

Gas Exchange Characteristics of Leaves of Four Species of Grain Amaranth

PETER C. HARLEY and JAMES EHLEINGER

Department of Biology, University of Utah, Salt Lake City, UT 84112 (U.S.A.)

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ABSTRACT

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Four species of the C₄ genus *Amaranthus*, *A. cruentus*, *A. caudatus*, *A. hypochondriacus* and *A. hybridus*, were grown at Salt Lake City, Utah for the determination of gas exchange characteristics of recently matured leaves.

The response of CO₂ assimilation to leaf temperature, measured at high quantum flux, was very similar in all species, each exhibiting a temperature optimum of approximately 37°C. Above about 40°C, all species showed high temperature inhibition, manifested as an irreversible time-dependent decline in CO₂ assimilation.

All four exhibited high rates of net CO₂ assimilation exceeding 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at quantum fluxes of 2.0 $\text{mmol m}^{-2} \text{s}^{-1}$, but none was completely light-saturated at such intensities. Leaf conductance to water vapor declined with decreasing quantum flux in all species, but less rapidly than assimilation, resulting in increasing values of internal CO₂ concentration (c_i). Quantum yield values in three species ($x = 0.048 \pm 0.003 \text{ mol(CO}_2\text{)/mol(photons)}$) were similar to those reported previously for NAD-malic enzyme type C₄ dicots, but leaves of *A. hybridus*, which were deep purple in color, exhibited a lower quantum yield, presumably due to light absorption by betacyanin pigments not involved in photosynthesis.

All four species had net photosynthesis versus c_i responses typical of C₄ species, with a steep initial linear response to c_i followed by a fairly abrupt transition to saturation in the region of 100-150 $\mu\text{l l}^{-1}$. Under near-optimal measurement conditions and high quantum flux, all species maintained c_i values close to the region at which saturation was reached ($x = 148 \pm 17 \mu\text{l l}^{-1}$).

Data pooled across species relating net photosynthesis measured at 2.0 $\text{mmol m}^{-2} \text{s}^{-1}$ quantum flux and 35°C to Kjeldahl nitrogen content revealed a linear relationship, the slope of which was not significantly different ($P=0.05$) from those reported in two other studies employing C₄ species.

INTRODUCTION

In the past decade, considerable attention has been directed towards several members of the C₄ genus *Amaranthus* as potentially valuable crop plants (NAS, 1984; Tucker, 1986). Several species, notably *A. tricolor* and *A. dubius*, are

commonly grown as leafy vegetables in Eastern Asia, as is *A. cruentus* in West Africa. *Amaranthus cruentus*, *A. hypochondriacus* and *A. caudatus* are pale-seeded cultivated varieties, developed in pre-Columbian times for their edible grain; these continue to be grown on a small scale in Mexico, Central America and parts of South America. The discovery by Downton (1973) that the seeds of *A. edulis* (considered a race of *A. caudatus* (NAS, 1984)) yielded very high protein contents focused attention on these so-called grain amaranths. Subsequent studies have reported protein contents for grain amaranths between 12.5 and 17.6% (Teutonico and Knorr, 1985), which compares favorably with values reported for traditional grain crops.

There is considerable genetic diversity within these species (Hauptli and Jain, 1984) and large-scale collecting has resulted in the accumulation of a sizeable germ plasm collection (Kauffman and Reider, 1984). *Amaranthus* species have been used in studying aspects of C₄ photosynthetic metabolism, particularly those features characterizing the C₄ group in which decarboxylation utilizes NAD-malic enzyme (Hatch et al., 1975). However, little has been done to describe the photosynthetic responses to environmental variables of different species or cultivars of *Amaranthus*. The data reported here compare the basic gas exchange responses of four species of grain amaranth.

MATERIALS AND METHODS

The Rodale Research Center, Kutztown, PA, provided seed of *A. hypochondriacus* (RRC Accession #1024), *A. cruentus* (RRC #1041) and *A. hybridus* (RRC #385), and seed of *A. caudatus* was obtained in Peru by author Ehleringer. *Amaranthus hypochondriacus*, *A. cruentus* and *A. caudatus* are pale-seeded cultivated varieties, while *A. hybridus* is a dark-seeded, weedy species from the same subsection of the genus and the presumed progenitor of *A. hypochondriacus* (NAS, 1984), or perhaps of all three cultivated grain species (Hauptli and Jain, 1984).

Plants were grown and measurements taken at the University of Utah, Salt Lake City, Utah. Seeds of experimental plants were germinated in vermiculite and seedlings transplanted into 9-l pots containing a mixture of potting soil, sand, and perlite (2:1:1, v/v). Plants were then grown either under natural conditions outdoors during frost-free periods or under greenhouse conditions, with natural light supplemented by a mixture of metal halide, sodium vapor and incandescent lamps (14/10 h photoperiod). Day/night air temperatures in the greenhouse averaged approximately 30/20°C. Plants were watered to field capacity twice daily, the water containing fertilizer (20:20:20, N:P:K) at a concentration of 150 ppm. Micronutrients were added weekly; plants appeared healthy and no nutrient deficiency symptoms were noticed.

All measurements, except where noted otherwise, were made on recently fully expanded leaves. Simultaneous measurements of photosynthesis and

transpiration were made with an open gas-exchange system previously described (Ehleringer, 1983), in which incident photon flux, leaf temperature, ambient CO_2 concentration and air-to-leaf water-vapor pressure difference (Δw) were controlled. Light was provided by a 1000-W sodium vapor HID lamp, and reduced stepwise using neutral-density filters. Ambient atmospheric pressure averaged 86 kPa.

When measuring the response of CO_2 assimilation to leaf temperature, initial measurements were made at approximately 30°C , and temperatures were then reduced in 4°C increments to about 14°C . The leaf was then returned to the initial conditions to determine whether full recovery from low temperatures was attained. Temperatures were then increased to well above the temperature optimum. If full recovery at 30°C was not attained, the recovery point was corrected to the initial value and high temperature data scaled proportionally. To avoid confounding effects of varying Δw , we attempted to maintain Δw at approximately 25 mPa Pa^{-1} . At extreme temperatures, this was not possible, and consequently Δw values during the temperature measurements varied between 12 and 40 mPa Pa^{-1} , but averaged 25 mPa Pa^{-1} between 20 and 35°C .

Measurements of leaf responses to incident quantum flux and internal CO_2 concentration were made at leaf temperatures of 35°C and Δw values between 22 and 28 mPa Pa^{-1} . During light responses, CO_2 concentration in the cuvette was maintained between 340 and $360 \mu\text{l l}^{-1}$; quantum flux during measurements of response to CO_2 varied between 2.1 and $2.3 \text{ mmol (photons) m}^{-2} \text{ s}^{-1}$. Curves were begun at the highest level of either light or CO_2 concentration. Quantum flux or CO_2 was then reduced stepwise to near compensation point.

Leaf absorptances in the 400 – 700 nm range were estimated by measuring absorptance at 625 nm using an Ulbricht integrating sphere as described by Ehleringer (1981), and leaf amino nitrogen contents were determined by microKjeldahl analysis (Allen et al., 1974) using an autoanalyzer; this technique excludes nitrate nitrogen which may be present in considerable quantity in amaranths.

RESULTS

Each curve in Figs. 1, 2, 3 and 5 below represents an average response based on three replicates. In order to calculate means and standard errors for the data, it was necessary to estimate CO_2 assimilation or stomatal conductance from each measured curve by interpolation at given values of the independent variable.

The measured temperature dependency of net CO_2 assimilation for each of the four amaranth species under study is shown in Fig. 1. At temperatures 2 – 3°C above the optimum, it was not possible to attain steady-state conditions, and photosynthesis declined with time. In this region therefore, measurements were obtained at approximately 15-min intervals.

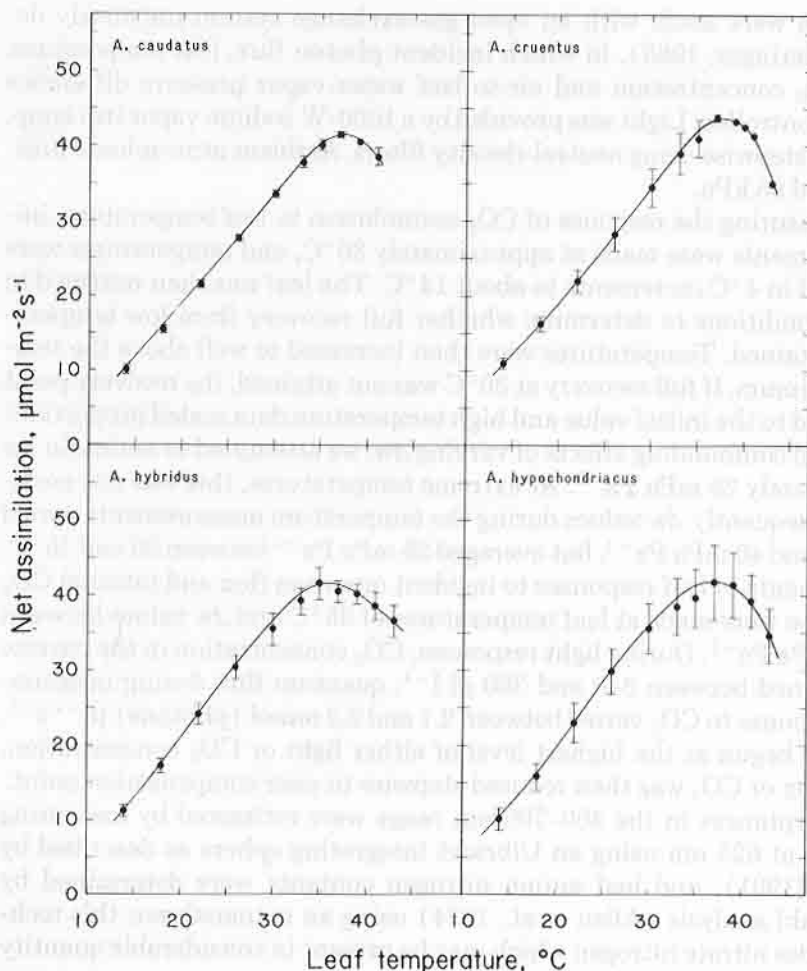


Fig. 1. Responses of net CO₂ assimilation to leaf temperature in leaves of four *Amaranthus* species. Measurement conditions were incident quantum flux of 2.0–2.2 $\text{mmol m}^{-2} \text{s}^{-1}$ and CO₂ concentration of 340–360 $\mu\text{l l}^{-1}$. Each point represents a mean of three determinations; bars represent \pm one standard error.

The light dependency of CO₂ assimilation in these cultivars is shown in Fig. 2. As is typical of many C₄ plants when grown under high light, the response was not saturated even at quantum fluxes exceeding full sunlight. Quantum yields for two leaves of each species, based on careful measurements at quantum fluxes below 0.2 $\text{mmol (photons) m}^{-2} \text{s}^{-1}$, are given in Table 1, along with the absorbances of those leaves.

Leaf conductance to water vapor (g ; Fig. 3) declined more or less in parallel

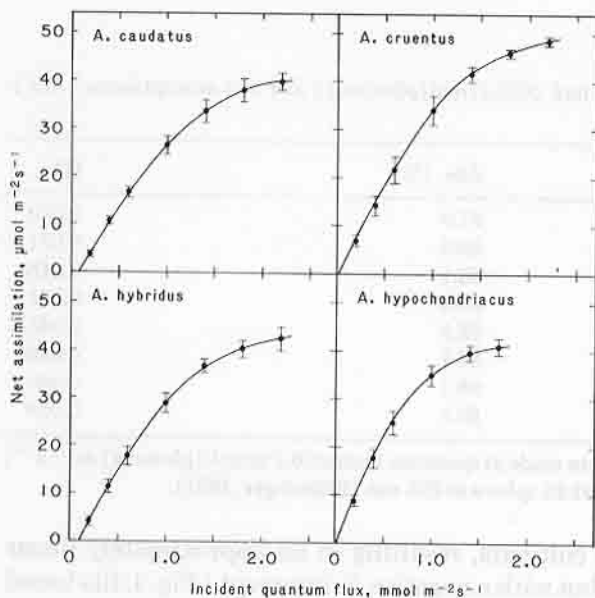


Fig. 2. Responses of net CO₂ assimilation to incident quantum flux in leaves of four *Amaranthus* species. Measurement conditions were leaf temperature of 35°C, CO₂ concentration of 340–360 $\mu\text{l l}^{-1}$ and Δw of 22–28 mPa Pa⁻¹. Each point is a mean of three determinations; bars represent \pm one standard error.

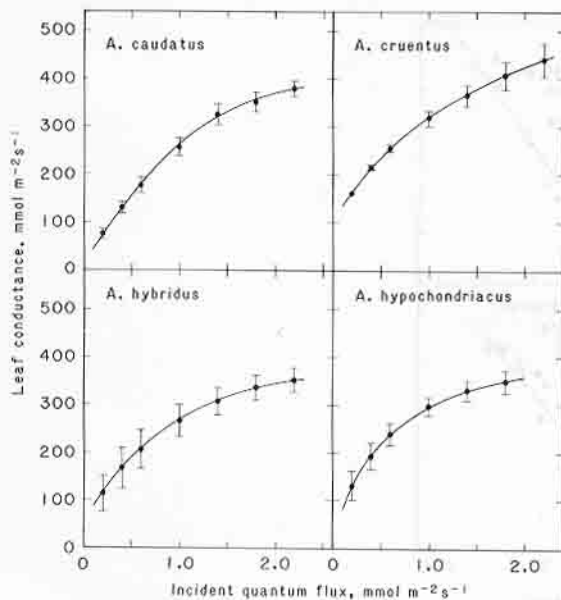


Fig. 3. Responses of leaf conductance to incident quantum flux in leaves of four *Amaranthus* species. Measurement conditions were leaf temperature of 35°C, CO₂ concentration of 340–360 $\mu\text{l l}^{-1}$ and Δw of 22–28 mPa Pa⁻¹. Each point is a mean of three determinations; bars represent \pm one standard error.

TABLE I

Quantum yield determinations (QY; mol (CO₂)/mol(photons)) and leaf absorptances (Abs.) for four species of *Amaranthus*.

Species	Abs. (%)	QY
<i>A. caudatus</i>	87.9	0.050
<i>A. caudatus</i>	89.0	0.051
<i>A. cruentus</i>	83.1	0.048
<i>A. cruentus</i>	85.8	0.051
<i>A. hypochondriacus</i>	82.5	0.043
<i>A. hypochondriacus</i>	86.1	0.046
<i>A. hybridus</i>	88.7	0.040
<i>A. hybridus</i>	89.5	0.038

Net photosynthesis measurements were made at quantum fluxes ≤ 0.2 mmol (photons) m⁻² s⁻¹, and absorptances measured in an Ulbricht sphere at 625 nm (Ehleringer, 1981).

with assimilation (*A*) for all cultivars, resulting in an approximately linear relationship between *A* and *g*, but with a negative Y-intercept (Fig. 4; fits based on linear regressions shown).

The dependency of net CO₂ assimilation on the intercellular CO₂ concentration for all four species (Fig. 5) was typical of C₄ plants. The CO₂ compensation point was close to zero and saturation occurred at approximately 150 μ l

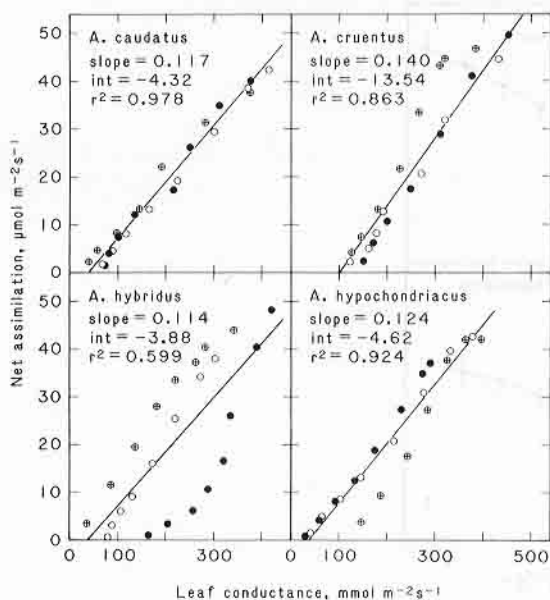


Fig. 4. The relationship between net CO₂ assimilation and leaf conductance in leaves of four *Amaranthus* species, with three replicates per species. Measurement conditions were leaf temperature of 35°C, CO₂ concentration of 340–360 μ l l⁻¹ and Δw of 22–28 mPa Pa⁻¹. Lines are fits based on linear regression equations shown.

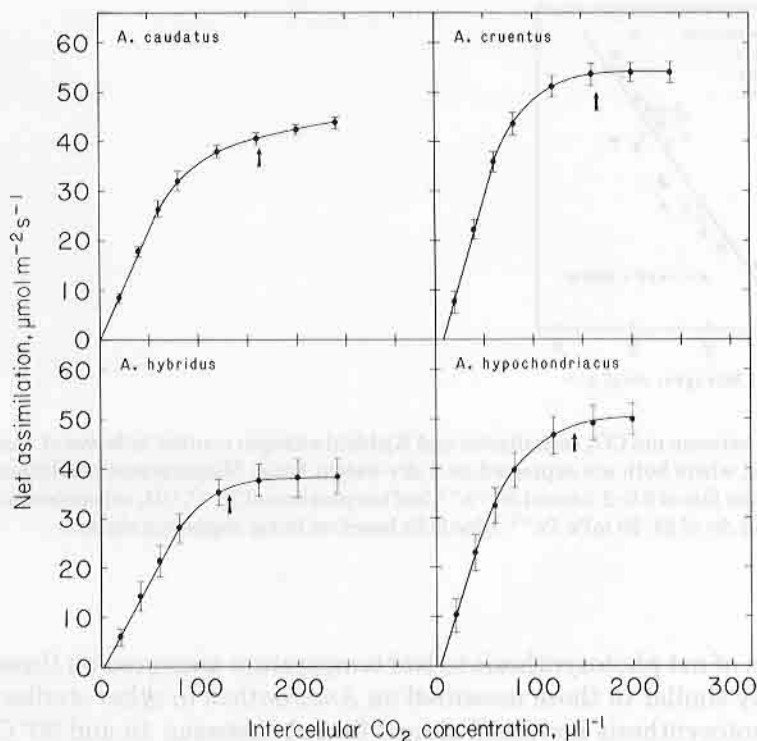


Fig. 5. Responses of net CO₂ assimilation to intercellular CO₂ concentration in leaves of four *Amaranthus* species. Measurement conditions were incident quantum flux of 2.0–2.2 mmol m⁻² s⁻¹, leaf temperature of 35°C and Δw of 22–28 mPa Pa⁻¹. Each point is a mean of three determinations; bars represent one standard error. Arrows denote average internal CO₂ concentration at an external CO₂ concentration of 350 μl l⁻¹.

l⁻¹ CO₂. Leaf conductances at ambient CO₂ concentration (350 μl l⁻¹), high light and moderate Δw (≈ 25 mPa Pa⁻¹) resulted in c_i values between 125 and 170 μl l⁻¹ (denoted for each species in Fig. 5 by an arrow). The average c_i in this study was 148.5 ± 17.4 μl l⁻¹. Note that the c_i value at which these plants operate occurred near the point at which CO₂ saturation was reached.

In Fig. 6, the rate of net CO₂ assimilation, expressed on a dry-weight basis and measured at approximately 35°C, 2.0 mmol (photons) m⁻² s⁻¹, 350 μl l⁻¹ external CO₂ concentration and a Δw of 25 mPa Pa⁻¹, is related to Kjeldahl N content (mmol g⁻¹), and the data fit by linear regression. High assimilation rates and N contents were obtained on leaves grown under optimal greenhouse conditions and measured at their physiological peak. Lower leaf N contents and correspondingly lower photosynthesis rates were obtained on immature or post-mature leaves.

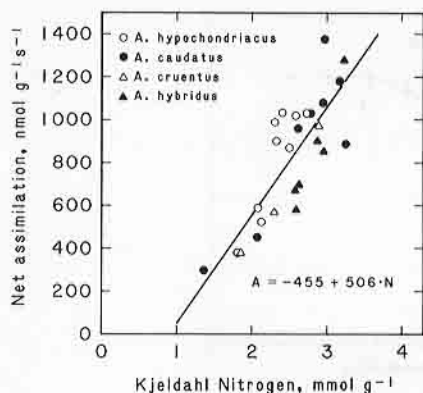


Fig. 6. Relationship between net CO_2 assimilation and Kjeldahl nitrogen content in leaves of four *Amaranthus* species, where both are expressed on a dry-weight basis. Measurement conditions were incident quantum flux of $2.0\text{--}2.2 \text{ mmol m}^{-2} \text{ s}^{-1}$, leaf temperature of 35°C , CO_2 concentration of $340\text{--}360 \mu\text{l l}^{-1}$ and Δw of $22\text{--}28 \text{ mPa Pa}^{-1}$. Line is fit based on linear regression shown.

DISCUSSION

The responses of net photosynthesis to leaf temperature measured on these cvs. are generally similar to those measured on *Amaranthus* in other studies, in which net photosynthesis increased almost linearly between 10 and 30°C and a fairly sharp temperature optimum was achieved, above which rates dropped rapidly. The maximum rates achieved and the temperature optimum varied from study to study, reflecting species differences and/or differences due to temperature acclimation, a phenomenon demonstrated for other C_4 dicots (Percy, 1977), arising from different growth temperature regimes. All four cvs. used in this study had a temperature optimum of about 37°C .

Using *A. edulis*, El-Sharkawy et al. (1968) obtained maximum rates of approximately $38 \mu\text{mol m}^{-2} \text{ s}^{-1}$, similar to those reported here, but with a temperature optimum of about 40°C . Lin and Ehleringer (1983) measured the temperature response of *A. tricolor*, and obtained rates between 40 and $45 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at a temperature optimum of 35°C , perhaps reflecting temperature acclimation in the direction of the growth temperature of 25°C . Ehleringer (1983) obtained extremely high maximum rates ($80 \mu\text{mol m}^{-2} \text{ s}^{-1}$) at 42°C , the temperature optimum of *A. palmeri*, a Sonoran Desert summer annual, reflecting both the thermal characteristics of its native habitat and the high summer temperatures in Salt Lake City where it was grown. At the other extreme, the temperature optimum of *A. lividus*, a vegetable type, was near 30°C (Imbamba and Tieszen, 1977), quite low for a C_4 plant, perhaps reflecting the fact that it is a shade-adapted species.

The temperature responses obtained in this study are typical of C_4 species, in which photorespiration is apparently suppressed by a CO_2 -concentrating

mechanism and any released CO_2 is refixed. The irreversible time-dependent decline in assimilation observed at temperatures above the optimum in this study is also typical (Mooney et al., 1978; Berry and Björkman, 1980), and presumably reflects a change in lipid properties leading to the deterioration of chloroplast membranes (Raison and Berry, 1979), rather than enzyme denaturation, which generally occurs at higher temperatures.

As is typical for C4 species grown under high light, and as shown previously for *A. palmeri* (Ehleringer, 1983), *A. tricolor* (Lin and Ehleringer, 1983) and *A. edulis* (El-Sharkawy et al., 1968), photosynthesis is not light-saturated in these cvs. even at quantum fluxes above that of full sun. Inasmuch as leaves of the cvs. in this study were not observed to change orientation and track the sun during the day as do those of *A. palmeri* (Ehleringer, 1983), incident light is presumably a major limitation to net photosynthesis for much of the day under natural conditions.

Quantum yield values, measured at 35°C and based on absorbed quantum flux at 625 nm (Table 1), averaged $0.048 \pm 0.003 \text{ mol (CO}_2\text{) mol}^{-1}$ (photons), slightly below values reported for other dicot species possessing the NAD-malic enzyme C4 pathway (Ehleringer and Pearcy, 1983). Subsequent absorptance measurements, made with a new light sensor, however, indicated the absorptances shown in Table 1 are 5–10% too high, so the quantum yields reported here may be underestimated by an equal amount. Leaves of *A. hybridus* cv. 385 are deep purple in color, and presumably contain large amounts of betacyanins, the reddish pigments which replace anthocyanins in the Amaranthaceae (Malbry, 1977). If betacyanin absorbs photosynthetic wavelengths in competition with chlorophyll and other photosynthetic pigments, quantum yield will be reduced. A similar phenomenon, involving anthocyanins, was noted in the C3 species *Antidesma platyphyllum*, a Hawaiian understory species (Ehleringer and Pearcy, 1983).

These quantum yield values (Table 1) are roughly 20–25% below those found in C4 species possessing other decarboxylation pathways, or in C4 grasses possessing the NAD-malic enzyme pathway (Ehleringer and Pearcy, 1983), perhaps because there is more leakage of CO_2 out of the bundle sheath cells (Hatch and Osmond, 1976; Farquhar, 1983). In all C4 monocots except NAD-malic enzyme pathway types, the wall separating mesophyll and bundle sheath cells contains a well-defined suberized lamella (O'Brien and Carr, 1970; Hatch and Osmond, 1976), which may act as a barrier to CO_2 diffusion into or out of bundle sheath cells. All C4 dicots studied lack such a suberized lamella, and CO_2 leakage out of the bundle sheath would lead to reduced quantum yields since additional ATP would be required to refix the CO_2 lost (Ehleringer and Pearcy, 1983). Additionally, the bundle sheath cells of NAD-malic enzyme grasses have a higher relative apoplastic surface area than do those in grasses utilizing other decarboxylation pathways (Hattersley, 1982); this trend may

hold for C4 dicots (Ehleringer and Pearcy, 1983) and could also lead to potentially greater CO_2 leakage and reduced quantum yield.

Net photosynthesis as a function of c_i in each of the four species in this study was at least 95% saturated at a c_i value of $150 \mu\text{l l}^{-1}$ (Fig. 5). This is typical of C4 plants (Percy and Ehleringer, 1984) and similar to the situation in *A. tricolor* (Lin and Ehleringer, 1983). Thus, the c_i values obtained under near-optimal measurement conditions (denoted by arrows in Fig. 5; average $c_i = 148 \mu\text{l l}^{-1}$ for all species) were quite near the point at which saturation was reached. Note that increases in conductance leading to c_i values greater than $150 \mu\text{l l}^{-1}$ would lead to a proportional increase in transpiration, with little appreciable gain in CO_2 assimilation, adversely affecting water-use efficiency (assimilation/transpiration). Ehleringer (1983) found in *A. palmeri* that under near-optimal measurement conditions, c_i remained in the range $130\text{--}140 \mu\text{l l}^{-1}$ during a drying experiment in which leaf water potentials fell from -0.5 to -2.2 MPa. On the other hand, Lin and Ehleringer (1983) reported that *A. tricolor*, under light and temperature conditions identical to this study and a Δw of 15 mPa Pa^{-1} , maintained a mean internal CO_2 concentration of $208 \mu\text{l l}^{-1}$; this is quite high for a C4 species, but comparable to values reported for two unusual Hawaiian *Euphorbia* species (Percy et al., 1982).

The ability of C4 plants to adjust conductance and assimilatory capacity enabling them to operate at or near their maximum potential at c_i values between 100 and $150 \mu\text{l l}^{-1}$ is well documented (Körner et al., 1979; Wong et al., 1979) and leads to significantly higher water-use efficiencies than in C3 species which generally operate at c_i values above $200 \mu\text{l l}^{-1}$ (Percy and Ehleringer, 1984). Ramos and Hall (1982) found a linear relationship between CO_2 assimilation and conductance for *A. hypochondriacus* described by the equation

$$A = -6.62 + 0.282 \cdot g$$

They point out that a linear relationship with a zero intercept implies a constant c_i value; a negative Y-intercept, however, as in this study (Fig. 4), implies that c_i increases as photosynthesis declines. In this study, as CO_2 assimilation fell from 40 to $10 \mu\text{mol m}^{-2}\text{s}^{-1}$, c_i increased from about 148 to $210 \mu\text{l l}^{-1}$, resulting in reduced water-use efficiency as quantum flux declined.

CO_2 compensation points in C4 plants are generally near zero, but high CO_2 compensation points have been reported for *A. edulis* and *A. tricolor* grown under greenhouse conditions (Lester and Goldsworthy, 1973), presumably due to leakage of photorespiratory CO_2 out of the bundle sheath. Oxygen sensitivity of photosynthesis (Ku and Edwards, 1980) and release of $^{14}\text{CO}_2$ into CO_2 -free air (Laing and Forde, 1971) also suggest that leakage of photorespiratory CO_2 may occur in *Amaranthus*, at least under certain growth conditions. CO_2 compensation points were not measured directly in this study, but if the initial slopes of the measured A vs. c_i response curves are extrapolated to zero assimilation, values for all cultivars are below $10 \mu\text{l l}^{-1}$.

Brown (1978) suggested that, because CO_2 is concentrated in the bundle-

sheath cells of C4 species, they could achieve comparable or greater assimilation rates than C3 species with much less investment in RuBP carboxylase-oxygenase. Furthermore, the N invested in phosphoenolpyruvate (PEP) carboxylase and associated enzymes of mesophyll cell metabolism in C4 species was relatively small compared to the massive nitrogen investment in RuBP carboxylase/oxygenase in C3 species. Thus, he suggested that C4 plants were inherently more N-use efficient than C3 species, and presented supporting data based on C3 and C4 grasses. He noted that the situation was less clear for C4 dicots, and commented that N values were quite high in several *Amaranthus* species (3.5–4.5% dry weight), comparable to those of C3 species.

Although a linear relationship between CO_2 assimilation rate and leaf N is well established for C3 plants (Field and Mooney, 1986), few studies have looked at the relationship in C4 species. The slope of the relationship between maximal CO_2 assimilation rates at 35°C and leaf Kjeldahl N in this study (Fig. 6), is $506 \text{ nmol } (\text{CO}_2) \text{ mmol } (\text{N})^{-1} \text{ s}^{-1}$ ($r=0.66$) when both photosynthesis and N are expressed on a leaf dry-weight basis. Using identical units, Pearcy et al. (1982) related CO_2 assimilation at 30°C to Kjeldahl N content for eleven *Euphorbia* species in Hawaii, and obtained a slope of 361 ($r^2=0.86$). Due to the considerable scatter in the *Amaranthus* data, these slopes are not significantly different (F-test at $P=0.05$), but the higher value in amaranth may reflect the 5°C higher measurement temperatures. Hunt et al. (1985) related CO_2 -saturated photosynthesis rates in *Amaranthus powelli* ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), measured at 35°C , to Kjeldahl N content (mmol m^{-2}) in a study in which N was altered by employing different NO_3^- levels during growth, and obtained a slope of $240 \text{ nmol } (\text{CO}_2) \text{ mmol } (\text{N})^{-1} \text{ s}^{-1}$ ($r^2=0.96$). Converted to leaf area-based units, the slope in the present study was 308 ($r^2=0.50$), and again the two slopes are not significantly different at $P=0.05$. Singh et al. (1974) found a linear relationship between protein content and photosynthesis in *A. retroflexus* up to rates of $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

Field and Mooney (1986) obtained a slope of $149 \text{ nmol } (\text{CO}_2) \text{ mmol } (\text{N})^{-1} \text{ s}^{-1}$ for a large collection of C3 species when both photosynthesis and nitrogen content were expressed on a dry-weight basis. Thus, although *Amaranthus* leaves often contain large amounts of N, high photosynthesis rates confer substantially greater N-use efficiency than in C3 species, presumably for reasons outlined above.

Amaranthus represents the only genus of C4 dicots to be utilized extensively as crop plants. Based on this study, it is clear that under non-stressful greenhouse growth conditions, amaranth is capable of high net photosynthesis rates, comparable to those of other highly productive C4 crop species such as corn and sorghum. Furthermore, the excellent nutritional qualities of *Amaranthus* increase its attractiveness as a subject of future research.

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