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REVIEW

From zero to hero: the past, present and future of grain amaranth breeding

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Abstract

Key message **Grain amaranth is an underutilized crop with high nutritional quality from the Americas. Emerging genomic and biotechnological tools are becoming available that allow the integration of novel breeding techniques for rapid improvement of amaranth and other underutilized crops.**

Abstract Out of thousands of edible plants, only three cereals—maize, wheat and rice—are the major food sources for a majority of people worldwide. While these crops provide high amounts of calories, they are low in protein and other essential nutrients. The dependence on only few crops, with often narrow genetic basis, leads to a high vulnerability of modern cropping systems to the predicted climate change and accompanying weather extremes. Broadening our food sources through the integration of so-called orphan crops can help to mitigate the effects of environmental change and improve qualitative food security. Thousands of traditional crops are known, but have received little attention in the last century and breeding efforts were limited. Amaranth is such an underutilized pseudocereal that is of particular interest because of its balanced amino acid and micronutrient profiles. Additionally, the C_4 photosynthetic pathway and ability to withstand environmental stress make the crop a suitable choice for future agricultural systems. Despite the potential of amaranth, efforts of genetic improvement lag considerably behind those of major crops. The progress in novel breeding methods and molecular techniques developed in model plants and major crops allow a rapid improvement of underutilized crops. Here, we review the history of amaranth and recent advances in genomic tools and give a concrete perspective how novel breeding techniques can be implemented into breeding programs. Our perspectives are transferable to many underutilized crops. The implementation of these could improve the nutritional quality and climate resilience of future cropping systems.

Introduction

Agricultural industrialization and globalization have provided a steady increase in food supplies worldwide through improved yields. However, the green revolution favored a small number of crops with few high performing varieties, leading to a loss of agrobiodiversity and the replacement of minor crops. The loss in diversity of crop species contributing to the world's food supplies is a potential threat to global food security (Khoury et al. 2014). The few major crops (rice, wheat and maize) which provide the largest proportion of daily nutrition for billions of people, suffer from an imbalanced nutrient profile (Pedersen et al. 1990). While these crops provide sufficient calories, they lack essential minerals and vitamins for a balanced nutrition, resulting in malnutrition of over two billion people worldwide who almost solely rely on these crops (Cheng et al. 2017). The incorporation of alternative crops with

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favorable nutrient composition could improve dietary diversification and be a key component to improve food quality to fight hidden hunger and increase biodiversity.

Amaranth is one such crop, which has high potential to act as alternative food grain in most parts of the world. There are three grain amaranth species (Fig. 1) which are predominantly self-pollinating diploids with 16–17 chromosome pairs and a total genome size of approximately 500 Mbp (Lightfoot et al. 2017; Stetter and Schmid 2017). Two of these species originate from Central and North America (*A. cruentus* L. and *A. hypochondriacus* L.), and one from South America (*A. caudatus* L.). Amaranth has wide adaptability and can be grown from temperate to tropical conditions. In the last decades, there has been an increased interest in amaranth related to its potential as a nutritional substitute in food formulations, and diverse pharmaceutical uses. Moreover, amaranth has the ability to adapt to environmental stresses such as high temperature, drought and low input cultivation (Barba de la Rosa et al. 2009). The high nutritional value and oil quality make it a highly valuable crop. In recent years, major advances in amaranth research have been made that may allow the adaptation of amaranth to modern cropping systems and make it an ecologically and economically viable future crop. In the present work, we review the benefits, origin, history, genetic resources, breeding and genomic advancements of amaranth and suggest future prospects that can accelerate amaranth breeding. Our results and perspectives can be transferred to a wide range of minor crops in order to increase yields and quality in changing environments.

A new crop with nutraceutical values

Amaranth grain and leaves are an excellent source of high-quality protein and lipids with higher contents of minerals, such as Ca, K and P than cereal grains (Fig. 2, Calderon de la Barca et al. 2010). Amaranth was found to have higher nutritional value than rice and contains more than three times the average amount of calcium than major cereals and is high in iron, magnesium, phosphorus and potassium. (Nascimento et al. 2014). Especially in rural low-income communities, amaranth could provide essential nutrients required for body growth and development and for prevention of nutritional disorders (Kachiguma et al. 2015).

Amaranth has a particularly favorable composition in essential amino acids, and its protein quality is much higher than conventional food sources like wheat, barley and maize (Venskutonis and Kraujalis 2013). Most cereal grains are generally deficient in the essential amino acid lysine and contain excess of leucine, isoleucine and valine (Table 1), while amaranth is rich in lysine (5.2–6.1 g/100 g protein) and therefore has a well-balanced composition of amino acids (Mlakar et al. 2009). Similarly, sulfur-containing amino acids in amaranth (2.6–5.5 g/100 g) are comparatively higher than in most of the legume species (1.4 g/100 g; Juan et al. 2007). The sum of essential amino acids ranged from

Fig. 1 Inflorescence of three grain amaranth species. **a** *A. hypochondriacus*; **b** *A. caudatus*; **c** *A. cruentus*

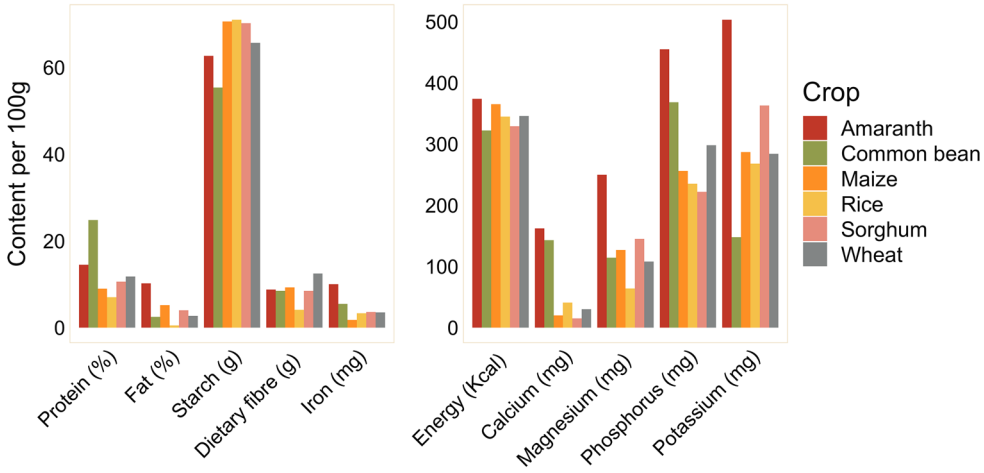

Fig. 2 Comparison of nutrient content of amaranth and other crops. Values are per 100 g of seeds, units for each component are indicated in labels. (Data from Rastogi and Shukla 2013; Petry et al. 2015; Kumar et al. 2016)

Table 1 Nutritional composition of three grain amaranth species in comparison to major cereals. (Data from Rastogi and Shukla 2013; Das 2016)

Components	*A.cruentus*	*A.hypochondriacus*	*A.caudatus*	Rice	Wheat	Maize
Proximate composition (% dry weight basis)						
Crude protein	13.80–21.50	15.00–16.60	13.10–21.00	6.80	13.20	10.00
Crude fat	5.60–8.10	6.10–7.30	5.80–10.90	1.00	2.70	5.20
Crude fibre	3.10–4.20	4.90–5.00	2.70–4.90	4.10	12.20	9.30
Carbohydrate	63.10–70.00	67.90–70.00	63.70–76.50	78.20	65.70	72.80
Amino acids (% of total protein)						
Tryptophan	0.90	1.80	1.40	1.00	1.20	0.60
Methionine	4.60	1.60	4.20	3.00	3.50	3.20
Threonine	3.90	3.30	3.40	3.70	2.70	4.00
Isoleucine	4.00	2.70	3.60	4.50	4.10	4.60
Valine	4.50	3.90	4.20	6.70	4.30	5.10
Lysine	6.10	5.90	5.20	3.80	2.60	1.90
Phenylalanine	8.50	8.52	6.00	9.10	8.10	10.60
Leucine	6.10	4.20	5.10	8.20	6.30	13.00

31.22 to 44.88 g/100 g total protein, making amaranth a good source of high-quality protein and nutritive substitute for some cereals in functional foods (Akin-Idowu et al. 2013), as well as conventional feed in the feed mixtures of animals (Pisarikova et al. 2005). On average, amaranth grain is composed of 13.1–21.0% of crude protein which is mainly composed of easily digestible albumins and globulins (50–60% of total protein), 20.8% of alkali-soluble protein glutelins, which are close to albumins and globulins by their nutritive value, and only 12% of alkali-soluble proteins prolamines that are poor in essential amino acids (Konishi et al. 1985; Zheleznov et al. 1997). Protein contents vary between amaranth species and varieties (Kaur et al. 2010), and wild (weedy) species are reported to contain higher amount of proteins, amino acids and other nutrients than the cultivated ones (Table 1; Gorinstein et al. 1991; Guil et al. 1997; Shukla et al. 2010; Andini et al. 2013).

In the USA and Europe, amaranth is especially preferred as a substitute for wheat in diets of patients with celiac disease (Huerta-Ocampo and Barba de la Rosa 2011; Tosi et al. 2001) due to its properties as functional gluten-free ingredient of bread, pasta and confectionary products (Alvarez-Jubete et al. 2009). Amaranth seeds can be subjected to several treatments such as puffing, toasting or grinding to be consumed as instant drinks with water or milk or to be included in bread, tortillas, cookies or other preparations (Sanchez 1983; Carlos-Mendoza and Bressani 1987; Bhat et al. 2015). Gluten-free amaranth seed flour can be used to improve the nutritional value and digestibility of various cereal products, enhancing the protein quality, fat content and amino acid profile without losing physical attributes (Bressani et al. 1992).

While the most widely known health benefit of amaranth is that the grains are effectively gluten free, there are several reports on a variety of medically active compounds in amaranth. Medicinal properties of amaranth are attributed to the presence of mixed tocopherols, 0.3–0.4% phytosterols and 4–6% squalene in its oil (Khamar and Jasrai 2014)

along with rich amounts of bioactive flavonoids (Rastogi and Shukla 2013). Amaranth oil is the best plant-based source of squalene, which is a strong antioxidant protecting the skin from premature aging by preventing cell damage (Khamar and Jasrai 2014). Various other compounds of amaranth, such as saponins, tannins, phenols, flavonoids, alkaloids, cardiac glycoside, steroid and triterpenoids, have been reported to have anti-inflammatory and anticancerous effects (Reyad-ul-Ferdous et al. 2015). Historically, amaranth has been used in traditional medicines around the world for numerous purposes (Kumar et al. 2012). It has been reported that seed protein of *A. hypochondriacus* which showed resemblance to tumor inhibiting lunasin proteins of soybean has anticancerous properties (Silva-Sanchez et al. 2008). The numerous potential compounds with several medical applications provide new avenues for amaranth breeding, although the effectiveness of specific molecules needs extensive scientific investigation prior to medical application.

Phylogeny, origin and history

The genus *Amaranthus* is part of the *Amaranthaceae* family and includes 50–70 species (Costea and Demason 2001). Most of these species are native to the Americas, and only 15 species are native to Africa, Europe and Asia (Das 2016). The taxonomic position and interspecific relationship of the genus *Amaranthus* are poorly understood due to the high phenotypic variation and mostly based on the inflorescence characters (Sauer 1955). While Sauer (1955) divided the genus into two subgenera the most recent taxonomy separates the genus into three subgenera, *Acnida*, *Amaranthus* and *Albersia* (Mosyakin and Robertson 1996; Costea and Demason 2001). These results have recently been partially reproduced using genome-wide molecular markers. However, the *Acnida* subgenus was split into two separate phylogenetic groups, potentially because of a polyploidization event within the subgenus (Stetter and Schmid 2017). The *Amaranthus* subgenus contains the hybridus complex that includes the three grain amaranth species and their two potential wild ancestors, *A. hybridus* and *A. quitensis*. These five species are closely related and readily cross within the complex (Stetter et al. 2016; Stetter and Schmid 2017).While the taxonomic identification remains a difficulty in *Amaranthus*, genetic markers provide a clear and inexpensive solution for species identification.

Grain amaranth was first cultivated in the Americas with archaeological records of collected seeds from Northern Argentina that date back to the initial mid-Holocene (8000–7000 BP; Arreguez et al. 2013). In Central America, the oldest findings of grain amaranth come from a cave in Tehuacan, Mexico, where seeds of *A. hypochondriacus* and *A. cruentus* were dated 1500 and 6000 years old, respectively (Brenner et al. 2000). Archaeological evidence suggests that amaranth was an integral part of Aztec civilization and grown in a large acreage in Mexico during the 1400s. Amaranth production strongly declined after the arrival of the Spanish, who later spread it to Europe, Africa and Asia. The distribution suggests though that both light (domesticated) and dark seeded (wild) genotypes of *A. hypochondriacus* were probably introduced to Asia from Latin America around early 1700s by both land and sea routes (Sauer 1993).

Several domestication hypotheses for the three grain amaranth species have been suggested over the last 50 years. Sauer (1967) suggested several models, including multiple domestication events from different ancestors and a single domestication event giving rise to all three grain amaranths, but also that all three grain amaranth were domesticated from *A. hybridus*. Reports based on meiotic behavior of hybrid chromosomes, allozyme analyses and DNA polymorphism provided supporting evidences in favor of that hypothesis and suggest that *A. hybridus* is a common ancestor to the three cultivated grain amaranth species (Sauer 1957; Pal et al. 1982; Pandey 1999). Recent studies based on SSRs and genotyping-by-sequencing agree that *A. hybridus* is the ancestor of all three grain amaranth, but it has not yet been fully resolved if in independent domestication events or from one single domestication event (Kietlinski et al. 2014; Stetter and Schmid 2017; Stetter et al. 2017). Phylogenetic and population genetic analysis indicates a clear geographic grouping of *A. hybridus* from South America with *A. quitensis* and *A. caudatus* and of *A. hybridus* from Central America with the two Northern crop species, suggesting separate domestication events in the different regions (Stetter and Schmid 2017). Nevertheless, the status and contribution of the closest wild relative *A. quitensis* remains unclear. *A. quitensis* might have contributed through gene flow to the domestication of the South American *A. caudatus* or be an intermediate stage of the domestication from *A. hybridus* (Kietlinski et al. 2014; Stetter and Schmid 2017; Stetter et al. 2017).

Botanical and agronomic attributes

All *Amaranth* species efficiently bind CO_2 through the C_4 photosynthetic pathway and perform better than most C_3 commodity crops at high temperatures and moisture stress environments (Stallknecht and Schulz-Schaeffer 1993). Grain amaranth has a wide adaptability and can grow in wide geographic areas ranging from tropical lowlands to 3500 m in the Himalayas (Joshi and Rana 1991). The plant is a tall, robust annual herb, simple or branched and grows up to 300 cm height (Joshi and Rana 1991). The three grain amaranth species exhibit variation for inflorescence characteristics, morphological features, plant type and can be

identified by mature inflorescence alone (Fig. 1). In the field, grain amaranth is an annual crop with a life cycle of 4–6 months from planting to harvest (Sooby et al. 1998).

Generally, the conditions suitable for maize cultivation also favor the grain amaranth cultivation. Therefore, it is often intercropped with maize and quinoa by the farmers in the Andes (Das 2016). Temperature plays a major role in germination and early growth of amaranth. The recommended temperature for optimum germination and early seedling growth of amaranth is reported to be between 20 and 30 °C (ISTA 2010). For proper growth of the plant, the optimum temperature range is 25–33 °C and low temperature (below 18 °C) generally ceases the growth and affects the plant development (Das 2016). Seeds germinate after 4–5 days of sowing and maintenance of proper spacing and adequate moisture during this stage is critical for the proper stand establishment and obtaining maximum yield potential of the crop (Bhatia 2005). The three species of grain amaranth differ in their day-length requirements and respond differently to changes in photoperiodism. Among the grain types, *A. caudatus* and *A. cruentus* are short-day species and flowers and sets seed when day length is less than 12 h, while *A. hypochondriacus* is day neutral (Mbwambo 2013). Long photoperiod conditions are reported to delay the grain maturation and drying of plants leading to substantial grain losses (Gimplinger et al. 2008). Flowering of amaranth species usually starts 4–8 weeks after sowing (Grubben and Denton 2004) but varies between species and cultivars depending on photoperiodism and cultivation practice. Grains mature in about 35–45 days after the reproductive phase begins, while the plant stays green for longer (Das 2016). It is crucial to harvest before the plant senesce to prevent heavy grain shattering which leads to substantial yield losses (Tucker 1986). In the Northern USA immature plants die off due to frost and seeds can be harvested easier thereafter (Brenner et al. 2000). Overall amaranth is a low maintenance crop that needs little fertilizer and pesticide input, but proper management during seedling establishment and before harvest is crucial for high yields.

Genetic resources and ex situ conservation

Amaranth and its wild relatives harbor a wide diversity, and considerable efforts have been made for ex situ conservation of amaranth genetic resources across the world. At present, approximately 61 diverse collections of amaranth genetic resources are being maintained in at least 11 countries of the world (Table 2; Das 2016). The first major effort to assemble a germplasm collection of amaranth was made in the 1970s by the Rodale Research Centre (RRC), Pennsylvania, USA. A total of 1400 accessions belonging to different species were assembled at the center from different countries (Kauffman and Weber 1990) and are now part of the United States Department of Agriculture (USDA) National Plant Germplasm System (Brenner et al. 2000). At present, the USDA germplasm collection is the major repository for amaranth world wide with a total of 3300 accessions from 40 countries (Trucco and Tranel 2011). The collection is estimated to represent about 42 species of the genus amaranth. While the hot spots of amaranth diversity are well represented, gaps in these collections exist for wild species and landraces from

Table 2 Amaranth germplasm accessions conserved in major gene banks globally

Institute/organization	Country	Number of species	Major species	Number of countries	Total accessions	References
North Central Regional Plant Introduction Station (NCRPIS)	USA	42	*A. hypochondriacus*	40	3300	Trucco and Tranel (2011)
National Bureau of Plant Genetic Resources (NBPGR)	India	10	*A. hypochondriacus*	40	3081	Das (2016)
National Botanical Research Institute (NBRI)	India	20	*A. hypochondriacus*	–	2500	Mathews (2001)
Univ. Nacional San Antonio Abad del Cusco (UNSAAC/CICA)	Peru	4	*A. caudatus*	12	740	Kalinowski et al. (1992) and IPGRI (1999)
Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP)	Mexico	–	*A. hypochondriacus*	5	495	Espitia (1992) and IPGRI (1999)
Universidad Nacional del Altiplano Puno	Peru	–	*A. caudatus*	–	440	IPGRI (1999)
Institute of Crop Germplasm Resources (CAAS)	China	–	–	–	438	IPGRI (1999)
World Vegetable Centre	Taiwan	18	–	–	520	http://seed.worldveg.org/

regions where amaranth is not a major crop. It is of great importance to study and fill germplasm gaps to make the collections more comprehensive by enriching them with rare valuable alleles and to preserve landraces before they are lost.

To categorize collections taxonomic keys and descriptors for the identification and characterization of amaranth genetic resources have been developed (Grubben and van Sloten 1981). Large-scale, well-documented phenotypic characterization of the germplasm collections conducted in India, Peru, the USA and Mexico revealed extensive variation in amaranth (Espitia 1986; Joshi 1986; Das 2016). Germplasm evaluation revealed a wide range of variability for important morpho-agronomic characters in indigenous and exotic accessions of amaranth. The centers of diversity in Mexico and Guatemala harbor a particularly rich variation of *A. cruentus* and *A. hypochondriacus* landraces (Espitia 1992).

Together, the genetic resources collected from a wide distribution of the genus contain a large genetic diversity (Kietlinski et al. 2014; Stetter et al. 2017; Wu and Blair 2017) that is currently being explored. This existing genetic diversity provides high potential for adaptation and improvement of grain amaranth and can be integrated at different steps in breeding programs.

The past and present of amaranth breeding

Breeding behavior

Amaranth is a predominantly autogamous crop, but outcrossing rates (5–39%) are sufficient to facilitate gene flow among populations (Hauptli and Jain 1985; Mohindeen and Irulappan 1993). While obligate allogamous diecious wild species of amaranth exist in North America (Sauer 1955, 1957), the cultivated species of grain amaranth are monoecious. Under field conditions amaranth has tens of thousands of intricate flowers (< 1 mm diameter) with male and female flowers on the same inflorescence where several female flowers are arranged circularly around a male flower. The complex arrangement of floral structure in amaranth hinders hand emasculation and artificial hybridization. Consequently, most of the present day amaranth cultivars are the outcome of first and second-generation selection cycles from a heterogeneous bulk of local collections and landraces resulting in only a handful of varieties developed through hybridization followed by pedigree based selection.

In order to establish successful breeding programs, efficient hybridization techniques are prerequisite to cross superior lines, introgress exotic alleles into amaranth breeding programs and ultimately to produce hybrid varieties. Stetter et al. (2016) compared the efficiency of three crossing techniques (open pollination, hot water emasculation and hand emasculation) in amaranth and showed that while hand emasculation has the highest success rate, hot water emasculation at 45 °C for 10 min is simple to perform and suitable for large-scale production of hybrids.

Genetic male sterility, which prevents the seed parent (mother) from producing viable pollen, is considered to be more efficient way to produce hybrids. Such a male sterile plant has to be pollinated by foreign pollen from the pollen parent (father), allowing to choose the parental lines and seed set of only hybrid seeds. For grain crops, the fertility has to be restored in the hybrid and male sterile seed parents have to be maintained. Therefore, restorer and maintainer genes are needed and have to be introduced into the pollen parent gene pool (Bohra et al. 2016). This method is well established in a variety of hybrid crops, such as rye (Geiger and Schnell 1970), sugar beet (Curtis 1967) and maize (Laughnan and Gabay 1978). In one of the grain amaranth species (*A. hypochondriacus*) male sterility governed by a single recessive nuclear gene, *ms* has been identified (Peters and Jain 1987; Gudu and Gupta 1988). A fully male sterile F_1-hybrid accession, with fertile offspring after cross-pollination has been developed recently (David Brenner, personal communication). However, the maintenance of genetic male sterility has to be improved and the exact genetic location of the *ms* gene should be identified to use this system for efficient breeding in numerous genetic backgrounds.

Breeding objectives

Major crops are well adapted to modern agroecosystems and mechanical harvest. Many minor crops, including amaranth, are less adapted to these systems. This leads to a different set of primary breeding targets. Major breeding objectives in amaranth include reduced seed shattering, reduced plant height (1.0–1.5 m) and flowering above the leaf canopy for mechanical harvest. Besides these basic traits, grain yield, synchronized maturity and grain quality are important breeding targets. Higher yield can be reached by improving yield components, such as grain size, which would be additionally desirable as the very small seeds of amaranth are causing difficulties for mechanical planting and harvest. Synchronized and medium maturity (100–120 days) would strongly reduce post-harvest drying requirements and improve storage properties of the crop. Quality traits for grain amaranth are white or golden seed color, puffing quality and taste (Kauffman 1992). In contrast to major crops amaranth suffers only little from pests and diseases, but these traits should be maintained in breeding pools as their importance might increase once amaranth becomes more abundant. One potential pest is *Lygus lineolaris* (tarnished plant bug), which can cause crop losses in the USA (Sooby et al. 1998) and Mexico (Espitia 1994). Apart from this, stem-boring insects, *Sciaria*,

Hypolixus and *Lixus*, are known to cause minor crop losses in Mexico (Grubben 1976; Burki et al. 1997; Louw et al. 1998). Germplasm screenings have already identified resistance sources to these pests (Espitia 1994).

There is high potential for improvement in amaranth, but increased seeds size and yield might lead to dilution effects for many of the nutritionally valuable components in the seeds, which has been observed in cereals (Evers and Millar 2002). Domestication and breeding have strongly increased the seed endosperm, which is low in protein and oil and consequently lowered the share of these nutrients in the grain (Harlan et al. 1973). To maintain the high nutritional quality of amaranth, such a dilution effect should be avoided when breeding for higher yields.

Genetic architecture of breeding targets

Understanding the genetic architecture of important target traits allows to adapt breeding strategies. A number of traits have been studied in amaranth for their genetic architecture (Table 3). While simple traits such as seed coat (Kulakow et al. 1985), flower and seedling color (Gupta and Gudu 1990) follow a simple Mendelian inheritance, other traits have a more complex genetic architecture (Kulakow and Jain 1987). Other important traits such as harvest index, yield per plant and 1000 seeds weight showed dominance pattern (Pandey 1984). Economically important traits such as anthesis time, plant height, inflorescence length, seed yield, protein content and oil content have been reported to have moderate to high heritabilities in amaranth (Kulakow and Jain 1987; Rana et al. 2005; Shukla et al. 2010; Pandey and Singh 2011). Based on these implications, efficacy of different selection procedures has been determined for genetic improvement of amaranth and showed that there is sufficient trait variation for selection (Ayiecho 1986; Kulakow and Jain 1987; Vaidya and Jain 1987).

Genetic mapping populations are important resources to gain further insight into the underlying genes for the traits of economic importance. Quantitative trait loci (QTLs) governing these traits have been identified in amaranth utilizing mapping populations (Maughan et al. 2011; Lightfoot et al. 2017). However, F_2 populations allow only the mapping of large regions, due to high linkage disequilibrium. Recombinant Inbred Lines (RILs), Multiple Advanced Generation Intercross (MAGIC) and Nested Associated Mapping (NAM) populations break down linkage and allow a more precise mapping of QTLs (Mackay and Powell 2007; Korte and Farlow 2013; Huang et al. 2015). Information on the genetic determinants (QTLs) of breeding targets identified through biparental and association mapping is lacking in grain amaranth due to the lack of robust mapping populations. With the availability of optimized growth conditions to facilitate six crop cycles per year (Stetter et al. 2016) and a genetic male sterility system (Gudu and Gupta 1988),

Table 3 Genetic basis of important agronomic and morphological traits in amaranth

Traits	Population	Genetic control	References
Flowering time	Backcross-derived generations of a cross between *A. retroftexus*×*A. cruentus*	Three major genes	Kulakow and Jain (1985)
Plant height	F_2 progenies derived from a cross between two landrace populations of *A. cruentus*	Non-additive effect	Kulakow and Jain (1987)
Leaf length	F_2 progenies derived from a cross between two landrace populations of *A. cruentus*	Non-additive effect	Kulakow and Jain (1987)
Leaf width	F_2 progenies derived from a cross between two landrace populations of *A. cruentus*	Non-additive effect	Kulakow and Jain (1987)
Panicle length	F_2 progenies derived from a cross between two landrace populations of *A. cruentus*	Non-additive effect	Kulakow and Jain (1987)
Panicle width	F_2 progenies derived from a cross between two landrace populations of *A. cruentus*	Non-additive effect	Kulakow and Jain (1987)
Harvest index	6×6 complete diallel	Over dominance effect	Pandey (1984)
1000 seed weight	6×6 complete diallel	Over dominance effect	Pandey (1984)
Grain yield	6×6 complete diallel	Dominant effect	Pandey (1984)
Starch content of grain	500 progenies of a single heterozygous plant	Single major gene	Okuno and Sakoguchi (1982)
Grain protein percentage	F_1 and F_2 of a diallel cross of six *A. hypochondriacus* genotypes	Additive and non-additive effects	Pandey and Pal (1985)
Seed coat color	F_2 population segregating for contrasting traits	Two dominant genes	Kulakow et al. 1985
Seedling color	F_2 population segregating for contrasting traits	Single dominant gene	Gupta and Gudu (1990)
Inflorescence color	F_2 population segregating for contrasting traits	Single dominant gene	Gupta and Gudu (1990)
Purple leaf mark	F_2 population segregating for contrasting traits	Two dominant genes	Gupta and Gudu (1990)

next-generation mapping populations (MAGIC, NAM) might become available to dissect the genetic control of complex quantitative traits in amaranth.

Little attention has been directed to estimate levels of heterosis on economically important traits within grain amaranth species. Lehman et al. (1991) reported midparent heterosis up to 88% for grain and biomass yield in an interspecific cross between *A. hypochondriacus* and *A. hybridus*. Genetic information regarding influence of genotype × environment interaction on quantitative traits for grain amaranth is lacking. Therefore, systematic and comprehensive studies should be carried out to understand the contributing factors for enhancing productivity and quality in amaranth. The reportedly high interspecific heterosis and trait variation could have very high potential for hybrid breeding programs and needs to be extensively investigated.

Historical breeding efforts

In the early 1970s, two amaranth species, *A. cruentus* and *A. hypochondriacus*, were recovered from the germplasm collection in the USA and was used to establish breeding material (Kauffman 1979). This initiative led to reintroduction of grain amaranth into North America followed by its increased cultivation in Central and South America (Kauffman 1992). The breeding efforts have achieved only little genetic enhancement in amaranth, although a number of cultivars have been released for cultivation across the world. The most successful cultivar development was achieved by the introduction of earliness into a high yielding *A. hypochondriacus* genotype. The effort has resulted in the release of Plainsman, one of the most widely grown grain amaranth cultivars in the USA (Baltensperger et al. 1992). Plainsman has proven to be a source of useful traits such as lodging resistance, shattering resistance, early maturity and high grain yield and played an important role in boosting the amaranth production in North America (Trucco and Tranel 2011). Much of the variability reported in amaranth gene pool remains poorly used in breeding programs. It has been reported that only the germplasm lines of RRC working collection appear in the parentage of most the cultivars released in the USA (Stallknecht and Schulz-Schaeffer 1993) and China (Corke et al. 1997). The extensive evaluation of a large collection of indigenous landraces and exotic genetic resources in Mexico led to improved selections for high grain yield (> 2000 kg/ha), medium maturity (130 days) and dwarf plant types suitable for mechanical harvesting (Espitia 1992). In India, the release of cultivar Annapurna, which was a direct selection from a local germplasm line, is a notable example of effective utilization of amaranth germplasm (Joshi et al. 1983). Nonetheless, amaranth breeding has been limited mostly by the lack of efficient breeding methods and was mainly performed at nonprofit institutions for research purposes.

The future of amaranth breeding: integrating advanced breeding methods

Hybrid breeding

In many crop species, the introduction of hybrid breeding has strongly improved yield potential and yield stability (Stuber 1994). Heterosis, the superiority of offspring over their parents, is observed when diverging parents from different heterotic pools are crossed. The resulting F_1 generation is genetically identical and outperforms the parental lines (Kaeppler 2012). The high phenotypic uniformity provides agronomic advantages, for instance for mechanical harvest. Amaranth varieties are bred as line varieties with only little breeding advances, but enormous heterotic effects have been identified in interspecific crosses (Lehman et al. 1991). To introduce hybrid breeding into amaranth breeding programs, a few tools have to be improved and applied.

Hybrid breeding programs rely on heterotic pools which should be diverging, but still have to cross readily. The three grain species of amaranth have been grown separately for a long time, but intercross easily which makes them good candidates as heterotic groups (Stetter et al. 2016). Such interspecific heterotic groups are successfully being used in sunflower breeding programs (Reif et al. 2012). Heterotic groups in amaranth can be identified from landraces and germplasm collections using genetic data, which has recently been shown for wheat (Boeven et al. 2016). The efforts of characterizing germplasm collections will provide valuable information about genetic distance between populations that can be used to construct heterotic pools (Kietlinski et al. 2014; Stetter et al. 2017; Wu and Blair 2017). The three grain species have different levels of genetic similarity, while *A. hypochondriacus* and *A. cruentus* are closely related, and *A. caudatus* is more distant from these groups, providing a range of similarity for hybrid pool identification. Potential heterotic groups should be verified by test crosses between the different pools.

Additionally, homozygous parental lines are needed for hybrid production. These can be produced by successive selfing, which is unproblematic in amaranth, but time-consuming even with fast cycling generations. Double haploid technology allows to achieve fully homozygous lines within a single generation, which is broadly used in various crops (Forster and Thomas 2005). This technique has not been explored for amaranth, but could be promising tool for improvement in genetic gain manifested in the form of line development and hybrid breeding.

The above-described crossing technique (Stetter et al. 2017) provides possibilities for experimental crosses, but

genetic male sterility should be further developed for efficient hybrid seed production in larger scale (Peters and Jain 1987; Gudu and Gupta 1988; Stetter et al. 2016). Hybrid breeding provides an opportunity to improve amaranth yield and yield stability and is particularly suitable for the crop as heterotic pools and most genetic tools are available. These should be further investigated and integrated into breeding programs.

Mutation breeding

Mutation breeding has been effectively utilized in amaranth for cultivar development and generating polygenic variability. So far, mutation breeding led to development of four cultivars in amaranth, 'Centenario' (improved grain yield) in Peru, 'New Asutake' (early maturity) in Japan, 'Sterk' (tolerance to moisture and heat stress) in Russia, 'Pribina' in Slovakia (Gomez-Pando et al. 2009; Das 2016). Gamma irradiation significantly enhanced 1000 seed weight in *A. cruentus*, and promising mutant lines (C26 and C82) with higher 1000 seed weight have been developed (Gajdošová et al. 2008; Hricová et al. 2016). Likewise, putative mutant lines of *A. hypochondriacus* and *A. cruentus* containing 2% more protein than non-treated lines were developed through gamma irradiation (Keckesova et al. 2012).

Induced polyploidy is another mutational approach that has proven effective to improve yield and quality traits in grain amaranth (Pal and Khoshoo 1977; Behera et al. 1974; Sun and Yue 1993). Significant impact of induced polyploidy on grain size, protein and lysine content without affecting the fertility and grain quality has been well documented (Misra et al. 1971; Pal and Khoshoo 1977; Sun and Yue 1993). An increase of up to 50% in grain size has been reported in tetraploid *A. caudatus* (Pal and Khoshoo 1977; Sun and Yue 1993). Polyploids were reported to be stable over ten generations and allow significant enhancement in essential quality traits without any negative impact on fertility and plant performance (Pal and Khoshoo 1977). While breeding of diploids is far simpler than polyploids, the potential of terminal induced polyploidy should be further investigated. This would allow the initial breeding on a diploid level while using the polyploidy in the final generation to increase seed size, quality and yield.

Genome enabled breeding

In the recent years, substantial advances in understanding the genome and modern genetic marker systems in amaranth have been made (Maughan et al. 2011; Clouse et al. 2016); Lightfoot et al. 2017; Stetter et al. 2017). These resources can greatly improve the breeding methodology for amaranth. One of the most important resources for genome enabled breeding is the availability of a well-assembled reference genome. The most recent physical map of the *A. hypochondriacus* genome has 16 chromosome scale major scaffolds with an N50 of 24.4 Mb (Lightfoot et al. 2017). Before this high-quality assembly, there were already two draft genomes (Sunil et al. 2014; Clouse et al. 2016), a transcriptome (Delano-Frier et al. 2011; Clouse et al. 2016), chloroplast genomes (Chaney et al. 2016), as well as a genetic map (Maughan et al. 2011). In addition to these genomes, different genome-wide marker systems have been employed to explore the diversity in amaranth. These range from whole genome resequencing (Clouse et al. 2016), educed representation sequencing (Maughan et al. 2009; Stetter et al. 2017) to PCR-based low-cost SNP markers (Maughan et al. 2011; Stetter et al. 2016).

The different genetic marker systems can be implemented at different steps into breeding programs. Whole genome resequencing of hundreds of individuals is becoming feasible for crops with small genomes, as that of amaranth. This will be particularly important to assess diversity in ex situ collections and use this diversity to map quantitative trait loci (QTL) by genome-wide association studies. No such study has been reported in amaranth yet, but these will greatly improve our understanding of the genetic architecture of traits and provide targets for marker-assisted selection (MAS). Reduced representation sequencing markers are well suited for linkage mapping experiments where linkage groups are larger (Lightfoot et al. 2017), while low-cost single SNP markers are well suited for marker-assisted selection (MAS), when they are in linkage with the target QTL or to identify hybrid individuals (Stetter et al. 2016).

Marker-assisted breeding employs the linkage between known QTLs and genetic markers to select individuals. The method is well applicable for monogenic traits or traits that are controlled by only few genes, for example, resistance genes (Varshney et al. 2013). Genome-wide maps can be used to identify markers in linkage with these QTLs, and individuals can be genotyped already in the seedling stage long before the phenotype appears. Selection can be performed on the basis of the individual's genotype, which strongly reduces the growing space and allows early and efficient selection.

Lightfoot et al. (2017) identified a major QTL for flower color in *A. hypochondriacus* using linkage mapping. Other QTLs for simple traits like seed coat color (Table 3) will be identified in the near future and will allow early selection on these traits. Another use of marker-assisted breeding is marker-assisted backcrossing and advanced backcross QTL analysis, which can be used to introgress specific regions from wild relatives while removing linkage drag. This method is well suited for the integration of genetic resources from ex situ germplasm collections.

Comparative genomics is an approach to understand genome synteny and harness functional similarity to closely

related species for targeting genes governing traits (Paterson et al. 2000; Hardison 2003). Recent progress in assembling genomes of important genera of family *Amaranthaceae* such as quinoa (Zou et al. 2017) and sugar beet (Dohm et al. 2014) along with amaranth (Lightfoot et al. 2017) will allow a detailed structural and functional comparison of genes regulating various biological processes. Such genomic comparisons have already demonstrated their utility in exploring the functional sequence motifs in other minor crops. For instance, utilizing the genomic synteny and functional similarity with rice, maize and sorghum genomes, QTLs governing tryptophan and protein content has been identified in finger millet (Babu et al. 2014).

Genomic selection (GS) overcomes many of the drawbacks of MAS. Compared to MAS, GS uses a large number of genome-wide distributed DNA markers (e.g., SNPs) to predict genomic estimated breeding values (GEBV) and recently been utilized in many crops (Meuwissen et al. 2001; Varshney et al. 2013). The method allows to evaluate individuals on the basis of genetic information without having to test them in the field. In contrast to phenotyping large numbers of individuals in the field for traditional phenotype-based selection, only a subset of individuals (training population) is phenotyped and genotyped to train the genome-wide model. The estimated marker effects can be used to predict GEBVs for individuals that have only been genotyped but not phenotyped (Desta and Ortiz 2014). Based on genome-wide marker profiles, genotypes with superior GEBVs selection can be performed. Depending on the heritability of the trait, GS can help either to remove very low performing individuals (moderate heritability) or even to select most superior individuals that contribute to the next generation (high heritability). In order to exploit the full potential of GS in amaranth breeding, efforts are required to develop a robust training population that includes advanced breeding lines.

Genomic selection has been proven to be an effective technique to accelerate genetic gains for valuable but complex traits that are costly to phenotype, such as grain quality and nutritional traits. Recently, the great potential of GS for enhancing grain micronutrient concentrations has been demonstrated in spring wheat (Velu et al. 2016). Genomic selection has not been experimented in amaranth so far, although the use of genomic prediction could largely accelerate the genetic gain for nutritional traits per generation through early selection and holds great potential for biofortification breeding in grain amaranth.

Genetic transformation and genome editing

The success of utilizing genetic transformation technology in any crop largely relies on efficient in vitro regeneration techniques. Regarding in vitro culture of amaranth, tissue culture-based direct shoot regeneration from stem internode explants (Swain et al. 2010), and regeneration of amaranth plants from callus tissue derived from mature embryo (Jofre-Garfias et al. 1997) and epicotyl (Pal et al. 2013) are known (Table 4). Studies on transformation in amaranth indicated that it is primarily a recalcitrant crop for tissue culture and transformation (Brenner et al. 2000). To overcome this, Munusamy et al. (2013), have established a tissue culture-independent genetic transformation system for amaranth using mature inflorescence as an explant. Although a low transformation efficiency of 1.8% was recorded, this is a promising starting point for further improvement of transformation in amaranth by circumventing and avoiding the lengthy tissue culture period and somaclonal variation.

In the recent years, genome editing technology has emerged as an effective tool to revolutionize basic research and trait development in crop plants by modifying genomes in a rapid yet precise and predictable manner (Bortesi and Fischer 2015). Genome editing permits direct transformation of favorable alleles or gene complexes into an elite genetic background, even if these allele combinations are not occurring in the population. Different genome editing methods have been applied in plants. Zinc finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs)-based genome editing require complicated constructs and have therefore been mostly replaced by the simpler and most widely used CRISPR/Cas9 system (Ma et al. 2016). In contrast to protein guided ZFNs and TALENs mechanisms, the CRISPR/Cas9 gene editing system depends on DNA or RNA sequence homology (Zhang et al. 2017). Availability of an efficient transformation protocol is one of the most critical factors for the CRISPR/Cas9-based gene editing, because it is required to introduce the T-DNA construct carrying Cas9 and the single guide RNA (sgRNA) into the plant. To date, no gene editing has been developed for amaranth, but advancements in genetic transformation (Munusamy et al. 2013) present the opportunity to improve different traits of grain amaranth through genome editing in near future.

Another potential application of genome editing in amaranth research is in understanding the genetic mechanism underlying herbicide resistance in some of the amaranth species such as palmer amaranth (*A. palmeri*) (Legleite and Johnson 2013). Precise nucleotide changes in herbicide resistance genes through genome editing could help to understand the changes and processes underlying resistance evolution in *A. palmeri*. Furthermore, CRISPR/Cas9-based targeted molecular stacking of herbicide resistance genes in grain amaranth would strongly reduce the crop management cost and increase the production. The tools of genome editing could further be utilized for the improvement of the efficiency of genes influencing nutraceutical properties and

Table 4 Details of explants and media composition used for amaranth transformation

Explant	Amaranth species	Media composition			References
		Morphogenic/embryogenic callus induction	Shoot regeneration	Root formation	
Mature embryos	*A. hypochondriacus*	MS medium supplemented with 2,4 D (10 µM) and BA (10 µM) and 10% coconut liquid endosperm	MS medium supplemented with 2% sucrose	–	Jofre-Garfias et al. (1997)
Stem internodes	*A. tricolor*	–	MS medium augmented with 2.0 mg/l zeatin	Explant co-cultivation with *Agrobacterium rhizogenes* on growth regulator-free MS medium	Swain et al. (2010)
Epicotyls	*A. tricolor*	–	MS medium supplemented with BA (13.2 µM) and NAA (1.08 µM)	Half strength MS medium supplemented with IAA (1.4–11.4 µM), IBA (1.2–9.8 µM) or IPA (1.3–10.6 µM)	Pal et al. (2013)
Leaves of In vitro grown plant	*A. tristis*	MS medium supplemented with 2,4 D (0.5 mg/l) and BA (0.5 mg/l)	Shoot regeneration failed	–	Murugan and Sathishkumar (2016)

presence of potential medical compounds in amaranth for possible enhancement in desirable tissues.

Accelerating the genetic gain

Breeding of field crops is traditionally a slow process that generally requires 10–12 years to produce genetically stable cultivars. Recently, the concept of speed breeding has been brought to spotlight which greatly shortens generation time and demonstrated immense potential to accelerate breeding programs (Watson et al. 2018). Speed breeding is performed in fully enclosed, controlled-environment growth chambers and uses extended photoperiods through supplemental lightning and controlled temperature regimes to achieve rapid crop cycles. Under field conditions, the generation time for the three grain amaranth species is approximately 6 months (Sooby et al. 1998), but under fully controlled conditions up to six generations per year can be achieved (Stetter et al. 2016). High temperatures and short-day conditions induced very early flowering in a large number of amaranth genotypes leading to rapid cycles and less flowers that are easier to handle. Plants grown under controlled conditions are much smaller and therefore particularly useful for laboratory experiments. These plants can be used for transformation and genome editing, where offspring can be tested early for success. Genomic selection in combination with the short generation times under controlled conditions could be used to advance breeding pools during off seasons, when phenotyping is not possible. Advancing several generations per year, where only a fraction has to be grown in the field, could substantially improve the selective gain and reduce costly field experiments.

Next-generation phenotyping

Alongside the developments in crop genomics, cost-efficient and high throughput phenotyping assays are being developed to help understand trait variation and improve traits in breeding programs. Recently, the introduction of next-generation phenotyping platforms supported with remote sensing, 3D imaging and software tools has allowed to phenotype complex quantitative traits with high resolution, precision and accuracy (Cobb et al. 2013). For instance, spectral indices such as normalized difference vegetation index (NDVI), hydration status and pigment composition estimated through remote sensing have been significantly associated with plot based measurements of yield, biomass and adaptation (Cobb et al. 2013; Li et al. 2014). Likewise, the automated optical seed sorting assays have a great potential to improve breeding and seed production (Pearson 2010). Unlike conventional assays, automated optical seed sorting devices have potential to purify the large seed lots based on color, surface texture, shape and size in a rapid yet precise manner (Jahnke et al. 2016; Tanabata et al. 2012). In a small seeded crop such as amaranth, automated seed phenotyping platforms would be particularly beneficial as other methods are labor intensive and often not precise enough to distinguish seed size and. The combination of high-density genotyping data high throughput phenotypic records can in addition improve our understanding of genetic architecture of breeding targets in amaranth.

Integration of wild relatives and genetic resources into breeding programs

Crop wild relatives often harbor desirable traits that are missing in the mainstream gene pool, though introducing these traits might be difficult owing to pollination barriers or linkage drag. Reducing linkage drag often requires several generations of backcrossing or the use of genetic engineering, but allows to introduce variation that would otherwise not be available. Seed size is an important yield component but there is only little variation available in grain amaranth (Stetter et al. 2017). The wild relatives *A. pumilus* and *A. cannabinus* have much larger seeds than the crop species and could be sources to increase variation for seed size into grain amaranth (Brenner et al. 2000). An example for successful transfer is the non-dehiscence property of *A. powellii* which was transferred to *A. hypochondriacus* and *A. cruentus* to reduce grain shattering (Brenner 2002).

Substantial efforts in the past have been made for transferring herbicide tolerance from wild and weedy species to crop plants (Ellstrand et al. 1999; Legere 2005; Gaines et al. 2008). Such herbicide tolerance has been documented in *A. hybridus* and other *Amaranthus* species and has been transferred to grain amaranth species *A. hypochondriacus* and *A. cruentus* (Trucco et al. 2006). Herbicide resistance could be integrated into agronomic practices and has immense potential to improve grain yield for amaranth. The genus *Amaranthus* includes a large diversity of species with different phenotypic properties. Many of the species within the genus can hybridize with the grain amaranth species and could serve as source for missing desirable agronomic traits.

Conclusions and future prospects

By virtue of its unique nutritional profile and C_4 photosynthetic pathway, amaranth is a well-suited crop to diversify our cropping systems and adapt to changing environments. The increasing awareness about the nutritional value, health benefits, medicinal and industrial uses of amaranth has resulted in the renaissance of the crop. The abundant genetic variation available in the amaranth gene pool allows the development and improvement of nutritionally rich cultivars. Available genetic and phenotypic diversity for economic traits needs to be further assessed through genetic studies and multi-location evaluation. Further, interspecific hybridization between genetically distant species offers a promising avenue to leverage heterosis in grain amaranth. In the last 10 years, considerable advances have been made in the genomic interventions in amaranth which has immense potential to be adopted in future crop improvement programs. However, molecular breeding efforts utilizing diverse omics tools in amaranth lag considerably behind those in other crops. With the availability of the high-quality reference genome sequence of *A. hypochondriacus*, it will be possible to identify new targets of selection and use genome-wide markers for phenotype prediction. This will shorten breeding cycles considerably and allow simultaneous

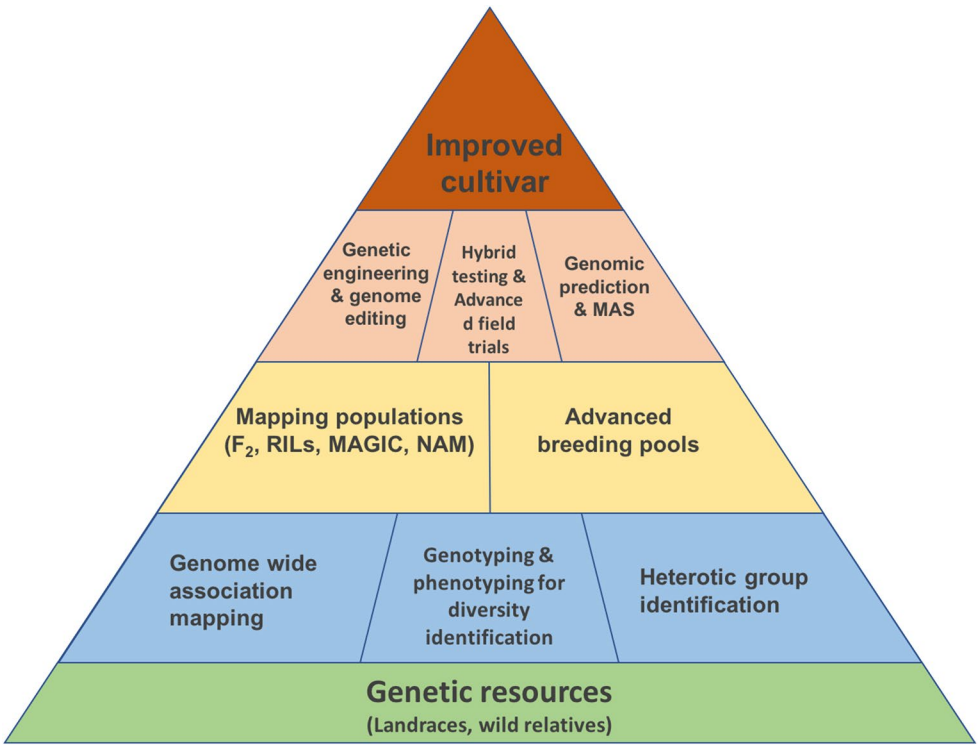

Fig. 3 Schematic representation of an integrative genomics and breeding approach for accelerated genetic improvement in amaranth. *NAM* (nested association mapping), *RIL* (recombinant inbred line), *MAGIC* (multiple advanced generation intercross), *MAS* (marker-assisted selection)

breeding gain for both, yield and quality traits. Along with cultivated species, genome sequencing of important wild and weedy species will be advantageous for various large-scale genotyping applications, including germplasm characterization, cultivar identification and QTL discovery (Fig. 3). The cross transferability of the reported markers across the species demonstrates their usability in understanding phylogenetics of this complex genus. Together these results will help to breed high yielding amaranth with high nutritional value for future agricultural systems.

In this review, we outlined the state of the art in grain amaranth research and breeding and suggest directions how to implement uprising molecular techniques to revive this ancient crop. With full use of these techniques on hand, amaranth research and breeding can bridge the gap to major crops that have been bred intensively for over 100 years. Our suggestions are widely transferable to many minor crops that have been neglected in the last decades. Improving these crops can play a crucial role in diversifying and adapting our cropping systems to future consumer needs and a changing environment.

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Author contribution statement DCJ and MGS conceived the idea, coordinated the manuscript layout and wrote the article. SS and RH wrote the section on nutraceutical value of amaranth and drafted Table 1. LK and AP improved the manuscript and provided revisions to the different sections of the manuscript. AK and DY improved the manuscript and provided inputs for the genomics and molecular breeding section. All the authors have read and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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