Photosynthetic Acclimation of Leaves of Three Apple Cultivars as Affected by Growth Under Full Sun Or 85 Percent Shade and Subsequent Transfer To the Contrasting Light Regime

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Abstract

Three cultivars of apple, "Granny Smith" (GS), "Golden Delicious" (GD), and "Red Delicious" (RD) were grown in full sun, or 85% shade. Trees grown in sun or shade were subsequently transferred to the light regime opposite of initial growth light for three weeks to determine the light acclimation potential for fully expanded leaves. Photosynthetic capacity was reduced in GS, GD, and RD apple leaves when grown under 85% shade as compared to full sun grown. Leaf nitrogen per area (N_a) was highly correlated ($p < 0.01$) with A, A_{max} and g'_m and the highest N_a was in leaves grown under the highest photosynthetic photon flux (PPF). This supports a hypothesis that nitrogen is re-distributed to leaves exposed to the greatest PPF to maximize daily carbon gain. Photosynthetic capacity was reduced to a greater extent in GS compared to GD or RD when grown under shade. However, GS acclimated photosynthetically to shade-to-sun transitions, whereas RD could not acclimate. Since photosynthetic capacity is greatly reduced by shade in GS and since RD and GD cannot acclimate to shade-to-sun transitions, the greatest photosynthetic productivity in these apple cultivars would be obtained by exposing the greatest portion of the canopy to full sun throughout the season.

Keywords: Malus domestica, CO_2 assimilation, carboxylation efficiency, mesophyll conductance, leaf nitrogen, specific leaf area

Abbreviations: A = CO_2 assimilation; A_{max} = CO_2 assimilation at saturating CO_2; g'_m = carboxylation efficiency; g'_s = stomatal conductance to CO_2; LMA = leaf dry weight per area; N_a = leaf nitrogen per area; PPF = photosynthetic photon flux; GS = "Granny Smith"; GD = "Golden Delicious"; RD = "Red Delicious"

Introduction

There has been a trend favoring high density trellised plantings in the production of fruit crops. High density orchards tend to come into production earlier and maximize yield per unit area. As canopies develop in fruit trees it has been shown that interior leaves receive much lower PPF than leaves in exposed positions (Weinbaum et al., 1989). Observations of early leaf senescence inside the canopies of a variety of fruit species indicate that reduced light intensity in high density trellised systems may have long-term negative effects on productivity, as dense canopies develop (Flore and Lakso, 1989).

Shade has been shown to reduce flower initiation (Cain, 1971; Jackson and Palmer, 1977), fruit set (Doud and Ferree, 1980; Stephenson, 1981), fruit size (Heinicke, 1966; Barritt et al., 1987), spur quality and longevity (Barritt et al., 1987; Ferree, 1989), and fruit quality (Fallahi et al., 1989; Ferree, 1989). These negative effects of shade

in fruit tree canopies are likely related to the reduction of photosynthetic capacity described in shaded leaves of many plants (Bjorkmann, 1981).

Leaves growing in high light environments are light saturated for A at higher PPF and have higher light compensation points. Differences in sun and shade plants have been related to protein content, leaf anatomy and physiology (Nobel et al., 1975; Chabot and Chabot, 1977; Bjorkmann, 1981; Anderson, 1986). Growth PPF has been correlated with leaf dry weight per area (Kapel and Flore, 1983; DeJong and Doyle, 1985; Jurik, 1986; Kwesiga et al., 1986; Walters et al., 1987; Weinbaum et al., 1989), A_{max} (Kwesiga et al., 1986), leaf nitrogen per area (DeJong, 1982; DeJong and Doyle, 1985; Weinbaum et al. 1989), CO_2 assimilation (DeJong, 1982; Kapel and Flore, 1983; DeJong and Doyle, 1985) carboxylation efficiency (DeJong and Doyle, 1985; Kwesiga et al., 1986) and dry matter production in apple (Palmer, 1988). Mooney and Gulmann (1979) hypothesized that growth PPF would integrate photosynthetic capacity by re-distributing N to leaves exposed to the highest light to maximize daily carbon gain. A similar hypothesis was proposed by Neumann and Stein (1983) which states that the most fully exposed leaves have the highest transpiration and receive the greatest proportion of mineral nutrients and hormones associated with high A. These hypotheses have been supported by the studies of Hunt et al. (1985) in a C_4 species Amaranthus powellii, by Field (1983) with a drought-deciduous chaparral shrub, and by DeJong and Doyle (1985) in peach tree canopies.

Since nitrogen acquisition, translocation and assimilation are costly in terms of energy, plants with long-lived leaves such as deciduous trees would benefit most by allocating more nitrogen to leaves exposed to the greatest PPF. However, this strategy may not be cost effective in trellised orchard environments where limbs that developed under full sun exposure are trained and tied down to wires in the shaded parts of canopies, or where summer pruning immediately exposes leaves which developed in shade to full sun. Canopy shade has been shown to reduce A and leaf dry weight per area in apple (Porpiglia and Barden, 1980), grape (Flore and Lakso, 1989), and citrus (Syvertsen, 1984). However, shade induced loss of photosynthetic ability is not readily reversible with all plant species. Skene (1974) has shown that grana thickness in apple leaves increases, and thereby reduces photosynthetic electron transport capacity when sun leaves are transferred to shade, whereas shade leaves do not have the capacity to reverse this trend when transferred to bright light. This is not true of all fruit trees as Syvertsen (1984) has shown that citrus leaves increased in density, and carboxylation efficiency was increased upon transfer from 90% shade to full sun.

The purpose of this study was to characterize N_a, leaf dry weight per area (LMA), and photosynthetic gas exchange in three common apple cultivars grown in full sun or 85% shade, and then to evaluate changes in these parameters when trees were transferred to the light regime opposite of the growth PPF. This will allow us to test the hypothesis of Mooney and Gulman (1979) that N_a and photosynthetic capacity is greatest in leaves grown under the highest PPF, and it will allow us to test a second hypothesis that apple does not have the capability to recover photosynthetic capacity by redistribution of nitrogen when transferred from shade to full sun. This should provide information relevant to managing densely planted trellised apple orchards. The current management strategy of allowing dense shade to develop until late in the season and then summer pruning to allow light for fruit size and color would be of questionable value if these cultivars could not increase photosynthetic capacity when exposed to increased light. If such were the case an alternative strategy would be to design trellised systems that expose the greatest amount of canopy to high PPF.

Materials and Methods

Plant Material

One-year-old trees of "Red Delicious" (RD), "Golden Delicious"(GD), and "Granny Smith" (GS) apple on M26 were potted into 20 l pots in a 1 soil:2 sphagnum peat:2 perlite (by volume) medium, pH 6.2. The medium was amended with 744 g of treble superphosphate, 496 g potassium nitrate, 496 g magnesium sulfate, 4 kg ground

calcitic limestone, and 62 g Peters Fruit Industries Trace Elements No. 555 (Peters Fertilizer Products, Fogelsville, Pa.) per cubic meter. Potted trees were pruned to one shoot and fertilized at each watering with 200 mg liter^{-1} each of N and K supplied from 517 mg liter^{-1} KNO_3 and 367 mg liter^{-1} NH_4NO_3. Fertilizer solution was maintained at pH 6.0 by injecting 75% (w/w) technical grade phosphoric acid into the irrigation system.

Trees of all three cultivars were randomized and grown for 10 weeks following bud break in full sun or in shade covered houses providing 85% reduction in light intensity. Midday irradiance (10-2PM PDT) during the course of the experiment averaged 2430 and 290 μmol m^{-2} s^{-1} for full sun and 85% shade respectively. Leaf length was measured every other day as they approached full expansion and were tagged when leaf length was the same for consecutive measurements. Three fully exposed leaves per tree were tagged at full expansion, and gas exchange response to increasing CO_2 was measured. Three trees per cultivar served as replicates, with three leaves per tree serving as a composite sample for each tree. These same three leaves per tree were removed and dried in a 80 C oven for 48 hours and measured for dry weight and leaf nitrogen. Dried leaves were ground to pass a 40-mesh screen and 0.1 g of tissue was used to measure nitrogen by a modified calorimetric indophenol technique (Keeney and Nelson, 1982). Three leaves per tree that were fully expanded were then tagged, and then trees grown in shade were moved to full sun, whereas those grown in full sun were moved to shade. Three weeks after transfer tagged leaves were again measured for gas exchange, dry weight, and leaf nitrogen. Data were analyzed as a completely randomized factorial design with each tree being a replication (n=3) and factors being grown in 100% sun, grown in 15% sun (85% shade), grown in 100% sun and transferred for 3 weeks to 15% sun, and grown in 15% sun and transferred for 3 weeks into 100% sun.

Gas Exchange

Gas exchange measurements were made using an open system and plexiglass chamber coated on the inside with clear teflon tape to reduce water vapor adsorption and absorption. Temperature within the chamber was controlled with a peltier plate (Thermoelectric Cooperation of America Model 150HC) and air circulation over a nickel plated aluminum heat exchanger was supplied with an small DC fan (Panmotor model L402). Oxygen, N_2, and CO_2 were mixed manually using multiple valves, and flow rates into the mixing chamber were measured with mass flow meters (Hastings Models ST 2663 and ST 2664). Response of CO_2 assimilation (A) to increasing CO_2 was monitored by measuring CO_2 gas exchange in step increments from low (< 100 μmol mol^{-1}) to high CO_2 (1000 μmol mol^{-1}). The reference, sample and the CO_2 differential concentrations between the inlet and outlet gas from the chamber were measured with an infrared gas analyzer (ADC Model LCA-2). Flow rate into the chamber was controlled at 4 liters min^{-1}, and the air temperature inside the chamber was controlled throughout at 25 +/- 0.5C. Air and leaf temperature were monitored using thin wire thermocouples. Vapor pressure deficit (VPD) was maintained at 0.5 to 1.0 KPa by saturating the gas stream in a temperature controlled water bath, and then drying part of the air stream with silica gel. Vapor pressure of the inlet gas was measured with a dewpoint hygrometer (EG & G Model 911). Outlet vapor pressure was measured directly within the chamber using a EG&G Model 200 dewpoint hygrometer. Light supplied by a 1000 W metal halide lamp was filtered through 8 cm of water and neutral density screens. The irradiance level was measured with a quantum sensor (LiCor Model LI-180) at the top of the leaves and was maintained between 1400 and 1600 (PPF μmol m^{-2} s^{-1}). Gas exchange was calculated using standard equations (Moon and Flore, 1986).

Data Analysis

A logarithmic curve was fitted to the data for CO_2 assimilation (A) versus intercellular CO_2 (C_i). CO_2 assimilation at saturating CO_2 levels (A_{max}) (C_i > 500 μmol mol^{-1}) was calculated from the plateau phase of the A/C_i curves. Reductions in A_{max} following an environmental stress are indications of non-stomatal limitation of A due to damage to photosynthetic electron transport and thereby regeneration of the substrate RuBP. Carboxylation efficiency (g'_m) was determined from linear regression using the linear portion of the A/C_i curve (0 to 250 μmol mol^{-1} CO_2). Estimates of carboxylation efficiency (g'_m) provide a means of assessing the non-stomatal process limiting CO_2 assimilation following a change in environment, e.g., imposition of water or temperature stress.

Results

A, g'_m, A_{max} and g'_s were lower in leaves grown in 15% sun or grown in 100% sun and transferred to 15% sun for 3 weeks, compared to controls grown and kept in full sun (Table 1, Fig.'s 1 and 2). Shade reduced gas exchange more in GS apple leaves (40% to 60%) compared to RD or GD (Fig.'s 1 and 2). When leaves of GS were grown in 15% sun and transferred to full sun, A increased by 135%, g'_m by 139%, A_{max} by 71%, and g'_s by 138%, whereas increases in GD were not as great (Fig.'s 1 and 2). Gas exchange in RD leaves showed almost no response to the transfer from shade to full sun (Fig. 1), as A increased by 8%, g'_m by 38%, and g'_s decreased 7% which gave a cultivar by light interaction (Table 1).

LMA was also reduced by shade, and the response to changes in growth PPF were similar to gas exchange responses (Fig. 2). N_a was lower in shade grown plants (Fig. 2), whereas transfer from full sun to shade reduced N_a by 19% or 27% respectively in GD and GS, but by only 7% in RD. Transfer of shade grown leaves to full sun caused N_a to increase 18% in GD, 30% in GS, and 42% in RD.

Photosynthetic gas exchange was highly correlated ($p<0.01$) with N_a (Table 2). Carboxylation efficiency (g'_m), g'_s, and LMA were also good predictors of A and photosynthetic capacity (Table 2).

Discussion

Leaves of all 3 apple cultivars had higher A, g'_m, A_{max} and LMA when grown under high PPF. Since these parameters are associated with high photosynthetic capacity, we suggest that growth PPF determines photosynthetic potential and efficiency in apple leaves. PPF level has been correlated with both A and g'_m in peach (DeJong and Doyle, 1985), and in tropical timber trees (Kwesiga et al., 1986). The higher LMA in leaves grown under high PPF observed here (Fig. 2), and reported for leaves of other tree species (Kapel and Flore, 1983; DeJong and Doyle, 1985; Jurik, 1986; Kwesiga et al., 1986; Walters et al., 1987; Weinbaum et al., 1989) could be due to increased soluble protein, but could also be due to structural changes affecting the leaf anatomy.

Stomatal conductance is 30% to 50% higher in high PPF grown apple leaves. The correspondingly higher transpiration rates associated with high g'_s may contribute to the high photosynthetic potential of the sun leaves by virtue of the fact that more nutrients and phytohormones associated with high A are accumulated via xylem conductance (Flore and Lakso, 1989). One such nutrient that would be accumulated through the transpiration stream would be leaf nitrogen. N_a has been highly correlated with A (DeJong and Doyle, 1985; Hunt et al., 1985; Sage and Pearcy, 1987; Sinclair and Horie, 1989), A_{max} (Seeman et al., 1987; Walters et al., 1987), and g'_m (DeJong and Doyle, 1985). The fraction of nitrogen invested in carboxylation enzymes has been shown to increase with increasing N_a (Sage et al., 1987; Seeman et al., 1987). In this study, N_a was about 30% higher in high PPF grown leaves (Fig. 2) and these higher levels of N_a were correlated with A, A_{max}, and g'_m. The higher N_a and photosynthetic capacity observed here in apple leaves supports the hypothesis of Mooney and Gulman (1972), which states that nitrogen will be distributed to leaves growing in the highest PPF in order to maximize daily carbon gain.

Photosynthetic gas exchange was lower in GS leaves grown under low PPF (15% sun) compared to RD and GD (Fig. 1). When grown under high PPF and transferred to 15% sun, A, A_{max}, g'_m were reduced from 40% to 50% in GS, whereas the reductions in these parameters was half as great in RD and GD. We suggest that shade during growth or repositioning limbs into shade will have a greater negative effect on the photosynthetic productivity of GS compared to RD or GD.

When grown in low PPF and transferred to full sun for 3 weeks, leaves of GS apple dramatically increased A (135%), g'_m (139%), and A_{max} (71%) (Fig. 1), whereas there was no increase in A or A_{max}, and only a small (38%) increase in g'_m in RD apple. Thus, it appears that GS has an acclimation potential to enable high A upon

transfer from shade to sun, whereas RD does not. Leaves of most fruit tree crops are similar to RD in that they cannot acclimate photosynthetically to shade-to-sun transitions (Skene, 1974, Flore and Lakso, 1989). However, increases in LMA and photosynthetic capacity have been reported in 'Red Yorking' apple (Barden, 1974), and citrus (Syvertsen, 1984). Ferrar and Osmond (1986) observed that a sun clone of Solanum dulcamara could increase photosynthetic capacity by increasing the primary carboxylating protein in C_3 plants (Rubisco) upon shade-to-sun transitions, whereas a shade clone could not acclimate and was damaged by photoinhibition. Since an increase in the amount and activity of the principal leaf protein, Rubisco, almost invariably accompanies acclimation to bright light (Bjorkmann, 1981), N_a could be an indicator of sun-to-shade acclimation capacity. N_a increased by 30% in GS and 42% in RD when transferred from 15% to 100% sun. Thus, the increase in N_a is not associated with Rubisco or other enzymes of photosynthetic machinery in RD apple leaves. The increased N_a in RD leaves are probably associated with structural proteins as indicated by the 32% increase in LMA, and/or in defense compounds. GD apple leaves also increased photosynthetic capacity when transferred from shade to sun, but the magnitude of the increase was only 20% to 50% as large compared to GS.

The inability to respond photosynthetically to shade-to-sun transitions leads us to suggest that photosynthesis will not be increased substantially when RD and GD are summer pruned. GS can acclimate to increases in PPF, but photosynthetic capacity is reduced to a much greater extent when grown in shade compared to RD or GD. An orchard management strategy that allows for dense canopy shade to develop for most of the season with summer pruning to increase light just before final sizing of fruit will not work optimally in RD and GD because they cannot respond to the light increase, whereas the same strategy would be deleterious in GS because of the dense canopy shade most of the season. Thus, we would suggest that photosynthetic productivity would be best maximized by training and pruning systems that expose the greatest amount of foliage to full sun over the entire growing season.

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Table 1. Gas exchange, leaf nitrogen (N), and leaf dry weight per area (LMA) in 'Granny Smith' (GS), 'Red Delicious' (RD), and 'Golden Delicious' (GD) apple grown under 100% or 15% full sun and percent change when transferred to the light condition opposite of growth light. CO_2 assimilation (A) was measured at 365 μmol mol^{-1} CO_2, 1500 μmol m^{-2} s^{-1} PPF, 25C; and vapor pressure deficits <1 KPa. A_{max} was measured at saturating internal CO_2 (C_i>600 μmol mol^{-1}). Carboxylation efficiency (g_m) was estimated from the linear portion of A/C_i curves (0 to 250 μmol mol^{-1} CO_2).

Parameter	Light Conditions												Significance		
	100%			15%			100 to 15%			15 to 100%					
	GS	RD	GD	GS	RD	GD	GS	RD	GD	GS	RD	GD	Cultivar	Light	Interaction
A (μmol m^{-2} s^{-1})	20.8	22.5	21.1	10.0	16.0	16.3	-41	-27	-19	+135	+8	+29	NS	***	NS
g_m (mmol m-2 s^{-1})	155	123	170	70	79	105	-53	-25	-34	+139	+38	+72	***	***	NS
A_{max} (μmol m^{-2} s^{-1})	36.9	35.8	40.1	20.1	28.5	30.8	-49	-22	-23	+71	0	+17	**	***	NS
g_s (mmol m^{-2} s^{-1})	138	174	196	73	139	86	-9	-18	-22	+138	-7	+114	NS	***	*
N (mmol m^{-2})	201	213	207	150	146	152	-27	-7	-19	+30	+42	+18	*	***	NS
LMA (mg cm^{-2})	9.3	9.9	10.3	7.5	6.8	8.0	-16	-5	-14	+33	+32	+26	NS	***	NS

NS = not significant; *P <0.05; ** P< 0.01; *** P< 0.001

Table 2. Summary of linear regressions relating leaf nitrogen (N), carboxylation efficiency (g_m'), stomatal conductance to CO_2 (g_s'), and leaf dry weight per area (LMA) to gas exchange measurements. Gas exchange conditions were the same as described in Table 1.[x]

Dependent variable	Independent variable	Y-intercept	Slope	Correlation coefficient (r)
N[y]	A	-3.33	0.177	0.709**[z]
N	g_m'	-26.81	0.812	0.552**
N	A_{max}	3.06	0.153	0.616**
g_m'	A	6.84	0.092	0.824**
g_m'	A_{max}	13.29	0.145	0.860**
g_s'	A	5.12	0.090	0.828**
LMA	A	-6.06	2.690	0.724**
LMA	A_{max}	3.28	2.970	0.536**
LMA	g_m'	-98.72	24.500	0.741**
N	A_N	7.40	-0.0015	-0.251NS

[x] n=36

[y] units: A (μmol CO_2 $m^{-2}s^{-1}$), g_m' (mmol CO_2 $m^{-2}s^{-1}$), A_{max} (μmol CO_2 $m^{-2}s^{-1}$), N (mmol m^{-2}) g_s' (mmol CO_2 $m^{-2}s^{-1}$), SLW (mg cm^{-2}), A_N (nmol CO_2 mg $N^{-1}s^{-1}$)

[z] **, NS, $p<0.01$ (**), not significant (NS)

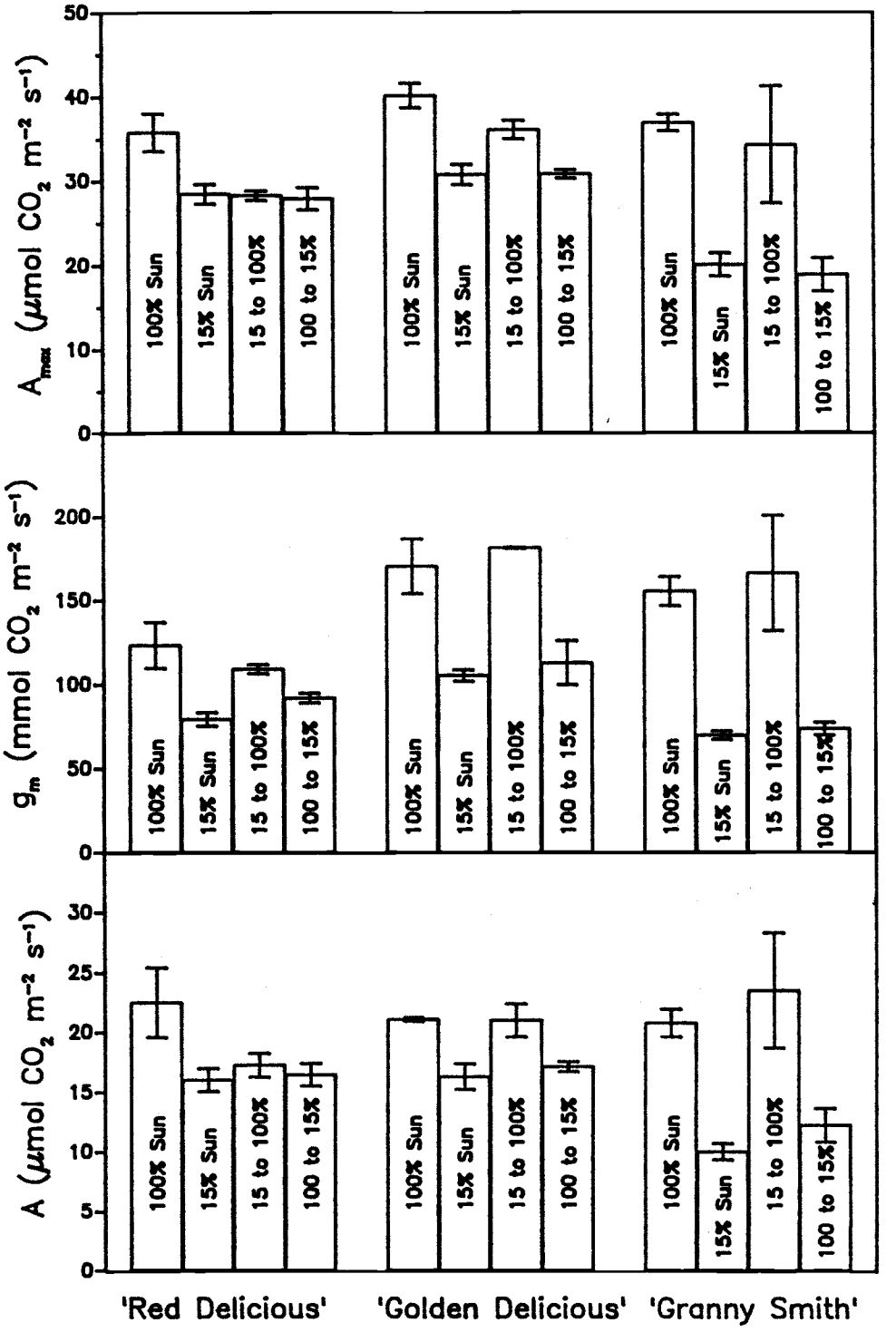

Figure 1. Gas exhange in RD, GD, and GS apple leaves. Gas exhange conditions are described in Table 1. Bars are the means of nine leaves +/- s.e.

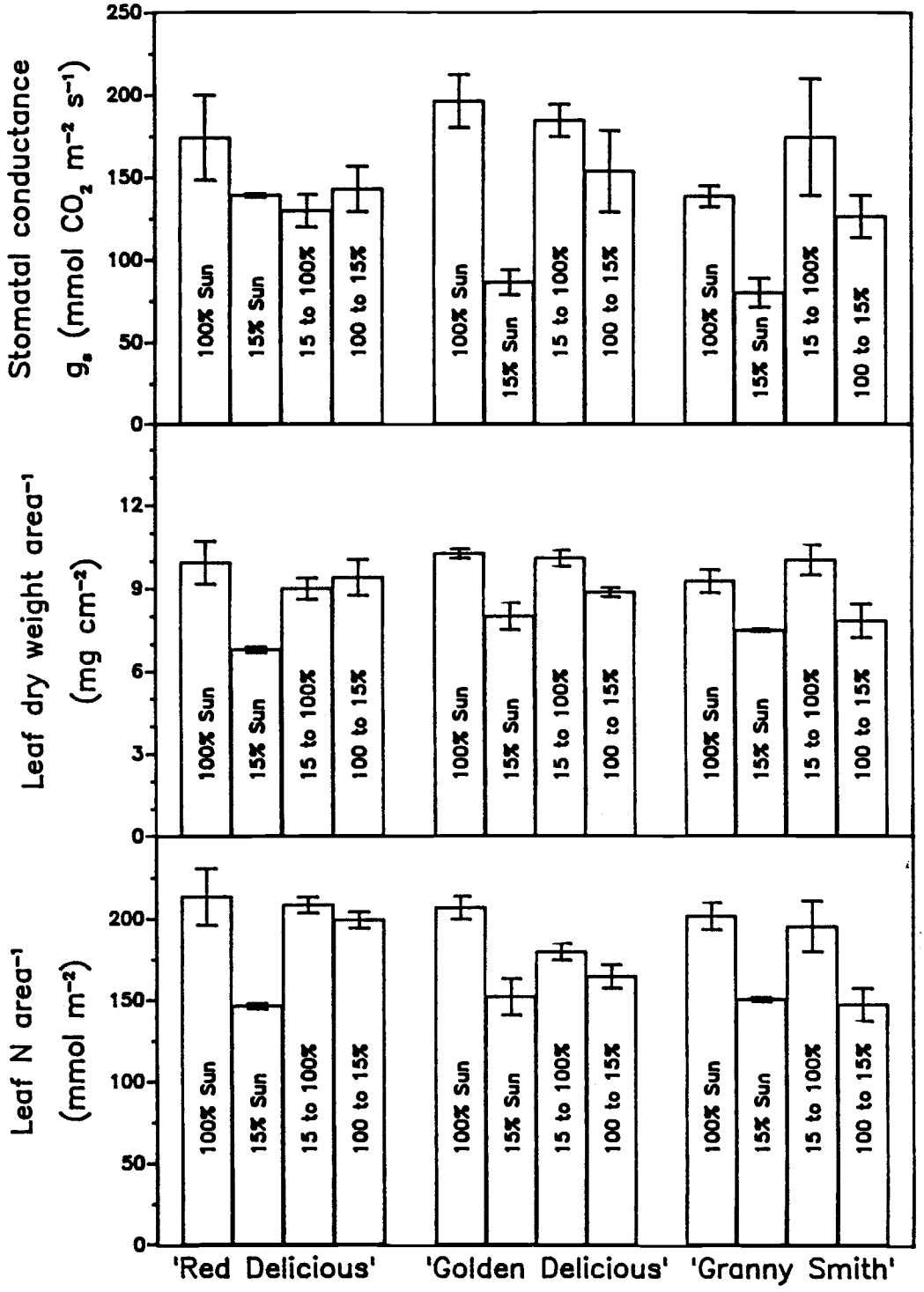

Figure 2. Gas exchange, LMA, and N in RD, GD, and GS apple leaves. Gas exchange conditions are described in Table 1. Bars are the means of nine leaves +/- s.e.