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The Solanaceae – A Review of Recent Research on Genetic Resources and Advances in the Breeding of Tomato, Pepper and Eggplant

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ABSTRACT

Plant breeding has played an important role in the improvement of the Solanaceae through the development of new cultivars with significantly increased yield and quality. Tomato, pepper and eggplant cultivars have been improved for adaptability to the greenhouse environment to enable year-round cultivation. Naturally occurring diversity and that artificially induced by intraspecific and interspecific crosses are a requisite for crop improvement. The plant genetic resources that have been used intensively in tomato breeding are wild species, while existing landraces still remain an untapped resource. Although conventional hybridization is still the main method of cultivar development in tomato, there are fast advances towards molecular techniques. Tomato is not only a highly commercial species, but also a model one against which the efficiency of novel techniques can be compared. Besides tomato, pepper and eggplant have also benefited from the application of new molecular breeding methods. Advances in pepper breeding have occurred at a greater rate than in eggplant, which still remains largely unexplored. Both pepper and eggplant have rich genepools in wild relatives and cultivated landraces, which need to be conserved, explored with new technological tools, and utilized for their improvement. In the present paper, we review the status of tomato, pepper and eggplant germplasm resources, breeding methodology, and the achievements of plant breeding in these three species during the current decade.

Keywords: breeding, *Capsicum annuum*, genetic engineering, genetic resources, genomics, marker assisted selection, molecular markers, *Solanum melongena*, *Solanum lycopersicum*, tissue culture
Abbreviations: **AARI**, Aegean Agricultural Research Institute; **AFLP**, amplified fragment length polymorphism; **AVDRC**, Asian Vegetable Research and Development Center; **BA**, benzyladenine; **BC**, backcross; **BSA**, bulk segregant analysis; **CAPS**, Cleaved Amplified Polymorphic Sequences; **CMS**, cytoplasmic male sterility; **DH**, doubled-haploid; **2,4-D**, 2,4-dichlorophenoxyacetic acid (2,4-D); **ECPGR**, European Cooperative Programme for Plant Genetic Resources; **EST**, Expressed Sequence Tag; **FAO**, Food and Agriculture Organization; **GA**, gibberellic acid (gibberellin); **GRIN**, Germplasm Resources Information Network; **GMS**, genic male sterility; **IL**, introgression lines; **INRA**, National Institute for Agronomic Research; **IPK**, Institute for Plant Genetics and Crop Plant Research**; ISSR**, inter simple sequence repeat; **LD**, linkage disequilibrium; **MAS**, marker-assisted selection; **MTA**, Material Transfer Agreement; **NAA**, napthaleneacetic acid; **NBPGR**, National Bureau of Plant Genetic Resources; **NGO**, non-governmental organization; **NIL**, near isogenic line; **PCR**, polymerase chain reaction; **PG**, polygalacturonase; **QTL**, quantitative trait locus; **RAPD**, random amplified polymorphic DNA; **RF**, Restorer Fertility; **RFLP**, restriction fragment length polymorphism; **SCAR**, sequence characterized amplified region; **SNP**, single nucleotide polymorphisms; **SOS activity**, superoxide scavenging activity; **SSAP**, sequence-specific amplification polymorphism; **SSR**, simple sequence repeat; **STMS**, sequenced tagged microsatellite site; **STS**, **s**equence tagged site; **UPLB-IPB**, University of the Philippines Los Baños – Institute of Plant Breeding; **USDA**, United States Department of Agriculture; **VIGS**, virus-induced gene silencing; **VNTR**, variable numbers of tandem repeats; **TDZ**, thidiazuron; **TGRC**, Tomato Genetic Resource Center

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Invited Review

INTRODUCTION

Tomato (*Lycopersicon esculentum* Mill. = *Solanum lycopersicum* L.), pepper (*Capsicum annuum* L.) and eggplant (*Solanum melongena* L.) are among the most important horticultural species of the Solanaceae family, with significant economic and nutritional value. They are particularly good sources of vitamins and antioxidants and provide variety to the daily diet.

Tomato and pepper originated in the New World (Central and South America) while eggplant is derived from the Old World (India-China). The time of their domestication is not known with certainty, but it surely spans the change from hunter-gatherer to more agriculturally orientated societies. The genetic changes associated with domestication include selection for phenotypic value-added characteristics and higher yield. Comparative morphology and genetic analysis have been employed to identify the wild progenitors of most crops, and the distribution and ecological range of wild relatives of tomato, pepper and eggplant have been identified.

More than 800 million people in the world are hungry or undernourished (UN-FAO 2008) and the nutritional basis of the world's food supply will become even more critical as the world population rapidly continues to increase and needs to be fed. To satisfy this need, food production on available land must increase and/or unfavourable land will have to be exploited. In both these cases, plant breeding and crop diversity will play a role.

Tomato, pepper and eggplant breeding programs will necessitate innovative, non-conventional methodologies to enhance genetic variation in order to keep up with the population's increasing food demands. New technologies can be used to exploit landrace genepools, as well as secondary and tertiary genepools for new sources of abiotic and biotic stress tolerance. This need is even greater now in view of the increasing loss of genetic diversity due to increased cultivar monoculture, which has resulted in erosion of the cultivated germplasm, and the increase of land under agriculture production that has resulted in the loss of natural habitats and spontaneous biodiversity. Strategies involving the systematic collection and conservation of tomato, pepper and eggplant germplasm and their wild relatives will secure the various genepools. This, together with an understanding of the evolutionary processes involved in the formation of the various members of the Solanaceae family and the integration of new genomic technologies with traditional plant breeding methods, will enable a more efficient restructuring of gene complexes to improve production and quality.

TOMATO

Taxonomy

According to the most recent and accepted taxonomic treatises (Peralta *et al.* 2006), cultivated tomato belongs to the genus *Solanum* section *Lycopersicon* and is referred to with the binomial *Solanum lycopersicum* L. (formerly *Lycopersicon esculentum* Mill.). *S. lycopersicum* is a herbaceous perennial that is cultivated as an annual. Co-specific forms occur spontaneously in the center of origin of the section *Lycopersicon*, which is located in the Andean region of Peru, whilst the cultivated form is thought to have originated in Mexico (the name tomato comes from the Aztec word 'tomatl', meaning "plump fruit") (Rick 1975; Bai and Lindhout 2007). From Central and South America, tomato was introduced into Europe at the beginning of the 16th century, where it was initially considered a botanical curiosity, and its potential as a foodstuff was hindered by the suspicion that it was poisonous due to the presence of alkaloids in the plant. It was only in the 17th century that the species began to be appreciated as a source of edible produce, and its cultivation rapidly spread through the Old World (Rick 1976; Bai and Lindhout 2007). Throughout the world, from the late 18th century onwards tomato was increasingly selected and bred within climates ranging from cool-temperate to tropical.

Tomato easily hybridizes with the co-generic taxa of the section *Lycopersicon*, although the fertility of the progeny depends on the species (Rick 1980). For example, compatibility is full with the self-fertilizing species close to *S. lycopersicum* (*S. cheesmaniae*, *S. neorickii*, S. *pimpinellifolium*), partial with those representing the evolutionary bridges between self-compatibility and self-incompatibility (unilateral, i.e. compatible only when the cultivated form is used as female; *S. chmielewskii*, *S. habrochaites*, *S. pennellii*), or naturally absent with the most distant self-incompatible species (a viable embryo is only recoverable after *in vitro* rescue; *S. chilense* and *S. peruvianum*). A comprehensive review of the interspecific crossing barriers in tomato and its relatives has been published by Mutschler and Liedl (1994).

Importance

Apart from being an important horticultural crop, tomato is ideal for physiological and molecular genetic studies and thus a species favoured by geneticists and molecular biologists. It is easy to cultivate and mostly autogamous, producing many seeds per plant; moreover it is amenable to various horticultural manipulations, including grafting and cutting. A large number of genes have been described and assigned to specific locations across the 12 chromosomes, and numerous monogenic mutants are available (Stevens and Rick 1986; http://tgrc.ucdavis.edu/). In addition, genetic maps are well developed (http//:www.sgn.cornell.edu/), the expressed genome is being increasingly sequenced (Emmanuel and Levy 2002; http://www.tigr.org/) and an international sequencing project is in progress (Mueller *et al.* 2005; Barone *et al*. 2008; http://www.sgn.cornell.edu/solanaceae-project/).

Genetic resources

In a report dated 1987, the estimated number of seed bank entries for tomato (and its relatives) worldwide was 32,000 (Plucknett *et al.* 1987). Today, it is estimated to have increased to over 75,000 accessions of *Solanum* sect. *Lycopersicon* germplasm, maintained in more than 120 countries (Robertson and Labate 2007). The biggest public gene banks collecting tomato germplasm are in the United States, where the United States Department of Agriculture (USDA) Plant Genetic Resources Unit holds about 6,000 accessions, with 15% wild species (http://www.ars.usda.gov/main/site_main.htm?modecode=19-10-05-00) and the Tomato Genetic Resource Center (TGRC) in the Department of Vegetable Crops of the University of California Davis holds about 3700 accessions, of which 30% are wild and 30% monogenic stocks (http://tgrc.ucdavis.edu/). In Asia, the biggest collection is hosted by the Asian Vegetable Research and Development Center (AVDRC) at Tainan in Taiwan (hosting more than 7200 accessions, 14% wild, http://www.avrdc.org/). Other important gene banks for tomato germplasm worldwide (>3,000 entries) are in Germany, at the Genebank of the Institute for Plant Genetics and Crop Plant Research (IPK) at Gatersleben (http://www.ipk-gatersleben.de/Internet/Forschung/Genbank), in the Russian Federation at the N.I. Vavilov All-Russian Scientific Research Institute of Plant Industry (http://www.vir.nw.ru/) and in the Philippines, at the National Plant Genetic Resources Laboratory (IPB/UPLB, http://community.uplb.edu.ph/ca/ipb/main/). A more complete list of gene banks hosting tomato germplasm has been reported by Robertson and Labate (2007).

Recently, under the initiative of the Solanaceae working group of the European Cooperative Programme for Plant Genetic Resources (ECPGR), a collaborative programme among most European countries aimed at facilitating long-term conservation and utilization of plant genetic resources in Europe, led to the establishment of a Tomato Database, hosted at Wageningen Agricultural University, The Netherlands. The database lists passport data for more than 21,000 accessions of tomato and tomato relatives held by 38 institutions in 26 European countries (http://documents.plant.wur.nl/cgn/pgr/tomato/default.htm). The database has been developed according to the IPGRI/FAO Multicrop Passport Descriptors List (IPGRI 1996; http://www.bioversityinternational.org/) and it is expected to have more fields added in the future to incorporate characterization data.

Procedures for seed maintenance and genetic resource collection, regeneration, and evaluation are available in specific reviews (Robertson and Labate 2007) or in the TGRC website. Specific care is needed for the regeneration of accessions of wild species in order to avoid loss of diversity and genetic identity through genetic drift or unwanted cross-pollination from other accessions. Genetic stocks belonging to the tomato primary and secondary genepool contain genetic variation that is used for breeding important traits, such as plant architecture, adaptability, fruit quality, yield and disease resistance. Such variation entails greater importance considering the strong bottleneck affecting the genetic diversity of the cultivated tomato due to domestication, migration and breeding (Tanksley and McCouch 1997; Saavedra and Spoor 2002). Important collections of genetic stocks include those of monogenic mutants derived from the mutagenesis efforts of geneticists like Hans Stubbe at the IPK of Gatersleben, who developed over 300 *S. lycopersicum* and 200 *S. pimpinellifolium* mutants (Rick 1975), and that of scientists like C.R. Rick, who funded the first reference collection of tomato genetic stocks worldwide, today known as TGRC. Mendelian mutants have been extensively used in both tomato basic research and breeding. In some instances, the selection of double or triple mutant lines allowed the achievement of synergistic, hardly predictable phenotypes. An emblematic example of this is given by the selection of the Micro-Tom line, that shows an extreme dwarf and compact plant architecture, based on a combination of the mutations *sp*, *dwarf* (*d*) and, probably, *miniature* (*mnt*). This genotype is deserving much interest as a very compact and short-lived experimental tomato line (Meissner *et al.* 1997; Martí *et al.* 2006).

Among specific genetic stocks, particularly important are the collections of near isogenic lines (NILs), where different mutations have been backcrossed into a single or common pool of genetic backgrounds. One of the most extended NIL collections was derived from work prompted by L. Butler and L.A. Darby, which introgressed dozens of different mutations in the backgrounds of cvs. 'Ailsa Craig' and 'Craigella' (Maxon Smith and Ritchie 1983). Similar work was carried out in Italy in the 1970s by G.P. Soressi, who introduced a panel of mutations and genes involved in

fruit ripening, colour and texture into five selected cultivars ('Marmande', 'San Marzano', 'New Yorker', 'Roma', 'Gimar') (G.P. Soressi pers. comm.). Another important NIL series was created by J. Philouze in France (Philouze 1991). In addition to being of great interest for conventional genetic and breeding research, these collections of NILs acquire a special importance in the era of molecular genetics as they are the choice material for research where near isogenicity is crucial, such as differential screening of transcripts, proteins or metabolites (Palmieri *et al.* 1978; Testa *et al.* 2002; Minoggio *et al*. 2003; Alba *et al.* 2005; Sgherri *et al.* 2007).

Other stocks with added value for genetic and genomic research applications are the libraries of introgression lines (ILs), where each IL carries a single region introgressed from a wild donor species showing characters of interest (or simply molecular polymorphisms) but identical for the rest of their genome. Libraries of lines have been selected in such a way that the whole genome is covered by different introgressions. The first of these resources to be developed, and the most widely used, is the set of ILs selected after introgressions from *S. pennellii* in the background of cv. 'M82' (Eshed and Zamir 1995). Among the wide range of application fields where this resource has been employed, the discovery of loci responsible for quantitative trait variation is probably the most important. It has been estimated that almost 2800 quantitative trait loci (QTLs) affecting important fruit quality traits have been described using this genetic resource (Lippman *et al.* 2007). Other important sets of ILs and other genetic stocks are listed in and generally available from the TGRC; they include material derived from crosses with *S. habrochaites*, *S. lycopersicoides* and *S. pimpinellifolium* (Monforte and Tanksley 2000; Bai and Lindhout 2007; Finkers *et al.* 2007; Robertson and Labate 2007).

The nearly exclusive focus of resource development on interspecific populations for genetic analyses and diversity studies has left a void in our understanding of genotypic variation within tomato breeding programs that focus on intra-specific populations. Only recently has interest been devoted to the diversity existing in landraces and heirloom varieties of tomato, which have evolved over centuries of cultivation and reciprocal adaptation with the environment and human selection (Bai and Lindhout 2007; Passam *et al*. 2007; Terzopoulos *et al*. 2009). Whereas the standard for large scale cultivation and marketing is rather uniform both for processing and fresh market tomatoes, an almost innumerable series of different typologies exist in several countries and are grown in backyards or for small-scale, local markets. These typologies, although generally lacking traits favoured by large-scale marketing, such as uniformity, productivity and long shelf-life, often maintain better organoleptic features and other fruit quality characteristics. In the following sections, examples of the usefulness of landraces in the perspective of their re-evaluation and use in tomato genetics and breeding are discussed.

Finally, new mutant populations have recently been established, based on insertional, chemical, or physical mutagenesis (Menda *et al.* 2004; http://zamir.sgn.cornell.edu/mutants/; http://www.agrobios.it/ricerca/genomfunz.htm), for use as platforms for functional genomics applications (Emmanuel and Levy 2002). From the classical germplasm collections, the constitution of a core subset of accessions including maximum morpho-physiological and molecular diversity is also being pursued in order to establish collections that can be used for applications that couple the potential of genomics to genetic resources, such as population genomics and linkage disequilibrium (LD) mapping. Thus, the availability of classical and new genetic stocks, together with the improvement of molecular maps and genomic information, offers a range of applications that are expected to maximize the potential of genetic resources for plant breeding.

Conventional tomato breeding

Conventional, modern tomato breeding began in the early 20th century with the crossing and selection of new, useful gene combinations to improve plant performance, yield and fruit quality. In this process, the genetic basis contributing to tomato breeding has been broadened by introgressions from wild accessions as donors of desirable traits, including but not limited to disease resistance and stress tolerance (Stevens and Rick 1986; Saavedra and Spoor 2002; Bai and Lindhout 2007; Passam *et al.* 2007). Specific focus in the following sections will be given to aspects related to plant architecture, reproductive biology and fruit quality.

Plant architecture

The most important modification to tomato plant architecture has been the adoption of mutants involved in the *Self pruning* (*Sp*) gene. Tomato behaves as a neutrodiurnal species and the main shoot differentiates the first inflorescence after producing a variable number of leaves depending on the genotype (most commonly 8 to 9). The inflorescence terminates the apex. Growth continues via an axillary meristem to give rise to the next sympodial segment usually producing three leaves and ending with a new inflorescence; this development can be repeated virtually indefinitely, giving the plant a potentially perennial habit and a height which requires support. Fruit production is therefore distributed in time and requires multiple harvesting.

Plants homozygous for the *sp* mutation, a lesion in the tomato ortholog of *CENTRORADIALIS* and *TERMINAL FLOWER1* genes (Pnueli *et al*. 1998) that maintains the indeterminate state of inflorescence meristems in *Antirrhinum majus* and *Arabidopsis thaliana* respectively, show a determinate growth habit and modified sympodial rhythm in which inflorescences form at an accelerated rate. Finally, many shoots lose their indeterminate habit and do not repeat the cycle. This determinate growth habit is greatly appreciated in cultivars of processing tomato because it reduces the need for support and results in more uniform flowering and fruit ripening, enabling a single mechanical harvest (Maggiore *et al.* 1973). Modern processing tomato varieties adapted to mechanical harvesting are all endowed with a determinate growth habit due to the *sp* allele.

Tomato plants normally produce adventitious shoots at the axil of each leaf which in indeterminate plants need to be removed to avoid the acquisition of a bushy habit with an excess of leaves. Tomato mutants impaired in the production of axillary shoots, as in the case of *lateral suppressor* (*ls*, modified in a member of the VHIID protein family, Schumacher *et al.* 1999) and *blind* (*bl*, alias *torosa*, impaired in the function of a MYB transcription factor, Schmitz *et al.* 2002), are of interest for breeding a tomato plant that is more compact and suitable for high planting densities (Soressi and Mapelli 1992), but to date such mutants have not proved successful.

As mentioned before, Micro-Tom, originally bred for ornamental purposes in the late 1980s (Scott and Harbaugh 1989), has been rediscovered as a useful genotype to allow very high plant densities in experimental greenhouses and growth chambers (Meissner *et al.* 1997; Martí *et al.* 2006). Thus, Micro-Tom has been adopted for a number of applications, ranging from the creation of new mutagenized populations by Ac/Dc insertional mutagenesis (Meissner *et al.* 2000), to EST sequencing (Yamamoto *et al*. 2005), genetic analysis (Martí *et al.* 2006) and metabolomics (Iijima *et al.* 2008). As a miniature model system endowed with a fleshy fruit, Micro-Tom has been adopted for experiments in devices simulating microgravity, to study the effect of space flight conditions on plant growth, fruit and seed development (Colla *et al.* 2007).

Reproductive biology

Tomato plants produce racemose scorpioid inflorescences

of various complexities, with flowers that are perfect, hypogynous and regular. The androecium is structured as a staminal cone that, in the modern cultivated germplasm, completely covers the stigma and ensures strict self-pollination. Thus, although flowers are protandrous, the complete self compatibility, the hanging position of the flower and the inserted position of the stigma inside the anther cone make selfing the preferred, if not the absolute, mating system of cultivated varieties (Rick 1980). The degree of stigma insertion, which in general is related to the degree of selfing, fruit set and yield, is regulated by a major QTL named *Style2.1* (Chen *et al.* 2007a). Knowledge of the mechanisms underlying stigma exertion is also very important because the trait is controlled by temperature and is one of the causes of impaired fertility under high temperatures (Fernández-Muñoz and Cuartero 1991).

Advances in our understanding of the control of flowering in tomato led to a knowledge of the genes underlying the most important reproductive processes of the species (reviewed by Quinet *et al.* 2006). The control and exploitation of this knowledge will offer new possibilities for breeding better-structured tomato plants with improved environmental adaptability and more suited to mechanical operations.

The tomato has also been a species of choice for the study of the mechanisms underlying fruit set (Gorguet *et al.* 2005). The phenotype of parthenocarpic mutants, which are capable of setting seedless fruit in the absence of fertilization, has raised considerable interest. This trait offers an opportunity for improving fruit set under conditions that are sub-optimal for pollen production, pollination and fertilization and of producing fruit without seeds that may be desirable for the consumers and/or for the processing industry. Interest in the mutations or introgressed genes conferring parthenocarpy led to several advances in the knowledge of fruit-set control (Nuez *et al*. 1986; Mazzucato *et al.* 1998; Beraldi *et al.* 2004; Gorguet *et al.* 2005, 2008), although genes for parthenocarpy are not intensively used nowadays.

Although studies on heterosis in tomato were initiated almost simultaneously with those on maize (*Zea mays* L.), the inclusion of tomato hybrids in cultivation came into practice some 30-35 years later than maize hybrids. However, their use increased dramatically from the early 1970s, and today the vast bulk of fresh and processing tomatoes is obtained from F_1 seed (Atanassova and Georgiev 2007; Bai and Lindhout 2007).

While no useful S-cytoplasm has been detected in tomato (Kaul 1988), a number of genic male-sterile (GMS) mutants have been described (Stevens and Rick 1986; Sawhney 1994). However, GMS has not been the choice material of plant breeders because most GMS lines are recessive mutations and therefore retain the major disadvantage that male-fertile segregants must be rogued out of hybrid seed fields, since the male sterile parent cannot be maintained by simple seed increase (Sawhney 1994). Consequently, the production of tomato hybrid seed still relies on manual emasculation and seed companies have transferred this activity to countries where labour costs are particularly low. The increasing need to protect property rights on parental lines and to increase quality control within the seed production chain (e.g. for organic seed production) create new interest on suitable male-sterility systems for hybrid tomato seed production in developed countries.

Genic male-sterile systems have been newly proposed, or re-proposed, based on mechanisms that facilitate the propagation of the sterile line or the execution of the cross. The *7B-1* mutant shows defects in stamen development and pollen production which are sensitive to photoperiod; mutant plants are sterile under long days, but recover considerable fertility under short days (Sawhney 2004). Unlike the wild-type flowers, the style and stigma of *7B-1* flowers are well exposed and this permits easy access for pollination without emasculation, thus greatly expediting the execution of manual crosses. Similarly, functional sterility has been regarded as a useful source of sterility, because in this case the sterile plant produces functional pollen grains that are not released into the environment because of defects in anther dehiscence. Such systems, based on the *positional sterile* mutant series, were extensively used in the past (Atanassova 1999) and recently deserved a renewal of interest (Gorguet *et al.* 2006). Although the interest raised by these mutations is high, their thorough genetic and molecular characterization is still under study. Because several mutants showing conditionality or functional sterility have been described in tomato, it is possible that in the future the cloning of the underlying genes, the identification of new alleles by reverse genetics and knowledge of the physiology of male development will contribute to a more efficient and economic production of tomato hybrid seed.

Fruit quality

For years, the main objectives of tomato breeding have been those imposed by growers and sellers (yield, adaptability to agronomic techniques, stress resistance or tolerance, increased fruit firmness and shelf life), with little attention paid to the organoleptic and nutritional quality of the fruit. More recently, greater attention has been paid to the content of nutritional compounds (lycopene and other carotenoids, ascorbic acid and other vitamins, phenolic compounds) and it has been demonstrated that such components can vary significantly among genotypes. Lycopene and ascorbic acid concentrations varied considerably among 12 genotypes (George *et al.* 2004). Cherry tomatoes showed the highest contents of antioxidants and highest antioxidant activity; moreover they presented additional quality value in terms of high total soluble solids and titratable acidity (George *et al*. 2004). In other analyses of diversity for nutritional compounds it was also shown that wide genotypic differences can be found; moreover an index of total antioxidant nutritional quality (I_{QUAN}), based on experimental data and on a literature survey of tomato composition, was proposed as a tool to address breeding programs for selecting tomato genotypes with better antioxidant nutritional qualities (Frusciante *et al*. 2007).

Antioxidant capacity is also highly diversified in fruit colour mutants: high-pigment mutants, such as *high pigment 1* (*hp-1*) and *hp-2*, generally showed increased levels of all antioxidants (ascorbic acid, chlorophyll and total carotenoids) (Torres and Andrews 2006) and flavonoids (Sapir *et al.* 2008), whereas *β-carotene* (*B*) accumulated mainly β-carotene (Minoggio *et al*. 2003). For greater tomato aesthetic and nutritional diversification, other mutations or genes have received the attention of geneticists and molecular biologists; among them, the *green flesh* (*gf*, involved in a STAY-GREEN protein, Barry *et al*. 2008) and the *Anthocyanin fruit* (*Aft*, involved in a MYB transcription factor, Sapir *et al*. 2008) genes. Deeper knowledge of these and other genes that confer value-added traits will greatly facilitate the use of such characters by breeders and their incorporation into present and future tomato cultivars and hybrids.

In a study of 55 North American traditional varieties, wide diversity was found in fruit colour, shape, weight, firmness, total soluble solids, titratable acidity, flavour intensity and ascorbic acid concentration, suggesting that some of the materials represented sources of variation of great interest for tomato breeding (Rodríguez-Burruezo *et al.* 2005). In addition, flavour volatiles can be quantitatively different and sometimes higher in traditional cultivars, thus biochemically explaining the supposed higher organoleptic value of landraces over hybrids, which have been improved for other characters (Ruiz *et al.* 2005).

Advanced breeding and biotechnology

Tissue culture

Tomato is a species that is amenable to *in vitro* techniques, including micropropagation, plant regeneration from tissue

Table 1 List (non exhaustive) of studies evaluating molecular diversity in accessions of tomato and related species using the most common classes of molecular markers.

Marker type	Reference	№ of primers/ primer combinations	№ of loci scored	№ of SSR alleles[a]	№ of accessions		Polymorphic loci (%)	
					Solanum lycopersicum	Other species	Only *Solanum lycopersicum*	Including wild species
RFLP	Miller and Tanksley 1990	-	198	-	46	98	41	100
	Fooland *et al.* 1993	-	25	-	3	1	16	100
	Williams and St. Clair 1993	-	48	-	46	42	25	35
	Saliba-Colombani *et al*. 2000	-	568	-	3	-	30	-
RAPD	Fooland *et al.* 1993	313	2035	-	3	1	63[b]	100[b]
	Williams and St. Clair 1993	24	215	-	46	2	25	37
	Nienhuis and Bosco dos Santos 1994	44	-	-	55	-	100[b]	-
	Rus-Kortekaas *et al*. 1994	89	-	-	15	6	4[b]	96[b]
	Villand *et al.* 1998	41	-	-	96	-	-	-
	Noli *et al.* 1999	6	104	-	67	8	32	56
	Egashira *et al.* 2000	10	438	-	4	46	-	99
	Saliba-Colombani *et al*. 2000	123	-	-	3	-	50	-
	Archak *et al.* 2002	42	174	-	27	-	63	-
AFLP	Saliba-Colombani *et al*. 2000	43	2530	-	3	-	15	-
	Suliman-Pollatschek *et al*. 2002	4	298	-	21	-	11	-
	Park *et al.* 2004	26	1092	-	74	-	9	-
	Tam *et al.* 2005	9	845	-	34	-	15	-
	García Martínez *et al.* 2006	7	470	-	48	-	40	-
SSR	Smulders *et al*. 1997	-	36	115	7	4	28	81
	Bredemeijer *et al.* 1998	-	20	60	18	-	90	-
	Areshchenkova 2000	-	46	125	12	13	72	96
	Alvarez *et al*. 2001	-	17	144	3	28	-	94
	Areshchenkova and Ganal 2002	-	21	53	11	-	95	-
	Bredemeijer *et al*. 2002	-	20	94	521	-	100	-
	Suliman-Pollatschek *et al.* 2002	-	114	-	13	3	52	82
	He *et al.* 2003	-	158	24	19	-	41	-
	Frary *et al.* 2005	-	109	602	7	12	56	99
	Tam *et al*. 2005	-	16	39	34	-	100	-
	García Martínez *et al.* 2006	-	19	77	46	2	74	95
	Mazzucato *et al*. 2008	-	29	111	60	1	69	86

(-) not available or not applicable, [a]calculated on the total accessions scored, [b]polymorphism is calculated over the number of primers, not over the number of loci.

or single cells, embryo rescue and somatic hybridization. However, notwithstanding more than 35 years of research to set up a protocol for anther culture in order to obtain haploid plants by androgenesis, to date there is no standardized method to obtain doubled-haploids (DHs) in this species due to the high instability of the haploid tomato cell and its tendency to diploidize (Zagorska *et al*. 2004). Recently, some advances have been reported in this field, demonstrating that both gametophytic and sporophytic calli occur in cultured tomato anthers, and describing some of the putative causes of loss of the haploid condition (Seguí-Simarro and Nuez 2007). These authors demonstrated that microspore embryogenesis is possible in tomato, but although the system is promising it must be optimized in order to be exploited as a developmental pathway for the production of DHs.

The frequency with which polyploids (mainly 4x) are recovered after *in vitro* regeneration of tomato hypocotyls has been exploited to obtain diploid and tetraploid somaclones in a pair of near-isogenic lines differing for the *parthenocarpic fruit* (*pat*) mutation (Habashy *et al*. 2004). Such lines were used to synthesize triploid plants that were completely sterile in the wild-type combination, but showed restored fruitfulness in the *pat* version; triploid fruits were bigger than diploid ones and showed a higher soluble solids content (Habashy *et al.* 2004). The total male and female sterility of triploid parthenocarpic plants makes them particularly suitable for transgenic applications where the containment of gene flow must be ensured with particular care, as in the case of genetically modified plants producing metabolites with pharmaceutical properties.

Recently, protocols to establish tomato cell cultures have been enriched with the knowledge to elicit the biosynthesis of fruit-specific carotenoids, thus offering a means to biosynthesize phytoene and phytofluene for prostate cancer cell culture studies (Campbell *et al.* 2006). These protocols open the perspective to switch the production of nutritional compounds to *in vitro* systems that can be automated, better controlled and more acceptable for the employment of genetically modified cell lines.

Molecular markers

Pioneering research with tomato molecular markers (*sensu lato*) started in the early 1980s, when the application of electrophoretic separation techniques to leaf extracts, coupled with colorimetric reactions, permitted the discernment of allelic forms of enzymes at the same locus (isozymes). Such isoenzymatic variation proved immediately useful for purity analysis of seed stocks and genetic mapping of Mendelian and quantitative traits (Rick and Tanksley 1983; Bernatzky and Tanksley 1986), but the low polymorphism encountered readily indicated that it was not sufficient for the analysis of intraspecific diversity (Foolad *et al.* 1993). Since then, almost all different classes of molecular markers have been developed in tomato and utilized for genetic studies ranging from gene mapping and QTL analysis to phylogeny and diversity assessment (Saavedra and Spoor 2002; Labate *et al.* 2007; Passam *et al.* 2007).

The use of molecular markers for the taxonomy, phylogeny and analysis of genetic diversity of cultivated tomato and its close relatives has employed several marker types (Robertson and Labate 2007; **Table 1**). Marker-based studies of genetic diversity in the section *Lycopersicon* revealed that wild species contained degrees of diversity much higher than those found in the cultivated genepool (Stevens and Robbins 2007). A tight correlation between the level of diversity and the mating system, the former being higher in self-incompatible xenogamic taxa, was revealed by restriction fragment length polymorphisms (RFLPs) (Miller and Tanksley 1990), random amplified polymorphic DNAs (RAPDs) (Egashira *et al*. 2000), simple sequence re-

peats (SSRs) (Alvarez *et al*. 2001) and the analyses of DNA sequences (Baudry *et al*. 2001). **Table 1** summarizes some of the results obtained with the most commonly adopted classes of molecular markers (RFLPs, RAPDs, amplified fragment length polymorphisms (AFLPs) and SSRs). Despite the variability of the information given in the reports, differences in the type and size of the sample of accessions, the marker type and the marker efficiency in terms of preselection, the table highlights the drop of polymorphism rates encountered when wild species are left out of the investigation. This drop would be even more marked if the *S. lycopersicum* sub-sample were separated from the *S. lycopersicum* var. *cerasiforme* accessions that still enclose much of the genetic diversity of the species (Williams and St. Clair 1993). Similar results were obtained by analyzing F_2 populations which were constituted for broadening the genetic base of tomatoes (Saavedra and Spoor 2002).

Markers used for assessing genetic diversity showed that while old improved cultivars are less variable than modern ones (probably because the former did not experience introgression of exotic germplasm) the range of genetic diversity found in collections of landraces is nevertheless generally larger than that encountered in modern cultivars (Miller and Tanksley 1990; Bredemeijer *et al.* 2002; García-Martínez *et al*. 2006; Mazzucato *et al*. 2008; Terzopoulos and Bebeli 2008). By comparing a number of studies that have used the same SSR loci, it appears that the degree of genetic variation is positively correlated with the number of wild accessions that are included in the analyses. In cultivated germplasm, greater variation is found in collections that include landraces (**Table 2**). Even if the highly polymorphic locus *LEEF1Aa* is not considered, collections of a relatively small number of diverse landraces from relatively small geographical regions (García-Martínez *et al*. 2006; Mazzucato *et al*. 2008) can encompass the same amount of genetic diversity that is shown by very large collections of cultivars (Bredemeijer *et al.* 2002).

In addition to those summarized in the tables, other markers have been used by different authors for studying genetic diversity in tomato, such as variable numbers of tandem repeats (VNTRs) (Vosman *et al*. 1992; Rus-Kortekaas *et al*. 1994; Andreakis *et al*. 2004), rRNA (Marshall *et al.* 2001), single nucleotide polymorphisms (SNPs) (Suliman-Pollatschek *et al*. 2002; García-Gusano *et al*. 2004; Labate and Baldo 2005) and sequence-specific amplification polymorphisms (SSAPs) (Tam *et al*. 2005). As a good, cost-effective technology, inter-SSR (ISSR) markers have been successfully used to study genetic diversity among tomato-related species and among cultivars and landraces (Tikunov *et al*. 2003; Terzopoulos and Bebeli 2008).

The ready availability of markers and genetic resources differentiated for several traits has facilitated the search for marker-trait associations in tomato based on linkage disequilibrium (LD). In a small-scale experiment, 59 accessions of cultivated tomato (including mainly Italian landraces) were phenotyped for 15 morpho-physiological traits and genotyped at 20 polymorphic SSR loci (Mazzucato *et al.* 2008). The association analysis, combining the results of non-parametric and parametric approaches, revealed that about 5% of the total number of associations was highly significant ($P \leq 0.01$) in both tests. The reliability of such associations was supported by the fact that markers selected as being located in the same genomic region of QTLs controlling fruit size and shape showed a higher proportion of significant associations when compared to traits directly involved in these characteristics than to traits that were not involved. Accordingly, markers not mapped or not linked to known QTLs for size and shape showed a lower frequency of significant associations (Mazzucato *et al*. 2008). The possibility of detecting significant associations even using a low number of markers implies that a high level of LD exists in the material used. Such a hypothesis was recently supported by the estimation that reasonable LD can be detected between markers that span a distance of up to 20 cM (van Berloo *et al*. 2008). The reasons for such elevated LD levels in tomato, which are higher than those reported in other selfers such as *Arabidopsis* or barley (*Hordeum vulgare* L.), may lay in the mating system and greatly reduced variability, due to the strong selection pressure exerted by breeders, which means that the time for recombination and LD breaking has been relatively short (van Berloo *et al.* 2008).

The advances in marker technology enabled the development of several highly saturated genetic maps that are a basis for gene targeting, positional cloning and the creation of sets of introgression lines. This resulted in new tools and greater efficiency in breeding for both qualitative and quantitative traits through marker assisted selection (MAS) (reviewed by Foolad 2007; Labate *et al*. 2007) and gave new inputs for the genetic engineering of traits of interest. For example, in tomato the identification of the molecular bases of mutations involved in (delayed) ripening, such as *ripening inhibitor* (*rin*), *non ripening* (*nor*), *colourless non-ripening* (*cnr*) (Moore *et al.* 2002; Giovannoni 2007) and the increased knowledge of the metabolic changes occurring during ripening (Alba *et al*. 2005; Carrari and Fernie 2006) are opening the perspective for a more targeted and tailored breeding for delayed ripening and other ripening-related traits. Similarly, most of the genes that have been selected for during tomato domestication and breeding have been molecularly identified and thus represent better targets for marker assisted breeding and applied biotechnology. Most of these genes affect fruit traits, including size, shape, colour and nutritional quality (Bai and Lindhout 2007; Paran and van der Knaap 2007). Comparative genetics has also shown that many loci associated with similar fruit traits are co-localized in tomato, pepper and eggplant; thus tomato may serve as a model species for the study of the genetic control of fruit morphology and physiology in other members of the Solanaceae and in other families.

Tomato fruit traits are among the best characterized experimental systems for the identification of QTLs and an elevated number of QTLs involved in the definition of fruit size, shape, texture, biochemical composition and nutritio-

Table 2 Comparison of the number of alleles found by different authors at common SSR loci (Smulders *et al*. 1997).

Authors	№ of accessions		№ of alleles at SSR loci							Mean № of alleles per locus
	Solanum lycopersicum	Other species	LE20592	LEMDDNa	LE21085	LELEUZIP	LELE25	LEEF1Aa	LESSRPSPGb	
Smulders *et al*. 1997	7	4	7	4	5	4	3	8	5	5.14
Bredemeijer *et al*. 1998	18	0	3	3	2	2	3	7	-	3.33
Alvarez *et a*l. 2001	3	28	-		12	5	-	-	-	8.50
Bredemeijer *et al.* 2002	521	0	4	7	4	2	4	-	-	4.20
He *et al*. 2003	19	0	-	4	3	1	3	-	-	2.75
García Martínez *et al*. 2006	46	2	6	5	4	2	4	10	3	4.90
Mazzucato *et al*. 2008	60	1	6	3	3	5	3	13	8	5.90

(-) not available

Table 3 Synopsis of contributions describing QTL involved in the control of fruit size, shape, texture and chemical attributes in tomato.

Trait category	Trait	References[a]
Physical traits	Fruit weight	(1)(2)(3)(4)(7)(9)(11)(12)(13)(14)(17)(18)(19)(21)(24)(25)(27)(28)(31)(32)(37)
	Fruit diameter	(4)(12)(17)(19)(21)
	Fruit shape	(4)(5)(9)(11)(12)(15)(17)(18)(20)(28)(37)(43)
	Shape-related traits	(7)(9)(13)(20)(23)(25)(28)(32)(36)(37)(43)
	Locule number	(4)(17)(25)(26)(37)
	External color	(4)(9)(10)(11)(14)(18)(19) (21)(28)(32)
Chemical traits	Dry matter weight	(19)(21)
	Soluble solids	(1)(2)(3)(4)(7)(9)(10)(11)(12)(18)(19) (21)(22)(27)(28)(31)(32)(37)
	Sugar(s) content	(19)(21)(22)(27)(30)(31)(32)(33)(37)
	Titratable acidity	(19)(21)(22)(27)(31)(32)(37)
	pH	(1)(9)(11)(12)(14)(19) (21) (22)(27)(32)
	Citric acid	(27)(22)(33)
	Malic acid	(27)(22)(33)
	Ascorbic acid	(34)(39)(42)
	Lycopene content	(12)(19) (21)(32) (34)
	Carotene content	(19)(21)(32)(34)
	Phenolics content	(34)
	Antioxidant capacity	(34)
	Other metabolites	(16)(19) (21)(22)(33)(35)(41)
Texture traits	Firmness	(7)(9)(10)(11)(16)(19)(21)(28)(31)(32)(37)(38)
	Meltiness	(16)
	Juiciness	(16)(38)
	Mealiness	(16)(38)
	Skin toughness	(16)(38)
	Fruitiness	(22)
	Viscosity	(9)(22)
	Elasticity	(19)(21)
Taste-related traits	Sweetness	(19)(21)
	Sourness	(19)(21)
Other traits	Inflorescence and floral traits	(4)(8)(9)(25)(29)
	Seed number	(4)(9)(17)(25)
	Seed weight	(4)(17)
	Ripening	(7)(11)
	Yield	(3)(7)(9)(10)(11)(18)(28)(32)

[a] (1) Paterson *et al*. 1991, (2) Goldman *et al.* 1995, (3) Eshed and Zamir 1996, (4) Grandillo and Tanksley 1996, (5) Grandillo *et al.* 1996, (6) Tanksley and Nelson 1996, (7) Tanksley *et al.* 1996, (8) Bernacchi and Tanksley 1997, (9) Fulton *et al*. 1997, (10) Bernacchi *et al*. 1998a, (11) Bernacchi *et al.* 1998b, (12) Chen *et al*. 1999, (13) Grandillo *et al.* 1999, (14) Frary *et al.* 2000, (15) Ku *et al.* 2000, (16) Causse *et al*. 2001, (17) Lippman and Tanksley 2001, (18) Monforte *et al*. 2001, (19) Saliba-Colombani *et al*. 2001, (20) van der Knaap and Tanksley 2001, (21) Causse *et al.* 2002, (22) Fulton *et al*. 2002, (23) van der Knaap *et al.* 2002, (24) Liu *et al*. 2003, (25) van der Knaap and Tanksley 2003, (26) Barrero and Tanksley 2004, (27) Causse *et al.* 2004, (28) Frary *et al.* 2004a, (29) Frary *et al.* 2004b, (30) Fridman *et al.* 2004, (31) Lecomte *et al*. 2004, (32) Yates *et al*. 2004, (33) Overy *et al.* 2005, (34) Rousseaux *et al.* 2005, (35) Schauer *et al*. 2006, (36) Brewer *et al.* 2007, (37) Causse *et al.* 2007, (38) Chaib *et al*. 2007, (39) Stevens *et al*. 2007, (40) Gonzalo and van der Knaap 2008, (41) Schauer *et al*. 2008, (42) Stevens *et al.* 2008, (43) Xiao *et al*. 2008

nal and organoleptic quality have been described in a wide number of reports which are (non exhaustively) summarized in **Table 3**. Reviews of such recent work have been published (Bai and Lindhout 2007; Foolad 2007; Labate *et al*. 2007; Lippman *et al*. 2007; Passam *et al*. 2007). Knowledge of the location of important QTLs together with the availability of saturated genetic maps is likely to cause a switch from classic phenotypic selection to selection based exclusively on genotypes. This strategy would lead to the exploitation of a number of alleles that are locked in phenotypically unappealing genetic resources (Tanksley and McCouch 1997). Indeed, it has been demonstrated that alleles useful to increment tomato fruit size may be offered by *S. pimpinellifolium* (formerly *L. pimpinellifolium*), a very small-fruited species (Tanksley *et al*. 1996), and that lycopene content may be increased through gene introgressions from *S. habrochaites* (formerly *L. hirsutum*), a green-fruited species (Bernacchi and Tanksley 1997; Bernacchi *et al*. 1998a, 1998b). A further informative example was derived from the pyramiding of three yield-related QTLs identified in introgression lines from *S. pennellii*, a drought-tolerant, green-fruited relative of cultivated tomato, which in the hybrid condition increased yield by 50% in comparison with the control market leader cultivars (Gur and Zamir 2004).

The discovery and localization of a great number of QTLs that control the most important agronomic characters has introduced the concept of "Breeding by Design™", implying the tailored introgression of the most important qualitative traits and the major QTLs into an elite genotype (Peleman and van der Voort 2003) not only by using cultivated germplasm, but also from wild species. The implementation of MAS would reveal critical traits not only for fruit related QTLs but also for any other trait where phenotypic selection is costly or inefficient. Gene targeting studies and the cloning of many resistance genes offer efficient and widely applicable systems for MAS for disease resistance in tomato breeding. The use of molecular markers linked to resistance genes can thus greatly improve breeding schemes aimed at both deploying and pyramiding resistance genes (Barone *et al*. 2005).

Transgenic plants

Historically, tomato has proved to be a species that is amenable to genetic engineering, the most widely adopted technique being *Agrobacterium*-mediated transformation of nuclear DNA using cotyledons as explants (Van Eck *et al.* 2006). Additionally, effective protocols have been set up for virus-induced gene silencing (VIGS), allowing large-scale functional analysis and the constitution of useful genotypes by gene silencing (Liu *et al.* 2002) and transplantomic (plastid genetic) engineering that permits good transgene expression in fruit and reduced risks of gene flow through the pollen (Ruf *et al*. 2001). Transgenic approaches allow the transfer of resistance genes across the species barrier to obtain the same effects in the heterologous host as those observed in the source organism; for example, the transfer of a resistance gene against root-knot nematode (*Meloidogyne* spp.) isolated in pepper (*C. annuum*) into susceptible tomato plants. The transgene was constitutively expressed

by the 35S Cauliflower Mosaic Virus promoter, and nematode assays showed that the resistance to root-knot nematodes was significantly improved in some transgenic lines compared to untransformed susceptible plants, and this resistance was inheritable (Chen *et al*. 2007b).

The modification of ripening behaviour was the first objective of tomato genetic engineering and an increase in the lifespan of fruit tissues was achieved by hampering the synthesis of ethylene through antisensing of the *ACC synthase* gene (Oeller *et al.* 1991) or by silencing the polygalacturonase (PG) activity. The tomato cultivar Flavr-Savr™, which is silenced for PG activity, was the first food crop for which transgenic fruits were commercially available (Gray *et al.* 1992). Since then, a wide variety of transgenic constructs have been introduced into tomato including those conferring resistance to herbicides, viruses and insects.

The extensive research carried out to understand the molecular genetics (Testa *et al*. 2002; Pascual *et al*. 2007; Vriezen *et al.* 2008) and physiological basis (Mazzucato *et al.* 1999; Fos *et al.* 2000; Olimpieri *et al*. 2007; Pandolfini *et al*. 2007) of fruit set inspired many transgenic approaches to engineer parthenocarpy in tomato. These addressed auxin biosynthesis (Ficcadenti *et al*. 1999; Rotino *et al.* 2005a), response (Wang *et al*. 2005; Goetz *et al*. 2007) and sensitization (Carmi *et al*. 2003). Other studies highlighted the importance of gibberellins (GA) in the control of tomato fruit set (Fos *et al*. 2000; Olimpieri *et al*. 2007; Serrani *et al.* 2007; Serrani *et al*. 2008); accordingly, parthenocarpy in tomato was also engineered by increasing GA signalling after silencing negative regulators of the GA response pathway (Martí *et al.* 2007). Although parthenocarpic fruits produced by UC82 tomato plants transgenic for the *DefH9-iaaM* gene were often malformed, a *DefH9-iaaM* derivative gene modified in its 5′ ULR decreased transgene expression and produced parthenocarpic fruits of higher quality (Pandolfini *et al*. 2002). Thus, not only the modification of genes involved in hormone metabolism and perception may stimulate the parthenocarpic development of the fruit, but also the modulation of the transgene expression may help address tailored fruit quality. In addition to modifying ripening *per se*, many metabolic engineering approaches have addressed the biosynthesis of carotenoids. By constitutively expressing tomato lycopene beta-cyclase (*tLcy-b*) plants, a significantly higher production of β-carotene and orange fruits was obtained (Rosati *et al*. 2000; D'Ambrosio *et al.* 2004). This phenotype, which mimics the *Beta* gene (Ronen *et al*. 2000) has been confirmed in a trial aimed at assessing agronomic performance, and the stability and penetrance of the transgene (Giorio *et al.* 2007). Similar success has been achieved with the increase of xanthophyll content (Dharmapuri *et al.* 2002; Davuluri *et al*. 2005) or the introduction of novel flavours by engineering the plastidial terpenoid pathway (Davidovich-Rikanati *et al.* 2007), thus demonstrating that metabolic engineering offers the means for fine control of the tomato fruit content in terms of compounds of high nutritional value.

PEPPER

Taxonomy

The genus *Capsicum* includes 25-30 species, of which only five, *C. chinense*, *C. baccatum*, *C. frutescens*, *C. pubescens* and *C. annuum* are cultivated. Among the cultivated species, *C. annuum* is the most economically important. *C. annuum* is both a vegetable and a spice crop, and can also be grown as an ornamental; however, it is best known as a vegetable. It includes a wide range of fruit types, from large-fruited bell peppers to small pungent types (Heiser 1995; Bosland and Votava 2000; Stummel and Bosland 2007; Stommel and Griesbach 2008). The other two species with hot or pungent berries are *C. frutescens* L. and *C. chinense* Jacq., which form a species complex with *C. annuum* (De Masi *et al*. 2007; Paran *et al.* 2007). *C. baccatum* and *C. pubescens* are grown primarily in South America, with the latter being both morphologically and molecularly distinct from the rest of the domesticated species. No known wild form of *C. pubescens* exists, though it does have some relationship with a few South American wild species (Heiser 1995; Paran *et al.* 2007). *Capsicum pubescens* is a perennial species that also originated in South America (Perez-Grajales *et al.* 2004).All cultivated species show various degrees of cross-compatibility, which depend on the direction of the cross and the species involved, and produce hybrids with varying degrees of fertility (Heiser 1995; Sharma and Sharma 2007).

Genetics of pepper

Capsicum species are generally diploid (2n=2x=24), the nuclear DNA content ranges from 7.65 to 9.72 pg per nucleus for *C. annuum* and *C. pubescens* respectively and the genome size has been estimated between 2702 and 3420 Mb (Pickersgill 1991; Barchi *et al* 2007; Paran *et al.* 2007). A few wild species of the genus have a basic chromosome number x=13 (Moscone *et al.* 2003; Pozzobon *et al.* 2006). Trisomic lines are available in pepper and chromosome rearrangements have been characterized (Paran *et al.* 2007). Genes for horticultural characteristics have been identified and the inheritance of vegetative and fruit traits, as well as their correlations, have been studied (Wang and Bosland 2006; Stommel and Griesbach 2008).

Capsicum genetic resources

Pepper was one of the earliest domesticated plants in the Americas. Archeological microfossils from the pungent fruits of *C. annuum* are estimated to be 6000 years old (Perry *et al*. 2007). The centers of domestication are in Central America and in the Andes. The Spanish introduced it to Europe in the 15th century and it soon spread to other parts of the world, where new, variable, cultivated forms were developed, which significantly increased the wealth of genetic resources beyond that found in the centers of origin (Heiser 1995; Paran *et al.* 2007).

Pepper genetic resources include all cultivated and *Capsicum*-related wild species. The cultivated species embrace all landraces, which can be found wherever the crop was and is still grown. Many farmers still prefer the traditional varieties to the improved commercial cultivars. Wild species are found in the center of domestication. Large collections are kept *ex situ* in various genebanks of the world. AVRDC-The World Vegetable Center, hosts one of the largest genebanks in the world for *Capsicum*, conserves one of the most diverse collection of *Capsicum* germplasm and contains eight species comprising 7500 accessions from 95 countries (Hanson *et al*. 2004). The USDA collection contains several thousand accessions of all cultivated species (Antonious *et al.* 2006). Genetic resources from *C. chinense* stored in the Horticultural Germplasm Bank in Brazil present a high degree of variability in fruit traits important for processing and the fresh market (Lannes *et al*. 2007).

Within the ECPGR, the working group Solanaceae deals, among other crops, with cultivated and wild relatives of *Capsicum*. The Vegetable Research Institute of Budapest focuses exclusively on pepper. In 2000, the total number of pepper accessions held in genebanks, universities, institutes and NGOs in ECPGR countries was estimated to be over 20,000 (Daunay *et al.* 2006). The European Database for Pepper is being developed by the Aegean Agricultural Research Institute (AARI), Izmir, Turkey (http://www.bgard.science.ru.nl/WWW-IPGRI-Capsicum/Pepperdb.htm) having the structure of the eggplant database including similar passport data.

The vast number of accessions in any germplasm collection often leads to the necessity of developing core collections for efficient utilization of genebank material in plant improvement. A core collection consists of a limited number of diverse accessions that represents the genetic composition of the whole collection (Brown 1995). Zewdie *et al*. (2004) evaluated different ways to form a core collec-

tion of *C. annuum*, *C. chinense* and *C. baccatum* from the USDA pepper collection. Initially, stratification by species was applied and subsequently cluster analysis was carried out based on morphological descriptors of a given species. Systematic selection of a number of accessions per cluster based on unique traits proved to be the best method since it would retain all the morphological variation known in the whole collection (Zewdie *et al.* 2004).

Plant genetic resources of wild species can be conserved *in situ* to avoid a reduction of their diversity. For example, wild populations of *C. annuum* from Mexico conserved *in situ* maintained more RAPD polymorphism and isozyme variation than that estimated from accessions conserved *ex situ* (Hernández-Verdugo *et al.* 2001b; Oyama *et al.* 2006). The total molecular diversity was equally partitioned within and among populations in both wild and domesticated accessions (Oyama *et al.* 2006).

Diversity assessment, maintenance and use of *Capsicum* genetic resources

Studies of germplasm collections followed by the promotion of their utilization will ultimately broaden the crop's genetic base and will help to slow genetic erosion. Diversity assessment of any crop genetic resource is of vital importance for monitoring the crop's vulnerability. The presence of a narrow genetic base means that the genepool of the crop can lack the wealth of alleles needed for reshuffling, through crosses or other methods, for crop improvement. The enrichment of germplasm through well-characterized collections and introductions will significantly widen the available genepool.

Diversity can be measured on the basis of phenotype or genotype using a combination of phenotypic and molecular markers. Traditionally, genetic resources are characterized by a set of descriptors. In depth characterization and evaluation of the genetic material has been, and still is being, carried out by breeders according to the needs of their respective crop improvement programs. Characterization and evaluation can follow descriptors published for *Capsicum* by Bioversity International (formerly the International Plant Genetic Resources Institute; http://www.bioversity international.org/Publications/pubfile.asp?ID_PUB=345), or use other marker types whenever appropriate (IPGRI 1995). Molecular markers are currently employed for monitoring diversity in wild and cultivated *Capsicum* collections that are maintained either *ex situ*, or *in situ* and *on farm*. Understanding genetic variability among and within wild species populations is well known to provide valuable information related to conservation efforts (Votava *et al*. 2002). Limited genetic diversity and the close relatedness of pepper species were estimated in accessions of cultivated species collected near the center of domestication in the Amazon basin (Toquica *et al.* 2003).

Capsaicinoid, carotenoid and vitamin A and C content varies among different *Capsicum annuum* cultivars and breeding material with high nutritional and functional components can be selected (Topuz and Ozdemir 2007). Based on the existing inter- and intra-specific variation for total phenolic compounds, ascorbic acid and capsaicin, which has antioxidant properties, parents can be selected and crosses can be designed to produce cultivars with value-added traits (Antonious *et al.* 2006). Variation in antioxidant activity and the content of antioxidant compounds existing in a subset of the AVRDC-The World Vegetable Center *Capsicum* core collection can be exploited in cultivar improvement (Hanson *et al.* 2004).

Wild species

The various *Capsicum* species contain vast resources of unexploited genetic diversity that can be utilized before breeders will need to turn to wearisome interspecific gene transfer (Pickersgill 1997). Nevertheless, the wild species, along with the cultivated, are the subject of current research. Some of the wild species offer valuable sources of genes, particularly for disease resistance (Heiser 1995). Their potential use as donors of agronomically important value-added traits through hybridization and introgression of the gene(s) of interest is currently being evaluated (Egea-Gilabert *et al.* 2008). Based on isozymic analysis, wild populations of *C. annuum* possess high levels of diversity, which indicates that they are a valuable genetic resource whose need for conservation is urgent (Hernández-Velugo *et al*. 2001b).

Capsicum landraces

Pepper landraces are part of the culinary tradition of local communities world wide, and this is the main reason that they have been maintained despite the introduction of modern cultivars. *Capsicum* landraces are cultivated in small fields for local markets and in gardens for personal consumption in many regions of the world (Baral and Bosland 2002; Lanteri *et al.* 2003; Perez-Grajales *et al*. 2004; Portis *et al.* 2004; Guzman *et al*. 2005; Votava *et al*. 2005; Portis *et al.* 2006; De Maci *et al*. 2007). As expected, *Capsicum* landraces collected from or near the center of origin in South America and Mexico are more diverse than those cultivated in other regions of the world (Baral and Bosland 2002). Nevertheless, cultivated landraces remain a vast untapped reservoir of genetic diversity, which is evident in morphological traits, yield, quality, and genetic profiles revealed by various molecular markers (Lanteri *et al*. 2003; Perez-Grajales *et al.* 2004; De Maci *et al.* 2007). The extent and distribution of this diversity should be further characterized for a more efficient resource management and their successful *on farm* conservation (Lanteri *et al.* 2003). Since *Capsicum* landraces are heterogeneous populations, the diversity can be partitioned among and within populations. Appropriate sampling during seed production will avoid genetic drift and erosion within *Capsicum* landraces (Lanteri *et al*. 2003; Portis *et al*. 2004). *Capsicum* landraces are highly diverse at the phenotypic level, particularly for the value-added traits of interest to farmers and consumers (Portis *et al.* 2006). Molecular markers, particularly RAPDs and AFLPs, have become an efficient tool in *Capsicum* landrace diversity studies (Baral and Bosland 2002; Lanteri *et al.* 2003; Portis *et al.* 2004; Votava *et al.* 2005; Portis *et al.* 2006; De Maci *et al*. 2007). The physiological and agronomic variability that has been observed in "Manzano" hot chile pepper landraces (*C. pubescens* R & P) revealed interesting traits that can be exploited in breeding programs (Perez-Grajales *et al.* 2004).

Capsicum landraces have been recognized as a special germplasm base with distinctive organoleptic traits and an adaptability that can increase the income of farmers through their value-added products (Portis *et al.* 2004). The European Union and national governments encourage *on farm* conservation of *Capsicum* landraces, and there is clearly an increased demand for landrace identification and characterization (Portis *et al.* 2006). The *Capsicum* landraces are highly diverse phenotypically, but a comparison of *C. annuum* landraces and commercially available cultivars has shown a decrease in genetic variability as estimated by RAPDs (Votava *et al.* 2005).

From classical to molecular breeding

The objectives of pepper improvement programs differ according to location, end use of the fruit and the available resources. However the common goals for each program are high yield, stability, high fruit quality, and resistance to abiotic and biotic stress. Landraces were the initial raw material from the primary genepool for plant improvement. Parental selection and hybridization followed by selection resulted in the first *Capsicum* cultivars. Secondary genepool interspecific crosses between *Capsicum* species have been used to recombine genes and create new germplasm pools for selection. Even though pepper is considered a self-pol-

linated crop, high percentages of outcrossing (2-90%), often associated with presence of insect pollinators, have been recorded (Bosland 1993; Pickersgill 1997; Bosland and Votava 2000).

Commercial hybrid cultivars are commonly produced using hand-emasculation which is a laborious and costly process (Bosland and Votava 2000). Heterosis has been reported for yield, desirable fruit characters and early ripening (Geleta and Labuschagne 2004). Classical breeding based on crosses is used to produce hybrids with quality characters such as high capsaicinoid content and good agronomic and technological (processing) characteristics (Ayuso *et al.* 2008). Due to their distinctive qualities and adaptation to local soil and climatic conditions, local pepper varieties are often used as parents. C*apsicum* breeding has been assisted by parallel progress in genetics and cytogenetics as well as tissue culture, particularly with the production of double haploids. Molecular markers have already shown their efficiency in assisting breeding with their application in fingerprinting, diversity studies, gene mapping and MAS (Bosland and Votava 2000; Paran *et al.* 2007).

Molecular markers and applications in *Capsicum*

Different types of molecular markers, such as RFLP, AFLP, SSR, SSAP, STS, and CAPS, have been used in pepper research for phylogenetic and diversity studies, population genetic structure characterization, genetic map construction, fingerprinting, cultivar identification, purity test of F_1 hybrid stocks, marker-assisted selection, and QTL analysis.

Phylogenetic relationships and diversity studies

Molecular markers are often used in combination with morphological data and together they contribute to a holistic picture of the genetic diversity or phylogenetic relationships (Curley and Jung 2004).

Plastome analysis using microsatellites in the genus *Capsicum* revealed phylogenetic relationships similar to those obtained from analysis of nuclear DNA and phenotypic observations (Ryzhova and Kochieva 2004). Furthermore, plastome analysis revealed intraspecific variation in *C. baccatum* while *C. annuum* showed conservation and low variability (Ryzhova and Kochieva 2004). Cluster analysis based on RAPD data clearly separated accessions of *C. frutescens* and *C. chinense* (Baral and Bosland 2004).

Molecular markers have been used extensively to assess genetic diversity in *Capsicum* species, cultivars, and landraces, and to describe the genetic structure of wild and domesticated *C. annuum* populations (Oyama *et al*. 2006; De Masi *et al*. 2007). RAPDs applied to Nepalese germplasm revealed that since its introduction it has diversified to a degree that unique RAPD bands were present in Nepalese accessions which revealed considerable diversity; however, such diversity, was still lower than that present in Mexican accessions (Baral and Bosland 2002). Landrace-specific AFLP fragments were detected in genetic relationship analysis between Italian pepper landraces (Portis *et al*. 2006). RAPD markers identified accessions belonging to *C. annuum*, *C. frutescens*, *C. baccatum*, *C. chinense* and revealed genetic variation within and among species (Da Costa *et al.* 2006). AFLPs have been successfully used for monitoring the genetic diversity present in home garden chili peppers, and comparing the *in situ* maintained diversity with the diversity conserved *ex situ* (Guzman *et al.* 2005). AFLP and RAPD markers were used to assess the diversity present within one *Capsicum* landrace and characterize the divergence among populations comprising the landrace (Lanteri *et al.* 2003). Microsatellite markers detected polymorphism in wild and cultivated *Capsicum* genotypes (Nagy *et al.* 2007). Research on EST-based SSR analyses is providing new markers useful for mapping and for diversity studies (Portis *et al.* 2007). RAPD and microsatellite markers applied on somaclones also revealed variations (Hossain *et al.* 2003; Ryu *et al.* 2007).

Cultivar identification and purity test of F_1 hybrid pepper

Pepper cultivars are traditionally registered on the basis of phenotypic data. Molecular markers have been used to assist the task of cultivar registration. RFLP, RAPD and AFLP data have been shown to be suitable for detecting polymorphism and genotyping, which has resulted in the discrimination of closely related pepper cultivars and inbred lines (Lefebvre *et al*. 2001; Ilbi 2003; Kochieva and Ryzhova 2003). SSR markers have been used to complement tests of pepper variety identification (Kwon *et al.* 2005). Among AFLP, SSR and morphological traits and their combinations that were compared for cultivar identification studies, the combination of the latter two proved more efficient (Kwon *et al.* 2007). All molecular and morphological data can be combined to calculate genetic distances between cultivar pairs and a minimum genetic distance could be used to protect the plant breeder's rights (Kwon *et al.* 2007). Different marker systems have clustered pepper genotypes in a similar way (Geleta *et al.* 2005; Kwon *et al*. 2007). Significant positive correlation was found between genetic distances calculated on the basis of AFLPs and 20 morphological traits in 39 *Capsicum* genotypes by Geleta *et al*. (2005) while Kwon *et al*. (2007) did not find a correlation between DNA markers (AFLPs and SSRs) and 40 morphological traits in 60 commercial pepper cultivars. This difference may relate to the fact that correlation between phenotypic and molecular distances depends on the association between marker loci and quantitative trait loci (QTLs) and decreases when the number of loci involved in the quantitative trait increases (Geleta *et al.* 2005). Retrotransposon-based SSAP markers, AFLP, and SSR have been used to assess the genetic diversity of industrial lines of pepper and showed general agreement with pepper types (Tam *et al.* 2005).

Seed companies and marketing regulations for hybrid *Capsicum* seeds require simple, quick and accurate tests that are suitable for large-scale quality control. PCR markers provide assays that can satisfy this requirement. RAPD markers were able to determine seed purity in all tested hybrid varieties (Ilbi 2003; Mongkolporn *et al.* 2004), while ISSR could not identify all F_1 hybrids (Mongkolporn *et al.* 2004). SCAR markers developed from RAPD markers identified male and female parents, and both SCARs and RAPDs could detect seed contamination (Jang *et al.* 2004).

Linkage map construction

The first markers used in molecular mapping were RFLPs (Tanksley *et al.* 1988 cited in Paran *et al.* 2007), followed by the introduction of RAPDs, AFLPs and SSRs (Lefebvre *et al.* 1995; Livingstone *et al.* 1999; Ben Chaim *et al*. 2001b; Kang *et al*. 2001; Lee *et al*. 2004; Minamiyama *et al.* 2006). An early-integrated genetic linkage pepper map included AFLP, RFLP, RAPD, several known gene sequences, isozymes, and morphological markers (Paran *et al*. 2004). Since then, AFLPs, SSRs, RFLPs, STS and SSAPs have been used in the construction of a high-resolution intraspecific linkage map of pepper (Barchi *et al*. 2007), while aiming at QTL analysis for resistance to *Phytophthora capsici*, a high density, SSR-based map has also been constructed (Minamiyama *et al.* 2007).

Marker-assisted selection

The use of molecular markers, linked to desirable genes that control traits of agronomical importance, to accelerate selection in a breeding program, is one of the most attractive applications of molecular marker technology. SCAR markers have been developed that may improve selection for various resistances. A SCAR developed from AFLP marker conversion is linked to the *L4* locus that confers resistance to tobamoviruses in pepper (Kim *et al*. 2008a). Five SCAR markers, two of which were codominant, were developed for the early detection of non-pungent genotypes (Lee *et al.*

2005).

MAS is successful if the trait to be selected is controlled by a single gene or a major QTL. RAPD and SCAR markers that are linked to the *PV4* locus, which confers resistance to PVY, and SCAR for the detection of a major QTL for resistance to Phytophthora blight (*Phytophthora capsici* Leon.) in pepper have been developed (Arnedo-Andrés *et al*. 2002; Quirin *et al.* 2005). SSR markers linked to QTLs for controlling resistance to *P. capsici* may be used for breeding Phytophthora rot-resistant pepper cultivars (Minamiyama *et al.* 2007), whereas SNPs associated with pungency in several *Capsicum* species can be used for quick, reliable and low cost screening of this important quality attribute at an early stage of plant growth and thus accelerate breeding programs and reduce costs (Garcés-Claver *et al*. 2007).

Cytoplasmic male sterility (CMS), controlled by plastidial or mitochondrial genes but overcome by restorer fertility (*Rf*) genes in the nuclear DNA, results in the production of non-functional anthers or pollen. Marker-assisted selection requires molecular markers linked to the genes related to fertility restoration. Using AFLP markers and bulk segregant analysis (BSA), a CAPS marker was developed and proposed for the selection of fully fertile lines during the generation of new inbred restorer lines in chili pepper (Kim *et al*. 2006). Another CAPS marker, PR-CAPS associated with partial restoration has been reported by Lee *et al.* (2008a). The partial restoration (*pr*) gene is closely linked to another *Rf* locus (Lee *et al*. 2008b). Earlier RAPD and SCAR markers were also developed that could assist with the identification of CMS genotypes and *Rf* genes (Zhang *et al*. 2000; Kim and Kim 2005).

Genetic maps, gene mapping and QTLs

A recent review emphasizing *Capsicum* mapping referred to classical genetic mapping achievements and limitations, the history of mapping efforts with reference to comparative maps, the construction of first and second generation genetic maps, and the combined efforts of both the public and private sectors to create a dense map with the integration of molecular markers based on microsatellites (Paran *et al.* 2007). The first pepper map containing RFLP markers, was constructed by Tanksley *et al.* (1988). Livingstone *et al.* (1999), by including RFLP, RAPD and AFLP markers of pepper origin and also tomato probes, created the most comprehensive comparative pepper map. Pepper maps have since been constructed using F_2, BC_1, BC_2 or DH populations derived from intraspecific crosses between *C. annuum* plants (Ben Chaim *et al*. 2001b; Lefebvre *et al*. 2002; Ogundiwin *et al*. 2005; Sugita *et al*. 2005; Minami-yama *et al*. 2006, 2007), as well as interspecific crosses, such as *C. annuum* x *C. chinense* (Kang *et al.* 2001; Yi *et al.* 2006), or *C. annuum* x *C. frutescens* (Rao *et al.* 2003; Ben Chaim *et al.* 2006).

Populations developed using interspecific crosses have the advantage of a high level of desirable polymorphism, especially since *C. annuum* contains low levels of polymorphism. However, interspecific crosses present other problems such as low fertility, segregation distortion and major structural rearrangements (Barchi *et al*. 2007). In order to increase the pepper map marker density, segregation data obtained from different populations have been merged resulting in an integrated pepper consensus map (Paran *et al.* 2004). However, a more reliable and accurate map will be produced using only a single high resolution mapping population containing a large number of individuals per progeny and a large number of markers (Barchi *et al.* 2007).

A number of value-added agricultural traits have been mapped using different mapping populations (Ben Chaim *et al.* 2001a, 2001b; Thabuis *et al.* 2003, 2004a, 2004b; Ben Chaim *et al.* 2006; Minamiyama *et al*. 2007). Markers such as RFLPs, RAPDs, AFLPs and CAPS have been linked to several genes conferring resistance to potyviruses, tomato spot wilt virus, root-knot nematode, bacterial spot, and tobacco mosaic virus (Paran *et al*. 2007). RFLP markers have also been linked to pepper fruit traits, such as the *C* locus for the level of pungency (Blum *et al.* 2002) and capsaicinnoid biosynthesis genes (Blum *et al.* 2003). A list of QTLs detected in pepper has been published by Paran *et al.* (2007). During the present decade, QTLs have been reported for resistances to CMV, Phytophthora root-rot, foliar-blight diseases, powdery mildew, and anthracnose (Ben Chaim *et al.* 2001a; Lefebvre *et al*. 2003; Thabuis *et al.* 2003; Voorrips *et al*. 2004; Ogundiwin *et al*. 2005). Current research is concentrating on QTLs related to fertility restoration (Wang *et al*. 2004), yield, fruit shape, size and capsaicinoid content (Rao *et al.* 2003; Zygier *et al*. 2005; Ben Chaim *et al*. 2006) and resistance to fungal pathogens (Quirin *et al*. 2005; Sugita *et al.* 2006; Minamiyama *et al*. 2007).

Tissue culture

In vitro plant regeneration of *Capsicum* species is a prerequisite for genetic manipulation. Crop species respond differently to *in vitro* culture techniques. Pepper has been characterized as recalcitrant and not amenable to differentiation and *in vitro* plant regeneration, and consequently to genetic transformation (Joshi and Kothari 2007). Nevertheless, tissue culture has been used in pepper and a review on the successful techniques and progress has been published by Ochoa-Alejo and Ramírez-Malagón (2001). Various procedures with potential applications in pepper breeding are micropropagation, embryo culture, anther culture, the induction of somaclonal variation, somatic cell hybridization, and genetic transformation.

Micropropagation

In vitro clonal propagation of shoot tips excised from aseptic *Capsicum* seedlings leads to high rates of shoot proliferation. *In vitro* propagation, via meristem culture, can produce large numbers of true-to-type healthy plant material provided that there is no adventitious shoot production and somaclonal variation is avoided (Sanatombi and Sharma 2007). Shoot meristems are considered an ideal explant for genetic transformation in maize, but in *Capsicum* the shoot proliferation rate was very low. However, experimentation and optimization of media composition and growth regulator concentrations increased the frequency of shoots formed from shoot meristems excised from *Capsicum* seedlings (Venkataiah *et al.* 2006). Among various cytokinins studied in shoot meristem explant cultures, thidiazuron (TDZ) was found to stimulate the highest shoot proliferation in *C. annuum*, *C. baccatum*, *C. frutescens* and *C. praetermissum* (Venkataiah *et al*. 2006). Sanatombi and Sharma (2008) studied different genotypes from various cultivated pepper species (*C. annuum*, *C. chinense* and *C. frutescens*), different explant types (leaf, cotyledon, hypocotyl), and different auxin types at various concentrations. They concluded that there is a strong genotypic component in the response to *in vitro* clonal propagation in all the species studied, that the hypocotyl is less responsive than the other two explants studied, and that different combinations of auxins and their concentrations are required for shoot bud induction, elongation of shoot buds and efficient rooting of the shoot buds (Sanatombi and Sharma 2008). Axillary shoot proliferation was induced when rooted plantlets of *C. frutescens* were decapitated, which led to a large number of plants being derived from a single seedling (Sanatombi and Sharma 2007).

Modified micropropagation techniques aimed at germplasm conservation were used for minimal growth of *C. chinense* (Montalvo-Peniche *et al.* 2007). The micropropagation medium was optimized by manipulating nitrate, sorbitol, mannitol and sucrose concentrations. When the minimal growth period had been completed the regenerated plants were checked and found to be normal (Montalvo-Peniche 2007).

Organogenesis

Plant regeneration can be initiated via organogenesis or somatic embryogenesis. Through organogenesis, adventitious shoots may arise either from callus or directly from the explant. *In vitro* regeneration has been achieved by direct organogenesis in *C. annuum*, *C. chinense* and *C. frutescens* (Santana-Buzzy *et al.* 2005; Kumar *et al*. 2007; Sanatombi and Sharma 2008).

Factors affecting organogenesis, shoot formation and regeneration have been the subject of research in *Capsicum* for many years. Among these factors, the type of explant, genotype and culture medium seem to play a critical role. The explants that have been used for direct organogenesis include seedlings, leaves, cotyledons, hypocotyls, nodes and stem segments (Santana-Buzzy *et al.* 2005; Golegaonkar and Kantharajah 2006; Khan *et al*. 2006; Venkataiah *et al.* 2006; Sanatombi and Sharma 2008). Leaf and cotyledon explants regenerated more shoots than hypocotyl explants (Sanatombi and Sharma 2008).

The components of the nutrient medium have an influence on the success of *Capsicum* tissue culture, the process of which starts with shoot production from the cultured explant, followed by elongation of shoot buds, rooting of the elongated shoots and hardening prior to transplantation to the soil. The medium, and in particular the type and concentration of growth regulators, may differ during the various steps of regeneration (Sanatombi and Sharma 2008). Among the growth regulators, kinetin, benzyladenine, thidiazuron and naphthaleneacetic acid were evaluated for adventitious shoot bud induction (Santana-Buzzy *et al.* 2005; Golegaonkar and Kantharajah 2006). Media efficiency improvement by manipulating copper and silver levels had beneficial results (Joshi and Kothari 2007). Multiple shoot production derived from TDZ supplement in the induction medium resulted in improved regeneration ability of phenotypically and cytologically normal red pepper plants (Ahmad *et al*. 2006). The culture conditions, such as continuous light, influenced the success of organogenesis and had a positive effect on *C. frutescens* shoot bud induction (Kumar *et al*. 2007).

Anther and microspore culture

Anther culture or microspore culture are very useful for obtaining homozygous pure lines and speeding up cultivar development. Whole anthers containing immature pollen grains have been the most common explant used for haploid production. However, isolated microspore culture has become more popular due to several advantages over anther culture (Kim *et al.* 2008b). Anther culture has been successfully used to obtain haploid and doubled-haploid (DH) plants in pepper (Ochoa-Alejo and Ramírez-Malagón 2001). DH populations obtained by anther culture of F_1 hybrids derived from crosses between susceptible and resistant pepper lines have been used in *Capsicum* genetic mapping (Sugita *et al.* 2006; Minamiyama *et al*. 2007; Paran *et al*. 2007).

The low frequency of recovery of haploid plants has been a limiting factor in the utility of anther culture for cultivar development. The recovery is low probably due to variable androgenetic ability, depending on many parameters, and the formation of embryos with shoot abnormalities which fail to develop into normal plants (Supena *et al.* 2006). The main parameters that influence anther, microspore culture and DH production in pepper are the growing season and age of the donor plant, the physiological stage of the explant and the developmental stage of the pollen, the medium composition and growth regulator concentration, the culture conditions, type of stress treatment and the genotype of the plant (Bal *et al.* 2003; Buyukalaca *et al*. 2004; Ercan *et al*. 2006; Supena *et al.* 2006; Koleva-Gudeva *et al.* 2007; Kim *et al.* 2008b). Genotypes derived from a paprika population showed different abilities to form haploid embryos from cultured anthers and the explants taken from plants grown in the greenhouse showed a higher morphogenetic response than plants grown under field conditions (Buyukalaca *et al.* 2004). Despite these difficulties, research has produced protocols with increased efficacy of DH *Capsicum* plant production. An efficient shed-microspore culture protocol was developed that produced DH plants in a hot pepper and might be routinely used in breeding programs (Supena *et al.* 2005). Kim *et al.* (2008b) also developed a protocol with a high frequency of embryo production and plant regeneration from isolated microspores. Microspore culture is preferred to anther culture because the regenerated plants are either haploids or DH, and single microspore cells are an attractive material for genetic transformation. Additionally, the optimum culture conditions are easily learnt since there is direct access to the microspores, while in comparison with anthers, microspores produce a higher number of embryos (Kim *et al.* 2008b).

Somatic embryogenesis

Somatic embryogenesis has been recorded in *C. annuum* and related species with various degrees of success (Steinitz *et al.* 2003; Zapata-Castillo *et al.* 2008). Somatic embryos have been directly developed on the surface of the explant or indirectly on the callus surface following callogenesis of the initial explant (Steinitz *et al.* 2003; Zapata-Castillo *et al.* 2008). Somatic embryogenesis is affected by many factors, including genotype, medium composition, growth regulator type and concentration, explant type, and culture conditions. Recent research has concentrated on pepper somatic embryogenesis in *C. annuum* and *C. chinense* (Kintzios *et al.* 2001; Steinitz *et al.* 2003; Khan *et al*. 2006; López-Puc *et al.* 2006; Koleva-Gudeva *et al*. 2007; Zapata-Castillo *et al.* 2008).

In pepper anther culture, the frequency of regenerated haploid plants through somatic embryogenesis is highly dependent on the genotype (Koleva-Gudeva *et al*. 2007). Zygotic embryos, stem segments and shoot tips have been used successfully for direct somatic embryogenesis in *C. annuum* (Steinitz *et al.* 2003; Khan *et al*. 2006). Node, internode, hypocotyl, half seeds, and fruit segments were evaluated for indirect somatic embryogenesis in *C. chinense* (Zapata-Castillo *et al.* 2007). Somatic embryos were formed directly on cotyledons, zygotic embryos, germinated zygotic embryos, cotyledonary leaves and hypocotyls of *C. chinense*, with hypocotyls being the most efficient explant and generating an average of 175 somatic embryos per segment of hypocotyl (López-Puc *et al*. 2006). Stem segments and shoot tips of *C. annuum* were also very successful explants for the induction of somatic embryos and subsequent normal plant regeneration in terms of morphology and growth characteristics (Khan *et al.* 2006). Different media have been evaluated for somatic embryogenesis in *C. annuum* (Koleva-Gudeva *et al.* 2007). Many protocols use different media for each step of the somatic embryogenesis process, while others use the same medium throughout the whole procedure from induction to regeneration of the somatic embryos (Khan *et al.* 2006; Koleva-Gudeva *et al.* 2007). Growth regulators have different effects on pepper somatic embryogenesis. TZD and three auxin-type herbicides, namely 2,4-dichlorophenoxyacetic acid, (4-chlorophenoxy) acetic acid 2-(dimethylamino)ethyl ester (centrophenoxine) and quinolinecarboxylic acid (quinclorac) induced somatic embryogenesis in *C. annuum* (Steinitz *et al*. 2003; Khan *et al.* 2006). Benzyl adenine and zeatin reduced somatic embryogenesis, while kinetin had no significant effect (Kaparakis and Alderson 2008). Kintzios *et al*. (2001) showed that the addition of nicotinic acid and an increase in copper concentration increased somatic embryos proliferation by 9.2% over the control.

Heat shock treatment and illumination or darkness are some of the culture conditions that have been evaluated to optimize pepper somatic embryogenesis (Kintzios *et al.* 2000; Koleva-Gudeva *et al.* 2007). Various incubation treatments, interchanging cold-darkness and light conditions or heat conditions in darkness, and combinations of different

media are known to either stop at callogenesis or form directly somatic embryos (Koleva-Gudeva *et al*. 2007).

The number of somatic embryos developed per explant determines the embryogenetic response. High percentages of explants can produce somatic embryos (Steinitz *et al*. 2003). Somatic embryos have both root and shoot apices and normally can develop into plantlets. However, pepper (*C. annuum*) regenerants obtained by direct somatic embryogenesis failed to develop shoots (Steinitz *et al.* 2003). The problem appears to relate to the inability of the apical meristem to elongate, although somatic embryos germinated (Kaparakis and Alderson 2008). It has also been observed that if the embryos germinate, the regenerants may lack cotyledons or have deformed cotyledons. Non-shoot regenerants were observed irrespective of the media and responsive genotypes (Steinitz *et al*. 2003). However, successful induction, maturation, germination, and regeneration has been reported in *C. annuum* and *C. chinense* (Khan *et al*. 2006). This success can be attributed to a favorable combination of parameters affecting regeneration, such as explant type, hormone type and concentration. Nevertheless more research is needed to overcome the barriers to the germination of the somatic embryo and the efficient regeneration of normal plants in order to increase the application of this method to *Capsicum* species.

Somaclonal variation

The occurrence of genetic variation is not unusual in plants regenerated from *in vitro* culture (somaclonal variation). Useful inherited somaclonal variation has been measured in both qualitative and quantitative traits of chili pepper (*C. annuum*) regenerated plants and their progenies. Variation in plant growth habit, stem and flower color, the color of unripe fruits, and yield components has been demonstrated (Hossain *et al.* 2003). Somaclonal variation in pepper has been found to be genotype dependent, and inheritable somaclonal variation has been observed in pepper fruit characters and quality (Anu *et al*. 2004).

Genetic transformation

Genetic transformation in pepper (*C. annuum*) had been hampered by the lack of an efficient transformation system. Various protocols have been tested to investigate the factors affecting transformation, and progress has been achieved. Transgenic plants have been regenerated with *Agrobacterium*-mediated gene transfer (Li *et al.* 2003; Moon *et al.* 2007). PEG-mediated transformation using the β-glucuronidase (gus) gene delivery in mesophyll protoplasts of *C. annuum* has resulted in transient expression and transformation (Jeon *et al*. 2007). Transgenic pepper plants were obtained using the shooter mutant-based transformation system which can be applied to many pepper genotypes (Balázs *et al.* 2008). A review of genetic transformation in *Capsicum* has been published recently (Sharma *et al.* 2008). Genetically modified peppers have been developed and a virus resistant genetically modified sweet pepper has been approved for commercialization in China (James 2007).

Breeding for resistance

Pepper cultivars with improved genetic resistance to destructive disease pathogens are among breeders' high priorities. A resistant cultivar is a cost effective and environmentally friendly solution to control fungal, bacterial and viral diseases. Researchers have tried to relate pepper morphological traits to resistance in *P. capsici* (Egea-Gilabert *et al*. 2008). The pepper genepools should be searched for resistance genes and major QTLs, and valuable germplasm should be used to improve pepper cultivars. For instance, pepper germplasm that showed variable reactions to *Sclerotium rolfsii* Sacc. could be used to develop southern blight-resistant pepper (*C. annuum*) cultivars (Fery and Dukes 2005). Extensive research is being carried out on detecting QTLs for resistance to various diseases so as to accelerate conventional breeding with MAS. QTLs have been detected for resistance to powdery mildew and Phytophthora blight (*P. capsici*) (Lefebvre *et al.* 2003; Thabuis *et al.* 2004a; Sugita *et al.* 2006).

Resistance to pepper huasteco virus (PHV) has been discovered in the relatively unexploited wild species genepools (Hernández-Verdugo *et al.* 2001a). Resistance to potyviruses, tomato spotted wilt virus and tobaco mosaic virus has been introduced to commercial pepper cultivars (Paran *et al.* 2007). Mapping of resistance genes against potyviruses has shown that they are localized in genomic regions that are colinear between the tomato and pepper genomes (Parella *et al.* 2002). RAPD and SCAR markers linked to the *Pvr4* locus for resistance to potato virus PVY in pepper have also been developed (Arnedo-Andrés *et al*. 2002).

The diversity of the root knot nematode species that are destructive for pepper urges breeders to search and breed for nematode resistance. Resistance of the pepper line 'CM334' to root knot nematode species appears to be related to phenolic compounds accumulation (Pegard *et al.* 2005). Nematode resistance gene N has been incorporated into commercial pepper cultivars (Paran *et al.* 2007). Several major resistance genes to root knot nematodes (*Meloidogyne* spp.), the *Me* genes, have been identified in different pepper lines. Map construction showed that AFLP markers are tightly linked to the *Me3* resistance gene (Djian-Caporalino *et al.* 2001). Comparative mapping studies showed that six *Me* genes are clustered in a single genomic region on the pepper chromosome P9 (Djian-Caporalino *et al.* 2007).

Breeding for quality

In recent years, attention has been given to quality traits, particularly those that contribute to the nutritional and functional properties of the crops. Pepper contains antioxidants, such as ascorbic acid, carotenoids, capsaicin and total phenolic compounds. Various types of peppers contain vitamins A, C and E in high concentrations. Studies on the genetic inheritance of traits related to quality, such as vitamin composition, and hence gene manipulation through breeding procedures, are in their infancy (Geleta and Labuschange 2006). There is enormous variability in the carotenoids, capsaicinoids, and ascorbic acid composition of pepper cultivars (Topuz and Ozdemir 2007). Accessions conserved in AVRDC - The World Vegetable Center include a vast variation in antioxidant activity and antioxidants that can contribute to the genetic improvement of these traits and increase the nutritional value of pepper cultivars (Hanson *et al*. 2004). Knowledge of the combining ability of different genotypes with regard to these traits will help in the development of hybrids of superior quality (Geleta and Labuschange 2006). Since 2000 an increasing number of research papers have been devoted to fruit composition in *C. annuum* and other related species (Hanson *et al*. 2004; Lannes *et al*. 2007; Ayuso *et al.* 2008; Frary *et al*. 2008) and because of the increasing awareness of the value of antioxidants and vitamins to human nutrition this trend is likely to continue.

Capsicum cultivars are also characterized by different degrees of pungency depending on the quantitative and qualitative capsaicinoid content of the fruit (Stewart *et al.* 2005). Capsaicinoids are alkaloid compounds formed in the placental tissue adjacent to the seeds. The most pungent capsaicinoid is capsaicin and two capsaicinoids (capsaicin and dihydrocapsaicin) can be responsible for more than 90% of the pungency (Antonious and Jarret 2006). Pungency is a major market-determining trait of *Capsicum* cultivars and a major breeding objective. Thus research has been carried out on the genetic inheritance and gene mapping of pungency. Single genes and QTLs involved in *Capsicum* pungency have been identified (Stewart *et al.* 2005; Lang *et al*. 2006; Prasad *et al*. 2006) and MAS for this trait has progressed. A CAPS marker has been developed and a SNP associated with this trait has been identified and validated (Minamiyama *et al.* 2005; Garces-Claver *et al.* 2007).

EGGPLANT

Taxonomy, genetics, genebanks

Eggplant (*Solanum melongena* L.), also known as brinjal, aubergine or Guinea squash, is a non-tuberous species of the family Solanaceae. Other cultivated species of eggplants are known as scarlet eggplant (*S. aethiopicum* L.) and gboma eggplant (*S. macrocarpon* L.). Cultivated eggplants and their wild relatives belong to the subgenus *Leptostenomum* (Dunal) Bitter, which includes more than 450 species distributed among 22 sections (Kantharajah and Golegaonkar 2004; Van Eck and Snyder 2006). The time frame for eggplant domestication is not known, but according to distribution patterns, domestication took place in the area between India and China, where the crop is extremely variable and wild relatives can be found (Choudhury 1995; Dauny and Janick 2007; Frary *et al.* 2007). From the Indo-China region, eggplant species spread to various areas of the world where many diverse forms (landraces) appeared and through natural and anthropic selection formed secondary centers of diversity (Prohens *et al.* 2005). The progenitor of *S. melongena* is probably a complex of wild species known as *S. incanum* L. while a very primitive cultivated and later wild form of eggplant is *S. insanum* (Frary *et al.* 2007). Eggplant is a diploid (2n=2x=24) inbreeding species with only an average of 6-7% natural cross-pollination (Choudhury 1995). However, research showed that cross-pollination levels could approach 70% depending on cropping and environmental factors (Frary *et al.* 2007). The genome size is approximately 956 Mbp (Frary *et al.* 2007).

Genetic resources of eggplant are comprised of both *S. melongena* cultivated forms and related wild species. They are conserved *ex situ* in various genebanks worldwide, with large collections maintained in China (Mao *et al.* 2008). In India, the centre of eggplant domestication, the National Bureau of Plant Genetic Resources (NBPGR) maintains over 2,500 accessions (Kumar *et al.* 2008). Additional genebanks that collect and keep eggplant accessions and related species are the National Institute and Agrobiological Resources in Japan, the AVRDC in Taiwan, the USDA Beltsville Research Station in the USA, and the Vavilov Institute in Russia. The European genebanks containing eggplant accessions are at INRA (France), Nijmegen Botanical Garden (The Netherlands), and the University of Birmingham in the UK (www.sgn.cornell.edu/documents/solanaceae-project/docs/solanaceae-crop.pdf). A European project and network, EGGNET connects all the European eggplant collections and has developed primary and secondary descriptors for eggplant germplasm characterization (www.ecpgr.cgiar.org). The European eggplant database (http://www.bgard.science.ru.nl/WWW-IPGRI/eggplant.htm) includes genetic resources of the common eggplant (*S. melongena*), the African eggplant species (*S. aethiopicum* and *S. macrocarpon*), pepino (*S. muricatum*), naranjilla (*S. quitoense*), cocona (*S. sessiliflorum*), other edible *Solanum* species, and wild relatives (Daunay *et al*. 2006). The total accessions held in various institutions in Europe (genebanks, universities, institutes and NGOs) number about 6,000 (Daunay *et al*. 2006). The eggplant database provides passport data as well as primary and some secondary data, and access to the eggplant accessions in Europe is facilitated with a standard Material Transfer Agreement (Daunay *et al*. 2006).

Classical eggplant breeding programs are based on inter-varietal crosses followed by selection and inbreeding. In many countries, the advantages of hybrid vigor, identified within breeding programs, has led to the progressive replacement of landraces and traditional cultivars by F_1 hybrids (Dauny and Janick 2007; Mao *et al.* 2008). Breeding program objectives have identified yield, quality, biotic, and abiotic stress as being of major importance. The vast genepool of landraces and related wild species represents a rich source of desirable value-added traits that has not been fully exploited, probably due to the difficulties that accompany the making of inter-specific crosses of wild species and the fact that the vast majority of landraces are in regions that so far have been less amenable to modern forms of genetic improvement. However the recent advances in biotechnology have entered the eggplant genetic improvement arena and promise to overcome many difficulties of successful gene introgression into eggplant via inter-specific and inter-generic hybridization. Molecular marker technology can quickly reveal the secrets of gene transfer and at the same time eliminate any undesirable linkage drag from the wild species. In comparison to tomato, which has been the focus of molecular research utilization in breeding programs, molecular tools have only recently been exploited in eggplant improvement. Molecular techniques are expensive and eggplant, unlike tomato, is not a plant favored by private breeding due to a lack of high return on investments. Classical mapping efforts have also been very limited in eggplant compared to other Solanaceae and the first molecular map was developed just a decade ago (Frary *et al.* 2007). Only few papers describe the application of molecular markers such as RAPD or AFLP in eggplant (Karihaloo *et al*. 1995; Mace *et al.* 1999) before 2000. However, due to the existing colinearity between eggplant and tomato genomes, tomato molecular markers can be used in eggplant, thus the knowledge that has been obtained from the long and intensive work in tomato can be applied to construct genetic maps in eggplant, and in MAS breeding programs.

Phylogenetic relationships

Even though genebanks collect, characterize, and maintain the world's genetic heritage, the massive work of regeneration, characterization, and maintenance of numerous plant species accessions does not permit a scrupulous study of their genetic profiles. However, it is of major importance to understand phylogenetic relationships for the efficient utilization of the germplasm resources available for plant improvement (Furini and Wunder 2004; Behera *et al.* 2006). The relationship between eggplant and related species remains unclear, and clarification of the evolutionary relationship between eggplant and its more than 300 related *Solanum* species is needed for the effective exploitation of eggplant-related species (www.sgn.cornell.edu/documents/solanaceae-project/docs/solanaceae-crop.pdf) (Behera *et al*. 2006). The established phylogenetic relationships are based on morphological characters, hybridization between different species, crossability and hybrid fertility studies, the results of which are often controversial (Behera *et al*. 2006). Allozymes were among the first molecular markers to be used to detect variations and phylogenetic relationships between eggplant and related species (Isshiki *et al.* 1994; Karihaloo and Gottlieb 1995), but more recently, new molecular tools, combined with already characterized morphological traits, have been employed (Mace *et al.* 1999; Furini and Wunder 2004). The analysis of biochemical markers for seed proteins revealed the same interrelationships in *Solanum* subgenus *Leptostemonum* as the conventional taxonomy tools of morphological markers and crossability tests (Karihaloo *et al.* 2002). The employment of STMS (sequence-tagged microsatellite site) markers revealed closer genetic similarity of *S. melongena* and the closely-related *S. insanum*, while it clustered together both species with the weedy species *S. incanum*, but clearly placed the distant species *S. sysimbriifolium* in a separate cluster. The molecular relationships of the four species confirmed phylogenetic relationships based on crossability relationships (Behera *et al*. 2006). The application of AFLP markers to *Solanum* accessions from various genebanks (USDA, Birmingham, INRA, Nijmegen) showed that, in general, the molecular data gave results consistent with those obtained from existing morphological, biochemical or other marker systems such as ITS-1 sequences. The successful classification of unknown *Solanum* species, the re-classification of previously misidentified taxa, and the efficient determination of genetic relationships among *Solanum* species has clearly in-

dicated the necessity of including molecular marker technology in germplasm management programs (Mace *et al.* 1999; Furini and Wunder 2004). ISSRs distinguished eight related *Solanum* species (*S. incanum* L., *S. macrocarpon* L., *S. virginianum* L., *S. torvum* Swartz, *S. aethiopicum* L., *S. anguivi* Lam., *S. violaceum* Ort. and *S. kurzii* Brace and Prain) and detected discrepancies in previous studies, thus proving that molecular marker systems can be efficient tools for phylogenetic analysis (Isshiki *et al.* 2008). ISSR studies indicated that *S. macrocarpon* and *S. virginianum* should be placed outside the section Melongena (Isshiki *et al.* 2008). Molecular analysis with mt DNA and ISSR markers identified distant relationships of *S. torvum* with the other related *Solanum* species (Isshiki *et al.* 2003; Isshiki *et al.* 2008).

Interspecific hybridization

Interspecific hybridization involving *S. melongena* has attracted eggplant breeders since it is an approach to introgress genes of interest that are present only in the wild or other cultivated eggplant species (Collonnier *et al.* 2001a, 2001b, 2003; Kashyap *et al.* 2003). Depending on the direction of the cross and the species involved, interspecific hybrids with varying degrees of fertility have been produced (Choudhury 1995; Bletsos *et al.* 1998; Collonnier *et al.* 2001a; Behera and Singh 2002; Bletsos *et al.* 2004). The conclusions derived from various studies on the crossability between *S. melongena* and its related species are not consistent and this may be attributed to the use of different parental genotypes and environmental conditions (Behera and Singh 2002). Hybridization experiments showed that *S. melongena* was crossable with several species of the same subgenus *Leptostemonum* (Collonnier *et al*. 2001a). Interspecific hybrids were produced from crosses between different genotypes of *S. melongena* with *S. macrocarpon* and *S. torvum*. However, interspecific hybrids have not been produced with *S. sisymbriifolium* Lam. (Bletsos *et al.* 1998, 2004).

Interspecific hybridization via sexual crosses has illustrated various degrees of limitation to crossability, possibly due to sexual barriers (Collonnier *et al*. 2001a; Behera and Singh 2002). The degree of hybrid crossability and fertility are affected by the eggplant genotype used and by which species is used as the female parent (Bletsos *et al.* 2004). Different parental genotypes should be tested since differences in fertility arise depending on the genotype of the parents involved in the cross (Behera and Singh 2002). Wide cross-hybridization and fertility barriers can be overcome by the utilization of new biotechnological tools (Collonnier *et al*. 2001a, 2001b, 2003; Kashyap *et al.* 2003). Among the techniques used for successful interspecific and intergeneric hybridizations is embryo rescue, which was a prerequisite for the formation of a viable progeny between two different species (Bletsos *et al.* 1998; Kashyap *et al.* 2003; Bletsos *et al.* 2004).

Wild species

Breeding resistant varieties is one of the most important contributions of plant breeding to agriculture and is a never-ending effort to confront pathogens and prevent diseases. Wild species related to *S. melongena* can be used as sources of resistance and other desired characters in eggplant breeding. Resistance to pests and pathogens has been well identified in several wild species (Kashyap *et al*. 2003). *Solanum integrifolium* shows resistance to *Fusarium* and bacterial wilt, as well as to fruit and shoot borers and spider mites (Kashyap *et al.* 2003). Resistance to powdery mildew, caused by *Leveillula taurica*, has been found in *S. quinquangolare*, *S. linnaeanum*, *S. aculeatissimum*, *S. aviculare*, *S. pseudocapsicum* and *S. spinosissimum*. *Solanum sisymbriifolium* showed a variable disease reaction (Bubici and Cirulli 2008). *Solanum torvum* has resistance to *Verticillium* wilts and to root-knot nematodes *Meloidogyne* spp. and also proved to be a useful source of resistance or tolerance against *Ralstonia solanacearum* and *Fusarium* for eggplant improvement (Kashyap *et al*. 2003; Clain *et al*. 2004; Gousset *et al*. 2005).

The importance of the wild species for eggplant improvement clearly underlines the need for their conservation *in situ* in their natural habitats, and *ex situ* in genebanks. Most of the wild relatives have not been collected and many of those that are conserved have not been studied; so their potential for plant improvement in most cases has not been exploited. Representative *ex situ* collections from eggplant wild relatives need to be readily available to breeders. The collection, use and maintenance of wild relatives require sampling strategies that can be optimized through knowledge of the genetic diversity patterns of the wild species. Studies of the genetic diversity of wild species are required for their efficient conservation and management. Diversity studies of the endangered relatives, *S. vespertilio* Aiton and *S. lidii* Sunding, endemic to the Canary Islands, showed that these two species are clearly differentiated from the continental species. The analysis of the populations within the species *S. vespertilio* and *S. lidii* showed relatively low differentiation. These kinds of analyses help in the development of appropriate strategies for species conservation (Prohens *et al*. 2007a).

Other species

The ghoma eggplant (*S. macrocarpon*) and scarlet eggplant (*S. aethiopicum*) are cultivated species that are related to eggplant (*S. melongena*). They are grown mainly in Africa and are known as the African eggplants (Daunay *et al.* 2006; Daunay and Janick 2007; Mao *et al.* 2008). Based on morphological data, it has been proposed that *S. anguivi* is the wild ancestor of *S. aethiopicum*, which has developed within species groups that are morphologically distinct. On the basis of RAPD analysis, accessions from the *S. anguivi* and *S. aethiopicum* groups Gilo and Shum, respectively, originating from Uganda, could not be clearly clustered according to species and group classifications (Stedje and Bukenya-Ziraba 2003). *S. macrocarpon* gives fertile hybrids with common eggplant through sexual hybridization (Bletsos *et al.* 2004), it is resistant to spider mite and represents a promising genetic resource for eggplant improvement. *Solanum aethiopicum* gr. *gilo* and *S. aethiopicum* gr. *aculeatum* (= *S. integrifolium*) carry resistance to soil-borne wilt caused by *F. oxysporum* f. sp. *melongenae* (Toppino *et al*. 2008a).

Eggplant landraces

Eggplant landraces (local heirlooms, local varieties or traditional cultivars) comprise a very attractive genetic resource because they have a close relationship with the modern cultivars and can be readily used as breeding material without the negative consequences that follow any cross involving a wild species (linkage drag). Eggplant landraces are still cultivated in many parts of the world probably because eggplant, in comparison to tomato and pepper, is still conceived as 'a poor man's crop' (Choudury 1995), and in Asia is produced by small-scale farmers as an important source of income (Rashid 2003 cited in Hanson *et al.* 2006). Eggplant landraces conserve the initial 'cultivated' diversity, while commercial cultivars present a narrower genetic base that is revealed in many different characters either in the phenotype or in the genotype, ranging from morphological to quality traits and can be fingerprinted with molecular markers. Eggplant landraces are not only used as a breeding resource but they are cultivated *per se* for their good organoleptic quality. In the last decade, informed consumers have demanded different and variable types that can be found in local heirlooms, thus increasing the market value of eggplant landraces. This has led to the need for a list of landraces that can be registered and protected. The list requires the identification of landraces so that they can be recognized and distinguished from other types. For example,

local Spanish, striped eggplants, known as 'Listada', have shown a characteristic morphological and molecular profile that can be used as an identity and protection label (Muñoz-Falcón *et al.* 2008).

Eggplant landraces can be found in the centre of diversity but also in other places where the crop was introduced early and, via natural and farmer influence, developed into new pools of variability and formed secondary centres of diversity, or simply variable cultivated forms. Collections of eggplant from secondary centres have revealed the presence of a vast morphological and molecular diversity (Prohens *et al.* 2005). Landraces are cultivated in many regions of the world (e.g. India, Japan, Sri Lanka, Taiwan and Bangladesh) and present a wide diversity of morphological, phenological and agronomic traits that can be exploited in breeding programmes (Prohens *et al.* 2005; Kumar *et al.* 2008).

Diversity studies

There is a vast phenotypic diversity in eggplant and its related species, which has been traditionally measured with morphological markers. Fruit is the most diverse unit (color, shape and size) of the plant, since this is the consumers' target for particular uses. The genetic variability of cultivated eggplant resources (hybrid and non-hybrid cultivars, landraces, and hybrids between landraces), related cultivated species, and wild related species has been studied with respect to their value-added agronomic traits, and morphological characters (Prohens *et al*. 2005; Wang *et al*. 2007; Muñoz-Falcón *et al.* 2008; Rodríguez-Burruezo *et al.* 2008). Several morphological and agronomic characters present polymorphism; among them growth habit and plant vigour, prickliness, fruit color, shape and size and other yield and quality related traits. Traits that characterize morphological diversity have been included in the descriptors list available from Bioversity International Publications (www.bioversityinternational.org). Biochemical markers, such as isozymes, have been used to evaluate genetic diversity among eggplant accessions from the species *S. melongena*, *S. insanum*, and *S. incanum* (Kaur *et al.* 2004), while seed protein diversity was assessed in *S. melongena* and its related taxa in subgenus *Leptostemonum* (Dunal) Bitter. (Karihaloo *et al*. 2002). DNA-based markers, such as RAPDs (Clain *et al.* 2004; Wang *et al*. 2007), SSRs (Nunome *et al*. 2003a, 2003b; Behera *et al*. 2006), AFLPs (Prohens *et al*. 2005, 2007a; Muñoz-Falcón *et al*. 2008; Rodríguez-Burruezo *et al*. 2008), or ISSRs (Isshiki *et al*. 2008) have also been used to study genetic relationships between cultivars, landraces and other genetic resources. Exotic and indigenous accessions maintained at the Indian Agricultural Research Institute revealed extensive genetic diversity using STSM markers with similarities that ranged from 0.37 to 0.90 within *S. melongena* (Behera *et al.* 2006). Significant variation has been detected in eggplant and *S. aethiopicum* accessions for superoxide scavenging (SOS) activity, total phenolics, ascorbic acid, soluble solids, minerals and other biochemical traits (Hanson *et al.* 2006; Prohens *et al.* 2007b; Raigòn *et al.* 2008). Intra-specific diversity in related or wild relatives of eggplant has also been studied using molecular markers or based on agronomic characters, such as the levels of resistance. RAPDs showed that *S. torvum* had complete homogeneity in accessions that were collected long after the introduction of the species in Reunion Island in the Indian Ocean (Clain *et al*. 2004).

Conventional breeding

Breeders using conventional methods have developed F_1 hybrids with high yield and quality and desirable horticultural traits such as earliness and reduced bitterness and prickliness that can successfully adapt in the greenhouse environment (Frary *et al*. 2007). Crosses between eggplant landraces have been used to produce F_1 hybrids, which were compared with commercial hybrids in open field cultivation in terms of yield, fruit and quality (Rodríguez-Burruezo *et al*. 2008). Morphological and molecular distances between the parents were used to predict the progeny performance, the yield of which was shown to be similar to that of commercial hybrids in several cases. Eggplant landraces as breeding populations or crossing parents have been found to increase the diversity of fruit types in commercial cultivars (Rodríguez-Burruezo *et al*. 2008).

Genetic systems, for the easy and low-cost production of commercial hybrids are essential for hybrid production. Both genic and cytoplasmic male sterility systems have been identified in eggplant (Phatak and Jaworski 1989; Phatak *et al.* 1991; Isshiki and Kawajiri 2002). Cytoplasmic male-sterile eggplants resulted from the transfer of *S. melongena* chromosomes into *S. violaceum* cytoplasm (Isshiki and Kawajiri 2002). *Solanum gilo* (*S. aethiopicum* gilo groups) has been used as a source of cytoplasmic male sterility (Fang *et al.* 1985), while recent research has shown that the cytoplasm of *S. virginianum* can also be used to develop functional male sterile (anther-indehiscent) eggplant with stable expression of male sterility and seed fertility, but fertility restorer genes are needed for the utility of the system (Khan and Isshiki 2008).

Unfavorable climatic conditions may induce flowering and fertilization problems that can be overcome by a laborious and costly hormone treatment. Plant improvement by the development of parthenocarpic cultivars aims at overcoming this problem. To achieve this goal, eggplant breeding is using both classical and molecular methods involving asexual gene transfer through transformation. Transgenic parthenocarpic eggplants, combining high fruit quality with high fruit set, continue to be the target of research (Donzella *et al.* 2000; Acciarri *et al.* 2002). Conventional crossbreeding has been used for the development of a new parthenocarpic eggplant cultivar with desirable fruit quality in Japan (Kikuchi *et al.* 2008).

Biochemical markers

Morphological markers have frequently been used to confirm hybridity (Bletsos *et al*. 2004). The development of biochemical markers has assisted in the confirmation of hybridity with precise and reliable methods devoid of environmental influence (Bletsos *et al.* 2004). Biochemical markers have been employed to describe phylogenetic relationships and genetic variation in eggplant and related species (Isshiki *et al.* 1994; Karihaloo and Gottlieb 1995), and have been used extensively in eggplant breeding to verify intentional genomic changes. In crosses between *S. melongena* and the species *S. macrocarpon* and *S. torvum* isozymes have proved effective in confirming hybridity (Bletsos *et al.* 1998, 2004). Isozymes have also been used to identify the hybridity in somatic hybrids between *S. melongena* and the species *S. torvum* and *S. aethiopicum*, *Aculeatum* group (Daunay 1993). Five enzymes, aspartate aminotransferase (AAT), glutamate dehydrogenase (GDH), glucose-phosphate isomerase (GPI), shikimate dehydrogenase (SKDH) and triose-phosphate isomerase (TPI), were used to study diversity in the eggplant complex that includes *S. melongena*, *S. insanum* and *S. incanum*, and according to the electrophoretic patterns *S. melongena* proved more homogeneous than the other two species (Kaur *et al*. 2004).

Molecular markers

Several types of molecular markers have been used to study the relationships between the cultivated *S. melongena* and related species (Furini and Wunder 2004; Behera *et al.* 2006). Recently, AFLPs distinguished domesticated and wild forms of eggplants and supported their morphological characterization (Furini and Wunder 2004). Molecular markers have also been successfully used to assess genetic diversity. The first markers used in the study of eggplant genetic diversity were RAPDs, which supported the notion that the two species *S. melongena* and *S. insanum* were not taxonomically different (Karihaloo *et al.* 1995). RAPD and

ISSR markers were used for the assessment of diversity within the wild species *S. torvum* introduced to Java in Indonesia and Reunion Island in the Indian Ocean (Clain *et al*. 2004; Gousset *et al*. 2005).

Microsatellites in eggplant have been identified, characterized, and successfully exploited in linkage mapping so as to assess polymorphism in eggplant accessions, and wild *Solanum* species (Nunome *et al.* 2003a, 2003b; Behera *et al.* 2006). ISSR markers have also been used for the assessment of genetic diversity relationships in eggplant and related species (Isshiki *et al.* 2008), while ISSR markers, isozymes and RAPDs were employed to characterize di-haploids obtained through anther culture of tetraploid somatic hybrids between *S. melongena* and *S. aethiopicum* group Gilo (Rizza *et al*. 2002). ISSR markers proved more efficient than isozymes, cpDNA and mt DNA, in discriminating *S. kurzii* and *S. violaceum*, which belong to the same section *Oliganthes* (Isshiki *et al.* 2008). Japanese eggplant cultivars showed either no or low levels of molecular polymorphisms using allozyme, cpDNA or microsatellite markers. Despite the low polymorphism levels detected, ISSRs provided an identification pattern, combining the marker bands amplified by only a few ISSR primers (Isshiki *et al.* 2008).

RFLP analysis has been used in the construction of an eggplant genetic linkage map using an F_2 population derived from an interspecific cross of *S. melongena* with *S. linnaeanum* Hepper & Jaeger (Doganlar *et al*. 2002b). Phylogenetic relationships in eggplant and the related species *S. surattense* Burm. (= *S. virginianum* L.), *S. torvum* Swartz, *S. gilo* Raddi (= *S. aethiopicum*), *S. integrifolium* Poir. (= *S. aethiopicum*), *S. indicum* auct. non L. (= *S. violaceum* Ort.) and *S. sanitwongsei* Craib were assessed by exploiting variations of organellar DNA (Isshiki *et al*. 1998, 2003).

In order to identify organelle inheritance in F_1 hybrid and backcross progenies between *S. virginianum* and *S. melongena*, their cpDNA and mt DNA were studied using different enzymes in PCR-RFLP analysis. Restriction patterns of F_1 and BC_1 revealed maternal inheritance for mt DNA and parental and biparental for cpDNA (Khan and Isshiki 2008).

Linkage maps, MAS and QTLs

Classical mapping efforts have been very limited and the construction of molecular maps in eggplant started only in the last decade, but since then several kinds of markers, such as RAPDs, AFLPs, SSRs, RFLPs, have been mapped in various eggplant interspecific and intraspecific populations (Nunome *et al.* 2001; Nunome *et al.* 2003a, 2003b; Doganlar *et al.* 2002b; Frary *et al*. 2007). The eggplant RFLP linkage map primarily used single copy tomato cDNA, genomic DNA and expressed sequence tag probes previously mapped in tomato (Doganlar *et al.* 2002b). Despite large evolutionary differences, the eggplant and tomato genomes are largely colinear, thus making comparative map construction possible (Doganlar *et al.* 2002a, 2002b). Genomic resources based on markers common to tomato and pepper maps can be used in eggplant (Frary *et al*. 2007). Efforts have been made to map genes and QTLs controlling traits such as eggplant fruit shape and weight, fruit, stem, and calyx color, plant prickliness, flower size and shape, plant height and hairiness and other fruit, leaf, flower and plant traits (Nunome 2001; Doganlar *et al.* 2002a; Frary *et al*. 2003, 2007).

MAS technology can help crop improvement programs to rapidly select progeny carrying markers linked to genes of interest controlling value-added trait (either monogenic or polygenic) instead of by slow phenotype selection. This MAS process expedites the introgression of the desired genes and reduces the linkage drag of undesired genes (Frary *et al.* 2007).

Tissue culture

Reviews of eggplant biotechnology have described the techniques and applications with particular emphasis on somaclonal variation, somatic hybridization, somatic embryogenesis, and genetic transformation (Collonnier *et al.* 2001a; Kashyap *et al*. 2003; Kantharajah and Golegaonkar 2004). Eggplant is amenable to tissue culture and plant regeneration from various explants (leaf, cotyledon, hypocotyl, root, anther, embryo, cell and protoplast). Somaclonal variants have been observed in regenerated eggplant plants and somatic hybrids have been produced by the fusion of cells derived from various types of *S. melongena* tissues, as well as from its wild relatives, and has facilitated geneflow from wild *Solanum* species (Collonier *et al*. 2001a, 2001b). Anther culture has been extensively used not only for the production of haploids and then DHs but recently for the production of di-haploids derived from anther culture of somatic hybrids in order to reduce the ploidy level and bring the hybrid back to normal ploidy. Somatic hybrids of special interest are the cybrids and asymmetric hybrids (Collonnier *et al.* 2001a).

Genetic engineering via transformation has been successful to *Bt* gene transfer and parthenocarpy (Rotino *et al*. 1997; Acciarri *et al.* 2000, 2002). A genetic transformation of particular interest would be to increase the nutritive value of eggplant fruit, for this could have a major impact in the countries of South Asia where eggplant is virtually a staple food.

Organogenesis

Organogenesis of various species of eggplant involving callus, shoot and root formation has been described in a review (Kashyap *et al.* 2003). Since then, only a few papers have been published with regard to organogenesis in eggplant and related species (Franklin *et al*. 2004; Gisbert *et al.* 2006; Sarker *et al.* 2006). Efficient regeneration was obtained for the African eggplant species scarlet (*S. aethiopicum*) and gboma (*S. macrocarpon*) (Gisbert *et al.* 2006).

Somatic embryogenesis

Eggplant is particularly amenable to somatic embryogenesis, and factors affecting the induction and maturation of somatic embryos, molecular aspects, and practical applications have been extensively reviewed by Kantharajah and Golegaonkar (2004). These authors concluded that even though much research has been carried out on the induction of eggplant somatic embryogenesis, the practical utility of the method has not been fully exploited and artificial seeds are not routinely used.

Protoplast culture

Efficient protocols for protoplast regeneration have been developed using *S. abutiloides*, *S. integrifolium*, *S. scabrum* and *S. toxicarium* (Iwamoto and Ezura 2006). Plant regeneration from protoplast culture is a prerequisite for the production of somatic hybrids through cell fusion and for transformation systems that use protoplasts for the reception of foreign DNA. Eggplant explants that can be used as protoplast sources are hypocotyls, cotyledons, and leaves (Iwamoto and Ezura 2006).

In vitro grown plants can be used as a competent source of protoplasts, and procedures involving chemical and electrical fusion have been utilized for the production of somatic hybrids in eggplant (Kashyap *et al.* 2003). Plant regeneration from leaf protoplasts of wild species such as *S. virginianum* has also been achieved (Borgato *et al*. 2007b).

Rootstock grafting has led to breeding not only for resistant scions but also for rootstock cultivars resistant to various soil borne diseases. The required regeneration from protoplasts for the successful somatic hybridization of rootstocks has expanded the development of protocols on eggplant rootstock cultivars and wild relatives (Iwamoto and Ezura 2006).

Anther culture

A review of anther culture studies in eggplant was presented by Kashyap *et al*. (2003). Anther culture has been utilized in eggplant to produce completely homozygous diploid plants for use in conventional breeding (Rotino 1996). More recently anther culture has been employed to produce dihaploids and bring back the diploid level in the interspecific somatic hybrids (Rizza *et al.* 2002; Rotino *et al.* 2005b; Toppino *et al*. 2008b).

Somatic hybrids

Somatic hybridization is the fusion of plant protoplasts from somatic cells of different species followed by the regeneration of hybrid plants. It is a popular biotechnological application of plant breeding in cases where wide crosses through sexual hybridization fail to produce hybrid seed. Somatic hybridization is the only technique that provides a means of increasing cytoplasmic variability. Eggplant has a vast number of related species that can be potentially fused to *S. melongena*.

A chronology of somatic hybridization in eggplant is given in the review of Collonier *et al.* (2001a). The species reviewed that have been fused with *S. melongena* are *S. sisymbriifolium*, *S. khasianum*, *S. torvum*, *S. nigrum*, *S. sanitwongsei*, *S. aethiopicum* gr. a*culeatum*, and others from the genera *Nicotiana* and *Lycopersicon*. The attempts involved the transfer of various resistances (nematodes, mites, *Verticillium* wilt, *Fusarium* wilts, *Ralstonia solanacearum,* etc.) to eggplant (Collonier *et al*. 2003; Kashyap *et al*. 2003).

Somatic hybrids between eggplant-related species have been produced with emphasis on the improvement of eggplant rootstocks. Thus somatic hybridization was used between *S. integrifolium* and *S. sanitwongsei* (syn. *S. kurzii*) for the production of fertile hybrids that showed increased resistance to bacterial wilt (Iwamoto *et al.* 2007). Protoplasts from *S. melongena* fused with protoplasts from *S. marginatum* and produced arboreous, fertile somatic hybrids (Borgato *et al.* 2007a). Since somatic hybrids between eggplant and its wild relatives are sterile, anther culture of tetraploids is used for the development of dihaploids.

Genetic transformation

Eggplant is susceptible to many diseases, nematodes and pests. As previously discussed, various value-added traits can be introgressed from wild germplasm sources. Besides the techniques of embryo rescue and somatic hybridization, *Agrobacterium*-mediated genetic transformation has proved very effective for gene introgression into eggplant. Eggplant is among the crop species that have been genetically transformed with foreign DNA; however only a few genetically transformed eggplant cultivars have been released.

Since the first successful eggplant transformation in 1988, many transformation protocols have been developed that used various selection markers and reporter genes (Kashyap *et al*. 2003). *Agrobacterium*-mediated transformation has been employed in all successful attempts to develop transgenic eggplants. Leaves, roots and seedling explants were used for transformation and regeneration (Van Eck and Snyder 2006). Transgenic eggplants have been produced with tolerance to abiotic stress, increased resistance to fungal diseases, insect resistance, and parthenocarpy (Acciarri *et al.* 2000, 2002; Prabhavathi *et al.* 2002; Prabhavathi and Rajam 2007a, 2007b).

Breeding for tolerance of abiotic stress

Abiotic stress can dramatically reduce the yield of any crop. Even though eggplant is relatively more tolerant to high temperatures than tomato and pepper, there are many other forms of stress that the crop may face. The first efforts to produce transgenic eggplants with tolerance to abiotic stress involved the introduction of a bacterial mannitol phosphodehydrogenase gene (Prabhavati *et al*. 2002). The same research team released the results of *Agrobacterium*-mediated transformation of eggplant with a key polyamine biosynthetic gene, arginine decarboxylase (Prabhavathi and Rajam 2007b). Transgenic eggplants with increased levels of polyamines demonstrated tolerance to multiple stresses such as salinity, drought, extreme temperatures and heavy metals.

Breeding for resistance to diseases

Eggplant is susceptible to several pathogens, but the most destructive diseases are bacterial and fungal wilts. Breeding for disease resistance is the most economic and environmental friendly way to confront diseases. The steps for improving eggplant resistance to diseases include screening resistant germplasm within the cultivated species and then in the wild relatives, followed by the transfer of desirable disease resistance traits through sexual hybridization and recombination. However interspecific crosses in eggplant have been hindered due to sexual barriers. Biotechnological techniques such as somatic hybridization and *Agrobacterium*-mediated transformation have been used to overcome such barriers.

Fusarium oxysporum f. sp. *melongenae* causes wilt that is destructive for greenhouse and open-field crops. Eggplant relatives such as *S. aethiopicum* gr Gilo and *S. integrifolium* show resistance to this pathogen. In an attempt to transfer the resistance to *S. melongena* and avoid sexual hybridization, somatic hybrids were produced between *S. aethiopicum* and *S. melongena,* and *S. aethiopicum* and *S. integrifolium* through mesophyll protoplast electrofusion. Di-haploids derived from anther culture using as explants somatic hybrids between *S. melongena* and *S. aethiopicum* group Gilo were used as a source of resistance to *Fusarium oxysporum* f. sp. *melongenae* (Rizza *et al*. 2002). In addition, polyamine or mannitol-accumulating transgenic plants showed resistance to fungal wilts (Prabhavathi and Rajam 2007a, 2007b).

Resistance to powdery mildew was detected in *S. melongena* accessions, as well as in the wild related species *S. laciniatum*, *S. nigrum*, *S. quinquangolare*, *S. linnaeanum*, *S. aculeatissimum*, *S. aviculare*, *S. pseudocapsicum*, *S. spinosissimum*, *S. gilo*, *S. capsicoides* and *S. sisymbriifolium.* Some *S. melongena* selected lines derived from the accessions and some wild species showed resistance that can be exploited through conventional or biotechnological breeding methods (Bubici and Cirulli 2008).

Breeding for pest resistance

One of the achievements of transgenic eggplants involves resistance to Colorado potato beetle (*Leptinotarsa decemlineata* Say) (Acciarri *et al*. 2000). The plants were transformed with the *Bt* gene. The eggplant fruit and shoot borer (*Leucinodes orbonalis*) can infect eggplant and cause a yield loss of up to 40% in Asia, where eggplant is a major crop. A project has been undertaken to develop genetically engineered eggplants that are resistant to the fruit and shoot borer and commercialize the resulting cultivars through a public-private partnership in India, Bangladesh, and the Philippines (http://www.news.cornell.edu/stories/Sept07/EggplantBt.kr.html). Analysis of the adoption of insect-resistant *Bt* eggplant technology in India has demonstrated the benefits of such a project to all parties involved (Krishna and Qaim 2007).

Breeding for nutritional quality

Eggplant breeding follows the needs of producers, processors and consumers and the main goals can be different in different areas. In the past, increased yield was the primary goal, whereas, quality is currently the primary aim, with particular emphasis on nutritional value. In developed countries there is a growing demand for high nutritive value

food that will provide antioxidants, minerals, protein and vitamins, and health-conscious consumers are willing to pay extra for such a high-value product. Breeding eggplant varieties with high antioxidant activity will be beneficial for both consumers and farmers. Improved cultivars of a higher nutritional value could have an impact on the diet of many individuals around the world, particularly those in less developed areas, where eggplant is virtually a staple food. Traits related to fruit nutritional value include the content of phenolic compounds with antioxidant properties, various vitamins, minerals such as P, K, Ca, Na and Mg as well as micronutrients such as Fe, Cu and Zn, the dry matter and protein content.

Total phenolics

In eggplant, phenolics are found both in the skin and pulp. The content is two times greater in the skin and specific types of phenolic compounds differ between the skin and the pulp. Eggplant presents considerable variation in the type and level of phenolic compounds that can be exploited in breeding for increased nutritional value (Stommel and Whitaker 2003; Hanson *et al*. 2006; Prohens *et al*. 2007b; Raigón *et al*. 2008). This variation seems to be affected by the environment, thus extensive experimentation is required for the evaluation of eggplant accessions with regard to phenolic content (Hanson *et al*. 2006). Total phenolic content positively correlated with SOS activity (Hanson *et al.* 2006).

Eggplant cultivars, landraces and landrace hybrids vary in phenolics content, with landraces containing on average a higher concentration of phenolics than commercial cultivars (Raigon *et al.* 2008). However, a high phenolic concentration increases the susceptibility of the fruit to browning and so negatively affects the commercial value. Eggplant breeders try to combine nutritional value with good fruit appearance. Based on the wide variation present in eggplant germplasm this goal may be materialized (Prohens *et al*. 2007b).

Superoxide scavenging activity

Eggplant is among the top vegetables for SOS activity (Hanson *et al.* 2006), with sufficient genetic variation with-in the cultivated germplasm to be exploited in breeding programmes. *Solanum melongena* originated in diverse geographical regions and not only produces fruits of variable color, shape and size but also demonstrates significant genetic differences for SOS that have followed the same rank throughout the years, despite environmental factors (Hanson *et al.* 2006). Thus plant breeders prefer direct selection for increased antioxidant activity rather than indirect selection of phenolic compound content, which is not consistent with different environments (Hanson *et al.* 2006). The negative correlation between SOS and fruit size will be a challenge for plant breeders because they will need to develop big fruits with high SOS activity (Hanson *et al.* 2006).

Ascorbic acid

Eggplant accessions present significant differences in ascorbic acid content. However, because, ascorbic acid is relatively low in eggplant it does not seem to play an important role in the antioxidant activity of this species (Hanson *et al.* 2006).

CONCLUSIONS AND FUTURE PERSPECTIVES

The reduction of available genetic diversity in the commercial varieties of the world's cultivated crops has awakened plant breeders and consumers to the urgent need for conservation of all available genetic resources and the optimization of management systems. The genetic erosion of the wild relatives of crops due to the global destruction of habitats and agronomic practices geared toward a narrowing of cultivar genetic composition, have led to national policies and international treaties stressing the conservation of plant diversity.

The Solanaceae is a very large family with species that include genes potentially beneficial for the improvement of economically important vegetables such as tomato, pepper and eggplant. Scientific groups and countries have united in their efforts to collect, characterize, document and evaluate the Solanaceous plant genetic resources. These resources are very important for future international genomic research, which will unravel the genetic potential of the wild and cultivated germplasm resources to feed an ever-increasing world population. European, USDA-GRIN, and other genebank databases provide public access to existing passport data information. However this access is still very limited in many genebanks, and in regions that have a tremendous wealth of Solanaceae genetic resources. The European Plant Genetic Resources Search Catalogue (EURISCO) is an example to be followed, but a global documentation system is the required target for the efficient management of the Solanaceae resources worldwide.

Vegetable landraces are not well represented in many genebanks, and existing inventories do not adequately record the cultivated diversity present in landraces. Therefore, landraces should be further collected and conserved *ex situ* and incentives should be offered to farmers for landrace cultivation and *on farm* conservation. The promotion of landraces in regions where they can perform well and produce conserved germplasm in addition to value-added products would assist their maintenance. Registration and the protection of landraces are of high priority, but should be done in a relaxed way that will not obstruct their cultivation due to marketing complexities. Landraces are valuable genetic resources for the world, but we should also keep clearly in mind that they are the farmers' varieties and should continue to be made available to them.

Policies should be developed for the protection of *in situ* habitats in the regions of domestication and variability, and where wild *Solanum* species currently exist. *On farm* conservation and *in situ* maintenance should become more efficient in all regions of genetic diversity. Management policies that will promote landrace cultivation in marginal areas are needed. The use of *on farm* plant genetic resources is the most efficient method to conserve them. Introgression, incorporation and pre-breeding will continue to play a major role in the utilization of genetic resources, but new technologies should work side-by-side to assist the classical methods.

The vast diversity of the Solanaceae family and the adaptation to numerous habitats make it an attractive model to investigate the basis of adaptation and variation using genomic tools. The International Solanaceae Genomics Project (SOL), (http://www.sgn.cornell.edu/solanaceae-project/), embraced Solanaceae scientists in a common goal of sequencing tomato euchromatin. A comparative genomics approach can be used to transfer genome information from tomato to pepper and eggplant. Molecular markers are beginning to have significant applications in many crops. Marker-assisted selection (MAS) is an application that can significantly improve the efficiency, precision and speed of conventional plant breeding. Although MAS applications have been successful in tomato, and a few examples exist in pepper, MAS is still in its infancy in eggplant. MAS is currently the most powerful molecular technique available for the Solanaceae breeders to accelerate crop improvement.

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