

Photosynthetic characteristics of *Amaranthus tricolor*, a C₄ tropical leafy vegetable

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Abstract. The gas exchange characteristics are reported for *Amaranthus tricolor*, a C₄ vegetable amaranth of southeastern Asia. Maximum photosynthetic capacity was $48.3 \pm 1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and the temperature optimum was 35°C. The calculated intercellular CO₂ concentration at this leaf temperature and an incident photon flux (400–700 nm) of $2 \text{ mmol m}^{-2} \text{ s}^{-1}$ averaged $208 \pm 14 \mu\text{l l}^{-1}$, abnormally high for a C₄ species. The photosynthetic rate, intercellular CO₂ concentration, and leaf conductance all decreased with an increase in water vapor pressure deficit. However, the decrease in leaf conductance which resulted in a decrease in intercellular CO₂ concentration accounted for only one fourth of the observed decrease in photosynthetic rate as water vapor pressure deficit was increased. Subsequent measurements indicated that the dependence of net photosynthesis on intercellular CO₂ concentration changed with water vapor pressure deficit.

Introduction

Amaranthus, a relatively large genus of C₄ photosynthetic pathway plants, found in diverse habitats, includes both weedy and agronomically useful species [10, 18, 19]. The agronomic species consist of both grain types and leafy vegetable types, and both forms are valued for their high protein content and balanced amino acid composition [7, 10, 20]. Amaranths are known to have high lysine (5.0%) and sulfur-containing amino (4.4%) contents, especially in comparison with other plant protein sources [7, 12]. Protein contents of the dry matter of leaves are reported to be greater than 27% [3, 5, 14].

Associated with the high leaf protein contents, one would expect to observe high intrinsic photosynthetic capacities since a large fraction of the leaf proteins are associated with the photosynthetic process. The gas exchange characteristics of the grain and weedy amaranth species measured thus far support this prediction [4, 8, 15, 21]. In fact, Singh et al. [21] showed a linear relationship between protein content and photosynthesis in *A. retroflexus* up to rates of $40 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ S}^{-1}$.

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Little is known, however, about the productivity characteristics of the leafy vegetable amaranths, although they are an important component in the diets in many subtropical countries [12]. The data which do exist suggest that vegetable amaranths are highly productive. Deutsch [3] conducted trials on six species and found that one species, *A. tricolor*, yielded 20 metric tons per hectare of leaf material in 25–30 days. Leafy vegetable yields of 26 metric tons per hectare in *A. caudatus* have been reported by Oke [16]. These plants are frequently ratooned for multiple harvests over a 2–3 month period.

The purpose of the current study was to investigate the basic photosynthetic gas exchange characteristics of a common leafy vegetable amaranth. The species used in this study was *A. tricolor*, which is commonly grown throughout the southeastern Asia and western Pacific regions.

Materials and methods

Seeds of *Amaranthus tricolor* were collected from Guangzhou, People's Republic of China and were greenhouse grown in Salt Lake City, Utah, during the winter and spring of 1982. Plants were grown individually in 10 l pots in a mixture of potting soil and perlite. They were watered daily and fertilized weekly. In the greenhouse natural sunlight was supplemented by metal halide and sodium vapor high intensity discharge lamps to create midday irradiances of approximately $1.6\text{--}1.8\text{ mmol m}^{-2}\text{ s}^{-1}$ (400–700 nm). Daily incident quantum flux in the 400–700 nm waveband averaged near 40 mol m^{-2} during the 14 h/10 h day/night cycle. The daily greenhouse temperature cycle was approximately 25/15°C and the midday relative humidity 25%.

Simultaneous measurements of photosynthesis and transpiration were made with an open gas exchange system described previously by Ehleringer [4], in which irradiance, leaf temperature, ambient CO₂ concentrations, and water vapor pressure deficit could be controlled. Single attached leaves were initially exposed to an irradiance of $2\text{ mmol m}^{-2}\text{ s}^{-1}$ (400–700 nm), a leaf temperature of 35°C, an ambient CO₂ concentration of $330\text{ }\mu\text{l l}^{-1}$, and a water vapor pressure deficit of 1.5 kPa. The boundary layer conductance to water vapor in the chamber was approximately 50 mm s^{-1} . Three to five replicates were run for each analysis.

Carbon isotope ratios were determined on leaves at Brigham Young University using standard techniques as described by Smith and Brown [22].

Results and discussion

The temperature dependence of net photosynthesis was measured at high irradiances and under normal atmospheric conditions on recently matured leaves (approximately 10–15 days old) (Figure 1). At an irradiance of

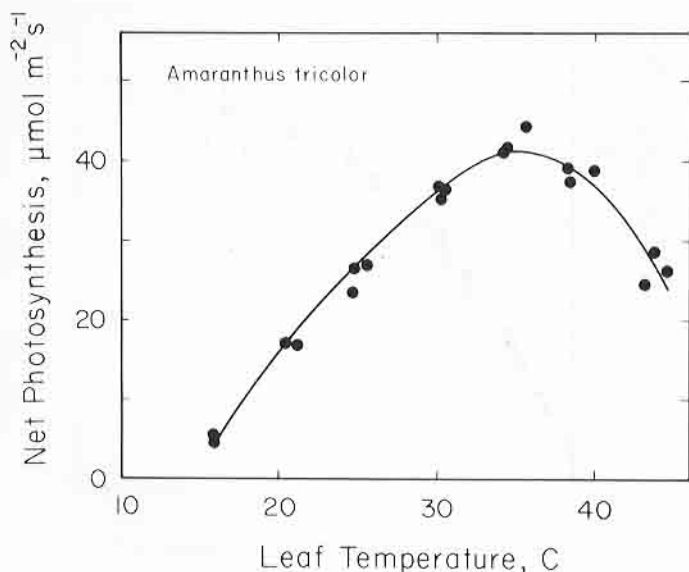


Figure 1. The response of net photosynthesis in leaves of *Amaranthus tricolor* to changes in leaf temperature. Irradiance in the 400–700 nm waveband was $1.7\text{--}1.8 \text{ mmol m}^{-2} \text{s}^{-1}$, ambient CO_2 concentration $330 \mu\text{l l}^{-1}$, 21% O_2 , and VPD 1.5 kPa.

$1.7\text{--}1.8 \text{ mmol m}^{-2} \text{s}^{-1}$ (400–700 nm), the temperature optimum was 35°C with the peak photosynthetic rate averaging $42.3 \pm 1.3 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ($\bar{x} \pm \text{s.e.}$). At the temperature optimum, the leaf conductance to water vapor averaged $14.8 \pm 1.2 \text{ mm s}^{-1}$ and the intercellular CO_2 concentration $208 \pm 14 \mu\text{l l}^{-1}$. The photosynthetic rate exhibited only a small temperature dependence between 30 and 40°C . However, below 30°C photosynthesis decreased rapidly at an approximate rate of $2.2 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1} \text{C}^{-1}$. Above 40°C , the photosynthetic rate again decreased rapidly and became unstable (= equilibrium rates could not be obtained) at temperatures above 44°C .

The photosynthetic response to irradiance at a leaf temperature of 35°C showed no saturation even at an irradiance of $2 \text{ mmol m}^{-2} \text{s}^{-1}$ (400–700 nm), although it seemed clear that photosynthetic rate was approaching a maximum (Figure 2). At the highest irradiance, the photosynthetic rate averaged $48.3 \pm 1.0 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$.

Below an incident irradiance of $0.5 \text{ mmol m}^{-2} \text{s}^{-1}$, the relationship between photosynthesis and irradiance was linear. The calculated quantum yield over this range (assuming a leaf absorptance of 85%) was 0.056. This value is well within the range of values reported for other NAD-malic enzyme C_4 dicot species [5, 6].

The maximum net photosynthetic rates measured in *A. tricolor* were at the high end for the range of values reported for other grain and vegetable

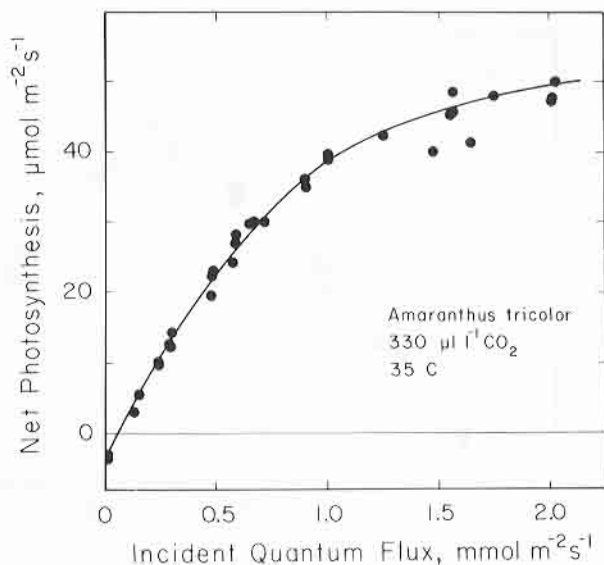


Figure 2. The response of net photosynthesis in leaves of *Amaranthus tricolor* to changes in the incident quantum flux (400–700 nm). Leaf temperature was 35 C, ambient CO_2 $330 \mu\text{l l}^{-1}$, 21% O_2 , and VPD 1.5 kPa.

amaranthus. Imbamba and Tieszen [15] reported a maximum photosynthetic rate of approximately $33 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *A. lividus*, an African vegetable. El-Sharkawy et al. [8] reported a maximum photosynthetic rate of approximately $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *A. edulis*, an Argentinian grain type. On the other hand, Ehleringer [4] reported an upper maximum photosynthetic rate of approximately $80 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *A. palmeri*, a weedy Sonoran Desert species.

The dependence of net photosynthesis on intercellular CO_2 concentration in *A. tricolor* exhibited a steep rise up to approximately $200 \mu\text{l l}^{-1}$ and plateaued shortly thereafter (Figure 3). Under high irradiances and ambient conditions of $330 \mu\text{l l}^{-1} \text{CO}_2$, leaves operated with an intercellular CO_2 concentration which close to the transition point in the response curve.

The intercellular CO_2 concentrations in leaves of *A. tricolor* under normal ambient conditions were much higher than the $125\text{--}150 \mu\text{l l}^{-1}$ values typically reported for C_4 species [1, 2, 17]. The abnormally high values of approximately $208 \mu\text{l l}^{-1}$ were consistently observed under repeated measurements on plants grown at different times of the year. Such high intercellular CO_2 values are not unknown for C_4 species. Pearcy et al. [17] have investigated the gas exchange characteristics of a number of C_4 *Euphorbia* species native to the Hawaiian Islands. While most of the *Euphorbia* species have intercellular CO_2 concentrations in the $125\text{--}150 \mu\text{l l}^{-1}$ range under normal atmospheric conditions, there are two notable exceptions. *E. remyi* and

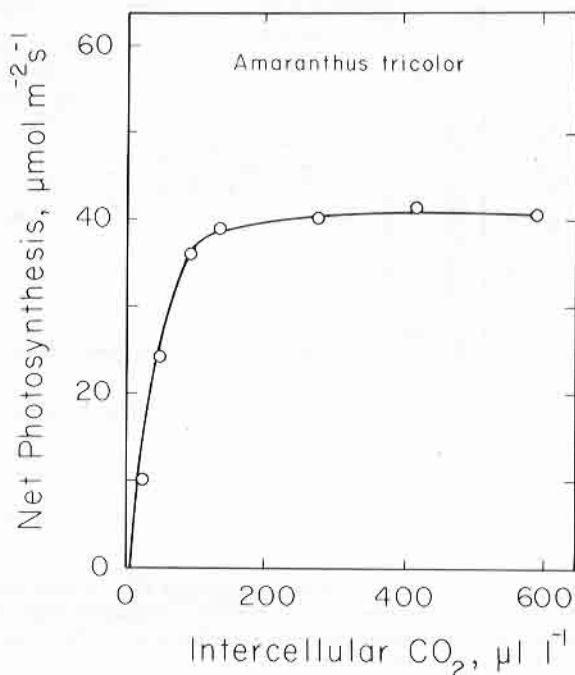


Figure 3. The response of photosynthesis in leaves of *Amaranthus tricolor* to changes in the intercellular CO₂ concentration. Irradiance in the 400–700 nm waveband was 2.0 mmol m⁻² s⁻¹, leaf temperature 35 °C, 21% O₂, and VPD 1.5 kPa.

E. halemanui have intercellular CO₂ concentrations of 235 ± 12 and $171 \pm 19 \mu\text{l l}^{-1}$, respectively. The basis for the unusually high intercellular CO₂ concentrations in these two *Euphorbia* species or in *A. tricolor* is not known.

The carbon isotope discrimination ratios, $^{13}\text{C}/^{12}\text{C}$, were determined for *A. tricolor* to determine if the value was consistent with or different from other C₄ species. The average carbon isotope discrimination was -14.9 ‰ , higher than typically observed with other C₄ species [23].

On a daily basis under the greenhouse growth conditions and also under natural conditions in the field, leaves are exposed to a great change in the water vapor pressure deficit as air temperature and relative humidity fluctuate. Such changes in microclimate are known to effect stomatal conductance and thus photosynthetic rates [13]. In order to determine the extent to which photosynthesis was influenced by vapor pressure deficits, the gas exchange parameters were measured as a function of water vapor pressure deficit (VPD) between 0.6–3.4 kPa. The photosynthetic rate in leaves of *A. tricolor* decreased almost linearly as VPD increased (Figure 4). Over the VPD change of 1.5 kPa to 3.4 kPa, net photosynthesis decreased from 44 to 36 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, an 18% increase. Over the same VPD change,

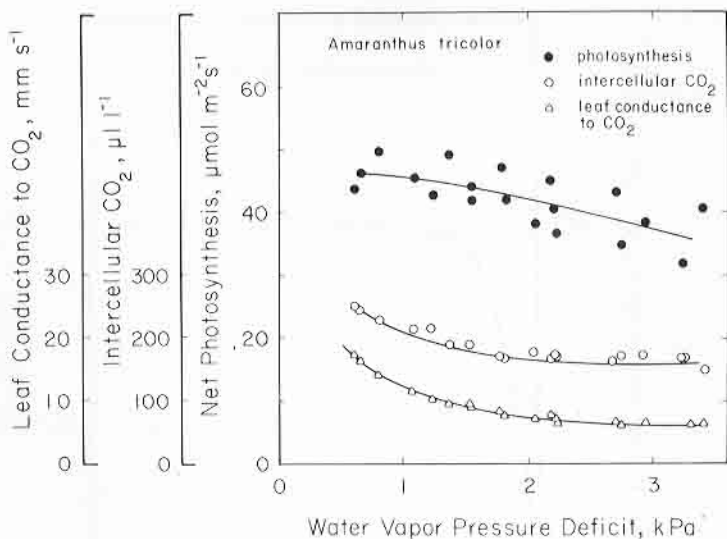


Figure 4. The responses of photosynthesis, intercellular CO_2 concentration, and leaf conductance to CO_2 in leaves of *Amaranthus tricolor* to changes in water vapor pressure deficit. Irradiance in the 400–700 nm waveband was $2.0 \text{ mmol m}^{-2} \text{s}^{-1}$, leaf temperature 35°C , ambient CO_2 $330 \mu\text{l l}^{-1}$, and $21\% \text{ O}_2$.

the leaf conductance to CO_2 decreased 9 to 6 mm s^{-1} , a 33% decrease. As a consequence, the calculated intercellular CO_2 concentration decreased from 195 to $160 \mu\text{l l}^{-1}$, a 18% decrease.

Although intercellular CO_2 concentration decreased with increasing vapor pressure deficit, it could not have been completely responsible for the decrease in photosynthetic rate. Using the intercellular CO_2 dependence response curve from Figure 3, we can calculate the expected relationship between photosynthesis and leaf conductance. Similar analyses have been done by Björkman et al. [2] and Farquhar and Sharkey [9]. Given the 33% reduction in leaf conductance, the intercellular CO_2 concentration should have declined to approximately $157 \mu\text{l l}^{-1}$, resulting in a direction in net photosynthetic rate to approximately $42 \mu\text{mol m}^{-2} \text{s}^{-1}$. The decline in net photosynthetic rate was much greater, down to $36 \mu\text{mol m}^{-2} \text{s}^{-1}$. From this we conclude that as the VPD decreased from 1.5 kPa to 3.4 kPa, stomatal factors were responsible for approximately one fourth of the decline and non-stomatal factors were responsible for three fourths of the decrease.

When the intercellular CO_2 dependence of photosynthesis was measured on the same leaf at two different vapor pressure deficits, the response curves differed (Figure 5). The photosynthetic capacity of the leaf decreased by 11% when exposed to the higher vapor pressure deficit. Thus, it would appear that in response to increasing vapor pressure deficits, photosynthetic rate declines in part due to stomatal closure (through decreased intercellular CO_2

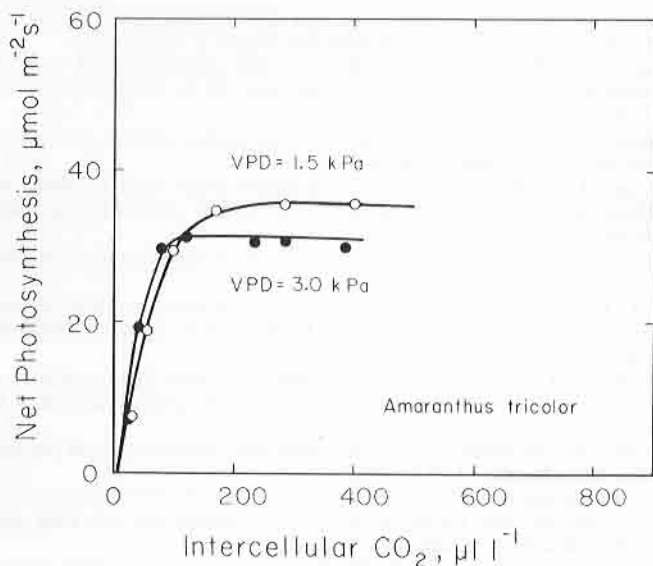


Figure 5. The response of photosynthesis in leaves of *Amaranthus tricolor* to changes in the intercellular CO₂ concentration at two different vapor pressure deficits.

concentration) and in part due to a decrease in photosynthetic capacity. This, seemingly direct effect of vapor pressure deficit on photosynthetic capacity has also been observed in C₃ plant *Malvastrum rotundifolium* [11] and is discussed independently as unpublished results by Farquhar and Sharkey [9].

In summary, photosynthetic capacities in *A. tricolor* were somewhat higher than values previously reported for other grain or vegetable amaranths, but lower than values for weedy amaranths. The CO₂ dependence of photosynthesis was somewhat atypical of the pattern commonly observed in C₄ species and intercellular CO₂ concentration was maintained near 208 μl l⁻¹ under ambient conditions. In other gas exchange characteristics, *A. tricolor* was typical of the pattern observed in other high light adapted C₄ plants.

Acknowledgements

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