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Biosystematics and Agronomic Potential of Some Weedy and Cultivated Amaranths

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Summary. Three weedy amaranths (*Amaranthus hybridus, A. retroflexus* and *A. powellii*) from nine California sites, three domesticated species (*A. caudatus, A. hypochondriacus* and *A. cruentus*) from the USDA plant inventory as well as other sources and a naturally-occurring crop-weed hybrid were studied for numerical taxonomy using morphological and allozyme variation data. The crop and weedy species groups were easily separated and the hybrid populations were found to be intermediate. Surprisingly, very little intraspecific variation was present. Crop, weed and hybrid amaranths were also compared for their yielding ability, harvest index, seed efficiency of grain production and protein, popping quality and other agronomic traits. Although field plot yields were similar among the three groups of species (700 Kg/ha seed without fertilizer treatment and water, ranging to 3000 Kg/ha with fertilizer applications of 170 Kg N/ha, and abundant water), the harvest index of the weedy group was much higher (25-40%) than the domesticated species (10-15%). The allocation of biomass to seed production is positively correlated with seed yield in the domesticated but not in the weedy types, whereas the percentages of biomass as stem material and as seeds are negatively correlated. Several weedy and crop characteristics together should provide the basis of new improved cultivars through genetic recombination and selection.

Key words: Amaranths – Biosystematics – Agronomic Potential

Introduction

Grain amaranths are currently enjoying revived interest as an agronomic crop by diverse groups (Lexander 1970; Ruttle 1963; Marx 1977). This ancient New World pseudocereal is attractive because of its high leaf and seed protein content, nutritious amino acid complement and high digestibility of this protein (Lexander 1970; Downton 1973), possession of the C_4 photosynthetic pathway and the availability of domesticated types with favorable crop morphology. Although weedy amaranths are used as a vegetable crop, enriching the protein-or lysine poor diets of many people worldwide (Martin and Roberté 1975), and grain amaranths are grown as leafy vegetables in many parts of Africa, there are rather few published reports of yield, cultural and harvesting techniques or comparability with other agronomic crops as a grain crop (Singh 1961; El Sharkawy et al. 1968; National Academy of Sciences 1975).

Sauer (1967) provided a thorough review of the systematics of cultivated amaranths and their wild and weedy relatives. Previously amaranth taxonomy was confusing, as one notes from this quote: 'In published works, *A. leucocarpus* is commonly reduced to a variety or synonym of either *A. caudatus* L. or *A. hybridus* L. Herbarium specimens of this group are commonly identified as either *A. paniculatus* L. or *A. hypochondriacus* L.' (Sauer 1967). Much of the taxonomic synonymy in the genus was simplified by Sauer (1967) who listed three crop species: *Amaranthus hypochondriacus, A. caudatus* and *A. cruentus*. Coons (1975) recently attempted further simplification through her careful study of some new collections from Ecuador. She concluded that the two weedy species, *A. hybridus* and *A. quitensis*, cannot be separated morphologically; likewise *A. hybridus* and *A. caudatus* show overlap in their variation patterns. Overall, the crop taxonomy is confused by the lack of many discrete qualitative characters defining species, the extremely wide range of phenotypic plasticity among species and by the possible introgression and hybridization involving weedy and crop species. Species are now mainly defined by the continuously ranging size and shape characteristics of minute flower parts 1.5-5 mm long. These were chosen by Sauer (1967) because they were relatively less affected by en-

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vironmental variation; however, they do vary under certain environmental conditions and are quite variable from flower on the same plant. Some gross inflorescence characteristics such as branching and size have also been considered diagnostic. Many of these taxonomic studies involved specimens from native habitats and little biosystematic or population genetic work has been done.

This study was undertaken to characterize several weedy and domestic amaranths using Sauer's (1967) list of characteristics as well some additional traits. Two populations from the delta region of Central California, where Tucker and Sauer (1958) postulated that extensive interspecific hybridization had occurred, were included. Very few accessions were available for most species. Numerical taxonomy involving quantitative traits and other measures of genetic similarity based on qualitative traits was useful in defining species and hybrids as clusters. Yield components were estimated from among the 25 traits measured on the crop, weed and crop x weed hybrid amaranths grown in field and in greenhouse in order to evaluate their potential for grain production.

Materials and Methods

A total of 504 plants from the collections listed in Table 1 were grown in 15 cm wide pots in a uniform greenhouse environment from February to April 1977 at Davis, California. Each collection was represented by a row of five plants randomly arranged in six replications. Incandescent lights were utilized to increase day-length to 16 hours for four weeks in an attempt to synchronize flowering. Each pot was fertilized every week with 1/2 gram of 10:10:10 NPK pelleted fertilizer.

Twenty five traits were scored on each plant: 1) seed color (1 = pink, 2 = white, 3 = brown and 4 = black); 2) bract length, in tenths of mm (largest bract on a random glomerule was used); 3) tepal length, in tenths of mm (largest tepal of female flowers of a different random glomerule seed); 4) excurrency of bract spine

Table 1. Collections used in taxonomic study

A. cruentus

1. (CHI-1) sent from Tanzania, where they were used as potherbs. Two increases in greenhouse, 1975. (Collection we received came from a single plant grown by M.P. Coons at Indiana University.)
2. (76-42) Escaped ornamental at campus of Universidade Federal de Vicosa, Vicosa, MG, Brazil – in mixed stand with *A. spinosus*, 1976; one seed increase at Davis.
3. (Africa) Unnumbered accession of USDA plant inventory from Africa. Probably used as potherb.
4. (Rodale) From Mexico, obtained through Rodale Press. (One increase in Pennsylvania). Used as a pseudocereal, popped to make alegrias.

A. caudatus

5. (BP352) Collected at Quinoa, near Ayacucho, prov. ayacucho, Peru, 1971. Grown for use as a pseudocereal.
6. P.I.166107 from USDA plant inventory. A mixed collection of *A. caudatus* and *A. hypochondriacus*. Mali Chua, India, 1948. No use specified.

A. hypochondriacus

7. P.I.337611 from USDA plant inventory. Originally collected from Kitoba market, in Uganda, 1968. No use specified.
8. P.I.288282, from USDA plant inventory. Originally collected from Bhrugupur, Surendranagar district, India, in 1963. No use specified.
9. P.I.166107 from USDA plant inventory. Mixed collection of *A. caudatus* and *A. hypochondriacus*. Mali Chua, India, 1948. No use specified.
10. (DN306B3) from Central Mexico originally collected by David Nelson. Seeds used to make confections. Common name is Chia.

A. retroflexus

11. (La Grange) Roadside ditch 2.5 miles west of La Grange Hwy 132. July, 1975.
12. (Walnut Grove) gravelly roadside stand just east of Staten Island bridge, near Walnut Grove, Calif. 1975.
13. (Road 132) Corn crop border weeds along Hwy 132,30 miles east of Modesto, Calif. 1975.
14. (Sutter Buttes) Roadside weed stand 1 mile north of intersection of Acacia Rd. and Butte House Rd., on the latter, Sutter Co., Calif. 1975.

A. hybridus

15. (Moorpark) Vacant corner at intersection of Evelyn and Moorpark Roads, Mountain View, Santa Clara Co., Calif. 1975.
16. (Howard Rd) Roadside weed stand on edge of safflower field, 3 miles from intersection of Howard Rd. and Hwy 4, near Stockton, Calif. July, 1975.

A. powellii

17. (Tulelake) Collected at Agricultural Experiment Station at Tulelake, California. Aug. 1975.

Delta Hybrid populations

18. (Acampo) One half-mile east of Center Rd. on Acampo Rd. near Lodi, California weed in grape vineyard. Aug. 1975.
19. (Thornton) Weed on edge of cornfield on Thornton Road, 5 miles north of its junction with Hammer Lane. Aug. 1975.

Table 2. Estimates of means ($\bar{x}$) and standard errors (SE)

		Seed Color	Bract Length	Tepal Length	Excurrent spine	Tepals recurving	Tepals spatulate	Leaf blade length	Petiole : blade length × 100	Blade length width × 100	Degree of bifurcation	# of branches	Branching polarity	Inflorescence leaves	Erectness	Erectness (laterals)	Utr. Abscission	Space between laterals	Leaf axil Inflorescences	Fibrous stem structures	Leaf Area	Length of longest lateral branch	# of plants
cruentus																							
CHI-1	$\bar{X}$	4	26.4	18.9	+	–	–	187.5	54.8	223.9	1.8	4.1	+	–	2	1	2	1.0	–	2	124.5	5.1	30
	±SE		5.1	1.7				16.0	7.1	20.0	0.3	1.8						0.2			20.6	3.9	
76.42	$\bar{X}$	4	26.7	20.3	+	–	1	244.4	34.4	238.4	1.8	4.1	+	–	2	1	2	1.0	–	2	199.0	5.2	30
	±SE		1.3	1.8				29.5	8.2	23.7	0.3	2.4						0.0			40.0	2.7	
Africa	$\bar{X}$	4	24.3	18.0	+	–	1	187.8	56.2	210.7	2.0	5.3	+	–	2	1	2	1.0	–	2	132.9	3.75	24
	±SE		2.5	2.0				17.3	7.1	19.7	0.0	1.8						0.0			23.4	1.5	
Rodale	$\bar{X}$	2	25.7	21.2	+	–	2	165.3	56.4	176.4	1.2	1.9	+	–	1	2	2	1.0	–	2	123.6	12.5	30
	±SE		2.5	2.0				13.3	56.4	176.4	1.2	1.9	+					0.2			23.9	4.6	
caudatus																							
BP352	$\bar{X}$	1	22.2	19.1	+	–	2	159.5	54.6	292.2	1.5	1.8	+	–	3	3	2	1.1	–	2	99.9	19.8	29
	±SE		2.7	1.8				10.8	7.0	15.7	0.5	1.0						0.3			16.0	9.2	
166107	$\bar{X}$	1	23.1	19.5	+	–	2	169.8	48.7	203.4	1.7	2.7	+	–	3	3	2	1.0	–	2	113.2	12.8	7
hypochondriacus																							
337611	$\bar{X}$	2	43.7	22.1	+	–	1	195.2	34.7	230.3	1.6	2.2	+	–	1	1	2	1.0	–	2	130.9	6.8	28
	±SE		2.8	2.2				14.3	5.3	18.8	0.5	1.2						0.0			18.8	2.5	
288282	$\bar{X}$	4	42.6	23.4	+	–	1	140.6	54.8	209.4	2.2	6.9	+	–	1	1	2	2.3	–	2	74.5	32.2	30
	±SE		2.1	2.5				10.6	9.4	13.3	0.4	1.5						0.6			9.5	4.9	
DN306B3	$\bar{X}$	2	44.8	24.1	+	–	1	179.0	46.5	256.0	1.7	3.6	+	–	1	1	2	1.0	–	2	99.9	26.0	28
	±SE		2.6	2.4				22.1	9.0	24.2	0.4	2.2						0.0			22.7	5.2	
166107	$\bar{X}$	2 (14%)	44.2	23.4	+	–	1	131.7	53.0	195.7	2.3	3.7	+	–	1	–	2	2.8	–	2	70.8	30.4	14
	±SE	4 (86%)	2.9	2.7				16.4	12.7	17.9	0.5	1.3						1.5			17.0	10.9	
Delta hybrids																							
Acampo	$\bar{X}$	4	31.6	25.3	+	+	3	92.3	97.8	165.9	3.0	10.1	+	+	1	2	+	4.6	+	2	40.9	26.4	30
	±SE		2.6	1.5				6.9	11.6	14.1	0.0	1.2						1.2			7.0	3.7	
Thornton	$\bar{X}$	4	40.6	21.9	+	–	3	158.5	61.1	169.3	2.9	10.5	–	–	1	2	1	1.1	+	2	117.2	10.6	30
	±SE		2.6	2.3				10.6	6.7	6.5	0.3	1.5						0.1			14.5	2.8	
retroflexus																							
Rd 132	$\bar{X}$	4	45.6	31.7	–	+	3	69.0	67.0	150.5	2.9	5.3	–	+	1	2	1	4.5	+	1	25.5	12.2	28
	±SE		5.1	2.4				12.1	10.1	10.9	0.2	1.0						3.0			8.3	1.5	
Walnut	$\bar{X}$	4	44.0	29.3	–	+	3	69.0	63.1	154.6	2.8	5.5	–	+	1	2	1	5.6	+	1	25.1	13.2	30
	±SE		4.9	1.8				10.3	8.2	10.8	0.3	0.9						1.8			7.4	3.3	
Sutter	$\bar{X}$	4	45.4	30.5	–	+	3	66.9	66.9	140.6	2.9	5.5	–	+	1	2	1	4.1	+	1	25.7	11.1	26
	±SE		5.3	2.4				11.1	15.5	10.2	0.2	1.0						1.5			6.7	2.6	
La Grange	$\bar{X}$	4	47.1	31.2	–	+	3	63.4	64.1	146.6	2.9	5.5	–	+	1	2	1	4.8	+	1	23.0	13.6	25
	±SE		3.4	2.7				8.6	9.7	13.4	0.2	0.8						1.5			6.7	2.6	
hybridus																							
Moorpark	$\bar{X}$	4	42.6	23.9	+	–	1	72.1	56.1	179.6	4.0	6.8	–	+	1	1	1	4.4	+	1	23.0	15.9	25
	±SE		4.5	2.0				7.1	8.4	18.4	0.5	1.3						0.8			4.8	2.2	
Howard	$\bar{X}$	4	42.1	24.5	+	–	1	71.5	52.4	193.7	3.7	7.8	–	+	1	1	1	4.2	+	1	22.1	17.6	25
	±SE		5.2	2.8				16.7	14.6	20.1	0.5	1.4						1.1			9.2	5.3	
powellii																							
Tulelake	$\bar{X}$	4	51.5	25.7	–	–	1	60.1	53.2	187.6	2.2	4.6	–	+	1	1	1	3.7	+	1	15.4	9.6	29
	±SE		5.2	2.3				10.8	8.2	14.8	0.4	0.8						1.0			5.0	2.4	
cruentus × *hybridus* F_1's																							
Africa	$\bar{X}$	4	38.6	18.8	*	–	1	109.0	58.1	175.3	3.0	8.8	–	+	1	2	1	6.8	+	2	53.5	34.6	6
	±SE		3.3	2.1				7.9	4.6	8.8	0.0	1.4						0.9			6.6	3.5	

(+ = spine excurrent, – = not excurrent; measured bract scored); 5) recurving of tepals (– = erect, + = recurving); 6) tepal shape (1 = acuminate, 2 = semispatulate, 3 = spatulate); 7) leaf blade length in mm (largest leaf); 8) petiole length (mm): blade length (mm) X 100 (largest leaf); 9) blade length (mm): blade width (mm) X 100 (largest leaf); 10) degree of bifurcation of stems; 11) number of branches along main stem; 12) lateral branches longest near top(+) or bottom(–) of stem; 13) % of total dry weight as stems; 14) % of total dry weight as leaves; 15) % of total dry weight as flowers; 16) % of total dry weight as seeds (harvest index); 17) presence of leaves throughout terminal inflorescence (+ = at least one inflorescence lateral is not in a leaf axil, – = all inflorescence laterals are present in leaf axils); 18) erectness of central inflorescence stem (1 = erect, 2 = horizontally drooping at approximately 45°-90°, 3 = vertically drooping at 180°); 19) erectness of inflorescence laterals (1 = erect, 2 = partially lax at 45°-90° from main inflorescence stem, 3 = completely lax, drooping with gravity); 20) utricle abscission (1 = utricle base abscises from flower, 2 = utricle base persistent); 21) space on main stalk between uppermost and second inflorescence laterals (in cm); 22) presence of inflorescence in branch axils (+ = presence, – = absence); 23) presence of fibrous structures on stem epidermis (1 = absence, 2 = presence); 24) area of largest leaf (calculated from length and width); and 25) length of longest inflorescence lateral.

All characters were scored or measured at maturity except for the leaf size characters which were measured two weeks after anthesis because of early leaf abscission. Abscised leaves were saved and included in the biomass partitioning data (characters 13-16). Plants were considered mature when all seeds were set, tepals were dry, and no new flowers were being produced.

The same 19 populations were compared electrophoretically for banding phenotypes of five enzyme systems: Alcohol dehydrogenase, leucine amino peptidase, acid phosphatase, glutamine-oxalacetic transaminase and esterase. Standard 12.8% starch gels were used with Triscitrate buffers, at pH 7.5 and 8.3, after the method of Scandalios (1974). Whole seedlings grown in greenhouse flats until three weeks of age were crushed in .014 M mercaptoethanol and .1M Tris citrate, pH 7.0 buffer, for crude enzyme extraction.

Each of the twenty field plots consisted of eight 76 cm beds, 4.5 m long. Each bed was planted with two rows 25 cm apart. Plants were thinned at 3 weeks of age to a within row spacing of 13 cm. Ten plots received fertilizer application (170 Kg N/ha), abundant irrigation and meticulous weeding; the others were given no fertilizer application whatsoever, sparse watering and no weeding. These will be designated as Treatments 1 and 2, respectively. Besides overall plot grain yields, 25 individual plants were harvested from each plot and scored for individual plant seed yield, harvest index (% of total above-ground mature dry weight as seed), % protein (in seed) and 100-seed/weight. The popping quality was estimated on two samples per population by heating seed on an open fry pan (ca. 800° F) for 30 seconds. In all statistical tests, a t-test for two independent samples was used.

Results and Discussion

Morphology and Biosystematics

Table 2 describes all 20 populations used in this study in terms of 25 morphological characters scored on individual plants grown in the greenhouse. Eleven of these characters are qualitative, scored in terms of a few discrete phenotypic classes. The characters, scored by Sauer (1967) in his taxonomic studies of amaranths, are quantitative. When taken singly they show a great deal of overlap among different taxa, with CV's in the range of 10% and 70%. For example, tepal length is significantly larger in *A. retroflexus*, but all the other five species overlap greatly. Likewise, leaf blade length is significantly different between the domesticated and weedy groups, and delta populations are like the weedy group or even transgress them (eg. Acampo population). Branching and leaf area bring out the difference between the weedy and domesticated groups.

Inflorescence characteristics have been emphasized by the other workers (Coons 1975; Sauer 1967; Singh 1961) and here too, important taxonomic differentiation is shown. Utricle abscission is clearly an important feature of weedy taxa (including the delta populations) but is absent in the domesticates. As also noted by previous workers, seed colors are black in weedy amaranths and in a few cultivated forms (e.g. *A. cruentus*, grown either as ornamental or for pot herb). These data largely confirm the main domestication changes as discussed by Pal and Khoshoo 1974), Sauer (1976) and others.

The partitioning of biomass into stems, leaves, flowers and seeds (Fig. 1) is of special interest as a measure of the harvest index (in plant breeding) and reproductive effort (in population biology). Histograms show that weedy types have higher harvest indices (or reproductive efforts) than the domesticated taxa. Of course, domesticated taxa are expected to have a wide range since they are used for ornamental purposes, leaf protein and food grain. In our

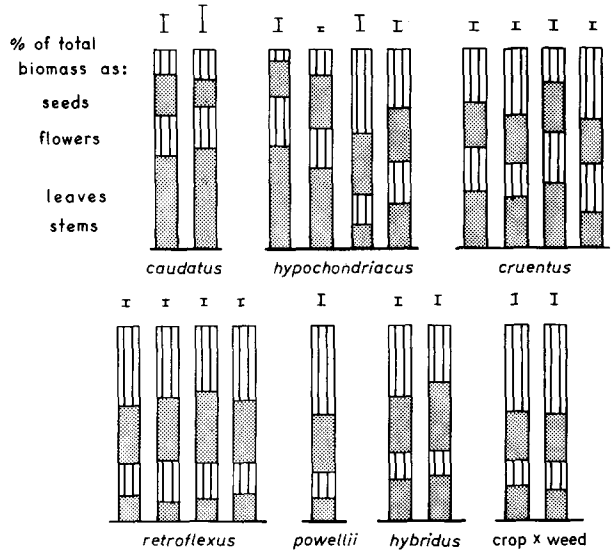

Fig. 1. Population mean values of % total biomass partitioned to seeds, flowers, leaves, and stems (greenhouse dats). These correspond to quantitative traits 13, 14, 15, and 16, respectively. Standard deviations were calculated using values for seed proportions

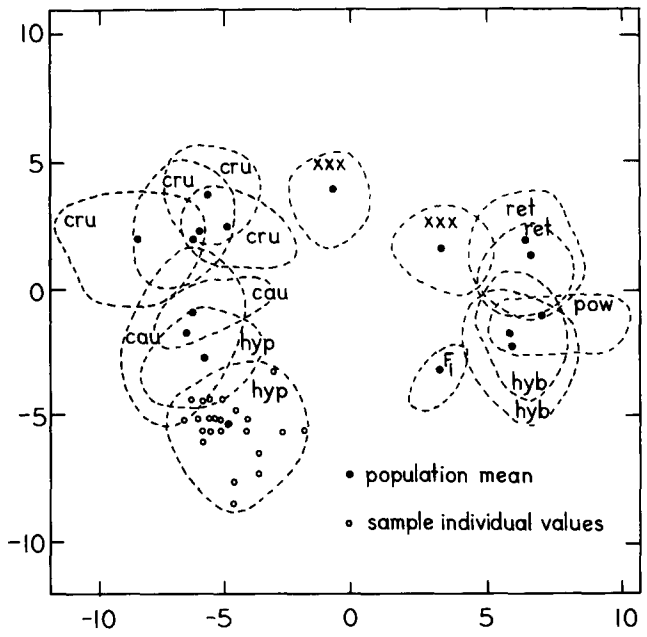

Fig. 2. Results of principal component analysis showing the relationships among the taxa listed here. cru = *A. cruentus*, cau = *A. caudatus*, hyp = *A. hypochondriacus*, pow = *A. powellii*, ret = *A. retroflexus*, hyb = *A. hybridus*, xxx = delta hybrid populations, and F_1 = *cruentus* X *hybridus* F_1 population. The dotted boundaries are drawn to emphasize the overlap of various 'clusters'. Each 'cluster' represents one population. Individual values for only one population are shown as an example of dispersion within 'clusters'

present limited collection, we apparently did not have a broad and extensive array of accessions.

All 14 quantitative characters were used in a discriminant analysis (using the BMDO7M program). Results are presented in Fig. 2, in terms of two canonical variables, showing clusters for each of the populations. Note that domesticates and weedy groups are well differentiated and the 'hybrid' populations from the delta region are intermediate with a closer affinity with the domesticated group. Hotelling's T test showed significant differences ($P < .05$) among these groups and the probability of misclassification was nearly zero. The hybrid (*cruentus* X *hybridus*), raised at Davis, showed a very close resemblance with the *hybridus* parent. This analysis showed that quantitative characters can be effectively used on plants grown in the same environment for identifying various taxa, especially in conjunction with the qualitative traits.

Allozyme Variation Among and Within Populations

Results of electrophoretic survey of variation were scored in terms of bands that are repeatable and discrete. Zymograms showed that alcohol dehydrogenase (*ADH*) is governed by a single locus, with fast, slow and null alleles (.43, .36, null), heterozygotes are triple banded (.36, .40, .43), and that leucine amino peptidase (*LAP*) is controlled by a single monomeric locus (two alleles scored as fast and slow) for which no heterozygotes were found so that genetics could not be ascertained. Acid phosphatase (*Acph*) was interpreted in terms of four alleles (fast, medium, slow, null). Glutamine oxalacetic transaminase (*GOT*) was described in terms of four 'phenotypes' by the presence and absence of three dark bands, but the genetics cannot be checked out until we can produce hybrids and segregating generations. Esterases (*EST*) were interpreted in terms of two loci, with three alleles each; heterozygotes are triple-banded (dimeric) but the number of plants scored was too small to estimate allelic frequencies.

Table 3 summarizes data in terms of these postulated 'alleles' or 'phenotypes.' Note that most populations are monomorphic for almost all the loci scored and that even polymorphic ones show one allele to be common. This pattern of low or no variation is very surprising since both domesticated and weedy taxa are widespread, highly adapted in many different regions and postulated to have hybridization in their historical background. Three explanations come to mind: (1) most populations have originated from a single ancestral stock and have been subsequently grown in similar environments even though, geographically speaking, continents apart, (2) random drift in nature and (3) loss of variation during the maintenance of these stocks. Hypotheses (3) and (2) are probable and could account for monomorphism, but similarity among populations of different regions within most taxa is rather unlikely under random drift alone. Explanation (1) is also unlikely since adaptive differences are known to exist for other traits (e.g. seed dormancy, flowering). Perhaps we do not have large enough samples yet and any further attempts to explain these results appear futile. We need more accessions, collected properly and in sufficient numbers, from natural stands and agricultural fields. Electrophoretic data were used to compute genetic distances (Table 4). The domesticated group shows intragroup homogeneity (mean distance 0.83 on a scale of 0 to 5), whereas mean distances among the weedy species and between the weedy vs domesticated groups are 2.17 and 2.84, respectively. The 'hybrid' populations from the delta region gave distance estimates in the range of 0.17 with *A. hypochondriacus* and up to 3.0 with *A. powelli*. These are in line with the cluster analysis presented above (Fig. 2).

Although domesticated species showed similarity in the alleles or band phenotypes included within each species, there were alleles that seemed to be unique for several species, and may be used as qualitative markers of particular species if this pattern persists in more than the few populations represented here (see table 3). Electrophoresis could then become a powerful tool in identifying spon-

taneous hybrids that may be incorrectly identified using quantitative morphology.

As an example, on the basis of the proximity of hybrid population clusters to the *A. cruentus* and *A. retroflexus* groups in the discriminant analysis graph, their similarity to *A. retroflexus* and *A. cruentus* in qualitative traits, and the fact that only *A. cruentus* alleles and phenotypes appear in their electrophoretic makeup, it should be concluded that these populations arose from hybridization between *A. cruentus* and *A. retroflexus* alone, and not the 3 to 5 species proposed by Sauer. A single, or few, hybridization events followed by segregation of major genes or groups of genes in subsequent selfed generations could have caused the creation of these two different morphological forms from the same two parents.

Agronomic evaluation

Plot yields were not much different across species (Table 5). Individual plant seed yield was tested in a series of paired t-tests, and none of the pair comparisons proved significant at the 5% level.

Although single plant seed yield was not significantly different between the two groups of weedy and domesticated collections, the harvest index was dramatically divergent between the two groups, the weedy species being much more efficient seed producers. Interestingly, the hybrids were intermediate between the crop and weedy groups (Fig. 3).

For seed protein, the crop collections were generally higher than the weedy collections, and the hybrid population (Acampo) was equal to the lowest weedy levels, although seed weight was more equivalent to the larger value in the crop group (Table 5).

On the whole, it seems that amaranth would be a competitive crop. Grain yields of 1000 to 2500 kg/ha are good for a preliminary study, but may not be economically feasible at this time. Some reasons for the low yields and

Table 3. Estimates of allelic or phenotypic frequencies

		caudatus BP 352	*cruentus* Rodale	*cruentus* 76-42	*cruentus* CHI-1	*hypochondriacus* P.I. 337611	*hypochondriacus* P.I. 288282	*retroflexus* Walnut Grove	*retroflexus* Sutter Buttes	*hybridus* Howard Rd.	*hybridus* Moorpark	*powellii* Tulelake	delta hybrids Thornton Rd.	delta hybrids Acampo Rd.
Adh	F	1.0	1.0	1.0	1.0	1.0	1.0	–	–	0.09	–	–	1.0	1.0
	S	–	–	–	–	–	–	0.90	1.0	0.91	1.0	0.60	–	–
	FS	–	–	–	–	–	–	–	–	–	–	0.07	–	–
	null	–	–	–	–	–	–	0.10	–	–	–	0.33	–	–
Lap	F	1.0	0.82	1.0	1.0	1.0	1.0	–	–	1.0	1.0	–	1.0	1.0
	S	–	0.18	–	–	–	–	1.0	1.0	–	–	0.65	–	–
	null	–	–	–	–	–	–	–	–	–	–	0.35+	–	–
Got	a	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.40	0.17	1.0	1.0	1.0
	b	–	–	–	–	–	–	–	–	–	0.03+	–	–	–
	c	–	–	–	–	–	–	–	–	0.05+	0.14+	–	–	–
	d	–	–	–	–	–	–	–	–	0.55+	0.66+	–	–	–
Acph	F	–	0.35	–	–	–	–	–	–	–	–	–	–	–
	M	–	0.63	1.0	1.0	1.0	1.0	1.0	0.97	1.0	1.0	1.0	1.0	1.0
	S	1.0+	–	–	–	–	–	–	–	–	–	–	–	–
	Null	–	0.02	–	–	–	–	–	0.03	–	–	–	–	–
Est-1	F	–	–	–	–	–	–	–	–	0.89+	1.0+	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–
	S	1.0	1.0	1.0	0.97	1.0	0.97	1.0	1.0	0.03	–	0.78	0.86	1.0
	Others (incl. heterozygotes)	–	–	–	–	–	0.03	–	–	0.08	–	0.22	0.14	–
Est-2	F	–	–	–	–	–	–	–	–	–	1.0	0.78	–	–
	M	–	–	–	–	–	–	0.76+	1.0+	–	–	–	–	–
	S	1.0	0.92	1.0	0.23	1.0	1.0	–	–	–	–	–	1.0	1.0
	Others (incl. heterozygotes)	–	0.08	–	0.77	–	–	0.24	–	1.0	–	0.22	–	–
# Plants scored		40	35	30	25	30	50	30	35	40	30	20	50	30

*F = fast, M = medium, S = slow, FS = heterozygotes; a, b, c, d are phenotypes
+ = potentially species-specific bands or alleles

Table 4. Mean electrophoretic distance between taxa, utilizing five enzyme systems

	A. caudatus	*A. hypochondriacus*	*A. cruentus*	*A. retroflexus*	*A. hybridus*	*A. powellii*
A. hypochondriacus	0.83					
A. cruentus	1.00	0.67				
A. retroflexus	2.50	2.50	2.50			
A. hybridus	3.17	3.00	2.83	3.50		
A. powellii	3.17	3.00	2.83	1.50	1.50	
crop X weed hybrid	0.42	0.17	0.58	2.50	2.67	3.00

(least distance) 0 = both populations fixed for same allele or band
1 = shared allele is fixed in one population, high frequency in other (polymorphic) population
2 = both populations polymorphic, but have the same allele in highest frequency
3 = both populations polymorphic, but shared allele is common in one population, rare in the other
4 = common alleles different
(most distance) 5 = populations fixed for different alleles

Table 5. Grain yield and quality in field plots

		A. cruentus	*A. hypochondriacus*	crop X weed hybrids	*A. retroflexus*	*A. powellii*
Mean plot see yield, Kg/Ha						
Treatment 1		1621	2136	2332	2646	1993
Treatment 2		598	1128	978	1105	1440
Seed yield gm/plant						
Treatment 1	$\bar{X}$	7.91	10.08	11.40	12.64	9.60
	±SE	10.40	8.07	16.04	13.78	8.68
Treatment 2	$\bar{X}$	2.85	5.37	4.79	5.06	5.75
	±SE	5.99	4.35	4.41	5.59	4.22
% Protein in seed	$\bar{X}$	15.76	16.49	14.22	15.30	14.36
	±SE	1.75	0.98	0.84	0.97	0.58
Seed weight	$\bar{X}$	71.0	54.4	57.8	36.5	40.6
(mg/100 sd)	±SE	10.9	8.0	9.4	2.6	4.9
Popping	$\bar{X}$	98.8	98.7	3.0	0.6	0.2
quality (%)	±SE	1.9	2.2	4.9	1.1	0.4

Table 6. Correlation coefficients is domesticates (top) and weedy (bottom) species (pooled as two groups; $n_1 = 249$; $n_2 = 187$)

Character	Bract length	Tepal length	Leaf blade length	Petiole: blade ratio	Degree of bi-furcation	No. of. main branches	Largest infl. branch	Leaf area	Harvest Index
Tepal	.63**								
length	.17*								
Leaf	−.24**	−.20**							
blade	−.04								
length		.05							
Petiole:	−.25**	−.10	−.58**						
blade	−.16*								
ratio		.35**	−.17*						
Degree of	.23**	.09	−.09	.09					
bifurcation	−.35**	−.26**	.39**	−.13					
# main	.19**	.09	−.00	.04	.66**				
branches	−.27**	−.28**	.45**	−.17*	.62**				
Longest	.52**	.50**	−.57**	.18**	.25**	.21**			
infl. br.	−.17*	−.12	.56**	−.07	−.52**	.57**			
Leaf	−.36**	−.26**	.94**	−.49**	−.12	−.04	−.59**		
area	−.03	.26**	.88**	.05	.29**	.34**	.47**		
Harvest	.13*	.02	−.33**	.45**	.16*	.35**	.40**	−.21**	
index	.18*	.01	−.10	−.03	−.21**	−.20**	−.11	−.11	
Seed	−.44**	−.23**	−.02	.37**	−.07	.12	−.14*	.12	.77**
yield	−.20**	−.31**	.39**	−.24**	.62**	.61**	.55**	.25**	.12

** $P < .01$
* $.01 < P < .05$

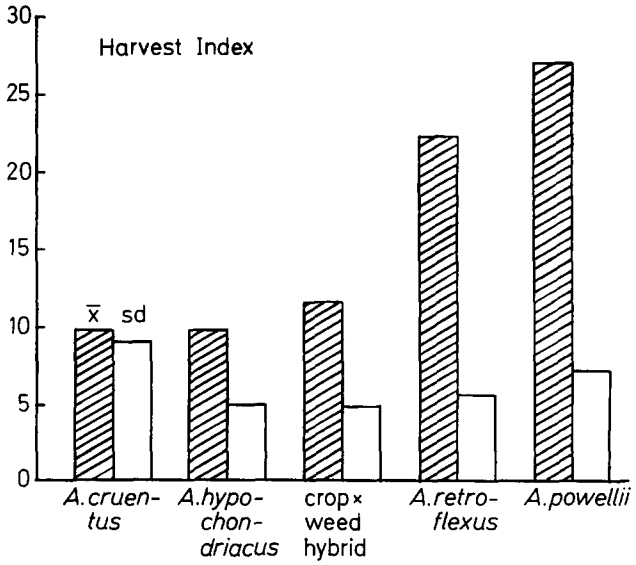

Fig. 3. Mean field harvest index over both treatments. Note the difference between domestic and weedy groups, and the high standard deviation (sd) of the *A. cruentus* population

extremely low harvest index of the crop species in this experiment may be the following:

1) The worst two crop collections may have been unknowingly selected for this field study. Some factor in the outdoor environment, perhaps the lack of humidity, may have consistently interfered with the fertility of either pollen or ovules in the *A. cruentus* (Rodale) collections used here. In contrast, harvest indices of 35-40% were obtained in the greenhouse. The other domestic collection, *A. hypochondriacus*, produced the lowest yields and harvest index of any crop accession in the field, greenhouse or in outdoor plots.

2) The extremely high CV's of harvest index in the crop accessions in contrast to the estimates of CV's associated with the weedy accessions indicate that field conditions were not at all uniform or optimal for crop production.

From the greenhouse data, a correlation matrix (Table 6) for all the morphological traits within populations, within species, and overall species pool was performed in order to ascertain if any of the traits are obvious contributors to yield, or if there are any obvious functional relationships between traits. Within various domestic species, different traits are highly correlated with yield, implying that different breeding strategies will need to be applied to different species. For instance, for *A. hypochondriacus*, the length of the longest inflorescence branch is highly correlated with seed yield, implying that the number of seeds per glomerule is relatively constant and that branch length controls yield by controlling the amount of glomerules produced. For *A. caudatus* and *A. cruentus*, however, inflorescence branch length and seed yield are unrelated, indicating that glomerule development is indeterminate, and that their number contributes most to the yield.

Over all three domesticated species, a few characteristics are consistently related to seed yield. They are:

1) Petiole: blade length ratio (shorter petiole length is desirable)

2) Leaf shape (rounder leaves are preferable to extremely ovoid or elliptic leaves)

3) Partitioning characters. (% seeds and % flowers are highly positively correlated with yield, whereas % leaves and % stems are highly negatively correlated with yield)

These partitioning data indicate that flowering time is important more from a partitioning standpoint than anything else. Earlier flowering varieties may have more time to make seeds, and fewer leaves. Crop accessions used in this study may have been previously selected for different uses; for example, the ornamentals and vegetable leaf forms may have been selected for an extremely late flowering time.

For the future study of amaranths as a grain crop, the highest return for research time would probably be in the study of basic agronomic properties, such as control of flowering time, optimal and cardinal temperatures, best planting densities, response to watering and fertilizer regimes, etc. to develop the highest harvest index possible (Hauptli and Jain 1977). For instance, a collection of *A. cruentus* gave a harvest index of 35-40% in greenhouse cultures while in the field it was less than 10%. The next step therefore would be the agronomic description of populations into classes or types based upon flowering times, inflorescence types, and partitioning characters, as has been done for other agronomic crops. New collections of most amaranth species are needed for population genetic and ecological studies (Frost and Cavers 1975; Pal 1972; Hauptli and Jain unpub. data) and agronomic work as outlined in this study. Although there is some polemic about natural species barriers (Sauer 1976; Pal and Khoshoo 1974), it would be extremely valuable to hybridize many of these species for recombining their desirable characteristics of plant type, flowering requirements, seed output, differing yield components, and physiological adaptations.

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