Chapter 4
Eggplant Breeding and Improvement for Future Climates

Mark A. Chapman

Abstract The Asian eggplant, *Solanum melongena* (also known as aubergine or brinjal), is a widely grown and economically important crop, especially in South and Southeast Asia and the Mediterranean. A large amount of morphological diversity is present in eggplant, suggesting that genetic variation is high; however, limited work has been carried out on traits which could be of importance in a future climate. Here I discuss what is known about biotic and abiotic tolerances in eggplant, and in particular highlight that the variation in the crop-wild relatives, found throughout Africa and Southern Asia, is likely to be very important for breeding eggplants for future climates. I also discuss the limited knowledge we currently have on two other domesticated eggplants, the scarlet eggplant (*S. aethiopicum* L.) and the Gboma eggplant (*S. macrocarpon* L.). The chapter ends with some considerations for future work, and I highlight that the development of introgression populations, the study and conservation of eggplant wild relatives, and the genetic dissection of adaptive traits should be prioritized.

Keywords Crop-wild relatives · Eggplant · Pathogen resistance · Pest resistance · Stress tolerance

4.1 Overview

Globally, with climate change, we expect increase in temperature and CO_2, as well as additional unpredictability with regard to droughts, floods, and storms (Coumou and Rahmstorf 2012; Trenberth et al. 2013; Poppy et al. 2014), and this is occurring at the same time as the world population is dramatically increasing in size (Godfray et al. 2010). Increasing temperatures are predicted to have a significant effect on crop yields (Zhao et al. 2017) and the rapid development of novel tolerant varieties is required to counteract this (Challinor et al. 2016; Atlin et al. 2017).

With this increasing world population, efforts need to be made to produce more food and utilizing sub-optimal land (Tilman et al. 2002). It is clearly important to

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increase crop yields; however, if we wish to expand the growing areas of crops, we need to develop varieties with ability to tolerate poor soils, more erratic precipitation, and/or salinity (Ahuja et al. 2010).

Coupled with the immediate abiotic pressures of climate change and poor growing conditions, future crops may have to tolerate novel suites of pests and pathogens. It is estimated that crop yields are reduced by 20–40% due to these biotic pressures (e.g., Oerke et al. 1994), and with climate change it is predicted that the natural geographic ranges of many pathogens will change (Garrett et al. 2006; Savary et al. 2012). This additional (and currently somewhat unpredictable; Donatelli et al. 2017) pressure, novel pests, and diseases could result in a significant drop in yield even if climate-tolerant varieties are developed.

Asian eggplant (*S. melongena*) is an important vegetable crop, especially in parts of the Mediterranean, the Middle East, and Southern/Southeastern Asia. It is the third most widely grown crop in the Solanaceae, after tomato and potato, grown on about 1.86 million (M) ha and with a total production of 52.3 M tons globally in 2017 (FAO 2017). The majority of eggplant (over 80%) is grown in China and India. India in particular is at extreme threat from climate change, with the expectation of increased temperatures, varied precipitation patterns, and unpredictability of the monsoons that millions of farmers rely on (World Bank 2013). Two-thirds of agriculture in India is rain-fed; therefore, >250 M farmers and associated landless agricultural laborers currently rely on the monsoon.

Adaptation of eggplant to the future climate could be achieved through (1) the identification of stress-tolerant eggplant varieties, (2) the breeding of eggplant with stress-tolerant wild relatives, and/or (3) mutational/transgenic approaches. These will be discussed in turn in this review, after an introduction to the Asian eggplant.

While the focus of this chapter is the Asian eggplant, two other eggplant species can be described as domesticated; these are the Ethiopian or scarlet eggplant (*S. aethiopicum* L.) and the African or Gboma eggplant (*S. macrocarpon* L.). Less research has been carried out on these other eggplants (in general, as well as specifically looking at climatic tolerances); however, the research that is available is reviewed in Sect. 4.6.

4.2   Origin of Asian Eggplant and Phylogenetic Relationships to Wild Relatives

Eggplant was domesticated in the Old World, in contrast to its New World congeners tomato and potato, most likely in or near to present-day Malaysia, Thailand, and Vietnam (Page et al. 2019b). Enormous morphological variation exists in the eggplant gene pool, most notably in fruit size, shape, and color characteristics, and also in plant stature, length of growing period, and flower shape and color. The wild progenitor is *Solanum insanum* L., a widespread species found as far West as Madagascar,

extending throughout India to Thailand, Indonesia, and Malaysia in the East (Ranil et al. 2017).

Recent analysis based on ca. 5,000 nuclear single nucleotide polymorphisms (SNPs) demonstrates that eggplants with fruit the shape and size of hen's eggs, previously named *S. ovigerum*, represent primitive domesticates, with further selection resulting in landraces with larger and more diverse shapes and sizes of fruits (Page et al. 2019b). The domestication bottleneck (the loss of diversity expected due to humans selecting only a subset of the genetic variation present in the wild) is estimated to have resulted in a ca. 50% reduction in genetic diversity in *S. melongena* relative to *S. insanum*. The cultivated species is roughly split into Eastern (Chinese, Thai, Indonesian, Filipino, and Malaysian) and Western (Indian) landrace groups based on the same panel of SNPs.

Several recent taxonomic works have provided more detail into the relationships between *S. melongena* and related wild eggplants. The eggplant clade, along with the wild relatives of *S. melongena* (Knapp et al. 2013), is a well-supported monophyletic group of 10–13 species (Vorontsova et al. 2013; Aubriot et al. 2018) distributed throughout Africa, the Middle East, and into Southeast Asia. It appears that the eggplant clade originated in the Middle East/Northeast Africa and then expanded into Africa (where most eggplant clade species are found) and into South Asia (where *S. insanum* is found and domestication took place) (Aubriot et al. 2018).

4.3 Climate Change-Relevant Genetic and Phenotypic Variation in Eggplant

In a review of the World Vegetable Center Eggplant Collection, Taher et al. (2017) highlight that while yield and fruit quality have been relatively well characterized, screening for biotic and abiotic stress tolerance has lagged behind. More generally, while the genetic basis of stress tolerance is being explored in a number of crops, there are scant examples of where this has been applied to breeding programs (Gilliham et al. 2017).

There are several pathogens which cause damage to eggplants, ranging from bacteria to fungi to insects. Screening investigations have identified accessions with the strongest resistance to Fusarium wilt (Boyaci et al. 2012), bacterial wilt (Daunay 2008; Lebeau et al. 2011), and *Ralstonia* (Daunay 2008; Salgon et al. 2018). Within the eggplant gene pool there also exist varieties resistant to leafhopper, aphids, and eggplant root and shoot borer (reviewed in Taher et al. 2017). Resistance to *Verticillium* wilt or root-knot nematodes (*Meloidogyne* spp.) has not been found (Daunay et al. in press), and the breeding of eggplants resistant to these latter pests relies on wild relatives (see next section). The genetic basis of resistance to Fusarium wilt has been determined based on crossing resistant and susceptible eggplant varieties (Mutlu et al. 2008; Boyaci et al. 2012; Miyatake et al. 2016). Similarly, resistance to *Ralstonia* has been mapped (Lebeau et al. 2013; Salgon et al. 2018).

Salt tolerance and chilling tolerance have been investigated in small numbers of cultivars (Minghua et al. 2001; Yasar 2003); however, drought tolerance in the eggplant gene pool appears to be understudied. In one eggplant cultivar, fruit production and leaf area are positively correlated with the number of lateral roots (Rouhani et al. 1987), which suggests that variation in root growth parameters is important to analyze. Recently, Bui et al. (2015) compared nine *S. melongena* accessions (and one *S. linnaeanum* Hepper and P.-M.L. Jaeger accession) for root traits thought to be correlated with drought tolerance. Rate of adventitious root emission showed considerable variation among the genotypes, which could play an adaptive role in adaptation to low water. Further, genotypes with high growth rate also had fast-growing densely branched roots (Bui et al. 2015) indicating that above-ground growth can be taken as a proxy for root growth without the need for extensive below-ground phenotyping.

While different varieties can have different levels of resistance to a stress, variation in pathogen resistance and stress tolerance can often be affected by external factors, for example, the presence of other stresses, a scenario likely to be encountered in the wild (Mittler 2006). These multiple stresses can give rise to synergistic or antagonistic responses, increased damage, or in some cases one stress can result in tolerance of a second stress. For example, tomato plants under drought conditions can be more resistant to fungal infection (Achuo et al. 2006) and *Arabidopsis* plants exposed to *Verticillium dahlia*, a fungal pathogen, demonstrated an increase in drought tolerance (Reusche et al. 2012).

In eggplant, simultaneous application of *Verticillium* infection and drought affected two eggplant cultivars in different ways, and not in the way as predicted by the effect of each stress applied individually. For example, *Verticillium* infection reduced relative growth rate (RGR) marginally in one cultivar under both control and drought conditions, whereas for the other cultivar a much greater reduction in RGR was observed under drought relative to control (Tani et al. 2018).

Other studies have examined the effect of the environment on trait expression. For example, phenolic compounds, common in eggplant fruit and with health benefits to the consumer, were significantly more abundant in spring-harvested than summer-harvested fruits (García-Salas et al. 2014), and in quantitative trait loci (QTL) mapping studies, some QTLs are found in only a subset of the environments in which the population is grown (e.g., Doganlar et al. 2002b; Toppino et al. 2016).

The examination of eggplant genotypes as a rootstock deserves investigation too. Eggplant is an important rootstock for a number of other crops because of tolerance to certain biotic and abiotic factors. In some countries more than half of the tomatoes produced are from plants which were grown on a rootstock (Lee et al. 2010), and eggplant is a commonly used rootstock. As an example, eggplants serve as a bacterial wilt-resistant rootstock for peppers and tomatoes (Sadashiva et al. 2001), and waterlogging tolerance is greater in tomato grafted onto eggplant rootstocks than in non-grafted tomato plants (Bahadur et al. 2015). Varieties typically used as rootstock have been identified based on tolerance in the current climate, but there appears to be no work analyzing these varieties under varying environmental pressures.

4.4 Climate Change-Relevant Genetic and Phenotypic Variation in Eggplant Wild Relatives

It has become evident that crop-wild relatives (CWRs) can contain adaptive genetic variation that is absent from domesticated crops (Maxted et al. 2007). This comes from the domestication bottleneck (i.e., only a subset of genetic variation present in the progenitor is found in the domesticated species), and also because each crop typically has many CWRs, likely to be found in diverse environments adapted to different selection pressures. Maxted and Kell (2009)reported that ca. 1,000 plant species can be considered CWRs very closely related to some of the world's most important food crops; however, 75% of these are threatened in the wild and/or poorly represented in gene banks (Dempewolf et al. 2014).

If the CWRs can be bred with the crop, then there is the potential for this novel variation to be crossed into the crop. In a relatively small number of generations, and enhanced by molecular breeding techniques, such as marker-assisted selection (MAS; Morrell et al. 2011), stress or pest tolerance from a wild species can be introgressed into a crop genetic background (Tanksley and McCouch 1997; Warschefsky et al. 2014). Hajjar and Hodgkin (2007) reported that the majority of CWR usage (ca. 80%) is for the crossing of pest and disease resistance into crops, highlighting how environmental tolerance was a low priority just a decade ago.

The success of breeding attempts between a crop and its wild relatives gives rise to the concept of gene pools (Harlan and de Wet 1971). The crop primary gene pool is expected to contain the wild progenitor species, which usually freely interbreeds with the crop. The secondary gene pool contains species which can be crossed to the crop, but exhibit partial reproductive isolation, for example, the crosses generate weak or partially sterile hybrids. The tertiary gene pool contains species which can only be crossed with the crop if embryo rescue or a bridging species is used. For eggplant, the primary gene pool contains only *S. insanum*, and the extent of free interbreeding between these two species is evidenced by several reports of gene flow in the wild (Davidar et al. 2015; Page et al. 2019b). The secondary gene pool of eggplant contains potentially 48 species (although taxonomic revision may change this number) and the tertiary gene pool only a handful (Syfert et al. 2016).

Eggplant is one of the 29 species prioritized by The Millennium Seed Bank (Royal Botanic Gardens, Kew) and the Global Crop Diversity Trust for the collection and conservation of CWRs (https://www.cwrdiversity.org/), highlighting the potential importance of CWRs toward the breeding of climate-resilient eggplant.

A number of eggplant CWRs have been identified with resistance to specific pests (reviewed in Kashyap et al. 2003; Syfert et al. 2016); however, in some cases, the generation of plants beyond the F_1 has proved difficult or impossible. For example, *S. sisymbriifolium* Lam. and *S. torvum* Sw. are resistant to *Ralstonia* and *Fusarium* wilts and root-knot nematodes (*Meloidogyne* spp.) and attempts have been made to cross these species with eggplant. In one case, F_1 hybrids between *S. sisymbriifolium* and *S. melongena* produced sterile seeds (Collonnier et al. 2003) and crosses between *S. torvum* and *S. melongena* could only be produced using embryo rescue (Bletsos

et al. 1998; Kumchai et al. 2013) or protoplast fusion (Jarl et al. 1999). Backcrosses between *S. torvum* x *S. melongena* F₁s and the parents were only possible when *S. melongena* was the male parent, and even then only some eggplant cultivars were successful fathers (Bletsos et al. 1998).

Better success has come from crossing two *Fusarium* wilt-resistant species, *S. incanum* L. (Lester and Kang 1998; Plazas et al. 2016) and *S. violaceum* Ortega (Rao and Kumar 1980, named *S. indicum* L. in their study), with *S. melongena*. The variable success of multiple attempts at the former cross, however, highlights how there can be extensive variability observed by different authors (reviewed in Daunay et al. 2019). Some successful crosses have been made between *S. linnaeanum*, a species with resistance to *Verticillium* wilt, and *S. melongena*; however, only one of four eggplant cultivars would successfully cross with *S. linnaeanum* (Liu et al. 2015).

While being less-studied than pest and pathogen resistance, the development of eggplant varieties with improved or novel environmental tolerances will be crucial to managing the risks associated with climate change. The large natural distribution of eggplant's progenitor, *Solanum insanum* (Ranil et al. 2017; Fig. 4.1), as well as other related species, for example, *S. campylacanthum*, suggests that different populations of these species are likely to be locally adapted (Knapp et al. 2013). Some
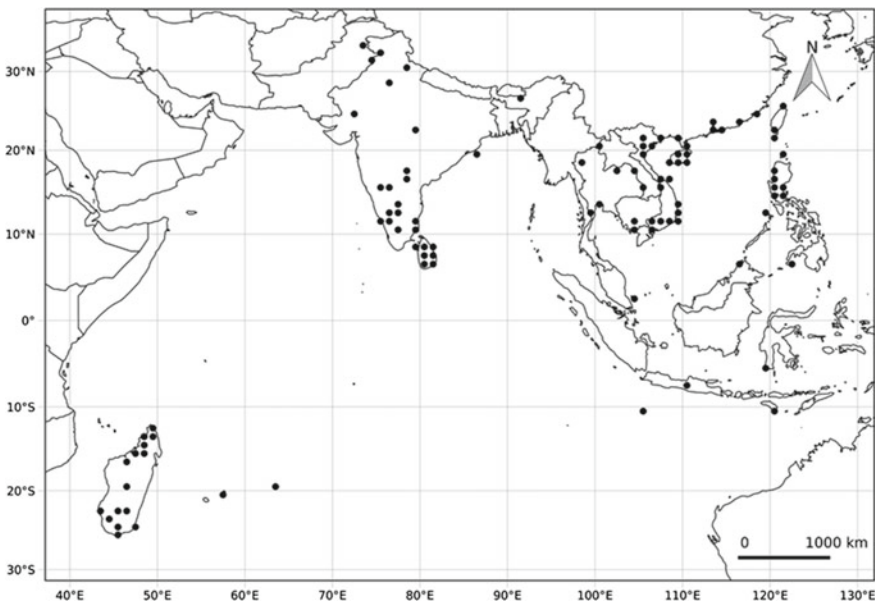
Fig. 4.1 Distribution of *S. insanum*, the wild progenitor of Asian eggplant, *S. melongena* according to herbarium collections observed by Ranil et al. (2017). Gaps in the distribution reflect gaps in collecting efforts and/or countries where herbaria have not been thoroughly examined. Figure taken from Ranil et al. (2017) under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/)

populations could therefore contain alleles at genes involved in adaptation to temperature, precipitation, and other stresses. Identifying adaptive variation in these species would be a significant first step in selecting material for breeding with eggplant. It is noteworthy that *S. campylacanthum* is a tetraploid, whereas *S. melongena* and many of the CWRs are diploid (Page et al. 2019b); hence, breeding attempts with *S. campylacanthum* might be met with initial sterility problems. Drought-tolerant *S. elaeagnifolium* (Christodoulakis et al. 2009; Fita et al. 2015) could not be crossed with eggplant by Plazas et al. (2016), but a single fruit with a small number of viable embryos was produced by Kouassi et al. (2016).

Significant advances have been made recently in regard to the detailed phenotyping of eggplant CWRs and (eggplant x CWR) F_1 hybrids (Kaushik et al. 2016; Fig. 4.2) and using these F_1 hybrids to generate backcross populations to eggplant (Kouassi et al. 2016). Although phenotyping of these crosses so far is limited to morphological descriptors with obvious agronomic benefits (for example, fruit size and shape), some of the traits might be of adaptive value in climate change scenarios (e.g., spininess/prickliness as herbivore deterrent and plant height under abiotic stress; Fig. 4.2).

The generation of backcross populations has utilized a range of CWRs, including the progenitor species *S. insanum*, as well as *S. anguivi*, *S. dasyphyllum*, *S. incanum*, *S. lichtensteinii*, and *S. tomentosum* (Kouassi et al. 2016). These species have several important traits which could be of adaptive value, including resistance to *Ralstonia* (*S. anguivi* [Schippers 2002]), drought tolerance (*S. incanum* [Daunay 2008; Lester and Hasan 1991] and *S. lichtensteinii* [Vorontsova and Knapp 2012]), and salinity tolerance/resistance to Verticillium wilt (*S. linnaeanum* [Daunay et al. 1991; Liu et al. 2015]). Genetic mapping in *S. linnaeanum* x *S. melongena* F2 populations has provided knowledge concerning the genetic basis of agronomic phenotypes (Doganlar et al. 2002b) and Verticillium resistance (Sunseri et al. 2003). Recombinant inbred lines (RILs) from the cross between *S. melongena* and *S. linnaeanum* used by Doganlar et al. (2002a, b) have been developed (M-C Brand-Daunay, personal communication).

An introgression line (IL) population is being developed in which *S. incanum* genome fragments are present in a *S. melongena* background, and preliminary phenotyping indicates that drought tolerance and other valuable traits are variable (Gramazio et al. 2017).

An analysis of drought tolerance (specifically the maintenance of growth under a 50% water deficit) in eggplant and CWRs was undertaken by Fita et al. (2015) in which nine eggplant varieties and six CWRs were investigated. One eggplant accession exhibited good tolerance to water deficit as did the tertiary gene pool species *S. elaeagnifolium*. Interestingly, tolerance was afforded by different mechanisms in different genotypes, intimating that crosses between these types could afford an even greater level of drought tolerance. Root vigor and plant architecture are also being investigated in *S. elaeagnifolium–S. melongena* crosses, with the potential for these traits to be linked to the observed drought tolerance (Garcia-Fortea et al. 2019).
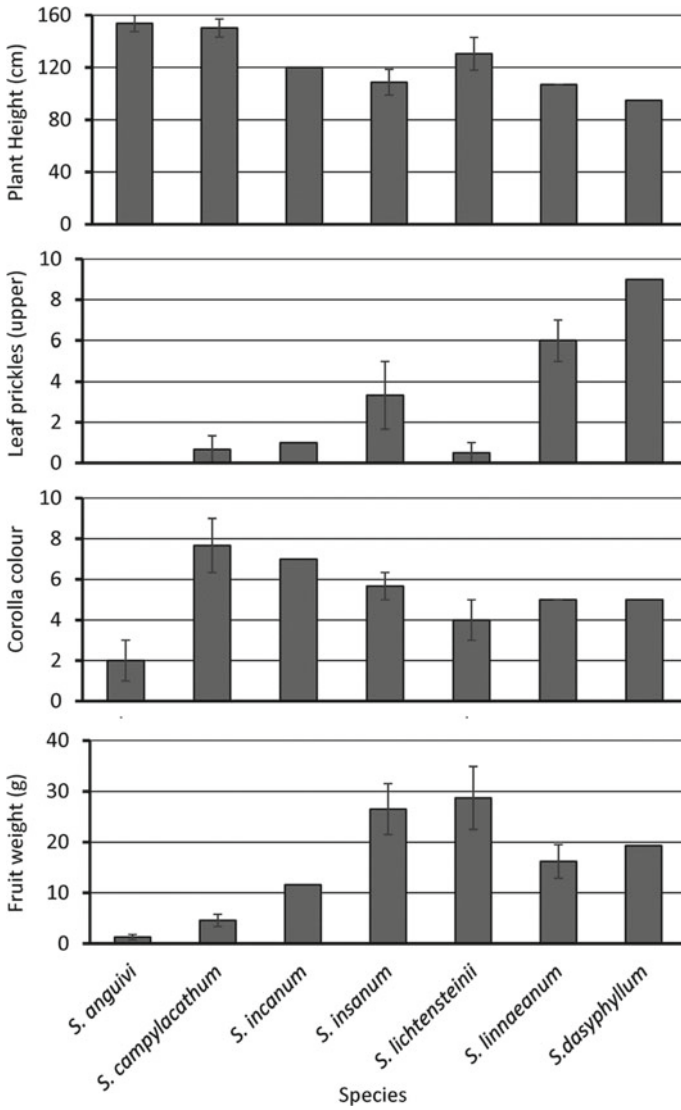
Fig. 4.2 Average (± SE) values for potentially adaptive traits based on accession means for several wild relatives of cultivated eggplant. Bars without SE are based on a single accession. Data taken from Kaushik et al. (2016) under the terms of the Creative Commons Attribution License (CC BY)

4.5 Mutational/Transgenic Approaches to Develop Climate-Resilient Eggplant

4.5.1 Mutagenic Approaches

A range of approaches have been applied to eggplant to induce mutations. Several studies have demonstrated morphological mutants, and in some cases these have led to the genetic characterization of pathways involved in these traits.

Of relevance to this article are fruit color mutants, which potentially have altered nutritional benefits (Xiao et al. 2016, 2017a). Xiao et al. have identified white, green, and black-purple fruits in a mutagenized population of the purple-fruited eggplant and demonstrated their anthocyanin contents differed. In addition, a number of dwarfing mutants were identified (Xiao et al. 2017a), and these could be resilient to lower water input, although was not tested, and may depend on the pathway which has been affected by the mutation (Lafitte et al. 2006). In another study, the total number of fruit was reduced in mutagenized eggplant populations, although the mass and size of fruits were generally increased (Prakash and Kumar 2018).

Improving eggplant biotic and abiotic tolerances through mutagenesis, however, is untested currently.

4.5.2 Transgenic Approaches

Eggplant is relatively amenable to *Agrobacterium*-mediated transformation, and this has been used since the late 1980s. Most studies have utilized information from other crops to identify suitable target genes for transformation, and have, in general, focused on pest and pathogen resistance. Early studies demonstrated that mutated forms of the *Bt* toxin from *Bacillus*, when transformed into eggplant, provided resistance to Colorado potato beetle, a major European and North American eggplant pest (Arpaia et al. 1997) and shoot and fruit borer (Kumar et al. 1998). In another study, resistance to the root-knot nematode *Meloidogyne* was conferred by the transformation of eggplant with the rice cystatin locus (Papolu et al. 2016).

In terms of resistance to abiotic stresses, one of the earliest successes in eggplant was the improved drought, chilling, and salinity tolerance in eggplants transformation with bacterial *mannitol-1-phosphodehydrogenase* (*mtlD*; Prabhavathi et al. 2002; Table 4.1). This study highlights the observation, which has been made in other crops too (reviewed in Golldack et al. 2014), that the genetic basis of different stresses maybe be identical, similar, or at least share some of the genetic components; thus, development of germplasm resistant to one stress may be in addition tolerant of other stresses. What was probably less expected was that the mannitol-producing eggplants also exhibited increased tolerance to a range of fungal wilts (Prabhavathi and Rajam 2007).

Table 4.1 Fresh weight (mean ± SE) for eggplant *mtlD* T1 transgenic seedlings (M) and untransformed controls grown in test tubes containing vermiculite: soil mix (1:1) and one-tenth MS liquid medium for 1 month with 200 mM NaCl (salt stress) and 10% PEG (drought)

	Salt		Drought	
	Seedling height (cm)	Fresh weight (mg)	Seedling height (cm)	Fresh weight (mg)
Control (with stress)	7.33 ± 0.33	0.026 ± 0.003	7.73 ± 0.37	0.03 ± 0.005
Control (no stress)	10.00 ± 0.00*	0.20 ± 0.003*	11.00 ± 0.58*	0.16 ± 0.005*
M1	9.66 ± 0.33*	0.24 ± 0.03*	7.13 ± 0.09	0.14 ± 0.005*
M8	8.66 ± 0.07*	0.21 ± 0.005*	6.16 ± 0.72	0.09 ± 0.005*
M9	9.21 ± 0.08*	0.18 ± 0.02*	8.77 ± 2.51	0.17 ± 0.01*
M16	9.71 ± 0.23*	0.16 ± 0.005*	7.71 ± 0.33	0.06 ± 0.01*

*indicates significant difference from control (with stress) at 5% level. Modified from Prabhavathi et al. (2002) with permission from Springer-Nature

Other studies have shown that a range of foreign genes can be transformed into eggplant to increase their tolerance to abiotic stresses. Transfer of *isopenty-transperase* (*IPT*) under control of a senescent-specific promoter delayed senescence and increased tolerance to drought and chilling (Xiao et al. 2017b). Transgenic introduction of a wheat Na +/H+ antiporter encoded by the *TaNHX2* gene into eggplant increased tolerance of saline conditions (Yarra and Kirti 2019).

The public perception of transgenic technologies, the widespread ban on transgenic foods, and the extensive assessments on nontarget organisms required, probably limits the study of eggplants transgenics to identifying candidate genes and for scientific curiosity, and may explain why relatively little research is currently being undertaken, and why alternative approaches (specifically introgression from CWRs; see above) are more common.

4.6 Other Eggplants

The scarlet eggplant (*S. aethiopicum* L.) and the Gboma eggplant (*S. macrocarpon* L.) are grown for human consumption; however, not to the same extent as *S. melongena*. The leaves of both species are also consumed. Both are in the secondary gene pool of *S. melongena*, and results from crosses between the cultivated eggplants are extremely variable (reviewed in Daunay et al. 2019). Crosses between *S. aethiopicum* and the other two species generally result in a vigorous F_1 with fertility from sterile to partially fertile, whereas the cross between *S. macrocarpon* and *S. melongena*, the F_1,

is generally weak. However, in all cases, the F_1 have set seed, and/or later generation crosses have been obtained (reviewed in Daunay et al. 2019).

Phenotyping of *S. aethiopicum* and *S. macrocarpon* has been carried out on smaller number of accessions than phenotyping of the Asian eggplant, however, has revealed some important characters that distinguish these species (Plazas et al. 2014; San José et al. 2016). In addition, it was found that the two African eggplants had greater fiber and vitamin C content than Asian eggplant, and that *S. macrocarpon* contains more phenolics (powerful antioxidants) than *S. aethiopicum* (San José et al. 2016). The African eggplants are differently adapted to *S. melongena* and could provide some interesting focal species with respect to resistance to warmer climate and varying precipitation.

Overall it seems that these African eggplants contain certain nutritional benefits over *S. melongena*; however, ensuring that these properties are maintained under climate change-relevant environments has rarely been assessed. However, in one study, the content of various carotenoids in multiple accessions of the two African eggplants was assessed in control and drought-affected plants (Mibei et al. 2017). The study revealed that carotenes, chlorophylls, neoxanthin, and violaxanthin decreased under water stress, however zeaxanthin content increased under stress and lutein was unaffected. This valuable insight tells us that climate change could affect the nutrient content of these eggplants, and more attention should be paid to the effect of the changing climate on nutritional compounds.

Solanum aethiopicum and *S. macrocarpon* exhibit good resistance to *Fusarium* (Daunay et al. 1991) and the former has been crossed with Asian eggplant via protoplast fusion and callus regeneration to make segregating populations (Toppino et al. 2008). The analysis identified a single locus controlling resistance to *Fusarium* and PCR (polymerase chain reaction)-based markers were developed to allow the expedited breeding of further backcross progenies.

Interestingly, the potential for *S. melongena* to improve the African eggplants has not been studied, but hypothetically, introgression of *S. melongena* alleles into *S. macrocarpon* could be used to increase variation in fruit shape, which is currently rather invariant (Page et al. 2019a).

4.7 Future Perspectives

From this review, it appears there are many research avenues being explored which assess the ability of eggplant to cope with future climates, and to identify adaptive germplasm. However, the research also appears to be progressing at a relatively slow pace, compared to other crops, which poses a risk to the development of climate change-resilient eggplant which could be needed in just the next few decades. Until recently, the eggplant genome available (Hirakawa et al. 2014) was quite highly fragmented, whereas it is anticipated that a significantly better assembly will be made available soon (Gramazio et al. 2018).

I highlight here three research avenues which should be prioritized for the enhancement of eggplant tolerance to future climates.

4.7.1   Development of Introgression Lines

The development of introgression lines (ILs; crop varieties with introgressed genome segments from a related species), has the potential to help gain an understanding of the genetic basis of adaptive traits, and serve as pre-breeding material. These are only just being developed in eggplant (Kouassi et al. 2016), and are only well-developed for one IL population (Gramazio et al. 2017). In contrast, IL populations are extensively used in understanding adaptive phenotypes in tomato (e.g., Eshed et al. 1996; Fridman et al. 2000) and were developed over 25 years ago (Eshed et al. 1992).

The development of these lines is relatively time-consuming, but once developed they can be "immortalized" as populations that the research community can share. This means multiple investigations into adaptive traits can take place in the same germplasm. Because the presence of genome sequences greatly aids in the identification of genetic variants underlying said traits, the parents of the ILs can be sequenced and then used as a resource by multiple groups, reducing the need for different research groups to obtain genome sequences of multiple IL populations.

Early steps have been taken to develop ILs in a range of wild x cultivated eggplant crosses (Kouassi et al. 2016) and it is hoped that these can be developed further. Utilizing genetic markers and targeting specific introgressions, it can be relatively quick to recover cultivar-like plants containing the wild-like trait of interest (Tanksley and McCouch 1997).

4.7.2   Conservation and Study of Eggplant Crop-Wild Relatives

Future climates will require a range of adaptations not present in the eggplant gene pool and introgression from the wild is a potential source of these adaptations. As made evident earlier in this chapter, eggplant crop-wild relatives (CWRs) host a range of important adaptations that could be utilized in breeding eggplant for future climates. This ranges from drought (e.g., *S. lichtensteinii* and *S. incanum*) and salinity tolerance (*S. linnaeanum*) to the tolerance of a range of pathogens (*S. torvum* and *S. linnaeanum*). In some cases, adaptive traits from CWRs have been introgressed into eggplant (Liu et al. 2015; Rotino et al. 2014), although these studies are not common. Further studies of wild species are needed; however, it is also important that a range of germplasm from the more widespread species which inhabit diverse environments

(e.g., *S. campylacanthum* and *S. insanum*) are investigated, instead of relying on one or a few accessions.

This may be difficult currently because a number of eggplant CWRs are poorly represented in gene banks (Taher et al. 2017). In a systematic survey of eggplant CWRs, cross-referenced with gene banks, it was recently shown that several eggplant CWRs should be considered high priority for future collection, and this included a number of species previously mentioned in this review which are known for their biotic and abiotic tolerances (Syfert et al. 2016). In addition, 14 eggplant CWRs are threatened or near-threatened in the wild (Syfert et al. 2016). Given that, in other crop-CWR groups, climate change is estimated to have a significant negative impact (Jarvis et al. 2008), it is important we identify and conserve eggplant CWRs now.

4.7.3 Functional Analysis of Adaptive Traits

While ILs and large mapping populations aid in the understanding of QTLs underlying traits of interest, gaining knowledge of the specific genes controlling these traits would provide several advantages.

First, identifying the gene controlling an adaptation is useful in applying MAS to breeding material. In MAS, large numbers of crosses can be rapidly screened for the presence of molecular markers flanking QTLs of interest, and those crosses not containing the markers (and therefore the QTL) removed early on, expediting the process.

Second, we can screen for novel variation across germplasm (both eggplant and the CWRs) and assess if the same or different genes control the trait of interest. If different genes control the same trait in different germplasms, then there is the potential to further increase tolerance or resistance by introgressing from multiple sources.

Third, to employ modern gene editing technologies, one needs to understand the genetic basis of the trait being investigated. CRISPR/Cas9, a widely employed gene editing technology (Jinek et al. 2012), requires guide RNAs to be designed which complements the locus of interest, upon which the Cas9 endonuclease makes a targeted lesion.

Understanding the genetic basis of certain traits in eggplant is being carried out, but is generally in its infancy, especially when comparing to other crops. Successful identification of genes controlling resistance to Fusarium wilt has been carried out (Mutlu et al. 2008; Boyaci et al. 2012), and functional characterization of bacterial wilt resistance is a current focus of study (Xiao et al. 2015; Morel et al. 2018).

4.8 Conclusions

In order to prepare for a warmer climate, more prone to droughts and floods, and with the potential for novel pests and pathogens to become a threat, it is vital that current research identifies crop varieties and CWRs with adaptive tolerance to these stresses. While this is being carried out for eggplant, it appears that progress is slow and, until very recently, has lacked behind other crops. While eggplant is not globally one of the most important vegetables, it plays a significant part in the diet of many countries and cultures, and any loss of production could harm these populations. In this review, I have highlighted what we already know about eggplant tolerances that may be of use in a future climate, and also highlight some important research avenues which should be prioritized.

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