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# Conventional and new genetic resources for an eggplant breeding revolution

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Running title: Eggplant conventional and new genetic resources

## Highlight

This review emphasizes the importance of genetic resources, including germplasm accessions and new experimental populations, for a breeding revolution in eggplant in the context of climate change.

## Abstract

Eggplant (*Solanum melongena*) is a major vegetable crop with great potential for genetic improvement owing to its large and mostly untapped genetic diversity. Eggplant is closely related to over 500 species of *Solanum* subgenus *Leptostemonum,* belonging to its 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, most of which have yet to be evaluated. Nonetheless, eggplant breeding using the cultivated *S. melongena* genepool has yielded significantly improved varieties. 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 can greatly contribute to a revolution in eggplant breeding. The recent creation of new genetic resources, such as mutant libraries, core collections, recombinant inbred lines (RILs), and sets of introgression lines (ILs) will be another crucial element for an eggplant breeding 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 a much-needed eggplant breeding revolution to address the challenges posed by climate change.

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

## Introduction

Eggplant (*Solanum melongena* L.), also known as common eggplant, brinjal or aubergine, was domesticated 9,000-10,000 years ago from its wild ancestor *S. insanum* L. in the Indian subcontinent and southeast Asia (Page *et al.*, 2019*a;* Barchi et al, unpublished). Apart from the intra-specific diversity of eggplant over 500 species of *Solanum* subgenus *Leptostemonum* (Vorontsova and Knapp, 2016; Knapp *et al.*, 2019), belonging to its primary, secondary and tertiary genepools provide a formidable source of additional diversity (Syfert *et al.*, 2016). As the sixth most important vegetable crop in production globally, following tomato, onion, watermelon, cucumber and cabbage (FAOSTAT, 2023), eggplant holds significant agricultural value. Its global production has increased by 24% over the past decade, from $47.3\cdot10^6$ t in 2012 to $58.6\cdot10^6$ t in 2021 (FAOSTAT, 2023). As a warm-climate crop, it is mostly cultivated in tropical, subtropical, and temperate regions of the world, and is an important part of the cuisine from East Asia, the Indian subcontinent, Southern Asia, the Middle East, and the Mediterranean basin. Eggplant contributes to alleviating "hidden hunger" by providing significant dietary amounts of K, P, Mn,Cu and folate, but also high concentrations of bioactive phenolics beneficial for human health (Plazas *et al.*, 2013; Rosa-Martínez *et al.*, 2021).

In recent years, the impact of climate change on agricultural production has become a significant concern, and eggplant cultivation is expected to be strongly affected by its effects (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).

Although significant advances have occurred in eggplant breeding (Daunay and Hazra, 2012; Chapman, 2020; Toppino *et al.*, 2021; Arafa *et al.*, 2022) they have not kept pace with other major vegetable crops, such as tomato. 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). While eggplant breeding programs have been successful in developing new improved cultivars, until now only a few of them have involved the introgression of useful traits. For example, resistance to the fungal wilts *Fusarium oxysporum* f. sp. *melongenae* (*Fom*) and *Verticillium dahliae* from *S. aethiopicum* (Toppino *et al.*, 2007, 2008*b*, 2009) and *S. linnaeanum* (Liu *et al.*, 2015) has been exploited with considerable success and new resistant materials of eggplant to these diseases have been obtained (Toppino *et al.*, 2021).

In addition to brinjal 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 mostly 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). The fact that both species are cross-compatible with common eggplant (Bletsos *et al.*, 2004; Oyelana and Ugborogho, 2008; Rotino *et al.*, 2014) is of great relevance for the breeding of the latter crop, as they share many domestication traits, facilitating the introduction of resistance to some pests and diseases from these species to common eggplant without dragging undesirable traits present in wild species (Toppino et al., 2021; Arafa et al., 2022).

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 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 traits (Daunay *et al.*, 2004; Portis *et al.*, 2015; Toppino *et al.*, 2016; Mangino *et al.*, 2021; Arrones *et al.*, 2022; Guan *et al.*, 2022), and the overall genetic variation of the crop is narrow (Acquadro *et al.*, 2017; Barchi *et al.*, 2019*a*; Liu *et al.*, 2019). Therefore, the exploitation of the genetic diversity present in other cultivated eggplants (*S. aethiopicum* and *S. macrocarpon*) and wild relatives represents a promising avenue for developing improved eggplant materials by incorporating unique traits from these exotic materials (Oyelana and Ugborogho, 2008; Prohens *et al.*, 2012; Toppino *et al.*, 2021).

## Eggplant breeding challenges for the present and the future: the need for a breeding revolution

Eggplant yield increased dramatically from a global average of 10.2 t/ha in 1961-1970 to 28.0 t/ha in the 2012-2021 decade (FAOSTAT, 2023). There is not much information on the genetic vs. agronomic factors that have driven this dramatic yield increase, although Muñoz-Falcón *et al.* (2009) found that modern varieties of black eggplants yielded on average 29.8% more than landraces, suggesting that improvement of cultural techniques such as protected cultivation, irrigation, improved fertilization and pest and pathogens management, may have had a major role in yield increase in the last decades. This suggests that major genetic advances that occurred in the past in other major staple and vegetable crops (Hedden, 2003; Díez and Nuez, 2008) may still have to occur in the coming decades for eggplant breeding, resulting in dramatically improved varieties, adapted to the new conditions posed by climate change. So far, breeding advances and actual exploitation of genetic resources in eggplant, particularly those from related species, are not comparable to those obtained in other major vegetable crops such as tomato (Schouten *et al.*, 2019). Although tomato has a narrow genetic diversity and exhibits limited crossability with only a few CWRs, considerable broadening of the genetic base and genetic advances have been achieved in this species through introgression breeding using wild relatives as donors. Among these achievements, the introgression of multiple genes for tolerance to diseases and fruit quality traits, the development of heterotic hybrids, the improvement of shelf-life, the diversification of varietal types, and the adaptation to multiple environments (Díez and Nuez, 2008), enabled the production of a large number of highly productive tomato varieties of many different typologies, resistant to the major diseases and suited to different environments. The success obtained in the extensive use of genetic resources in tomato breeding suggests that in eggplant, which exhibits an even greater diversity of cross-compatible relatives, the advances in breeding for adaptation to climate change and other traits, achievable with a systematic use of its genetic resources may be extraordinary.

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) - a genotyping technique that employs targeted amplification of specific genomic regions using a single specific primer - (Scaglione *et al.*, 2019), 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 both species, which in turn impacts on the applicable breeding methods.

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 (i.e., when a hybrid displays superior quantitative traits, such as yield, with respect to the standard parent) (Kakizaki, 1931; Sambandam, 1964) and heterobeltiosis (i.e., when a hybrid displays superior quantitative traits with respect to the best parent)) 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 of eggplant with excellent yields are also available and extensively cultivated (Muñoz-Falcón *et al.*, 2009; Taher *et al.*, 2017). However, further improvement of the yield potential is a significant challenge in eggplant breeding, which will undoubtedly benefit from the incorporation of new genetic diversity to allow additional genetic advances (Muñoz-Falcón *et al.*, 2009; Daunay and Hazra, 2012).

One of the major current challenges in eggplant breeding is the development of breeding lines with an improved tolerance or resistance to major pests and diseases (Toppino *et al.*, 2021), which may cause crop losses of up to 100% (Daunay and Hazra, 2012; Arafa *et al.*, 2022). Eggplant is affected by numerous diseases, although the most relevant in terms of economic impact is the bacterial wilt caused by *Ralstonia solanacearum*, which is highly prevalent in tropical regions (Lebeau *et al.*, 2013; Barik *et al.*, 2020). In many cases, bacterial wilt prevents eggplant cultivation unless plants are grafted onto resistant rootstocks (Namisy *et al.*, 2019). Verticillium and Fusarium wilts, as well as nematodes, are also important eggplant pathogens in many regions of the world (Arafa *et al.*, 2022). So far, most eggplant modern commercial varieties do not carry genes for disease resistance (Srinivasan, 2009). Introgression breeding from the multiple sources of resistance found in eggplant-related species can result in the development of a new generation of materials with resistance to the main eggplant pathogens, mimicking the process occurred in tomato breeding,, where the incorporation of disease-resistant genes introgressed from wild relatives are crucial technical innovations for the success of modern commercial varieties (Díez and Nuez, 2008; Schouten *et al.*, 2019).

The eggplant fruit and shoot borer (*Leucinodes orbonalis*), is the most damaging and difficult pest to control in the Indian subcontinent, Southern and East Asia, where multiple insecticide sprays are used to partially control it (Srinivasan, 2008). This pest is such a damaging and limiting factor in eggplant cultivation that two countries (Bangladesh and the Philippines) have authorized the use of genetically modified *Bt* eggplants expressing the cry1Ac gene from *Bacillus thuringiensis* to control the eggplant fruit and shoot borer (Shelton *et al.*, 2018; Gonzalvo *et al.*, 2022). Additional pests 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 such as CleanLeaf® (Rijk Zwaan, De Lier, The Netherlands) has improved biological pest control in greenhouse cultivation, as the pests are more accessible to their predators and parasites. The development of new resistant or tolerant varieties can benefit from the use of eggplant genetic resources, as sources of variation to the main diseases are available in these materials (Arafa *et al.*, 2022).

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). 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); however, 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 as well as to soil flooding are also important breeding objectives. Despite being a warm-climate 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 is impaired by low temperatures (Toppino *et al.*, 2022). To this purpose, 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 a more sustainable agriculture. In this context, breeding for better root systems could lead to more sustainable production (Chapman, 2020).

Diversification and improvement of fruit quality (Daunay and Hazra, 2012) represent other important challenges in breeding. Eggplant displays a large diversity of fruit sizes, shapes, and colors, facilitating breeding for outer fruit quality and appearance traits. QTLs (quantitative trait loci) 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), although 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). The identification of causative genes underlying other important traits for fruit appearance, such as the presence of fruit stripes, fruit netting or prickliness, will provide additional tools for eggplant breeding. Eggplant is one of the vegetables with the highest antioxidant and bioactive properties, resulting from its high content of phenolic acids (Kaushik *et al.*, 2015), which are also associated with increased browning of the fruit flesh (Mishra *et al.*, 2013; Docimo *et al.*, 2016; Kaushik *et al.*, 2017), a non-desirable trait. Breeders, by directly selecting genotypes with low fruit browning, indirectly selected for low content in phenolic acids (Prohens *et al.*, 2007). Selection for low polyphenol oxidase (PPO) activity has been proposed to improve the phenolic acid content while limiting the effects of browning, (Plazas *et al.*, 2013). Indeed, CRISPR/CAS9 editing of *PPO* genes expressed in the fruit has been shown to reduce fruit flesh browning without affecting phenolic acid content (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). Finally, saponins present in the fruit flesh tissues contribute to the bitterness of some accessions, which is also an undesirable trait (Aubert *et al.*, 1989). In summary, research on the above traits for a more efficient development of improved eggplant cultivars.

Eggplant CWRs often exhibit concentrations of glycoalkaloids above those considered safe for human consumption (Aubert *et al.*, 1989; Rosa-Martínez *et al.*, 2022*a*). This represents a challenge in introgression breeding of eggplant, although several works showed that most introgression lines display glycoalkaloid concentrations similar to those of the cultivated recurrent parent (Mennella *et al.*, 2010; Rosa-Martínez *et al.*, 2022*a*). This indicates that, although levels of glycoalkaloids have to be monitored in the introgressed breeding lines, most of them will be safe for consumption.

Rootstock development is another important 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 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).

The systematic exploitation of genetic diversity and the use of modern technologies, such as molecular markers, for introgression breeding in eggplant will facilitate 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 a successful breeding 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, so far, the large genetic diversity present in CWRs has been barely exploited and used in eggplant breeding. Moreover, speed breeding techniques, such as cold priming at the expanded cotyledon stage, K fertilization supplementation, and embryo rescue, have proven to be efficient tools for reducing generation cycles in tomato and pepper (Manzur *et al.*, 2014; Ayenan *et al.*, 2019; Gimeno-Páiz *et al.*, 2023), need to be developed for a faster and more efficient eggplant breeding revolution.

## The eggplant genepools and their potential for eggplant breeding enhancement

The large diversity present in cultivated eggplant for morphological and agronomic traits of interest (Figure 1) has facilitated the development of new varieties with improved performance and new combinations of traits (Taher *et al.*, 2017). However, intra-specific variation is reduced for some traits, particularly tolerance to some biotic and abiotic stresses (Arafa *et al.*, 2022) and improving such traits will require accessing inter-specific diversity. In addition, the vast number of eggplant relatives, with their diverse phenotypic (Figure 1) and physiological characteristics and environmental adaptation 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 are adapted to a wide range of environments of all tropical and subtropical regions of the world (Vorontsova and Knapp, 2016; Knapp *et al.*, 2019). Many of these wild relatives can be crossed with eggplant (Daunay and Hazra, 2012; Rotino *et al.*, 2014; Plazas *et al.*, 2016), facilitating conventional breeding methods to introgress the traits of interest in eggplant from allied species. Interspecific hybrids between eggplant and wild relatives as well as backcrosses with eggplant 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 include many species from the Old World (Rotino *et al.*, 2014; Plazas *et al.*, 2016; Toppino *et al.*, 2021), as well as 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). 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). *S. 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*). *Solanum insanum* has a high potential 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 already 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 change, which could be easily transferred to 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 such as 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 populations have been obtained, while many other interesting GP2 species still unexploited in breeding hold great potential.  Moreover, the two cultivated eggplants (*S. aethiopicum* and *S. macrocarpon*) are also valuable for eggplant breeding, since 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 2) (Knapp *et al.*, 2013; Syfert *et al.*, 2016). As expected, the success of hybridization of eggplant with GP3 species is very low, although attempts to obtain interspecific hybrids with eggplant have been successful in several 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 with adaptation to climate change and meeting the urgent need for an eggplant breeding revolution.

## Eggplant germplasm collections

Based on the recent Global Strategy for the Conservation and Use of Eggplants (Solberg *et al.*, 2022), 19,020 accessions of cultivated eggplants and relatives are conserved in 110 germplasm banks and collections around the world (Figure 3) (FAO, 2010). The largest genebank collections of eggplant are conserved at the National Bureau of Plant Genetic Resources (India; 4,236 accessions), the World Vegetable Center (an international organization with eggplant germplasm collections headquartered in Taiwan; 3,036 accessions), the INRAE Genebank of France (2,388 accessions), the National Genebank for Vegetable Germplasm Resources of China (1,601 accessions) and the NARO Genebank of Japan (1,501 accessions) (Taher *et al.*, 2017; Salinier *et al.*, 2022; Solberg *et al.*, 2022).

When considering the Genesys (https://www.genesys-pgr.org/) and WIEWS (World Information and Early Warning System on Plant Genetic Resources for Food and Agriculture; https://www.fao.org/wiews/en/) global germplasm databases, most of the conserved materials of the eggplant genepools correspond to cultivated *S. melongena* (12,665 accessions), *S. aethiopicum* (1,004) and *S. macrocarpon* (208) while the wild species of the GP1, GP2 and GP3 genepools are much less represented (2,351 accessions in total) (Solberg *et al.*, 2022). Among the wild species, *S. incanum* is the most abundant (GP2; 423 accessions), followed by *S. torvum* (GP3; 358 accessions), *S. aculeatissimum* (GP3; 210 accessions), *S. virginianum* (GP2; 187 accessions) and *S. grandiflorum* (GP3;

184 accessions). However, apart from these five wild species, the number of remaining wild species accessions from GP2 and GP3 of eggplant is dramatically low, with just 14 species having more than 10 accessions conserved, while for many others no accessions are conserved 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 six of them (including S. *ruvu*, which is considered extinct in the wild) no accessions are conserved in germplasm banks 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. Seventy *S. aethiopicum* accessions, mostly belonging to the *gilo* group, were assessed for morpho-physiological traits, AFLP (amplified fragment length polymorphism) and SSR (simple sequence repeat) molecular markers and chlorogenic acid content, revealing 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 a breakthrough in eggplant breeding, it is essential to systematically evaluate the available variation and identify sources of variation for adaptation to climate change.

## Use of genetic resources in breeding: achievements and challenges

Selections of eggplants started very early in breeding, with accessions having improved characteristics already present in seed catalogues in the late 19th and early 20th centuries (Daunay and Janick, 2007). In addition, heterosis for yield was already reported in 1931 (Kakizaki, 1931), which opened the door for the development of hybrid varieties with improved features. Genetic improvements in eggplant have relied on the use of germplasm, and breeders have been using the eggplant germplasm (mostly of cultivated *S. melongena*) for breeding and developing new selections, lines and hybrids. According to a survey of germplasm banks (Solberg *et al.*, 2022), the number of eggplant accessions distributed per year ranged between 0 and 503, revealing that some germplasm banks make a significant distribution to users, many of whom are breeders.

The genetic improvements of eggplant are evident in the characteristics of modern cultivars, which are considerably better in yield and overall quality than landraces. For example, by considering the western market modern F1 hybrid cultivars found in western markets have no prickles, greater earliness, intense black color and epidermal shininess, and lower fruit flesh browning (Prohens *et al.*, 2007; Muñoz-Falcón *et al.*, 2009) or increased yield (Sambandam, 1964; Rodríguez-Burruezo *et al.*, 2008; Daunay and Hazra, 2012; Kaushik *et al.*, 2018; Kumar *et al.*, 2020). The development of modern eggplant cultivars has been mainly carried out employing the cultivated genepool. This resulted in a reduction of the genetic base of eggplant elite breeding lines and materials used for developing modern F1 hybrids. For instance, Muñoz-Falcón *et al*. (2009) evaluated the 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 F. oxysporum f. sp. *melongenae* (Fom) have been obtained by introgressing the *Rfo-sa1* resistance locus from *S. aethiopicum* (Toppino *et al.*, 2008b). 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

*Fom*-resistant lines introgressed from *S. aethiopicum*, along with associated molecular markers, are of great interest for the development of commercial cultivars.

*Solanum linnaeanum* has also been used in introgression breeding for the development of early backcross eggplant materials with resistance to Verticillium wilt (Acciarri *et al.*, 2004; Liu *et al.*, 2015). However, no eggplant commercial cultivars with resistance derived from *S. linnaeanum* have been produced until now.

First backcross generations of eggplant with *S. aethiopicum* as a donor displayed a wide morphological variability (Prohens *et al.*, 2012). Similarly, high morphological diversity and a wide range of values for phenolic acid contents were found in the first backcross generations using *S. incanum* as the donor parent (Prohens *et al.*, 2013). However, introgression lines (ILs) derived from these early *S. incanum* backcrosses were largely similar to the recurrent parent, although two lines with higher plant vigour were identified (Mangino *et al.*, 2020). Some advanced backcrosses with *S. elaeagnifolium* exhibited a higher yield than the recurrent *S. melongena* parent (Villanueva *et al.*, 2021). However, these materials are still in an early stage of development and have not been used for the development of new cultivars. In addition, several species such as *S. aethiopicum*, *S. anguivi*, *S. grandiflorum*, *S. kurzii*, *S. violaceum* and *S. virginianum* have been used for the development of alloplasmic lines of eggplant that display cytoplasmic male sterility (Khan and Isshiki, 2016). These male-sterile lines have potential interest in the production of hybrids. However, to our knowledge, alloplasmic male sterility has not been used so far in the commercial production of eggplant hybrids.

Eggplant wild species and interspecific hybrids have also been explored for their use as rootstocks, mainly to obtain resistance to diseases and enhanced vigor (King *et al.*, 2010; Schwarz *et al.*, 2010). In this way, apart from selections of *S. torvum* and interspecific hybrids between eggplant and *S. aethiopicum* used as commercial rootstocks, other wild species, such as *S. anguivi*, *S. incanum*, *S. insanum*, *S. 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 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 some toxic alkaloids synthesized in the roots can move in the epigeal part of the plant, in the case of using wild species or interspecific hybrids with high alkaloid contents as rootstocks, the content in the fruit should be checked to ensure the safety of the potential new commercial varieties.

Although considerable improvements have been made in eggplant breeding, the diversity used mostly relied on the cultivated eggplant *S. melongena* (Daunay and Hazra, 2012; Taher *et al.*, 2017; Kumar *et al.*, 2020). Furthermore, breeding efforts have been made in using eggplant CWRs for breeding, even if they did not have a major impact on the modern cultivars presently grown. As in other important crops, a qualitative leap forward in genetic advances in eggplant will require unleashing the huge potential of CWRs, which is still largely unexploited.

## A new generation of genetic resources

Besides germplasm accessions of eggplant cultivated and CWRs, during the last years a new generation of eggplant genetic resources, consisting of core collections, recombinant inbred lines (RILs), and ILs (Table 2) have been generated (Toppino *et al.*, 2008*b*, 2018, 2020; Gangopadhyay *et al.*, 2010; Mennella *et al.*, 2010; Lebeau *et al.*, 2013; Gramazio *et al.*, 2017; Barchi *et al.*, 2018; Miyatake *et al.*, 2019; Mishra *et al.*, 2020; Arrones *et al.*, 2022; Ro *et al.*, 2022; Gaccione *et al.*, 2022; Mangino *et al.*, 2022). These materials are considered immortal since they can be regenerated by selfing for seed propagation. This is in contrast to F2 and early backcross materials, for which several populations have been obtained in eggplant (Daunay and Hazra, 2012; Prohens *et al.*, 2012, 2013; Clarke *et al.*, 2014; Portis *et al.*, 2014; Toppino *et al.*, 2016; Boyaci *et al.*, 2021; Qian *et al.*, 2022), and where each individual has a variable degree of heterozygosis and can be thus maintained only by vegetative propagation.

We should also point out that few mutant collections exist so far for eggplant (Xi-ou *et al.*, 2017; Du *et al.*, 2022). Two ethyl methane sulfonate (EMS) mutant libraries of 400 and 790 $M_2$ lines (Table 2) were generated and used to identify mutants for phenotypic traits, including dwarf mutant plants (Xiao *et al.*, 2016; Xi-ou *et al.*, 2017; Lu *et al.*, 2021; Du *et al.*, 2022).

Core collections allow a representation of most of the diversity of large germplasm set in a reduced number of accessions (Odong *et al.*, 2013) exploitable for genotype to phenotype studies. The first eggplant core collection of 181 eggplant accessions was developed by Gangopadhyay *et al.* (2010) from an original set of 1,798 accessions by using 14 morphological descriptors (Table 2). In a first attempt to apply a GWAS (genome-wide association study) approach in eggplant, Ge *et al.* (2013) were able to identify several phenotype/genotype associations related to eight fruit-related traits. Subsequently, a selected eggplant association panel of 191 selected accessions (Cericola *et al.*, 2013), comprising a mixture of breeding lines, old varieties and landrace selections originating from Asia and the Mediterranean Basin, was genotyped and phenotyped. This allowed the identification and positioning of several marker/trait associations related to fruit, plant and leaf morphological traits relevant to eggplant breeding (Cericola *et al.*, 2014; Portis *et al.*, 2015) as well as to identify contrasting genotypes for nitrogen use efficiency (NUE) (Mauceri *et al.*, 2020) and, most recently, to identify the gene networks responsible of such diversity (Mauceri *et al.*, 2021).

Subsequently, Miyatake *et al.* (2019) genotyped 893 accessions, mostly from Asia, with 831 SNP and 50 SSR markers and established a core collection of 100 accessions (World Eggplant Core; WEC). More recently, a core collection of 288 accessions from an initial set of 587 accessions by using 52 SNP markers complemented with agro-morphological traits (Ro *et al.*, 2022). The combination of both types of data resulted in the identification of significant associations of SNPs with six traits, which allowed the identification of several candidate genes. Another core collection of 322 *S. melongena* accessions was obtained from an original set of over 3,600 accessions

(Gaccione *et al.*, 2022), most of which were genotyped with the 5k probes eggplant SPET platform (Barchi *et al.*, 2019*a*). This core collection has been re-sequenced and phenotyped at three locations for multiple agronomic and composition traits (Gaccione *et al.*, 2022) and has already proved useful in identifying allelic variants for the *SmAPRR2* transcription factor responsible for chlorophyll pigmentation in the eggplant fruit peel (Arrones *et al.*, 2022).

RILs from bi-parental or multi-parental crosses are genetic resources of great relevance, as each of them is a different genetic mosaic of the parents (Arrones *et al.*, 2020). Therefore, new genotypes of interest for breeding combining desirable characteristics present in the set of parents may be recovered in the set of RILs. In addition, in the absence of selection, bi-parental or multi-parental RIL sets do not present genetic structure, which makes them a powerful tool for the detection of major genes and QTLs involved in traits of interest (Cockram and Mackay, 2018). Several RIL populations of eggplant (Table 2), which have in common one eggplant relative (*S. aethiopicum* or *S. incanum*) in their pedigree, have been obtained from bi-parental crosses (Lebeau *et al.*, 2013; Toppino *et al.*, 2020). A first RIL population composed of 178 F6 lines was obtained by single seed descent from the F2 generation obtained after crossing an eggplant line (MM738) susceptible to bacterial wilt with a resistant breeding line (AG91-25) derived from the crossing of a resistant *S. melongena* and an *S. aethiopicum* accession (Lebeau *et al.*, 2013). Genotyping of this RIL population with AFLP, SSR and SRAP (sequence-related amplified polymorphism) markers allowed the construction of a genetic map with 119 polymorphic markers in which a major dominant gene and several QTLs were detected. Interestingly, some RILs displayed better performance than the resistant parent (AG91-25) for some of the resistance traits evaluated (Lebeau *et al.*, 2013). More recently, Toppino *et al.* (2020) developed a RIL population of 163 F7 lines derived from single seed descent of the F2 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 *Fom*, as well as tolerance to Verticillium wilt (Barbierato *et al.*, 2016; Barchi *et al.*, 2018; Toppino *et al.*, 2018). This RIL population was sequenced at low coverage 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 (random amplified polymorphic DNA), ISSR (inter-simple sequence repeat), SCoT (start codon targeted) 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 is a MAGIC (multi-parent advanced generation inter-cross) set of lines of eggplant (MEGGICS3), constituted of 420 S3 lines (Table 2) 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 descent from the S0 quadruple hybrid recombinant generation (Mangino *et al.*, 2022) and has been genotyped with the eggplant 5k SPET panel (Barchi et al.), 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 core collection developed within the H2020 programme project G2P-SOL (Linking genetic resources, genomes and phenotypes of Solanaceous crops; https://www.g2p-sol.eu/), the MAGIC population allowed identifying the gene *SmAPRR2* as responsible for fruit chlorophyll pigmentation in the fruit peel (Arrones *et al*., 2022).

The occurrence of interspecific gene exchanges between eggplant and its relatives is a fundamental prerequisite for enlarging the eggplant genetic pool and, therefore, exploiting the variation resident in the allied germplasm for the improvement of the cultivated species. As an example, the occurrence of tetrasomic inheritance, including chromatid recombination, disclosed in the population of dihaploids obtained from anther culture of the tetraploid somatic hybrid between *S. melongena* and *S. aethiopicum* gr. Gilo (Toppino *et al.*, 2008*a*) it opened up the possibility to introduce this material into advanced breeding programs. The first ILs of *S. melongena* with related species were obtained after recurrent backcrossing of two hybrids between *S. melongena* lines 1F5(9) and Dourga and *S. aethiopicum,* towards cultivated eggplant (Toppino *et al.*, 2008b). Also, ILs 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 IL sets displayed similar glycoalkaloid levels to the recurrent parents, 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*), highlighting several stable QTLs, as well as low levels of glycoalkaloids. 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 (Caliskan *et al.*, 2023), as well as to whitefly (Taher *et al.*, 2020). New sets of ILs with *S. insanum*, *S. dasyphyllum* and *S. elaeagnifolium* are in advanced stages of development (Plazas *et al.*, 2020) and will soon increase the diversity available to eggplant breeders from so far unexplored exotic genetic resources. Advanced backcrosses containing *S. elaeagnifolium* introgressions, screened under low N conditions have revealed a great potential for low-input agriculture (Villanueva *et al.*, 2021).

These new generations of genetic resources make extant eggplant genetic diversity more accessible to breeders, allowing the development of new recombinant genotypes and representing powerful tools for identifying genes/alleles and QTLs associated with traits of interest, including complex traits such as those related to climate change (Prohens *et al.*, 2017; Chapman, 2020). The extended use of these materials has already started to demonstrate their tremendous potential for eggplant breeding (Lebeau *et al.*, 2013; Barchi *et al.*, 2018; Mangino *et al.*, 2020, 2022; Arrones *et al.*, 2022).

## Genomic and biotechnological tools to enhance the exploitation of genetic resources

New genomic tools such as high-throughput genotyping derived from NGS technologies, reference genomes, pangenomes and resequencing projects, can efficiently contribute to the enhancement of eggplant genetic resources and are essential for the breakthrough in eggplant breeding  (Gramazio *et al.*, 2018; Lanteri and Barchi, 2019; Simko *et al.*, 2021). Although DNA molecular markers of different types, such as RAPDs, AFLPs and SSRs have been widely used for eggplant genotyping and genetic mapping since the early 1990s (Collonnier *et al.*, 2001; Gramazio *et al.*, 2014, 2018), the availability of NGS technologies allowed an easier genotyping of large sets of accessions and experimental 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 chromosome-anchored eggplant genome assemblies have not been available until recently (Barchi et al, 2019b; 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 enhance the management of eggplant genetic resources. The availability of resequencing data from eight accessions (Gramazio *et al.*, 2019) allowed the development of an eggplant 5k.

SPET platform (Barchi *et al.*, 2019*a*), which is the first specific eggplant genotyping platform. This 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 ILs (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 and allowed the identification of additional genes compared to the reference genome used, as well as of 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 eggplant with adaptive genes to specific environmental conditions has not been exploited yet. Both genomics approaches have a lot of potential for contributing to the eggplant breeding revolution. The genetic/genomic data and the phenotypic information available on the eggplant genetic resources (i.e. core collection and experimental populations) might lay the foundation to start applying genome-enable prediction methods to both accelerate eggplant breeding and increase the efficiency of the selection processes.

New Plant Breeding Techniques (NPBTs) such as those based on CRISPR (clustered regularly interspaced short palindromic repeats) and Cas (CRISPR-associated protein) genome editing represent valuable tools useful to create novel genetic variation as well as to determine the function of genes via targeted mutagenesis. However, only two studies have been published so far on CRISPR/Cas gene editing in eggplant (Maioli *et al.*, 2020; Kodackattumannil *et al.*, 2023), probably as a consequence of the recalcitrance of *S. melongena* to *in vitro* regeneration (García-Fortea *et al.*, 2020) and genetic transformation. In the study of Maioli *et al.* (2020), polyphenol oxidase (PPO) genes *PPO4*, *PPO5*, and *PPO6* were knocked out, which resulted in reduced fruit flesh browning demonstrating how the creation of new allelic variation contributed to the improvement of an important trait. In a subsequent study, Kodackattumannil *et al*. (2023) found that CRISPR/Cas mutation of *PPO2* resulted in the inhibition of fruit flesh browning, but also had multiple pleiotropic effects in morphological and agronomic traits.

## Conclusions and future perspectives

The exploration of the cultivated and wild eggplant germplasm both at the phenotypic and molecular levels is required for the identification of sources of variation for new traits barely explored so far, such as tolerance to new stresses caused by climate change as well as for improved sustainability, such as water and fertilizers use efficiencies. The establishment of core collections, such as the ones already existing (Gangopadhyay *et al.*, 2010; Miyatake *et al.*, 2019; Gaccione *et al.*, 2022; Ro *et al.*, 2022), as well as the FIGS approach of identification of potentially useful germplasm (Street *et al.*, 2016), genebank and landscape genomics (Li *et al.*, 2017; Mascher *et al.*, 2019) may help in facilitating the identification accessions of interest carrying novel and/or superior alleles.

The eggplant breeding revolution requires coordinated activities and programs for an improved exploitation of its genetic resources enhancement of its genetic resources. Two major international initiatives, the "Adapting Agriculture to Climate Change" (2011-2021) initiative of the Global Crop Diversity Trust (Dempewolf *et al.*, 2014), and the H2020 project G2P-SOL (2016-2021) have demonstrated the enormous potential of international collaboration in the improved conservation and utilization of eggplant genetic resources. In this way, the eggplant activities and projects performed under the "Adapting Agriculture to Climate Change" (2011-2021) initiative allowed the identification of gaps in the eggplant CWRs germplasm collections and proposed priorities for collection and *in situ* conservation (Syfert *et al.*, 2016), as well as the collection of 474 new accessions of eggplant and CWRs (32 different species) for the completion of these gaps (Eastwood *et al.*, 2022). Also, this initiative allowed the development of advanced backcrosses and ILs with four different eggplant CWRs (*S. dasyphyllum*, *S. elaeagnifolium*, *S. incanum* and *S. insanum*) (Gramazio *et al.*, 2017; Plazas *et al.*, 2020; Villanueva *et al.*, 2021). Characterization of these sets of ILs for multiple traits and stress conditions is expected to result in new materials with improved adaptation to climate change (García-Fortea *et al.*, 2019; Plazas *et al.*, 2020). The "Adapting Agriculture to Climate Change" initiative has also contributed to the development of the Germinate platform (Raubach *et al.*, 2021), which includes a database on eggplant (https://ics.hutton.ac.uk/cwr/eggplant) that contains 59 datasets with genotypic and phenotypic data from cultivated eggplant, wild species and pre-breeding materials.

The H2020 project G2P-SOL represents another landmark for the enhancement of genetic resources of *S. melongena* and the species of its genepools, in which the 5k SPET platform was developed (Barchi *et al.*, 2019*a*) and used for the largest genotyping effort in eggplant germplasm (around 3,500 accessions), allowing the evaluation of diversity of the eggplant genepool, establishment of relationships, identification of duplicates, and in combination with historical characterization data the identification of hundreds of QTLs (Barchi *et al.*, 2022; Gaccione *et al.*, 2022). By using these data, a core collection of 322 eggplant accessions was created, which has been resequenced and phenotyped in multiple locations as well as evaluated for several biotic (*Fusarium* wilt, *Verticillium* wilt, *Meloidogyne* nematodes) and abiotic (drought tolerance and salinity tolerance) related to climate change (Gaccione *et al.*, 2022; Salinier *et al.*, 2022). In addition, fruit metabolomic analyses of the core collection have been performed (Sulli *et al.*, in preparation).

Although these two initiatives represented a starting point for the eggplant breeding revolution, new international, preferably global, actions are needed for a coordinated and systematic exploitation of the advances obtained so far. In this way, the Global Strategy for the Conservation and Use of Eggplants (Solberg *et al.*, 2022) calls for seven priority activities: (i) establishing a global eggplant working group, (ii) developing an Eggplant Knowledge Platform; (iii) improve passport data accuracy and completeness in the collection databases; (iv) facilitate and encourage collaborative plant health-related activities; (v) support collaborative activities associated with accessions regeneration and safety duplication, (vi) characterize the global eggplant collection morphologically and genetically, and (vii) encourage collaborative efforts to involve CWR in breeding programmes. However, the implementation of this strategy, which would represent an additional boost for an eggplant breeding revolution is still in the phase of funding acquisition for its effective fulfilment. 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 breeding revolution. As for 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 climate change challenges.

## Conflict of interest

The authors declare that there is no conflict of interest.

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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); Caliskan et al. (2023) |
| 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)<br>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).

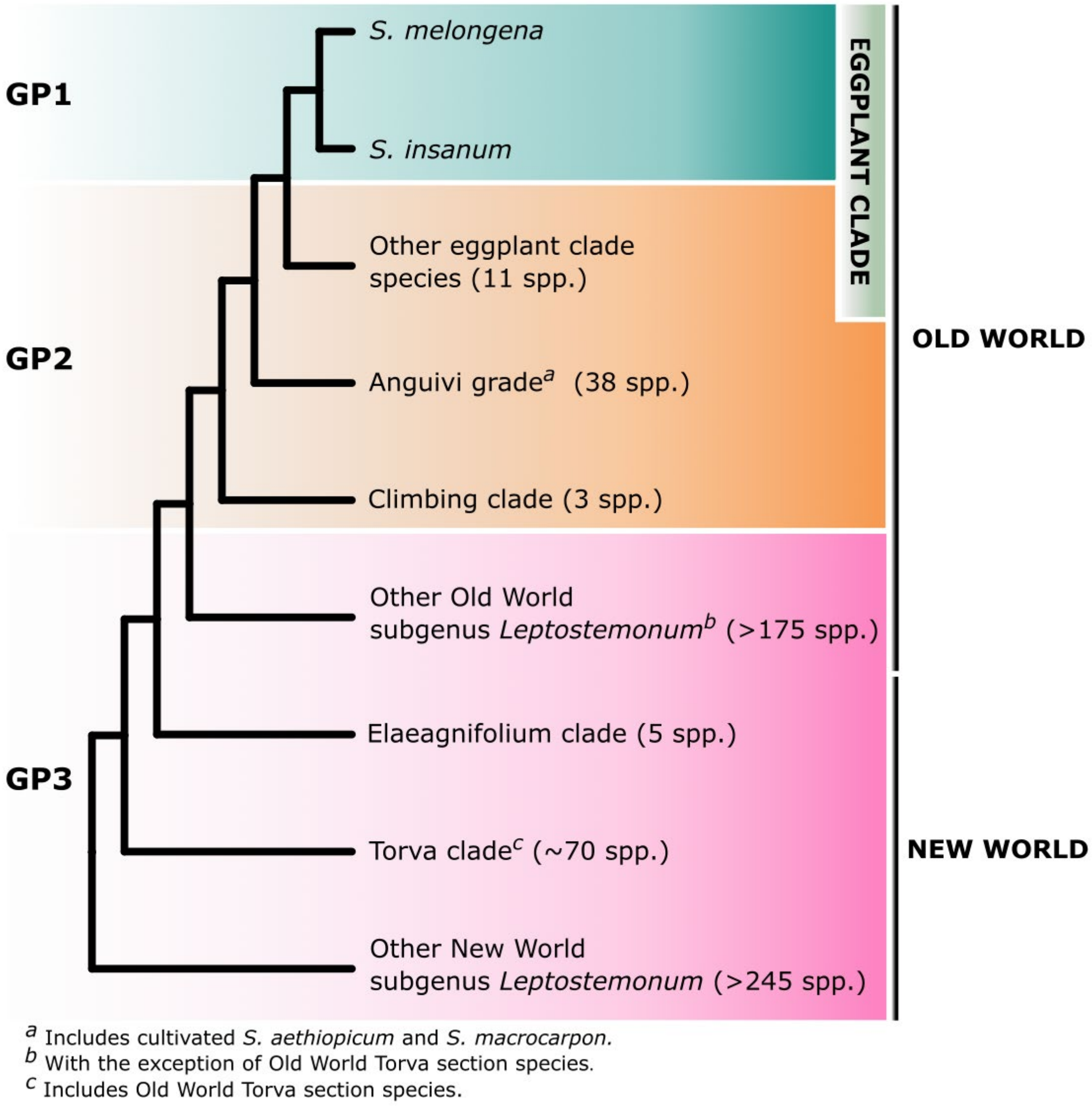

Figure 2. Dendrogram representing relationships of the most relevant groups of the primary (GP1), secondary (GP2) and tertiary (GP3) genepools of *S. melongena*. Based on. Whalen, 1984; Vorontsova *et al.*, 2013; Aubriot *et al.*, 2016; Knapp and Vorontsova, 2016 and Knapp *et al.*, 2019.

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).

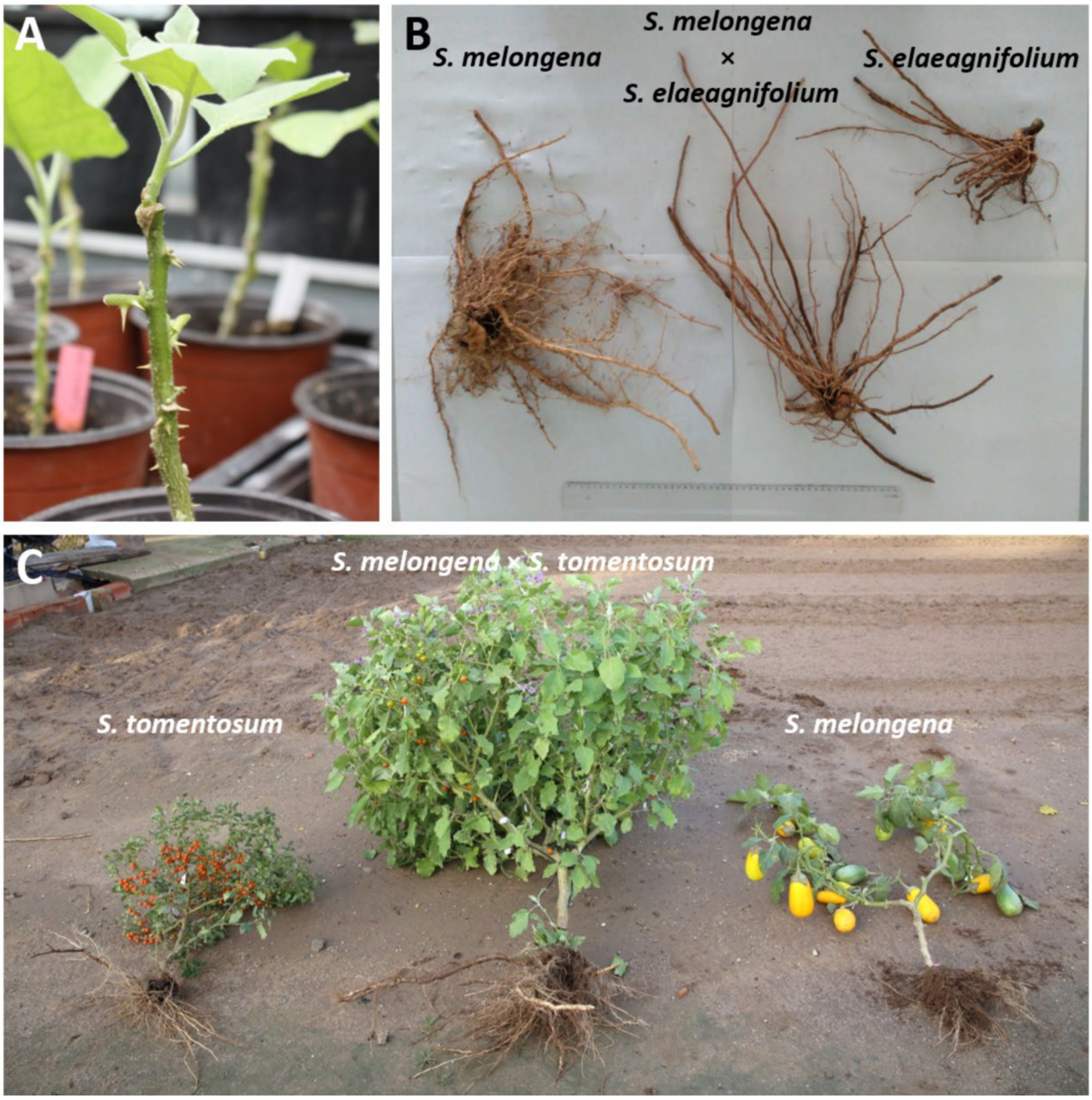

Figure 4. Unexploited eggplant wild relatives and interspecific hybrids as potential roortstocks for eggplant: highly prickly rootstocks are challenging for commercial rootstock utilization as prickles difficult the manual grafting process (above left; A); interspecific hybrids of eggplant (*S. melongena*)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