Nitrogen Fertilization and Light Intensity Affects the Agronomic Performance and Leaf Blade Oxalate and Nutrient Concentrations of Vegetable Amaranth

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ABSTRACT

A study was undertaken to determine if vegetable amaranth (*Amaranthus tricolor* L.) leaf oxalates and mineral nutrients are affected by nitrogen fertility and simulated cloudy weather conditions prior to harvest. Three-week-old transplants of 'RRC 241' (RC) and 'Hinn Choy' (HC) were given applications of 0, 50 and 100 kg N/ha on 8 July and 15 July 1992. In the 3rd week after transplanting, plants were exposed to 100, 70, and 50% of ambient solar radiation for nine (HC) and ten (RC) days, respectively. Plants were harvested in the seventh week. Cultivars differed in leaf number and area, yield, height, mineral uptake, and stem fresh and dry wt. HC was higher in leaf blade K, Mg, Na, Fe, Zn, Cu, NO_3, chlorophyll (chl), and carotenoids, but lower in Ca and total oxalic acid than RC. Light reduction or shading had no effect on leaf area or plant fresh wt., but decreased the dry wt. of stems, leaf blades, and plants while increasing plant water content. Increasing shade had a linear (L) effect on leaf blade soluble oxalic acid, NO_3, protein, K, Mg, S, P, Al, Fe, and Cu (dry wt. basis). There were L and quadratic (Q) increases in chl and carotenoids as shading increased. Photosynthesis (Ps) rates were reduced with 50% shade. Nitrogen application increased stem length, and plant fresh and dry wt. Increasing N increased leaf blade protein (L,Q), Na (L), Mn (L), chls (L,Q), carotenoids (L,Q), but decreased Mg (L), P (L,Q), Zn (L,Q), and soluble oxalic acid (L in RC). As supplemental N increased, nitrate levels increased in RC (L) and HC (Q).

RESUMEN

Se realizó un estudio para determinar si los oxalatos y nutrientes minerales foliares en el amaranto (*Amaranthus tricolor* L) eran afectados por la fertilización con nitrógeno y por las condiciones climáticas simuladas de nubosidad precedentes a la cosecha. Transplantes de 3 semanas de edad de 'RRC 241' (RC) y Hinn Choy' (HC) recibieron aplicaciones de 0, 50 y 100 Kg de N/ha en Julio 8 y 15 de 1992. En la tercera semana después del transplante, las plantas se expusieron a 100, 70, y 50% de radiación solar ambiental por nueve (HC) y diez (RC) días, respectivamente. Se cosecharon las plantas en la séptima semana. Los cultivares difirieron en el número y el área de las hojas, el rendimiento, la altura, la incorporación de minerales, y el peso fresco y seco. La lámina foliar de HC presentó mayor contenido de K, Mg, Na, Fe, Zn, Cu, NO_3, clorofila(cl) y carotenoides, pero menor contenido de Ca y ácido oxálico total que RC. La reducción de la luz o sombreado no tuvo efecto en el área foliar o el peso fresco de la hoja, pero disminuyó el peso seco de tallos, láminas foliares, y de las plantas mientras que aumentó el contenido de agua de la hoja. El incremento de sombra tuvo un efecto linear (L) sobre el ácido oxálico soluble de la lámina foliar, NO_3, proteína, K, Mg, S, P, Al, Fe y Cu (en base a peso seco). Hubo incrementos lineares y cuadráticos (C) y en clorofila y carotenoides a medida que se incrementó el sombreado. Las tasas de fotosíntesis se redujeron con el 50% de sombreado. La aplicación de nitrógeno incrementó la longitud del tallo y el peso fresco y seco de la planta. El aumento de N aumentó la proteína de la lámina foliar (L, C), Na (L), Mn (L), cl (L, C), carotenoides (L, C), pero disminuyó el Mg (L), P(L, C), Zn (L, C), y el ácido oxálico soluble (L en RC). A medida que se incrementó el N suplementario, los niveles de nitrato se incrementaron en RC (L) y HC (C).

Additional index words. Amaranthus tricolor, pigments, mineral nutrition, shading, leafy greens

Fresh vegetable amaranth (Amaranthus spp.) is being grown, imported, and consumed in the U. S. in increasing amounts (Makus, 1990). Dehydrated leaves of *A. cruentus* L. are grown and presently marketed in the Republic of South Africa (A. D. Goosen and W. J. Van der Bank, 1993, personal communication).

Shading can effect leaf composition. Several cool-season leafy greens are known to accumulate anti-nutritional factors, such as nitrates and oxalates, under weather conditions that are cool and/or cloudy in combination with high levels of applied nitrogen (N). Periods of low light intensity, shortened photoperiods, and lower growing temperatures were reported to increase leaf oxalate (Kitchen et al., 1964) and nitrate levels

(Cantliffe, 1972) in spinach. Shading or a reduction in light intensity can increase oxalate levels in Chenopodium spp. (Singh, 1974). Shading, induced by a corn canopy, reduced dry matter accumulation, leaf area, plant height, and main stem branches in *A. retroflexus* L. (McLachlan et al., 1993). Shading can accelerate the remobilization of mineral nutrients from leaves (Marschner, 1986).

Increasing total N fertilization levels from 0 to 200 kg N/ha decreased oxalic acid levels in spinach leaves from 839 to 303 mg /100 g fresh leaf weight (Verma et al., 1970). *Amaranthus cruentus* leaves accumulated more soluble oxalate, total oxalate, and nitrate when grown in soil of 'high' vs 'medium' fertility (Schmidt et al., 1971). Provided there is adequate soil P, supplemental N can increase *Amaranthus tricolor* L. leaf blade chlorophyll and protein and plant biomass (Makus, 1986; Makus, 1992).

The objective of this experiment was to determine the effect of shade or reduced light intensity and N application on vegetable amaranth performance, biomass partitioning, and several leaf blade constituents (protein-N, mineral nutrients, nitrate, and oxalates) associated with human nutrition. In the interest of brevity, the term shade or shading will generally be substituted for expressions relating to the 'reduction in light intensity'.

MATERIAL AND METHODS

On 8 July 1992, three-week-old containerized plants of vegetable amaranth RRC 241 (now USDA PI 2153) and 'Hinn Choy' were transplanted into a Leadvale silt loam soil (fine-silty, siliceous, thermic, Typic Fragiudults) with a 6.8 pH. Plants were spaced 15x15 cm apart in 4 rows on 0.12 high X 0.6 wide x 1.35 m long raised beds. Beds were on 1.2 m centers. Plant density was 215,270 plants/ha. The beds received 90 kg P/ha, 90 kg K/ha, and one-half the N rate of 0, 100 or 200 kg/ha (broadcast basis) on the day of transplanting. The remaining 0, 50 or 100 kg N/ha was applied one week later. Two weeks after transplanting, the 36-plant plots were covered 50 cm above the soil line with 0, 30, and 50% shade fabric (Chicopee, Cornelia, Ga.) in order to simulate overcast weather. After 5 days, the shade fabric was removed for 2 days, then re-installed for a total of 9 (HC) or 10 (RC) days before the final harvests on 4 Aug. and 5 Aug., respectively. The earlier maturing HC was harvested on 4 Aug.

During the shading period, ambient air temperatures were measured with shielded thermocouples at 15 cm above the soil. LI-190SA quantum sensors (Li-Cor, Lincoln, Neb.) were used to measure photosynthetic photon flux density (PPFD) at each shade level, and the cumulative output was expressed in radiometric units (McCree, 1972). Wetness sensing grids (Campbell Sci., Logan, Utah) were used to measure leaf wetness (Gillespie and Kidd, 1978). Temperature, light, and wetness measurements were recorded hourly with a CR-10 data logger (Campbell Sci.) or in the case of the wetness, every 15 min. when grid resistance was < 20 k ohms. Soil moisture (by neutron probe and recording tensiometers) were similarly monitored in one replicate. Trickle irrigation was used to restore soil moisture to field capacity when soil moisture fell below -20 k Pa.

Table 1. Agronomic responses of 'Hinn Choy' and 'RRC 241' amaranth accessions given supplemental N at 0, 100 or 200 kg/ha and exposed to 0, 30, or 50% shade 9 and 10 days, respectively, prior to harvest.

Main Effects	Yield	Plant dry wt	Plant water content	Stem length	Stem dry wt	Leaf blade dry wt	Petiole dry wt	Stem dry wt	Leaf dry wt
	mt/ha	g	%	cm	g	g	as % total	as % total	as % total
Cultivar (C)									
RRC 241	11.7 a	5.78	88.5	20.8 a	1.14 a	4.26	6.6 b	19.7 a	80.2
Hinn Choy	8.2 b	5.42	88.3	16.6 b	0.92 b	3.85	10.9 a	17.0 b	83.0
	**[z]	NS	NS	**	*	NS	**	**	**
Shade (S)									
0%	9.6	6.56 b	86.4 b	17.6 b	1.15	4.73 a	9.3	17.6 b	82.4 a
30%	10.7	5.63 ab	88.9 ab	19.8 a	1.11	4.02 ab	9.0	19.4 a	80.6 b
50%	9.5	4.61 b	90.0 a	18.7 ab	0.85	3.41 b	7.8	18.0 ab	82.0 ab
	NS	**	*	*	NS	**	NS	*	*
Polynomial fit	Q*[y]	L**	L**	Q*[y]	L*	L**	--	Q**[y]	Q**[y]
Nitrogen (N)									
0 kg/ha	8.3 b	4.93 b	89.2	17.5 b	0.83 b	3.43 b	11.3 a	17.3 b	82.7 a
100 kg/ha	10.9 a	5.93 a	88.1	19.7 a	1.15 a	4.35 a	7.5 b	19.0 a	81.0 b
200 kg/ha	10.6 a	5.95 a	87.9	18.9 ab	1.12 a	4.39 a	7.4 b	18.7 ab	81.3 ab
	**	*	NS	*	**	*	*	*	*
Polynomial fit	L*, Q*[y]	L*	--	Q*[y]	L**[y]	L**	L*, Q**[y]	L*[x]	L*[x]
Interactions:									
C x S	NS	NS	NS	NS	NS	NS	NS	NS	NS
C x N	NS	**	*	NS	NS	*	NS	NS	NS
S x N	NS	NS	NS	NS	NS	*	NS	NS	NS
C x S x N	NS	NS	NS	NS	NS	NS	NS	NS	NS

[z]NS, *, ** = Not significant or significant at P=0.05, P=0.01, respectively; L = linear, Q = quadratic.
[y]'RRC 241' only.
[x]'Hinn Choy' only.

Table 2. Main effects of cultivar, shade intensity, and supplemental nitrogen on total leaf blade nitrogen (N) and leaf blade mineral nutrients (dry wt. basis).

Main Effects	N	P	K	Ca	Mg	Na	S	Mn	Fe	Zn	Cu	Al	NO_3
	---------------------------------%---------------------------------							--------------------------μg/g--------------------------					
Cultivar (C):													
RCC 241	4.51	.366	4.62 b	3.56 a	0.771 b	.054 b	.453	265	432 b	55.2 b	47.4 b	622	3144 b
Hin Choy	4.62	.350	5.06 a	3.23 b	1.035 a	.125 a	.444	293	521 a	67.1 a	62.6 a	704	4992 a
	NS[z]	NS	**	*	**	**	NS	NS	**	**	**	NS	**
Shade (S)													
0%	4.45 b	.313 b	4.60 b	3.48	.858	.082	.414 b	258	442	59.9	52.0	622	3718 b
30%	4.49 b	.365 a	4.74 b	3.35	.884	.096	.458 a	303	475	61.4	55.1	648	3724 b
50%	4.76 a	.396 a	5.18 a	3.34	.966	.090	.472 a	277	511	62.2	57.9	720	4763 a
	**	**	**	NS	NS	NS	**	NS	NS	NS	NS	NS	**
Polynomial fit:	L**	L**	L*	--	L*	--	L**	--	L**	--	L*	L*	L**,Q*
Nitrogen (N):													
0 kg/ha	3.91 c	.398 a	4.87	3.35	.983 a	.065 b	.445	253 b	487 a	70.8 a	57.2	709 a	1632 c
135 kg/ha	4.79 b	.344 b	4.92	3.54	.852 b	.096 a	.460	267 b	435 b	55.5 b	53.1	602 b	4808 b
270 kg/ha	5.00 a	.332 b	4.74	3.29	.872 b	.107 a	.441	318 a	506 a	57.1 b	54.8	679 a	5765 a
	**	**	NS	NS	**	**	NS	**	*	**	NS	**	**
Polynomial fit:	L**,Q**	L**,Q*	--	--	L*	L**	--	L**	--	L**,Q**	--	--	L**,Q**
Interactions:													
C x S	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
C x N	NS	NS	NS	NS	*	*	NS	*	NS	NS	NS	NS	**
S x N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
C x S x N	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS

[z]NS, *, ** = Not significant or significant at P=0.05, P=0.01, respectively, L=linear, Q=quadratic.

On 25 July leaf temperatures were taken with an infrared (IR) thermometer (Omega OS-2101, Omega Engineering, Stamford, Conn.) between 1115 and 1200 hrs in treatments receiving only the 100 kg N/ha rate. On 6 Aug., between 1445 and 1545 hrs, CO_2 fixation rates (Ps), in treatments receiving only the 100 kg N/ha rate, were measured with a LI-6200 portable photosynthesis system (Li-Cor).

Twelve plants, selected from the middle two rows of each four-row plot, were used to determine yield, plant height, and to supply leaf blades for nutrient analysis. Leaf blades located approx. 1/3 the distance from the base of the plant were then washed, frozen, lyophilized, ground through a 40 mesh (0.36 mm^2) screen and stored at -20C until analyzed. A single representative plant from each replicate was used to determine the following plant biomass attributes: fresh and dry weight of the stem, petiole, leaf blade, and corresponding fresh and dry weights of these plant parts, as a percent of the total plant fresh and dry weights. Stem length, plant water content, and leaf area were also determined from these plants. Leaf area was determined with a CID Model 201 area meter (CID, Vancouver, Wash.) for a main-axis leaf located 1/3 the distance from the base of the stem.

Nitrate and P were determined colorimetrically, protein-N and S by the Leco combustion method, and mineral elements by ICP spectrometry (Plank, 1992). Leaf pigments were determined by the method of Welburn and Lichtenthaler (1984), and oxalates by an A.O.A.C method (1984).

The experiment was analyzed as a split plot, with 4 replications in a randomized complete block design. Cultivars (2) and shade levels (3) were randomized as whole plots and nitrogen fertilizer levels (3) were randomized as sub-plots.

Table 3. Effect of shading and supplemental soil nitrogen rate on leaf blade oxalates (dry wt. basis) of two vegetable amaranth cultivars.

Main Effects	Oxalates soluble	Oxalates insoluble	Oxalates Total	Soluble: insoluble ratio
	---------------mg/g---------------			
Cultivar (C)				
RCC 241	27.0	9.5 a	36.8 a	3.0 b
Hin Choy	25.5	6.8 b	32.6 b	4.4 a
	NS[z]	**	**	**
Shade (S)				
0%	22.9 b	9.0	32.2	3.2
30%	27.6 a	8.1	35.4	3.6
50%	28.2 a	7.5	36.7	4.2
	*	NS	NS	NS
Polynomial fit	L**,Q*[y]	L**[y]	L**[y]	L**[y]
Nitrogen (N)				
0 kg/ha	27.7 a	8.0	35.8 a	3.8
135 kg/ha	25.8 b	8.5	34.6 ab	3.7
270 kg/ha	25.2 b	8.0	33.5 b	3.7
	**	NS	*	NS
Polynomial fit	L*[y]	--	--	--
Interactions				
C x S	NS	NS	NS	NS
C x N	*	NS	NS	NS
S x N	**	NS	**	NS
C x S x N	*	**	NS	NS

[z]NS, *, ** = Not significant or significant at P=0.05, P=0.01, respectively; L=linear, Q=quadratic.
[y]RRC241 only.

Means were compared by 't' tests using the PDIFF option of LSMEANS statement in PROC GLM of SAS (Ver. 6.04, Cary, N.C.).

RESULTS AND DISCUSSION

Environment. The 0 and 30% shade treatments required 27 and 11 mm of supplemental water, respectively, when soil moisture fell below -20 k Pa. From 7 July until 31 July, 84 mm of rainfall occurred, much of this during the shading period, so that no further supplemental irrigation was required. Shade did not affect leaf wetness, as measured by moisture grids, or soil moisture, as measured by the neutron probe (data not shown).

During shading, average cumulative daily irradiance was 53.2, 35.1, and 22.7 kW•m^{-2} (as PAR) for 0, 30, and 50% shade, respectively. Corresponding average maximum air temperatures 15-cm above the soil line were 35.0, 33.1, and 32.3C. Corresponding average daily air temperatures, measured every 60 s, was 25.4, 25.0, and 24.9C, respectively. Corresponding average daily soil temperatures at 15-cm depth were 25.9, 25.6, and 25.6C, respectively. Corresponding tensiometer readings at 30-cm soil depth were -11.8, -11.6, and -8.6 k Pa, respectively. Leaf temperatures, measured on 25 July by IR thermometry, were 31.8, 30.6, and 28.8C, respectively, and were different at each level of shade ($P<0.01$). The decrease in leaf temperature was linear as shade level increased ($P<0.05$).

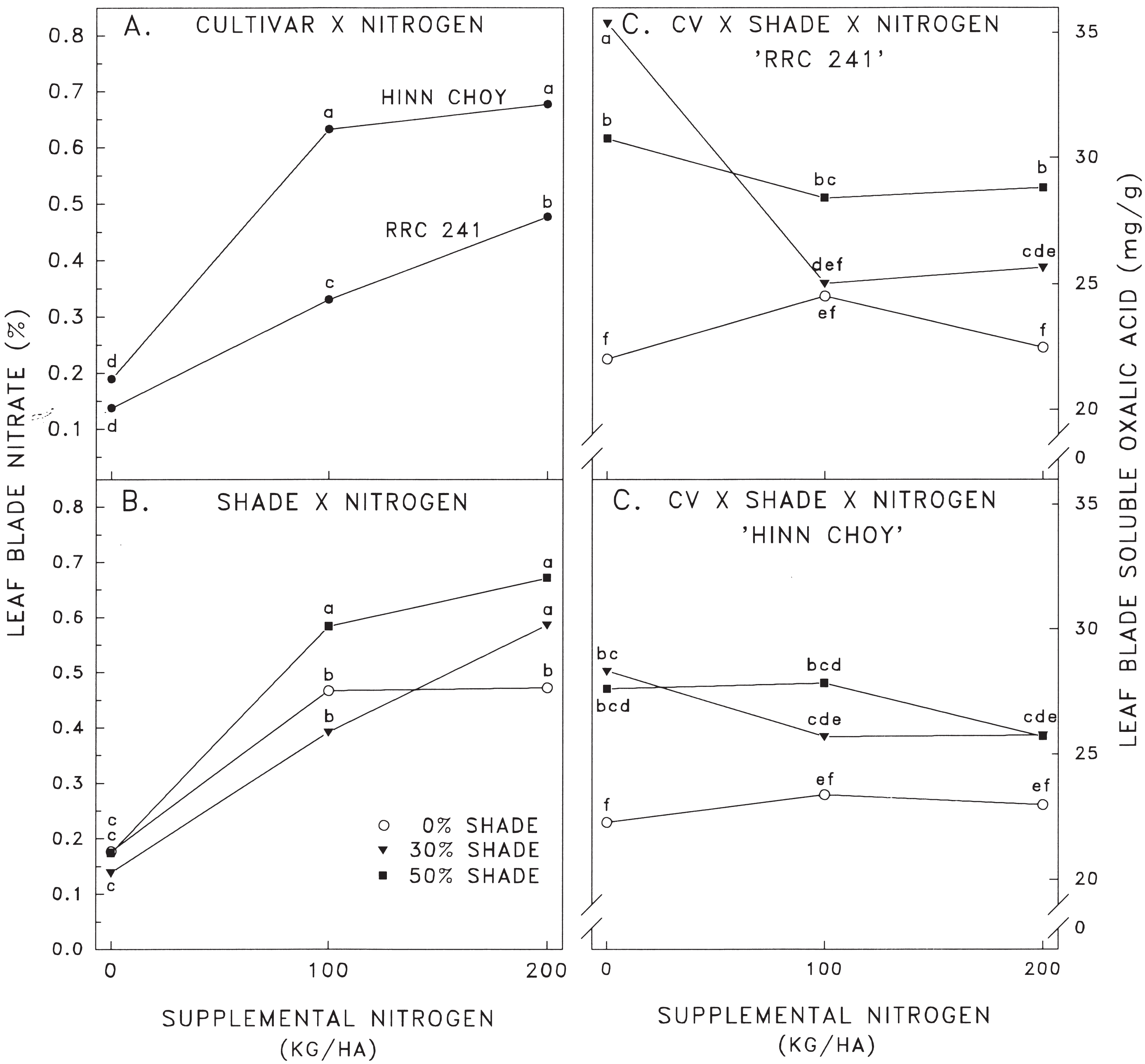

Fig. 1. Interactions are shown between cultivar x nitrogen rate (Fig.1A) and shade x nitrogen rate (Fig. 1B) for leaf blade nitrates, and between cultivar x shade x nitrogen rate for 'RRC 241' (Fig. 1C) and for 'Hinn Choy' (Fig. 1D) for leaf blade soluble oxalates. Lower case letters are used to separate mean differences (P<0.05).

Agronomic. RC was higher in yield, stem length, stem dry weight, and stem dry wt. (as % total plant dry wt.), but lower in petiole dry wt. (as % total plant dry wt.) and leaf dry wt. (as % total dry wt.) compared to HC (Table 1). There were no differences in plant dry wt., plant water content or leaf blade dry wt. between cultivars. HC leaves were greater in area (50 vs 67 cm^2 per leaf) than corresponding RC leaves ($P<0.01$). The mean number of leaves on the main axis stem for RC and HC were 17.8 and 16.9, respectively ($P<0.015$). No additional main effects or interactions were observed in leaf number or leaf area (data not shown).

Increasing shade from 0% to 50% linearly (L) reduced plant dry wt., stem dry wt. and leaf blade dry wt. Plant water content was increased by shading (L). Response of RC to increased shade was quadratic (Q) in terms of yield, stem length, stem dry wt. (as % total plant dry wt.), and leaf dry wt. (as % total plant dry wt.). There were no differences in yield and petiole dry wt. (as % total plant dry wt.) when plants were shaded to 50% of ambient light (Table 1).

Increasing N application rate from 0 to 200 kg/ha increased yield (L, also Q in RC), plant dry wt. (L), stem length (Q in RC), stem dry wt. (L in RC), blade dry wt. (L), petiole dry wt. (as % total) (L, also Q in RC), stem dry wt. (as % total plant dry wt.) (L in HC) and leaf dry wt. (as % total plant dry wt.) (L in HC).

Agronomic responses not affected by shade and N level were leaves per plant, stem fresh wt., petiole fresh wt., leaf blade fresh wt., leaf area, petiole dry wt., avg. plot plant height, plant fresh wt., leaf blade fresh wt. (as % total plant fresh wt.), petiole fresh wt. (as % total plant fresh wt.), stem fresh wt. (as % total plant fresh wt.), leaf fresh wt. (as % total plant fresh wt.), and leaf blade dry wt. (as % total plant dry wt.) (data not shown).

Supplemental N reduced plant water content (%) in RC; HC was not affected (data not shown for interactions). Leaf blade dry wt. was lowest in RC in the absence of supplemental N, but was not effected by any level of supplemental N in HC. Leaf blade dry wt. increased with added N when cultivars were exposed to full sunlight before harvest. Under 30 and 50% pre-harvest shade, there was no increase in leaf blade dry wt. from either 100 or 200 kg/ha of supplemental N (Table 1).

Leaf blade constituents. HC was higher in leaf blade K, Mg, Na, Fe, Zn, Cu, NO_3 (Table 2), chlorophylls (chl) and carotenoids (Table 4), but lower in Ca and insoluble and total oxalates (Table 3) than was RC. No significant differences between cultivars were found in leaf blade protein-N, P, S, Mn, Al, and soluble oxalic acid.

Decreasing light intensity before harvest linearly increased protein-N, P, K, Mg, S, Fe, Cu, Al, NO_3 (also Q), soluble oxalate and total oxalates (in RC), chl a, b, and total (also Q), and total carotenoids (also Q) in leaf blades.

Increasing N rates increased protein-N (L, Q), Na (L), Mn (L), NO_3 (L, Q), chl a, b and total (L, Q), and carotenoids (L, Q), but decreased P (L, Q), Mg (L), Zn (L, Q), and soluble oxalates (L in RC only) in leaf blades.

Leaf blade NO_3 levels increased linearly in RC and quadratically in HC when supplemental N was applied (Fig. 1A). Leaf NO_3 levels were not affected by shading when supplemental N was not applied. When 100 kg N/ha was applied, leaf blade NO_3 concentration was similar in 0% and 30% shaded leaves, but higher at 50% shade. At the 200 kg N/ha application rate, leaves exposed to full sun were lowest in NO_3 (Fig. 1B).

In *Amaranthus*, the effect of plant maturation or harvest date on leaf nitrates and mineral nutrients can vary. Plant age and leaf position of *A. tricolor* sp. *tristis* did not influence

Table 4. Main effect of shade and nitrogen rate and cultivar on leaf blade chlorophyll and total carotenoids of vegetable amaranth.

	Chlorophylls[y]				
Main Effects[z]	'a'	'b'	Total	Total carotenoids[y]	Chl:carot ratio
Cultivar					
RCC 241	8.24 b	1.99 b	10.23 b	2.52 b	3.55 b
Hin Choy	8.96 a	2.23 a	11.19 a	2.68 a	3.66 a
	**[x]	**	**	**	*
Shade					
0%	7.82 b	1.91 b	9.73 b	2.41 b	3.53
30%	8.97 a	2.21 a	11.19 a	2.70 a	3.63
50%	9.01 a	2.20 a	11.22 a	2.69 a	3.65
	**	**	**	**	NS
Polynomial fit	L**,Q**	L**,Q*	L**,Q**	L**,Q*	L*
Nitrogen					
0 kg/ha	7.65 b	1.85 b	9.50 b	2.39 b	3.48 b
100 kg/ha	8.86 a	2.20 a	11.05 a	2.68 a	3.61 ab
200 kg/ha	9.30 a	2.28 a	11.58 a	2.73 a	3.73 a
	**	**	**	**	**
Polynomial fit	L**,Q*	L**,Q**	L**,Q*	L**,Q**	L**

[z]The C x S x N interaction for chl:carot ratio was significant (P<0.03).
[y]mg/g dry wt.
[x]NS, *, ** = Not significant or significant at P=0.05, P=0.01, respectively; L=linear, Q=quadratic.

leaf nitrate levels in either 4- or 8-week-old plants (Prakash and Pal, 1991). However, in *A. cruentus* and *A. dubius*, Walters et al. (1988) reported leaf nitrate levels increased when soil applied N was increased to 100 kg/ha and that leaf nitrate levels decreased with later harvest dates or plant age. Nitrate reductase activity, in *A. retroflexus*, appears to be stimulated by light intensity, leaf age, and soil nitrate availability (Chu et al., 1980). Mineral nutrients were reported to decrease in *A. cruentus* after seven weeks from sowing (Olufolaji and Tayo, 1980).

Supplemental N had no effect on leaf blade soluble oxalates in HC and RC plants exposed to full sun (Fig. 1C). However, when shaded, RC accumulated more soluble oxalates as supplemental N was applied, when grown in 50% shade than in 30% shade. Soluble oxalate levels in HC leaf blades were similar at both shade levels when N was applied. In the presence of reduced light, leaf blade soluble oxalate levels were similar between cvs when supplemental N was applied, but were higher in RC than in HC at 50% shade when plants were given 0 and 200 kg N/ha. Ammonium nitrate application rates, similar to those used in this study, were found to increase total oxalic acid levels in HC leaf blades, and nitrogen source (nitrate vs ammoniacal) modulated leaf blade oxalate levels (Makus, 1999).

In either full sun or 50% shade, increasing levels of supplemental N increased the chl:carotenoid ratio in HC but not RC (P=0.028). Under conditions of 30% shade, the ratio increased in both cultivars when N was added (data not shown). In the case of HC, the ratio of chl to carotenoids linearly increased with N application. This relationship also has been reported for another C_4 plant, corn (Khamis et al., 1990).

Net photosynthesis, measured 6 Aug. under 0, 30 and 50% shade, was 23.8, 22.0 and 16.5 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, respectively. Corresponding levels of PPFD were 1328, 938, and 569 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. Both net Ps and PPFD decreased linearly as shading increased (P<0.05) but internal leaf CO_2 concentration, leaf temperature, and stomatal conductance were similar (data not shown). Under conditions of natural irradiance of between 1500 - 2200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR, *Amaranthus edulis* L. showed little decline in net CO_2 assimilation, stomatal conductance, and net internal CO_2 over the duration of an 8 h photoperiod (340 μbar CO_2, 21% O_2) (Blechschmidt-Schneider et al., 1989). Leaf Ps increased in *A. retroflexus* when plants were given increasing levels of N (Byrd et al., 1992); growth rates and maintenance respiration were also higher at higher leaf N levels. Jajoo and Bharti (1993) reported that anions, such as oxalate, interfered with photosynthesis system I in spinach chloroplasts, *in vitro*. Oxalates were found in higher concentrations under shade in this study and may affect amaranth in a similar way.

Johnston et al., (1984) found that Na deficient *A. tricolor* plants had lower chl a:b ratios. In this study, leaf blade Na levels were 57% higher in HC and HC leaves were also significantly higher in chl a:b ratio compared to RC. Sodium ions can stimulate the regeneration of phosphoenolpyruvate in mesophyll chloroplasts of *A. tricolor* (Murata et al., 1992). The higher Na in HC leaf blades may help facilitate the higher Ps rates in HC vs RC observed here.

In this study, the response of *Amaranthus tricolor*, a C_4 plant, to supplemental N and reduced light levels was similar to those reported for spinach, a C_3 plant, with respect to leaf nitrate and oxalate. Supplemental N fertilizer and lower light levels increased leaf blade nitrates. Supplemental N reduced leaf blade soluble oxalate levels (in RC, only), whereas decreased light levels increased soluble oxalates and most mineral nutrients in both accessions. The darker-green accession, HC, was higher in leaf blade nitrate, chl and carotenoid pigments, most mineral nutrients and lower in total oxalates and yield than was RC.

Although cloudy weather and N fertilizers can increase leaf NO_3 and soluble oxalate levels in vegetable amaranth, the modest increases in these anti-nutrients should not be of concern to producers or consumers.

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