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Conventional and new genetic resources for an eggplant breeding revolution

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1 Conventional and new genetic resources for an eggplant Green Revolution

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3 Pietro Gramazio^{1,†}, David Alonso^{1,†}, Andrea Arrones¹, Gloria Villanueva¹, Mariola
4 Plazas¹, Laura Toppino², Lorenzo Barchi³, Ezio Portis³, Paola Ferrante⁴, Sergio Lanteri³,
5 Giuseppe Leonardo Rotino², Giovanni Giuliano⁴, Santiago Vilanova¹ and Jaime
6 Prohens^{1,*}

7
8 ¹Instituto de Conservación y Mejora de la Agrodiversidad Valenciana, Universitat
9 Politècnica de València, Camino de Vera 14, 46022 Valencia, Spain

10 ²CREA Research Centre for Genomics and Bioinformatics, Via Pauledese 28, 26836
11 Montanaso Lombardo (LO), Italy

12 ³Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), Plant Genetics,
13 University of Turin, Largo P. Braccini 2, 10095 Grugliasco (TO), Italy

14 ⁴Agenzia Nazionale Per Le Nuove Tecnologie, L'energia e Lo Sviluppo Economico
15 Sostenibile (ENEA), Casaccia Research Centre, Rome, Italy

16
17 † These authors contributed equally to this work.

18 * Correspondence: jprohens@btc.upv.es

19
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.

26 **Abstract**

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

44

45 **Keywords:** eggplant, gene pools, genetic resources, germplasm banks, Green Revolution,
46 introgression breeding, *Solanum melongena*, wild relatives

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51 **Introduction**

52 Eggplant (*Solanum melongena* L.), also known as common eggplant, brinjal or
53 aubergine, was domesticated from its wild ancestor *S. insanum* L. around 9,000-10,000
54 years ago in the region that includes the Indian subcontinent and southeast Asia (Page *et*
55 *al.*, 2019a). Eggplant is globally one of the most important vegetable crops, ranking sixth
56 in production among vegetables after tomato, onion, watermelon, cucumber and cabbage
57 (FAOSTAT, 2023). Its global production has increased by 24.0% in the last decade, from
58 $47.3 \cdot 10^6$ t in 2012 to $58.6 \cdot 10^6$ t in 2021 (FAOSTAT, 2023). As a warm-loving crop, it is
59 mostly cultivated in tropical, subtropical and temperate regions of the world, with most
60 of its production coming from East Asia, the Indian subcontinent, Southern Asia, the
61 Middle East and the Mediterranean basin. In these regions, eggplant is a common
62 constituent of the diet, providing significant amounts of K, P and Cu, as well as high
63 concentrations of bioactive phenolics beneficial for human health (Plazas *et al.*, 2013;
64 Rosa-Martínez *et al.*, 2021). However, agricultural production in main eggplant
65 cultivation areas is expected to be strongly affected by climate change (del Pozo *et al.*,
66 2019; Habib-ur-Rahman *et al.*, 2022). Increased spells of extreme events such as intense
67 drought periods may have a dramatic impact on crops sensitive to water stress, such as
68 eggplant (Plazas *et al.*, 2022).

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

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

80 In addition to eggplant, two other related minor crops, namely the scarlet eggplant
81 (*S. aethiopicum* L.) and the gboma eggplant (*S. macrocarpon* L.), were domesticated in
82 Africa (Page *et al.*, 2019b) and are mostly grown in the sub-Saharan region (Schippers,
83 2000). Although they have local importance, they are relevant crops, particularly *S.*
84 *aethiopicum*, in some parts of the world such as Brazil and the Caribbean, as well as in
85 Southern Italy, where a Protected Denomination of Origin exists for the *S. aethiopicum*
86 landrace ‘Melanzana Rossa di Rotonda’ (Schippers, 2000; Sunseri *et al.*, 2010). Little
87 research has been performed on these two minor African eggplant species. However,
88 given that they share many characteristics, pathogens and pests with the common
89 eggplant and the three domesticated eggplant species are cross-compatible (Bletsos *et al.*,
90 2004; Oyelana and Ugborogho, 2008; Rotino *et al.*, 2014), they are genetic resources of
91 interest to each other.

92 Eggplant displays a wide morphological diversity, even within a single varietal
93 group, particularly for fruit traits such as size, color and shape (Figure 1), as well as for
94 agronomic traits and adaptation to different environments (Cericola *et al.*, 2013; Taher *et*
95 *al.*, 2017; Chapman, 2020; Kouassi *et al.*, 2020; Ro *et al.*, 2022; Salinier *et al.*, 2022;
96 Toppino *et al.*, 2022). The diversity present within the cultivated eggplant is a valuable
97 genetic resource of great interest for eggplant breeding and has allowed the development
98 of significantly improved modern cultivars (Daunay and Hazra, 2012). However, as
99 occurs with many other vegetables, this high morphological diversity is mostly the
100 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.*, 2019a; 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.

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

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

141 Breeding in eggplant traditionally relies on selection from both within and among
142 landraces as well as in the development of F1 hybrids, which are predominant in high-
143 value markets (EU Plant Variety Database, 2022). It is known since long ago that F1
144 hybrids in eggplant generally display heterosis for yield (Kakizaki, 1931; Sambandam,
145 1964) and heterobeltiosis is also common (Rodríguez-Burruezo *et al.*, 2008; Kumar *et al.*,
146 2020). Selection of parents for heterotic hybrids is possible by evaluating the parents'
147 combining ability, as well as by selecting parents with high genetic distance using
148 molecular markers (Rodríguez-Burruezo *et al.*, 2008). It is worth remembering that
149 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

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

179 Abiotic stresses are expected to increase in the areas where eggplant is cultivated
180 due to climate change (Toppino *et al.*, 2022; Khalid *et al.*, 2023). Although eggplant is
181 mildly tolerant to water and salinity stresses (Heuer *et al.*, 1986; Díaz-Pérez and Eaton,
182 2015; Kouassi *et al.*, 2020; Toppino *et al.*, 2022), developing new varieties with better
183 resilience is needed, particularly in drought-prone areas or where water and soil salinity
184 is a problem for eggplant cultivation. Tolerance to extreme temperatures is also an
185 important breeding objective. Despite being a warm-loving plant, high temperatures
186 affect pollen viability and fruit set (Toppino *et al.*, 2022) and heat-tolerant varieties are
187 needed for production in the warm seasons. Tolerance to cold is also important in off-
188 season production in temperate areas, as growth and development are arrested, and fruit
189 set impaired (Toppino *et al.*, 2022). To this purpose, some parthenocarpic materials have
190 been developed which can set fruit even under cold conditions affecting pollen viability
191 (Kikuchi *et al.*, 2008). Improving water and nutrient use efficiencies is also necessary for
192 more sustainable agriculture as well. In this context, breeding for better root systems,
193 which is in its infancy in eggplant, can lead to more sustainable production (Chapman,
194 2020).

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

200 2016, 2020; Barchi *et al.*, 2019c; Mangino *et al.*, 2021), few causative genes have been
201 identified. One exception is the *APRR2* gene (Arrones *et al.*, 2022), which controls the
202 synthesis of fruit peel chlorophyll, as well as several genes involved in anthocyanin
203 synthesis (Florio *et al.*, 2021; He *et al.*, 2022; Li *et al.*, 2022). However, the causative
204 genes underlying other important traits for fruit appearance such as the presence of fruit
205 stripes, fruit netting or prickliness remain to be identified. Eggplant is one of the
206 vegetables with higher antioxidant and bioactive properties, resulting from its high
207 content of phenolic acids (Kaushik *et al.*, 2015), which unfortunately are indirectly
208 associated with increased browning of the fruit flesh (Mishra *et al.*, 2013; Docimo *et al.*,
209 2016; Kaushik *et al.*, 2017). Breeders therefore directly selected genotypes with low fruit
210 browning led to the indirect selection of genotypes with low content in phenolic acids
211 (Prohens *et al.*, 2007). To improve the phenolic acid content while limiting the effects of
212 browning, selection for low polyphenol oxidase (PPO) activity has been proposed (Plazas
213 *et al.*, 2013). In this way, CRISPR/Cas knocking out of PPOs expressed in the fruit has
214 been shown to reduce fruit flesh browning (Maioli *et al.*, 2020; Kodackattumannil *et al.*,
215 2023)). Parthenocarpic fruit set is also of interest for reducing fruit browning, as browning
216 is more intense in the tissues surrounding the seeds (Sarengaowa *et al.*, 2022). Saponins
217 present in the fruit flesh tissues contribute to the bitterness of some materials, which is an
218 undesirable trait (Aubert *et al.*, 1989). However, little information is available on the
219 genetics of bitterness in eggplant.

220 One of the major drawbacks of the use of wild relatives in eggplant introgression
221 breeding is represented by glycoalkaloids, since eggplant CWRs often exhibit
222 concentrations of these metabolites above those considered safe for human consumption
223 (Aubert *et al.*, 1989; Rosa-Martínez *et al.*, 2022a). Rootstocks development is an
224 emerging field in eggplant breeding. Rootstocks with robust root systems have been

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

233 Unlike tomato and other major vegetable crops, the systematic exploitation of
234 genetic diversity and the use of modern technologies, such as molecular markers, for
235 introgression breeding in eggplant have not sufficiently benefited the development of
236 highly productive and resilient varieties with traits such as disease and pest resistance,
237 yield heterosis through genetic diversity, tolerance to abiotic stresses, including improved
238 rootstocks, removal of undesirable traits such as prickliness, and the development of long-
239 shelf life or seedless materials (Daunay and Hazra, 2012; Chapman, 2020; Arafa *et al.*,
240 2022; Toppino *et al.*, 2022). To achieve an eggplant Green Revolution, systematic efforts
241 must be made to efficiently and rapidly utilize the high genetic diversity present in
242 eggplant and its close wild relatives (CWRs). In particular, the large genetic diversity
243 present in CWRs has been barely exploited and used in eggplant breeding. Moreover,
244 speed breeding techniques, which have proven to be an efficient tool for reducing
245 generation cycles in tomato and Capsicum pepper (Ayenan *et al.*, 2019; Liu *et al.*, 2022;
246 Gimeno-Páiz *et al.*, 2023), are currently absent in eggplant breeding and should be
247 developed for the eggplant Green Revolution.

248

249 **3. The eggplant gene pools and their potential for eggplant breeding enhancement**

250 The vast number of eggplant relatives, with their diverse phenotypic (Figure 1)
251 and physiological characteristics and environmental adaptation differences greatly
252 expands the access to exotic and wild genetic diversity for eggplant breeding. Indeed,
253 eggplant can be hybridized with many wild relatives from the subgenus *Leptostemonum*,
254 which contains over 500 species found in all tropical and subtropical regions of the world,
255 exhibiting specific adaptations to a wide range of environments (Vorontsova and Knapp,
256 2016; Knapp *et al.*, 2019). Conventional breeding methods to introgress the traits of
257 interest in eggplant from allied species were used only sporadically, as many wild
258 relatives displayed partial cross-compatibility with the cultivated species, thus often
259 hampering their effective employment for the crop improvement (Ano *et al.*, 1991;
260 Bletsos *et al.*, 1998). Nevertheless, interspecific hybrids between eggplant and wild
261 relatives have been obtained through sexual crosses using several wild and allied species
262 (Daunay and Hazra, 2012; Rotino *et al.*, 2014; Premabati Devi *et al.*, 2015; Plazas *et al.*,
263 2016; Daunay *et al.*, 2019); This includes species from the Old World (Rotino *et al.*,
264 2014; Plazas *et al.*, 2016; Toppino *et al.*, 2021), as the American species such as *S.*
265 *elaeagnifolium*, *S. torvum*, *S. viarum* and *S. sisymbriifolium* (Daunay and Hazra, 2012;
266 Rotino *et al.*, 2014; Kouassi *et al.*, 2016; Plazas *et al.*, 2016), which diverged from
267 eggplant approximately 6.7, 7.7, 8.3 and 8.9 million years ago, respectively (Särkinen *et*
268 *al.*, 2013). However, most of the studies have been conducted for taxonomic purposes
269 and preliminary breeding works and no information is available about the outcomes of
270 possible attempts of further backcrosses with eggplant (Toppino *et al.*, 2021). The
271 accessibility for breeding of the available genetic diversity of eggplant-related species
272 depends mainly on the genepool (primary, secondary, or tertiary) they belong to (Prohens
273 *et al.*, 2017), although there are significant differences within the secondary and tertiary

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

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

298 The secondary gene pool (GP2) is very broad in terms of number of species
299 (Eggplant clade, Anguivi grade, and Climbing clade), geographic distribution (Africa,
300 Indian subcontinent, Southeast and Eastern Asia), and environmental adaptation (from
301 desertic areas to wet forests; from sea level to 3,300 m) (Vorontsova and Knapp, 2016;
302 Syfert *et al.*, 2016; Knapp *et al.*, 2017). The wild ancestor of eggplant (*S. insanum*)
303 diverged from all GP2 species between 1.5 and 4.6 million years ago (Särkinen *et al.*,
304 2013). Within the GP2, eggplant hybridization and introgression are easier with Eggplant
305 clade species, showing a higher hybridization success, hybrid seed viability and pollen
306 fertility than in the *Anguivi* grade and Climbing clade (Rotino *et al.*, 2014; Plazas *et al.*,
307 2016). Generally, embryo rescue is unnecessary to obtain hybrids and backcrosses with
308 *S. melongena*, although hybridization with GP2 species is more challenging than with
309 GP1 materials (Kouassi *et al.*, 2016; Plazas *et al.*, 2016; Daunay *et al.*, 2019) and
310 sometimes alternative breeding strategies of somatic hybridization were necessary to
311 obtain fertile hybrids (Rotino *et al.*, 1998; Särkinen *et al.*, 2013). Several species
312 belonging to the GP2 such as *S. anguivi*, *S. dasyphyllum*, *S. incanum*, *S. linnaeanum* and
313 *S. tomentosum* (Table 1) have been identified as of great interest for eggplant breeding
314 due to their tolerance to biotic and abiotic stresses and high contents of bioactive
315 compounds beneficial for human health (Syfert *et al.*, 2016; Kaushik *et al.*, 2017; Arafa
316 *et al.*, 2022; Toppino *et al.*, 2022) and for some of them, introgressed and backcrossed
317 population have been obtained, while many GP2 species remain unexplored. Moreover,
318 the two cultivated eggplants (*S. aethiopicum* and *S. macrocarpon*) are also valuable for
319 eggplant breeding, as aside from presenting characteristics of interest for eggplant
320 breeding, they display the typical traits associated to the domestication syndrome, which
321 facilitates their use in breeding (Särkinen *et al.*, 2013; Plazas *et al.*, 2014).

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

342 Overall, the large genetic, phenotypic and physiological diversity present in the
343 three genepools represents an enormous potential for eggplant breeding, which has been
344 barely explored, particularly in the case of wild species (Daunay and Hazra, 2012; Rotino
345 *et al.*, 2014; Taher *et al.*, 2017; Toppino *et al.*, 2021, 2022; Arafa *et al.*, 2022; Salinier *et*
346 *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

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

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

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

397 aiming at evaluating the morphological diversity of cultivated eggplant (Cericola *et al.*,
398 2013; Kumar *et al.*, 2013; Liu *et al.*, 2018; Oladosu *et al.*, 2021; Ro *et al.*, 2022). These
399 studies revealed a large diversity of morpho-agronomic characteristics in the cultivated
400 eggplant genepool and provided relevant information for their utilization in breeding.
401 Large screening for evaluation traits in germplasm collections of eggplant relatives is
402 more limited. Field evaluation of 70 *S. aethiopicum* accessions, mostly belonging to *gilo*
403 group, was assessed for morpho-physiological, molecular (AFLP and SSR markers) and
404 chlorogenic acid content highlighted a wide genetic diversity (Sunseri *et al.*, 2010). A
405 total of 125 accessions of *S. aethiopicum* and *S. macrocarpon* were evaluated by Taher *et*
406 *al.* (2019) for resistance to the two-spotted spider mite (*Tetranychus urticae*), resulting in
407 the identification of high levels of resistance in two accessions of *S. macrocarpon*. In
408 another large evaluation study, Stommel and Whitaker (2003) studied the phenolic acid
409 profiles of 115 accessions, mostly of cultivated *S. melongena*, but also including some
410 accessions of *S. aethiopicum*, *S. anguivi*, *S. incanum* and *S. macrocarpon*. Another study
411 on 73 accessions, most of which were of *S. melongena*, but also included *S. aethiopicum*
412 and *S. macrocarpon*, also found large variations in total phenolics content (8.4-fold), and
413 fruit flesh browning (7.3-fold), but less in ascorbic acid (2.3-fold) (Prohens *et al.*, 2007).

414 Overall, given the large number of species in the GP2 and GP3 of eggplant, the
415 Focused Identification of Germplasm Strategy (FIGS), which is based on the assumption
416 that wild accessions growing in specific environments must have adaptive genes to these
417 conditions (Street *et al.*, 2016), might help in identifying putative species or accessions
418 of interest for tolerance to a certain biotic or abiotic stress (Prohens *et al.*, 2017).
419 However, the exploration of eggplant and relatives germplasm collections for traits
420 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

424 **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

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

460 Accessions of wild species of eggplant GP2 and GP3 species, as well as from the
461 cultivated *S. aethiopicum*, have been employed for introgression breeding (Mennella *et*
462 *al.*, 2010; Liu *et al.*, 2015; Gramazio *et al.*, 2017; Plazas *et al.*, 2020; Villanueva *et al.*,
463 2021). Eggplant lines fully resistant to *Fusarium* wilt have been obtained by introgressing
464 the *Rfo-sal* resistance locus from *S. aethiopicum* (Toppino *et al.*, 2008). Interestingly, the
465 response mechanism to *Fom* inoculation triggered by this locus is also able to protect the
466 plant from *Verticillium* wilt (Barbierato *et al.*, 2016; Barchi *et al.*, 2018) when the two
467 fungi are used in a combined artificial inoculation. These elite *Fusarium* wilt-resistant
468 lines introgressed from *S. aethiopicum*, along with associated molecular markers, are of
469 great interest for the development of commercial cultivars.

470 *Solanum linnaeanum* has also been used in introgression breeding 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*

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

500 It is worth considering that interspecific hybrids of eggplant with some wild
501 species such as *S. tomentosum* or *S. elaeagnifolium* (Figure 4) are highly vigorous and
502 have an extended root system (García-Forteza *et al.*, 2019), making them exploitable as
503 rootstocks. However, in some cases such as the hybrids between *S. melongena* and *S.*
504 *elaegnifolium*, the obtainment of hybrids is very challenging and requires embryo rescue
505 (Kouassi *et al.*, 2016), limiting their exploitation. Introgression breeding with wild
506 species that display high contents of glycoalkaloids (solasonine and solamargine) might
507 result in the inadvertent increase of these glycoalkaloids in the recurrent eggplant parents.
508 However, studies performed by Mennella *et al.* (2010) with *S. aethiopicum* and *S.*
509 *linnaeanum* and by Rosa-Martínez *et al.* (2022a) with *S. incanum* did not detect
510 significantly higher levels of glycoalkaloids in introgression lines (ILs) with these species
511 than in the recurrent parents. However, given that these ILs did not represent the whole
512 genome of the donor parents, the evaluation of glycoalkaloids should be performed in the
513 elite materials obtained after the introgression process with eggplant relatives that exhibit
514 high contents in potentially harmful glycoalkaloids. Similarly, given that in Solanaceae
515 glycoalkaloids synthesized in the roots can move up in the plant (Kodama *et al.*, 2021),
516 in the case of using wild species or interspecific hybrids with high contents of
517 glycoalkaloids as rootstocks, the content in the fruit should be checked to ensure the safety
518 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 al.*
541 *et al.*, 2017; Du *et al.*, 2022). Two ethyl methane sulfonate (EMS) mutant libraries of 400
542 and 790 M₂ 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.*, 2019a). 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

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

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

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

621 The first ILs of eggplant with related species were obtained after backcrossing two
622 somatic hybrids or dihaploids derived from them resulting from the crossing between
623 eggplant lines 1F5(9) and Dourga and two *S. aethiopicum* lines (Toppino *et al.*, 2008).
624 Also, introgression lines were obtained after hybridization of several eggplant lines with
625 *S. linnaeanum* (Mennella *et al.*, 2010). In total, 57 ILs derived from these programmes
626 after 6-7 cycles of backcrossing were studied for several health-related compounds and
627 PPO activity (Mennella *et al.*, 2010). The results revealed that both ILs sets displayed
628 similar levels to the recurrent parents for glycoalkaloids, indicating their safety for human
629 consumption, while a significant number of ILs displayed better values for antioxidant
630 compounds. Subsequently, Gramazio *et al.* (2017) used marker-assisted selection in the
631 repeated backcrossings (up to BC6) and subsequent selfings between *S. melongena*
632 accession ANS26 and *S. incanum* accession MM577. This resulted in 25 ILs with single
633 introgressions that covered 61.7% of the *S. incanum* genome, which was recently
634 increased to over 70% of the *S. incanum* MM577 genome (Plazas *et al.*, 2020). A subset
635 of these ILs have been characterized for morphological and agronomic traits (Mangino *et*
636 *al.*, 2020; Rosa-Martínez *et al.*, 2022b), fruit shape characteristics (Mangino *et al.*, 2021),
637 and composition (Rosa-Martínez *et al.*, 2022a,b), putting in evidence several stable QTLs
638 and revealed the low levels of glycoalkaloids found in the ILs. Toppino *et al.* (2018)
639 recently developed 90 ILs carrying introgressions from the wild relative *S. tomentosum*,
640 which may be of great interest for breeding for resistance to several traits present in this
641 wild relative, such as resistance to *Fusarium*, *Verticillium* or nematodes as well as to
642 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

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

674 A first draft of the eggplant genome was published in 2014 (Hirakawa *et al.*,
675 2014), but improved eggplant genome assemblies have not been available until recently
676 (Wei *et al.*, 2020; Barchi *et al.*, 2021, 2022; Li *et al.*, 2021) and this has delayed the
677 application of the potential of resequencing and pangenome projects to eggplant genetic
678 resources enhancement and management. Also, the availability of resequencing data from
679 eight accessions (Gramazio *et al.*, 2019) allowed the development of the eggplant 5k
680 probes SPET platform (Barchi *et al.*, 2019a), which is the first specific eggplant
681 genotyping platform. The SPET genotyping platform has been used for the genotyping of
682 germplasm of eggplant and wild relatives and the first MAGIC population (Barchi *et al.*,
683 2019a, 2022; Gramazio *et al.*, 2020; Arrones *et al.*, 2022) as well as the marker-assisted
684 selection for the development of introgression lines (Plazas *et al.*, 2020; Villanueva *et al.*,
685 2021). The first eggplant pangenome, which included the resequencing data of 23
686 accessions of *S. melongena* and two of CWRs (*S. incanum* and *S. insanum*) is very recent
687 (Barchi *et al.*, 2021). This eggplant pangenome allowed the identification of additional
688 genes compared to the reference genome used, as well as selective sweeps during
689 domestication and the associated underlying candidate genes (Barchi *et al.*, 2021).

690 Genebank genomics can help in the management and utilization of eggplant germplasm
691 collections (Mascher *et al.*, 2019), but so far no studies have been performed on eggplant.
692 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-enabled 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-Forteza *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

712 **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-Forteza *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 gene pools, in which the 5k
745 probes SPET platform was designed (Barchi *et al.*, 2019a) and used for the largest
746 genotyping effort in eggplant germplasm (around 3,500 accessions), allowing the
747 evaluation of diversity of the eggplant gene pool, 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

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

774

775 **Conflict of interest**

776 The authors declare that there is no conflict of interest.

777

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810

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Tables

Table 1. *Solanum* species from the primary (GP1), secondary (GP2) and tertiary (GP3) gene pools (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 <i>S. melongena</i>	References
Primary gene pool (GP1)			
<i>S. insanum</i>	Drought and salinity tolerance, phytochemical composition	Advanced backcrosses	Ranil <i>et al.</i> (2017); Brenes <i>et al.</i> (2020); Plazas <i>et al.</i> (2020); Nadeeshani <i>et al.</i> (2021); González-Orenga <i>et al.</i> (2023)
Secondary gene pool (GP2)			
<i>S. aethiopicum</i>	Resistance or tolerance to <i>Fusarium</i> and bacterial wilts and nematodes, vigor of F1 hybrids as rootstocks, spider mite resistance	Lines with introgressed resistance to <i>Fusarium</i> and <i>Verticillium</i> wilt	Collonnier <i>et al.</i> (2001); Toppino <i>et al.</i> (2008); Prohens <i>et al.</i> (2012); Calvo-Asensio <i>et al.</i> (2014); Barbierato <i>et al.</i> (2016); Barchi <i>et al.</i> (2018); Taher <i>et al.</i> (2019); Zhuang & Wang (2009)
<i>S. anguivi</i>	Drought tolerance, high content of phenolics	Second backcross generation	Kaushik <i>et al.</i> (2019); Plazas <i>et al.</i> (2020); Kouassi <i>et al.</i> (2021)
<i>S. dasyphyllum</i>	Drought tolerance, two-spotted spider mite and silverleaf whitefly tolerance	Advanced backcrosses	Plazas <i>et al.</i> (2020); Kouassi <i>et al.</i> (2021); Taher <i>et al.</i> (2020); Villanueva <i>et al.</i> (2023)
<i>S. incanum</i>	Drought tolerance, bacterial wilt resistance, fruit and shoot borer resistance, silverleaf whitefly tolerance, high content of phenolics	Introgression lines	Bletsos and Olympios (2008); Prohens <i>et al.</i> (2013); Gramazio <i>et al.</i> (2017); Namisy <i>et al.</i> (2019);

<i>S. lichtensteinii</i>	Drought tolerance, silverleaf whitefly tolerance	Second backcross generation	Mangino <i>et al.</i> (2020); Taher <i>et al.</i> (2020) Vorontsova and Knapp (2016); Plazas <i>et al.</i> (2020); Taher <i>et al.</i> (2020)
<i>S. lidii</i>	Unexplored so far	Second backcross generation	Plazas <i>et al.</i> (2020)
<i>S. linnaeanum</i>	Salinity tolerance, Verticillium wilt resistance	Lines with introgressed resistance to Verticillium wilt	Mennella <i>et al.</i> (2010) Acciarri <i>et al.</i> 2007; Zhuang <i>et al.</i> (2014); Liu <i>et al.</i> (2015)
<i>S. tomentosum</i>	Fusarium and Verticillium wilts and nematodes resistance, silverleaf whitefly tolerance	Introgression lines	Toppino <i>et al.</i> (2018); Taher <i>et al.</i> (2020)
Tertiary genepool (GP3)			
<i>S. elaeagnifolium</i>	Drought tolerance, high content of phenolics	Advanced backcrosses	García-Fortea <i>et al.</i> (2019); Plazas <i>et al.</i> (2020); Villanueva <i>et al.</i> (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			
<i>S. melongena</i> accession E31-1	790	Ethyl methane sulfonate	Xi-ou <i>et al.</i> (2017)
<i>S. melongena</i> line 14-345	400	Ethyl methane sulfonate	Du <i>et al.</i> (2022)
Core collections			
1,798 accessions of <i>S. melongena</i>	181	14 morphological descriptors	Gangopadhyay <i>et al.</i> (2010)
392 accessions of <i>S. melongena</i>	191	314 SNPs, 33 morphological traits, NUE	Cericola <i>et al.</i> (2013), 2014, Portis <i>et al.</i> (2015), Mauceri <i>et al.</i> (2020); Miyatake <i>et al.</i> (2019)
893 accessions of <i>S. melongena</i>	100	831 SNPs and 50 SSRs	Miyatake <i>et al.</i> (2019)
587 accessions of <i>S. melongena</i>	288	52 SNPs and 17 agromorphological traits	Ro <i>et al.</i> (2022)
3,600 accessions of <i>S. melongena</i> and wild relatives	322	5k probes SPET platform	Gaccione <i>et al.</i> (2022)
Biparental recombinant inbred lines			
<i>S. melongena</i> lines MM378 and AG91-25	178 F6	AFLP, SSR and SRAP	Lebeau <i>et al.</i> (2013)
<i>S. melongena</i> lines 305E40 and 67/3	163 F7	GBS (10 k polymorphic markers)	Toppino <i>et al.</i> (2020)
<i>S. melongena</i> landrace Ramnagar Giant and <i>S. incanum</i> accession W-4	114 F8	282 polymorphic RAPD, ISSR, SCoT and SSR	Mishra <i>et al.</i> (2020)
Multiparental recombinant inbred lines			

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