition, whereas an effective sunscreen would be expected to match the absorption spectrum of the target photodynamic chlorophyll molecules (Manetas 2006). Green light, with a lower probability of absorption by chlorophyll, penetrates deeper into the leaf and drives photosynthesis at a distance from the exposed surface, whereas red light is absorbed in the more superficial layers, exhibiting a steep gradient across the leaf (Gould et al. 2002c).

Nishio (2000), seeking an adaptive significance for the green color of chlorophyll, argued that the green chlorophyll window allows the leaf to acquire a mechanically acceptable thickness, with successively deeper layers effectively using different spectral bands for photosynthesis. We further argue that green-light-absorbing anthocyanins impose a ceiling on leaf thickness, making the development of additional layers unproductive. This produces not a “shade leaf,” but a thinner leaf, the missing layers being that part of a green leaf possessing more “shade” characteristics, i.e., its lower part. Gradients in shade acclimation characteristics have been reported in successive paradermal leaf slices (Terashima and Inoue 1984). This interpretation may explain the absence of differences between green and red leaves in dry-mass-based chl_{sb} concentrations and carotenoid:chl_{sb} ratios, and the lower dry-mass-based CO₂ assimilation rates. However, the presence of green and yellow absorbing anthocyanins may disturb the relative proportion of photons available for use by PSII and PSI. Green and yellow light is better absorbed by PSI, whereas red and dark-red light is better absorbed by PSI (Melis et al. 1985). There are reports that growth of plants in red-enriched and green- and yellow-depleted light results in a changed photosystem stoichiometry by increasing the PSII:PSI ratio (Chow et al. 1990). This adjustment is believed to be an adaptation to light quality to compensate for an uneven absorption of light by PSI and PSII. As a result, the chl a:b ratio is decreased (Chow et al. 1990), as was the case in the anthocyanic leaves we studied.

Our interpretation of a light-quality-dependent adjustment of morphology and photosynthesis in red leaves is also corroborated by the work of Brown et al. (1995) and Yu and Ong (2003), who found that acyanic (i.e., green-leaved) plants grown in red light displayed lower CO₂ assimilation rates, electron transport rates and leaf mass per area than plants grown in white light, whereas stomatal conductance and dry mass-based chlorophyll concentrations were unaffected by the light quality.

In conclusion, field evidence from predawn and daytime chlorophyll fluorescence parameters did not allow confirmation of a photoprotective advantage of anthocyanic leaf pigmentation, even after prolonged water stress. Red leaves developed a higher intrinsic capacity for non-photothermal quenching, despite their anthocyanic screen. However, we cannot exclude a photoprotective function of anthocyanins in other test systems or under different conditions. The assumed shade acclimation of red leaves was supported only partly by the comparative data collected from an array of characteristics linked to the shade syndrome. The results were more compatible with mesophyll adjustments to an altered spectral distribution of internal light characterized by a relative lack of green photons.

References


