Chapter 7
Genomics-Assisted Design of Biotic Stress Resistant Vegetable Amaranths

Darshan T. Dharajiya, Gauravi N. Trivedi, Nevya J. Thakkar, Karen P. Pachchigar, Basavaraj Teli, Kapil K. Tiwari, and Matthew W. Blair

Abstract The *Amaranthus* genus contains various species showing differential economic importance based on the use of various plants parts, from leafy vegetables, to biomass fodder to high protein grain. The genus has ~75 species across the world with most being wild or weedy and a few are edible plants. Among the species those used for vegetable purpose are *A. hybridus*, *A. tricolor*, *A. dubius*, *A. blitum*, *A. lividus*, *A. viridis*, *A. spinosus*, *A. graecizans* and some others; while those that are primarily grain crops are *A. caudatus*, *A. cruentus*, and *A. hypochondriacus*.The latter species are from the New World while the former species are mostly of Asian origin with worldwide spread due to them having been consumed in many different ways. Amaranth plants contain multiple nutritional components with high nutraceutical value that provide several health benefits. Climate change and associated disease and pest outbreaks are projected to have extensive impacts on agricultural production in the future. Several diseases and insect pests have been reported to have adverse effect on yield and quality of vegetable and grain amaranths. A small number of diseases including leaf blight, *Choanephora* rot, white rust, and damping-off are found on various amaranths. Meanwhile, a large number of pests including leaf beetles, leaf miners, stem weevils, and lepidopteran caterpillars are of

D. T. Dharajiya · G. N. Trivedi · K. K. Tiwari
Bio Science Research Centre, Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar, Gujarat 385506, India

N. J. Thakkar
School of Agriculture and Environment, Assiniboine Community College, Brandon, MB R7A 2A9, Canada

K. P. Pachchigar
Department of Biotechnology, College of Basic Science and Humanities, Sardarkrushinagar Dantiwada Agricultural University, Sardarkrushinagar, Gujarat 385506, India

B. Teli
Department of Mycology and Plant Pathology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, UP 221005, India

M. W. Blair (✉)
Department of Agricultural and Environmental Sciences, Tennessee State University, Nashville, TN 37209, USA
e-mail: mblair@tnstate.edu

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major concern in reducing yield and marketability of vegetable amaranths in particular. Although, some efforts have been made towards the improvement of amaranth through conventional breeding approaches, an efficient and comprehensive breeding work for the species has yet to be adopted using modern breeding approaches such as molecular breeding. The advanced approaches like genomics assisted breeding, transgenics, or genome editing could be useful in amaranth improvement for biotic stress resistance.

Keywords Amaranth · Diseases · Insect pests · Biotic stress · Genomics assisted breeding

7.1 Introduction

7.1.1 Amaranths: Crop of the Future

The *Amaranthus* genus belongs to the Amaranthaceae family and includes monoecious and dioecious herbs of various heights and ecological adaptations with a total of 75 species across six continents (Stetter and Schmid 2017). Species of *Amaranthus* are commonly known as amaranths. They are mostly wild species of drylands, forests and swamps or annual weeds growing in disturbed soils (Das 2016). However, a few have been domesticated as vegetables, pseudo cereals, and ornamentals hence; they have been categorized based on their uses (Sauer 1967; Singh et al. 2019).

Among the vegetable types are *A. hybridus* (worldwide) and *A. blitum*, *A. dubius*, *A. graecizans*, *A. lividus*, *A. spinosus*, *A. tricolor*, and *A. viridis* whose leaves are excellent sources of dietary fibers, protein, certain vitamins (pro-vitamin A carotenoid), and essential minerals (e.g. Ca, Fe, Mn, Mg, Cu, P, and K) (Peter and Gandhi 2017). Amaranth leaves are also an outstanding source of some antioxidant leaf pigments: including betalain, β-xanthin, β-cyanin, and a source of amaranthine, carotenoids, anthocyanin, and other bioactive, nutraceutical compounds (Rashad and Sarker 2020; Riggins et al. 2021).

Amaranth is known as "a crop of the future" due to of its incredible nutritional quality (Tiwari et al. 2021). The seeds of the pseudocereal types (*A. caudatus*, *A. cruentus* and *A. hypochondriacus*) have tremendous nutritional value because their grains are rich in lysine and tryptophan amino acids, in overall proteins (18%), and complex starches (75–80%). The grains also contain health enhancing oils, vitamin A, vitamin C, vitamin E, some vitamin B, cholesterol-reducing soluble fibers, and some minerals (e.g. Fe, Ca, Zn, Mn) (Peter and Gandhi 2017).

Meanwhile, *A. tricolor* and sometimes *A. caudatus* are considered as ornamental species given their attractively colored leaves and flower panicles, respectively (Das 2016). Other *Amaranthus* spp. namely, *A. retroflexus*, *A. gracilis*, *A. paniculatus*, *A. gangeticus*, and *A. hybridus* have been considered as weedy amaranths and/or wild relatives of some domesticated or cultivated amaranths. Some weedy amaranths have been considered as weedy but can also be used as vegetable amaranths viz., *A.*

graecizans, *A. hybridus*, and *A. viridis.* Some of weedy amaranths are monoecious (*A. albus*, *A. blitoides*, *A. hybridus*, *A. powellii*, *A. retroflexus*, and *A. spinosus*) and some are dioecious (*A. arenicola*, *A. palmeri*, *A. rudis*, and *A. tuberculatus*) (Sauer 1967; Das 2016; Singh et al. 2019).

7.1.2 Economic Importance of Amaranths for Healthy Diets and Increasing Human Populations

Humans in the modern world have tended to modify their diets to stay fit and healthy. This has involved shifting food habits, increased vegetarianism, and avoiding consumption of highly processed foods or ready to eat market and street foods that pose health risks from contamination (Alimi 2016). The United Nation launched the Zero Hunger campaign through the World Food Program (WFP) to meet enough, safe and nutritional food and human dietary requirements for people to lead healthy and active lives (Li and Siddique 2020).

Consumption of amaranth is good for healthy lifestyles because of its high nutritional quality which are helpful against diabetes, heart issues, and osteoporosis. Amaranths can be immunity boosters for various gastrointestinal issues, and treatment of diarrhea, excessive menstruation, internal bleeding, and even nosebleeds, snake bites, stomach disorders, ulcerated mouths, vaginal discharges, and wound healing (Sarker et al. 2020).

The leaves, shoots, and tender stems of several cultivated vegetable amaranth and young leaves of grain amaranth are used as a food and as an animal feed (Dharajiya et al. 2021). Some amaranth species possess potential phytoremediation ability to uptake of heavy metals in soil (Ziarati and Alaedini 2014). Amaranth species are used to extract natural nutritive pigments (red-violet betacyanins) and oil for the food industry (Cai et al. 1998). Amaranth grains are used in making custards, pastes, and salad dressings; grain flour in bread, cookies, and bakery products; and starch in thickening of sauces, soups, and gravies (Jimoh et al. 2018). Amaranth seeds are an underexploited plant source of squalene, a very important compound in the cosmetic, food, and pharmaceutical industries (Krulj et al. 2016).

By 2050, the Food and Agriculture Organization (FAO) estimates that the food demand will be increased over 60% to feed the 10 billion people on the Earth (Miladinovic et al. 2021). It can reduce poverty, malnutrition, and food insecurity by diversifying our food supplies and reducing the risks associated with our reliance on a few basic crops. The adaptation of many amaranths to reduced water supply compared to other leafy vegetables or even most grain crops, means that this genus if very important in the face of growing worldwide droughts and rainfall variability due to climate change effects. Many amaranths are also adapted to marginal soils and are very successful at capturing nutrients before these are leached from soils. Furthermore, they are deep rooted and capable of growing in a variety of soil types from sandy to silt-loams to heavy clays.

7.1.3 Limitations of Traditional Breeding and Rational of Genome Designing

Some efforts have been made towards the improvement of amaranth over the past few decades but the achievements have not met consumer demand. The result has mostly occurred because most yield- or quality-related characters are quantitative. Conventional breeding alone is insufficient in simultaneous improvement of multiple quantitative complex characters due to low heritability, genotype–environment (G × E) interaction and linkage drag (Zhang 2007). Implementation of advanced breeding approaches along with novel selection approaches can accelerate gains from crop improvement programs. Marker assisted breeding or genomics assisted breeding have not been much employed yet due to unavailability of genomic information for vegetable amaranths, although some advances for grain amaranths have been made (Maughan et al. 2011; Lightfoot et al. 2017; Tiwari et al. 2021).

In the last decade, some molecular markers have been made available in different amaranth species; however, most have been deployed only for improvement or understanding of abiotic stress tolerance (Jamalluddin 2020; Kreiner et al. 2021; Murphy et al. 2021). The study of the genetics of biotic stress resistance has been limited in all kinds of amaranths. Resistances and tagged genes for both types of resistances are needed for rational genomic design of new varieties, the subject of this chapter. Genomic design requires abroad collection of molecular tools and genetic data about important agronomic traits and biotic stress resistance in various amaranth species of interest; and has been recommended to enhance the precision and efficacy of selection and to shorten the duration required for trait improvement and pyramiding multiple desirable traits in crop plants (Qian et al. 2016).

Conventional breeding has facilitated to improve food security and crops with improved yield and resistance/tolerance to biotic and abiotic stresses along with increased quality characters (Miladinovic et al. 2021). However, the changing climate and greater consumer demands in recent time resulted in increased challenges for plant breeders expected to be overcome. Climate changes (increasing temperatures, droughts or floods in a certain geographical area) are projected to have extensive adverse impacts on agricultural production, disturbing food production in future. Furthermore, climate changes could result in damaging effects which might be associated with diseases and pests' outbreaks resulting in reduced crop production and quality of the harvested products (Raza et al. 2019). These conditions will have adverse effects on plants and demand new improved varieties and altered production systems in different geographic regions. Although seemingly efficient, it is not resilient to sudden changes in yield shocks posed by environmental changes or changed trading due to changed demands or changed financial market balance.

Genomics assisted breeding and genome editing approaches provide new tools for the designing of crops with improved characters (e.g. disease/pest resistance). These approaches will enable rapid development of new crop varieties with better adaptability to any biotic or abiotic changes through precision breeding. Although few examples of marker assisted selection of the priority biotic stresses exist for

vegetable amaranths, we discuss in this chapter which diseases and pest challenges and resistances would be amenable to this approach. Hence, we review the biotic stresses of amaranth below and then describe the genomic resources developed for certain grain and weed amaranths and the implications these will have combined with plant breeding and genetic engineering on the vegetable species. We hope to touch on the state-of-the-art for amaranth improvement as it currently exists even if it is in initial stages of development.

7.2 Biotic Stresses

7.2.1 Diseases and Pests of Amaranth

Amaranth is relatively less susceptible to pathogens and insect pests than most comparable vegetable and agronomic crops. However, several diseases can be of major importance (including leaf blight, wet rot/Choanephora rot, white rust, and damping-off) and all amaranths, even weeds but especially leaf and grain species, host numerous insect pests (including flea beetles, leaf miner, stem weevil, and lepidopteran caterpillars among others). Here we concentrate on those biotic stresses of greatest concern for reducing yield and marketability of the amaranth crop (Mureithi et al. 2017).

The main fungal diseases include anthracnose, damping-off, wet rot/Choanephora rot, white rust, leaf spot, Alternaria leaf spot, root rot, and white blister rust of amaranth. Bacterial diseases of amaranth have been poorly studied but seem to be mostly irrelevant. Meanwhile amaranth has a few well-characterized viruses such as *Amaranthus leaf mottle virus* (*AmLMV*) and *Amaranthus mosaic virus* (*AMoV*) but seems to host many others as well especially from other vegetables that grow in similar conditions. Details of the diseases of grain amaranths, their causal organisms and symptoms have been annotated in Table 7.1.

The major insect groups causing losses to amaranth belong to the orders Lepidoptera, Coleoptera, Hemiptera, and Diptera (Mureithi et al. 2017). These affect various plant parts, but mostly leaves which being broad and single petiole can be rapidly consumed. Amaranth leaves of domesticated species are characteristically large compared to those of weedy species which have small leaves, less susceptible to attack. Insect pests can also be troublesome to stem tissues at the base of the plant or near the panicle, resulting in plant collapse or failure of seed formations.

The major insects on vegetable amaranth crops include stem weevil, pigweed weevil (Coleoptera), leaf miner (Diptera), cutworms/leaf worms, fall armyworm, leaf webber, lepidopteran defoliator, and Amaranthus caterpillar (Lepidoptera). Leaf beetles cause more damage on grain amaranth but are considered minor pests of vegetable types, although they cause cosmetic damage that may influence consumer purchases of leaves. These include flea beetle, leaf twisting weevil, and tortoise beetle (Coleoptera). Meanwhile, other pests include mealy bugs, aphids

Table 7.1 Diseases of amaranth

Disease	Causal organism	Symptoms	References
Fungal diseases			
Alternaria leaf spot	*Alternaria* spp., *A. tenuissima*	Brown to black, circular to oval, necrotic lesions on leaves, may cause complete crop loss	Blodgett and Swart (2002)
Anthracnose	*Colletotrichum gloeosporioides*, *Glomerella cingulata*	Necrotic lesions on leaves, dieback of leaves and branches	Kwon and Park (2003)
Cercospora leaf spot	*Cercospora* spp.	Leaf spots are amphigenous, circular or irregular, 2–5 mm in diameter, coalescent, necrotic, light brown, with dark brown margin, sometimes with chlorotichalo	Vieira et al. (2019)
Damping-off	*Pythium* spp., *P. aphanidermatum*, *P. myriotylum*,	Poor germination, seedling collapse, brown-black lesions girdling stem close to soil line	Lopez et al. (2018)
Leaf spot	*Cercospora* spp., *C. brachiata*	Brown spots and necrosis on leaves	Vieira et al. (2019)
Root rot	*Fusarium* spp., *F. oxysporum*, *F. sambucinum*, *Rhizoctonia* spp.	Severe stunting of plants with chlorotic and wilted foliage, amber to brown discoloration of taproot and secondary roots, white mycelium on diseased tissue	Chen and Swart (2000)
Wet rot (choanephora rot)	*Choanephora cucurbitarum*	Water-soaked lesions on stems, lesions have hairy appearance based on fungal spores, may have leaf loss	Awurum and Uchegbu (2013)
White rust	*Albugo candida*, *A. bliti*, *A. occidentalis*, *A. amaranthi*	Defoliation and withering of whole plant	Talukder et al. (2012); Islam (2019)
White blister rust disease	*Wilsoniana amaranthi*, *W. bliti*	Yellow spots on the upper surface of leaves and typical white rust pustules on the lower surface of leaves	Kim et al. (2019); Lee et al. (2020)

(continued)

Table 7.1 (continued)

Disease	Causal organism	Symptoms	References
Viral diseases			
Amaranthus leaf mottle virus (AmLMV)	*AmLMV* (Potyviridae)	Leaf mottling, blistered mosaic, and growth reduction	Casetta et al., (1986); Sastry et al. (2019); Segundo et al. (2007)
Amaranthus mosaic virus (AMV)	*AMoV*	Severe mosaic, mottling, and curling of leaves with stunting	Kareem et al. (2011); Sastry et al. (2019)
Capsicum chlorosis virus (CaCV)	*CaCV*	Characteristic symptoms of tospoviruses	Sharma and Kulshrestha (2014)
Chili leaf curl virus (ChiLCV)	*ChiLCV* begomovirus (Geminiviridae)	Plants displaying leaf curling, leaf distortion, leaf crinkling and yellow leaf margins	George et al. (2014)
Cucumber mosaic virus (CMV)	*CMV*	One isolate causing leaf crinkle and severe mosaic	Raj et al. (1997)
Iris yellow spot virus (IYSV)	*IYSV tospovirus* (Bunyaviridae)	Thrips damage on leaves indicate overwintering host of onion disease	Karavina and Gubba (2017)
Telfairia mosaic virus (TeMV)	*TeMV*	Photosynthetic pigments of *A. viridis* were decreased by *TeMV* infection	Mofunanya et al. (2021)

(Hemiptera), grasshopper (Orthoptera), thrips (Thysanoptera), and root-knot nematode (Tylenchida). The details of insect pests damaging amaranth, their common names, species identification and damage characteristics are provided in Table 7.2.

7.2.2 Reduction in Yield and Quality Due to Biotic Stresses

Some of the diseases and insect pests listed above cause considerable reduction in yield and quality of amaranth. For instance, yield losses of 20–100% by major arthropod pests have been reported in Kenya (Sithanantham et al. 2003; Mureithi et al. 2017). Massive yield losses to Amaranthus caterpillar (*Spoladea recurvalis*) have been reported in Nigeria (Aderoluet al. 2013). Extensive yield losses to amaranths by another lepidopteran, *Spodoptera littoralis* (Lepidoptera; Noctuidae), have been reported in both Nigeria and Mexico (Aragón et al. 1997; Aderolu et al. 2013). This same species of insect is widely distributed in most parts of sub-Saharan Africa and

Table 7.2 Insect pests of amaranths

Order	Family	Common name	Scientific name	Damage	References
Major insect pests					
Coleoptera	Chrysomelidae	Flea beetles Cucumber beetles	*Disonycha melanocephala* *D. bicolor*, *Diabrotica balteata*	Amaranth bulging flea beetle, leaf beetles	Aragón-García et al. (2011)
	Curculionidae	Pigweed weevil	*Hypolixus haerens*, *H. nubilosus*	Withering plants, stems bending and collapsing	Kagali et al. (2013); Anil (2017)
		Stem weevil	*Hypolixus truncatulus*	Scratching on stem and branches, eat up tender margin of leaves	Tara et al. (2009)
Diptera	Agromyzidae	Leaf miner	*Liriomyza* spp., *L. huidobrensis*	Creates tunnels inside leaves resulting in leaf yellowing and shed. Death of seedlings follows in severe infestation	Mureithi et al. (2017)
Lepidoptera	Noctuidae	Cutworms or leaf worms	*Spodoptera* spp.	Cuts through the stem of young plants just above/below ground level causing plant wilt and death	Mureithi et al. (2017)
		Fall armyworm	*Spodoptera frugiperda*	Skeletonizing upper epidermis, spaces on leaves, and faecal pellets in the whorls	Maruthadurai and Ramesh (2020)
	Pyraustidae	Leaf webber	*Hymenia recurvalis*, *Psara basalis*	Attack on stem and leaves, larvae fold/web leaves and feed within leaves	Kagali et al. (2013); Aragón-García et al. (2011); Mureithi et al. (2017); Oliveira et al. (2012); Anil (2017)

(continued)

Table 7.2 (continued)

Order	Family	Common name	Scientific name	Damage	References
	Crambidae	Lepidopteran defoliator (white grubs)	*Herpetogramma bipunctalis*	Defoliation of plants	
		Amaranthus caterpillar	*Spoladea recurvalis*	Feed within leaves, cause yield loss	
	Heliodinidae	Lepidopteran defoliator	*Eretmocera impactella*	Leaf feeding	
Minor insect pests					
Coleoptera	Curculionidae	Leaf twisting weevil	*Apoderus tranquebaricus*	Leaf rolling	Anil (2017)
	Cassididae	Tortoise beetle	*Aspidiomorpha exilis*	Feed by scrapping outer tissues of leaves, defoliation	Sultan et al. (2008)
Hemiptera	Coreidae	Bugs	*Cletus* spp., *Cletomorpha* spp.	Insects damage flowering head, feed on seeds, cause discoloration, shrivelling, and premature drying of seeds, reduce seed yield and viability	Oke and Ofuya (2011)
	Pseudococcidae	Mealy bugs	*Ferrisia virgata*	Sap-feeding, reduced plant growth, sticky exudate which favours fungal growth, leaf discoloration and drop	McCorquodale and Hodges (2017)
	Aphididae	Aphids	*Aphis craccivora*, *Myzus persicae*	Curling, wrinkling, and discolouring of leaves, stunting of plants, seed deformation, plants may dry out	Yarou et al. (2020)

(continued)

Table 7.2 (continued)

Order	Family	Common name	Scientific name	Damage	References
Orthoptera	Acrididae	Grasshopper	*Atractomorpha crenulata*	Feed by scrapping outer tissues of leaves, defoliation	Seni (2018)
Thysanoptera	Thripidae	Thrips	*Haplothrips ceylonicus*	Infest inflorescence	Iftikhar et al. (2016)
	Phlaeothripidae		*Euryaplothrips crassus*		
Tylenchida	Heteroderidae	Root-knot nematode	*Meloidogyne* spp. (*M. javanica*, *M. incognita*, *M. arenaria*)	Galls formation on roots, reduced branching of roots, reductions in shoot height, leaf area and shoot and root dry weight	Vaingankar et al. (2018)

affects leaf production and income generation as amaranths are the most important leafy vegetable of this region (Mureithi et al. 2017). Another caterpillar, the fall armyworm (*Spodoptera frugiperda*) (Lepidoptera: Noctuidae) damages amaranth in India and causing c. 13% yield loss (Mureithi et al. 2017).

Amaranth stem weevils (*Hypolixus* spp.) are among the most serious coleopteran pests of amaranth. Infestation by stem weevil of 81% has been reported in India for vegetable amaranths (Mureithi et al. 2017). The leaf miner (*Liriomyza huidobrensis* Blanchard) (Diptera; Agromyzidae) is widespread in the Mediterranean and reduces production of any type of amaranth. This species also has colonized other areas of the world from Asia to America. Even if scanty data on geographical distribution, host range, virus transmission, and economic importance of some of these pests are available, they are of concern in amaranth production due to the capacity for long distance migration, temporal spread, quarantine issues and moderate to severe damages they cause.

7.2.3 Control of Diseases and Pests

The use of chemicals to control diseases and pests has not been recommended due to their excessive cost, residue, and environmental issues. Therefore, research has focused on implementing non-chemical methods of pest control, which are cheap, safe, easy to use, and available to farmers. Botanicals from various plants have shown considerable potential for pest control (Yarou et al. 2020).

Integrated pest management (IPM) combines host plant resistance and cultural methods of control as options for pest and disease management (Vaingankar et al. 2018). Many plant species contain biocidal components which can be utilized in controlling insect pests, leading to reduced use of synthetic pesticides and to increase the quality of vegetable crops (Yarou et al. 2020). For example, *Ocimum* spp. (*O. gratissimum* L. and *O. basilicum* L.) can be used as an alternate method to control aphids (*Aphis craccivora* Koch, *A. fabae* Scopoli, and *Myzuspersicae* Sulzer) in *A. hybridus* and can help to avoid the use of synthetic pesticides (Yarou et al. 2020). Plants of *Ocimum* spp. have an ability to repel pests and they can also be harvested, providing a direct economic return to the farmer (Yarou et al. 2020).

Vegetable oil-based extracts of *Xylopia aethiopica*, *Eucalyptus globolus*, and *Alium sativum* can reduce the infestation of nine pests (major, minor or occasional) belonging to three orders namely, Orthoptera, Coleoptera, and Lepidoptera in *A. hybridus* (Borisade et al. 2019). African marigold (*Tageteserecta* L.) has been reported to destroy nematodes as an intercrop (Hooks et al. 2010; Vaingankar et al. 2018). Biorational insecticides from different plants (e.g. *Jatropha curcas*, *Azardirachta indica*, *Ocimum gratisimum*, *Vernonia amygdalina*, and *Chrysanthemum* spp.) and microorganisms (e.g. *Bacillus thuringiensis* and *Saccharopolyspora spinosa*) are effective in pest management of leafy vegetables including amaranth (Iwuagwu et al. 2019; Muralikrishna et al. 2019; Vorsah et al. 2020).

Trap cropping has been proven to be an effective strategy to control nematodes (Vaingankar et al. 2018). Nematodes enter and grow in the susceptible host plant of an intercrop which is consequently detached before the completion of nematode's life cycle (Vaingankar et al. 2018). Plant color (green or red) has been associated with the preference of insect in feeding and oviposition. Host preference differences can also be exploited for pests. For example, many insects prefer green plants and tend to avoid red plants because it indicates that red plants are defended by phytochemicals or that red compounds are accompanied by colorless phenolics (Niveyro et al. 2013). The development and use of red plants/varieties might decrease the incidence of insects.

7.3 Glimpses on Classical Genetics and Traditional Breeding

7.3.1 Breeding Objectives for Vegetable Amaranth

Efficient and comprehensive breeding programs for grain or vegetable amaranth improvement have yet to be established, except in a few locations mostly within universities and non-profit organizations (Das 2016). Experimental approaches and breeding objectives are very important for continuous genetic improvement and they are quite different in grain and vegetable amaranths. The breeding objectives for vegetable amaranth are tolerance to heat, improved seedling establishment, improved nutritional profile, improved seedling vigor, increased leaf size, reduced length of petiole, improved leaf/stem ratio (should be >1), attractive leaf color (dark green is preferable), reduced antinutritional compounds (e.g. nitrates, oxalates etc.), more days to 50% bolting (late bolting lines are preferable), increased yield, increased tolerance to drought, and increased resistance to biotic stresses. Breeding objectives for grain amaranths have to do with seed yield and ease of threshing. Across both types, drought tolerance and adaptation to marginal soils has been important.

7.3.2 Classical Breeding Achievements

Conventional (or classical) breeding has played a key role in the genetic improvement of grain and vegetable amaranths. Commercial amaranths have been selected from field studies in many developing countries eager for new crop alternatives and heat tolerant vegetables such as in China, Peru, Kenya, India, Mexico, and Thailand (Das 2016). A collection of world germplasm and breeding lines was established in Taiwan at WorldVeg Center (previously known as Asian Vegetable Research and Development Center or AVRDC). Among developed countries, only the United States has had an interest in amaranth cultivar selection and mainly for hot or dry areas in

the South and West. In India, various research organizations and universities are actively involved in amaranth improvement for promising varieties (Dua et al. 2009; TNAU 2017; KAU 2020). All the varieties have been developed through conventional breeding methods e.g. selection and hybridization. Some varieties are resistant to one or more disease(s)/pest(s) e.g. varieties 'Kashi Suhaavani' (VRAM-42), 'Arka Arunima', and 'Arka Suguana' are tolerant, highly resistant and moderately resistant to white rust, respectively. CO-1 is resistant to Rhizoctonia leaf blight, and PLR-1 is moderately resistant to several pests and diseases. These resistant varieties can be exploited in developing new varieties resistant to various diseases or pests.

Field evaluation in Tanzania has been important for the identification of amaranth genotypes resistant to biotic stresses in other parts of the world as well. Two accessions of *A. cruentus* (TZ51 and TZ53), one of *A. dubius* (TZ34), and one of unknown *Amaranthus* spp. (TZ39) have moderate resistance against Lepidopteran insects [*Spoladea recurvalis* (Crambidae), *Spodoptera exigua* (Noctuidae), and *Spodoptera littoralis* (Noctuidae)] (Smith et al. 2018). In the same study, *A. cruentus* (TZ06 and TZ27) had moderate resistance against stem weevils [*Neocleonussannio* Herbst, *Gasteroclisus* pr. *rhomboidalis* Boheman, *Hypolixus* pr. *haerens* Boheman, and *Baradine* spp. (Curculionidae)]. Furthermore, Othim et al. (2018) also working in Tanzania reported that breeding lines VI036227 (*A. blitoides*), RVI00027 (unknown *Amaranthus* sp.), VI054569 (*A. gracilis* Desf.), VI033487 (*A. cruentus*), VI044432 (*A. viridis*), VI048076 (*A. tricolor*), VI049639 (*A. viridis*), VI049530 (unknown *Amaranthus* spp.), and VI049698 (*A. viridis*) were highly resistant against Lepidopteran (leaf-webbers and leaf-worms). Three accessions namely, VI047517-B (*A. tricolor*), VI036227 (*A. blitoides*), and VI056563 (*Amaranthus* spp.) have been reported for resistance against stem weevil while VI048076 (*A. tricolor*), VI056563 (*Amaranthus* sp.) and VI047555-B (*A. tricolor*) shown moderate resistance against *Spoladea recurvalis*.

Breeding in the United States has produced one main grain amaranth variety, 'Plainsman', with good plant architecture for row crop production. However, a number of dual-purpose amaranth selections are mass marketed for sale such as 'Burgundy' and 'Hopi Red' by seed companies selling to the ornamental and home gardener. The details of vegetable amaranth varieties released in India and Unites States are given in Table 7.3.

Mutation breeding has been used in amaranth for development of new cultivars and generation of variability. These include, 'New Asutake' for early maturity in Japan, 'Centenario' for improved grain yield in Peru, 'Sterk' for tolerance to moisture and heat stress in Russia, and 'Pribina' and 'Zobor' in Slovakia (Gómez-Pando et al. 2009; Das 2016). Promising mutant lines of *A. cruentus* namely, lines C26 and C82 with enhanced 1000-seed weight have been developed through gamma irradiation (Gajdošová et al. 2008; Hricova et al. 2016). Putative mutant lines of *A. cruentus* and *A. hypochondriacus* with higher protein have been developed through gamma irradiation (Kečkešová et al. 2021). Two mutant varieties 'Pribina' and 'Zobor' belonging to *A. cruentus* and *A. hypochondriacus* × *A. hybridus*, respectively have been developed by gamma irradiation in Slovakia. They showed changes in quantitative traits

Table 7.3 Some varieties of vegetable and grain amaranth released in India and the United States

Name of variety	Species	Pedigree and breeding method	Year of release	Green yield (t/ha)	Resistant to biotic stress	Developed by
CO-1	*A. dubius*	Selection from local germplasm introduced from Tirunelveli	1968	8	Resistant to leaf blight and white rust	HCRI, TNAU, Coimbatore
CO-2	*A. tricolor*	Selection from local germplasm introduced from Thanjavur	1979	10.78	–	
CO-3	*A. tristis*	Selection from local germplasm	1988	30.72	–	
CO-4	*A. hypochondriacus*	Selection from local germplasm	1989	8.2	–	
CO-5	*A. tricolor*	–	1998	40.7	–	
PLR 1	–	Selection from Tiruvannamalai	2013	8–9	Moderately resistant to pests and diseases	VRS, Palur, TNAU
Pusa Chhoti Chaulai	*A. blitum*	Selection at IARI	–	–	–	ICAR-IARI, New Delhi
Pusa Badi Chaulai	*A. tricolor*	Selection at IARI	–	–	–	
Pusa Kirti	*A. blitum*	–	1991	55	–	
Pusa Kiran	*A. tricolor*	Hybridization between *A. tricolor* and *A. tristis*	1991	35	–	
Pusa Lal Chaulai	*A. tricolor*	–	1991	45–49	–	
Arka Suguana	*A. tricolor*	Pure line selection from IIHR Acc. No. 13560, an exotic introduction from Taiwan	–	25–30	Moderately resistant to white rust	ICAR-IIHR, Bangalore

(continued)

Table 7.3 (continued)

Name of variety	Species	Pedigree and breeding method	Year of release	Green yield (t/ha)	Resistant to biotic stress	Developed by
Arka Arunima	*A. tricolor*	Pure line selection from IIHR Acc. No. 18384	–	26–28	Resistant to white rust	
Arka Samraksha (IlHR-1-21) (green stem)	–	Modified bulk method of selection from F_6 population of IIHR-4× IIHR-70	2018	10–12	–	
Arka Varna (pink stem)	–	Modified bulk method of selection from F_6 population of IIHR-7× IIHR-30	2018	10–12	–	
Arun	–	Palapoor local (mass selection)	1992	–	–	KAU, Kerala
Renusree (green)	–	Selection	2006	15.5	–	
Krishnasree (red)	–	Selection	2006	14.8	–	
KAU Vaika	–	Local collection from Vellarada	2019	–	–	
Kashi Suhaavani (VRAM-42)	–	–	2019	30–33	Tolerant to white rust	ICAR-IIVR, Uttar Pradesh
Plainsman	*A. cruentus*	Breeding line for Nebraska ADAP	1992		Architecture, drought	Rodale

Abbreviations: DBSKKV: Dr. Balasaheb Sawant Konkan Krishi Vidyapeeth; HCRI: Horticultural College and Research Institute; IARI: Indian Agricultural Research Institute; ICAR: Indian Council of Agricultural Research; IIHR: Indian Institute of Horticultural Research; IIVR: Indian Institute of Vegetable Research; KAU: Kerala Agricultural University; VRS: Vegetable Research Station

of seed along with higher oil and squalene content compared to commercial cultivars. Additionally, 'Zobor' also showed significantly higher linoleic acid content (Szabóová et al. 2020).

7.3.3 Global Collection of Amaranth Germplasm

The maximum number of amaranth germplasm accessions have been collected and conserved by the Indian Council of Agricultural Research within the National Bureau of Plant Genetic Resources (ICAR-NBPGR). This National Gene Bank of India has 6,309 amaranth accessions (ICAR-NBPGR 2020). The next largest Gene Bank is held by the United States Department of Agriculture Agricultural Research Services (USDA-ARS) at its North Central Regional Plant Introduction Station (NCRPIS) location in Ames, Iowa, USA with 3,502 accessions. Other smaller collections are held at institutes in Bolivia, Ecuador, Mexico, Peru and Taiwan or within University programs in India and the United States, primarily (Fig. 7.1) (Jacobsen and Mujica 2003; AVGRIS 2020; GENESYS 2020; ICAR-NBPGR 2020; TNAU 2021).

These germplasm collections are useful for finding sources of resistance against different biotic (disease pathogens and insects), soil (low nitrogen and phosphorus) or weather related (heat, drought and cold climates) stresses. These sources of resistance can be further utilized to develop new variety or population resistance against particular disease or insect through conventional breeding or advanced biotechnological approaches. Some of the Gene Banks emphasize on a few species of *Amaranthus*, such as those in Latin America while others particularly those of South Asia and North America emphasize on multiple *Amaranthus* species.

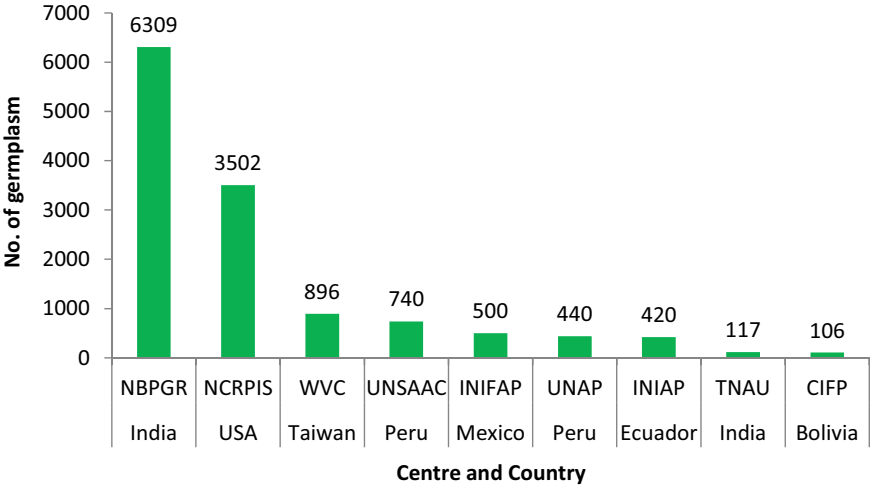

Fig. 7.1 Amaranth germplasm collections found around the world. Abbreviations: NBPGR: National Bureau of Plant Genetic Resources, New Delhi, India; NCRPIS: North Central Regional Plant Introduction Station, USDA-ARS, Ames, Iowa, USA; WVC: World Vegetable Centre, Taiwan; UNSAAC: Universidad Nacional de San Antonio Abad del Cusco, Peru; INIFAP: Instituto Nacional de Investigaciones Forestales, Agrrícolas y Pecuarias, Mexico; UNAP: Universidad Nacional del Altiplano, Escuela de Peru; INIAP: Instituto de Investigaciones Agropecuarias EE. Santa Ecuador; TNAU: Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India; CIFP: Centro de Investigaciones Fitoecogenéticas de Pairumani, Cochabamba, Bolivia

7.4 Genetic Diversity in Amaranths and Their Wild Relatives

Amaranth species have great genetic variability in morphological characteristics, particularly in relation to growth habit, inflorescence type and color, leaf shape and color, stem color, as well as resistance to diseases and pests (Nyonje et al. 2021). Elucidation of genetic diversity is very advantageous to a plant breeder to ascertain diverse parents in creating segregating populations with genetic variability. It also enables introgression of desirable genes from a diverse germplasm into the prevailing population (Thompson et al. 1998). Although, vegetable amaranth is used as an inexpensive source of antioxidants, minerals, other nutrients, and the main food crop in many countries of the world, not many efforts have been made towards its genetic improvement (Shukla et al. 2006).

Genetic variability can be evaluated by collecting information on morphological, cytological, biochemical, or molecular markers (Dharajiya et al. 2021). The phylogenetic relationships to study extents of variation among different species of amaranths have been studied (Das 2016). The extensive genotypic diversity in *Amaranthus* spp. could be due to frequent interspecific and intervarietal hybridizations or introgression events (Suresh et al. 2014). Two different major groups of amaranths: namely the grain and vegetables types have evolved from their specific wild relatives through individual domestication events in different parts of the world. There is much confusion in evolutionary relations of amaranth species which can be resolved by assessing genetic diversity (Dharajiya et al. 2021).

7.4.1 Morphological Diversity in Amaranth

Characterization and morphological diversity assessment of plant genetic resources of crop species provides essential information for breeding programs of crops (Gerrano et al. 2017). Morphological characterization of amaranth can play an important role in resolving taxonomic obscurities in *Amaranthus* spp. Morphological characters of different plant parts like inflorescence, flowers, seed, leaves, stem, pollen, and phyllotaxy are considered as an important part in distinguishing taxa (Das 2016). On the bases of morphological characters, intra-specific and interspecific genetic diversity have been assessed in some *Amaranthus* species (Table 7.4). A wide range of intraspecific diversity in vegetable *Amaranthus* spp. viz. *A. tricolor* (Shukla et al. 2010; Ahammed et al. 2013), *A. hybridus* (Oboh 2007), and *A. lividus* (Rashad and Sarker 2020) has been evaluated. Interspecies genetic diversity among *A. tricolor* var. *tristis*, *A. tricolor*, *A. blitum*, and *A. dubius* has been assessed and resulted in heterogeneous clusters concerning species and geographical origin (Anuja and Mohideen 2007). Accessions belonging *A. hybridus*, *A. dubius*, *A. tricolor*, and *A. cruentus* have been evaluated for the assessment of genetic diversity resulted in formation of clusters on the basis of morphological characters and their geographical

Table 7.4 Diversity analysis in amaranth species based on morphological and biochemical characters

Sr. no.	Species	No. of genotypes	Characters		References
			Type	No.	
1	*A. hybridus*	16	Quantitative	14	Oboh (2007)
2	*A. tricolor*	39	Quantitative	16	Shukla et al. (2010)
3	*A. hypochondriacus*, and *A. tricolor*	13	Quantitative	11	Erum et al. (2012)
			Qualitative	4	
4	*A. cruentus*, *A. tricolor*, *A. dubius*, and *A. hybridus*	28	Quantitative	22	Shankar et al. (2012)
5	*A. tricolor*	22	Quantitative	12	Ahammed et al. (2013)
6	*A. blitum*, *A. caudatus*, *A. dubius*, *A. hybridus*, *A. spinosus*, *A. tricolor*, and *A. viridis*	53	Quantitative	9	Andini et al. (2013)
			Qualitative	3	
7	*A. caudatus*, *A. viridus*, *A. graecizans*, *A. tricolor*, and *Amaranthus* sp. (unknown)	32	Quantitative	14	Gerrano et al. (2015)
8	*A. spinosus*, *A. gracilis*, *A. hybridus*, and *A. tricolor*	18	Quantitative	12	Gueco et al. (2016)
			Qualitative	8	
9	*A. caudatus*, *A. viridus*, *A. graecizans*, *A. cruentus*, *A. tricolor*, and *Amaranthus* sp. (unknown)	32	Qualitative	16	Gerrano et al. (2017)
10	*A. cruentus*, *A. hypochondriacus*, *A. caudatus*, *A. hybridus*, *A. quitensis*, *A. powellii*, *A. retroflexus*, *A. palmeri*, and *Amaranthus* sp. (Unknown)	293	Qualitative	9	Thapa and Blair (2018)
11	*A. spinosus*, *A. atropurpureus*, *A. cruentus*, *A. viridis*, *A. thunbergii*, *A. caudatus*, *A. graecizans*, *A. mantegazzianus*, *A. hypochondriacus*, *A. blitum*, *A. lecuocarpus*, *A. dubius*, *A. retroflexus*, *A. gracilis*, *A. tricolor*, *A. hybridus*, and *A. palmeri*	50	Quantitative	8	Kiruthika et al. (2019)
			Qualitative	14	
12	*A. lividus*	20	Quantitative	9	Rashad and Sarker (2020)
13	*A. albus*, *A. blitiodes*, *A. caudatus*, *A. graecizans*, *A. hybridus*, *A. lividus*, *A. retroflexus*, *A. spinosus*, *A. tricolor*, and *A. viridis*	10	Quantitative	4	Taia et al. (2021)
			Qualitative	22	

origin along with the co-existence of accessions native to different geographic regions (Shankar et al. 2012). Evaluation of morphological diversity can be helpful in identifying superior genotype for particular character. Amaranth genotypes belonging to *A. viridis*, *A. tricolor*, *A. dubius*, *A. blitum*, *A. spinosus*, *A. hybridus*, and *A. caudates* have been assessed for morphological diversity which indicated that *A. dubius* and *A. viridis* genotypes could be used as valuable parental lines in breeding programs for yield improvement and protein content, respectively (Andini et al. 2013). The clustering of the accessions can be useful in the recognition and selection of genetically diverse parents having the greatest inter-cluster distance which may give high levels of heterosis for the desired traits in breeding programs (Anuja and Mohideen 2007).

7.4.2 Molecular Diversity in Amaranth

Molecular markers are powerful tools to identify, characterize, and elucidate origin and diversity of genotypes (Dharajiya et al. 2020). Various molecular markers viz., random amplified polymorphic DNA (RAPD) (Ray and Roy 2009; Sammour et al. 2020), internal transcribed spacer (ITS) (Xu and Sun 2001), amplified fragment length polymorphism (AFLP) (Chandi et al. 2013), inter-simple sequence repeat (ISSR) (Gelotar et al. 2019), simple sequence repeat (SSR) (Oo and Park, 2013; Nguyen et al. 2019), and single nucleotide polymorphism (SNP) (Xu et al. 2020) have been utilized in the diversity analysis among and/or within *Amaranthus* spp. Work done on inter- and/or intra-specific diversity analysis in vegetable amaranth have been shown in Table 7.5.

Suresh et al. (2014) grouped 348 amaranth accessions from 33 vegetable species into seven groups collected from different geographical locations in order to investigate relationship among 33 weedy, grain and vegetable *Amaranthus* using 11 SSR markers. The cluster analysis showed that weedy type appeared to be more diverse based on expected heterozygosity (H_E) and polymorphic information content (PIC) followed by vegetable type having and then grain types. In that study, simple grouping did not strictly follow geographic affiliations (Suresh et al. 2014) as was the case for Thapa and Blair (2018). By characterizing the genetic diversity using a combination of morphological, biochemical, physiological, and molecular data, accessions with superior stress resistance traits can be interpreted.

7.5 'Omics' Assisted Breeding

The advent of molecular biology applied to higher plants especially crops in agronomy and horticulture has led to a revolution in plant breeding based on more accurate genotyping of breeding lines. "Omics" are bodies of knowledge about genes (genomics), messenger RNAs (mRNAs) and expression (transcriptomics), proteins

Table 7.5 Genetic diversity among grain and vegetable amaranth species using molecular markers

Sr. no	Species	Type	No. of accessions	Molecular marker	Coefficient used and range	References
1	*A. caudatus*, *A. cruentus*, *A. hypochondriacus*, *A. hybridus*, *A. powellii*, *A. retroflexus*	Grain, Wild	179	SSR	H: 0.14 to 0.83	Mallory et al. (2008)
2	*A. gangeticus* (syn. *tricolor*), *A. paniculatus*, *A. viridis*, *A. hypochondriacus*, *A. caudatus*, and *A. cruentus*	Grain, Wild	30	RAPD	J: 0.16–0.97	Ray and Roy (2009)
3	*A. caudatus*, *A. cruentus*, *A. hypochondriacus*, *A. hybridus*, *A. powellii*, *A. retroflexus*, *A. tuberculatus*	Grain, Wild	480	SNP-Kasp	MAF: 0.05–0.5	Maughan et al. (2011)
4	*A. blitum*, *A. Deflexus*, *A. graecizans* subsp. *sylvestris*, *A. mantegazzianus*, *A. standleyanus*, *A. viridis*, *A. quitensis*, *A. caudatus*, *A. hybridus*, *A. tricolor*, and *Amaranthus* spp. (unknown)	Wild, Vegetable, Ornamental	75	SSR	N: 0.03–0.89	Oo and Park (2013)

(continued)

Table 7.5 (continued)

Sr. no	Species	Type	No. of accessions	Molecular marker	Coefficient used and range	References
5	*A. acutilobus*, *A. albus*, *A. arenicola*, *A. australis*, *A. blitoides*, *A. blitum*, *A. blitum*var. *oleraceus*, *A. bouchonii*, *A. caudatus*, *A. caudatus*var. *albiflorus*, *A. crassipes*, *A. crispus*, *A. cruentus*, *A. deflexus*, *A. dubius*, *A. fimbriatus*, *A. floridanus*, *A. gangeticus* var. *melancholicus*, *A. hybridus*, *A. hypochondriacus*, *A. lividus*, *A. mangostanus*, *A. mantegazzianus*, *A. palmeri*, *A. powellii*, *A. powellii* subsp. *bouchonii*, *A. quitensis*, *A. retroflexus*, *A. spinosus*, *A. standleyanus*, *A. tricolor*, *A. tuberculatus*, *A. viridis*, and *Amaranthus* sp. (unknown)	Grain, Wild, Vegetable	348	SSR	CS: 0.48–0.91	Suresh et al. (2014)
6	*A. caudatus*, *A. cruentus*, *A. hypochondriacus*, *A. powellii*, *A. quitensis*, *A. retroflexus*	Grain, Wild	10,668	SNP-GBS	n/a	Wu and Blair (2017)

(continued)

Table 7.5 (continued)

Sr. no	Species	Type	No. of accessions	Molecular marker	Coefficient used and range	References
7	*A. tricolor* and *A. hypochondriacus*	Vegetable, Grain	300	SSR	–	Nguyen et al. (2019)
8	*A. hypochondricus*, *A. cruentus*, *A. caudatus*, *A. hybridus*, *A. palmeri*, *A. retroflexus*, *A. quitensis*, *A. powellii*, *A. tricolor*, and *A. spinosus*	Grain, Wild, Vegetable	25	RAPD	J: 0.11–0.88	Sammour et al. (2020)
9	*A. albus*, *A. arenicola*, *A. blitoides*, *A. blitum*, *A. bouchonii*, *A. capensis*, *A. caudatus*, *A. crispus*, *A. cruentus*, *A. deflexus*, *A. dubius*, *A. fimbriatus*, *A. graecizans* ssp. *sylvestris*, *A. hybridus*, *A. hypochondriacus*, *A. palmeri*, *A. polygonoides*, *A. powellii*, *A. retroflexus*, *A. spinosus*, *A. standleyansus*, *A. tennuifolius*, *A. tricolor*, *A. tuberculatus*, *A. tuberculatus* var. *tuberculatus*, *A. viridis*	Grain, Wild, Vegetable	26	SNP	–	Xu et al. (2020)

Abbreviations: CS: Chord distance; D: Dice similarity coefficients; J: Jaccard's similarity coefficient; H: Heterozygosity; MAF: Minor allele frequency; N: Nei's genetic distance matrix; NL: Coefficient

(proteomics) and metabolites (metabolomics) which assist in both basic and applied sciences.

Each area of omics has many of its own technologies, under-laid with the central dogma of transcription and translation as well as modifications in gene regulation, protein modification and metabolic pathways. The characterization of these pools of biological molecules provide a context for functional genomics which allows for a deeper understanding of each gene and its manipulation via selection and targeted modifications such as clustered regularly interspaced short palindromic repeat (CRISPR). Within the scope of functional genomics are studies for gene discovery through marker tagging by association or other statistical means all the way to the creation of genetically modified organisms (GMOs). The initial part of the spectrum of science, especially gene tagging, is the one most useful in the immediate future of amaranth breeding, as gene modification, transgenesis and protein/metabolite study are still in its infancy for the genus.

7.5.1 Association Mapping Studies

Genome-wide association study (GWAS) and population genomic methods have been employed not surprisingly in the weedy species of the *Amaranthus* genome, where economic losses are high for major industrial agriculture. A case in point is the study of the genetic architecture of glyphosate resistance in waterhemp, *A. tuberculatus*, an important weed species in the United States. GWAS enabled appropriate recognition of the gene targeted by glyphosate and additional 250 genes related to non-target site resistance (NTSR) (Kreiner et al. 2021). Genome-wide SNPs showed a remarkable variation in glyphosate resistance to monogenic mechanisms and under-appreciated polygenic contribution to the evolution of herbicide resistance in *A. tuberculatus* (Kreiner et al. 2021). In one of the first studies in a vegetable amaranth, GWAS in *A. tricolor* was used to discover 25 marker trait associations (MTAs) associated with branching index, inflorescence color, petiole pigmentation, and terminal inflorescence shape and attitude (Jamalluddin 2020). The markers associated with specific characteristics can then be used for marker-assisted selection (MAS) for the respective traits under stress or non-stress conditions.

7.5.2 Molecular Mapping of Resistance Genes and Quantitative Trait Loci (QTLs)

Gene tagging is often assisted by molecular maps or whole genomes. To this end, Maughan et al. (2011) characterized the first complete genetic linkage map in the *Amaranthus* genus using SNP markers. This study followed up the partial sequencing of the *A. caudatus* genome through 454 pyro-sequencing (Maughan et al. 2009).

For the genetic mapping study, PI 481125 (female parent; *A. hypochondriacus*) and PI 642741 (male parent; *A. caudatus*) were crossed to develop an interspecific F_2 population (Maughan et al. 2011). Pairwise linkage analysis clustered all 411 SNP markers into 16 linkage groups (LGs) at a minimum logarithm of the odds (LOD) score of 5. The number of markers within the linkage groups varied from 9 to 47 SNPs/LG. The total map contained 411 SNP loci and covered 1288 cm. This map was a preliminary first step in the genetic dissection of agronomically important traits in cultivated grain amaranths.

In a similar study, but with weedy amaranths, two large-effect QTLs were recognized governing 4-hydroxyphenylpyruvate dioxygenase (HPPD)-inhibitor resistance in *A. tuberculatus* which was the first QTL mapping study to characterize herbicide resistance in a weedy amaranth species (Murphy et al. 2021).

7.5.3 Transcriptomics and Metabolomics

Although less well studied, certainly than the genes of *Amaranthus*, some mRNA, and metabolite studies have been conducted. For example, transcriptomics and metabolomics of edible amaranth cultivars (*A. mangostanus*) under salinity stress helped in acquiring a comprehensive view of the expression of key enzymes and alterations in metabolites, respectively (Guo et al. 2018, 2020).

Similarly, transcriptomics and metabolomics approaches can provide better understanding of plant's response to biotic stresses and the underlying mechanisms of resistance at the metabolite level. The expression levels of two candidate genes viz., *Ah-2880* and *Ah-HFR* were assessed through qRT-PCR and their high expression levels was observed under several stress conditions. The expression of the *Ah-HFR* gene was increased in response to herbivory, defoliation, and salinity whereas the expression of *Ah-2880* was increased at high salinity stress and infection by *Pseudomonas syringae* pv. *syringae* (avirulent bacteria) (Álvarez et al. 2017; Cabrales Orona 2017).

7.5.4 Genome Research in Amaranth

In recent times, advanced research towards understanding the amaranth genome and modern genetic marker systems have been conducted (Maughan et al. 2009, 2011; Clouse et al. 2016; Lightfoot et al. 2017; Stetter and Schmid 2017). Such information and resources can be of great use in the development of markers for the improvement of breeding methodologies for various amaranths (Joshi et al. 2018).

A well-assembled reference genome is one of the most important resources for genome assisted breeding. Genome sequencing of *Amaranthus* spp. was first attempted on a weed amaranth, waterhemp (*A. tuberculatus*) by Lee et al. (2009)

and on a grain amaranth (*A. caudatus*) by Maughan et al. (2009). Recently, a more complete *A. tuberculatus* genome has been published (Kreiner et al. 2019).

Within the grain amaranths, physical mapping of *A. hypochondriacus* and *A. caudatus* genomes provided chromosome scale scaffolds (Maughan et al. 2008; Lightfoot et al. 2017). Along with these high-quality assemblies, two draft genomes of *A. hypochondriacus* (Sunil et al. 2014; Clouse et al. 2016), chloroplast genomes of *A. hypochondriacus*, *A. cruentus*, *A. caudatus*, and *A. hybridus* (Chaney et al. 2016), a transcriptome (Delano-Frier et al. 2011; Clouse et al. 2016), and a genetic map (Maughan et al. 2011) were made available. The details of various genome sequences of various amaranth species have been provided in Table 7.6.

Genome-wide SNPs (Maughanet al. 2011) and SSRs (Tiwari et al. 2021) have been developed for *A. caudatus* and *A. hypochondriacus*, respectively and their cross-species transferability has been evaluated. These multiple reference and draft genomes of various amaranth species, along with the reported SSRs, SNPs, and InDel, is an important genetic resource will boost up genomic studies in amaranth to understand evolution and diversity within *Amaranthus*. Sources of resistance to biotic and abiotic sources can be identified and tracked through new genetic markers and available genomic information in amaranth. Various molecular marker systems can be applied at different stages in breeding programs. The study of diversity in ex situ collections and use of this genetic diversity to map QTLs by GWAS will impressively increase our knowledge of the genetic architecture of traits and provide targets for MAS. Genomic selection has not been investigated in amaranth so far, although the use of genomic prediction could generally increase the speed of the genetic gain for nutritional traits per generation via early selection and possesses great potential for biofortification breeding in amaranth (Joshi et al. 2018).

Table 7.6 Details of genome sequences of amaranth species

	A. hypochondriacus			*A. tuberculatus*			*A. palmeri*	*A. hybridus*
Quality of genome assembly	Draft	Draft	Reference	Draft	Reference	Draft	Draft	Draft
Cultivar	Domesticated cultivar from farmers in northern Karnataka	Plainsman[a]	Plainsman	Local collection	Female plant	–	-	-
Sequencing platform	Illumina GAIIx (Illumina)	Illumina HiSeq (Illumina)	Illumina paired-end (Illumina)	454-pyrosequencing Genome Sequencer FLX system (Roche)	HiSeq 3000 instrument (Illumina)	HISEQ 3000 instrument (Illumina)	HISEQ 3000 instrument (Illumina)	HISEQ 3000 instrument (Illumina)
Estimated genome size (Mb)	431.8	431.8	431.8	675.6	675.6	675.6	421.8	503.8
The assembled genome size (Mb)	318.8	376.4	403.9	42.8	663.7	572.9	408.1	403.0
Total no. of contigs	491,569	17,366	1589	19,925	2,514	841	638	640
N_{50} contig length (Mb)	0.0019	0.0445	1.254	–	1.74	2.58	2.54	2.26
Total no. of scaffolds	367,441	3,518	908	–	16	16	303	16
N_{50} scaffold length (Mb)	0.035	0.37	24.36	–	43.1	34.7	20.11	24.5
Annotated genes	24,829	23,059	23,847	10,620	56,936	26,784	29,758	24,325

(continued)

Table 7.6 (continued)

	A. hypochondriacus			*A. tuberculatus*			*A. palmeri*	*A. hybridus*
Quality of genome assembly	Draft	Draft	Reference	Draft	Reference	Draft	Draft	Draft
References	Sunil et al. (2014)	Clouse et al. (2016)	Lightfoot et al. (2017)	Lee et al. (2009)	Kreiner et al. (2019)	Montgomery et al. (2020)	Montgomery et al. (2020)	Montgomery et al. (2020)

[a] Plainsman is a release variety from Baltensperger et al. (1992)

7.6 Genetic Engineering in Amaranth

Transformation methods in amaranth are still undeveloped. Only few reports are available on the development of transgenic amaranth plants. Munusamy et al. (2013) developed the protocol for *Agrobacterium*-mediated transformation in female reproductive system of amaranth. A standard floral dip protocol for amaranth floral transformation was developed by introduction of *p5b5*, *p5d9*, and *p5f7* individually in pDRB6b vector for *Agrobacterium*-mediated transformation using *A. tumefaciens* strain AGL1 which resulted in more than 95% seed productivity. It was reported that transgenic amaranth (*A. retroflexus*) plants obtained by floral dip transformation method containing *ARGOS-LIKE* gene (derived from *A. thaliana*) along with the dahlia mosaic virus promoter showed increased (190%) fresh weight due to increased length of stem and leaf (Kuluev et al. 2017).

A different plant regeneration protocol via somatic embryos of transgenic *A. hypochondriacus* (grain) and *A. hybridus* (vegetable) produced from hairy roots was established by Castellanos-Arévalo et al. (2020) by using *A. rhizogenes*. Castellanos-Arévalo et al. (2020) also proposed that genetic factors were affecting the transformation as only *A. hypochondriacus* among grain amaranth species, was efficiently transformable in the generation of transgenic hairy roots, while *A. caudatus* (grain) and *A. cruentus* (grain) remained recalcitrant. *A. hybridus* (vegetable) considered to be a common ancestor of all three grain amaranths (Stetter and Schmid 2017), was also acquiescent to *A. rhizogenes*-mediated transformation.

In whole plant transformation, transgenic plants of *A. caudatus* cv. "Kremoviyrannii" and "Karmin" resistant to herbicide—phospinotricin (PPT) were obtained after treatment with *A. tumefaciens* using the floral-dip method (Yaroshko et al. 2018). Few other successful transformation protocols have been developed in *Amaranthus* spp., including *A. hypochondriacus* (Jofre-Garfias et al. 1997), *A. tricolor* (Swain et al. 2010; Pal et al. 2013a), *A. spinosus* (Pal et al. 2013b), *A. cruentus* (Taipova et al. 2020), and *A. caudatus* (Yaroshko et al. 2020; Mani et al. 2021).

Experimental uses of transgenesis with amaranth sequences have proven valuable for study of gene function. For example, transformation of *Ah24* gene of *A. hypochondriacus* into *Nicotina tabacum* and *A. thaliana* has confirmed its role in defense against mechanical damage and herbivory due to higher jasmonic acid expressed in young or developing tissues (Massange-Sanchez et al. 2015).

In another example, the gene*AhDGR2* from *A. hypochondriacus* showed expression of abiotic stress-induced DUF642 protein in transgenic *A. thaliana* which modified cell wall structure and composition and caused salt and ABA hypersensibility (Palmeros-Suárez et al. 2017). It has been reported that overexpression of *A. hypochondriacus* transcription factors namely, *AhDOF* and *AhERF* in *A. thaliana* increased salt stress and water deficit tolerance, respectively (Massange-Sanchez et al. 2016). Some developed methods of transformation in few amaranth species can be applicable to develop faster and efficient genetic transformation methods in different vegetable amaranth species.

7.7 Role of Bioinformatics

Bioinformatics of various amaranth species is incipient. Apart from sequences deposited in Phytozome by authors of sequencing papers, Amaranth GDB (https://amaranthgdb.org/) is a resource combining amaranth genomics and population genetics (Gonçalves-Dias and Stetter 2021). According to the authors, popAmaranth is an intuitive and user-friendly population genetic genome browser for grain *Amaranthus* and their wild relatives, including three grain amaranth species (*A. hypochondriacus*, *A. cruentus*, and *A. caudatus*) and two wild relatives (*A. hybridus* and *A. quitensis*) providing statistical analysis of genes from all five species through whole genome sequencing data. Total twelve tracks in the database are grouped in five categories of gene annotation, differentiation, diversity, selection, and variant call. Annotation provides sub-features including coding sequence (CDS), mRNAs, and untranslated region (UTRs). Differentiation provides statistical summary of fixation index, average pairwise differences, estimator of genetic diversity population observed and expected heterozygosity for SNP genotype, inbreeding coefficient (F) for each variant and Nei's nucleotide diversity (Gonçalves-Dias and Stetter 2021).

7.8 Recent Concepts and Strategies Developed

The progress in genomics and transformation described above can lead to expanded progress in other areas of research and applied biotechnology such as those listed below, including gene editing as a more directed method of mutagenesis and nanotechnology as a way to develop biocontrol methods for many plants. This will aid in the development of new varieties, as to date plant breeders have utilized only existing natural mutations combined with some chemical and physical mutagens enabling fast 'genebanking' of large sets of genetic variation. However, as a consequence of the evolutionarily slow generation of random mutations, the recognition of desired mutations is a long and laborious procedure.

7.8.1 Gene Editing

The development of sequence-specific engineered endonucleases, the homing endonucleases (HENs) or mega-nucleases, zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and clustered regularly interspaced short palindromic repeat (CRISPR)/CRISPR-associated protein 9 (Cas9), has improved the techniques of targeted gene editing in plant genomes (Vats et al. 2019). These engineered nucleases enable the generation of double-stranded DNA breaks (DSBs) at specific target sites. The induced DSBs can be repaired either end-joining

pathway or via the homology-directed repair (HdR) pathway which can be responsible for the introduction of gene modifications at the target loci (Gaj et al. 2016). In the past few years, highly versatile genome-technology, CRISPR–Cas9 has transformed genome engineering by providing investigators with the ability to introduce sequence-specific alterations into the genomes of a broad range of cell types and organisms (Gaj et al. 2016). These methods of gene editing can be used in amaranth for the trait improvement for biotic stress resistance.

7.8.2 Nanotechnology

Nanotechnology combines biological elements with engineered molecules to deploy for various purposes. An area of research that is having nanotechnology success is that of nanoparticles (NPs) for combating disease organisms, especially fungi. Resistant fungal strains emerge constantly and to combat them green NPs biosynthesized by plants have found useful. For example, silver nanoparticles (AgNPs) synthesized with leaf extract of *A. retroflexus* possessed antifungal activity against plant pathogenic fungi namely, *Alternaria alternata*, *Macrophomina phaseolina,* and *Fusarium oxysporum* (Bahrami-Teimoori et al. 2017). Some other species have also been utilized in the synthesis of NPs. These include *A. cruentus*, *A. gangeticus*, *A. dubius*, and *A. tricolor* leaf extracts for synthesis of AgNPs, *A. spinosus* for gold nanoparticles (AuNPs), and *A. caudatus* for zinc oxide nanoparticles (ZnONPs) all showing antimicrobial activity (Das et al. 2012; Kolya et al. 2015; Sigamoney et al. 2016; Jeyabharathi et al. 2017; Baghani and Es-haghi 2019; Fatimah and Aftrid 2019). NPs developed by various plant extracts can be screened against pathogens and insects of vegetable amaranth to identify suitable NP-based control of biotic stress.

7.9 Future Perspectives

Various modern approaches are now available for crop improvement but limited efforts have been made in amaranth breeding. Combining conventional and advanced approaches can speed up crop improvement with more accuracy. The breeding of any crop starts with the genetic resources available. World-wide collections of germplasm and their conservation in gene banks include natural populations, wild relatives, landraces, varieties, and breeding lines. They contain both beneficial and harmful alleles which can be utilized as breeding lines or as parents in the development of mapping populations. The germplasm must be evaluated for diversity to analyze the extent of variation among different populations or genotypes. The diversity at morphological, biochemical, cytological, and molecular levels provides a collection of information for selecting parents or lines as a source of resistance against particular biotic stress. The diversity estimation aids in identification and selection

of diverse lines with superior alleles/haplotypes (heterotic group). High-throughput phenotyping at multiple locations with diverse environments helps in recognizing the superior plants/genotypes. Moreover, study G × E interaction by GGE biplot or related models can aid in determining response of genotype in specific environment (Pagi et al. 2017). Next-generation sequencing (NGS) including whole genome sequencing (WGS), whole exome sequencing (WES), and transcriptome sequencing (RNA-seq) provides genome annotation and other genetic information.

The sequencing data have been used in the discovery and development of reliable and co-dominant genetic markers (e.g. SSRs, SNPs, and InDels) which can be employed in genotyping, linkage mapping, and other genomics application. The identified heterotic groups are used in the development of mapping populations (e.g. F_2, recombinant inbred lines (RILs), multi-parent advanced generation inter-cross (MAGIC), nested association mapping (NAM) etc.) to identify QTLs, genes, or linked markers for the trait of interest. The data collected from the phenotyping of population are combined with the data of genotyping of the population for GWAS. Combination of multi-omics approaches and phenotyping under field condition offers a great way to associate genomic variations with the important phenotypes. After identification of a gene-trait association, functional validation leads to identification of a causative gene. Information of genes responsible for key characters/traits of plant creates the way for haplotype-based breeding/genomic assisted breeding or de novo domestication.

Simultaneously, genome-wide genotyping information leads to genomic prediction approach which can also be used in breeding programs. Identified functional markers or genes can be used in MAS and marker assisted backcrossing (MAB). Genetic transformation can be utilized to insert specific gene of interest into the plant or gene editing methods (e.g. CRISPR/Cas9) can be used to eliminate undesired gene or to modify of the targeted gene.

A proposed work flow of genome design of amaranths resistant to biotic stress is shown in Fig. 7.2. Execution of these new breeding methods and tools will help in accumulation of desired alleles or deletion of undesired alleles in plant population leading to improvement in genetic gains of breeding programs for designing future crops.

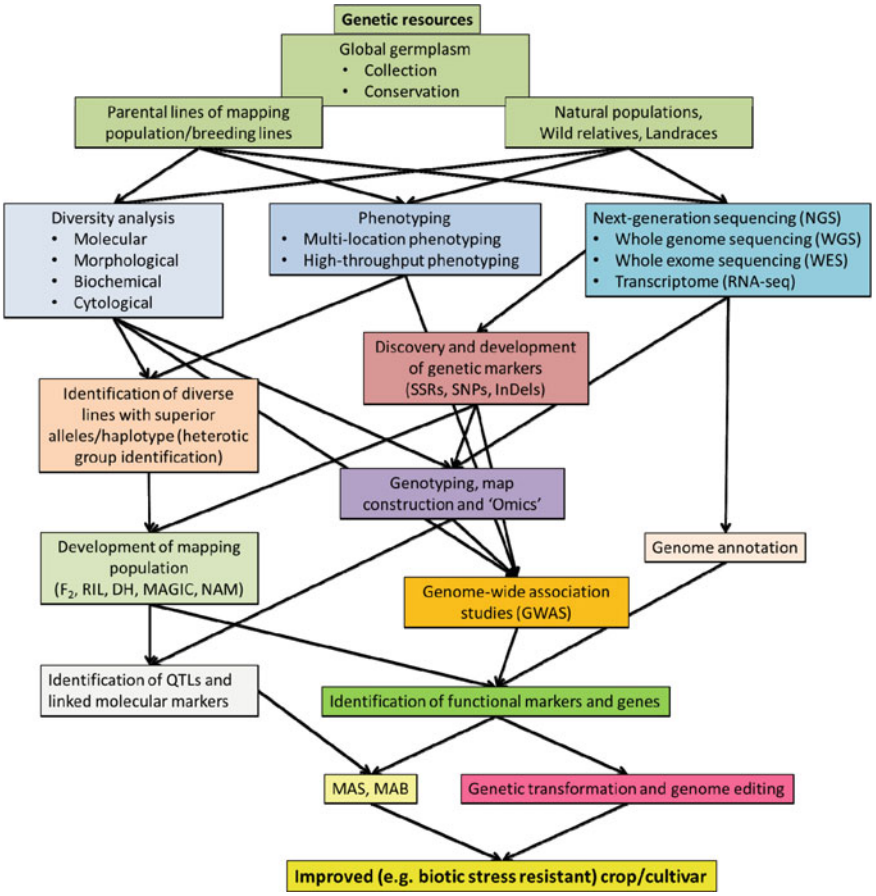

Fig. 7.2 Approaches to accumulate desired alleles or eliminate harmful alleles in the plant genomes for designing future crops resistant to biotic stress

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