

## Chapter 2

# Maize

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**Abstract** During the domestication process of cultivated crop species, the variability has decreased considerably rendering them more susceptible towards vagaries of environment and biotic stresses. Alien genes from wild relatives are not only the source of imparting new genetic variability but are also storehouses of novel traits which are linked with wider adaptability towards biotic and abiotic stresses. Transfer of alien genes from wild species to maize has been undertaken for a number of traits of agronomic value and for imparting resistance to stresses using both conventional and biotechnological tools. This chapter covers the problems encountered in transfer of alien chromatin into maize and the tools to overcome those problems including direct gene transfer of alien DNA beyond taxonomical boundaries. It also presents various achievements in introgression of alien genes via various methods and also the impact of such introgressions on maize improvement.

**Keywords** Alien gene transfer • Achievements • Biotechnology • Direct gene transfer • Impacts • *Teosinte* • *Trypsacum* • Somatic hybridization

### 2.1 Introduction

Maize (*Zea mays* L.), also known as corn, is the third most important cereal after wheat and rice that is grown and consumed in the form of food, animal feed and in several industrial processes. Maize, the queen of cereals, is one of the oldest domesticated plants dating back to as far as 7,000 years ago in Central Mexico by

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Mesoamerican natives. The crop seems to develop as a result of gradual selection upon primitive annual teosinte (*Zea mexicana*), an ancient grass found in Mexico and Guatemala, although opinions vary as to whether maize is a domesticated version of teosinte (Galinat 1988). Maize is being cultivated in the tropical, subtropical and temperate climatic regions of Asia, Africa, Europe and North and South America. Currently, the area under this crop is nearly 162 m ha, out of which, nearly 100 million ha is covered by 125 developing countries with global production reaching a mark of 845 m tonnes with global productivity of 5.21 tonnes/ha, 67 % coming from low- and lower middle-income countries (Anonymous 2012). In terms of international trade, although maize accounts for only 12 % of worlds cereal production, it represents over one-third of cereal trade. About 30 % of world's production is used for direct human consumption and as an industrial input, while 70 % is used as an animal feed (Turrent and Serratos 2004).

Maize along with wheat and rice provides at least 30 % of the food calories to more than 4.5 billion people in 94 developing countries where one-third of children are malnourished (Hoisington et al. 1999; Von Braun et al. 2010). By 2050, the demand for maize in the developing world will be almost double the current demand (Rosegrant et al. 2008), and with the current scenario of production which is lagging far behind, estimates are not quite optimistic for the poor and marginal farm families. Under the changing climate scenario, there is a further threat to maize production, and the low- and middle-income countries will be the most affected by climate change. Spatial analyses in recent years have consistently predicted an average of 10 % or even more decline in maize yields by 2050 for sub-Saharan Africa and Latin America (Thornton et al. 2010; Lobell et al. 2011). In addition to abiotic stresses, increasing maize production is threatened by as much as about 110 diseases on a global basis caused by fungi, bacteria and viruses and 130 insect-pests.

## 2.2 Maize Improvement

Although a rapid boost in maize production was achieved as a result of using single, double and three-way crosses, the hybrid technology has also posed a challenge on meeting the target growth in maize production due to narrowing down of genetic variability. Concerns over the lack of genetic diversity in maize used for production go beyond the realms of academic argument and theory. The devastating 1970 epidemic of southern corn leaf blight (caused by the fungal pathogen *Bipolaris maydis* race T) was due to the widespread deployment of genetically uniform varieties, all containing T-cytoplasm. In addition to increased susceptibility to diseases and pests, low diversity levels do not bode well for yield plateaus lurking on the horizon. Exotic maize germplasm contains significant variation for many quality traits that have remained untapped (Hoisington et al. 1999). Also, the threat of genetic vulnerability can be overcome by use of wild and distant relatives of maize to broaden the genetic base of maize germplasm and also to introgress resistance against biotic and abiotic stresses.

Genetic variability is a basic element necessary to any plant breeding programme. If genetic variability is not present in the breeder's populations, selection will not be.

Plant breeders devote considerable effort and time to the development of genetically variable populations for future selection. The mechanisms used for creating genetic variability include hybridization of adapted material, mutagenic agents and introduction of germplasm from other sources (Hallauer and Sears 1972). Introduction of exotic maize germplasm to improve and broaden local maize genetic base is a widely used method across the world especially for agronomically important traits (Albrecht and Dudley 1987; Vasal et al. 1992a, b; Ron Parra and Hallauer 1997; Goodman 1999; Abadassi and Hervé 2000; Li et al. 2001; Ho et al. 2002; Chen et al. 2010). Moreover, when the variability for certain traits is not available in the exotic germplasm, distant relatives are used to introgress alien genes into genetic background.

## 2.3 Sources of Alien Genes

Maize belongs to the family Poaceae and tribe Maydeae which comprises seven genera, viz. *Coix* ( $2n=10$  or  $20$ ), *Chionachne* ( $2n=20$ ), *Sclerachne* ( $2n=20$ ), *Trilobachne* ( $2n=20$ ) and *Polytoca* ( $2n=20$ ) (Old World groups) and *Zea* and *Tripsacum* (New World groups). The genus *Zea* consists of four species of which only *Z. mays* L. ( $2n=20$ ) is economically important. The other *Zea* sp., referred to as teosintes, are largely wild grasses native to Mexico and Central America (Doebley 1990). Species belonging to both *Zea* and *Tripsacum* serve as important sources of alien genes for introgressing desirable traits into genetic background of bread wheat (Table 2.1).

### 2.3.1 Teosintes

Teosintes are wild grasses native to Mexico and Central America with limited distribution. Among teosintes, the nearest teosinte relative to *Z. mays* is *Z. mays* sp. *mexicana* (Schrader) Iltis ( $2n=20$ ), distributed across central highlands of Mexico. The other teosintes include perennial teosintes, viz. *Z. diploperennis* ( $2n=20$ ) and *Z. perennis* ( $2n=40$ ), distributed in Jalisco, Mexico. The annual teosintes include *Zea luxurians* from southeastern Guatemala, *Zea mays* ssp. *parviglumis* of southern and western Mexico and *Zea mays* ssp. *huehuetenangensis* from the western highlands of Guatemala (Reeves and Mangelsdorf 1942; Hitchcock 1951; Iltis et al. 1979; Iltis and Doebley 1980; Doebley 1990; Watson and Dallwitz 1992).

### 2.3.2 Tripsacum

The genus *Tripsacum* is comprised of about 12 perennial and warm season species that are mostly native to Mexico and Guatemala but are widely distributed throughout warm regions in the USA and South America, with some species present in Asia

**Table 2.1** Classification of the genus *Zea* within the tribe Maydeae and the genus *Tripsacum*

Species	Chromosome number ( $2n$ )	Common name
<i>Zea mays</i> subsp. <i>mays</i> (L.) Iltis	20	Maize
<i>Zea mays</i> subsp. <i>mexicana</i> (Schrader) Iltis	20	Teosinte
<i>Zea mays</i> subsp. <i>parviglumis</i> Iltis and Doebley	20	Teosinte
<i>Zea mays</i> subsp. <i>huehuetenangensis</i> Doebley		Teosinte
<i>Zea diploperennis</i> Iltis, Doebley and Guzman	20	Perennial teosinte
<i>Zea luxurians</i> (Durieu) Bird	20	Teosinte
<i>Zea nicaraguensis</i>	20	—
<i>Zea perennis</i> (Hitchc.) Reeves and Mangelsdorf	40	Tetraploid teosinte
Genus <i>Tripsacum</i>		
<i>T. andersonii</i>	64	—
<i>T. australe</i>	36	—
<i>T. bravum</i>	36, 72	—
<i>T. cundinamarcae</i>	36	—
<i>T. dactyloides</i>	72	Eastern gamma grass
<i>T. floridanum</i>	36	—
<i>T. intermedium</i>	72	—
<i>T. manisuroides</i>	72	—
<i>T. latifolium</i>	36	—
<i>T. pereuvianum</i>	72, 90, 108	—
<i>T. zopilotense</i>	36, 72	—
<i>T. jalapense</i>	72	—
<i>T. lanceolatum</i>	72	
<i>T. laxum</i>	36?	
<i>T. maizar</i>	36, 72	
<i>T. pilosum</i>	72	

and Southeast Asia. Species of economic importance to agriculture in the genus are *Tripsacum dactyloides* (L.) (Eastern gama grass), *T. laxum* Scrib and Merr. Other species include *T. andersonii*, *T. latifolium*, *T. lanceolatum*, *T. floridanum* and *T. manisuroi-des* (deWet and Harlan 1972; deWet et al. 1983; Talbert et al. 1990; Watson and Dallwitz 1992).

### 2.3.3 Coix and Other Asiatic Genera

The Asiatic genera of the Maydeae tribe are native to an area extending from India to Southeast Asia and the Polynesian islands to Australia. They include *Coix* L. ( $2n=10$ , 20 and 40), *Sclerachne* R. Br. ( $2n=20$ ), *Polytoca* R. Br. ( $2n=20$  and 40), *Chionachne* R. Br. ( $2n=20$ ) and *Trilobachne* Schenk and Henrard ( $2n=20$ ). *Coix* sp. is the most familiar genera and includes several species. The species *Coix lacryma-jobi* Linn. (Job's Tears) ( $2n=20$ ) is native to Southeast Asia, Africa and warmer parts of the

Mediterranean and exists in the wild as well as cultivated races. *Chionachne* includes several species native to Southeast Asia. The species *C. semiteres* is cultivated as a fodder crop. *Polytoca* includes a few species, none of which however are commonly cultivated. One species has been described for *Trilobachne* and is not known to be cultivated. Both genera are native to Southeast Asia (Watson and Dallwitz 1992).

## 2.4 Crossability Potential and Barriers for Alien Gene Transfer

The success of a breeding programme depends upon the production of fertile hybrids especially while dealing with interspecific or intergeneric hybridization. Maize exhibits great sexual compatibility with all annual teosintes to produce fertile hybrids except for the tetraploid *Z. perennis* (Wilkes 1977). However, maize-teosinte hybrids exhibit low fitness and have little impact on gene introgression in subsequent generations (Galinat 1988). The tendency to form natural hybrids differs among teosintes where *Z. luxurians* rarely hybridizes with maize while *Zea mays* sp. *mexicana* frequently forms hybrids (Wilkes 1977). Molecular data confirms that gene flow occurs between Maize and teosintes and suggests that introgression of maize and teosintes occurs in both directions but at low levels (Doebley 1990). Intergeneric crosses are even more difficult with species belonging to genus *Tripsacum*. Nevertheless, *T. dactyloides*, *T. floridanum*, *T. lanceolatum* and *T. pilosum* have been successfully hand crossed with maize to form hybrids. These hybrids have a high degree of sterility and are generally unstable, yet the crossability and stability of *Tripsacum* sp. is genotype dependent (Kindiger and Beckett 1992). Infertility among maize  $\times$  *Tripsacum* crosses is common because of differences in chromosome number and lack of pairing between chromosomes (Eubanks 1997).

No reports are available regarding the crossability of Asiatic genera with maize; however, genetic and chromosomal studies indicate that the Asiatic genera are very distinct from both maize and teosintes. Nevertheless, the similarity in chromosome number suggests that there may be a potential for crossing to occur between maize and the Asiatic genera (Katiyar and Sachan 1992). Maize readily crosses with hexaploid wheat (*Triticum aestivum*) with high frequencies of fertilization and embryo formation; however, maize chromosomes are eliminated from the genome during the initial stages of meiosis and result in haploid wheat embryos (Laurie and Bennett 1986; Chaudhary et al. 2002; Singh et al. 2004; Sharma et al. 2005). Similarly, maize has also been reported to cross readily with triticale and triticale  $\times$  wheat derivatives (Pratap et al. 2005, 2006). There have been unsubstantiated reports of hybridization between maize and sugar cane (*Saccharum* sp.).

The low success of above-mentioned interspecific or intergeneric hybrids is result of cross incompatibility that may arise due to many factors which may be classified into (a) pre-fertilization and (b) post-fertilization barriers (Gutierrez-Marcos et al. 2003).

### **2.4.1 Pre-fertilization Barriers**

#### **2.4.1.1 Difference in Floral Structures and Asynchrony in Flowering**

The floral structure and synchrony in flowering time, a prerequisite for any hybridization programme, impose a barrier only during natural fertilization but are easily eliminated under planned hybridization programmes (Kiesselbach 1999; Lausser et al. 2010).

#### **2.4.1.2 Pollen-Style Incompatibility**

Partial and complete gametophytic incompatibility has been documented among cultivated maize, landraces and teosinte. The former is demonstrated by differential pollen growth and a skewed recovery of alleles linked to incompatibility genes (Kermicle and Allen 1990). Later Duan et al. (2008) observed that germinating pollen of *Coix lacryma-jobi* L., which elongated till the end of maize pistil, indicated strict reproductive isolation due to pollen-style incompatibility. The pollen-style incompatibility takes place at various levels, viz. competition on the receptive trichomes, inside the transmitting tracts, and elimination of the late-entering tubes at the stigma abscission zone and at a constricted zone of the transmitting tract in the upper ovary wall (Heslop-Harrison et al. 1984).

### **2.4.2 Post-Fertilization Barriers**

#### **2.4.2.1 Abortion of Embryo**

The incompatibility in the embryo sac was reported in maize  $\times$  *Tripsacum* L. and maize  $\times$  *C. lacryma-jobi* L. var. *frumentacea* by Duan et al. (2008). Partial embryo sac cross incompatibility have also been reported in maize  $\times$  *Z. mays* ssp. *parviglumis* interspecific crosses.

#### **2.4.2.2 Endosperm Failure**

Cooper and Brink (1942) were among the first to ascribe the major role of endosperm in the failure of seed production after interspecific hybridization. Histological studies on hybrid maize showed abnormalities of endosperm development at very early stages ranging from defects at the chalazal pole (Cooper and Brink 1940) to abnormal free nuclear division rates (Brink and Cooper 1940).

### 2.4.2.3 Hybrid Sterility

The wide hybrids may be sterile due to production of abnormal male and female gametes. Anomalies in the development of the microspore apparently occur because of the failure of chromosomes to congregate at the metaphase plate, development of a tripolar spindle and failure of cytokinesis at the first and second meiotic divisions (Kindiger 1993). The maize-*Tripsacum* hybrids generally have 28 chromosomes (10 from maize and 18 from *Tripsacum*) and exhibit pollen sterility with limited female fertility (Mangelsdorf and Reeves 1939; Newell and de Wet 1973; Mangelsdorf 1974).

## 2.5 Achievements in Alien Gene Transfer

### 2.5.1 Utilization of Sexual Hybridization

The wild relatives of any crop species have long been recognized by plant breeders and geneticists as sources of important genes, viz. agronomically desirable traits, resistance to diseases and pests and tolerance to abiotic stresses. Maize has high genetic plasticity and hence is a good candidate for interspecific or intergeneric hybridization (Ramirez 1997). Genetic improvement of crops has traditionally been achieved through sexual hybridization between related or distant species, which has resulted in numerous cultivars with high yields and superior agronomic performance (Prescott-Allen and Prescott-Allen 1986). The desired introgressions from interspecific crosses in maize were not of major concern since fertile hybrids with intermediate phenotype could be recovered easily even as a result of natural hybridization (Ellstrand et al. 2007). The significance of interspecific hybridizations apart from introgression of desirable traits lies in the development of modifier complexes and maintenance of heterozygosity (Mangelsdorf 1952).

#### 2.5.1.1 Transfer of Traits of Agronomic Importance

The traits of agronomic importance are mostly governed by polygenes, and the role of alien germplasm to improve quantitative traits is less reported. The possible reason for this is limitation in introgressing large number of loci responsible for expression of a quantitative trait into the target host (dela Vina et al. 1995). In maize, alien introgression has been accomplished for improvement of agronomic traits using sexual hybridization. Cohen and Gallinat (1984) suggested improvement of maize inbreds with respect to quantitative traits like yield via introgression of alien chromatin segments both from teosintes and *Tripsacum*. The introgression of genetic segments from teosinte was accomplished by selection for modifications of the

female spike during the backcross generations and reported to positively affect quantitatively inherited traits. The *Tripsacum* chromosome was found to increase the combining ability of maize line in which it was incorporated. This segment of alien germplasm, homologous to maize chromosome, contributes increased yield, combining ability and affecting other quantitative traits hence adding new dimensions to the utility of *Tripsacum* germplasm. Sidorov and Shulakov (1962) developed hybrids between maize and teosinte that were having superior silage-making ability. Pásztor and Borsos (1990) reported that maize  $\times$  teosinte (*Z. mays* ssp. *mexicana*) produced F<sub>1</sub>s with profuse tillering and F<sub>2</sub>s with teosinte characteristics having more number of tillers, high green matter production and better nutritional quality with respect to lysine, aspartic acid and other amino acids. *Z. mays* ssp. *mexicana* has many important traits, viz. good vigour, high protein in kernel and tillering. Wang et al. (2008) crossed maize with *Z. mays* ssp. *Mexicana* and reported that 54.6 % of the hybrids had higher yield than the superior maize hybrid checks. The advanced backcross generations exhibited improved characters like large number of tillers, increased height, increased 100 seed weight and resistance to lodging. Many researchers use such traits of agronomic importance to confirm the hybridity of plants obtained by crossing maize with its wild relatives (Tang et al. 2004).

### 2.5.1.2 Transfer of Disease Resistance

Plant breeders have been exploiting wild relatives for introgressing resistance against biotic stresses from over a century. Over 80 % of the beneficial traits conferred by wild relatives involve pest and disease resistance. Findley et al. (1982) introgressed resistance against maize chlorotic dwarf virus (MCDV) into maize from *Zea diploperennis*. The hybrid between maize and *Zea diploperennis* exhibited sterility hence backcross generations were generated which revealed resistance to MCDV. Another teosinte was used to confer resistance against downy mildew in maize. The introgression of resistant genes from *Z. mays* ssp. *Mexicana*, *Z. diploperennis* and *Z. perennis* into maize was carried out by Ramirez (1997) using sexual hybridization. Disease resistance was also imparted from *Z. mays* ssp. *Mexicana* to maize for many diseases, viz. maize stalk rot, maize rough dwarf disease and MCDV. Introgression of resistance against *Fusarium* was reported in F<sub>1</sub> and F<sub>2</sub> generations of crosses between maize and *Z. mays* ssp. *mexicana* (Pásztor and Borsos 1990). Similarly, Bergquist (1979) reported introgression of resistance from distant relatives, viz. *T. dactyloides*, where sexual mating is difficult, against *Colletotrichum graminicola*, *Helminthosporium turcicum*, *H. maydis*, *Erwinia stewartii* and *Puccinia sorghi* by backcrossing into various maize genotypes. In BC<sub>5</sub>–BC<sub>10</sub> generations, resistance to each of the pathogens appeared to be dominant; however, a gradual breakdown of qualitative traits, including resistance, occurred in later generations. Later, Bergquist (1981) successfully transferred a dominant gene *Rp<sup>Td</sup>* conferring resistance against rust pathogen of corn *Puccinia sorghi*, from *T. dactyloides*. Similarly, *T. floridanum* was used to introgress resistance gene *Ht* into the genetic background of maize (Hooker and Perkins 1980). Zhou and his associates (1997) conducted the distant



hybridization involving maize  $\times$  teosinte (*Z. diploperennis* L.) in order to introduce novel genetic variability. They reported fourteen inbred lines resistant to diseases, insects and environmental stress after eighth-generation selfing and selection. Topcrossing of these 14 lines with normal testers produced 1,000 hybrids which showed strong heterosis. On the basis of success of maize  $\times$  teosinte (*Z. diploperennis*) crosses for introgression of desirable traits, *Z. diploperennis* was suggested as one of the potential sources for widening germplasm pool of maize and to overcome the static situation of maize production in China. Likewise, the alloplasmic inbred lines derived from maize  $\times$  *Zea diploperennis* interspecific hybrids were reported to exhibit resistance against *H. turcium* and *H. maydis* (Wei et al. 2003).

### 2.5.1.3 Transfer of Insect Resistance

Insect-pests cause huge yield losses by inducing direct damage to plants and by rendering the grains unfit for human and animal consumption. The major insect-pests of corn are stem and cob borers, rootworms and aphids which are generally polyphagous and damage almost all corn varieties. The wild relatives of maize, viz. *Z. mays* ssp. *mexicana*, *Z. mays* ssp. *diploperennis* and *Z. mays* ssp. *perennis*, have resistance against a number of insect-pests, and these species were used to impart resistance against Asiatic corn borer (Ramirez 1997). Pásztor and Borsos (1990) reported certain degree of resistance in the maize  $\times$  *Z. mays* ssp. *mexicana* hybrids for corn borer (*Ostrinia nubilalis*). *T. dactyloides* exhibits resistance to corn rootworms via non-preferences and or antibiosis as reported by Branson (1971), Moellenbeck et al. (1995) and Eubanks (2001). Eubanks (1997, 2001, 2002) crossed *Tripsacum* with diploid perennial teosinte and produced viable recombinants that were cross-fertile with maize. This allowed the incorporation of *Tripsacum* genetic material into corn and development of experimental lines, some of which exhibited rootworm resistance, as evidenced in insect bioassays and field root damage ratings (Eubanks 2002; Eubanks 2006). Similarly, Prischmann et al. (2009) produced *Tripsacum*-introgressed maize germplasm in breeding programmes to enhance plant resistance or tolerance to corn rootworms.

### 2.5.1.4 Resistance Against Parasitic Weed

The parasitic weed *Striga* threatens cereal grain production in tropical and subtropical regions of Asia and Africa. The slow pace of development and deployment of *Striga*-resistant cultivars is mostly attributable to paucity of sources of resistance, complex genetics of resistance and scant knowledge about specific mechanisms associated with expression of resistance in maize to the parasite. Sources of *Striga* resistance in maize have been scarce, perhaps because early evolution and adaptation of the maize crop took place in the absence of this parasite. There have been a few reports which indicated the presence of resistance to *Striga* in wild relatives of maize. Lane et al. (1997) reported that some plants among the wild progenitor of

maize, *Z. diploperennis*, restricted parasite penetration of its roots and impaired the development and survival of parasites. Introgression of resistance genes from *Z. diploperennis* into genetic background of maize against *Striga* has been reported independently by Amusan et al. (2008) and Yallou et al. (2009). Gutierrez-Marcos et al. (2003) reported that *Striga* failed to develop on another wild relative of maize, *T. dactyloides*; however, no post-attachment resistance to *Striga* has been found in cultivars of maize (Oswald and Ransom 2004).

### 2.5.1.5 Transfer of Abiotic Stress Resistance

#### Tolerance to Flooding

Flooding damage to maize is highly dependent on the developmental stage of plant, the length of the flooding period and the soil-air temperatures. Maize is affected most by flooding in the early stages of growth and hence is a major concern for maize growers due to huge yield losses and limited availability of flooding-tolerant lines. Although a few maize lines were reported to form adventitious roots at the soil surface during experimental flooding conditions (Mano and Omori 2007), teosintes obtained from regions that are known to receive frequent rainfall may provide a superior genetic resource for the development of flooding-tolerant maize. The teosintes, viz. *Z. nicaraguensis* (Bird 2000; Iltis and Benz 2000), *Z. luxurians* and *Z. mays* ssp. *huehuetenangensis* (Mano et al. 2005a), have been observed to exhibit a higher capacity for adventitious root formation than some maize inbreds. *Z. mays* ssp. *huehuetenangensis* seedlings were observed to exhibit a high adaptability to flooding by developing adventitious roots above the soil surface (Mano and Omori 2007). As a consequence, the adventitious roots of this teosinte can obtain oxygen, and this characteristic may play an important role in its adaptation to flooding conditions. Similarly *Z. nicaraguensis* and *Z. luxurians* were reported to develop well-formed aerenchyma in adult plants (Ray et al. 1999) hence imparting tolerance to flooding conditions.

#### Salt Tolerance

Since corn has been one of the most sensitive crops to soil salinity and the growth of the crop is highly affected, techniques such as remote hybridization and in vitro selection have been extensively used to accelerate breeding processes with respect to this trait. *T. dactyloides* was suggested as source to resistance against salt stress by Pesqueira et al. (2003) on the basis of their evaluation of hybrids between *Z. mays* ssp. *mays* and *T. dactyloides*. The organogenic calli, induced from immature maize × *Tripsacum* hybrid embryos, were exposed to different NaCl concentrations, and the survival and regeneration percentage was calculated. Plants of the hybrid, obtained from the organogenic calli, were exposed to NaCl concentrations considered harmful for normal growth of maize. The shoot dry weights of plants exposed

to 250 mM NaCl did not show significant differences with respect to the control ones. Although sodium content in shoots was incremented up to two- to fivefold, yet it was not toxic for this material (Pesqueira et al. 2006).

#### 2.5.1.6 Transfer of Apomixis

Apomictic reproduction defines an asexual process that substitutes for sexual reproduction in many species of the family Gramineae. It has been suggested that the development of apomictically reproducing forms provides a major contribution towards food security since it helps in fixation of heterotic, and this effect can be exploited without the need of producing hybrid seed every year. Petrov (1984) advocated the possibility of transferring genes conferring apomixis in *T. dactyloides* L. to maize for the development of true breeding hybrids. The diploid *Tripsacum* reproduce sexually, whereas triploids and tetraploids ( $2n=4x=72$ ) reproduce as facultative or near obligate apomicts. Savidan and Berthaud (1994) reviewed the potential of maize  $\times$  *Tripsacum* crosses for the transfer of alien genes controlling the diplosporous apomictic mode of reproduction. Likewise, Leblanc et al. (1995) carried out bulk-segregant analysis of  $F_1$  population of maize  $\times$  *Tripsacum* to identify molecular markers linked to diplospory in *T. dactyloides*. On the basis of maize RFLP probes, three restriction fragments co-segregating with diplospory were identified in one maize-*T. dactyloides*  $F_1$  population that segregated 1:1 for the mode of reproduction. The markers were also found to be linked in the maize RFLP map, on the distal end of the long arm of chromosome number 6. These results support a simple inheritance of diplospory in *Tripsacum*. Later efforts were made to transfer apomixis from diplosporous tetraploid *Tripsacum* into maize through conventional backcrossing. The polyhaploid hybrid plants were totally male sterile, whereas the apomictically produced seeds were viable. Apomictic reproduction in such polyhaploids revealed diploid-like chromosomal complement, confirming diplosporous apomixes. It was also suggested from this investigation that diplosporous apomixes and polyploidy are not totally linked and diploid crops such as maize can also reproduce apomictically (Leblanc et al. 1996).

#### 2.5.1.7 Genetic Analysis

The alien introgressions from wild relatives are not only transfer desirable genes and genetic variability into the cultivated backgrounds but have also proved to be highly useful in revealing the genetic mechanisms at molecular level. The genus *Zea* has been reported as one of the most complex genera, and the direct progenitor of maize is still unknown. To unravel this mystery, the interspecific and intergeneric crosses have been utilized by a number of researchers to understand the events that took place during evolution of *Z. mays*. Recently developed novel molecular cytogenetic tools have been more efficiently used to study the genomic affinities and establish relationship among different species (González et al. 2006).

Other than investigation regarding evolution and species relationships, the wild relatives also helped in dissection of complex traits. Doebley and Stec (1993) investigated two populations derived from interspecific hybrids between maize and two teosintes (*Z. mays* ssp. *parviglumis* and *Z. mays* ssp. *mexicana*) by employing molecular marker loci to map quantitative trait loci (QTLs). Studying these populations, they suggested that in both the populations a relatively small number of loci with large effects were involved in the early evolution of the key traits that distinguish maize and teosinte and are not a specific feature of crop evolution but rather a common phenomenon in plant evolution whenever a species invades a new niche with reduced competition. Similarly, the genetic control for kernel weight, which determines the differences between maize and its probable progenitor *Z. mays* ssp. *parviglumis*, was studied using QTL mapping (Doebley et al. 1994), which revealed that a QTL on chromosome 3 of maize had large effect on kernel weight and has contributed to early evolution of maize, hence implying that there may have been evolutionary periods during which the fixation of these genes brought relatively rapid change in a reasonably short period of time. Later, Doebley et al. (1995) investigated two QTL controlling differences in plant and inflorescence architecture between maize and its progenitor, one mutant locus *teosinte branched1* (*tb1*) located on chromosome arm 1L reported to influence inflorescence sex and the number and length of internodes in the lateral branches and inflorescences and second QTL, located on chromosome arm X. While the *tb1* locus has strong phenotypic effects in teosinte background, the other QTL had enhanced effect in maize-teosinte  $F_2$  population. The potential of these QTLs to substantially transform inflorescence architecture of both the plants suggests the role of *tb1* locus on morphological diversification of teosinte taxa as well on the domestication of maize. Recently, Studer and Doebley (2012) investigated the occurrence of a natural allelic series for complex traits at the *teosinte branched1* (*tb1*) gene in natural populations of teosinte (*Zea mays* ssp. *parviglumis*, *Z. mays* ssp. *mexicana* and *Z. diploperennis*). The effects of the three allelic classes also correspond to known morphological differences between the teosinte taxa. Likewise in another study, three QTLs on chromosomes 4, 5 and 8 have been identified by using *Z. mays* ssp. *huehuetenangensis* for formation of adventitious roots under flooding conditions (Mano et al. 2005b); three QTLs for controlling roots aerenchyma formation using *Z. nicaraguensis* on chromosomes 1, 5 and 8 (Mano et al. 2006); five QTLs controlling root aerenchyma formation in maize  $\times$  *Z. luxurians* mapping population (Mano et al. 2008); and five QTLs for root angle in maize  $\times$  *Z. luxurians* mapping population. The QTL on chromosome 7 influencing second and third root angle was considered most significant for flooding tolerance (Omori and Mano 2007).

### 2.5.2 Biotechnology Assisted Hybridization

Introgression of variability or novel traits into any crop species requires development of complex hybrids involving distant species (Harlan 1976). Since the complex

hybrids are not stable meiotically, they are difficult to produce through conventional hybridization, and hence the need of specific techniques is required to introgress alien chromatin into the genetic background of crop species. Biotechnology, which includes cell and molecular biology techniques, was developed in the early 1980s. For plant breeders, biotechnology is a powerful tool to assist in introgressive hybridization programmes. Biotechnological tools have helped in overcoming crossing barriers, and using biotechnological tools genes from unrelated sources and even beyond the taxonomic boundaries can be introgressed.

### 2.5.2.1 Embryo Rescue

The low frequency of hybrid recovery in wide hybridization programmes due to different levels of crossability barriers among maize and its wild relatives is a major hindrance in the corn wide hybridization programmes. The efficiency of hybridization work can be enhanced utilizing the biotechnological tools such as embryo rescue followed by organogenesis. Although, the teosintes are easily crossable with maize under natural conditions, the response of scutella cultures to enhance the efficiency of maize-teosinte hybridization for introgression of desirable traits into genetic background of maize was investigated by Dhaliwal and Lorz (1979). They reported that organogenesis in immature embryos of maize  $\times$  teosinte (*Z. mexicana*) hybrids resulted in numerous plantlets. The utilization of this biotechnological tool has more significance in the intergeneric hybridizations due to more severe crossability barriers than interspecific crosses leading to low frequency of hybrid recovery. Embryo rescue was used to produce intergeneric maize-*Tripsacum* hybrids by Farquharson (1957). Garcia and Molina (1999) investigated the use of embryo rescue in maize  $\times$  *Tripsacum* hybrids and in maize  $\times$  *Zea mays* ssp. *parviglumis* crosses (Garcia and Molina 2001) to enhance the efficiency of wide hybrid production. The response of wide crosses involving a number of maize inbreds as female parents and the morphological characteristics of the hybrids regenerated was evaluated. Nevertheless, the number of hybrids obtained could be increased through the induction of long-term embryogenic callus cultures from the rescued embryos (Furini and Jewell 1995). The success of embryo rescue in intergeneric crosses involving maize and *Tripsacum* was also revealed by Li et al. (1998) and in trihybrid of *Zea mays*  $\times$  *Zea perennis*  $\times$  *Zea diploperennis* by Rapela (1984).

### 2.5.2.2 Somatic Hybridization

Sexual hybridization is the easiest and most successful method of gene transfer; however, it has certain limitations, viz. the plants across taxonomic boundaries cannot be mated and there is no chance of recombination of cytoplasmic genomes. Somatic hybridization through the fusion of somatic protoplasts of two different plant species or varieties allows full genetic recombination involving both nuclear and cytoplasmic genomes. Somatic hybrids were utilized in wide crosses that were

not feasible through sexual hybridization even by utilizing biotechnological tools. The maize protoplasts are isolated from cell suspensions, and the tissue for extraction of protoplasts is selected specifically so as to be able to differentiate later on between somatic hybrids and unfused protoplasts. Polyethylene glycol (PEG) treatment at high pH and high concentration of calcium ions are reported to work well for fusion of maize protoplasts with other protoplasts. The somatic hybrids are selected on the basis of physiological complementation and are singled out from the cell colonies and subcultured followed by their complete regeneration into haploid plants. Somatic hybrids have been reported between maize and *Triticum* sect, *trititrigia* MacKey (*trititrigia*,  $2n=35$ ), a perennial hybrid of *T. durum* Desf. and *Elytrigia intermedium* (host) Nevski by (Wang et al. 1993). The regenerated hybrid plants were identified using restriction patterns of nuclear, ribosomal, mitochondrial and chloroplast genes which revealed that all the hybrids carried only the organellar DNAs of *trititrigia*, which excluded the possibilities of a chimeric callus or any DNA contamination. The potential of gene transfer between *Zea* and *Triticum* species was thus conclusively established. Later, intergeneric somatic hybridization was performed between albino maize protoplasts and mesophyll protoplasts of wheat by PEG treatment. The hybrid plants though sterile despite having male and female flowers were reported to exhibit maize phenotype by Szarka et al. (2002). The cytological analysis of cells from callus tissues and root tips revealed 56 chromosomes, but intact wheat chromosomes were not observed. Genomic in situ hybridization using total wheat DNA as a probe revealed the presence of wheat DNA islands in the maize chromosomal background. Similarly in another study, the flow cytometry analysis of wheat-maize somatic hybrids showed intermediate DNA concentration in hybrid nucleus although; other intermediate morphological traits of plants with hybrid origin were not reported (Göntér et al. 2002). Xu et al. (2003) in a similar experiment tried to combine the genome of wheat and maize in order to generate some valuable breeding material, understand the chromosome elimination mechanism and detect certain interactions between maize and wheat nuclear and cytoplasmic genomes. Unlike earlier workers, they reported that the somatic hybrids were more like wheat instead of maize. Though somatic hybridization seems like a potential alternative for sexual hybridization and success has been achieved in development of hybrid plants, the technique is cumbersome and encompasses limitations at various levels for alien gene transfer owing to difficulty in fusion of protoplasts, fusion of nuclei, elimination of chromosomes and nuclear or cytoplasmic incompatibility.

### 2.5.3 Direct Gene Transfer

Recombinant DNA techniques have provided plant breeders the opportunities to transfer genes of interest from plants, animals and microbes. Due to the worldwide predominance of cereal grains in the human diet, cereal crops were the prime targets for improvement by genetic transformation. Initially cereal transformation was problematic, due to recalcitrant in vitro cultures, low response to *Agrobacterium-mediated*

transformation and low level activity of some of the promoters in monocot cells and tissues. Maize was among the first cereals in which transgenics were obtained via fusion of recombinant DNA directly in the protoplast cultures derived from immature embryos. The DNA was introduced into the protoplasts by electroporation; a chimeric gene-encoding neomycin phosphotransferase (*neo*), a selectable marker, was introgressed into maize immature embryos or callus (D'Halluin et al. 1992). Also, Silicon carbide whiskers-mediated techniques have also been successfully used to transform maize cell suspension cultures (Frame et al. 1994). Nonetheless, the development of super-binary vector systems contributed to the breakthrough of *Agrobacterium*-mediated transformation of maize (Ishida et al. 1996), for which transformation frequencies of 5–30 % were reported.

### 2.5.3.1 Herbicide Resistance

Weed flora competes with the crop plants for available nutrients and light energy and thus reduces crop yields by an average of 10–15 %. Through direct gene transfer, it has been possible to provide crop plants with resistance to a certain herbicide, which allows selective elimination of weeds. In general, production of herbicide-resistant crops has involved insertion of only one or two genes that encode inactivation of the herbicide by either overproduction of a herbicide-sensitive biochemical target, structural alteration in biochemical target resulting in altered binding to the herbicide or detoxification or degradation of the herbicide, before it reaches its target site in the plant cell (Stalker et al. 1988). Gordon-Kamm et al. (1990) reported transformation of cells from embryogenic maize suspension cultures with the bacterial gene *bar* encoding for the enzyme phosphinothricin acetyltransferase (PAT) that inactivates the herbicidal compound phosphinothricin (PPT) by acetylation. Fertile transformed maize plants (R) were regenerated, to evaluate the stability of the gene which reduced in the R<sub>1</sub> generation. Likewise now resistance to maize has been incorporated for non-selective herbicides such as glufosinate, glyphosate, imidazolinone, dimethenamide-P, S-metolachlor, flufenacet and terbuthylazine (Zhu et al. 2000; Devos et al. 2008).

### 2.5.3.2 Insect Resistance

Development of crops that is resistant to insects is expected to increase crop yields since pest infestation can cause reduction in the yield to the tune of up to 10–40 %. This can also save a huge amount of agrochemicals used for crop protection thereby saving considerable amount of money and also the environment. The development of insect-resistant crops was initiated by the discovery that a Gram-positive soil bacterium, *Bacillus thuringiensis* (*Bt*), produces insecticidal crystal proteins ( $\delta$ -endotoxins) during sporulation. The initial attempts to confer insect resistance by insertion of the gene (*cry*) coding for  $\delta$ -endotoxin did not provide expected levels of insect resistance due to low *cry* expression, partly due to the high A–T content of the



bacterial gene, which was subsequently modified to fit the higher level G–C content of plant genes, and especially monocot genes. Expression of the altered versions of *cry* genes, *cryIA(b)* and *cryIA(c)*, resulted in a 100-fold higher level of  $\delta$ -endotoxin production in corn. Transgenic corn expressing the *Bt*-gene *CryIAb* was developed in the USA for protection against the devastating European corn borer, *Ostrinia nubilalis*, and was approved for commercial cultivation in the 1990s (Koziel et al. 1993; Armstrong et al. 1995). In elite tropical maize lines, CML67, CML72 and CML216, direct transformation of  $\delta$ -endotoxin (*cryIAc*) expressing for varying levels of resistance to Southwestern corn borer was carried out by Bohorova et al. (1999). Transgenic corn plant (MON 810), expressing the *Bt* protein, *CryIAb*, was reported to provide effective protection against maize stem borer, *Chilo partellus*, even under high level of larval infestation in the greenhouse (Singh et al. 2005). Various *Cry* proteins entailing resistance genes against insect-pests, namely, *cryIA(b)*, *cryIA(c)*, *cryIF*, *cry3B(b)*, *Cry34Ab1*, *Cry35Ab1*, modified *Cry3A*, *CryIA.105*, *Cry2Ab2* and *Vip3Aa20*, have been widely used in maize transformation. The *cry* genes exhibit specificity for different insect species, and each protein is active in only one or a few insect species, specificity to a large extent determined by the toxin-receptor interaction, although solubility of the crystal and protease activation also play a role. The members of the *Cry* gene family are grouped in subfamilies according to their specificity for members of the insect families Lepidoptera (caterpillars), Diptera (flies and mosquitoes) and Coleoptera (beetles). Some *Bt* strains have also been reported to be active against other insect families and also mites, nematodes, flatworms and protozoa, but few details as to their practical use are available. It is also significant that several important insect-pests appear to be insensitive to known *Cry* proteins (e.g. the corn rootworm, aphids and white flies). To overcome this limitation another source of resistance against insect-pests was used, gene *gna* encoding for snowdrop lectin under control of phloem-specific promoter taken from *Galanthus nivalis* L. This toxic agglutinin is toxic to insects such as corn leaf aphid (*Rhopalosiphum maidis* Fitch) under greenhouse conditions (Wang et al. 2005). The toxicity of the endotoxins was significantly enhanced by use of fusion proteins like BtRB, combining the endotoxin *cryIAc* with the galactose-binding domain of the nontoxic ricin B-chain (RB) which provides the toxin with additional binding domains, thus increasing the potential number of interactions at the molecular level in target insects. Apart from increased toxicity from the *Bt* gene, the resistance was also transferred against a wider range of insects, including important pests that are not normally susceptible to *Bt* toxins (Mehlo et al. 2005).

### 2.5.3.3 Abiotic Stress Tolerance

Drought is a major abiotic stress that limits crop productivity and engineering plants with enhanced tolerance of abiotic stresses such as drought is a major objective of plant biotechnology that is expected to be commercialized in the near future. Tolerance to abiotic stress may be achieved through the modification of endogenous plant pathways, often by manipulating important regulatory proteins such as



transcription factors. Altering the level of expression of key transcription factors involved in abiotic stress pathways has been shown to enhance tolerance to drought stresses in maize (Nelson et al. 2007). Van Breusegem et al. (1999a, b) reported introgression of transgenes expressing for manganese superoxide dismutase that entails foliar tolerance to chilling and oxidative stress and for iron superoxide dismutase entailing enhanced tolerance towards methyl viologen and increased growth rates, respectively.

#### 2.5.3.4 Biofortification

Micronutrient deficiency in developing nations, especially where populations subsist on a monotonous diet of cereal grains that lack essential vitamins and minerals, is a major challenge to health organizations and governments throughout the world, with an estimated 40–50 % of the world's population suffering at one time from diseases caused by a lack of such essential minerals and vitamins. Pyramiding of genes controlling the nutritional quality is difficult via sexual hybridization because large number of loci control the pathway of nutrient accumulation in the plants. Hence, biofortification of staple food grains can be an effective way to provide essential nutrients to consumers whose diets rely heavily on these grains. Biofortification of maize has been carried out for vitamins, iron and zinc. Vitamin deficiency affects up to 50 % of the world's population. Transgenic plants offer an effective way to increase the vitamin content of staple crops, but thus far it has only been possible to enhance individual vitamins. Transgenic corn plants have been developed with the levels of  $\beta$ -carotene, ascorbate and folate vitamins increased specifically in the endosperm to the tune of 169-, six- and twofold, respectively, through the simultaneous modification of three separate metabolic pathways (Naqvi et al. 2009). Similarly, Drakakaki and co-workers (2005) generated transgenic maize expressing both an *Aspergillus* phytase and soybean ferritin in the kernel increasing the concentration of Fe up to 50 % along with 95 % of phytate degradation directly correlated with Fe bioavailability and uptake. Biofortification of maize was also carried out for amino acids lysine and tryptophan, reduction in bitter-tasting sinapinic acid and raising the content of vitamin E.

## 2.6 Impact of Alien Gene Transfer in Maize

Maize being an allogamous crop promotes heterozygosity and hence possesses genetic plasticity in the populations. Therefore, it has an advantage over any other crop in terms of yield potential, adaptability and natural genetic variability. The evolutionary developments and natural hybridization between maize and its relatives in isolated niches have contributed a lot in the available genetic diversity in its primary gene pool. Nonetheless, maize exhibits vast potential for introgression of alien genes due to availability of diverse sources of genes belonging to seven

species and subspecies of genus *Zea* and 16 species of genus *Tripsacum*. The transfer of desirable genes has been successfully achieved via utilizing both conventional and modern biotechnology (Repellin et al. 2001). Introgressive hybridization programmes involving alien genes are extensively time consuming and result in development of breeding lines that are further used in breeding programmes instead of having direct use as commercial cultivar. Use of alien genes has been reported for improvement of agronomic and yield traits; resistance to disease, insect-pests and parasitic weeds; and tolerance to abiotic stresses through conventional hybridization methods. Likewise, biotechnological tools were also employed for the purpose among which the most successful method with practical implication was genetic engineering of maize through recombinant DNA technology. Genetically modified maize covers 42 million ha area contributing to a total of 26 % of cultivated area under maize throughout world.

Genetic engineering has allowed incorporation of traits hitherto not available in the crop germplasm, viz. herbicide resistance. A number of maize cultivars are commercially available with resistance against otherwise non-selective herbicides. Nevertheless, the herbicide-tolerant corn in field has sparked a new debate over the risk of transfer of these herbicide-resistant genes to wild species and hence leading to development of superweeds (Devos et al. 2008). Similarly the insect-resistant genetically modified crop is being cultivated throughout the world and is successful in controlling insect-pests, saving tremendous cost on production and use of harmful chemicals and also having a positive environmental impact. However, there are concerns on the other side of using the transgenic maize varieties as it is opined that such transgenes are affecting the nontarget species also is considered as the negative aspect of this technique. The most useful facet of genetic engineering lies in the biofortification of maize for increasing the amount and availability of minerals and vitamins for which this crop is otherwise deficient. Biofortified maize has provided nutritional security to the people who are solely dependent on corn as staple food. Likewise, genetic engineering of corn has also been focussed towards increasing the content of bio-products like bioethanol or amylase and production of plastics, which are of industrial importance. The use of maize as industrial raw material has further enhanced its value as a cultivated crop.

## 2.7 Conclusion

Since the commencement of systematic maize improvement endeavours, the breeding objectives were to attain high productivity which were well exploited using available variability within the crop germplasm. However, uniformity and narrow genetic base among the commercial cultivars and their parents served as a bottleneck in genetic upgradation of maize for which distant hybridization programmes were taken up for introgression of desirable alien genes. The prevalence of various fertilization barriers has reduced the possibility of alien introgressions into the cultivated background of maize through sexual hybridization. To overcome the sexual barriers

encountered during wide hybridization endeavours, biotechnological tools have assisted the maize breeders to a great extent. The utilization of recombinant DNA technology for genetic engineering of corn has not only helped in increasing yield but has also provided nutritional security and industrial advantage. Conclusively, the transfer of alien genes either through conventional or biotechnological methods has contributed significantly in enhancing the value of this crop.

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