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1 **Conventional and new genetic resources for an eggplant Green Revolution**

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20 Running title: Eggplant conventional and new genetic resources

21

22 **Highlight**

23 This review emphasizes the importance of genetic resources, including germplasm

24 accessions and new experimental populations, for a Green Revolution in eggplant in the

25 context of climate change.

Abstract

Eggplant (*Solanum melongena*) is a major vegetable crop that has yet to undergo a Green Revolution. It is closely related to over 500 species of *Solanum* subgenus *Leptostemonum* belonging to the primary, secondary, and tertiary genepools and exhibits a wide range of characteristics, including adaptive traits to climate change, that are useful for eggplant breeding. Germplasm banks worldwide hold more than 19,000 accessions of eggplant and related species, but the exploration of germplasm collections has generally been limited. Nonetheless, eggplant breeding using the cultivated *S. melongena* genepool has yielded significantly improved varieties. However, to overcome current breeding challenges and adaptation to climate change, a qualitative leap forward in eggplant breeding is necessary. The initial findings from introgression breeding in eggplant indicate that unleashing the diversity present in eggplant relatives from different genepools can greatly benefit the eggplant Green Revolution. The recent creation of new genetic resources, such as mutant libraries, core collections, recombinant inbred lines, and sets of introgression lines will be another crucial element of the eggplant Green Revolution, which will require the support of new genomics tools and biotechnological developments. The systematic utilization of eggplant genetic resources supported by international initiatives will be critical for the much-needed eggplant Green Revolution.

Keywords: eggplant, genepools, genetic resources, germplasm banks, Green Revolution, introgression breeding, *Solanum melongena*, wild relatives

Introduction

Eggplant (*Solanum melongena* L.), also known as common eggplant, brinjal or aubergine, was domesticated from its wild ancestor *S. insanum* L. around 9,000-10,000 years ago in the region that includes the Indian subcontinent and southeast Asia (Page *et al.*, 2019*a*). Eggplant is globally one of the most important vegetable crops, ranking sixth in production among vegetables after tomato, onion, watermelon, cucumber and cabbage (FAOSTAT, 2023). Its global production has increased by 24.0% in the last decade, from $47.3 \cdot 10^6$ t in 2012 to $58.6 \cdot 10^6$ t in 2021 (FAOSTAT, 2023). As a warm-loving crop, it is mostly cultivated in tropical, subtropical and temperate regions of the world, with most of its production coming from East Asia, the Indian subcontinent, Southern Asia, the Middle East and the Mediterranean basin. In these regions, eggplant is a common constituent of the diet, providing significant amounts of K, P and Cu, as well as high concentrations of bioactive phenolics beneficial for human health (Plazas *et al.*, 2013; Rosa-Martínez *et al.*, 2021). However, agricultural production in main eggplant cultivation areas is expected to be strongly affected by climate change (del Pozo *et al.*, 2019; Habib-ur-Rahman *et al.*, 2022). Increased spells of extreme events such as intense drought periods may have a dramatic impact on crops sensitive to water stress, such as eggplant (Plazas *et al.*, 2022).

Despite its importance as a prominent vegetable crop in many areas, research on eggplant lags behind other major vegetable crops. For instance, tomato breeding programs have made extensive use of genetic resources, including the introgression of multiple genes from crop wild relatives (CWRs) that have been incorporated into modern cultivars (Díez and Nuez, 2008; Schouten *et al.*, 2019). Conversely, to our knowledge, until now only a few concrete breeding programs involving introgression of useful traits have been carried out aimed at improving the resistance to the fungal wilts *Fusarium oxysporum* and

Verticillium dahliae by exploiting the sources residing in the two relatives *S. aethiopicum* (Toppino *et al.*, 2007, 2008, 2009) and *S. linnaeanum* (Acciarri *et al.*, 2007), respectively, although no eggplant cultivars carrying the introgressions have been released so far (Toppino *et al.*, 2021).

In addition to eggplant, two other related minor crops, namely the scarlet eggplant (*S. aethiopicum* L.) and the gboma eggplant (*S. macrocarpon* L.), were domesticated in Africa (Page *et al.*, 2019*b*) and are mostly grown in the sub-Saharan region (Schippers, 2000). Although they have local importance, they are relevant crops, particularly *S. aethiopicum*, in some parts of the world such as Brazil and the Caribbean, as well as in Southern Italy, where a Protected Denomination of Origin exists for the *S. aethiopicum* landrace 'Melanzana Rossa di Rotonda' (Schippers, 2000; Sunseri *et al.*, 2010). Little research has been performed on these two minor African eggplant species. However, given that they share many characteristics, pathogens and pests with the common eggplant and the three domesticated eggplant species are cross-compatible (Bletsos *et al.*, 2004; Oyelana and Ugborogho, 2008; Rotino *et al.*, 2014), they are genetic resources of interest to each other.

Eggplant displays a wide morphological diversity, even within a single varietal group, particularly for fruit traits such as size, color and shape (Figure 1), as well as for agronomic traits and adaptation to different environments (Cericola *et al.*, 2013; Taher *et al.*, 2017; Chapman, 2020; Kouassi *et al.*, 2020; Ro *et al.*, 2022; Salinier *et al.*, 2022; Toppino *et al.*, 2022). The diversity present within the cultivated eggplant is a valuable genetic resource of great interest for eggplant breeding and has allowed the development of significantly improved modern cultivars (Daunay and Hazra, 2012). However, as occurs with many other vegetables, this high morphological diversity is mostly the consequence of genetic variation in a few major genes, particularly those related to fruit

101 traits (Daunay *et al.*, 2004; Portis *et al.*, 2015; Toppino *et al.*, 2016; Mangino *et al.*, 2021;

102 Arrones *et al.*, 2022; Guan *et al.*, 2022), and the overall genetic variation of the crop is

103 narrow (Acquadro *et al.*, 2017; Barchi *et al.*, 2019*a*; Liu *et al.*, 2019). Therefore, other

104 cultivated eggplants (*S. aethiopicum* and *S. macrocarpon*) and wild eggplant relatives

105 represent a largely unexplored genetic resource of paramount interest to eggplant breeders

106 (Oyelana and Ugborogho, 2008; Prohens *et al.*, 2012; Toppino *et al.*, 2021).

107

108 **Eggplant breeding challenges for the present and the future: the need for a Green**

109 **Revolution**

110 Although eggplant yield increased from a global average of 10.2 t/ha in the 1961-

111 1970 decade to 28.0 t/ha in the 2012-2021 decade (FAOSTAT, 2023), the Green

112 Revolution that occurred in other major staple and vegetable crops (Hedden, 2003; Díez

113 and Nuez, 2008) has not taken place yet in eggplant. Breeding advances and actual

114 exploitation of genetic resources in eggplant, particularly those from related species, are

115 not comparable to those obtained in other major vegetable crops such as tomato (Schouten

116 *et al.*, 2019). Despite the narrow genetic diversity and the availability of only a few CWRs

117 exploitable for tomato, considerable broadening of the genetic base and genetic advances

118 contributing to the tomato Green Revolution were achieved through introgression

119 breeding. Among the achievements made using wild relatives as donors, the introgression

120 of multiple genes for tolerance to diseases and fruit quality traits, the development of

121 heterotic hybrids, the improvement of shelf-life, the diversification of varietal types, the

122 adaptation to multiple environments (Díez and Nuez, 2008), enabled the production of a

123 large number of highly productive tomato varieties of many different typologies, resistant

124 to the major diseases and suited to different environments.

5

Several eggplant commercial varieties display undesirable traits for modern markets and distribution chains, suggesting that eggplant breeding needs a leap forward to bring itself to the level of other vegetable crops. As an example, many cultivars display prickles on the calyx of the fruit, which not only represents a nuisance for farmers, marketers, and consumers but also results in the damage of fruits due to their prickling during storage and manipulation, leading to postharvest losses (Prohens *et al.*, 2009; Miyatake *et al.*, 2020).

Like tomato, eggplant is self-compatible and mostly autogamous (Daunay and Hazra, 2012), Indeed, in a study involving eggplant and tomato accessions genotyped by Single Primer Enrichment Technology (SPET), the heterozygosity of eggplant and tomato was reported to be 0.67% and 0.65%, respectively (Barchi *et al.*, 2019*a*), confirming the mostly autogamous reproduction of the species, which in turn impacts on the breeding methods applicable. However, high levels of cross-pollination can occur when the circumstances are favourable, such as in open field conditions with the presence of pollinators (Quamruzzaman, 2021). Avoiding cross-pollination is highly relevant for maintaining purity in the case of reproduction of landraces or germplasm accessions.

Breeding in eggplant traditionally relies on selection from both within and among landraces as well as in the development of F1 hybrids, which are predominant in high-value markets (EU Plant Variety Database, 2022). It is known since long ago that F1 hybrids in eggplant generally display heterosis for yield (Kakizaki, 1931; Sambandam, 1964) and heterobeltiosis is also common (Rodríguez-Burruezo *et al.*, 2008; Kumar *et al.*, 2020). Selection of parents for heterotic hybrids is possible by evaluating the parents' combining ability, as well as by selecting parents with high genetic distance using molecular markers (Rodríguez-Burruezo *et al.*, 2008). It is worth remembering that landraces and pure line selections with excellent yields are also available and cultivated

150 (Muñoz-Falcón *et al.*, 2009; Taher *et al.*, 2017). However, further improvement of the

151 yield potential remains a significant challenge in eggplant breeding, which could benefit

152 from the incorporation of new genetic diversity to allow additional genetic advances

153 (Muñoz-Falcón *et al.*, 2009; Daunay and Hazra, 2012).

154   One of the major current challenges in eggplant breeding is the development of

155 breeding lines with an improved tolerance or resistance to major pests and diseases

156 (Toppino *et al.*, 2021), which may cause crop losses of up to 100% (Daunay and Hazra,

157 2012; Arafa *et al.*, 2022). Eggplant is affected by numerous diseases, although the most

158 relevant in terms of economic impact is the bacterial wilt caused by *Ralstonia*

159 *solanacearum*, which is highly prevalent in tropical regions (Lebeau *et al.*, 2013; Barik

160 *et al.*, 2020). In many cases, bacterial wilt prevents eggplant cultivation unless plants are

161 grafted onto resistant rootstocks (Namisy *et al.*, 2019). Verticillium and Fusarium wilts,

162 as well as nematodes, are also important eggplant pathogens in many regions of the world

163 (Arafa *et al.*, 2022). However, unlike in tomato where the incorporation of disease-

164 resistant genes introgressed from wild relatives are crucial technical innovations for the

165 success of modern commercial varieties (Díez and Nuez, 2008; Schouten *et al.*, 2019),

166 most eggplant modern commercial varieties do not carry genes for disease resistance

167 (Srinivasan, 2009).

168   The eggplant fruit and shoot borer (*Leucinodes orbonalis*), is the most damaging

169 and difficult pest to control in the Indian subcontinent, Southern and East Asia, where

170 multiple insecticide sprays are used to partially control it (Srinivasan, 2008). This pest is

171 such a damaging and limiting factor in eggplant cultivation that two countries

172 (Bangladesh and the Philippines) have authorized the use of genetically modified *Bt*

173 eggplants expressing the cry1Ac gene from *Bacillus thuringiensis* to control the eggplant

174 fruit and shoot borer (Shelton *et al.*, 2018; Gonzalvo *et al.*, 2022). Additional pests

7

attacking *S. melongena* are spider mites, whiteflies and aphids, which affect other solanaceous crops as well (Srinivasan, 2009). To this purpose, the development of eggplant hairless materials (CleanLeaf®) has improved biological pest control in greenhouse cultivation, as the pests are more accessible to their predators and parasites.

Abiotic stresses are expected to increase in the areas where eggplant is cultivated due to climate change (Toppino *et al.*, 2022; Khalid *et al.*, 2023). Although eggplant is mildly tolerant to water and salinity stresses (Heuer *et al.*, 1986; Díaz-Pérez and Eaton, 2015; Kouassi *et al.*, 2020; Toppino *et al.*, 2022), developing new varieties with better resilience is needed, particularly in drought-prone areas or where water and soil salinity is a problem for eggplant cultivation. Tolerance to extreme temperatures is also an important breeding objective. Despite being a warm-loving plant, high temperatures affect pollen viability and fruit set (Toppino *et al.*, 2022) and heat-tolerant varieties are needed for production in the warm seasons. Tolerance to cold is also important in off-season production in temperate areas, as growth and development are arrested, and fruit set impaired (Toppino *et al.*, 2022). To this purpose, some parthenocarpic materials have been developed which can set fruit even under cold conditions affecting pollen viability (Kikuchi *et al.*, 2008). Improving water and nutrient use efficiencies is also necessary for more sustainable agriculture as well. In this context, breeding for better root systems, which is in its infancy in eggplant, can lead to more sustainable production (Chapman, 2020).

Diversification and improving fruit quality (Daunay and Hazra, 2012) represent other important challenges in breeding. Eggplant displays a large diversity of fruit sizes, shapes and colours, but unlike tomato, it is slightly available to the consumers. Furthermore, the genetics of these traits is still poorly understood, and although QTLs have been identified for fruit morphological traits (Portis *et al.*, 2015; Toppino *et al.*,

2016, 2020; Barchi *et al.*, 2019*c*; Mangino *et al.*, 2021), few causative genes have been

identified. One exception is the *APRR2* gene (Arrones *et al.*, 2022), which controls the

synthesis of fruit peel chlorophyll, as well as several genes involved in anthocyanin

synthesis (Florio *et al.*, 2021; He *et al.*, 2022; Li *et al.*, 2022). However, the causative

genes underlying other important traits for fruit appearance such as the presence of fruit

stripes, fruit netting or prickliness remain to be identified. Eggplant is one of the

vegetables with higher antioxidant and bioactive properties, resulting from its high

content of phenolic acids (Kaushik *et al.*, 2015), which unfortunately are indirectly

associated with increased browning of the fruit flesh (Mishra *et al.*, 2013; Docimo *et al.*,

2016; Kaushik *et al.*, 2017). Breeders therefore directly selected genotypes with low fruit

browning led to the indirect selection of genotypes with low content in phenolic acids

(Prohens *et al.*, 2007). To improve the phenolic acid content while limiting the effects of

browning, selection for low polyphenol oxidase (PPO) activity has been proposed (Plazas

et al., 2013). In this way, CRISPR/Cas knocking out of PPOs expressed in the fruit has

been shown to reduce fruit flesh browning (Maioli *et al.*, 2020; Kodackattumannil *et al*.,

2023)). Parthenocarpic fruit set is also of interest for reducing fruit browning, as browning

is more intense in the tissues surrounding the seeds (Sarengaowa *et al.*, 2022). Saponins

present in the fruit flesh tissues contribute to the bitterness of some materials, which is an

undesirable trait (Aubert *et al.*, 1989). However, little information is available on the

genetics of bitterness in eggplant.

One of the major drawbacks of the use of wild relatives in eggplant introgression

breeding is represented by glycoalkaloids, since eggplant CWRs often exhibit

concentrations of these metabolites above those considered safe for human consumption

(Aubert *et al.*, 1989; Rosa-Martínez *et al.*, 2022*a*). Rootstocks development is an

emerging field in eggplant breeding. Rootstocks with robust root systems have been

shown to improve yield and confer tolerance to soil diseases and abiotic stresses in eggplant (Gisbert *et al.*, 2011; Barik *et al.*, 2020). In this way, wild eggplant relatives, as well as interspecific hybrids have demonstrated a high potential as rootstocks for improving eggplant production (Sabatino *et al.*, 2018; Toppino *et al.*, 2021). For example, the eggplant wild relative *S. torvum*, which is resistant to most soil diseases and nematodes, and hybrids between eggplant and scarlet eggplant, which provide vigor and good performance under cold conditions, are used as rootstocks at the commercial level (King *et al.*, 2010; Schwarz *et al.*, 2010; Calvo-Asensio *et al.*, 2014; Ranil *et al.*, 2015).

Unlike tomato and other major vegetable crops, the systematic exploitation of genetic diversity and the use of modern technologies, such as molecular markers, for introgression breeding in eggplant have not sufficiently benefited the development of highly productive and resilient varieties with traits such as disease and pest resistance, yield heterosis through genetic diversity, tolerance to abiotic stresses, including improved rootstocks, removal of undesirable traits such as prickliness, and the development of long-shelf life or seedless materials (Daunay and Hazra, 2012; Chapman, 2020; Arafa *et al.*, 2022; Toppino *et al.*, 2022). To achieve an eggplant Green Revolution, systematic efforts must be made to efficiently and rapidly utilize the high genetic diversity present in eggplant and its close wild relatives (CWRs). In particular, the large genetic diversity present in CWRs has been barely exploited and used in eggplant breeding. Moreover, speed breeding techniques, which have proven to be an efficient tool for reducing generation cycles in tomato and Capsicum pepper (Ayenan *et al.*, 2019; Liu *et al.*, 2022; Gimeno-Páiz *et al.*, 2023), are currently absent in eggplant breeding and should be developed for the eggplant Green Revolution.

3. The eggplant genepools and their potential for eggplant breeding enhancement

The vast number of eggplant relatives, with their diverse phenotypic (Figure 1) and physiological characteristics and environmental adaptation differences greatly expands the access to exotic and wild genetic diversity for eggplant breeding. Indeed, eggplant can be hybridized with many wild relatives from the subgenus *Leptostemonum*, which contains over 500 species found in all tropical and subtropical regions of the world, exhibiting specific adaptations to a wide range of environments (Vorontsova and Knapp, 2016; Knapp *et al.*, 2019). Conventional breeding methods to introgress the traits of interest in eggplant from allied species were used only sporadically, as many wild relatives displayed partial cross-compatibility with the cultivated species, thus often hampering their effective employment for the crop improvement (Ano *et al.*, 1991; Bletsos *et al.*, 1998). Nevertheless, interspecific hybrids between eggplant and wild relatives have been obtained through sexual crosses using several wild and allied species (Daunay and Hazra, 2012; Rotino *et al.*, 2014; Premabati Devi *et al.*, 2015; Plazas *et al.*, 2016; Daunay *et al.*, 2019); This includes species from the Old World (Rotino *et al.*, 2014; Plazas *et al.*, 2016; Toppino *et al.*, 2021), as the American species such as *S. elaeagnifolium, S. torvum*, *S. viarum* and *S. sisymbriifolium* (Daunay and Hazra, 2012; Rotino *et al.*, 2014; Kouassi *et al.*, 2016; Plazas *et al.*, 2016), which diverged from eggplant approximately 6.7, 7.7, 8.3 and 8.9 million years ago, respectively (Särkinen *et al.*, 2013). However, most of the studies have been conducted for taxonomic purposes and preliminary breeding works and no information is available about the outcomes of possible attempts of further backcrosses with eggplant (Toppino *et al.*, 2021). The accessibility for breeding of the available genetic diversity of eggplant-related species depends mainly on the genepool (primary, secondary, or tertiary) they belong to (Prohens *et al.*, 2017), although there are significant differences within the secondary and tertiary

genepools in the crossability and ease of hybridization and subsequent introgression breeding (Kouassi *et al.*, 2016; Plazas *et al.*, 2016).

The primary genepool (GP1) of eggplant consists of the cultivated eggplant *S. melongena* and its ancestor *S. insanum* L. (Syfert *et al.*, 2016), which was previously considered a botanical variety of *S. melongena* (*S. melongena* var. *insanum*) (Knapp *et al.*, 2013; Ranil *et al.*, 2017). Although two genetic groups, named Occidental (predominantly grown in the Middle East, Europe and Africa) and Oriental (mostly grown in the Indian subcontinent, Southeast Asia and eastern Asia), have been recognized within *S. melongena* (Vilanova *et al.*, 2012; Cericola *et al.*, 2013) no genetic barriers exist between them or with *S. insanum*, and hybridization within and between *S. melongena* groups or between *S. melongena* and *S. insanum* is equally successful (Plazas *et al.*, 2016; Daunay *et al.*, 2019). *Solanum insanum* grows as a wild or weedy species in a wide range of environments in its natural distribution (Indian subcontinent, Southeast and Eastern Asia, Madagascar and some Indian Ocean islands) (Ranil *et al.*, 2017). In these areas, *S. melongena* and *S. insanum* form a genetic continuum with intermediate forms resulting from hybridization, and genetic flow between both species has been documented (Knapp *et al.*, 2013; Davidar *et al.*, 2015; Mutegi *et al.*, 2015; Page *et al.*, 2019*a*). Despite its high potential interest (Table 1), *S. insanum* remains unexploited for the development of improved cultivars (Ranil *et al.*, 2017). Nonetheless, due to the natural genetic flow between *S. insanum* and *S. melongena*, it is plausible that some unknown introgressions from the former have been inadvertently incorporated and utilized in eggplant breeding. This species, therefore, represents a reservoir of potential superior untapped alleles for traits of interest, including those related to climate changes, which could be easily incorporated into the *S. melongena* genepool.

The secondary genepool (GP2) is very broad in terms of number of species (Eggplant clade, Anguivi grade, and Climbing clade), geographic distribution (Africa, Indian subcontinent, Southeast and Eastern Asia), and environmental adaptation (from desertic areas to wet forests; from sea level to 3,300 m) (Vorontsova and Knapp, 2016; Syfert *et al.*, 2016; Knapp *et al.*, 2017). The wild ancestor of eggplant (*S. insanum*) diverged from all GP2 species between 1.5 and 4.6 million years ago (Särkinen *et al.*, 2013). Within the GP2, eggplant hybridization and introgression are easier with Eggplant clade species, showing a higher hybridization success, hybrid seed viability and pollen fertility than in the *Anguivi* grade and Climbing clade (Rotino *et al.*, 2014; Plazas *et al.*, 2016). Generally, embryo rescue is unnecessary to obtain hybrids and backcrosses with *S. melongena*, although hybridization with GP2 species is more challenging than with GP1 materials (Kouassi *et al.*, 2016; Plazas *et al.*, 2016; Daunay *et al.*, 2019) and sometimes alternative breeding strategies of somatic hybridization were necessary to obtain fertile hybrids (Rotino *et al.*, 1998; Särkinen *et al.*, 2013). Several species belonging to the GP2 such as *S. anguivi*, *S. dasyphyllum*, *S. incanum*, *S. linnaeanum* and *S. tomentosum* (Table 1) have been identified as of great interest for eggplant breeding due to their tolerance to biotic and abiotic stresses and high contents of bioactive compounds beneficial for human health (Syfert *et al.*, 2016; Kaushik *et al.*, 2017; Arafa *et al.*, 2022; Toppino *et al.*, 2022) and for some of them, introgressed and backcrossed population have been obtained, while many GP2 species remain unexplored. Moreover, the two cultivated eggplants (*S. aethiopicum* and *S. macrocarpon*) are also valuable for eggplant breeding, as aside from presenting characteristics of interest for eggplant breeding, they display the typical traits associated to the domestication syndrome, which facilitates their use in breeding (Särkinen *et al.*, 2013; Plazas *et al.*, 2014).

Hybridization of eggplant with around 20 GP2 species has been achieved, including the *Anguivi* grade cultivated species *S. aethiopicum* and *S. macrocarpon*, as well as with *S. linnaeanum*, *S. incanum* and *S. tomentosum* (Daunay and Hazra, 2012; Särkinen *et al.*, 2013; Rotino *et al.*, 2014; Plazas *et al.*, 2016; Daunay *et al.*, 2019; Toppino *et al.*, 2021). Different kinds of introgression materials were obtained with eggplant relatives from the GP2, mostly aimed at exploiting resistance traits to pathogens and adverse environmental conditions. The tertiary genepool (GP3) is genetically very diverse, including species found in Africa and Madagascar, as well as in Australia, Pacific Islands, Asia and in distant American species of subgenus *Leptostemonum* (Figure 3) (Knapp *et al.*, 2013; Syfert *et al.*, 2016). As expected, the success of hybridization of eggplant with GP3 species is very low, although attempts of obtaining interspecific hybrids with eggplant have been reported and achieved only in a few cases, including the Madagascar species *S. pyracanthos* and the American *S. elaeagnifolium*, *S. sisymbriifolium*, *S. torvum*, and *S. viarum* (Rotino *et al.*, 2014; Kouassi *et al.*, 2016; Plazas *et al.*, 2016; Daunay *et al.*, 2019). In many cases, embryo rescue was necessary, especially in crosses with American species. Although interspecific hybrids between eggplant and American species are highly sterile, some backcrosses to eggplant were obtained when the interspecific hybrid with *S. elaeagnifolium* was used as maternal parent, suggesting the possibility to exploit previously untapped GP3 genetic material for introgression breeding (Plazas *et al.*, 2016; García-Fortea *et al.*, 2019).

Overall, the large genetic, phenotypic and physiological diversity present in the three genepools represents an enormous potential for eggplant breeding, which has been barely explored, particularly in the case of wild species (Daunay and Hazra, 2012; Rotino *et al.*, 2014; Taher *et al.*, 2017; Toppino *et al.*, 2021, 2022; Arafa *et al.*, 2022; Salinier *et al.*, 2022). Unlocking this high diversity will be essential for developing new materials

347 with adaptation to climate change and meeting the urgent need for an eggplant Green

348 Revolution.

349

350 **4. Eggplant germplasm collections**

351 Based on the recent Global Strategy for the Conservation and Use of Eggplants

352 (Solberg *et al.*, 2022), 19,020 accessions of cultivated eggplants and relatives are

353 conserved in 110 germplasm banks and collections around the world (Figure 3). (FAO,

354 2010)The largest genebank collections of eggplant are conserved at the National Bureau

355 of Plant Genetic Resources (India; 4,236 accessions), the World Vegetable Center (an

356 international organization with eggplant germplasm collections headquartered in Taiwan;

357 3,036 accessions), the INRAE Genebank of France (2,388 accessions), the National

358 Genebank for Vegetable Germplasm Resources of China (1,601 accessions) and the

359 NARO Genebank of Japan (1,501 accessions) (Taher *et al.*, 2017; Salinier *et al.*, 2022;

360 Solberg *et al.*, 2022).

361 When considering the Genesys and WIEWS databases, most of the conserved

362 materials correspond to cultivated *S. melongena* (12,665 accessions), *S. aethiopicum*

363 (1,004) and *S. macrocarpon* (208) while the wild species of the GP1, GP2 and GP3

364 genepools are much less represented (2,351 accessions in total) (Solberg *et al.*, 2022).

365 Among the wild species, *S. incanum* is the most abundant (GP2; 423 accessions),

366 followed by *S. torvum* (GP3; 358 accessions), *S. aculeatissimum* (GP3; 210 accessions),

367 *S. virginianum* (GP2; 187 accessions) and *S. grandiflorum* (GP3; 184 accessions).

368 However, apart from these five wild species, the number of remaining wild species

369 accessions from GP2 and GP3 of eggplant is dramatically low, with just 14 species having

370 more than 10 accessions conserved, while for many others no accessions are conserved

371 at all (Solberg *et al.*, 2022). This is particularly evident for the 14 eggplant CWRs

classified as at risk of extinction (one critically endangered, nine threatened, three near threatened, and one extinct in the wild), for which no accessions are conserved in germplasm banks for six of them (including *S. ruvu*, which is considered extinct in the wild), and for the remaining, up to just four accessions are conserved *ex situ* (Syfert *et al.*, 2016).

Relevant information for the *in situ* conservation*, i.e.* the on-site management of genetic resources, is available thanks to Syfert *et al.* (2016). The study identified hotspots of diversity of eggplant crop wild relatives in southern and eastern Africa and the Indian subcontinent. These hotspots, found in protected areas of Kenya, Tanzania, and Uganda, are potential areas of interest for establishing *in situ* conservation policies and collecting genetic resources to fill germplasm gaps in *ex situ* collections. However, few *in situ* programmes are ongoing. A total of five eggplant wild relatives (*S. lidii*, *S. linnaeanum*, *S. marginatum*, *S. sisymbriifolium*, and *S. torvum*) are included in the European priority CWR taxa (Rubio Teso *et al.*, 2021), although none of them is native to continental Europe (Vorontsova *et al.*, 2013; Vorontsova and Knapp, 2016), and two (*S. sisymbriifolium* and *S. torvum*) are invasive (Alaniz *et al.*, 2020; Musarella, 2020). Two of these species (*S. lidii* and *S. marginatum*) are found only in one European country, and specific conservation sites exist only for *S. lidii*, which is an endangered endemism of the Canary Islands (Gramazio *et al.*, 2020; Rubio Teso *et al.*, 2021).

The level of exploration of the cultivated eggplant germplasm is variable, depending on the traits. While passport data are available for most accessions conserved in germplasm banks, the availability of characterization data, generally performed using standardized descriptors such as those of Bioversity (IBPGR, 1990), UPOV (2002) or EGGNET (van der Weerden and Barendse, 2007), is much more limited. On the one hand, some phenotypic studies were performed using a large number of accessions (>150) and

aiming at evaluating the morphological diversity of cultivated eggplant (Cericola *et al.*, 2013; Kumar *et al.*, 2013; Liu *et al.*, 2018; Oladosu *et al.*, 2021; Ro *et al.*, 2022). These studies revealed a large diversity of morpho-agronomic characteristics in the cultivated eggplant genepool and provided relevant information for their utilization in breeding. Large screening for evaluation traits in germplasm collections of eggplant relatives is more limited. Field evaluation of 70 *S. aethiopicum* accessions, mostly belonging to *gilo* group, was assessed for morpho-physiological, molecular (AFLP and SSR markers) and chlorogenic acid content highlighted a wide genetic diversity (Sunseri *et al.*, 2010). A total of 125 accessions of *S. aethiopicum* and *S. macrocarpon* were evaluated by Taher *et al.* (2019) for resistance to the two-spotted spider mite (*Tetranychus urticae*), resulting in the identification of high levels of resistance in two accessions of *S. macrocarpon*. In another large evaluation study, Stommel and Whitaker (2003) studied the phenolic acid profiles of 115 accessions, mostly of cultivated *S. melongena*, but also including some accessions of *S. aethiopicum*, *S. anguivi*, *S. incanum* and *S. macrocarpon*. Another study on 73 accessions, most of which were of *S. melongena*, but also included *S. aethiopicum* and *S. macrocarpon*, also found large variations in total phenolics content (8.4-fold), and fruit flesh browning (7.3-fold), but less in ascorbic acid (2.3-fold) (Prohens *et al.*, 2007).

Overall, given the large number of species in the GP2 and GP3 of eggplant, the Focused Identification of Germplasm Strategy (FIGS), which is based on the assumption that wild accessions growing in specific environments must have adaptive genes to these conditions (Street *et al.*, 2016), might help in identifying putative species or accessions of interest for tolerance to a certain biotic or abiotic stress (Prohens *et al.*, 2017). However, the exploration of eggplant and relatives germplasm collections for traits relevant to adaptation to climate change has been very scarce until now. To achieve an

421 eggplant Green Revolution, it is essential to systematically evaluate the available

422 variation and identify sources of variation for adaptation to climate change.

423

5. Use of genetic resources in breeding: achievements and challenges

425 Selections of eggplants started very early in breeding, with accessions having

426 improved characteristics already present in seed catalogues in the late 19th and early 20th

427 centuries (Daunay and Janick, 2007). In addition, heterosis for yield was already reported

428 in 1931 (Kakizaki, 1931), which opened the door for the development of hybrid varieties

429 with improved features. Genetic improvements in eggplant have relied on the use of

430 germplasm, and breeders have been using the eggplant germplasm (mostly of cultivated

431 *S. melongena*) for breeding and developing new selections, lines and hybrids. According

432 to a survey of germplasm banks (Solberg *et al.*, 2022), the number of eggplant accessions

433 distributed per year ranged between 0 and 503, revealing that some germplasm banks

434 make a significant distribution to users, many of whom are breeders.

435 The genetic improvements of eggplant are evident in the characteristics of modern

436 cultivars, which are considerably better in yield and overall quality than landraces.

437 Indeed, as an example by considering the western market, modern F1 hybrids cultivars

438 have no prickles, greater earliness, intense black colour and epidermis shininess, and

439 lower fruit flesh browning (Prohens *et al.*, 2007; Muñoz-Falcón *et al.*, 2009) or increased

440 yield (Sambandam, 1964; Rodríguez-Burruezo *et al.*, 2008; Daunay and Hazra, 2012;

441 Kaushik *et al.*, 2018; Kumar *et al.*, 2020). The development of modern eggplant cultivars

442 has been mainly carried out employing the cultivated genepool. This resulted in the

443 reduction of the genetic base of the eggplant elite breeding lines and materials used for

444 developing modern F1 hybrids. For instance, Muñoz-Falcón *et al*. (2009) evaluated the

445 genetic diversity of black eggplants of different groups and found that modern F1 hybrids

have a narrow genetic base and share a common genepool. This situation is in contrast to tomato, where the widespread use of CWRs, especially for introgressions of biotic resistance traits increased the genetic diversity of modern varieties (Díez and Nuez, 2008; Schouten *et al.*, 2019). The exploitation of cultivated eggplant germplasm allowed the development of new cultivars and elite materials with improved resistance or tolerance to pests and diseases. Indeed, sources of resistance to the most significant pests, including the eggplant fruit and shoot borer, leafhopper, aphids, spider mites, and whiteflies, as well as to the primary diseases such as bacterial wilt, Fusarium, and Verticillium wilts, have been identified (Taher *et al.*, 2017; Arafa *et al.*, 2022; Salinier *et al.*, 2022). Many of these cultivated accessions have been transferred to researchers and breeders to incorporate them into their breeding pipelines (Taher *et al.*, 2017). However, while some quantitative improvements have been achieved, resulting in cultivars with improved tolerance, the genetic diversity for resistance to these biotic stresses present in the primary genepool of eggplant seems to be limited (Taher *et al.*, 2017).

Accessions of wild species of eggplant GP2 and GP3 species, as well as from the cultivated *S. aethiopicum*, have been employed for introgression breeding (Mennella *et al.*, 2010; Liu *et al.*, 2015; Gramazio *et al.*, 2017; Plazas *et al.*, 2020; Villanueva *et al.*, 2021). Eggplant lines fully resistant to *Fusarium* wilt have been obtained by introgressing the *Rfo-sa1* resistance locus from *S. aethiopicum* (Toppino *et al.*, 2008). Interestingly, the response mechanism to *Fom* inoculation triggered by this locus is also able to protect the plant from *Verticillium* wilt (Barbierato *et al.*, 2016; Barchi *et al.*, 2018) when the two fungi are used in a combined artificial inoculation. These elite Fusarium wilt-resistant lines introgressed from *S. aethiopicum*, along with associated molecular markers, are of great interest for the development of commercial cultivars.

470 *Solanum linnaeanum* has also been used in introgression breeeding for the development

471 of early backcross eggplant materials with resistance to Verticillium wilt (Acciarri *et al.*,

472 2004; Liu *et al.*, 2015). However, no eggplant commercial cultivars with resistance

473 derived from *S. linnaeanum* have been produced until now.

474 First backcross generations of eggplant with *S. aethiopicum* as a donor displayed a wide

475 morphological variability (Prohens *et al.*, 2012). Similarly, high morphological diversity

476 and a wide range of values for phenolic acid contents were found in the first backcross

477 generations using *S. incanum* as the donor parent (Prohens *et al.*, 2013). However,

478 introgression lines derived from these early *S. incanum* backcrosses were largely similar

479 to the recurrent parent, although two lines with higher plant vigour were identified

480 (Mangino *et al.*, 2020). Some advanced backcrosses with *S. elaeagnifolium* exhibited a

481 higher yield than the recurrent *S. melongena* parent (Villanueva *et al.*, 2021). However,

482 these materials are still in an early stage of development and have not been used for the

483 development of new cultivars. In addition, several species such as *S. aethiopicum*, *S.*

484 *anguivi*, *S. grandiflorum*, *S. kurzii*, *S. violaceum* and *S. virginianum* have been used for

485 the development of aloplasmic lines of eggplant that display cytoplasmic male sterility

486 (Khan and Isshiki, 2016). These male-sterile lines have potential interest in the production

487 of hybrids. However, to our knowledge, aloplasmic male sterility has not been used so far

488 in the commercial production of eggplant hybrids.

489 Eggplant wild species and interspecific hybrids have also been explored for their

490 use as rootstocks, mainly with the aim of obtaining resistance to diseases and enhanced

491 vigour (King *et al.*, 2010; Schwarz *et al.*, 2010). In this way, apart from selections of *S.*

492 *torvum* and interspecific hybrids between eggplant and *S. aethiopicum* used as

493 commercial rootstocks, other wild species, such as *S. anguivi*, *S. incanum*, *S. insanum*, *S.*

494 *palinacanthum* or *S. sisymbriifolium* (Gisbert *et al.*, 2011; Rakha *et al.*, 2020; Kumbar *et*

al., 2021; Murata *et al.*, 2022) were proposed as potential new rootstocks. However, no commercial rootstocks have been developed so far from these latter species. One potential reason is that some of these species with potential interest have prickly stems (Vorontsova *et al.*, 2013; Vorontsova and Knapp, 2016), making the grafting procedure difficult and unusable for mass-scale grafting, typical of field cultivation (Figure 4).

It is worth considering that interspecific hybrids of eggplant with some wild species such as *S. tomentosum* or *S. elaeagnifolium* (Figure 4) are highly vigorous and have an extended root system (García-Fortea *et al.*, 2019), making them exploitable as rootstocks. However, in some cases such as the hybrids between *S. melongena* and *S. elaeagnifolium*, the obtainment of hybrids is very challenging and requires embryo rescue (Kouassi *et al.*, 2016), limiting their exploitation. Introgression breeding with wild species that display high contents of glycoalkaloids (solasonine and solamargine) might result in the inadvertent increase of these glycoalkaloids in the recurrent eggplant parents. However, studies performed by Mennella *et al.* (2010) with *S. aethiopicum* and *S. linnaeanum* and by Rosa-Martínez *et al.* (2022*a*) with *S. incanum* did not detect significantly higher levels of glycoalkaloids in introgression lines (ILs) with these species than in the recurrent parents. However, given that these ILs did not represent the whole genome of the donor parents, the evaluation of glycoalkaloids should be performed in the elite materials obtained after the introgression process with eggplant relatives that exhibit high contents in potentially harmful glycoalkaloids. Similarly, given that in Solanaceae glycoalkaloids synthesized in the roots can move up in the plant (Kodama *et al.*, 2021), in the case of using wild species or interspecific hybrids with high contents of glycoalkaloids as rootstocks, the content in the fruit should be checked to ensure the safety of the potential new commercial varieties.

519   Although considerable improvements have been made in eggplant breeding, the

520   diversity used mostly relied on the cultivated eggplant *S. melongena* (Daunay and Hazra,

521   2012; Taher *et al.*, 2017; Kumar *et al.*, 2020). Furthermore, breeding efforts have been

522   made in using eggplant CWRs for breeding, even if they did not have a major impact on

523   the modern cultivars presently grown. As in other important crops, a qualitative leap

524   forward in genetic advances for a "Green Revolution" in eggplant will require unleashing

525   the huge potential of CWRs, which is still largely unexploited.

526

527   **6. A new generation of genetic resources**

528   Besides germplasm accessions of eggplant cultivated and CWRs, during the last

529   years a new generation of eggplant genetic resources, consisting of core collections,

530   recombinant inbred lines, and introgression lines have been generated (Toppino *et al.*,

531   2008, 2018, 2020; Gangopadhyay *et al.*, 2010; Mennella *et al.*, 2010; Lebeau *et al.*, 2013;

532   Gramazio *et al.*, 2017; Barchi *et al.*, 2018; Miyatake *et al.*, 2019; Mishra *et al.*, 2020;

533   Arrones *et al.*, 2022; Ro *et al.*, 2022; Gaccione *et al.*, 2022; Mangino *et al.*, 2022). These

534   materials are considered immortal since they can be regenerated by selfing for seed

535   propagation. This is in contrast to F2 and early backcross materials, for which several

536   populations have been obtained in eggplant (Daunay and Hazra, 2012; Prohens *et al.*,

537   2012, 2013; Clarke *et al.*, 2014; Portis *et al.*, 2014; Toppino *et al.*, 2016; Boyaci *et al.*,

538   2021; Qian *et al.*, 2022), and where each individual has a variable degree of heterozygosis

539   and can be thus maintained only by vegetative propagation.

540   We should also point out that a few mutant collections exist so far for eggplant (Xi-ou *et*

541   *al.*, 2017; Du *et al.*, 2022). Two ethyl methane sulfonate (EMS) mutant libraries of 400

542   and 790 M_2 lines, which were generated and used to identify mutants for phenotypic traits,

543 including dwarf mutant plants (Xiao *et al.*, 2016; Xi-ou *et al.*, 2017; Lu *et al.*, 2021; Du

544 *et al.*, 2022).

545   Core collections allow a representation of most of the diversity of large germplasm

546 set in a reduced number of accessions (Odong *et al.*, 2013) exploitable for genotype to

547 phenotype studies. The first eggplant core collection of 181 eggplant accessions was

548 developed by Gangopadhyay *et al.* (2010) from an original set of 1,798 accessions by

549 using 14 morphological descriptors. In a first attempt to apply a GWA approach in

550 eggplant, Ge *et al.* (2013) were able to identify several phenotype/genotype associations

551 related to eight fruit-related traits. Subsequently, a selected eggplant association panel of

552 191 selected accessions (Cericola *et al.*, 2013), comprising a mixture of breeding lines,

553 old varieties and landrace selections originating from Asia and the Mediterranean Basin,

554 was SNP genotyped and phenotyped. This allowed the identification and positioning of

555 several marker/trait associations related to fruit, plant and leaf morphological traits

556 relevant to eggplant breeding (Cericola *et al.*, 2014; Portis *et al.*, 2015) as well as to

557 identify contrasting genotypes for Nitrogen Use Efficiency (Mauceri *et al.*, 2020) and,

558 most recently, to identify the gene networks responsible of such diversity (Mauceri *et al.*,

559 2021).

560   Subsequently, Miyatake *et al.* (2019) genotyped 893 accessions, mostly from

561 Asia, with 831 SNPs and 50 SSRs and established a core collection of 100 accessions

562 (World Eggplant Core; WEC). More recently, a core collection of 288 accessions from

563 an initial set of 587 accessions by using 52 SNP markers complemented with agro-

564 morphological traits (Ro *et al.*, 2022). The combination of both types of data resulted in

565 the identification of significant associations of SNPs with six traits, which allowed the

566 identification of several candidate genes. Another core collection of 322 *S. melongena*

567 accessions was obtained from an original set of over 3,600 accessions (Gaccione *et al.*,

568   2022), most of which were genotyped with the 5k probes eggplant SPET platform (Barchi

569   *et al.*, 2019*a*). This core collection has been re-sequenced and phenotyped at three

570   locations for multiple agronomic and composition traits (Gaccione *et al.*, 2022) and has

571   already proved useful in identifying allelic variants for the *SmAPRR2* transcription factor

572   responsible for chlorophyll pigmentation in the eggplant fruit peel (Arrones *et al.*, 2022).

573   Recombinant inbred lines from bi-parental or multi-parental crosses are genetic

574   resources of great relevance, as each of them is a different genetic mosaic of the parents

575   (Arrones *et al.*, 2020). Therefore, new genotypes of interest for breeding combining

576   desirable characteristics present in the set of parents may be recovered in the set of RILs.

577   In addition, in the absence of selection, bi-parental or multi-parental RILs sets do not

578   present genetic structure, which makes them a powerful tool for the detection of major

579   genes and QTLs involved in traits of interest (Cockram and Mackay, 2018). Several RILs

580   populations of eggplant, all of them have in common that they have one eggplant relative

581   (*S. aethiopicum* or *S. incanum*) in their pedigree, have been obtained from bi-parental

582   crosses (Lebeau *et al.*, 2013; Toppino *et al.*, 2020). A first RIL of 178 F6 lines was

583   obtained by single seed descend from the F2 generation obtained after crossing an

584   eggplant line (MM738) susceptible to bacterial wilt with a resistant breeding line (AG91-

585   25) derived from the crossing of a resistant *S. melongena* and an *S. aethiopicum* accession

586   (Lebeau *et al.*, 2013). Genotyping of this RIL population with AFLP, SSR and SRAP

587   markers allowed the construction of a genetic map with 119 polymorphic markers in

588   which a major dominant gene and several QTLs were detected. Interestingly, some RILs

589   displayed better performance than the resistant parent (AG91-25) for some of the

590   resistance traits evaluated (Lebeau *et al.*, 2013). More recently, Toppino *et al.* (2020)

591   developed a RIL population of 163 F7 lines derived from single seed descend of the F2

592   from the cross between eggplant lines '305E40' and '67/3'. The parent '305E40' derived

from the repeated backcrossing of a doubled haploid of the somatic hybrid between *S. melongena* and *S. aethiopicum* to two eggplant lines and carries the *Rfo-sa1* gene from *S. aethiopicum*, which confers resistance to *F. oxysporum* f. sp. *melongenae* (*Fom*), as well as tolerance to Verticillium wilt (Barbierato *et al.*, 2016; Barchi *et al.*, 2018; Toppino *et al.*, 2018). This RIL population was mild sequenced and employed to anchor the genome of the male parent '67/3' (Barchi *et al.*, 2019*b*). More recently the same population was genotyped by GBS, resulting in over 10k polymorphic markers, which allowed the development of a high-density genetic map and the identification of a large number of QTLs, as well as candidate genes, for multiple morphological and metabolic traits (Toppino *et al.*, 2020; Sulli *et al.*, 2021), together with the characterization of two major QTLs for resistance to *Fom* (Tassone *et al.*, 2022). Also, Mishra *et al.* (2020) developed a RIL population of 114 F8 RILs from the crossing between a cultivated landrace (Ramnagar Giant) and an accession of *S. incanum* (W-4), allowing the development of a genetic map after genotyping the population with 282 polymorphic RAPD, ISSR, SCoT and SSR markers.

Following the intercrossing of eight parental lines (seven *S. melongena* of different origins and characteristics and one *S. incanum*), the only multiparental RIL population (MAGIC) of eggplant (MEGGICS3) is available, constituted of 420 S3 lines that were resequenced at an average of an average depth of 20x (Gramazio *et al.*, 2019). The MEGGICS3 population was developed following a funnel scheme and single seed descend from the S0 quadruple hybrid recombinant generation (Mangino *et al.*, 2022) and has been genotyped with the eggplant 5k probes SPET, resulting in 7,724 high-confidence SNPs. The phenotyping of plant and fruit anthocyanic pigmentation as well as fruit peel chlorophyll presence has allowed the identification of several major QTLs and candidate genes for the traits evaluated (Arrones *et al.*, 2022; Mangino *et al.*, 2022). Interestingly,

in combination with the G2P-SOL core collection, the MAGIC population has allowed identifying the gene *SmAPRR2* as responsible for fruit chlorophyll pigmentation in the fruit peel.

The first ILs of eggplant with related species were obtained after backcrossing two somatic hybrids or dihaploids derived from them resulting from the crossing between eggplant lines 1F5(9) and Dourga and two *S. aethiopicum* lines (Toppino *et al.*, 2008). Also, introgression lines were obtained after hybridization of several eggplant lines with *S. linnaeanum* (Mennella *et al.*, 2010). In total, 57 ILs derived from these programmes after 6-7 cycles of backcrossing were studied for several health-related compounds and PPO activity (Mennella *et al.*, 2010). The results revealed that both ILs sets displayed similar levels to the recurrent parents for glycoalkaloids, indicating their safety for human consumption, while a significant number of ILs displayed better values for antioxidant compounds. Subsequently, Gramazio *et al.* (2017) used marker-assisted selection in the repeated backcrossings (up to BC6) and subsequent selfings between *S. melongena* accession ANS26 and *S. incanum* accession MM577. This resulted in 25 ILs with single introgressions that covered 61.7% of the *S. incanum* genome, which was recently increased to over 70% of the *S. incanum* MM577 genome (Plazas *et al.*, 2020). A subset of these ILs have been characterized for morphological and agronomic traits (Mangino *et al.*, 2020; Rosa-Martínez *et al.*, 2022*b*), fruit shape characteristics (Mangino *et al.*, 2021), and composition (Rosa-Martínez *et al.*, 2022*a,b*), putting in evidence several stable QTLs and revealed the low levels of glycoalkaloids found in the ILs. Toppino *et al.* (2018) recently developed 90 ILs carrying introgressions from the wild relative *S. tomentosum*, which may be of great interest for breeding for resistance to several traits present in this wild relative, such as resistance to *Fusarium*, *Verticillium* or nematodes as well as to whitefly (Taher *et al.*, 2020). New sets of ILs with *S. insanum*, *S. dasyphyllum* and *S.*

643 *elaeagnifolium* are in advanced stages of development (Plazas *et al.*, 2020) and will soon

644 increase the diversity available to eggplant breeders from so far unexplored exotic genetic

645 resources. In this way, advanced backcrosses with *S. elaeagnifolium* under low N

646 conditions have revealed a great potential of the introgressions from this species for

647 sustainable agriculture (Villanueva *et al.*, 2021).

648 These new generations of genetic resources make extant eggplant genetic diversity

649 more accessible to breeders, allowing the development of new recombinant genotypes

650 and representing powerful tools for identifying genes/alleles and QTLs associated with

651 traits of interest, including complex traits such as those related to climate change (Prohens

652 *et al.*, 2017; Chapman, 2020). The extended use of these materials, which has already

653 started to demonstrate their potential for eggplant breeding (Lebeau *et al.*, 2013; Barchi

654 *et al.*, 2018; Mangino *et al.*, 2020, 2022; Arrones *et al.*, 2022) will be of paramount

655 importance in the development of the eggplant Green Revolution.

656

657 **7. Genomic and biotechnological tools to enhance the exploitation of genetic**

658 **resources for the enhancement of genetic resources**

659 New genomic tools such as high-throughput genotyping derived from NGS

660 technologies, reference genomes, pangenomes, resequencing projects can efficiently

661 contribute to the enhancement of eggplant genetic resources and are essential for the

662 eggplant Green Revolution (Gramazio *et al.*, 2018; Lanteri and Barchi, 2019; Simko *et*

663 *al.*, 2021). Although DNA molecular markers of different types, such as RAPDs, AFLPs

664 and SSRs have been widely used for eggplant genotyping and genetic mapping since the

665 early 1990s (Collonnier *et al.*, 2001; Gramazio *et al.*, 2014, 2018), the availability of NGS

666 technologies allowed an easier genotyping of large sets of accessions and experimental

667 populations with hundreds to thousands of markers, contributing to the evaluation of the

eggplant and CWRs genetic diversity, the establishment of genetic relationships of germplasm sets and identification of QTLs (Barchi *et al.*, 2019*c*; Liu *et al.*, 2019; Miyatake *et al.*, 2019; Toppino *et al.*, 2020; Sulli *et al.*, 2021; Mangino *et al.*, 2022; Ro *et al.*, 2022; Tassone *et al.*, 2022; Gaccione *et al.*, 2023), which is of interest in identifying materials for breeding and germplasm management (Lanteri and Barchi, 2019; Arafa *et al.*, 2022; Toppino *et al.*, 2022).

A first draft of the eggplant genome was published in 2014 (Hirakawa *et al.*, 2014), but improved eggplant genome assemblies have not been available until recently (Wei *et al.*, 2020; Barchi *et al.*, 2021, 2022; Li *et al.*, 2021) and this has delayed the application of the potential of resequencing and pangenome projects to eggplant genetic resources enhancement and management. Also, the availability of resequencing data from eight accessions (Gramazio *et al.*, 2019) allowed the development of the eggplant 5k probes SPET platform (Barchi *et al.*, 2019*a*), which is the first specific eggplant genotyping platform. The SPET genotyping platform has been used for the genotyping of germplasm of eggplant and wild relatives and the first MAGIC population (Barchi *et al.*, 2019*a*, 2022; Gramazio *et al.*, 2020; Arrones *et al.*, 2022) as well as the marker-assisted selection for the development of introgression lines (Plazas *et al.*, 2020; Villanueva *et al.*, 2021). The first eggplant pangenome, which included the resequencing data of 23 accessions of *S. melongena* and two of CWRs (*S. incanum* and *S. insanum*) is very recent (Barchi *et al.*, 2021). This eggplant pangenome allowed the identification of additional genes compared to the reference genome used, as well as selective sweeps during domestication and the associated underlying candidate genes (Barchi *et al.*, 2021).

Genebank genomics can help in the management and utilization of eggplant germplasm collections (Mascher *et al.*, 2019), but so far no studies have been performed on eggplant. Similarly, the potential of landscape genomics (Li *et al.*, 2017) to identify materials of

693 eggplant with adaptive genes to specific environmental conditions has not been exploited

694 yet. Both genomics approaches have a lot of potential for contributing to the eggplant

695 Green Revolution. The genetic/genomic data and the phenotypic information available

696 on the eggplant genetic resources (i.e. core collection and experimental populations)

697 might lay the foundation to start applying genome-enable prediction methods to both

698 accelerate eggplant breeding and increase the efficiency of the selection processes.

699 New Plant Breeding Techniques (NPBTs) such as CRISPR/Cas genome editing

700 represent valuable tools useful to create novel genetic variation as well as to determine

701 the function of target genes via targeted mutagenesis. However, only two studies have

702 been published so far on CRISPR/Cas gene editing in eggplant (Maioli *et al.*, 2020;

703 Kodackattumannil *et al.*, 2023), probably as a consequence of the recalcitrance of *S.*

704 *melongena* to *in vitro* regeneration (García-Fortea *et al.*, 2020). In the study of Maioli *et*

705 *al.* (2020), polyphenol oxidase (PPO) genes *PPO4*, *PPO5*, and *PPO6* were knocked out,

706 which resulted in reduced fruit flesh browning demonstrating how the creation of new

707 allelic variation contributed to the improvement of an important trait. In a subsequent

708 study, Kodackattumannil *et al*. (2023) found that CRISPR/Cas mutation of *PPO2* resulted

709 in the inhibition of fruit flesh browning, but also had multiple pleiotropic effects in

710 morphological and agronomic traits.

711

Conclusions and future perspectives

713 The exploration of the cultivated and wild eggplant germplasm both at the

714 phenotypic and molecular level is required for the identification of sources of variation

715 for new traits barely explored so far, such as tolerance to new stresses caused by climate

716 change as well as for improved sustainability, such as water and fertilizers use

717 efficiencies. The establishment of core collections, such as the ones already existing

718   (Gangopadhyay *et al.*, 2010; Miyatake *et al.*, 2019; Gaccione *et al.*, 2022; Ro *et al.*, 2022),

719   as well as the FIGS strategy of identification of potentially useful germplasm (Street *et*

720   *al.*, 2016), genebank and landscape genomics (Li *et al.*, 2017; Mascher *et al.*, 2019) may

721   help in facilitating the identification accessions of interest.

722   The eggplant Green Revolution requires a coordinated enhancement of its genetic

723   resources. Two major international initiatives, the "Adapting Agriculture to Climate

724   Change" (2011-2021) initiative of the Global Crop Diversity Trust (Dempewolf *et al.*,

725   2014), and the H2020 project G2P-SOL (2016-2021) have demonstrated the enormous

726   potential of international collaboration in the improved conservation and utilization of

727   eggplant genetic resources. In this way, the eggplant activities and projects performed

728   under the "Adapting Agriculture to Climate Change" (2011-2021) initiative allowed the

729   identification of gaps in the eggplant CWRs germplasm collections and proposed

730   priorities for collection and *in situ* conservation (Syfert *et al.*, 2016), as well as the

731   collection of 474 new accessions of eggplant and CWRs (32 different species) for the

732   completion of these gaps (Eastwood *et al.*, 2022). Also, this initiative allowed the

733   development of advanced backcrosses and ILs with four different eggplant CWRs (*S.*

734   *dasyphyllum*, *S. elaeagnifolium*, *S. incanum* and *S. insanum*) (Gramazio *et al.*, 2017;

735   Plazas *et al.*, 2020; Villanueva *et al.*, 2021). Characterization of these sets of ILs for

736   multiple traits and stress conditions is expected to result in new materials with improved

737   adaptation to climate change (García-Fortea *et al.*, 2019; Plazas *et al.*, 2020). The

738   "Adapting Agriculture to Climate Change" initiative has also contributed to the

739   development of the Germinate platform (Raubach *et al.*, 2021), which includes a database

740   on eggplant (https://ics.hutton.ac.uk/cwr/eggplant) that contains 59 datasets with

741   genotypic and phenotypic data from cultivated eggplant, wild species and pre-breeding

742   materials.

743   The H2020 project G2P-SOL represents another landmark for the enhancement

744   of genetic resources of *S. melongena* and the species of its genepools, in which the 5k

745   probes SPET platform was designed (Barchi *et al.*, 2019*a*) and used for the largest

746   genotyping effort in eggplant germplasm (around 3,500 accessions), allowing the

747   evaluation of diversity of the eggplant genepool, establishment of relationships,

748   identification of duplicates, and in combination with historical characterization data the

749   identification of hundreds of QTLs (Barchi *et al.*, 2022; Gaccione *et al.*, 2022). By using

750   these data, a core collection of 322 eggplant accessions was created, which has been

751   resequenced and phenotyped in multiple locations as well as evaluated for several biotic

752   (*Fusarium* wilt, *Verticillium* wilt, *Meloidogyne* nematodes) and abiotic (drought tolerance

753   and salinity tolerance) related to climate change (Gaccione *et al.*, 2022; Salinier *et al.*,

754   2022). In addition, fruit metabolomic analyses of the core collection have been performed

755   (Sulli *et al.*, 2021).

756   Although these two initiatives represented the starting point for the eggplant

757   Green Revolution, new international, preferably global, actions are needed for a

758   coordinated and systematic exploitation of the advances obtained so far. In this way, the

759   Global Strategy for the Conservation and Use of Eggplants (Solberg *et al.*, 2022) calls for

760   seven priority activities: (i) establishing a global eggplant working group, (ii) developing

761   an Eggplant Knowledge Platform; (iii) improve passport data accuracy and completeness

762   in the collection databases; (iv) facilitate and encourage collaborative plant health-related

763   activities; (v) support collaborative activities associated with accessions regeneration and

764   safety duplication, (vi) characterize the global eggplant collection morphologically and

765   genetically, and (vii) encourage collaborative efforts to involve CWR in breeding

766   programmes. However, the implementation of this strategy, which would represent an

767   additional boost for the eggplant Green Revolution is still in the phase of funding

acquisition for its effective fulfillment. In any case, the foundations are set for the international networks already established, together with new projects and developments in the fields of genomics and biotechnology, to bring forward the eggplant Green Revolution. As in other crops, we foresee this will result in dramatic genetic improvements in eggplant cultivars that will increase yield and quality and will allow the development of more resilient materials able to cope with the climate change challenges.

Conflict of interest

The authors declare that there is no conflict of interest.

810

811 **References**

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Tables

Table 1. *Solanum* species from the primary (GP1), secondary (GP2) and tertiary (GP3) genepools (according to Syfert et al., 2016) for which introgression breeding with eggplant has been reported.

Species	Main traits of interest for eggplant breeding	Most advanced type of generations obtained with *S. melongena*	References
Primary genepool (GP1)			
S. insanum	Drought and salinity tolerance, phytochemical composition	Advanced backcrosses	Ranil *et al.* (2017); Brenes *et al.* (2020); Plazas *et al.* (2020); Nadeeshani *et al.* (2021); González-Orenga *et al.* (2023)
Secondary genepool (GP2)			
S. aethiopicum	Resistance or tolerance to *Fusarium* and bacterial wilts and nematodes, vigor of F1 hybrids as rootstocks, spider mite resistance	Lines with introgressed resistance to Fusarium and Verticillium wilt	Collonnier *et al.* (2001); Toppino *et al.* (2008); Prohens *et al.* (2012); Calvo-Asensio *et al.* (2014); Barbierato *et al.* (2016); Barchi *et al.* (2018); Taher *et al.* (2019); Zhuang & Wang (2009)
S. anguivi	Drought tolerance, high content of phenolics	Second backcross generation	Kaushik *et al.* (2019); Plazas *et al.* (2020); Kouassi *et al.* (2021)
S. dasyphyllum	Drought tolerance, two-spotted spider mite and silverleaf whitefly tolerance	Advanced backcrosses	Plazas *et al.* (2020); Kouassi *et al.* (2021); Taher *et al.* (2020); Villanueva *et al.* (2023)
S. incanum	Drought tolerance, bacterial wilt resistance, fruit and shoot borer resistance, silverleaf whitefly tolerance, high content of phenolics	Introgression lines	Bletsos and Olympios (2008); Prohens *et al.* (2013); Gramazio *et al.* (2017); Namisy *et al.* (2019);

			Mangino *et al.* (2020); Taher *et al.* (2020)
S. lichtensteinii	Drought tolerance, silverleaf whitefly tolerance	Second backcross generation	Vorontsova and Knapp (2016); Plazas *et al.* (2020); Taher *et al.* (2020)
S. lidii	Unexplored so far	Second backcross generation	Plazas *et al.* (2020)
S. linnaeanum	Salinity tolerance, Verticillium wilt resistance	Lines with introgressed resistance to Verticillium wilt	Mennella *et al.* (2010) Acciarri *et al.* 2007; Zhuang *et al.* (2014); Liu *et al.* (2015)
S. tomentosum	Fusarium and Verticillium wilts and nematodes resistance, silverleaf whitefly tolerance	Introgression lines	Toppino *et al.* (2018); Taher *et al.* (2020)
Tertiary genepool (GP3)			
S. elaeagnifolium	Drought tolerance, high content of phenolics	Advanced backcrosses	García-Fortea *et al.* (2019); Plazas *et al.* (2020); Villanueva *et al.* (2021)

Table 2. New eggplant genetic resources, consisting of mutant libraries, core collections, biparental and multiparental recombinant inbred lines and introgression lines sets.

Plant material used	Number of lines or accessions	Conventional and biotechnological tools used for the development	Reference
Mutant libraries			
S. melongena accession E31-1	790	Ethyl methane sulfonate	Xi-ou *et al.* (2017)
S. melongena line 14-345	400	Ethyl methane sulfonate	Du *et al.* (2022)
Core collections			
1,798 accessions of *S. melongena*	181	14 morphological descriptors	Gangopadhyay *et al.* (2010)
392 accessions of *S. melongena*	191	314 SNPs, 33 morphological traits, NUE	Cericola *et al.* (2013), 2014, Portis *et al.* (2015), Mauceri *et al.* (2020);
893 accessions of *S. melongena*	100	831 SNPs and 50 SSRs	Miyatake *et al.* (2019)
587 accessions of *S. melongena*	288	52 SNPs and 17 agromorphological traits	Ro *et al.* (2022)
3,600 accessions of *S. melongena* and wild relatives	322	5k probes SPET platform	Gaccione *et al.* (2022)
Biparental recombinant inbred lines			
S. melongena lines MM378 and AG91-25	178 F6	AFLP, SSR and SRAP	Lebeau *et al.* (2013)
S. melongena lines 305E40 and 67/3	163 F7	GBS (10 k polymorphic markers)	Toppino *et al.* (2020)
S. melongena landrace Ramnagar Giant and *S. incanum* accession W-4	114 F8	282 polymorphic RAPD, ISSR, SCoT and SSR	Mishra *et al.* (2020)
Multiparental recombinant inbred lines			

Seven *S. melongena* accessions (MM1597, DH ECAVI, AN-S-26, H15, A0416, IVIA-371 and ASI-S-1) and one *S. incanum* accession (MM577)	420 (S3 MAGIC)	5k probes SPET platform	Mangino *et al.* (2022)
		Introgression lines sets	
S. melongena lines 1F5(9), Dourga, Tal 1/1 and CCR3, two accessions of *S. aethiopicum* and one accession of *S. linnaeanum*	57	Selection for tolerance to Fusarium and Verticillium wilts	*Acciarri et al. (2007)* Mennella *et al.* (2010)
S. melongena AN-S-26 and *S. incanum* MM577	51	COSII, SSRs, SNPs (GBS and SPET)	Gramazio *et al.* (2017), Plazas *et al.* (2020)
S. melongena accession 67/3 and one *S. tomentosum* accession	90	HRM Molecular markers	Toppino *et al.* (2018)

Figure legends

Figure 1. Diversity for fruit morphology in the cultivated (*S. melongena*) gene pool (above), within a particular cultivar type (striped eggplant) (center) and in eggplant wild relatives from the primary (GP1), secondary (GP2) and tertiary (GP3) genepools (below).

Figure 2. Dendrogram representing relationships of the most relevant groups of the primary (GP1), secondary (GP2) and tertiary (GP3) genepools of *S. melongena*. Based on Whalen (1984), Vorontsova *et al*. (2013), Aubriot *et al*. (2016), and Knapp *et al.* (2016, 2019).

Figure 3. Map of global distribution of cultivated eggplant and its wild relatives in genebank holdings. Map elaborated according to data from FAO *et al.* (2010), Taher *et al.* (2017), Salinier *et al.* (2022) and Solberg *et al.* (2022).

Figure 4. Unexploited eggplant wild relatives and interspecific hybrids as potential roortstocks for eggplant: highly prickly rootstocks are challenging for commercial rootstock utilization as prickles difficult the manual grafting process (A); interspecific hybrids of eggplant (*S. melongena*) with some wild species such as *S. elaeagnifolium* (B) and *S. tomentosum* (C) are highly vigorous and/or have an extended root system which is great interest for improving resilience.