Chapter 16
Eggplant

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Abstract The eggplant is one of the most important solanaceous crops and is widely cultivated across the world for its fruits, mainly used as a vegetable. Wild relatives of eggplant have been shown to be important sources for transferring tolerance to biotic and abiotic stresses and other agronomically important traits in cultivated background. However, most of the wild relatives have shown partial cross-compatibility with the cultivated species. Efforts have been made to transfer alien genes controlling important traits into the cultivated gene pool of eggplant (*S. melongena*) using the sexual, somatic hybridisation and genetic transformation methods. Introgression lines and molecular markers have accelerated the identification of alien segments introgressed from wild species and helped assessing their impact on phenotypic expression. These approaches have opened new ways to solve constraints for accessing to the reservoir of alien alleles represented by the progenitors, allied and wild species of *S. melongena*. This chapter focuses on such developments and the major achievements made through alien gene transfer in eggplant.

Keywords Dihaploids • Genetic engineering • Genetic resources • Linkage drag • QTL • *S. melongena* • Somatic hybridisation

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16.1 Introduction

The eggplant, *Solanum melongena* L. ($2n = 24$), also known as brinjal, belongs to the *Solanaceae* family, and similar to the other popular and important solanaceous crop such as tomato, potato and pepper, is cultivated across all continents. Eggplant reached in 2010 a harvested area of 1,674,092 ha with a production of 43,891,773 tons of berries showing an increase, respectively, of 9 % and 60 % when compared to those of 2000 (FAOSTAT, http://faostat.org, 2012). This crop is especially cultivated in Asia (93 % of both the world production and harvested area) particularly in China, India, Indonesia and Iran followed by Africa and Europe with, respectively, about 3.3 % and 2.3 % of harvested area and 3.6 % and 2.1 % of world production, being Egypt and Italy the most interested countries. This crop needs warm weather for an extended period of time to give good yields; therefore the tropical and subtropical climates are considered optimal for its cultivation; however it is also grown in temperate and continental regions both in an open field and under protected cultivation for off-season production. Although eggplant is generally considered as a "low-calorie vegetable", its nutritional value is comparable to most of the other common vegetables. It contains vitamins, minerals, proteins, fibre and also important phytonutrients like phenolic compounds and flavonoids, many of which have antioxidant activity (Raigona et al. 2008). Besides, eggplant has been used in the traditional medicine. The tissue extracts are used for the treatment of asthma, bronchitis, cholera and dysuria; fruits and leaves are beneficial in lowering blood cholesterol. It has been shown that eggplant also possesses antimutagenic properties (Khan 1979; Hinata 1986; Kalloo 1993; Collonnier et al. 2001a; Kashyap et al. 2003; Rajam and Kumar 2006). As other solanaceous crops, eggplant contains the glycoalkaloids solasonine and solamargine, which may exert potential toxic effect on human beings but have also shown anticancer properties; in particular, skin neoplasias are efficiently treated with commercial cream based on eggplant-derived glycoalkaloids (Cham 2012).

The cultivated eggplant exhibits a wide diversity in phenotypic (e.g. colour, shape and size of plants, leaves and fruits; growth habit; prickliness and hairiness), physiological and biochemical characteristics, and it is susceptible to a variety of biotic and abiotic stresses, which may cause great yields and quality losses. The classical breeding methods, by exploiting mainly the intraspecific genetic diversity, have accomplished the development of several varieties of eggplant improved with regard to the fruit size, weight and shape and to the plant resistance to diseases and pests (Kalloo 1993). Moreover, interspecific crosses of eggplant with its wild and allied relatives have been attempted together with biotechnological approaches, such as somaclonal variation, somatic hybridisation and genetic transformation, to further enlarge the genetic variability for improving the resistance to pests and diseases, the quality and, more recently, the nutritional value of the fruit. This chapter reviews the progress made for introgression of alien genes into the cultivated eggplant and their potential use in breeding programmes.

16.2 Wild Genetic Resources

In Europe and some Asian countries, and particularly where the cultivation system became more intensive, the release of F_1 hybrids has contributed to the loss of eggplant landraces thus, unavoidably, causing genetic erosion in *S. melongena* (Daunay et al. 1997). Therefore, it is greatly needed, through conventional breeding methods and biotechnological approaches, to introgress the traits of resistance to diseases and pests from the *S. melongena* progenitors, landraces, allied and wild relatives into the gene pool of cultivated eggplant. Germplasm resources are an important reserve of potential genetic variability and allelic variation for the traits underlying many agronomic and qualitative features of the plant and fruit as well as for the content of nutritional and functional compounds. Since 1977, actions aimed at preserving the genetic resources of the cultivated eggplants (including *S. melongena*, *S. aethiopicum* and *S. macrocarpon*) and its relative have been undertaken in Europe, Asia and Africa (Lester et al. 1990; Collonnier et al. 2001a). In the case of eggplants, the controversial identification of its progenitors and of its centres of origin and domestication (Weese and Bohs 2010; Meyer et al. 2012) has also been a hindrance to the search for useful genetic variability with regard to the germplasm and to the geographical areas. In fact, taking into account the enormous contribution that the use of wild relatives and progenitors have given to the genetic improvement of the solanaceous species tomato and pepper (Lenne and Wood 1991), it emerges that for eggplant the potential usefulness of its allied and wild relatives is far to be fully exploited. The allied species *S. aethiopicum* gr. *gilo* and gr. *aculeatum* (Fig. 16.1a), *S. incanum* and *S. macrocarpon* have been frequently subjected to evaluation and utilised as source of genetic variability because they are considered genetically closer to *S. melongena*.

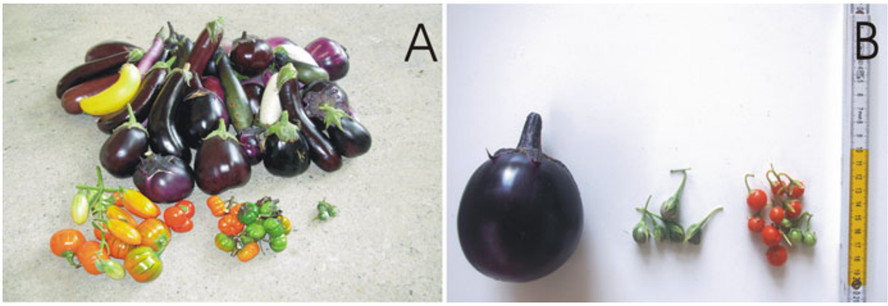

Fig. 16.1 (**a**) Fruits of different introgression lines of *Solanum melongena* and of three allied species utilised for somatic and sexual hybridisation (top of the image, eggplant introgression lines; bottom, from the left, *S. aethiopicum* group *gilo*, *S. aethiopicum* group *aculeatum* = *S. integrifolium* and *S. sodomaeum*) and (**b**) sexual hybrids between eggplant and *S. tomentosum*, from left: fruit of eggplant line from purpura typology, of the sexual F_1 hybrid with *S. tomentosum* and of *S. tomentosum*

16.3 Important Traits in Wild Relatives

Eggplant is susceptible to numerous diseases and pests. Particularly, soilborne diseases (bacterial and fungal wilts, nematodes) and insects are the most serious cause of yield losses both in greenhouse and in open-field cultivations (Sihachakr et al. 1994). Partial resistance/tolerance to most pathogens is also found within the eggplant gene pool, but its low efficacy, often, hindered an effective employment in breeding programmes (Daunay et al. 1991). Resistance to bacterial wilt (*Ralstonia solanacearum*) in some eggplant varieties has become ineffective during hot planting seasons or in badly drained fields (Ano et al. 1991). Only partial resistance or weak tolerance against root-knot nematodes (*Meloidogyne* spp.), *Verticillium* (*Verticillium dahliae*) and *Fusarium* (*Fusarium oxysporum* f. sp. *melongenae*) wilts, *Phomopsis* blight (*P. vexans*) and the insects *Leucinodes orbonalis* (shoot and fruit borer), *Amrasca biguttula* (leaf hopper) and *Aphis gossypii* has been reported in some varieties of eggplant (Yamakawa and Mochizuki 1979; Bindra and Mahal 1981; Chelliah and Srinivasan 1983; Sambandam and Chelliah 1983; Messiaen 1989; Ali et al. 1992; Rotino et al. 1997a). Table 16.1 shows the wild and allied species of eggplant which have been reported to carry traits of resistance to most diseases and pests affecting eggplant. It can be noted that *S. sisymbrifolium* and *S. torvum* have been recognised as resistant to the most severe diseases of eggplant, such as the soilborne

Table 16.1 Sources of resistance against diseases and pests in wild and allied species of eggplant

Pathogens/pests	Resistant species	References
Fungi		
Leveillula taurica	*S. laciniatum*, *S. nigrum*, *S. linneanum, S. aculeatissimum*, *S. aviculare*, *S. pseudocapsicum*	Bubici and Cirulli (2008)
Phomopsis vexans	*S. viarum*, *S. sisymbrifolium*, *S. aethiopicum* gr gilo, *S. nigrum*, *S. violaceum*, *S. incanum*	Kalda et al. (1977); Rao (1981)
Fusarium oxysporum	*S. violaceum* Ort., *S. incanum* agg. *S. mammosum* L., *S. aethiopicum* gr *aculeatum* and gr *gilo*, *S. torvum*	Yamakawa and Mochizuki (1979); Rizza et al. (2002)
Fusarium solani	*S. aethiopicum* L. gr *aculeatum*, *S. torvum* SW.	Daunay et al. (1991)
Verticillium dahliae and *V. albo-atrum*	*S. sisymbrifolium*, *S. aculeatissimum*, *S. Linnaeanum,* *S. hispidum*, *S. torvum* SW, *S. scabrum* Mill	Fassuliotis and Dukes (1972); Pochard and Daunay (1977); McCammon and Honma (1983); Daunay et al. (1991); Collonnier et al. (2003a, b); Gousset et al. (2005); Zhuang and Wang (2009)

(continued)

Table 16.1 (continued)

Pathogens/pests	Resistant species	References
Colletotrichum coccodes	*S. linnaeanum* Hepper and Jaeger	Daunay et al. (1991)
Phytophthora parasitica	*S. aethiopicum* L. gr *aculeatum*, *S. torvum* SW.	Beyries et al. (1984)
Cercospora solani	*S. macrocarpon* L.	Madalageri et al. (1988)
Bacteria		
Ralstonia solanacearum	*S. capsicoides* All., *S. sisymbrifolium* Lam. *S. sessiliflorum* Dun.	Beyries (1979); Mochizuki and Yamakawa (1979)
	S. stramonifolium, Jacq., *S. virginianum* L., *S. Aethiopicum*, *S. aethiopicum* gr *aculeatum*, *S. grandiflorum* Ruiz, *S. hispidum* Pers. *S. torvum* SW, *S. nigrum* L., *S. americanum*, *S. scabrum*	Messiaen (1989); Hebert (1985); Sheela et al. (1984); Daunay et al. (1991); Collonnier et al. (2001b, 2003a, b); Gousset et al. (2005)
Nematodes		
Meloidogyne spp.	*S. ciarum* Dun., *S. sisymbrifolium* Lam., *S. elagnifolium* Cav., *S. violaceum*, *S. hispidum* Pers., *S. torvum* SW	Sonawane and Darekar (1984); Fassuliotis and Dukes (1972); Di Vito et al. (1992); Verma and Choudhury (1974); Daunay and Dalmasso (1985); Messiaen (1989); Shetty and Reddy (1986); Daunay and Dalmasso (1985); Messiaen (1989); Shetty and Reddy (1986)
Insects		
Leucinodes orbonalis	*S. mammosum* L., *S. viarum* Dun., *S. sisymbrifolium* Lam., *S. incanum, S. aethiopicum* gr *aculeatum*, *S. grandiflorum S. aethiopicum* gr *aculeatum*, *S. grandiflorum*	Baksh and Iqbal (1979); Lal et al. (1976); Chelliah and Srinivasan (1983); Khan et al. (1978)
Epilachana vigintioctopunctata	*S. mammosum* L., *S. viarum* Dun., *S. torvum* SW.	Beyries (1979); Sambandam et al. (1976)
Aphis gossypii	*S. mammosum* L.	Sambandam and Chelliah (1983)
Tetranychus cinnabarinus	*S. mammosum* L., *S. sisymbrifolium* Lam., *S. pseudocapsicum* L.	Shalk et al. (1975)
Tetranychus urticae	*S. macrocarpon* L.	Schaff et al. (1982)
Viruses		
Potato virus Y	*S. linnaeanum* Hepper and Jaeger	Horvath (1984)
Eggplant mosaic virus	*S. hispidum* Pers.	Rao (1980)
Others		
Mycoplasma (little leaf)	*S. hispidum* Pers., *S. aethiopicum* L. gr *aculeatum*, *S. viarum* Dun., *S. torvum* SW	Rao 1980; Khan et al. (1978); Charkrabarti and Choudhury (1974), Datar and Ashtaputre (1984)

bacterial and fungal wilts and nematode as well as, respectively, to the insect *L. orbonalis* and *E. vigintioctopunctata*.

In eggplant, wild relatives have been shown as an important source for tolerance to abiotic stresses and other agronomically important traits. High tolerance to frost was reported in *S. grandiflorum*, *S. mammosum* and *S. khasianum* (Baksh and Iqbal 1979), and tolerance to drought has been reported in *S. macrocarpon* L. while tolerance to salinity in *S. linnaeanum* (Daunay et al. 1991). *S. torvum* is one of the eggplant relatives widely studied because it exhibited high tolerance to salts and a low translocation of cadmium in the shoot. Thanks to these characters and also to the resistance to many soilborne diseases, *S. torvum* has been widely utilised as a rootstock (Bletsos et al. 2003). With regard to salt tolerance, eggplant grafted onto *S. torvum* showed more vigorous growth and less adverse effects of salinity. Various physiological and biochemical attributes (shoot length and stem width, chlorophyll pigments, proline content and activities of peroxidase (POD), polyphenoloxidase (PPO) and phenylalanine ammonia-lyase (PAL)) of grafted eggplants resulted higher than those of self-rooted plants (Bai et al. 2005; Bao-li et al. 2010). Cadmium (Cd) concentration in eggplant fruits is reported to be drastically reduced by grafting onto *Solanum torvum*; a more detailed characterisation of the mechanism of Cd translocation in *S. torvum* with respect to cultivated eggplant revealed that although they displayed a similar rate of adsorption in the roots, the wild species showed a significant lower translocation of Cd in the stem, leaf and fruit. Thus, *S. torvum* has been proposed for soil phytoremediation (Mori et al. 2009). These responses prompted the study to identify the genes of *S. torvum* involved in the tolerance to the heavy metal Cd and also to *Verticillium* by transcriptome analyses (Wang et al. 2010a; Yamaguchi et al. 2010; Xu et al. 2012), and the pathogenesis-related gene *StDAHP* was cloned following inoculation with *Verticillium* (Wang et al. 2010b).

In most of the work aimed to assess the response of the allied species to the biotic and abiotic stresses, often, a single or a few accessions were analysed. It is worth to point out that the allied and wild species probably display an even huge allelic variation for the useful traits searched because they have been mainly subjected to environmental selection including the indirect effect of the human activities and not to the bottleneck of domestication. Therefore the collections of wild and allied species need to be implemented and also to be better characterised for their biological and biochemical properties; with regard to eggplant only a few example can be reported, like *S. torvum* (Gousset et al. 2005) and *S. aethiopicum* (Sunseri et al. 2010).

16.4 Introgression of Alien Genes from Allied and Wild Species

16.4.1 Conventional Breeding Approach

The use of conventional breeding methods to introgress the alien traits of interest into cultivated lines of eggplant has been performed only sporadically through interspecific crosses because of the presence of sexual barriers between *S. melongena* and its related wild species (Ano et al. 1991; Bletsos et al. 1998). The capability of eggplant to cross to species of other genera or subgenera is very low (Daunay et al. 1991). This may result from the lack of genetic information about the crossing partners or due to evolutionary divergence, which is known as incongruity (Franklin et al. 1995). Attempts at more distant crosses as that of *S. melongena* with *S. lycopersicon* resulted in sterile hybrids (Rao 1979).

Most of the published works about the sexual interspecific hybridisations between eggplant and its allied and wild relatives are listed in Table 16.2. More than 25 species have been employed in attempts to crossing with *S. melongena* in order to transfer useful traits. Only a limited number of them (*S. incanum* L., *S. linnaeanum*, *S. macrocarpon*, *S. aethiopicum* L., *S. viarum* and *S. virginianum*) were able to develop fertile or partially fertile F_1 hybrids which were successfully backcrossed to the cultivated *S. melongena*. Interspecific hybrids are also commercially employed as rootstock (e.g. cv "Taibyo VF" from a cross between eggplant and *S. grandiflorum*; Hasnumnahar et al. 2012) especially in Japan in field infested by fungal and bacterial wilt. It has been reported that interspecific hybrids with the wild relative *S. incanum*, which is more easily crossable with cultivated eggplant, display an acceptable level of tolerance to nematodes and produced fruits of good apparent and compositional quality compared to *S. torvum* (Gisbert et al. 2011).

The allied species, *S. linneanum* (=*S. sodomaeum*), which is efficiently cross compatible with eggplant has been used in development of mapping population for construction of a molecular map (Doganlar et al. 2002). Subsequently, it has been used in identification of QTLs for qualitative and quantitative traits (Frary et al. 2003). This species (Fig. 16.1a) has also been used to introgress the alien genes controlling to *Verticillium* wilt following backcross breeding, which resulted in the development of several wilt tolerant lines of eggplant (Acciarri et al. 2004). Also *S. tomentosum* has been successfully employed for alien genes introgression due to its partial fertility with cultivated species (Fig. 16.1b). The partially fertile hybrid obtained between this wild species and eggplant has been backcrossed with cultivated species for the improvement of agronomical and fruit quality traits (unpublished).

Most of the wild relative species, particularly *S. sisymbrifolium* and *S. torvum*, possess a large number of resistance traits to serious diseases of eggplant. However crossing of these species with cultivated eggplant gave no hybrids at all or only partially fertile hybrids through embryo rescue (Daunay and Lester 1988; Bletsos et al. 1998). Different eggplant lines showed a diverse capacity to be crossed with a given allied or wild relative and, sometimes, successful hybridisation of wild species with cultivated species had been obtained when wild species were used as female or *vice versa* (Rao 1979). For example, the interspecific hybrid with *S. anomalum* and *S. indicum* can produce seeded fruits only when they are employed as male parent and not as female (Behera and Singh 2002). Therefore, the employment of different accessions of the same wild relative with different lines of eggplant may improve the chance to obtain fertile interspecific hybrids. Interspecific crossing barrier may also be broken down by making several attempts of crossing to the same flowers along different days. A combination of the above approaches has allowed to obtain

Table 16.2 Interspecific crosses between the cultivated eggplant (*S. melongena* L.) and other *Solanum* species

Wild species	Status of crossability with cultivated species	References
S. melongena	Fertile F_1 plants	Pearce (1975)
S. incanum	Fertile F_1 plants	Pearce (1975); Behera and Singh (2002); Vilanova et al. (2010)
S. campylacanthum	Partially fertile F_1 plants	Pearce (1975)
S. linnaeanum (*S. sodomeum*)	Partially fertile or sterile F_1 plants	Pearce (1975); Pochard and Daunay (1977); Acciarri et al. 2004
S. macrocarpon	Partially fertile/sterile F_1 plants	Pearce (1975); Bletsos et al. (2004); Gowda et al. (1990)
S. marginatum	Partially fertile F_1 plants	Pearce (1975)
S. verginianum	Partially fertile F_1 plants or no F_1 plants	Pearce (1975); Rao (1979); Isshiki et al. (2000)
S. sodomeum	Fertile F_1 plants	Tudor and Tomescu (1995); Acciarri et al. (2004); Doganlar et al. (2002)
S. anomalum	Fertile F_1 plants	Behera and Singh (2002)
S. aethiopicum (gr. kumba, gr gilo *gr aculeatum*)	Partially fertile F_1 or sterile F_1 plants	Pearce (1975); Rao and Baksh (1979); Isshiki and Taura (2003); Prohens et al. (2012)
S. anguivi	Partially fertile F_1 plants	Pearce (1975)
S. cinereum	Sterile F_1 plants	Pearce (1975)
S. pyracanthos	No F_1 plants	Pearce (1975)
S. rubetorum	Partially fertile F_1 plants	Hassan (1989)
S. tomentosum	Partially fertile F_1 plants	Pearce (1975)
S. trilobatum	No F_1 plants, no seeds	Rao and Rao (1984)
S. violaceum	Partially fertile F_1 plants	Bulinska (1976); Isshiki and Kawajiri (2002)
S. hispidum	Partially fertile F_1 plants	Khan (1979); Magoon et al. (1962), Rao (1980)
S. torvum	Partially fertile or sterile or F_1 plants after embryo rescue	Pearce (1975), Bulinska (1976); McCammon and Honma (1983); Daunay et al. (1991); Bletsos et al. (1998)
S. capsicoides	No F_1 plants	Pearce (1975)
S. mammosum	No F_1 plants or abnormal seeds	Sambandam et al. (1976)
S. viarum = *khasianum*	Sterile F_1 plants after embryo rescue	Pearce (1975); Sharma et al. (1980)
S. grandiflorum	Partially fertile F_1 plants	Rao (1979)
S. lidii	Partially fertile F_1 plants	Hassan (1989)
S. sisymbrifolium	Sterile F_1 plants after embryo rescue	Sharma et al. 1984; Bletsos et al. (1998)
S. campanulatum	No F_1 plants or abnormal seeds	Pearce (1975)
S. stramonifolium	No F_1 plants, no seeds	Nishio et al. (1984)

interspecific hybridisation of *S. melongena* with *S. khasianum* (=*S. viarum*) and *S. sisymbrifolium* by using in vitro embryo rescue. In this case, it could only be possible when the wild relatives *S. khasianum* and *S. sisymbrifolium* were employed as female and male parent, respectively, during crossing with eggplant (Sharma et al. 1980, 1984).

The infertility of interspecific hybrids between *S. melongena* and others *Solanum* could be associated to self-incompatibility due to the wild parent, being the eggplant self-compatible (Daunay et al. 1991). However, the sterility is often attributable to lack of affinity of the genomes involved in the cross causing difficulty in correct pairing of chromosomes at the meiosis and the formation of irregular and sterile microspores and egg-cells. Reduced fertility or infertility is a common phenomenon in the interspecific hybrids of eggplant with other *Solanum* species (e.g. *S. macrocarpon*, *S. linneanum*) belonging to the *Melongena* section as well (Bletsos et al. 2004; Acciarri et al. 2007). However, fertility may be significantly improved or restored by doubling the ploidy level of the diploid (2x) hybrid, because synthetic amphidiploid has a more balanced chromosomes pairing during meiosis. For example, fertility restoration has been reported in the sexual hybrid between eggplant and *S. aethiopicum* (Isshiki and Taura 2003). Similarly, male-sterile plants were selected following the sexual hybridisation of eggplant with *S. violaceum* (Isshiki and Kawajiri 2002). Isshiki and collaborators employed *S. virginianum*, *S. aethiopicum* Aculeatum group and *S. grandiflorum* cytoplasms to develop male-sterile lines of eggplant through sexual hybridisation; the relative species were used as female parent and *S. melongena* as male to obtain the F_1 interspecific hybrids and the successive backcrossed progenies were selected for male sterility. Functional (indeishent anthers) and cytoplasmic (non-forming pollen) male-sterile introgression lines were developed. Furthermore, in the case of *S. grandiflorum*-derived cytoplasmic male sterility, two independent dominant restorer fertility (*Rf*) genes have been discovered to control pollen formation (Khan and Isshiki 2008, 2010; Hasnumnahar et al. 2012).

16.4.2 Somatic Hybridisation

Plant regeneration from protoplast has been efficiently set up in eggplant (Sihachakr and Ducreux 1987). This has provided an opportunity to apply the somatic hybridisation technology for introgression of alien genes in order to make genetic improvements of eggplant (Sihachakr et al. 1994; Collonnier et al. 2001a; Kashyap et al. 2003; Rajam and Kumar 2006). It offers the possibility of overcoming sexual barriers or improving the fertility of interspecific hybrids with respect to the correspondent ones which are obtainable by conventional breeding methods (Sihachakr et al. 1994). Moreover, with respect to sexual hybridisation, somatic fusion may lead to new and unique nucleo-cytoplasmic combinations with higher genetic variability from the mixture of nuclear and cytoplasmic genomes of the fusion partners. It is also associated to increase the possibility of obtaining somaclonal variants. For example, a salt-resistant line of eggplant has been isolated from cell culture in a medium containing 1 % sodium chloride (Jain et al. 1988). In field trials, potential useful genetic variation for agronomic traits was observed in both embryogenic and androgenic eggplant lines (Rotino 1996).

In eggplant, the first successful somatic hybridisation was obtained with *S. sisymbrifolium*. These somatic hybrids were resistant to root-knot nematodes and potentially resistant to spider mites. However, the strong sterility of these hybrids has prevented their practical utilisation (Gleddie et al. 1986). Other tetraploid somatic hybrids obtained with *S. sisymbrifolium* have shown resistant to *Ralstonia solanacearum* and culture filtrate of *V. dahliae* in in vitro tests (Collonnier et al. 2003a). The somatic hybrids with *S. khasianum*, a relative displaying resistance to shoot and fruit borer, despite it showed a promising percentage (12 %) of viable pollen, produced only seedless parthenocarpic fruits (Sihachakr et al. 1988). Resistance to the herbicide atrazine was achieved in somatic hybrids of eggplant with *S. nigrum* (Guri and Sink 1988b; Sihachakr et al. 1989). *S. torvum* was also widely employed in different fusion experiments; the somatic hybrids were found resistant to nematodes, partially resistant to spider mite and displayed good levels of resistance to *R. solanacearum* and culture filtrate of *V. dahliae*. However, greenhouse-grown plants resulted sterile (Guri and Sink 1988a; Sihachakr et al. 1989; Collonnier et al. 2003b). *S. torvum* was also employed to obtain highly asymmetric somatic hybrids tolerant to *Verticillium* wilt, which displayed a morphology similar to the cultivated eggplant (Jarl et al. 1999). The asymmetric hybrids were obtained following the X-ray treatment of the donor genotypes (*S. torvum*) in order to obtain hybrids bearing few chromosome fragments from the donor parent associated with a complete set of chromosomes from the other parent (Jones 1988; Sihachakr et al. 1994). Somatic hybridisation was accomplished between eggplant and a sexual hybrid of tomato with its wild relative, *Lycopersicon pennellii*, producing only hybrid calli with few leaf primordial (Guri et al. 1991). Subsequently highly asymmetric hybrid plants were regenerated after irradiation of one fusion partner with γ-rays (Liu et al. 1995; Samoylov and Sink 1996; Samoylov et al. 1996). Fertile tetraploid somatic hybrids were also obtained between eggplant and *S. marginatum* in view of converting the cultivated eggplant to an arborescent perennial species; the selfed progenies maintain the arboreous character but showed a low frequency of tetravalent formation during microsporogenesis (Borgato et al. 2007).

Somatic hybridisation with *S. aethiopicum* is an excellent example of successful incorporation of somatic hybrids in breeding programmes (Fig. 16.2a). The tetraploid somatic hybrid was obtained through electrofusion to introgress the traits of resistance to bacterial and fungal wilts from *S. aethiopicum* into cultivated eggplant (Daunay et al. 1993; Rotino et al. 2001). Most of the hybrids had the eggplant ctDNA. Field evaluation showed that the tetraploid somatic hybrids had a much better pollen viability and, most important, gave a high yield of fruits (up to 9 kg/plant) while the diploid sexual hybrids produced only few seedless fruits. The somatic hybrids resulted highly resistant to bacterial wilt in inoculation tests carried out in a contaminated field (Rajam et al. 2008). Similarly, other fertile somatic hybrids of eggplant with *S. aethiopicum* gr. *aculeatum* were resistant to *Fusarium* wilt (Fig. 16.2b; Rotino et al. 1998, 2001). These results support the previous reports that the tetraploid status significantly improves the fertility of the interspecific hybrid which produces seeded fruits. However, in order to incorporate the somatic hybrid in a practical eggplant breeding programme for introgression of traits of interest, two essential prerequisites still need to be accomplished beyond fertility: (1) occurrence of genetic recombination between the genomes of the two species and (2) reduction of the ploidy level to that of recurrent parent because generally the

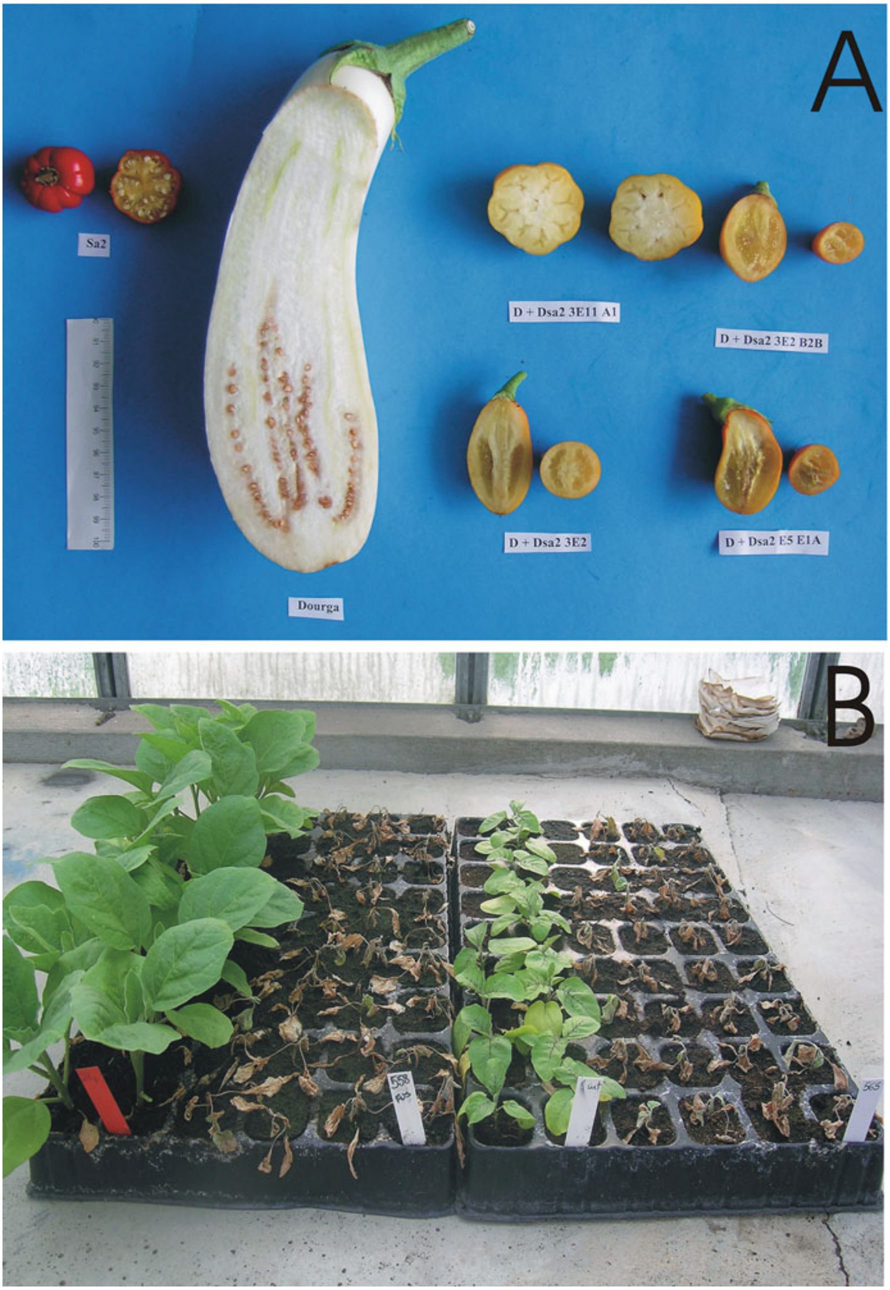

Fig. 16.2 Fruits from interspecific hybridisation of eggplant with allied species. (**a**) Somatic hybridisation between *S. melongena* and *S. integrifolium*; from *left*: *S. aethiopicum*, eggplant cv Dourga and four somatic hybrids. (**b**) Phenotypical evaluation of the progenies for the resistance to *Fusarium oxysporum* scored after 30 days from inoculation with the fungus; from the *left*, an introgression line from a somatic hybrid with *S. integrifolium* (resistant), a recurrent genotype of eggplant (completely dead), *S. integrifolium* (donor, resistant), another recurrent genotype of eggplant (completely dead)

somatic hybrids possess the sum of the genomes of the involved species. In case of first point, synthetic amphidiploids from sexual hybridisation are capable to form multivalents at meiosis leading to segregation in their selfed progenies (Isshiki et al. 2000; Isshiki and Taura 2003). However, the presence of multivalents at meiosis is necessary but not sufficient condition for genetic recombination because crossing over does not always occur after chromosome pairing. In relation to the second point, eggplant is quite responsive to the tissue and organ culture including the regeneration of androgenetic plants from microspore mainly through anther culture (Rotino 1996). This technology has been efficiently exploited to regenerate dihaploid plants either from the somatic hybrids (Rizza et al. 2002) or from a tetraploid BC_1 backcross (Rotino et al. 2005). Occurrence of an effective genetic recombination was demonstrated in the population of androgenetic dihaploids derived from anther culture of the somatic hybrid between *S. melongena* and *S. aethiopicum* gr. *gilo* (Rizza et al. 2002). A population of 71 dihaploids was elegantly employed to clearly demonstrate that crossovers (i.e. random chromatid segregation) occurred between the chromosomes of the two species by following the segregation of 280 ISSR markers and 5 isoenzymatic loci (Toppino et al. 2008a). The dihaploids, which were highly heterozygous, displayed a wide range of morphological variation and segregated for resistance to *Fusarium*. These variations were never showed off by the selfed progenies of the tetraploid somatic hybrids, which appeared phenotypically uniform and were all resistant to *Fusarium* (Rotino et al. 2005). Although first backcrossing of the dihaploids with the recurrent eggplants has been obtained with a certain difficulty, in subsequent backcross generations, morphology and fertility improved progressively (Rotino et al. 2005). Thus, these BC_1-derived dihaploids have been shown more useful in the breeding programme for faster and straightforward selection of introgression lines with resistance to *Fusarium* (Fig. 16.2b). The development of advanced backcross introgression resistant lines has been used to identify the molecular marker linked to resistance that behaves as a dominant monogenic trait (Toppino et al. 2008b).

Another interspecific hybrid using *S. viarum* has been successfully backcrossed to eggplant and after selfing for nine generations resulted in the identification of two lines having higher yield, good fruit quality and high tolerance to the devastating insect fruit and shoot borer (Pugalendhi et al. 2010). Further biochemical analyses of these lines showed that the tolerant introgression lines had increased activity of polyphenoloxidase and peroxidase and higher level of solasodine and total phenol (Prabhu et al. 2009). Backcrossed progenies obtained from the sexual hybrid of eggplant with *S. aethiopicum* gr. *aculeatum* showed the resistance to *Fusarium* (Zhuang and Wang 2009). Similarly backcross progenies (BC_1) derived from the crossing between the *S. incanum* gr. C and eggplant have been used to construct an interspecific linkage map and development of introgression lines (Vilanova et al. 2010). Interspecific hybridisation has also been accomplished in the less cultivated *S. aethiopicum* Kumba group, and its BC_1 progenies have been analysed in view of their possible exploitation for the improvement of eggplant (Prohens et al. 2012).

16.4.3 Linkage Drag of Undesirable Traits During Alien Gene Introgression

Introgression of alien genes from allied and wild species may result in linkage drag of undesirable agronomical traits such as susceptibility to (new) pest and diseases and/or a high level of unsafe compounds such as glycoalkaloids along with desirable traits. For example, the use of wild species *S. torvum* carries a very high susceptibility to *Colletotrichum gloeosporioides* (Collonnier et al. 2001a). The detailed analyses of glycoalkaloid levels in *S. macrocarpon* and *S. aethiopicum*, which have been shown potential genetic resources for improvement of eggplant, revealed that *S. macrocarpon* fruits had values 5–10 times higher than those considered to be safe in foods and might not be considered suitable for human consumption while fruits of *S. aethiopicum* presented values similar to those of *S. melongena* and could be considered as safe for consumption (Sanchez-Mata et al. 2010). *S. sodomaeum* also produces fruits very rich in glycoalkaloids; this species is very close to eggplant as they both belong to the section *Melongena* of Solanaceae and interspecific hybrids between them have been obtained and incorporated in breeding programmes (see above). A biochemical characterisation of the health-related compounds including glycoalkaloids (solamargine and solasonine) was carried out in advanced introgression lines from *S. sodomaeum* and also of *S. aethiopicum* gr *gilo* and gr. *aculeatum* (=*S. integrifolium*), in the eggplant recurrent genotypes and the three allied species (Mennella et al. 2010). This study demonstrated that most of the introgression lines, obtained after several cycles of backcross with eggplant, showed biochemical composition and functional properties similar to that of the recurrent eggplants, even though the selection was made only on the basis of morphological traits of interest and tolerance trait to *Verticillium*. However, it is to point out that some introgression lines from *S. sodomaeum* still presented significantly higher values (three to six times) than the recurrent eggplant (Mennella et al. 2010). Therefore, it could be advisable, as first step in an introgression breeding programme, to check the biochemical composition of the fruits in the allied and wild parents of the interspecific hybrids; then, according to the results obtained and the goals of the programme, the biochemical analyses might be also employed as a selection tool or limited to the last characterisation of the final genetic materials obtained.

16.5 Genetic Engineering

Eggplant, as many other members of the Solanaceae family, is highly responsive to genetic transformation (Rajam et al. 2008). The main achievements of genetic transformation via *Agrobacterium* are listed in Table 16.3. Transgenic plants were firstly

Table 16.3 Genetic transformation in eggplant (*Solanum melongena* L.)

Explant	Gene	Accomplishment	References
Leaf	*npt*II	Transgenic plant using a cointegrate vector	Guri and Sink (1988a)
Cotyledon/leaf	*npt*II	Stable transformation with a binary vector	Filippone and Lurquin (1989)
Leaf	*npt*II, *cat*	Transformation efficiency of 7.6 %	Rotino and Gleddie (1990)
Leaf	*npt*II, *gus*	In vivo selection of *npt* II gene in transgenics	Sunseri et al. (1993)
Cotyledon	*npt*II, *gus*	Transformation through organogenesis and embryogenesis	Fári et al. (1995); Akhter et al. (2012)
Hypocotyl	*Bt (cryIIIB)*	Resistance to CPB was not observed	Chen et al. (1995)
Cotyledon/Leaf	Mutagenised *Bt (cryIIIB)*	Resistance to CPB; Field trials; strategy of Bt-resistant eggplant deployment; spider mites preference; wide ecological study	Arpaia et al. (1997); Iannacone et al. 1997; Acciarri et al. (2000); Mennella et al. (2005); Rovenska´ et al. (2005); Arpaia et al. (2007)
Leaf	*Bt (cryIIIB)*	Effect of hormones and antibiotics on efficiency of transformation	Billings et al. (1997)
Leaf	Synthetic *Bt (cry IIIA)*	Resistance to CPB	Hamilton et al. (1997); Jelenkovic et al. (1998)
Cotyledon	Synthetic *Bt (cry1Ab)*	Resistance to *Leucinodes orbonalis*	Kumar et al. (1998)
Leaf	*Luc*	Stability of luciferase gene expression	Hanyu et al. (1999)
Cotyledon	*PAtgtrp-5::GUS*	Studies about factors influencing transformation efficiency	Magioli et al. (2000)
Cotyledon/leaf	*DefH9-iaaM*	Parthenocarpic transgenic plants; green house trial; green-house and open-field trials; biochemical and technological evaluation of parthenocarpic fruits	Rotino et al. (1997a, b); Donzella et al. (2000); Acciarri et al. (2002); Maestrelli et al. (2003)
–	Yeast Δ-9 desaturase	Increased resistance to *Verticillium* wilt	Xing and Chin (2000)
Cotyledon	*Mtl*D	Tolerance against osmotic stress	Prabhavathi et al. (2002); Prabhavathi and Rajam (2007a)
Root	*npt*II	Efficient and stable transformation	Franklin and Sita (2003)
Leaf, cotyledon, hypocotyl	*Gfp:gus,hpt, VirE:LacZ*	Increased transformation efficiency	Kumar and Rajam (2005)
Cotyledon	*Mi-1.2*	Resistance to root-knot nematode	Goggin et al. (2006)
Cotyledon	*Oryzacystatin*	Resistance to aphids	Ribeiro et al. (2006)

Leaf	*Dm-AMP1*	Resistance to *Botrytis cinerea*; release of the defensin in their root exudates; inhibitory effect on *Verticillium albo-atrum*	Turrini et al. (2004)
Cotyledon, hypocotyl	*npt*II	Influence of growth regulators and explants type on Agrobacterium transformation; hypocotyl regenerate better than cotyledons	Prakash et al. (2007a, b)
	Bt (Cry2Ab)- nptII-gus	Antibiotic marker-free transgenic plant obtained by using *A. tumefaciens* bearing two T-DNA plasmids	Narendran et al. (2007)
Hypocotyl	*Cry1Ac*	Complete resistance towards EFSB	Pal et al. (2009)
Hypocotyl	*Barnase, Cre/loxP*	A combined system to induce a restorable male sterility in eggplant	Cao et al. (2010)
Stem	*aadA*	Optimisation of plastid transformation protocol in eggplant	Singh et al. (2010)
Leaf, cotyledon	*SmTAF10,SmTAF13*	Developing of a reversible male sterility system	Toppino et al. (2010)
Cotyledon	*CMV-CP*	Resistance to CMV	Pratap et al. (2011)
Leaf, cotyledon	*Cry1Fa1*	Resistance to BFSB	Shrivastava et al. (2011)
Shoot tip	*DREB1A*	Moisture stress tolerant eggplant	Sagare and Mohanty (2012)

*npt*II, *neomycin phosphotransferase* II; *hpt*, *hygromycin phosphotransferase*; *cat*, *chloramphenicol acetyltransferase*; *Bt (cry IIIB)*, *Bacillus thuringiensis cry IIIB*; *Bt (cry IIIA)*, *Bacillus thuringiensis cry IIIA*; *Bt (Cry 1Ab)*, *Bacillus thuringiensis cry 1Ab*; *gus*, *β-glucuronidase*; *luc*, *luciferase*; *pAtgrp-5,* regulatory region of the *Arabidopsis thaliana* glycine rich protein 5; *DefH9-iaaM*, regulatory region of the *DEFICIENS 9* gene from snapdragon and the auxin-synthesising gene coding region *(IaaM)* from *Pseudomonas syringae* pv. *savastanoi; mtl*D, bacterial *mannitol-1-phosphodehydrogenase* gene; *Dm-AMP1*, *antimicrobial defensin from Dahlia merckii gene; Bt (Cry 2Ab)*, *Bacillus thuringiensis cry 2Ab; Barnase,* cell lethal gene*; Cre/loxP* site-specific recombination system; *aadA* gene for resistance to spectinomycin and streptomycin. *SmTAFs*, *Solanum melongena TBP-associated factors* gene. *CMV-CP*, *Cucumber mosaic virus coat protein* gene. *Cry1Fa1*-synthetic Bt gene. *DREB1A*, *Arabidopsis dehydration-responsive element* gene obtained by Guri and Sink (1988c), using leaf explants and a cointegrate vector carrying the *npt*II gene; in the following years, Filippone and Lurquin (1989) reported stable callus transformation and Rotino and Gleddie (1990) obtained transgenic plants using a binary vector. Since then, different *Agrobacterium* strains harbouring binary vectors were employed to raise transgenic eggplants carrying kanamycin resistance (*npt*II) as selective agent and different reporter genes, including *gus* (*β-glucuronidase*), *cat* (*chloramphenicol acetyl transferase*) and *luc* (*luciferase*).

Resistance to Colorado potato beetle (*Leptinotarsa decemlineata* Say) (CPB), which is a serious pest for eggplant cultivation in Europe and America as it develops resistance to synthetic insecticides (Arpaia et al. 1997), has been pursued by a number of groups. Chen et al. (1995) produced transgenic eggplant lines with the introduction of *Bacillus thuringiensis* (Bt) genes, but resistance to CPB was not observed. Later, different groups were able to obtain lines resistant to CPB by using mutagenised versions of *cryIIIB* (Arpaia et al. 1997; Iannacone et al. 1997) or a synthetic version of *cryIIIA* Bt genes by adjustment of the codon usage for expression in dicots (Hamilton et al. 1997; Jelenkovic et al. 1998). Field trials demonstrated high levels of resistance in transgenic plants for the mutagenised Bt *cryIIIB* gene, which ensured a significantly higher production than untransformed controls without detrimental effects on some nontarget arthropods (Acciarri et al. 2000). Moreover, strategies for field deployment of eggplant-Bt expressing were also evaluated (Mennella et al. 2005). A study in a greenhouse revealed that the transformed *cryIIIB*-eggplants were a food more preferred for spider mites and simultaneously less preferred by predatory mites. Such a shift in the preference of both the spider mites and their predators could result in lower effectiveness or even failure of biological control (Rovenska´ et al. 2005). A further wide open field 3-year study on species assemblage of herbivorous and insect biodiversity in experimental fields of Bt *cryIIIB*-expressing lines evidenced a comparable nontarget species assemblage between transgenic and near-isogenic eggplant cultivation areas (Arpaia et al. 2007).

Resistance to *Leucinodes orbonalis*, the eggplant fruit and shoot borer (EFSB), which is a lepidopteran insect very destructive in Asian countries, was firstly obtained using a synthetic *cry1Ab* gene modified for rice codon usage (Kumar et al. 1998). Antibiotic marker-free transgenic plants resistant to EFSB were also obtained by using *A. tumefaciens* bearing two T-DNA plasmids containing the Bt *cry2Ab* gene and the *nptII* plus the *gus* genes, respectively; *cry2Ab* and marker genes segregated independently in 44 % of the primary transformants demonstrating that the T-DNA insertions were unlinked (Narendran et al. 2007). A *cry1Ac* Bt gene expressed in an elite eggplant line gave also a complete resistance towards EFSB (Pal et al. 2009). Recently, a synthetic Bt gene (*cry1F*) effective against *Leucinodes orbonalis* was introduced into eggplant by means of targeted homologous recombination in a gene of the anthocyanin pathway *F3G* (*flavonoid-3-glucosyltransferase*) without the aid of any recombinase gene, and out of 956 kanamycin-resistant plantlets, 2 had the expected insertion of the 35S-*cry1F* in the *F3G* gene (Shrivastava et al. 2011).

In several field experiments, Bt-eggplant effectively controlled EFSB; efforts to commercialise in India and the Philippines eggplant hybrids expressing Bt protein have been done including extensive biosafety investigations, nutritional and substantial equivalence studies and relative toxicity and allergenicity assessment using animal models like Sprague Dawley rat, brown Norway rat, rabbit, fish, chicken and goat; however the final approval still has not been given (Kumar et al. 2011).

The transgenic eggplant expressing oryzacystatin, a cysteine proteinase inhibitor of rice, reduced the net reproductive rate, the instantaneous rate of population increase and the finite rate of population increase of the two aphids *Myzus persicae* and *Macrosiphum euphorbiae* with respect to the control line (Ribeiro et al. 2006). These results indicate that expression of oryzacystatin in eggplant has a negative impact on population growth and mortality rates of *M. persicae* and *M. euphorbiae* and could be a source of plant resistance for pest management of these aphids.

The tomato *Mi-1.2* gene which confers race-specific resistance against root-knot nematodes *(Meloidogyne* spp.), potato aphids (*Macrosiphum euphorbiae*) and the insect whiteflies (*Bemisia tabaci*) was successful transferred via *A. tumefaciens* transformation into eggplant and a susceptible tomato cultivar (Goggin et al. 2006). The transgenic eggplants expressing *Mi-1.2* displayed resistance to *Meloidogyne incognita* but not to *Macrosiphum euphorbiae*; on the contrary, the transgenic tomato was resistant to both nematode and aphids (Goggin et al. 2006). Thus, the tomato *Mi-1.2* resistance gene retains partial function when introduced into another related solanaceous species. The lack of resistance to insects in eggplant could be due, for example, to deficiencies in the *Mi-1.2* sequence translation or protein processing in eggplant leaves and/or to absence of conservation, between tomato and eggplant species, of factor(s) essential for aphid resistance (Goggin et al. 2006).

This result deserves a further consideration about the transferability of useful traits from one species to another through genetic engineering or by means of hybridisation. In the first case (based on the introduction of a single or a few genes), the knowledge of the genetic basis underlying the trait and, as evidenced for *Mi-1.2* gene, of its mechanism of action is an essential prerequisite. In the second case (based on interaction between entire genomes), theoretically, it is not necessary to have any genetic information about the trait of interest, provided that an efficient method to select the introgressed progenies for this trait is available.

Resistance to the *Cucumber mosaic virus* (CMV) was engineered by insertion of the coat protein (CP) of *CMV* gene under the control of the constitutive promoter *CaMV 35S*, independent primary T0 transgenics resulted either tolerant or completely resistant when challenged with CMV virus (Pratap et al. 2011).

Eggplant was also engineered for *Verticillium* wilt resistance by overexpression of a yeast Δ-9 desaturase gene, which increased the levels of 16:1, 18:1 and 16:3 fatty acids (Xing and Chin 2000). The transgenic eggplants showed improved resistance to *Verticillium* wilt and, when inoculated with the pathogen, displayed a marked increase in the content of 16:1 and 16:3 fatty acids; it was also shown that *cis*-Δ9 16:1 fatty acid inhibited *Verticillium* growth.

Resistance to the fungus *Botrytis cinerea* was achieved by constitutive expression of the antimicrobial defence gene *Dm-AMP1* from *Dahlia merckii*; the transgenic plants released the defensin in their root exudates that had an inhibitory effect on the pathogenic *Verticillium albo-atrum* while did not interfere with the symbiotic arbuscular mycorrhizal fungus *Glomus mosseae* (Turrini et al. 2004).

The bacterial *mannitol-1-phosphodehydrogenase* (*mtlD*) gene, which is involved in the mannitol synthesis when expressed in eggplant, caused tolerance to osmotic stress induced by salt, drought and chilling (Prabhavathi et al. 2002). Interestingly, these transgenic plants expressing *mtlD* gene with mannitol accumulation also exhibited increased resistance against three fungal wilts caused by *Fusarium oxysporum, Verticillium dahliae* and *Rhizoctonia solani* under both in vitro and in vivo growth conditions. Mannitol levels could not be detected in the wild-type plants, but the presence of mannitol in the transgenics could be positively correlated with the disease resistance (Prabhavathi and Rajam 2007a, b). Further, various transgenic eggplants overexpressing the oat *arginine decarboxylase* gene-encoding enzymes in the polyamine metabolic pathway were also generated. These transgenic plants showed increased tolerance to multiple abiotic (salinity, drought, extreme temperature and heavy metals) as well as biotic (fungal pathogens) stresses (Prabhavathi and Rajam 2007a). Tolerance to moisture stress was accomplished by expression of the transcriptional activator controlling the expression of genes containing C-repeat/dehydration-responsive element (*DREB1A*) under the control of the stress inducible promoter *rd29A*; morpho-physiological and biochemical analyses were performed, and transgenic plants, when subjected to extended stress condition, were in normal condition while control plants were completely dried (Sagare and Mohanty 2012).

Transgenic eggplants with parthenocarpic fruits were also developed by manipulating the auxin levels during fruit development through the introduction of *iaaM* gene from *Pseudomonas syringae* pv. *savastanoi* under the control of the ovule-specific promoter *DefH9* from *Antirrhinum majus* (Rotino et al. 1997b). These transgenics produced seedless parthenocarpic fruits in the absence of pollination without the external application of plant hormones, even at low temperature, which normally prohibit fruit production in untransformed lines. Further, these transgenics exhibited significantly higher winter yields than the untransformed plants and a commercial hybrid under an unheated glasshouse trial (Donzella et al. 2000). Trials in open field for summer production and greenhouse for early spring production confirmed that transgenic parthenocarpic eggplant F_1 hybrids gave a higher production coupled with an improved fruit quality with respect to the untransformed controls (Acciarri et al. 2002). Quality parameters of frozen parthenocarpic fruits did not show any significant changes when compared to their controls (Maestrelli et al. 2003).

Recently, a reversible male sterility system was developed in eggplant (Toppino et al. 2010). An anther-specific artificial microRNA-mediated silencing of two endogenous *TBP-associated factors* (*TAFs*) encoding genes was employed to obtain male-sterile eggplants (Fig. 16.3). Recovery of male fertility was successfully triggered by the addition in the unique transformation construct of an ethanol-inducible alternative form of the *TAF* genes insensitive to the amiRNA-mediated silencing; short treatments with ethanol allowed the formation of viable pollen able to perform pollination (Toppino et al. 2010) (Fig. 16.3a–c). The stability and the efficiency of this recoverable system make it interesting in view of the development of a transgene containment system but can also be adopted as a useful tool for commercial hybrid seed production. By combining this system with induced parthenocarpy

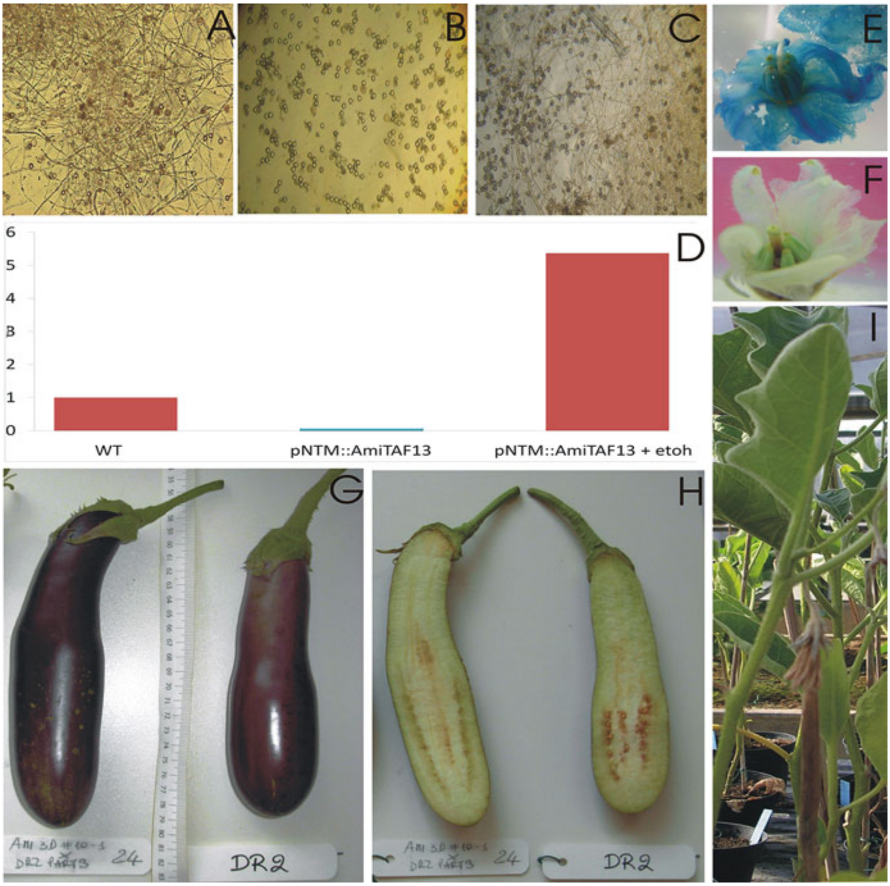

Fig. 16.3 Phenotypic and molecular evaluation of the eggplant lines transformed with the amiRNA targeting a TAF gene of eggplant. (**a**–**c**) Representative images of a pollen germination assay for wild-type and amiRNA-containing eggplant lines. (**a**) Wild-type germinating pollen. (**b**) Pollen of an eggplant transformed with the amiRNA construct, showing that pollen grains do not germinate. (**c**) Pollen of the same plant as shown in panel **b**, but after treatment of developing flowers with ethanol, pollen development and germination is restored. (**d**) Real-time analysis showing the TAF wild-type expression, the pNTM19: amiTAF13-mediated silencing of the TAF gene and the induction of the amiRNA-insensitive form of the TAF gene upon EtOH treatment of the same line. (**e**–**f**) Phenotypic evidence of the tissue-specific expression of the reporter gene GUS under the promoter pNTM (**f**), with respect to the systemic expression of the same reporter gene under constitutive 35S promoter (**e**). (**g**–**h**) Fruits from the cross between the amiRNA-transformed lines and parthenocarpic eggplant display identical phenotype with respect to the wild-type eggplant line DR2 but are completely seedless. (**i**) Inhibition of pollen fertility in the transformed lines of eggplant reflects in increment of the ratio of dried flowers on the plant

(Rotino et al. 1997b) (Fig. 16.3g, h), a novel example of complete transgene containment (male and female) in eggplant could be provided enabling biological mitigation measures for coexistence or biosafety purposes of GM crop cultivation. In addition, the growers could benefit of the increased yield of the parthenocarpic male-sterile eggplants and of the improved quality of seedless fruit produced (Donzella et al. 2000; Acciarri et al. 2002; Maestrelli et al. 2003).

A combined system to induce a restorable male sterility in eggplant was also developed by utilising a cell lethal (ribonuclease) gene *Barnase* under the control of the *TA29* promoter, which ensures the expression specifically in the tapetum, coupled to the *Cre*/*loxP* system (Cao et al. 2010). The eggplant line "E-38" was transformed with *Cre* gene and the line "E-8" with the *TA29-Barnase* chimeric gene situated between *loxP* recognition sites for *Cre*-recombinase. Four T_0-plants with the *Barnase* gene proved to be male-sterile and incapable of producing viable pollen. The crossing of male-sterile Barnase plants with *Cre* expression transgenic eggplants resulted in site-specific excision with the male-sterile plants producing normal fruits since pollen fertility was fully restored in the hybrids when the Barnase gene was excised (Cao et al. 2010).

16.6 Conclusion

Alien gene introgression from wild species has been attempted using conventional breeding approaches. However, cross-incompatibility of most of the wild species has restricted their use in crop improvement, although different strategies have deployed to overcome these problems. However, relevant knowledge acquired on eggplant regeneration from different organs, tissues, cells and protoplasts has resulted development of somatic hybrids (Rajam et al. 2008). Further development of new tools and techniques will certainly improve the use of wild species in alien gene introgression.

Considerable progress has been gathered in the genetic improvement of eggplant by exploitation of the biotechnological tools of androgenesis and, to certain extent, of genetic transformation and somatic hybridisation. However, the general controversial acceptance of the GM plants has stopped so far the possible practical utilisation of trans- and cis-genesis in eggplant, even though this species could greatly take advantage of these technologies for transferring foreign genes. Thus, it has become more urgent to fill in the gap about the understanding of the *S. melongena* genome structure and organisation through the development of molecular tools which may allow to drive the breeding, including the transfer of alien genes from its allied and wild relatives.

The first well-saturated intraspecific maps have been recently developed (Fukuoka et al. 2012; Barchi et al. 2012a), making available to the scientific community DNA sequence databases and collections of expressed sequence tags (ESTs) for genomic analysis and markers mining. These tools have facilitated the localisation of the first quantitative trait loci (QTLs) of agronomic interest (Miyatake et al. 2012; Barchi et al. 2012b; Lebeau et al. 2012). The huge variation shown by the progenitors, allied and wild relatives of *S. melongena* is still untapped and could be better evaluated and employed by the use of molecular tools and introgression lines. Introgression lines (ILs) are more powerful in QTL identification of favourable alleles of alien

QTL because they carry a single introgressed region and thus the phenotypic variation in these lines can be associated with individual introgression segments. For precise introgression of these favourable alleles into cultivated eggplant, marker-assisted selection will play an increasing crucial role as the map positions and markers linked to the QTLs will allow to plan optimal breeding strategies.

The recent released sequence of the potato (The Potato Genome Sequencing Consortium 2011) and tomato (The Tomato Genome Consortium 2012) genomes certainly will facilitate the genetic recognition of the putative synthetic genetic regions, the development of highly saturated comparative maps, and the identification of useful orthologous regulatory and structural genes in wild species eggplant. Until the entire eggplant genome will be deciphered, the availability of such heterologous genomic knowledge will make anyhow easier the development of molecular markers and isolation useful genes in the background of wild relatives. These genes can also be exploited through genetic transformation. Allelic variation underlying the traits of interest for biotic and abiotic stress resistance and other useful agronomical traits in *Solanum* relatives will be utilised using recent molecular tools and techniques.

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