Bronzing of Pecan Foliage

Bruce W. Wood, Charles C. Reilly, Ted Cottrell, and W. Louis Tedders
U.S. Department of Agriculture, Agricultural Research Service, Southeastern Fruit and Tree Nut Research Laboratory, Byron, GA 31008

Ida Yates
U.S. Department of Agriculture, Agricultural Research Service, Russell Agricultural Research Center, Athens, GA 30613

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ABSTRACT. The influence of pecan [Carya illinoinensis (Wangen.) K. Koch] leaflet bronzing, a discoloration of the lower (abaxial) leaf surface, on foliar physiology and nut-meat yield is unknown. Field investigations indicate that bronzing can adversely affect foliage by reducing net photoassimilation (A), stomatal conductance (gs), and transpiration (E) while also altering stomatal aperture and cellular structure, and increasing temperature. Kernel weight and fill percentage are also reduced. Research indicated that foliar A declined in proportion to degree of bronze coloration, with negative A exhibited by heavily bronzed foliage. A by bronzed foliage did not increase as light levels exceeded 250 μmol·m−2·s−1. Within the same compound leaf, nonbronzed leaflets adjacent to bronzed leaflets exhibited greater than normal A. Bronzed leaflets also exhibited lower gs to water vapor, less transpirational H2O loss, and higher afternoon leaf temperature. Light micrographs of bronzed foliage indicated abnormal epidermal and spongy mesophyll cells. Weight and percentage of kernel comprising the nut declined on shoots supporting foliage bronzing in July to August, but was unaffected when bronzing occurred in September to October. Bronzing of pecan foliage can therefore be of both physiological and economic significance.

A poorly understood foliar abnormality of pecan (Carya illinoinensis) is a bronze-like discoloration of the lower (abaxial) leaf surface; termed bronzing. Bronzing occurs occasionally between midsummer and leaf fall and ranges from a slight bronze tint to a deep bronze color. Its occurrence is sporadic, varying with crop season, cultivar, orchard, and geographic region, and is therefore difficult to study.

The cause of bronzing in pecan is unknown, but appears to be associated with unusually dry, hot summers. It is therefore often attributed to sunburn or high temperature stress. Mineral nutrient imbalances and damage by pesticides have also been blamed, yet objective supporting data are lacking. Use of dodine (n-dodecyiguanidine acetate), a pecan fungicide, has in certain cases, been associated with bronzing and it was therefore thought that bronzing was due to phytotoxicity of dodine. Bronzing also occurs in other crops and has been attributed to several factors. For example, a mite-induced bronze-like browning of adaxial leaf surfaces occurs in citrus (Citrus sinensis L.) (McCoy, 1976; McCoy and Albrigo, 1975; Yang et al. 1994) and apple [Malus sylvestris (L.) Mill. var. domestica (Borkh.) Mansf.] (Spieser et al., 1998); there is arsenic induced bronzing in rice (Oryza sativa L.) (Tsutsumi 1980), induction by zinc sulfate sprays in tung (Aleurites fordii) (Mowry and Camp, 1934); water-stress induction on banana fruit (Musa paradisiaca L.) (Daniells et al., 1987) and bean foliage (Phaseolus vulgaris L.) (Schwartz et al., 1983); and by air pollutants on beans (Hart and Saettler, 1982; Hucl et al., 1982).

The alternate-bearing nature of pecan is regarded as a major horticultural problem (Woodroof et al., 1928) that is linked closely to carbohydrate reserves of shoots (Smith et al., 1986) and roots (Wood, 1989). Factors influencing these reserves can therefore potentially reduce nut yields (Worley 1979a, 1979b). Thus, the influence of bronzing on pecan tree physiology and nut yield may be significant but as of yet is unknown. Therefore, the following investigation was conducted to study the influence of bronzing on net photoassimilation (A), water vapor exchange characteristics [stomatal conductance (gs) and transpiration (E)], and cellular integrity of pecan foliage, and also on kernel quality of nuts.

Materials and Methods

‘Desirable’ trees in certain central Georgia pecan orchards exhibited bronzing = 1 July 1998. This study evaluated foliage from =15- to 20-year-old ‘Desirable’ trees from two such orchards under commercial management. Trees were irrigated, fertilized, and managed for pecan scab disease [Cladosporium caryigenum (Ell. et Lang) Gottwald] [using SuperTin (fentin hydroxide) and Orbit (propiconazole)] according to standard extension service recommendations (Crocketer et al., 1996; Ellis et al., 1994). One orchard did not receive insecticide sprays during the growing season whereas the other received a single Lorsban [O, O-diethyl-0-(3,5,6-trichloro-2-pyridyl) phosphorothioate] spray.

PHOTOSYNTHETIC ASSIMILATION RATE (A). Leaves exhibiting different degrees of bronzing were measured for foliar gas exchange using a LI-6400 (LI-COR, Lincoln, Nebr.) open-system portable photosynthesis apparatus (Wood, 1997). Measurements were made at a photosynthetic photon flux of 1,500 μmol·m−2·s−1, at =400 ppm CO2, and between 1000 and 1200 HR on attached foliage from three trees receiving =50 L water per day via drip irrigation. Measurements were made on leaflets from the four basal compound leaves of randomly selected terminals from the southern exposed lower canopy of three trees. Levels of bronzing exhibited by samples ranged from none to heavy. Measurements were made 21 July and 15 Sept. from =30 leaflets differing in degree of bronzing from heavy to none. After measuring A, leaflets were removed, stored in a cool thermal insulated container and then color quantified by determining tristimulus color space coordinates.

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nates, as described below within 2 h of sampling. Photosynthetic assimilation rate (A) was regressed against color characteristics (h°, C, and L°) to identify relationships.

Leaf bronzing was quantified by measuring tristimulus color space coordinates using a Minolta chromameter (CR-200, D\(_65\); Minolta Corp., Osaka, Japan) measuring in CIELAB (L°, a°, b°) (Hunter and Harold 1987; McGuire 1992). The lightness coefficient, L°, ranges from black = 0 to white = 100; whereas a° = bluish-green/red-purple hue component; and b° = yellow/blue hue component. The a° and b° hue coordinates of the tristimulus colorimetry data were then converted to chroma \(C = \sqrt{(a°^2 + b°^2)}/2\) and hue angle \(h° = \arctan(b°/a°)\) to allow for color interpretation. Chroma refers to the degree of color saturation (i.e., vivid vs. dull colors) and h° refers to color (i.e., red, yellow, green, blue).

Foliation was also measured to determine if A of adjacent nonbronzed foliage compensates for bronzing induced reduction in A by nearby bronzed leaflets. Fifteen sun exposed ‘Desirable’ terminals, possessing a compound leaf supporting a bronzed leaflet adjacent to a nonbronzed leaflet and also adjacent to a compound leaf devoid of bronzing, were selected for A measurements. This arrangement allowed four treatments: a) bronzed leaflet (i.e., being adjacent to a nonbronzed leaflet), b) adjacent nonbronzed (i.e., a nonbronzed leaflet on the same compound leaf and immediately adjacent to the bronzed leaflet), c) bronzed control (i.e., a nonbronzed leaflet on the adjacent compound leaf occupying the same relative position as that of the bronzed leaflet), and d) nonbronzed control (i.e., leaflet on the adjacent compound leaf devoid of bronzing, with the leaflet occupying the same relative position in the leaflet array of the compound leaf as that of the adjacent nonbronzed leaflet). Measurements of A were made in September on foliage showing an initiation of bronzing in July. Gas exchange measurements were performed as described above. The design of the experiment was a randomized complete block consisting of 15 blocks of four treatments. Data were analyzed by analysis of variance and means separated by Duncan’s multiple range test (SAS Institute, Inc., 1995).

In another study, the responsiveness of bronzed foliage to different PPF was determined using the gas exchange methods described above. A readings were made at 125, 250, 500, 1000, and 2000 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) with 3 min for adaptation under new light conditions. Different levels of photosynthetically active radiation (PAR) (i.e., at 670 nm) were achieved used the LI-6400 portable photosynthetic system fitted with a light emitting diode light source providing actinic radiation for photosynthesis. Measurements were taken from leaves from the southern side of the canopy from adjacent terminals where one terminal supported a heavily bronzed leaflet and an adjacent terminal supported nonbronzed leaflets. This was done on three trees. Thus, the experimental design consisted of three randomized complete blocks consisting of bronzed and nonbronzed treatments. Leaves were simultaneously measured for stomatal conductance to water vapor \(s_w\) and for transpirational water loss \(E\). Measurements of A were then regressed against levels of PAR. Test trees exhibited bronzing that developed in September.

**Water relations and temperature.** The effect of bronzing on the water potential (\(\Psi_w\)) of affected leaflets was determined by measuring comparable normal vs. bronzed leaflets on adjacent terminal shoots from seven trees. Measured leaflets were selected from bronzed and normal leaflets from the same leaflet position on the terminal shoot, but from adjacent shoots because bronzing generally affected all leaflets of the shoot. Measurements were made by placing a single 0.5 \(\times\) 4 cm strip of leaflet in sample cups of a thermocouple psychrometer (Tru Psi-SC10X; Decagon Devices, Pullman, Wash.) so as to contact as much cup surface as possible to rapidly attain thermal equilibration. Sample cups were capped and stored in an insulated container at \(25^\circ C\) and equilibrated = 30 min in the sample chamber prior to measuring.

Leaflet temperature of bronzed and normal leaflets was measured using an Omega 450-AET thermocouple thermometer (Omega Engineering, Stamford, Conn.) with a 0.003 mm diameter chromel/constantan thermocouple appressed to the abaxial surface of leaflets. Measurements were made on sun leaves exposed to direct sunlight at \(1500\) HR. Measured bronzed and normal leaflets occupied the same position on the terminal leaflet hierarchy, but on different terminals of the same branch. This was repeated on five different trees.

The water status of affected foliage was assessed further by detaching heavily bronzed and normal leaflets at \(1030\) HR and monitoring for rate of water loss. Sample leaflets were sealed immediately in plastic bags and maintained at \(25^\circ C\) in an insulated container prior to measurement. Percentage water content and rate of drying were determined gravimetrically by measuring fresh weight upon reaching the laboratory and again weighed after drying at \(23^\circ C\) for 2 and 4 HR and at \(65^\circ C\) for 12 HR.

**Microscopy.** Leaflet samples, taken from bronzed and normal ‘Desirable’ terminals in July and October, were subjected to both light and electron microscopy. Light evaluation focused on the condition of epidermal and spongy mesophyll cells of normal vs. bronzed leaflets. Scanning electron micrograph (SEM) evaluation focused on stomatal aperture as related to time of day when leaves were sampled. For example, normal and bronzed leaflets were collected at \(0830\) and \(1500\) HR and fixed immediately in 60% ethanol : 35% formalin : 5% acetic acid. Leaflets were studied regarding surface and interior features. SEM analysis was by a SEM/ X-ray microscope (Leo 982, Leo Elektronenmikroskopik GmbH, Oberkochen, Germany). Leaf tissue was cut into 3 \(\times\) 5-mm sections and mounted for viewing, without metallic coating, at an accelerating voltage of 0.90 KV.

**Kernel filling.** The effect of foliar bronzing on total kernel weight and percentage of kernel comprising the nut (i.e., percentage kernel) was determined for two ‘Desirable’ orchards. One orchard exhibited early season (appearing in July) whereas the other exhibited late season bronzing (appearing in October). Fruit were sampled from southern exposed \(12\)- to \(20\)-cm-long terminals. These were sampled from a common limb supporting both bronzed and normal foliage. Sampled terminals supported only two fruit per cluster. The experiment was structured in both orchards as a randomized complete block design [20 blocks (i.e., trees) in the July to August bronzing period; 32 blocks (i.e., 32 trees) in the October bronzing period]. Effects of bronzing on nuts were determined from nuts collected upon ripening in mid October from terminals exhibiting either bronzed and normal foliage. Nuts were air dried, weighed in shell, shelled and the kernels weighed to determine percentage of kernel and total kernel weight. Data were subjected by ANOVA.

**Results**

**Photosynthetic assimilation rate (A).** \(A\) was substantially lower in foliage exhibiting heavy bronze coloration than in foliage with lesser coloration (Fig. 1). This negative relationship was nearly linear in both July and September for all three color
measures (i.e., h°, C, and L*) of bronzing (Figs. 1A–F). Thus, there is increasingly less photoassimilation as bronze coloration intensifies and foliage becomes duller, and more yellowish in color. Light micrographs of the lower surface of bronzed leaflets revealed that the bronze coloration was blotchy rather than continuous (micrographs not shown).

It was also observed that A of normal leaflets adjacent to bronzed leaflets exhibited higher A than either bronzed or control leaflets (Fig. 2). The effect of bronzing increased A of adjacent nonbronzed leaflets to ≈133% of normal rates. Thus, certain
Nonbronzed leaflets on terminals with bronzed leaflets have the ability to compensate partially for lower \( A \) by adjacent bronzed foliage.

Nonbronzed and bronzed foliage had similar \( A \) at \( \text{PAR} \) of 125 \( \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \), but \( A \) of bronzed leaflets did not respond to \( \text{PAR} \) levels > \( \approx 250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \) (Fig. 3A). \( A \) of nonbronzed foliage was as much as \( \approx 3 \)-fold greater than that of bronzed foliage at high \( \text{PAR} \) levels. The \( A \) response curve was sigmoidal for both nonbronzed and bronzed foliage. Nonbronzed foliage attained near maximum \( A \) at \( \approx 1,000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1} \text{PAR} \).

**Water relations and temperature.** Stomatal conductance (\( g_{sw} \)) of bronzed foliage to water vapor and transpirational water loss (\( E \)) during midmorning, regardless of \( \text{PAR} \) level, was much less (i.e., \( \approx 1/3 \) as high) than that of nonbronzed foliage (Fig. 3B).

| Table 1. Water and temperature status of ‘Desirable’ pecan foliage exhibiting bronzing. |
|-----------------------------------|-----------------|----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| **Treatment**                     | \( \Psi_w \) \( (\text{J} \cdot \text{kg}^{-1}) \) | **Temp** \( (\circ\text{C}) \) | **Leaf fresh wt** \( (\text{mg} \cdot \text{cm}^{-2}) \) | **Water content** \( (\%) \) | **Water loss** \( (\%) \) | 2 h | 4 h |
| Normal                            | -3310 a \(^{a}\) | 33.2 a | 21.4 a | 46.7 a | 65 a | 85 a |
| Bronzed                           | -3070 a \(^{a}\) | 34.7 b | 23.2 b | 48.3 b | 71 b | 92 b |

\(^{a}\)Percentage of water lost after detached foliage was exposed to an air temperature of 23 \( \circ\)C and \( \approx 40\% \) relative humidity for 2 and 4 h.

\(^{b}\)Mean separation within columns by ANOVA, \( P \leq 0.05 \).

| Table 2. Influence of bronzing occurring on ‘Desirable’ pecan foliage either in July or October on kernel weight and shell-out percentage. |
|-----------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| **Treatment**                     | **July**        | **October**     |
|                                   | Kernel wt \( (\text{g}) \) | Shell out \( (\%) \) | Kernel wt \( (\text{g}) \) | Shell out \( (\%) \) |
| Normal                            | 3.7 b \(^{a}\) | 44.2 b | 4.0 a | 50.3 a |
| Bronzed                           | 3.4 a | 40.5 b | 3.9 a | 50.2 a |

\(^{a}\)Bronzing occurring in either July or October persisted until leaf drop in November.

\(^{b}\)Shell out is the percentage proportion of the total weight of the nut due to kernel (i.e., nut meat).

\(^{c}\)Mean separation within columns by ANOVA, \( P \leq 0.05 \).

[Figs. 4A and 4B] Light micrographs of cross-sections of foliage from nonbronzed (A) and bronzed (B) foliage from leaflets bronzing in early season (July to August; 80\( \times \)). (C and D) Enlargements (200\( \times \)) of the above leaf sections, respectively. Mesophyll (m), epidermal (e), and stomatal guard cells (s) of nonbronzed tissue were turgid whereas these cells in the bronzed leaf were shrunken.
This relationship between PAR and \( g_{sw} \) and \( E \), was nearly linear for both nonbronzed and bronzed foliage and was also evident when measured in midafternoon (data not presented). Bronzed foliage therefore exhibits low conductance, or loss of water vapor, through the stomates and transpires less during midmorning than does nonbronzed. Although there was a difference in water loss between bronzed and nonbronzed foliage, leaflets of both classes maintained similar leaf water potentials (Table 1). Weight per unit area of bronzed foliage at \( \approx 1030 \text{ hr} \) was 108% of normal foliage and possessed a fresh weight water content of 103% of normal foliage.

**Microscopy.** Light microscopy of bronzed vs. normal leaflets, regardless of whether they bronzed in July to August or September to October, exhibited obvious differences in the epidermal cells of the lower leaf surface and the adjacent spongy mesophyll (Fig. 4A and B). Most intraveinal epidermal cells of bronzed leaves were collapsed; however, epidermal cells above nearby vascular tissues appeared undamaged (Fig. 4C and D). The spongy mesophyll also appeared abnormal—being somewhat shrunken in appearance. Certain stomatal guard cells also appeared abnormal and shrunken. Visual evaluation of numerous SEM electronmicrographs indicated a tendency for stomata aperture to be less in both the morning (Fig. 5A and C) and afternoon (Fig. 5B and D) for bronzed foliage.

**Kernel filling.** ‘Desirable’ shoots supporting foliage that began bronzing in July (i.e., early season) produced nuts with lighter kernels and less shell-out percentage than nonbronzed shoots (Table 2). Kernel weight and kernel percentage from these bronzed terminals was \( \approx 92\% \) of that from nonbronzed shoots. Conversely, these kernel traits were unaffected when bronzing occurred during October (i.e., late season).

**Discussion**

Data herein indicate that bronzing of the lower surface of pecan foliage can potentially disrupt normal leaf physiological processes and also affect nut quality. Bronzed foliage exhibits abnormal gas exchange physiology in that \( A \) and \( g_{sw} \) are reduced in a manner that is inversely proportional to the degree of bronzing. Heavily bronzed foliage exhibits negative \( A \)—with \( \text{CO}_2 \) evolution being greater than uptake. A similar decline in \( A \) occurs in mite-induced bronzed foliage of apple (Spieser et al., 1998). The ability of bronzed pecan foliage to utilize available radiant energy for carbon assimilation is also diminished in that \( A \) of sun leaves is maximized at \( \approx 12\% \) of full sunlight (i.e., \( \approx 250 \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)) whereas nonbronzed foliage is near maximum at \( \approx 50\% \) of full sunlight (Fig. 3).

The bronzing-associated reduction in foliar gas exchange is characterized, relatively to that of normal leaflets, by low stomatal conductance to water vapor during both midmorning and
mid afternoon. This relatively low conductance, plus darker surfaces due to the bronze coloration resulting in less evaporative cooling and greater absorption of solar radiation which in turn increases surface temperatures of affected foliage. Reduced stomatal conductance may also account for the greater fresh weight per unit area of foliage and the slightly higher water content of bronzed foliage. This is supported by SEM micrographs showing the stomatal aperture of bronzed foliage being less than that of nonbronzed foliage. The similarity of leaf water potential between bronzed and nonbronzed foliage is consistent with observations of the senior author that there is little correlation between stomatal conductance and leaf water potential in pecan except under extremes in moisture conditions (unpublished). The reason for the greater loss in percentage water content of detached bronzed foliage, than that of nonbronzed foliage, is problematic, but may be due to a subtle effect of bronzing on stomatal function or to the compromised integrity of the damaged epidermal cells or perhaps due to the effect of water-binding colloids and cell surfaces on rate of water loss (i.e., matric forces).

Assessment of the impact of bronzed foliage, and its associated decline in net assimilation, on tree vigor or crop yield is complicated by the ability of nonbronzed foliage to partially compensate by increasing A. A similar elasticity in A by pecan foliage was observed in shoots supporting fruit vs. those without fruit (Wood, 1988). Loss of A capacity by bronzed foliage may therefore be of little or no economic importance if the percentage of canopy displaying bronzed foliage is small or if bronzing develops late in the growing season. This may account for lack of reduced kernel weight or shell-out percentage in nuts from shoots becoming bronzed in September to October.

Reduced fruit quality, based on kernel weight and percentage kernel, appears to be a primary side-effect of excessive early-season foliar bronzing. The substantial negative influence of foliar bronzing on gas exchange is evidence that bronzing contributes potentially to alternate bearing related problems of pecan—because factors reducing leaf efficiency tend to increase alternate bearing and its associated side effects (Sparks, 1981; Sparks and Brack, 1972; Worley, 1979a, 1979b). Trees that are heavily bronzed throughout much of the growing season may produce lower quality fruit during the year of bronzing and set less fruit the following year.

These data indicate that bronzed pecan foliage is characterized by a) collapse of the epidermal cells of the lower foliar surface; b) abnormal spongy mesophyll cells, and c) reduced photosynthesis and conductance to water vapor. These, and perhaps other yet to be detected side effects, may reduce kernel quality. Because pecan nuts are generally sold on a percent kernel basis, severe bronzing occurring in July to August may be of economic significance whereas the likelihood of late-season bronzing (September to October) adversely affecting yields is much less. The strong linkage between foliage health and alternate-bearing-related problems however indicates that both early- and late-season bronzing may influence subsequent year yields. Thus, in addition to affecting tree appearance, bronzing possesses potential for being a yield limiting problem if the tree’s canopy is heavily bronzed for much of the growing season. The cause, control, and action threshold for bronzing, and effects on the next seasons crop yield, warrants further study.

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