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REVIEW

Current knowledge on *Amaranthus* spp.: research avenues for improved nutritional value and yield in leafy amaranths in sub-Saharan Africa

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Abstract In the past 20 years, very little progress has been achieved in reducing food insecurity, child malnutrition and hunger in Africa. Under-nutrition and micronutrients deficiencies are widespread and affect mainly women and children. To address these problems, increased consumption of African leafy vegetables is promoted as sources of both micronutrients and bio-active compounds. Widely promoted African leafy vegetables include *Amaranthus* spp., a taxonomic group cultivated worldwide. Species of this genus are used as pseudo-cereals in Europe and America, and are mostly planted as vegetables in Africa. *Amaranthus* has been rediscovered as a promising food crop mainly due to its resistance to heat, drought, diseases and pests, and the high nutritional value of both seeds and leaves. Leaves are rich in proteins and micronutrients such as iron, calcium, zinc, vitamin C and vitamin A. All parts of the plant are used as medicine to heal many diseases in African communities. This paper focuses on leafy amaranths traditionally utilized on the continent. It briefly reviews the current knowledge on taxonomy, ecology, nutritional and nutraceutical value, production and cultivation systems, reproductive biology, genetic resources and breeding of amaranths. Species of interest include: *A. blitum, A. caudatus, A. cruentus, A. dubius, A. hypochondriacus, A. spinosus, A. thunbergii, A. tricolor,* and *A. viridis*. Research and development opportunities on nutritive and nutraceutical properties, production and commercialization, taxonomic evaluation and breeding perspectives were explored.

Keywords *Amaranthus* · Leafy vegetables · Nutrients · Nutraceutical properties · Genetic resources

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Introduction

Africa has experienced mixed progress in reducing food insecurity and child malnutrition in the past 20 years (Garcia 2012). Approximately, one third of children under 5 years of age in Africa are stunted and more than a quarter are underweight. Micronutrient deficiencies affect mainly women and children and contributes significantly to the global disease burden of children by limiting proper cognitive development, impairing physical development, and increasing susceptibility to infectious diseases (Asare-Marfo et al. 2013). Most countries in Africa are still struggling to address problems of under-nutrition and micronutrient deficiencies (Lopriore and Muehlhoff 2003).

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African leafy vegetables are increasingly recognized as possible contributors of both micronutrients and bioactive compounds to the diets of populations in Africa (Smith and Eyzaguirre 2007). The continent is rich of vegetable species including amaranths which are among the most popular leafy vegetables on the continent (Maundu et al. 2009). Amaranths consist of 60–70 species (Xu and Sun 2001) and include at least 17 species with edible leaves and three grain amaranths grown for their seeds (Grubben and Denton 2004). Although several species are often considered weeds, people around the world value amaranths as leafy vegetables, cereals and ornamentals (Trucco and Tranel 2011).

Most of the amaranth species are harvested in the wild as food resource. Only a few are grown and are among the leafy types most common in markets in tropical Africa. Amaranths can also be grown for their seeds. This is the case of some introduced varieties of American origin (Wu et al. 2000). Grain amaranth is not commonly cultivated in Africa (Grubben and Denton 2004). More recently however, a few farmers have taken the growing of grain amaranth more seriously and are supplying millers and supermarkets in Zimbabwe, Kenya, Uganda and Ethiopia. Since about 1980, *Amaranthus* has been rediscovered as a promising food crop mainly due to its resistance to heat, drought, diseases and pests, and the high nutritional value of both seeds and leaves (Wu et al. 2000). According to Onyango (2010), improvement of amaranths through research and development could produce an easy and cost-effective way of eliminating malnutrition and promoting people's health as well as achieving food security. Unfortunately, there are still gaps in knowledge of some popular amaranths of Africa and there are confusions in the nomenclature of species, for instance, of the *hybridus* complex while comprehensive nutritional profiles are yet to be compiled (Grubben and Denton 2004). Moreover, little is known on the breeding potentials particularly of wild relatives that can be promoted for sustainable utilization.

Some interventions were carried out thanks to partnerships between research institutions and local NGOs and to promote indigenous vegetables including amaranths. For example, the Promotion of Neglected Indigenous Vegetable Crops (IV) for Nutritional and Health in Eastern and Southern Africa (ProNIVA) project led by the World Vegetable Center (AVRDC) have contributed to provide seeds of superior micro-nutrient rich amaranth (*Amaranthus cruentus*) cultuvars and increase production and consumption of leafy vegetables in Rwanda, Uganda, Malawi and Tanzania (AVRDC 2008). Another important project was the Bioversity International's African leafy vegetables programme conducted in Botswana, Cameroon, Kenya, Senegal and Zimbabwe which induced notable positive changes in growing, consumption, marketing and nutritional awareness of African leafy vegetables such as amaranths and nightshades (Gotor and Irungu 2010).

Unfortunately, there are still gaps in knowledge of some popular amaranths of Africa and there are confusions in the nomenclature of species, for instance, of the *hybridus* complex while comprehensive nutritional profiles are yet to be compiled (Grubben and Denton 2004). Moreover, little is known on the breeding potentials particularly of wild relatives that can be promoted for sustainable utilization.

Here we present an overview of studies carried out on amaranth species and identify future prospects for research and development with focus on leafy amaranths of sub-Saharan Africa. Particular emphasis is placed on ways to improve amaranth genetic diversity for increased production and consumption on the continent.

Systematic and taxonomy of economically important species

The species of *Amaranthus* are often difficult to characterize taxonomically, due to the overall similarity of many of them, small and difficult-to-see diagnostic parts, intermediate forms, and the broad geographical distribution, which is the reason for many synonyms (Mujica and Jacobsen 2003). Sauer (1967) described two subgenera: *Acnida* (which included the dioecious species) and *Amaranthus* (which included the monoecious species), while Mosyakin and Robertson (1996) recognized three subgenera, i.e. *Acnida*, *Amaranthus* and *Albersia* based on inflorescence and floral characteristics. The need for infrageneric classification or micro-classification of the genus was raised recently (Das 2012).

Species differentiation based on morphological features can be sometimes challenging. However, examination of floral parts can result in constant

Fig. 1 Inflorescences of selected *Amaranthus* species. **a** Apical and axillary inflorescences of *A. blitum*; **b** Hanging inflorescence of *A. caudatus*; **c** Terminal inflorescence of *A. cruentus*; **d** Terminal inflorescence of *A. dubius*; **e** Inflorescence of *A. hypochondriacus*; **f** Apical and axillary inflorescences of *A. spinosus*; **g** Axillary clusters of *A. tricolor*; **h** Terminal inflorescence of *A. viridis.* (Plants were grown at the National Agricultural Research Institute of Benin (INRAB), Agonkanmey, Republic of Benin using seeds requested from United States Department of Agriculture, Institut National des Recherches Agricoles du Bénin (INRAB) and Kenya Resource Centre for Indigenous Knowledge (KENRIK)

characters from which discontinuities can be used to define well-established taxa (Trucco and Tranel 2011). In this sense, tepal number and morphology are commonly used for taxonomic identification (Trucco and Tranel 2011). According to Das (2012) amaranth species can be classified into three categories, which represent more or less use-groups: (1) vegetable *Amaranthus* with for instance *Amaranthus tricolor* var. *tricolor*, *Amaranthus tricolor* var. *tristis;* (2) grain *Amaranthus* which includes *Amaranthus hypochondriacus*, *Amaranthus caudatus*, *Amaranthus cruentus*; and (3) weed *Amaranthus* with members such as *Amaranthus spinosus*, *Amaranthus viridis*, *Amaranthus retroflexus*, *Amaranthus graecizans*, *Amaranthus dubius*, and *Amaranthus hybridus*. Vegetable *Amaranthus* can be easily distinguished by inflorescence features like mostly or exclusively axillary glomerules or short spikes (Fig. 1a, g), origin of flower bud from leaf axil, 3 tepal lobes, 3 stamens, brownish black seed, indeterminate growth habit. Grain *Amaranthus* are characterized by apical large to moderately large complex inflorescence comprising aggregates of cymes (Fig. 1b–h), 5 tepal lobes, 5 stamens, seed with variable seed coat colour and well defined flange, utricle circumscissile (Das 2012). Table 1 gives an illustration of that classification (Das 2012) based on commonly used species in sub-Saharan Africa. As far as weeds are concerned some species showed morphological commonality with leafy vegetable form, others with grain form of *Amaranthus*. The seed character is also very useful in demarcating vegetable, grain and weed *Amaranthus*. Vegetable group shares striking similarity with weed group in having brownish-black or black seeds with undifferentiated folded

Table 1 Description and uses of selected amaranths species Adapted from Mosyakin and Robertson (1996), Grubben and Denton (2004) and Adjakidjè (2006)

Species	Status	Uses	Botany/description	Seed maturity period
Amaranthus blitum L. Fig. 1a	Wild and cultivated	Leafy vegetable; medicine	Inflorescence an axillary many-flowered cluster, forming a false spike at apex of plant, with male and female flowers intermixed; flowers unisexual, with 3(–5) tepals; leaves lamina broadly cuneate at base, often deeply notched at apex; smooth and wrinkled fruits, shiny blackish seeds indehiscent or bursting irregularly	8 weeks after sowing
Amaranthus caudatus L. Fig. 1b	Cultivated	Pseudo-cereal; leafy vegetable; ornamental; medicine	Inflorescences dense spikes. Female flowers with 5 broad tepals, 3 internal obovate, rounded at apex, mucronate, 2 external spatulate, not rounded at the apex; spikes hanging from their base. Seed almost globose, smooth and shining, pale coloured (ivory), reddish or dark brown	–
Amaranthus cruentus L. Fig. 1c	Cultivated	Leafy vegetable; grain; medicine; ornamental	Leaves lamina broadly lanceolate to rhombic-ovate; Inflorescence large and complex, consisting of numerous agglomerated cymes arranged in axillary and terminal racemes and spikes, the terminal one up to 45 cm long, usually with many lateral, perpendicular, thin branches. Flowers unisexual, subsessile, with 5 tepals 1–2 mm long, bracts as long as or slightly longer than the perianth. Seeds obovoid to ellipsoid, compressed, whitish to yellowish or blackish	12–20 weeks after sowing
Amaranthus dubius Marx. ex Thell. Fig. 1d	Wild and cultivated	Leafy vegetable; medicine	Inflorescence spikelike or paniculate, glomerules more or less isolated at base of inflorescence and clustered towards apex; leaves broadly triangular blade down; female flowers 5 tepals; Fruit an ovoid-urceolate capsule, dehiscing circularly, blackish seeds	6 weeks after sowing
Amaranthus hypochondriacus L. Fig. 1e	Cultivated	Pseudo-cereal, ornamental	Inflorescence stiff with thick branches, bracteoles always longer than the tepals; tepals 5, lanceolate, with one equal to or longer than the fruit, the other 4 shorter; Fruit an obovoid to rhombic capsule. Seed obovoid to ellipsoid, whitish to yellowish or blackish	–
Amaranthus spinosus L. Fig. 1f	Wild	Fodder, leafy vegetable, medicine	Inflorescence in spikes to upper nodes, axillary glomerules present or not. A pair of spines in the leaf axils, often dense presence of axillary 5–10 mm diameter fruit capsular, dehiscent. Seed shiny black or brownish-black with thin margin	–
Amaranthus thunbergii L.	Wild	Leafy vegetable	Leaves lamina narrowly elliptical to rhomboid or spatulate, sometimes with a dark purple blotch; Inflorescence an axillary cluster, bracts with long awn; flowers with 3 tepals; Fruit an ovoid-ellipsoid to pyriform capsule	4–8 weeks after sowing
Amaranthus tricolor L. Fig. 1g	Cultivated	Leafy vegetable, ornamental, medicine	Inflorescence an axillary, globose cluster up to 2.5 cm in diameter, the upper clusters sometimes forming a terminal spike, with male and female flowers intermixed; brown or shiny black seeds, faintly reticulate	6 weeks after sowing
Amaranthus viridis L. Fig. 1h	Wild and occasionally cultivated	Leafy vegetable; fodder; medicine	Inflorescences spikes slender, not spiky, trimers female flowers, fruits strongly verrucose, apiculate, as long as the perianth, tearing irregularly; Seed subglobose, slightly compressed, margin acute, glossy black	–

flange. The grain amaranths are characterized by having discoid grains with well-differentiated folded flange region and seed coat colour other than black or brownish-black. Some of the weedy types are cultivated and used as vegetables (Grubben and Denton, 2004). *A. dubius* for example is presently the most important leafy vegetable in Kenya. Das' classification (Das 2012) might be valid for some commonly used species with economic importance. However, this classification needs to be comprehensively evaluated for the whole range of species diversity within the *Amaranthus* genus.

There is a persistent confusion between *A. cruentus* and *A. hybridus*. One hypothesis states that there was a single domestication of *A. cruentus* from *A. hybridus* while the other two domesticated species, *A. hypochondriacus* and *A. caudatus* evolved secondarily by repeated crossing of *A. cruentus* with two other wild species, *A. powellii* and *A. quitensis*, as the primary crop spread into their native ranges (Chan and Sun 1997; Sauer 1967, 1976; Xu and Sun 2001). An alternative hypothesis is that each of the grain species was domesticated independently in different regions and from different wild species: *A. cruentus* from *A. hybridus* presumably in Central America, *A. hypochondriacus* from *A. powellii* in Mexico, and *A. caudatus* from *A. quitensis* in South America (Sauer 1967, 1976). A third hypothesis suggested that each of the three domesticated species were derived from independent domestication events from genetically differentiated populations of *A. hybridus* (Mallory et al. 2008; Maughan et al. 2011). These discrepancies might be related to taxonomic coverage or the type of markers used. That is why a combination of morphological and molecular markers should be used on comprehensively selected amaranth taxa to understand the linkages between phenotypes and genomes.

Chan and Sun (1997) suggested that the low level of genetic diversity observed in *A. cruentus* might be a result of a specialized domestication process where only a small subset of the original *A. hybridus* population was subjected to intense artificial selection for specific agronomic characteristics. Mallory et al. (2008) speculated that the uniform cultivation range of *A. cruentus* might have further reduced the level of genetic diversity within the species. Conversely, *A. hybridus*, the putative wild progenitor species of the grain amaranths, showed a high genetic diversity.

Some scientists prefer to put what is known locally as *A. cruentus* and *A. hybridus* (and even some forms of *A. hypochondriacus*) under one species, *A. hybridus*, with subsp. *cruentus* and subsp. *hybridus* (Maundu et al. 2009).

Geographical distribution and agro-ecology

Amaranth is extensively cultivated as a green, leafy vegetable and grain crop in many temperate and tropical regions. In pre-Columbian times, large areas were grown during the height of the Aztec civilization in Mexico (Brenner et al. 2000). Meanwhile, amaranth had spread around the world and had become established for food use (grain or leaves) in places such as Africa, Central America, Southeast Asia, the Andean highlands in South America and North America (Brenner et al. 2000).

Amaranths exhibit C_4 photosynthesis and grow rapidly under heat and drought stress, and they tolerate a variety of unfavorable abiotic conditions, including high salinity, acidity, or alkalinity, making them uniquely suited for subsistence agriculture. By implication, amaranth has the potential for significant impact on malnutrition (Maughan et al. 2011).

Vegetable amaranths grow well at day temperatures above 25 °C and night temperatures not lower than 15 °C. Shade is disadvantageous except in cases of drought stress. Amaranth is a quantitative short-day plant, which is an advantage in the subtropics where the generative stage is delayed during summer. Amaranths like fertile, well-drained alkaline soils ($pH > 6$) with a loose structure. The mineral uptake is very high (Grubben 2004a).

A. blitum is fairly resistant to adverse climate and soil conditions. *A. cruentus* is grown up to 2,000 m altitude in Indonesia. Although *A. cruentus* and *A. hypocondriacus* are fairly tolerant of adverse climate and soil conditions, escapes growing as a weed tend to disappear because they cannot compete with true weeds like *A. spinosus* (Grubben 2004a; Jansen 2004). In the tropics, *A. caudatus* performs well under cool, dry highland conditions. In South America it is found at elevations of 1,000–3,200 m. In Peru it is grown in regions with an average annual rainfall of 550 mm (Agong 2006). *A. dubius* is frequently found in tropical humid lowland from sea level up to 500 m

Table 2 Nutrient contents in the leaves of five *Amaranthus* species (on 100 g fresh weight of edible portion basis) source: adapted from Yang and Keding (2009)

Species	Protein (g)	Vitamin A (mg)	Vitamin C (mg)	Ca (mg)	Fe (mg)	Zn (mg)
Amaranthus blitum	3.5	1.7	42	270	3.0	–
Amaranthus cruentus	3.2	1.8	36	305	3.8	0.7
Amaranthus dubius	3.5	3.1	78	582	3.4	1.5
Amaranthus tricolor	3.9	1.8	62	358	2.4	0.8
Amaranthus viridis	4.6	5.7	64	410	8.9	–

altitude, but also less frequently at higher elevations up to 2,000 m. It is a common plant in waste places, roadsides, flood plains, riverbanks and cleared forest areas. Regarding flowering time, it shows a weak quantitative short-day reaction (Grubben 2004b).

Flowering of *Amaranthus* species can start 4–8 weeks after sowing (Grubben and Denton 2004). However, the growth and development patterns are highly variable from one species/cultivar from the other (Table 1) and might also depend on photoperiodism, altitude and cultivation practices. Overall, the three grain crops have a longer growth period than weedy species (Wu et al. 2000).

Nutritional value of amaranths

Amaranths have excellent nutritional value because of their high content of essential micronutrients such as β-carotene, iron, calcium, vitamin C and folic acid (Priya et al. 2007). *Amaranthus hybridus* has higher content of minerals than *Vernonia amygdalina* Delile, *Telfairia occidentalis* Hook.f. (Aletor et al. 2002), *Gnetum africanum* Welw., and *Cucurbita pepo* L. (Iheanacho and Udebuani 2009). Schönfeldt and Pretorius (2011) found that raw leaves of *A. tricolor*, *Cleome gynandra* L., and *Corchorus olitorius* L. contained the highest concentration of iron, zinc as well as phosphorus and calcium, respectively, compared with *Vigna unguiculata* (L.) Walp. and *Cucurbita maxima* Duschene. Cooked *Cucurbita maxima* and cooked *A. tricolor* had higher magnesium levels than other three cooked vegetables.

One cup of amaranth leaves, that are cooked, boiled, and drained contains 90 % vitamin C daily value requirement, 73 % vitamin A, 28 % calcium and 17 % iron. The vitamin composition of the plant is higher than those reported for *Aspilia africana* (Pers.) C.D. Adams, *Bryophyllum pinnatum* (Lam.) Oken, *Vernonia amygdalina*, *Eucalyptus globulus* L. and *Ocimum gratissimum* L. (Alabi et al. 2005).

Amaranthus leaves and stems are used as food in Southeast Asia and Equatorial Africa and can compete with spinach leaves in terms of protein content (van Le et al. 1998). The particularity of amino acid profile of *A. cruentus* leaves is its methionine and lysine levels, which are the limiting amino acids in most plant proteins (Fasuyi 2007).

Wesche-Ebeling et al. (1995) showed that the wild species *A. viridis*, *A. retroflexus*, *A. palmeri* and *A. blitoides* had higher protein levels than the cultivated one *A. hypochondriacus*. Akubugwo et al. (2007) reported that the crude protein content of *A. caudatus* was higher than the protein content of *A. hybridus*. The nutrient contents of five species of *Amaranthus* are shown in Table 2. The figures show interspecific variation in nutrient contents. Indeed, the highest amount of protein, vitamin A and iron were found in *A. viridis* while *A. dubius* showed highest amount of vitamin C, calcium and zinc.

A similar study done on four *Amaranthus* species, *A. blitum*, *A. spinosus*, *A. tricolor*, and *A. viridis* showed that the highest amount of proteins, carbohydrates and calcium were found in *A. spinosus* while *A. viridis* contained the maximum amount of iron and sodium (Srivastava 2011). Andini et al. (2013) compared the protein contents of the vegetable (*A. tricolor*), grain (*A. cruentus*, *A. hypochondriacus*, *A. caudatus*) and weedy (*A. blitum*, *A. dubius*, *A. viridis*) and indicated that the content of proteins in the leaves of the three weedy types was found to 2–2.5 higher than that found in *A. tricolor*.

Even though there is no doubt about the nutritional value of amaranth leaves, the processing methods influence the nutrient contents positively and/or negatively. For example, boiling leaves in distilled water significantly decreased their levels of ascorbic acid, phosphorus, nitrates and oxalates. However, the cooking losses of the nutrients were not excessive, while the antinutrients were substantially reduced (Mziray et al. 2001). Longer blanching periods result in higher losses in ascorbic acid and β-carotene contents of leaves (Yadav and Sehgal 1995a). The nutritional quality of minerals in food depends on their quantity as well as their bioavailability (Reddy and Love 1999). Blanching and cooking increases availability of minerals such as iron (Yadav and Sehgal 2002), calcium and zinc (Yadav and Sehgal 1995b) and significantly reduced antinutrient contents (Yadav and Sehgal 2003). Heat treatment of these vegetables by pressure-cooking, stir-frying and open-pan boiling had a beneficial influence on the bioaccessibility of β-carotene and stir-frying was the most effective method (Veda et al. 2010). Thermal processing can also enhance the bioavailability of thiamin, vitamin B-6, niacin and folate. However, there is no evidence that such improvements in bioavailability compensate for the losses in activity of heat-labile and water-soluble vitamins (Hotz and Gibson 2007).

Amaranth grain is also a good source of important minerals. It was reported that the amount of minerals such as calcium, magnesium, iron and zinc in wheat grain are 5.2-, 2.9-, 2.8- and 1.3-fold lower than in amaranth seeds, respectively (Alvarez-Jubete et al. 2010). Its high lysine content makes it particularly attractive for use as a blending food source to increase the biological value of processed foods. The lipids are rich in tocotrienols and squalene, which are natural organic compounds positively involved in lowering low-density lipoprotein blood cholesterol. However, whole grains contain significant amounts of phytic acid, a well-known inhibitor of iron absorption and other minerals (Sanz-Penella et al. 2012).

Nutraceutical properties of amaranths

According to Manikandaselvi and Nithya (2011), nutraceuticals are non-specific biological agents used to promote wellness, prevent malignant processes and control symptoms.

Several studies have shown that amaranth seed or oil may benefit those with hypertension and cardiovascular disease, regular consumption reduces blood pressure and cholesterol levels, while improving antioxidant status and some immune parameters. "In Benin, the dried plants are burned for the preparation of potash. Vegetable amaranths are recommended as a good food with medicinal properties for young children, lactating mothers and for patients with constipation, fever, hemorrhage, anemia or kidney complaints. In Senegal the roots are boiled with honey as a laxative for infants. In Ghana the water of macerated plants is used as a wash to treat pains in the limbs. In Ethiopia, *A. cruentus* is used as a tapeworm-expellant. In Sudan the ash from the stems is used as a wound dressing. In Gabon heated leaves were used on tumors" (Grubben 2004a).

Amaranthus tricolor and *A. caudatus* are used externally to treat inflammations, and internally as a diuretic (Agong 2006). According to Baral et al. (2011), the seed of *A. spinosus* is used as a poultice for broken bones. It is used internally in the treatment of internal bleeding, diarrhoea and excessive menstruation. In Southeast Asia, a decoction of the root is used to treat gonorrhoea and is also applied as an emmenagogue and antipyretic. The Nepalese and some tribes in India apply *A. spinosus* to induce abortion. In many countries, the bruised leaves are considered a good emollient. The leaves are also used for gastroenteritis, gall bladder inflammation, abscesses, arthritis and for the treatment of snakebites. The plant sap is used as an eye-wash to treat ophthalmia and convulsions in children. During the rainy season, *A. spinosus* bark decoction is taken to ward off malaria.

Production and cultivation systems

Because of its low production costs, amaranth is one of the cheapest dark-green leafy vegetables in tropical markets and is often described as the poor man's vegetable (Varalakshmi 2004). In Africa amaranths are among the most important leafy vegetables, a fact attributed to their easy of cultivation, wide occurrence, low pests and diseases incidence, low labour input, ease in cooking and high nutritional value (Maundu et al. 2009). Cultivation occurs in all agro-ecological zones of West Africa, from the coastal sector in the Guinean zone to the dry forests and herbaceous savannahs in the Sudanian zone. In Benin, *Amaranthus* species are the most commonly cultivated and consumed African leafy vegetables throughout the country. (N'Danikou et al. 2010). In East Africa, leaf amaranths are among the most important leafy vegetables. Although much of the production is still from plants growing spontaneously in farmland and wasteland, cultivation for both home and commercial use is on the increase particularly around urban centres. *A. dubius* is the most widely used in the coastal parts of Kenya and Tanzania and adjoining lowlands below 1,500 m a.s.l. *A. hybridus* is more important in central highlands of Kenya where it is produced by small-scale farmers at 1,700–2,500 m a.s.l for the urban market. *A. blitum* is more popular in the western zone of Kenya and in Uganda, at 1,500–2,600 m a.s.l. It is cultivated but also picked from spontaneous populations.

Vegetable amaranth is usually grown commercially as a sole crop on beds. It is also found intercropped with other food crops and in home gardens. The common cultivation practice is sowing in a nursery at a seed rate of 3–10 g/m^2 and transplanting after 2–3 weeks. In this way the grower gets 1,000–1,500 plantlets/m^2 for transplanting. For repeated cuttings, a density of about 20 plants/m^2 is appropriate. It is also possible to sow directly, either broadcast or in rows with at least 20 cm between the rows, with a seed rate of 2–5 g/m^2. Direct sowing is the common practice in Nigeria, Uganda and in western Kenya (Grubben 2004a). Harvesting can occur 4–5 weeks after sowing. In subsistence agriculture, the lateral shoots of plants growing near homes are harvested while the plant continues to produce seeds that will make subsequent plantings. In the case of multiple harvests, the main shoot is harvested first and side shoots are allowed to grow, these being picked as and when required. In regions infested by borers, harvesting by uprooting is preferred (Schippers 2004).

Amaranths like soils rich in nitrogen and high levels of nitrogen will delay the onset of flowering, thus providing higher leaf yield. The addition of well-rotted organic matter is beneficial, at 20–40 t/ha. Amaranth thrives on urban garbage or compost. This is one of the reasons for its popularity in Cotonou (Benin) and other urban or suburban areas. The application of compound fertilizer NPK 10-10-20 at a rate of 400 kg/ha is recommended. Lack of water causes early flowering. It is therefore essential to irrigate frequently in the case of a rapid growth and late flowering (Schippers 2004).

Wet rot or stemrot caused by the fungus *Choanephora cucurbitarum* is the main disease. Damping-off caused by *Pythium aphanidermatum* and *Rhizoctonia* is often serious in seedbeds. It is controlled by good drainage. Insects are a serious problem for amaranth growers (Grubben 2004a). Caterpillars (*Spodoptera litura*, *Helicoverpa armigera*, *Hymenia recurvalis, Psara basalis)* and sometimes grasshoppers are the most harmful (Grubben 2004a; James et al. 2006). The larvae of the stem borer *Lixus truncatulus* often cause serious damage. Many other insects such as aphids, leaf miners, stinkbugs, mole crickets and mites also attack amaranth but generally cause only minor damage. Biological insecticides derived from *Bacillus thuringiensis* (Bt) and *Beauveria bassiana* are fairly effective against caterpillars (Grubben 2004a; James et al. 2006). Amaranth is hardly or not susceptible to nematode damage. Harvesting by uprooting removes *Meloidogyne* larvae that have penetrated the roots, making the soil more suitable for a next crop of lettuce, okra, African nightshades (*Solanum* species), *Corchorus* or other vegetables susceptible to root-knot nematodes (Grubben 2004a).

Leafy amaranth yields of about 40 t/ha had been recorded in the region of Dar-Es-Salaam while in Benin and Nigeria, the yield of shoots of 4 weeks old *A. cruentus* was about 30 t/ha (Schippers 2004). Evaluation of harvesting techniques showed that continuous harvesting with topping (removal of flowers) gave the highest economic leaf yield (32.0 t/ha), while continuous harvesting without topping gave the lowest (17.8 t/ha). Uprooting the whole plant after two planting and two harvests was the second highest yielding method with 29.8 t/ha and plants harvested with this method had the smallest leaf size but it provided better marketable leaf quality (Oluoch et al. 2009). For many species, only the young new leaves are harvested as the older ones are bitter or hairy; but there are no hard-and-fast rules. Different communities favour different tastes and practice varying harvesting and cooking techniques to either reduce negative characteristics or to enhance the more desirable traits (Maundu et al. 2009). It is therefore important to tailor production and marketing systems on consumers' preferences as they are highly dependent on socio-cultural background.

Low crop productivity is a general problem facing most farming systems in sub-Saharan Africa. Low leaf yields of <1.2 tons per hectare in amaranth (Madulu and Chalamila 2005) could be attributed to several factors such as environmental, agronomic, low soil fertility and low yielding varieties which have short growth periods. In Benin, the early flowering of some amaranth fields is probably more a result of waterstress and the use of too old seedlings for transplantation than a photoperiodical symptom (Grubben 1975).

Reproductive biology

The structure of the inflorescence of *Amaranthus* spp. is complex. Flowers are small, green, unisexual, and develop in numerous dense clusters. Each cyme has a determinate main axis with a terminal male flower, followed by pairs of opposite, or occasionally single, lateral branches of female flowers. Each flower is subtended by 1–2 spinescent bracteoles, which increase the overall density of the inflorescence (Costea and Tardif 2003). The cymes are further arranged in numerous spikes that grow acropetally by the addition of new cymes. At any moment during flowering, toward the endings of the spiciform branches there are several newly developed male flowers that can pollinate female flowers from lower cymes. The formation of new male flowers decreases and stops towards the end of the growing season. All monoecious species of *Amaranthus* are self-compatible and probably are primarily self-pollinated (Brenner et al. 2000; Costea et al. 2001). The flowers lack nectar glands, and pollination occurs predominantly by wind or gravity. (Costea et al. 2001; Franssen et al. 2001). The pollen grains of *Amaranthus* spp. contain 1.2–7.5 % starch, which may play a role in protecting the pollen against desiccation. The pollen grain is covered with granules or spinules that facilitate adherence to the stigma hairs. The gynoecium of *Amaranthus* spp. does not have a style and consists of two or three united carpels. The unilocular ovary is sometimes narrowed toward the apex to form a "beak" filled with ramified cells and many intercellular spaces that are penetrated by the pollen tubes during fertilization. The receptive part of the stigma is dry and covered with 2–4 rows of uni- or bicellular hairs (Costea et al. 2001).

Pre-dispersal seed predators also may play a role in the reproductive biology of *Amaranthus* spp. in North America. Flower formation, pollination, and seed set proceed simultaneously because of the indeterminate growth habit of the plants. Pre-dispersal predation is common because of the dense terminal inflorescence and highly nutritious seeds. Insects such as *Coleophora lineapulvella* foraging in the inflorescence may accidentally carry or disperse pollen. When seeds are shed, eaten or damaged, the next pair of ovaries within each cyme begins to develop, with the result that a single lost seed stimulates the formation of two new ones (Costea et al. 2004). Seeds have a thin and structurally simple seed coat that is both impermeable and resistant to mechanical and chemical agents (Costea et al. 2001).

Seed production varies enormously with growing conditions. Seed production per plant could be estimated from plant height and basal stem diameter (Mohler and Callaway 1995). The size and weight of the seeds can vary between the populations of the same species, between the individuals of the same populations and even between seeds on the same plant.

Seed dispersal is accomplished by wind, farm machinery, water, birds, animals, and the spreading of manure and compost. *Amaranthus* seeds are lightweight, but not otherwise adapted for wind-dispersal, and seeds often fall near (0.2–2 m) the mother plant (Costea et al. 2004). Both seeds and fruits can float easily, and are dispersed by raindrops, streamlets produced on the soil by rain, surface irrigation, and water courses. Viable seeds can be dispersed after ingestion and elimination by mammals and birds. Storage under ambient conditions should not exceed 3 months for best performance of amaranth seeds (Kehinde et al. 2013). Probert et al. (2009) found that 84 % of amaranth seed collections displayed no significant drop in viability during 20 years storage at 15 % RH and −20 °C. In ageing conditions (45 °C, 60 % RH), amaranth (*Amaranthus caudatus*) seeds took about 70 days to fall to 50 % viability. For resource-constrained seed banks in the tropics, vacuum sealing with or without refrigeration may represent a viable alternative to other expensive and energy-intensive storage techniques (Croft et al. 2013).

Genetic resources and breeding

Current genetic resources

Correct genotype identification is important to evaluate the genetic diversity of local amaranths. It is estimated that there are 61 species of amaranth around the world. Identification and preservation of germplasm are necessary for maintaining genetic diversity, studying local genetic material in order to choose ecotypes having high nutritional interest in their place of origin, and initiating breeding programs (Perez-Gonzalez 2001). At its peak, the Rodale Research Center collection (Pennsylvania, USA) contained approximately 1,400 accessions mostly represented by *A. cruentus*, *A. hypochondriacus*, *A. caudatus*, *A. tricolor* and *A. dubius* (Brenner et al. 2000). The *Amaranthus* germplasm collection of the Plant Introduction Station (USDA) includes approximately 3,000 accessions, and half of the species in the genus. Most of the accessions are landrace types for grain production (Brenner et al. 2000); species in high numbers include *A. hypochondriacus*, *A. caudatus*, *A. cruentus*, *A. hybridus* and *A. tricolor*. The National Botanical Research Institute (NBRI, India) has one of the best qualitative collections of amaranth germplasm in the world with over 2,500 accessions referable to 20 species (Mathews 2001). The World Vegetable Center (AVRDC) holds a collection of circa 520 acessions of 18 amaranth species (AVRDC Vegetable Genetic Resources Information System, http://203.64.245.173/characterization.asp). Other germplasm collections are held by at least 60 different groups or institutions, although most of these tend to have fewer than 100 entries (Brenner et al. 2000). In general, non-domesticated germplasm is poorly represented in these collections. However, at the University of Illinois, for instance, seed collected from several weedy populations of the Midwestern USA are conserved for herbicide resistance research and genetic diversity studies (Trucco and Tranel 2011).

Evolutionary relationships and genetic variation in *Amaranthus*

Studies on chromosome number and hybrid fertility, random amplified polymorphic DNA (RAPD), restriction site variation of chloroplast and nuclear DNA have clarified some aspects regarding genetic diversity and evolutionary relationships among grain amaranths and their wild relatives (Popa et al. 2010).

Analysis of internal transcribed spacer (ITS) regions of nuclear ribosomal DNA (rDNA) showed that 12 of 92 *Amaranthus* accessions collected and identified by weed scientists were misidentified. Internal transcribed spacer (ITS) primers have proven to be a useful source of information for the resolution of phylogenetic relationships at the species level (Popa et al. 2010). However, taxonomic confusion remains among closely related taxa such as *A. cruentus, A. caudatus,* and *A. hypochondriacus*, and their putative wild progenitors, *A. hybridus, A. quitensis*, and *A. powellii*. Low Internal transcribed spacer divergence in these taxa resulted in poorly resolved phylogeny (Xu and Sun 2001).

Analysis of genetic diversity and evolutionary relationships among wild amaranth and grain amaranths using Random Amplified Polymorphic DNA (RAPD) and isozyme markers (Chan and Sun 1997) showed a monophyletic origin for grain amaranths, with *A. hybridus* as the common ancestor. Studies on isozymes have demonstrated a high degree of polymorphism between populations, in which it is possible to find intermediate stages of domestication, such as wild types of amaranth that live without human intervention, amaranths that survive despite the efforts to eradicate them, and cultivated species that require special care for survival (Mujica and Jacobsen 2003). Moreover, possible introgression of wild genes into cultivated populations has been suggested (Lanoue et al. 1996).

Genetic markers are essential tools for modern plant breeding research programs (Eathington et al. 2007). They are particularly important for germplasm conservation, characterization, and in breeding applications, such as marker-assisted selection (MAS) (Maughan et al. 2011). The first step toward the development of genetic markers for amaranth was the characterization of 179 microsatellite markers by Mallory et al. (2008). About 37 microsatellite markers segregated an intraspecific *A. cruentus* F2 mapping population resulting in a sparsely populated linkage map. A significant advance in the number of available markers occurred when Maughan et al. (2009) reported the utilization of a novel genomic reduction strategy linked with next-generation sequencing to identify 27,658 putative single nucleotide polymorphisms (SNPs) among four diverse amaranth accessions. Compared to microsatellites-based markers, SNPs exhibit a lower mutation rate and thus are less problematic in population genetic analyses (Xu et al. 2005). Within *A. caudatus*, *A. cruentus*, *A. hypochondriacus*, and *A. hybridus* subgroups, a total of 136, 35, 186, and 263 SNP assays were polymorphic, respectively. *Amaranthus hypochondriacus* showed the highest total number of polymorphic SNP markers, while *A. cruentus* showed the lowest genetic diversity of the grain species with 35 polymorphic markers only. The reduced level of genetic diversity observed in *A. cruentus* is consistent with other observations using different types of genetic markers, including microsatellites, restriction fragment length polymorphism (RFLP), isozyme, and amplified fragment length polymorphism (AFLP) (Chan and Sun 1997; Mallory et al. 2008; Xu and Sun 2001).

Hybridization in Amaranth species

Eight hybrids, namely *A. edulis* × *A. hypochondriacus, A. edulis* × *A. caudatus, A. edulis* × *A. caudatus* var. *atropurpureus, A. caudatus* × *A. hybridus, A. edulis* × *A. hybridus, A. caudatus* × *A. hypochondriacus, A. hybridus* × *A. hypochondriacus* and *A. powellii* × *A. hypochondriacus* were studied. The successful crosses were obtained for *A. powellii* × *A. hypochondriacus*, *A. edulis* × *A. hypochondriacus, A. caudatus* × *A. hypochondriacus, A. edulis* × *A. caudatus, A. edulis* × *A. caudatus* var. *atropurpureus* and *A. hybridus* × *A. hypochondriacus* (Pal and Khoshoo 1973).

Hybrids from crosses between *A. hypochondriacus* as the male parent and *A. hybridus* and *A. caudatus* showed the formation of 16 bivalent chromosomal associations. However, hybrids produced with *A. hybridus* showed much greater pollen fertility than hybrids produced with *A. caudatus*. Interestingly, in *A. hybridus* × *A. caudatus* hybrids seedling were lethal (Trucco and Tranel 2011). According to Ranade et al. (1997), the hybrid of *A. edulis* and *A. caudatus* is clustered together with *A. caudatus,* while the hybrid of *A. hybridus* and *A. hypochondriacus* is in the cluster of the latter species. The low values of genetic distance between these hybrids and other accessions of *A. caudatus* and *A. hypochondriacus*, respectively, indicated that these are not strongly differentiated genetically. Hybrids with wild species have been produced to address all major breeding objectives, which include yield improvement, pest management, and grain harvestability. Brenner et al. (2000) report that crop–wild hybrids have been produced to transfer *A. powellii* nondehiscence to *A. cruentus* and *A. hypochondriacus* breeding lines, in efforts to reduce grain shattering.

Future prospects for research and development

Despite several studies conducted on amaranths, there are still many unresolved issues regarding vegetable amaranths such as *A. blitum*, *A. cruentus*, *A. dubius*, *A. spinosus*, *A. thunbergii*, *A. tricolor*, and *A. viridis* in terms of nutrition and health benefits, genetic diversity, variety improvement, seed supply, assessment of the importance of these species in cropping systems and their integration in agricultural statistics. In contrast, grain amaranths have been much studied because of the potential nutritional impact of their seed consumption on human health in the temperate and tropical regions of Asia, Australia, Europe, America and Africa.

Nutritional and nutraceutical potential

In spite of the important level of knowledge on the nutritional value of vegetable amaranths, much still remains to be done. First, the nutrient composition of local species and varieties and its variations with respect to the environment and cultivation practices, especially fertilization have to be deeply investigated to determine most interesting species and practices that enhance both yields and nutritional value of these vegetables. Second, processing has an effect on nutrient contents and bioavailability as mentioned earlier. Yang and Keding (2009) reported that the potential contribution of food to micronutrient status depends upon the retention of the nutrients after processing and cooking. Data measured for a specific dish may not be applicable to another dish with the same ingredients. Thus, there is a need to assess the impact of processing and cooking methods commonly used in Africa on the nutritional value of species so as to suggest adequate combinations of foods including amaranths. Third, there is a dearth of scientific work related to nutraceutical properties of amaranths. Little information about pharmacologically active compounds for each species is available. Traditional knowledge may contribute to valorization of those properties and further to the promotion and conservation of less commonly cultivated species.

Addressing these issues will contribute to raising awareness on vegetable amaranths health benefits and increase their utilization and consumption.

Production and commercialization data

There is a lack of data on (1) the production of amaranth species in African countries, (2) the total cultivated areas for each species, and (3) commercialization and consumption. No statistical data was available for individual species since in most cases all leafy vegetables were recorded as one single group. In national or FAO statistics, they were not recorded at all (Grubben 2004a). Such data are important in assessing impacts of interventions, and hence both governments and research and development institutions should build strategic partnerships to address this lack of information. International collaborative efforts involving institutions such as the FAO, Bioversity International, Crops for the Future and the EU supported-ACP project and the three conferences on neglected and under-utilized species (NUS) (Arusha 2008; Kuala Lumpur 2011 and Accra, 2013) show the increasing recognition of the importance of these crops. However, at a national level, there is a need to raise public and political awareness of the benefits of NUS, to provide incentives for conservation of biodiversity, to improve policies, legal frameworks, stronger collaboration, and information sharing systems between research programmes, extension services, and farmers involved in the value chains of NUS.

Taxonomic re-evaluation

Many studies using biochemical (Das 2012; Drzewiecki 2001; Juan et al. 2007) and molecular markers (Costea et al. 2006; Lymanskaya 2012; Maughan et al. 2011; Ranade et al. 1997; Ray and Roy 2009; Wassom and Tranel 2005; Xu and Sun 2001) were conducted to analyze the genetic variability and phylogenetic relationships among *Amaranthus* species. However, taxonomic ambiguities regarding infrageneric classification, identification of each species and relationships among them, especially *A. hybridus* and *A. cruentus*, persist and must be clarified through comprehensive studies focusing on both grain and vegetable amaranths. This will help streamline characterization of local species and initiation of selection, conservation and genetic improvement programmes.

Seed supply systems

A crucial step in the promotion of amaranths is the production and supply of quality seeds. Seeds represent an important factor in food production, and their quality determines the performance of a crop (Achigan-Dako et al. 2014). Overall, the seed supply system is still weak for many major crops and worse for neglected and under-utilized species including amaranths crops. This situation calls for the development of local seed programmes including commercial seed supply by small-scale seed enterprises, and community-based seed supply systems that will ensure production and marketing of quality seed. In this regards, national seed services and research institutions should collaborate to ensure quality control and variety release and utilization. They should also to attend to the safeguarding of farmers rights related to the sustainable use of plant genetic resources as provided by the International Treaty on Plant Genetic Resources for Food and Agriculture.

Breeding perspectives

Given the importance of amaranths in the control of nematodes, their short cultivation cycle and strong growth, and despite their low selling price, they are among most commonly cultivated African leafy vegetables. Besides, *Amaranthus* is a wide taxonomic group with a large diversity of species, with particular traits such as resistance to biotic and abiotic stresses, high yields, nutritive, nutraceutical and market qualities. It is consequently important to identify and improve those traits through breeding programs. Several studies have been carried about the origin and interrelationship of different species, their reproduction, hybridization, germplasm characterization and their improvement. However, those studies have generally focused on grain amaranths which are selected for a high grain yield to the detriment of leaves production.

Expanding the research to vegetable amaranths will help strengthen the background necessary for any breeding work. This requires collection and diffusion of local communities' knowledge on the value of neglected amaranths species and an effective collaboration between farmers and scientists. According to Perez-Gonzalez (2001), identification and preservation of germplasm are necessary for maintaining genetic diversity and studying local genetic material in order to choose ecotypes of high nutritional interest in their place of origin.

Interspecific and intraspecific variations should be exploited to improve macro and micro-nutrients of cultivated amaranths including vitamin A, iron and zinc contents, especially of *Amaranthus cruentus*.

Identification of molecular markers associated with these traits may allow plant selection at an early stage. Indeed, marker-assisted selection has been tested on many species such as eggplant (Nunome et al. 2001), melon (Chiba et al. 2003) and rice (Jiang et al. 2012) to achieve various breeding objectives.

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