Grain Amaranths Amaranthus spp. (Amaranthaceae)

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Manuscript 17. October 2007

Introduction

Amaranthus could be a valuable alternative crop due to its high nutritional content, the many desirable traits expressed by the grain amaranths – and the unexplored potential of the wild relatives. Unlike the traditional monocot grains, the grain amaranths possess lysine in nutritionally significant levels. In addition, specific varieties of grain amaranths tolerate drought and heat, and, as a result, lessen the demand for costly irrigation. Peruvian varieties of *Amaranthus caudatus* have are known for their resistance to damping off and to root rot. Based upon phylogenecic studies (Lanoue et al., 1996) a number of wild species closely related to cultivated Amaranths should be explored for breeding purposes: *Amaranthus floridanus* and *A. pumilus* for salt tolerance, *A. powellii* and *A. fimbriatus* for drought resistance, and *A. hybridus* , *A. quitensis,* and *A. retroflexus* for pest, viral and bacterial resistance. Not only would these wild species be valuable for breeding with the cultivated Amaranths, but they would also be favourable target species to explore useful genes for other crop traits.

Origin and use

Amaranths have a long tradition in the New World, where they have been grown as pseudo-cereals by pre-Columbian civilizations on thousands of hectares. In Mesoamerica, amaranth developed as an important ritual and cash crop. They were grown as the principal grain crop by the Aztecs 5,000 to 7,000 years ago, until to the disruption of their culture(s) by the Spanish Conquistadors. The reasons of this decline is still unclear, since the Aztecs relied on the amaranths as an important staple. In fact, in Montezuma's time, the tribute in Amaranth almost equaled that of maize and beans according to the Codex Mendoza (Berdan & Anawalt Rieff, 1997). the tributes in *Amaranthus* (including Chenopods) under the name of 'huauhtli' were 8,100T, compared to maize (9,900T) and beans (7,000T) a major crop in those times. It was also called the 'Super Grain' of the Azteces, the 'Golden Grain of the Gods' and the grain was noted to be nourishing to infants and to provide energy and strength to soldiers on their extended trips (Itúrbide & Gispert, 1994; Kauffman & Weber, 1990; Macneish, 1976; Sauer, 1950; Smartt & Simmonds, 1988, 1995; Stallknecht & Schulz-Schaeffer, 1993; Teutonico & Knorr, 1984). Since amaranth was also part of important aztec rites which came close to the christian rites of the Lords supper, the Spanish conquistadores banned amaranth cultivation (Saunders & Becker, 1984). One of the most important sources of *Amaranth* history is (Sauer, 1950; Sauer, 1967; Sauer, 1995).
Amaranthus is still in use today, it is spread worldwide as a vegetable as well as a grain crop for food and feed. It has recently gone from an obscure plant to a recognized grain again. Credits for this go to the Rodale Foundation with the establishment of the American Amaranth Institute in Bricelyn, Minnesota. Numerous marketing companies have helped to

foster the importance of amaranth as a newly established crop (Myers, 2002). In both Mexico and Peru, wild amaranth leaves are gathered, boiled, and fried and the seeds are only popped eaten. In Mexico, the seeds are popped on a clay griddle *comal* with an *escoba* whisk broom. In Peru, a clay pot and drumstick like a spatula is often used (Early, 1990; Early & Capistran, 1987).
It is astonishing how extensively amaranths have been studied, despite the fact that it still counts as a minor crop; there are extensive bibliographies available (Ammann, 2006; Gates, 1992; Mnzava et al., 1999; Senft et al., 1981).
In the US, *Amaranthus* is used almost exclusively for seed production. The grain amaranth plant usually grows to around 150-180 cm and is maroon or crimson in color. The seeds of the plant number in the thousands and are quite small (0.9 to 1.7 mm diam.) and seed weights vary from 1,000 to 3,000 seeds per g.
Amaranth seeds are processed in popped, flaked, extruded, and ground flour forms. They are used in snacks and cereals, and in combination with other grains and flours in baking. *Amaranth* can also be used for ornamental or limited forage purposes. Farmers in China are reportedly growing over 40,000 hectares of amaranth as a forage for hogs. (Kauffman & Weber, 1990; Myers, 2002; Stallknecht & Schulz-Schaeffer, 1993).

Taxonomy and Diversity

Taxonomic position: *Magnoliopsida: Caryophyllidae: Caryophyllales: Amaranthaceae*
The *Amaranthaceae* have their centers of diversity in southwestern North America, Central America, South America, and Africa south of the Sahara Desert. Generic limits are not well defined in some groups (Robertson & Clemants, 2004). Consequently, the number of recognized genera varies from about 150 to 70, with a tendency of reduction. Kew Gardens databases reveal a recent number of ca. 70 recognized genera (Chase, 2004). A summary of grain amaranths is published by (Wegerle & Zeller, 1995). The genus *Amaranthus* contains ca. 70 species (38 in North America, including cultivated species): their distribution is mostly tropical, subtropical, and warm-temperate zones, some species in temperate zones; some taxa are at present almost worldwide in their distribution as introduced and naturalized weeds (Mosyakin & Robertson, 2004). Some segregate genera of *Amaranthus*, in the broad sense, have been proposed and sometimes recognized (see synonymy). In the present treatment, *Amaranthus* is accepted in its broad sense. Three subgenera are currently recognized (Mosyakin & Robertson, 1996): subg. *Acnida*, subg. *Amaranthus*, and subg. *Albersia*.
The Flora of China treats only 14 *Amaranthus* species, among those all important cultivars mentioned below (Shu, 2003). Recently, one of the Asian cultivars has been characterized more precisely and referred to *Amaranthus graecizans* (Costea et al., 2003).
The taxonomy of wild *Amaranthus* species is not easy , and even harder to understand for the vegetable and grain type cultivars. Specimens of *Amaranthus* are often difficult to identify by someone not familiar with the group. When using the key, one should closely study the tips of pistillate inflorescence branches for staminate flowers, to determine whether the plant is monoecious or dioecious; this is especially important for some monoecious species that produce few staminate flowers. Also, pistillate plants of dioecious species are usually required for positive identification. Additional difficulties stem from some misunderstandings of the morphologic terminology in *Amaranthus*, as used in different floristic and taxonomic treatments: especially regarding the terms applied to inflorescences and flowers. The traditional inflorescence terminology (Tutin et al., 2001) is mainly followed for brevity and convenience see (Fedorova, 2002) for a more complex and most probably more realistic scheme. A flower is subtended by a bract, often termed a "bracteole," and 0-2 lateral bracts, the true bracteoles. Structures that are clearly reduced green leaves subtending

portions of the inflorescence are sometimes incorrectly taken for bracts by key users (Mosyakin & Robertson, 2004). Excellent illustrations of morphological details can be found in: (Sauer, 1950) p. 598ff. These difficulties lead to misinterpretations on a species level. An example of existing taxonomic problems is the proposal to lump two commonly recognized species: *A. rudis* and *A. tuberculatus* as one (Pratt & Clark, 2001), see the summary in (Mosyakin & Robertson, 2004).
There is no clear distinction between the grain and vegetable cultivars, and young grain type plants can be eaten as greens. Many species are also found all over the globe as introduced plants, some have evolved into aggressive weeds (Maertens et al., 2004), and one of those, *Amaranthus retroflexus* (redroot pigweed), is ranking among the worst global weeds (Holm et al., 1977). Among the dozens of species there are three main ones to consider here: *A. hypochondriacus* 'Prince's feather', *A. cruentus*, 'Purple or Red Amaranth', and *A. caudatus* 'Love-lies Bleeding' as grain type species, *A. tricolor, A. dubius*, *A. lividus* and *A. cruentus* again are grown as vegetables.

Descriptions of the major grain amaranths after (Mosyakin & Robertson, 2004)
The economically most important group of species in the genus *Amaranthus* is the *A hybridus* species complex, including three cultivated grain amaranths, *A. cruentus*, *A. caudatus*, and *A. hypochondriacus*, and their putative wild progenitors, *A. hybridus*, *A quitensis*, and *A. powellii*.

1. Amaranthus hybridus Linnaeus, Sp. Pl. 2: 990. 1753.

Smooth amaranth, smooth pigweed, green amaranth, green pigweed, hybrid amaranth

Plants glabrous or glabrescent, or distal parts of stem and branches slightly pubescent when young. **Stems** erect, green or sometimes reddish purple, rarely under-developed plants ascending, branched to nearly simple, 0.3-2(-2.5) m. **Leaves:** petiole $^1/2$ as long as to equaling blade; blade ovate, rhombic-ovate, or lanceolate, (2-)4-15 × (1-)2-6 cm, base cuneate to broadly cuneate, margins entire, apex acute to obtuse, with mucro. **Inflorescences** terminal and axillary, erect or reflexed, occasionally nodding, green or olive green, occasionally with silvery or reddish purple tint, leafless at least distally, terrminal inflorescence often slightly nodding with numerous shorter branches at base. **Bracts** lanceolate-linear to subulate, 2-3.5(-4) mm, subequal to or 2 times as long as tepals **}**, apex spinescent. **Pistillate flowers:** tepals 5, lanceolate to lanceolate-linear, subequal or unequal, 1.5-3 mm, membranaceous, apex acute or acuminate, gradually narrowing into aristate tip; style branches erect, shorter than body of fruit; stigmas 3. **Staminate flowers** at tips of inflorescences; tepals 5; stamens (4-)5. **Utricles** obovoid or elongate-ovoid, 1.5-2.5 mm, shorter than tepals, smooth proximally, lid verrucose or rugose, dehiscence regularly circumscissile, or rarely in some presumably hybrid forms, irregularly dehiscent or indehiscent. **Seeds** black to dark reddish brown, lenticular to lenticular-globose, 1-1.3 mm, smooth, shiny.

Flowering summer-fall. Waste places, agricultural and fallow fields, railroads, roadsides, riverbanks, other disturbed habitats; 0-2500 m; Widespread and abundant in North America. Mexico; West Indies; Central America; South America; widely introduced or naturalized in tropical, subtropical, and warm-temperate regions worldwide.

Originally a riverside pioneer in eastern North America, now *Amaranthus hybridus* is extremely abundant in agricultural fields and other disturbed habitats. Related cultivated species have been reported from the flora area, including *A. caudatus, A. hypochondriacus,* and *A. cruentus*; there is no evidence that they are established; specimens identified as these species are often variants of *A. hybridus*.

Distribution of *Amaranthus hybridus* in North America needs clarification because the name was misapplied to other species, notably *A. powellii*, and specimens of *A. retroflexus, A. powellii,* and *A. hybridus* are frequently interchangeably misidentified. Forms of *A. hybridus* and *A. powellii* with reddish inflorescences are often misidentified as escaped and hence presumably naturalized, cultivated species: *A. caudatus* Linnaeus, *A. hypochondriacus* Linnaeus, and *A. cruentus* Linnaeus.

Amaranthus hybridus is extremely variable. In particular, there are numerous North American specimens with subobtuse tepals and thick inflorescences, suggesting hybridization with *A. retroflexus*. In Europe such presumably hybrid forms are known as *A.* ×*ozanonii* Thellung (A. Thellung 1914-1919).

2. Amaranthus cruentus Linnaeus, Syst. Nat. ed. 10. 2: 1269. 1759.

Blood amaranth, purple amaranth, caterpillar amaranth

Amaranthus hybridus Linnaeus subsp. *cruentus* (Linnaeus) Thellung

Plants almost glabrous or slightly pubescent distally, especially when young. **Stems** erect, green or reddish purple, branched distally, mostly in inflorescence, to nearly simple, 0.4-2 m. **Leaves:** petiole $^{1}/2$ as long as to ± equaling blade; blade rhombic-ovate or ovate to broadly lanceolate, 3-15(-20) × 1.5-10(-15) cm, occasionally larger in robust plants, base cuneate to broadly cuneate, margins entire, plane, apex acute or subobtuse to slightly emarginate, with mucro. **Inflorescences** terminal and axillary, erect, reflexed, or nodding, usually dark red, purple, or deep beet-red, less commonly almost green or greenish red, leafless at least distally , large and robust. **Bracts** narrowly spathulate, 2-3 mm, equaling or slightly longer than tepals, apex short-spinescent. **Pistillate flowers:** tepals 5, oblong to lanceolate, not clawed, equal or subequal, 1.5-3 mm, apex acute; style branches erect or slightly reflexed; stigmas 3. **Staminate flowers** at tips of inflorescences; tepals 5; stamens (4-)5. **Utricles** obovoid to elongate-obovoid, 2-2.5 mm, smooth or slightly rugose distally, dehiscence regularly circumscissile. **Seeds** usually white or ivory, with reddish or yellowish tint, sometimes dark brown to dark reddish brown, broadly lenticular to elliptic-lenticular, 1.2-1.6 mm diam., smooth or indistinctly punctate.

Flowering summer-fall. Near places of cultivation; Ariz., Calif., Conn., Ill., Ind., Ky., Maine, Md., Mass., Mich., Nebr., N.H., N.J., N.Y., N.C., Ohio, Oreg., Pa., R.I., S.C., Tex., Utah, Vt., Wash., W.Va., Wis.; Central America; South America; cultivated widely.

Amaranthus cruentus is cultivated as ornamental and pseudocereal almost worldwide from tropical to warm-temperate regions. While reported as naturalized in several states, most specimens identified as this species are referable to *A. hybridus* or other native species. Escaped plants of *A. cruentus* sometimes occur near places of cultivation (see note under *A. caudatus*). No attempt has been made to summarize distribution data for such escapes.

Amaranthus cruentus originated from *A. hybridus* (most probably in cultivation in Central America), with which it shares almost all major morphologic characteristics. Inclusion of cultivated forms in *A. hybridus* in a broad sense is thus rather justified. Cultivated species traditionally have been treated as separate taxa in horticultural and agricultural literature, and we prefer to maintain the current convenient usage of these names.

3. Amaranthus caudatus Linnaeus, Sp. Pl. 2: 990. 1753.

Love-lies-bleeding, purple amaranth, foxtail amaranth, quilete

Plants moderately pubescent distally, becoming glabrescent at maturity. **Stems** erect, usually green, moderately branched, rarely nearly simple, 0.5-1.5(-2.5) m. **Leaves:** petiole shorter than to equaling blade; blade rhombic-ovate, ovate, or elliptic to broadly lanceolate, 5-15(-20) × 2-10 cm, base cuneate, margins entire, apex acute to subobtuse, with mucro. **Inflorescences** terminal, drooping or nodding, usually red, purple, or white, less commonly green, silvery green, or yellow, usually much-branched at base, leafless at least distally, very large and robust. **Bracts** narrowly lanceolate to linear, equaling or subequal to tepals, not exceeding style branches, apex acuminate with excurrent midrib. **Pistillate flowers:** tepals 5, spatulate-obovate or lanceolate-obovate, not clawed, subequal, (1-)1.5-2(-2.5) mm, membranaceous, apex obtuse, slightly emarginate, or subacute with mucro; style branches spreading or reflexed; stigmas 3. **Staminate flowers** mostly at tips of inflorescences; tepals (4-)5; stamens 5. **Utricles** broadly ovoid to subglobose, 1.5-2(-2.5) mm, ± equaling tepals, dehiscence regularly circumscissile. **Seeds** dark brown to brownish black or reddish brown, yellowish white, or ivory, lenticular to subglobose, 1-1.2(-1.5) mm diam., smooth or indistinctly punctate.

Flowering summer-fall. Rarely occurs as escapes, persisting near the places of cultivation; introduced; Calif., Conn., Del., Ill., Kans., Maine, Mass., Mich., Mo., N.Y., Oreg., Pa., Tenn., Vt., Wis.; Central America; South America; cultivated elsewhere except cold-temperate, subarctic, and arctic zones.

While reported as naturalized in some states, most specimens identified as *Amaranthus caudatus* are referable to *A. hybridus* or other native species. *Amaranthus caudatus* is one of the most popular domesticated amaranths and is cultivated primarily as an ornamental, and, to a lesser degree, as a pseudocereal. Plants of *A. caudatus* may occur locally, usually close to places of cultivation and mostly in the southern regions of the flora. No reliable records of their successful naturalization are available. It is impossible at present to trace records of such ephemeral populations and individual escapes; maps and detailed distribution statements for cultivated species of amaranths are not presented here.

The origin of *Amaranthus caudatus* remains uncertain. It is generally believed that it originated in South America or Central America from some unspecified wild race of the *A. hybridus* aggregate, probably South American *A. quitensis* Kunth. At least some cultivated forms and strains of *A. caudatus* probably developed with some degree of hybridization with other cultivated species. Numerous infraspecific entities that are mostly of horticultural importance have been described within *A. caudatus*. Forms with erect and robust club-shaped inflorescences have been recognized as *A. mantegazzianus*.

4. Amaranthus powellii S. Watson, Proc. Amer. Acad. Arts. 10: 347. 1875 (as Amarantus).

Powell’s amaranth, green amaranth, Powell’s smooth amaranth

Amaranthus bracteosus Uline & W. L. Bray; *A. retroflexus* Linnaeus var. *powellii* (S. Watson) B. Boivin

Plants glabrous or moderately pubescent toward inflorescences, becoming glabrescent at maturity. **Stems** usually erect, green or sometimes reddish purple, branched, mainly in inflores-cences, to nearly simple, 0.3-1.5(-2) m, stiff. **Leaves:** petiole mostly equaling or longer than blade; blade rhombic-ovate to broadly lanceolate, 4-8 × 2-3 cm, occasionally larger in robust plants, base cuneate to broadly cuneate, margins entire, apex cuneate to obtuse or indistinctly emarginate, with mucro. **Inflorescences** mostly terminal, usually with spikes at distal axils, erect and rigid, green to silvery green, occasionally tinged red, leafless at least distally. **Bracts** lanceolate to linear-subulate, 4-7 mm, 2-3 times as long as tepals, rigid. **Pistillate flowers:** tepals usually 3-5, not clawed, unequal; outer tepals narrowly ovate-elliptic or elliptic, 1.5-3.5 mm, apex aristate; style branches spreading, shorter than body of fruit; stigmas 3. **Staminate flowers** clustered at tips of inflorescence branches; tepals 3-5; stamens 3-5. **Utricles** subglobose or compressed-ovoid, 2-3 mm, equaling or shorter than tepals, smooth or lid slightly rugose or minutely verrucose, dehiscence regularly circumscissile. **Seeds** black, subglobose to lenticular, 1-1.4 mm diam., smooth, shiny.

Flowering summer-fall. Disturbed habitats, agricultural fields, railroads, roadsides, waste areas, banks of rivers, lakes, and streams; 0-2500 m; Alta., B.C., Ont., P.E.I., Que., Sask.; Ariz., Ark., Calif., Colo., Conn., Fla., Idaho, Ill., Ind., Kans., Ky., La., Maine, Mass., Mich., Minn., Miss., Mo., Mont., Nev., N.H., N.J., N.Mex., N.Y., N.C., Ohio, Okla., Oreg., Pa., R.I., S.C., S.Dak., Tenn., Tex., Utah, Vt., Va., Wash., W.Va., Wis., Wyo.; Mexico; introduced or naturalized in South America, Eurasia, Australia.

Amaranthus powellii is originally native to southwestern United States and adjacent regions of Mexico; now, it is widely naturalized almost everywhere in temperate regions of North America. The distribution of *A. powellii* is probably underestimated both in North America and the Old World, and literature references are somewhat confusing, because *A. powellii* has been commonly confused with *A. hybridus*.

Forms of *Amaranthus powellii* with indehiscent or occasionally irregularly dehiscent utricles were described from Europe (southwestern France, the Gironde estuary) as *A. bouchonii* Thellung. Similar forms occasionally occur in North America. According to J. M. Tucker and J. D. Sauer (1958) and J. D. Sauer (1967b, 1972b), they are mostly "mutant or aberrant forms" of *A. powellii,* or hybrids of *A. powellii* and/or *A. hybridus* with other species. Recent comparative studies of morphology and isozymes of *A. bouchonii* (P. Wilkin 1992) indicated that that taxon, whatever its origin was, now differs from its presumably parental species and probably deserves recognition, at least as a separate subspecies. It seems that in North America, the situation with indehiscent-fruited forms is much more complicated than in Europe, and multiple entities are involved, including deviate forms of *A. powellii* and also partly sterile hybrids of dioecious taxa with species belonging to the *A. hybridus* group. The formal recognition of *A. bouchonii* in North American material would be premature.

The names *Amaranthus hybridus, A. chlorostachys* Willdenow, and *A. hybridus* subsp. *chlorostachys* (Willdenow) Hejný were occasionally misapplied to *A. powellii* in North America and Europe.

5. Amaranthus hypochondriacus Linnaeus, Sp. Pl. 2: 991. 1753.

Prince’s-feather, Prince-of-Wales-feather, prince’s-feather amaranth

Plants glabrous or moderately pubescent in distal parts, often becoming glabrescent at maturity. **Stems** usually erect, green or reddish purple, branched, mainly in inflorescences, to nearly simple proximally, 0.4-2(-2.5) m, coarse. **Leaves:** petiole of distal leaves equaling or slightly shorter than blade, becoming longer proximally; blade rhombic-ovate to broadly lanceolate 4-12 × 2-7 cm, larger in robust plants, base cuneate to broadly cuneate, narrowly cuneate in distal leaves, margins entire, apex cuneate to obtuse or indistinctly emarginate, mucronulate. **Inflorescences** predominantly terminal, often with few spikes at distal axils stiff, erect, dark red, purple, or deep beet-red, less commonly yellowish or greenish, leafless at least in distal part, usually robust. **Bracts** lanceolate to linear-subulate, subspinescent, 3-6(-8) mm, to 2 times as long as tepals, rigid. **Pistillate flowers:** tepals usually 5, proximal ones lanceolate, distal ones narrowly ovate-elliptic to elliptic, not clawed, unequal to occasionally subequal, 1.3-3(-3.5) mm, apex acute; style branches spreading; stigmas 3. **Staminate flowers** clustered at tips of inflorescence branches; tepals 3-5; stamens 3-5. **Utricles** compressed-ovoid to elongate-ovoid, (1.5-)2-3 mm, equaling tepals or nearly so, smooth or lid slightly rugose or minutely verrucose, dehiscence regularly circumscissile. **Seeds** white, ivory, pinkish white, or black to dark reddish brown, subglobose to lenticular, 1-1.4 mm diam., smooth, shiny.

Flowering summer-fall. Near places of cultivation; Ariz., Mass., Mich., Nebr., N.Mex., N.Y., Tex., Utah, W.Va., Wis.; cultivated widely.

Amaranthus hypochondriacus and its hybrids are widely cultivated as ornamental, pseudocereal, and fodder crops in many tropical to warm-temperate regions of the world. Occasionally, *A. hypochondriacus* occurs as escapes near the places of cultivation; there are no reliable reports of its successful naturalization in the flora area.

The wild progenitor of *Amaranthus hypochondriacus* seems to be *A. powellii* (J. D. Sauer 1967b); hybridization with other cultivated taxa (e.g., *A. cruentus*) probably also played some role. The initial cultivated form probably emerged in southwestern North America, within the original range of native *A. powellii*.

Agronomy

In Mexico, growers primarily monocrop amaranth as a cash crop. Techniques of monocultivation may date from the Aztec period when amaranth was grown as a presumably large scale "cash" (tribute) crop. On the outskirts of Mexico City amaranth had been cultivated in Aztec *chinampas* or "floating gardens," an ingenious agricultural system practiced in various forms by the Maya, pre-Inca Lake Titicaca peoples, and other South American cultures (Armillas, 1971). This type of sub-irrigation no longer seems to be a decisive factor (Crossley, 1995, 2004). The author concludes that while sub-irrigation is possible under certain combinations of field morphology, crop type, and soil properties, it was a relatively minor factor in the overall decision-making process of past chinampa farmers. It should not be a major determinant of future planning for chinampa preservation or reconstruction. For the enhancement of the present day production of modern amaranth traits The floating gardens may have a certain value in restoring historical agriculture to be shown to eco-tourists.

Twentieth century amaranth production is vastly different from that of early civilizations or even from primitive agriculture systems present today (Stallknecht & Schulz-Schaeffer, 1993). Grain amaranth entry into the marketing distribution arena has been confronted by numerous challenges. In contrast to many other established agricultural commodities, crop production challenges are even greater than marketing to the success of an amaranth industry. In regard to crop production, amaranth certainly is a specialty crop, since every aspect of production, from planting to harvest and storage requires special attention and consideration. Whereas ancient production relied essentially on small plots grown by hand, intercropped with numerous other crops, modern agronomic practices have changed this. Mechanization and extensive crop monoculture cause high disease and insect pressure and call for new management systems and integrated pest control to attain competitive economic crop returns (Myers, 2002; Stallknecht & Schulz-Schaeffer, 1993).

Weed control in amaranth is achieved by cultivation, hand weeding, delayed planting, and by manipulation of plant populations using narrow row spacing. Presently, there are no

herbicides labeled for weed control in amaranth, and it is unlikely that any chemicals will become cleared for commercial use.
Harvesting of *Amaranthus* is difficult. When plant populations of amaranth are low, the seed heads become extremely large and do not properly dry. When amaranth is harvested prior to a killing frost, plant moisture levels will complicate the harvest. It is thus not surprising that amaranth grain yields are extremely variable, dependent upon cultivar selection and the growing season, particularly with regard to available soil moisture.
The principal insect pest problem of *Amaranth* is the lygus bug (*Lygus lineolarius*) (Wilson & Olson, 1992), which can extensively damage the flowering head. Amaranths can also suffer injury from the fall armyworm (*Spodoptera frugiperda*), cabbage looper (*Trichoplusia ni*), corn ear worm (*Heliothis zea*), cowpea aphid (*Aphis craccavora*), and the blister beetle (*Epicuata vittata*). The amaranth weevil (*Conotrachelus seniculus*) can cause severe damage to the roots resulting in lodging and predisposition to root diseases (Stallknecht & Schulz-Schaeffer, 1993).
With the upcoming mechanization and monoculture practices the amaranth farmers are also confronted with diseases and insect pests, which will be described in detail in the section major constraints.

Nutritional Value

The nutritional value is well known (Becker et al., 1981; Teutonico & Knorr, 1984). Grain amaranth has higher protein (12 to 18%) than other cereal grains and has a significantly higher lysine content. The high lysine content of amaranth grain makes it particularly attractive for use as a blending food source to increase the biological value of processed foods (Pedersen et al., 1990; Pedersen et al., 1987). With modern breeding technologies, it should be easy to enhance those unique nutritional characteristics to even higher values.
In addition to the unique characteristics of the major components of proteins, carbohydrates, and lipids, amaranth grain also contains high levels of calcium, iron, and sodium when compared to cereal grains (Becker et al., 1981). A practical foundation has been established for breeding higher yield in the future (Lehmann et al., 1991). The nutritional value of the seed is so well balanced that an *Amaranthus hypochondriacus* 11S globulin cDNA, encoding one of the most important storage proteins (amarantin) of the seed, with a high content of essential amino acids, was used in the transformation of CIMMYT tropical maize genotype (Rascon-Cruz et al., 2004). Total protein and some essential amino acids of the best expressing maize augmented 32% and 8-44%, respectively, compared to non-transformed samples. The soluble expressed proteins were susceptible to digestion by simulated gastric and intestinal fluids, and it is suggested that they show no allergenic activity. These findings demonstrate the feasibility of using genetic engineering to improve the amino acid composition of grain crops.

Physiology

Amaranthus spp. are among the few dicot species with C_4 metabolism, which results in increased efficiency to use CO_2 under a wide range of both temperature and moisture environments (Kiirats et al., 2002, 2003; Sage, 2002; Sawada et al., 1999; Sawada et al., 2002). This is of importance for a future crop, since the crop could easily be adapted to a wider range of environmental conditions.

Seed germination is epigeal: the seedlings emerge three to four days after sowing and, at 2.5 months, the panicle begins to appear and later flowering occurs. The seeds do not have dormancy problems and maintain their viability at ambient temperature for more than five years, provided their humidity is less than 5 percent.
If there are secondary dormancy mechanisms in the seed, they occur mainly in the wild or weedy species. Amaranth has defence mechanisms against pest insects: its spiny panicles and seeds, which have a thick, pruinous testa, allow germination in later years (Itúrbide & Gispert, 1994).

Genetic Diversity

American *Amaranthus* species have different centres of domestication and origin, being widely distributed in North America (Canada, United States), Central America (Mexico, Guatemala), and the South American Andes (Peru, Bolivia, Ecuador), where also the greatest genetic diversity is found. *Amaranthus* as a genus has a broad genetic variability, with diversity in plant type (erect to prostrate), number of inflorescences (one to several), seed colour, earliness, protein content, plant height, seed and green matter yield, resistance to pests and diseases, and adaptation to soil type, pH, climate, rainfall and day-length (Kulakow, 1987; Kulakow & Jain, 1987; Mucjia & Jacobsen, 2005).
Genetic diversity and relationships of 23 cultivated and wild *Amaranthus* species were examined using both isozyme and RAPD markers. (Chan & Sun, 1997). A total of 30 loci encoding 15 enzymes were resolved, and all were polymorphic at the interspeciÞc level. High levels of inter-accessional genetic diversity were found within species, but genetic uniformity was observed within most accessions of cultivated grain amaranths (*A. caudatus*, *A. cruentus*, and *A. hypochondriacus*). Much higher levels of polymorphism were found in vegetable and other wild species. The evolutionary relationships between grain amaranths and their putative ancestors were investigated, and both the RAPD and isozyme data sets supported a monophyletic origin of grain amaranths, with *A. hybridus* as the common ancestor.
The phylogenetic relationships among the most important *Amaranthus* cultivars and their wild relatives have been studied using internal transcribed spacer, amplified fragment length polymorphism, and double-primer fluorescent intersimple sequence repeat markers . (Xu & Sun, 2001). The AFLP (amplified fragment length polymorphism) trees share many features in common with the ISSR trees: ISSR being intersimple sequence repeat with higher reproducibility than RAPD (Meyer et al., 1993). Both AFLP and ISSR showing a close relationship between *A. caudatus* and *A. quitensis*, placing *A. hybridus* in the same clade as all grain amaranths, and indicating that *A.powellii* is the most divergent taxon in the *A. hybridus* species complex.

Breeding history

The breeding biology of amaranth is complex in nature being strongly affected by the environment (Hauptli & Jain, 1985; Jain et al., 1982). Based on theoretical considerations decades ago (Allard, 1960; Fehr, 1987; Simmonds, 1976) the breeding method employed in the development of 'Plainsman' was built on conventional methods, self-pollination was assumed to be the prevalent reproductive system in the developing populations ((Kauffman &

Weber, 1990; Schulz-Schaefer et al., 1991). The single plant selection scheme allows for near homozygosity only in the F_5 generation, consequently preliminary yield trials may begin at F_6 generation with no guarantee of success. After lenghy hypothesizing and citing a lot of soft literature (Guillen-Portal et al., 1999) conclude:
The study showed the large extent to which environmental conditions affect the expression of morphological and agronomic traits in a population exhibiting a small degree of genetic variability, and that genetic improvement through a selfing–selection scheme would be limited.

The aforementioned composition, properties, and historical, current, and future applications of amaranth demonstrate the food potential of this underutilized crop. Nevertheless, there are problems in commercialization of amaranth, mainly because of lack of sufficient experimental data.
In the area of agriculture, the specific soil nutrient requirements of the amaranth plant, the effects of fertilization on its yield, and the plant composition at different stages of harvest still need to be explored in more detail. Also, selection is needed for those varieties that are most stress-tolerant and most productive in a temperate climate.

Modern breeding methods could make the difference

The main challenge for R&D is to incorporate amaranth into existing food formulations, to modify their functional and nutritional quality, as well as to create entirely new products from grain and vegetable amaranth. In order to reach such goals economy and marketing will play a decisive role.
Prospects of amaranth breeding have been also summarized some 14 years ago (Kauffman & Weber, 1990) it did not get a really successful follow up: Selection and mutational breeding seem to have limited success, an extensive literature survey on amaranth breeding did nor reveal any major breakthrough. Lots of promises in the breeding literature of the last decades have not been put into reality.
In a noteworthy concluding discussion (Guillen-Portal et al., 1999) point to the difficulties and the limited success of selection among self-pollinated populations. it is generally accepted that at the F_5 generation near homozygosity is reached, so preliminary yield trials may begin at F_6 generation (Allard, 1960; Simmonds, 1976). However, some residual genetic variability is retained, and it might be present indefinitely, the reasons are discussed and various hypothesis are discussed (Guillen-Portal et al., 1999). This calls for modern breeding methods, starting with marker gene control and also for a more targeted breeding strategy using transformation, but still, also with the transformed *Amaranthus* traits, some of those difficulties of genetic instability might remain.

Suggested sources for modern breeding programmes
Genetic analysis shows the way: Lots of characters have been spotted and linked more or less precisely to genes.
(Williams & Haq, 2002) show in Table 3.2.1. p. 14 in Asia and Latin America Amaranthus div. sp. as underutilized crops with a high priority to be developed further.
(Lanoue et al., 1996) demonstrate that many wild *Amaranthus* species possess agriculturally desirable traits such as drought and salt tolerance, and pathogen resistance. They detected through PCR analysis 11 potentially informative restriction-site mutations and seven length-polymorphisms among the 28 *Amaranthus* species. But they also state that genetic variation is not very promising, but still molecular phylogeny provides a basis for selection of species

pairs for crop development. They show that the two common grain amaranths, *A. caudatus* and *A. cruentus*, share identical character states across all three of their data sets, and are included in a group with *A. hybridus*. *A. dubius* and *A. quitensis* closely related, except for their length data. The putative progenitors of *A. caudatus* and *A. cruentus* are considered to be *A. quitensis* and *A. hybridus*, respectively, according to (Williams & Brenner, 2002). (Lanoue et al., 1996) conclude in accordance with (Doebley, 1992) that a crop species and its progenitor should maintain a close phylogenetic relationship due to the recent time of domestication.

Amaranthus powellii should be the favourable source for genes steering shattering, as discusse above. With a more precise location of such genes the creation of non-shattering transgenic *Amaranthus* can become a realistic option.

There are already experimental transgenic *Amaranthus* plants reported, in order to fight root rot, a bacterial disease, see section Contraints and what could be done bout them.

Major constraints and summary of what needs to be done with modern breeding methods

The high genetic diversity in the amaranth family offers opportunities for increasing desirable characteristics, such as yield, protein content, and height [McKell, 1983 #506]. (McKell, 1983).

Among the areas in which further research is needed are the following (Teutonico & Knorr, 1984):

1. Seed shattering

Most importantly, non shattering traits have to be developed. The hybridizing and selection field experiments described in (Brenner, 2002) have not yet produced a cultivar, which is competitive and regained all the favourable characteristics, which made *Amaranthus hypochondricus* ‘Plainsmen’ so successful. The best way to obtain non shattering characters in amaranth cultivars will be through genetic engineering. preferably with marker genes.

Selection of plant varieties with large and nonshattering seeds, as well as the development of harvesting and processing methods adapted to the seed characteristics (McKell, 1983), would improve processing of grain amaranth.

Shattering can cause serious losses in commercial grain production of amaranth (Fitterer et al., 1996). In Nebraska, amaranth grain is harvested after the plants are killed by frost and have dried. The predominant cultivar ‘Plainsman’ is favored partly because it maintains good stem strength after frost has killed it (Baltensperger et al. 1992), however, it does shatter (Fitterer et al., 1996). In certain years, the mature plants must remain standing for weeks before the plants are killed and dry enough to harvest.

Each amaranth seed is held in a separate papery utricle. In standard grain production cultivars each utricle has a seam that opens at maturity allowing for circumscissile abscission along the utricle’s equator. Taxonomists including (Sauer, 1967) have observed that some populations of *A. powellii* S. Watson have non-circumscissile utricles. *A. powellii* is a wild and weedy species closely related to the grain amaranths. Non-circumscissile utricles have also been observed infrequently in cultivated amaranths (Hauptli & Jain, 1980) p. 119, and some populations are so indicated in the GRIN database (USDA, ARS 2001). Jain et al. (1986) used the notation, *Dh* and *dh*, in *A. hypochondriacus*, with dh representing a recessive non-circumscissile allele, and *Dh* representing the dominant circumscissile allele. They noted that

the trait has potential for use in breeding programs. Brenner and Hauptli (1990) proposed breeding for non-shattering populations, described the abscission mechanisms, and suggested parental germplasm. The two germplasm releases described herein result from their proposal (Brenner and Hauptli 1990). Hauptli et al. (1980, p. 119) originated the idea of breeding for non-shattering in this way. Two distinct populations were developed because of the need to have cross-compatible germplasm for both grain species important in North America, *A. cruentus* L. and *A. hypochondriacus* L. Both of these non-shattering populations are adapted for seed maturity in the Midwestern United States.
Three grain amaranth interspecific hybrid populations with non-shattering (seed retaining) utricles, *Amaranthus* hybrids DB 92226, DB 9350, and DB 98246 were developed at the North Central Regional Plant Introduction Station (NCRPIS), Agronomy Department, Iowa State University. These populations have little or no abscission at the equator of the utricle or beneath the utricle. The first two are intended to be crossed with standard cultivars and provide a source of shattering resistance in newly developed cultivars. DB 98246 is intended for biomass production. The populations were released by Iowa State University in 1999, and 2000 (Brenner, 2002). Although the shattering problem seems to be solved after lengthy selection processes for a limited number of traits, non-shattering *Amaranths* are still not really adopted in a large scale.

2. Seed size

The small size of the amaranth seed has been considered a deterrent to commercialization, so either varieties must be bred for larger seeds or processing methods must be adapted to the small grain.
An interesting targeted way to learn more about the genetics of live history effects on increasing trade offs between size and reproductive traits when resources are more limited is suggested by (Arntz et al., 2002). Genetically based differences in photosynthate availability can affect the relationships between size and reproduction and therefore affect fitness. This might be a promising pathway to understand the complex genetics of seed size (besides having a closer look at wild *Amaranthus* species with particularly big seeds, such as *Amaranthus cannabinus* (Linnaeus) J. D. Sauer, with its seeds of 2-3mm, compared to the grain amaranth seeds of 1.2-1.6mm (Mosyakin & Robertson, 2004).

3. Salt and Drought tolerance

Although there are claims that amaranths can flourish in stressful environments where conventional crops cannot, little experimental evidence exists in the literature to document that amaranths are really that drought- or salt-tolerant (Saunders & Becker, 1984). A systematic evaluation for Missouri about drought tolerance with a close comparison of GIS controlled fields with various ecological characteristices also did not have any evident followup, although drought tolerance in summer for the amaranth traits tested seems to be noticable, but the GIS field tests need to be continued in order to provide conclusive results (Myers, 1993).
(Flores et al., 1982) provide tools like in vitro cultivation leading to full plant restoration and chloroplast isolation for future work. It will be important to foster natural drought- and salt tolerance, which is inherent in the families Amaranthaceae and Chenopodiaceae – genes will be available, knowing about the ecological span of numerous highly salt- and drought tolerant genera in both families. This should be done with more targeted methods than plain crossing and selection, i.e. the method to be used here is targeted transformation.

4. Insect resistance

Shoot diseases in humid climates (Adebanjo, 1994; Emoghene & Okigbo, 2001). (Blodgett & Louw, 2004; Blodgett & Swart, 2002) report significant yield losses in South Africa through

pigweed weevils being a vector for *Fusarium* pathogens.They also confirm that pathogenic fungal isolates of the *Alternaria tenuissima* group can infect and colonize *Amaranthus hybridus* leaves in a manner consistent with other endophytic fungi, and suggest that these fungi can act as latent leaf pathogens when the host is altered by wounding. Diseases of Amaranthus-Spp Caused by *Pythium-Aphanidermatum* and *Macrophomina-Phaseolina* are studied by (Mihail & Champaco, 1993). Two attempts of biological control are reported: (Rosskopf et al., 2000) for *Phomopsis amaranthicola*, and for the Shoot Disease of Amaranthus-Hybridus Caused by *Choanephora cucurbitarum* with *Bacillus-Subtilis* by (Ikediugwu et al., 1994).
Amaranthus hypochondriacus accumulates trypsin inhibitors and α-amylase inhibitors in seeds and leaves that are considered to act as herbivore deterrents. (Delano-Frier et al., 2004). It seems that *Amaranthus* has natural deterrents against herbivores which need to be studied carefully and located genetically.

5. Microbial resistance
Root rot in *Amaranthus* is reported from South Africa (Chen & Swart, 2001, 2002; Chen et al., 2003) including a specific case of tolerance against the disease in *Amaranthus hypochondriacus*:
A 30-residue antimicrobial peptide gene Ar-AMP was amplified by PCR, isolated from the seeds of amaranth *Amaranthus retroflexus* L. essentially by a single step procedure using reversed-phase HPLC, and its in vitro biological activities were studied. (Lipkin et al., 2005). The complete amino acid sequence of Ar-AMP was determined by Edman degradation in combination with mass spectrometric methods. In addition, the cDNA encoding Ar-AMP was obtained and sequenced. The cDNA encodes a precursor protein consisting of the N-terminal putative signal sequence of 25 amino acids, a mature peptide of 30 amino acids and a 34-residue long C-terminal region cleaved during post-translational processing. It effectively inhibited the growth of different fungi tested: *Fusarium culmorium* (Smith) Sacc., *Helminthosporium sativum* Pammel., King et Bakke, *Alternaria consortiale* Fr., and *Botrytis cinerea* Pers., caused morphological changes in *Rhizoctonia solani* Ku¨hn at micromolar concentrations and protected barley seedlings from H. sativum infection. The gene encoding for Ar-AMP may be of interest for general tranformation projects for various crops.
On the screening of 200 nonhost plants, an *Amaranthus gangeticus* extract was found to attract and subsequently inhibit the motility of Aphanomyces cochlioides zoospores. (Islam et al., 2004). Obviously, it would be good to know more about the genetics of those substances involved, isolate the genes and proceed to produce by transformation experimental GM crops.

6. Gene flow among Amaranths
What can be done to remedy the gene flow situation?
Certainly, the old rules in agriculture should not be forgotten: (Manley et al., 2001) proper weed management and crop rotation helps to control amaranths and other broad leaved weeds considerably.
Species of *Amaranthus* occasionally form interspecific hybrids. Such hybridization seems to be especially important and widespread in cultivated grain-amaranths, in wild representatives of the *A. hybridus* aggregate, between species of sect. *Amaranthus*, and between *A. tuberculatus* and species of sect. *Amaranthus*. The degree and scope of hybridization in *Amaranthus* are often overestimated, especially by European authors, and some taxa described as putative hybrids are in fact nonhybrid infraspecific forms of morphologically variable species. Hybrids between more distantly related species, if they occur at all, are usually highly sterile, such as hybrids between taxa of the subgenera *Amaranthus* and *Acnida*, or at least show much decreased fertility. There are no verified records of hybrids between representatives of the subgenera *Amaranthus* and *Albersia*. (Mosyakin & Robertson, 2004).

Nevertheless, *Amaranthus* will require some management of gene flow, at least farmers need to meet minimal safety distance of a few meters. It is known, that wild and weedy *Amaranthus* species can transfer herbicide tolerance, (Tranel et al., 2002) tested in greenhouses if a dominant allele encoding a herbicideinsensitive form of acetolactate synthase (ALS) could be transferred from a monoecious species, *A. hybridus*, to a dioecious species, *A. rudis*. Numerous F1 hybrids were obtained from controlled crosses in a greenhouse between *A. rudis* and herbicide-resistant *A. hybridus*, and most (85%) of these hybrids were herbicide-resistant.
There is general promiscuity between wild and weedy Amaranths in agricultural systems (Franssen et al., 2001; Jeschke et al., 2003; Lanta et al., 2003; Lehmann et al., 1991; Maertens et al., 2004; Santos et al., 2004). Field studies have established high potential for hybridization between two important and often coexisting weedy species, *Amaranthus hybridus* and *Amaranthus tuberculatus* (Steinau et al., 2003; Trucco et al., 2005a; Trucco et al., 2005b). Consequently, if *Amaranthus* traits are selected in agriculture for herbicidetolerance or if *Amaranthus* is transformed for herbicide tolerance, the chance of having outcrossing herbicide tolerance is real. Even then it depends on the management system whether this is a risk or not, since outside the fields no herbicide selection pressure is ocurring. (Gressel et al., 1983; Gressel, 1994) have shown that once a wild plant (in our case a wild relative) is through selection becoming herbicide tolerant and the plants are then not anymore under constant selection pressure from the given herbicide, then the herbicide tolerance is vanishing in a few years again.
If ever *Amaranthus* is receiving transgenes which could easily confer with their wild relatives enhanced competitiveness, then things look different, and some mitigation should be applied: Either male sterility should be involved (Peters & Jain, 1987) or the tandem solution should be seeked (Al-Ahmad et al., 2006; Al-Ahmad & Gressel, 2005; Al-Ahmad & Gressel, 2006; Gressel, 1999; Gressel & Al-Ahmad, 2005)

6. Biofortification

Only in later stages of modern breeding, i.e. when amaranth develops into a major crop, biofortification will be a serious topic. A more detailed analysis will show the needs, starting from the modern traits existing at that time. The fact that most of the seed volume is occupied by the embryo might account for the unusually high lysine content (Oke, 1983). This provides a good opportunity for the development of varieties of even higher nutritional quality.
Selection of vegetable amaranth and grain amaranth low in nutritional stress factors, such as nitrate and oxalate. Too much and regular oxalate intake can cause kidney problems, the formation of calcium crystals in the renal tubular cells is an important factor during the formation of urinary stones. It would be easy to antisense the known gene out. This has to be balanced against the good side of oxalate content: It provides the plant with resistance against herbivores. (Lou & Baldwin, 2006; Ramputh et al., 2002).

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