Consequences of Plant Breeding on Genetic Diversity

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ABSTRACT

It is generally perceived that activities related to plant breeding have reduced the genetic diversity within crop species. Therefore, the impact of plant breeders' activities i.e. introduction, selection and hybridization on plant genetic diversity have been reviewed. After examining a large number of scientific reports it may be generalized that losses of genetic diversity occurred but followed spatial and sometimes temporal trends. Furthermore, losses of genetic diversity in plant material occurred in a specific order i.e. the highest in elite open-pollinated cultivars or inbred lines and the lowest in wild germplasm followed by land races. Plant introduction increased genetic diversity when local germplasm was partially substituted or supplemented by introduced germplasm. Selection enhanced genetic differentiation at the expense of genetic diversity. Losses in genetic diversity were observed when plant populations were subjected to domestication during the pre-systematic plant breeding era and pedigree selection during the systematic plant breeding era. However, participatory plant selection effectively generated an allelically rich and broad genetic-based plant material. Intraspecifc hybridization lowered genetic diversity due to utilization of similar types of parents in generating trangressive segregation. Commercial hybrids, when used to substitute land races or diverse indigenous germplasm, also lowered the genetic diversity of the area. In order to broaden the genetic base of plant material, interspecific hybridization was performed in many crop species with some success. Transgenics were released as a product of biotechnology, spontaneous pollination between conventional cultivars and wild germplasm may enhance genetic diversity but may, on the other hand, raise the issue of genetic pollution. These are all pertinent issues as 2010 has been considered by the UN as the International Year of Biodiversity.

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INTRODUCTION

Plant breeding is a technology that deals with the evolution of crop varieties using the principles of various sciences and skills of the plant breeder gained over the years. Since its birth as a subject, systematic plant breeding has achieved two major landmarks i.e. pre (before 1965) and post (after 1965) green revolution (Perkins 1997; Neelu and Rajbir 2009). The pre-green revolution era is marked by the nobalization of sugarcane, utilization of commercial heterosis and development of plant breeding and biometrical techniques (Troyer 1996). This resulted in the evolution of crop varieties more uniform in yield and growth. A major leap in yield was achieved with the onset of the green revolution era, specifically in the Indian subcontinent. After the green revolution, the per capita availability of cereals increased from 275 to 370 kg (Ortiz 1998). The green revolution was

achieved when dwarfing genes were exploited in plant species. The genes characteristically reduced plant height, induced early maturity, increased harvest index (HI), stomatal conductance and defective plant growth regulators (PGRs) such as auxin and gibberellins (Reynolds *et al.* 1999; Salamini 2003; Feil 2006; Routray *et al.* 2007; Rauf and Sadaqat 2008a). Induction of dwarfing genes also helped to maintain high-density populations and a double cropping system (Neelu and Rajbir 2009). However, sustainability of high plant density and a double-cropping system was only possible after the introduction of inorganic chemicals in the form of fertilizers and pesticides (Troyer 1996). It has been estimated that plant breeding and better crop husbandry techniques have contributed in equal proportions to improve yield (Duvick 1986; Reynolds *et al.* 1999). Duvick (1986) indicated that there was a 50% increase in yield over the past 50 years due to plant breeding showing a linear annual

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rate of 1% increase in yield.

Plant breeding has frequently been affected by new innovations within other disciplines. The discovery of each novel technique convened great hopes and perceptions for the improvement of yield. In the beginning of the 19th century, rediscovery of Mendel's work resulted in the birth of the science of genetics, which established plant breeding on a scientific basis. Before Mendel, people indulged in the fluid-like inheritance mechanism, which gave a blended expression to the union of male and female gametes. Mendel's work has provided the basis for systematic plant genetic improvements and the notation (F_1, dominant and recessive) described by Mendel is valid and used even today in plant breeding. The discovery of various mutagens was the next major breakthrough, which made it possible to induce mutations in the genome. X-rays were first discovered for their mutagenic effect on barley (*Hordeum vulgare*) and maize (*Zea mays* L.) by Stadler (1928a, 1928b). Afterwards, large numbers of mutation breeding projects were started during the 1960s. Limited benefits in the form of few cultivars having high yielding potential and disease resistance were reaped from these mutation-breeding programs (Micke 1993; Ahloowalia *et al.* 2004). Ahloowalia *et al.* (2004) noted that more than 2250 cultivars were released in various mutation breeding programs by inducing radiations. In Pakistan, a cotton mutation breeding program was very fruitful, yielding many mutants (NIAB-78, NIAB999, NIAB-111) with high yield and early maturity. Cotton production in Pakistan increased from 7 to 11 million bales after the release of mutant NIAB-78 (Ahloowalia *et al.* 2004). Mutation breeding continues to be a fundamental science in ornamental plant breeding (see six chapters in Teixeira da Silva 2006).

Discovery of genome-doubling agents such as colchicine provided another exciting tool for plant breeders to set the foundation for polyploidy breeding. However, benefits of this technique were limited to evolution of a few cultivars meant for their vegetative parts or seedless fruits and vegetables (Lee 1998; Kloen and Speckmann 2004).

In the 1950s micropropagation techniques evolved which helped to multiply and produce disease-free plant breeding stocks, to overcome the interspecific incompatibility and isolation of somaclones, etc.

Today, plant breeding has gained the form of molecular breeding through the advancement and accumulation of knowledge in the field of biochemistry and molecular genetics. Molecular breeding is involved in the selection of appropriate parental material and genotypes in segregating and back cross populations. Furthermore, the development of DNA-based marker systems has also allowed us for marker-based selection of complicated traits without exposing them to the target environment.

Developments in the field of molecular biochemistry and genetics have also given birth to plant biotechnology, which often limits the existence of plant breeding. Co-existence or merging of both disciplines, either plant breeding into plant biotechnology or biotechnology into plant breeding, seems controversial among scientific communities and it may take some time to come to some conclusion. Plant biotechnology addresses yield-limiting factors through the production of transgenic crops. Production of transgenic crops through genetic engineering has gained significant popularity nowadays. Genetic engineering is a technique that inserts gene beyond the boundaries of species and genus to produce transgenic organisms. In the mid 1990s, many transgenic crop species were released for general cultivation and now these crops occupy a significant cropping area (James 2008; **Fig. 1**). However, release of such products resulted in wide debates about their safety for the ecosystem and their impact on biodiversity.

It is generally perceived that plant breeding has reduced genetic diversity in crop species. Therefore, this review will take into account the (i) status of genetic diversity in crop species (ii) consequence of systematic plant breeding on the genetic diversity. Systematic plant breeding is traditionally
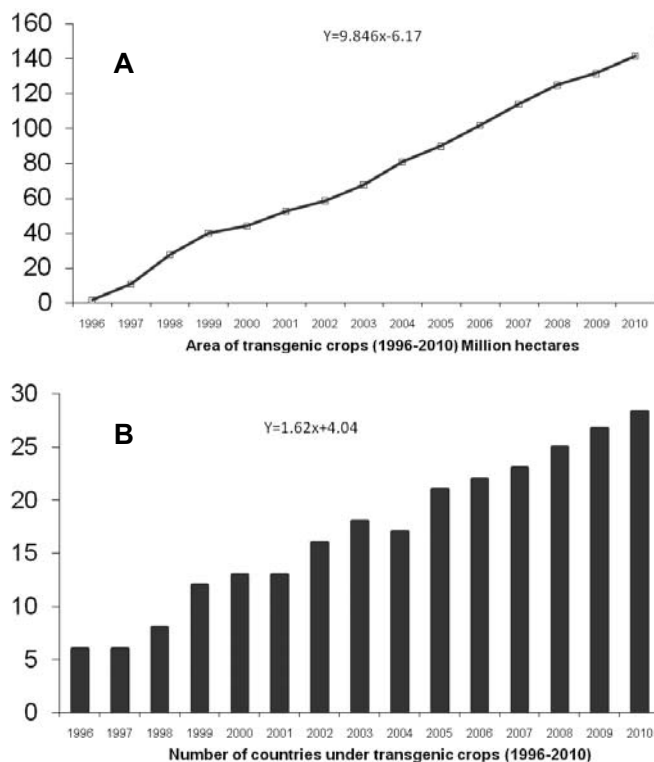

Fig. 1 Area (A) and (B) number of countries under various transgenic crop cultivation.

dependent on three activities i.e. introduction, selection and hybridization. Here we will also discuss the effects of these three major activities specifically on the genetic diversity.

Genetic diversity

Bio-diversity refers to the "variations" within the living world while genetic diversity is the sum of genetic characteristics within any species or genus (Rao and Hodgkin 2002). It differs from genetic variability, which describes the variation within these genetic characteristics (Genetic diversity 2009; Wikipedia). Greater bio-diversity is important for stability and sustainability of an ecosystem (**Fig. 2**). It has the potential to enhance pollination, soil processes such as continuous biomass cover, preventing soil erosion, water logging and aids the ecosystem to sequester carbon.

Genetic diversity is important for sustainable production in crop species since greater losses of characteristics in any population may limit its chances of survival and re-
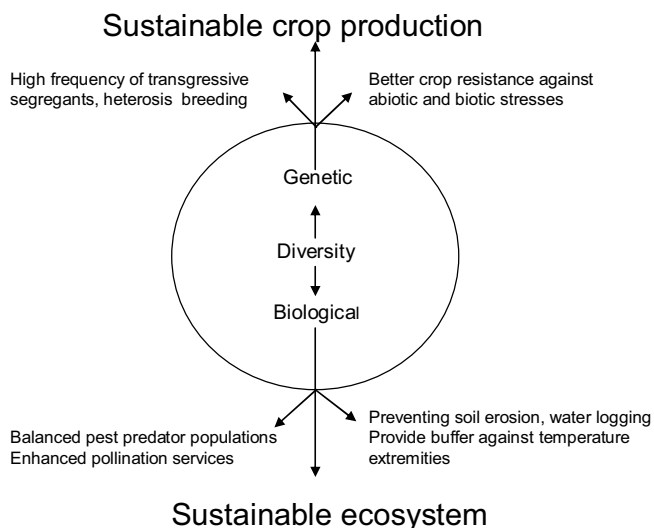
Fig. 2 Diagrammatic representation of diversity and its types.

Table 1 Effect of molecular marker on the estimates of genetic diversity in several crops.

Reference	Species	Marker	Genetic diversity
Thormann *et al.* 1994	*Cruciferous* species	RFLP vs. RAPD	Similar to show intraspecific relationship
			RFLP were better while depicting inter specific variation
Lu *et al.* 1996	*Pisum sativum* (pea)	PCR based marker vs. RFLP	All PCR-based markers were better than RFLP
Barrett *et al.* 1998	*Triticum aestivum* (wheat)	Phenotypic vs. AFLP	AFLP-based genetic diversity was more useful
Dubreuil and Charcosset 1998	*Zea mays* (maize)	Isozyme vs. RFLP	RFLP's were superior to identify the origin of an individual
Lima *et al.* 2002	*Saccharum* spp. (sugarcane)	Phenotypic vs. AFLP	AFLP-based genetic diversity was more useful
Davila *et al.* 2004	*Hordeurn vulgare* ssp. *spontaneum* (wild barley)	RAMP vs. SSR	Estimates given by two marker system were different; RAMP gave slightly better estimates; Genetic variation was revealed by different mechanism
Doldi *et al.* 2006	*Glycine max* (soybean)	RAPD vs. SSR	Combined used of both marker was useful and more reliable for estimating genetic diversity
Fuentes *et al.* 2005	*Oryza sativa* L. (rice)	RAPD vs. AFLP	RAPD was found superior than AFLP
Leal *et al.* 2010	*Zea mays* (maize)	RAPD vs. SSR	Both techniques were efficient

Conclusion:
Phenotypic data < Isozyme < RFLP < AFLP < SSR < RAMP < RAPD
where (<) means inferior capacity to detect the genetic diversity than other systems.
Abbreviations: **AFLP**, amplified fragment length polymorphism; **RAMP**, randomly amplified microsatellite polymorphism; **RAPD**, randomly amplified polymorphic DNA; **RFLP**, restriction fragment length polymorphism; **SSR**, simple sequence repeat

quires greater human efforts for successful production (Trethowan and Kazi 2008). Different author(s) have shown the value of genetic diversity in providing genetic barriers against different biotic and abiotic stresses (Hughes *et al.* 2004; Hajjar *et al.* 2008). Hajjar *et al.* (2008) showed that increasing genetic diversity is important for pest and disease management and provides chances for further improvement of the species. Beside these applied aspects, molecular marker-based genetic diversity is necessary for genetic mapping and marker-assisted selection in breeding (Lapitan *et al.* 2007).

Traditionally, factors such as urbanization, and the replacement of traditional agriculture systems by modern industrial methods have reduced biological diversity (Khlestkina *et al.* 2004a). It is also generally perceived that the overall genetic diversity in crop species has been reduced. Few reports have indicated that modern plant breeding methods and systems also regulate the magnitude of genetic diversity (Christiansen *et al.* 2002; Witcombe *et al.* 1996). Christiansen *et al.* (2002) showed that wheat genetic diversity was enhanced by plant breeding in the first quarter of the 20th century followed by a decrease and then again increased during the second quarter. Witcombe *et al.* (1996) showed that these differential responses arose due to the differential impact of different breeding methods and/or systems on diversity.

Comparison of different genetic diversity estimates methods

Genetic diversity has been conventionally estimated on the basis of different biometrical techniques (Meteroglyph, D^2, divergence analysis, and principal component analysis) such as phenotypic diversity index (*H*), or coefficient of parentage utilizing morphological, agronomical and biochemical data (Matus and Hayes 2002; Mohammadi and Prassana 2003; Jaradat *et al.* 2004; Ahmad *et al.* 2008). However, evaluation based on these phenotypic data was laborious and took years to draw a conclusion. The advent of different molecular techniques led breeders to estimate genetic diversity on the basis of data generated by different molecular markers, which provided a means of rapid analysis of germplasm and estimates of genetic diversity, which were often found to corroborate phenotypic data. These molecular markers are broadly categorized as non-PCR or PCR-based. Restriction fragment length polymorphism (RFLP) belong to the first category and polymorphism is restriction site-based and does not require a PCR reaction to amplify while amplified fragment length polymorphism (AFLP), single sequence repeats (SSR) and random amplified polymorphic DNA (RAPD) markers belong to second category which require a PCR reaction and offer several advantages over the first category i.e. rapid and low cost per analyses,

freedom from radio labeling and high or sometimes comparable polymorphism. All these markers are now being widely used for evaluating genetic relationships of crop germplasm. Since these markers differ in their properties they may result in different estimates of genetic diversity. Therefore it is worthwhile to review the studies comparing genetic diversity estimates generated by different marker systems. Comparing results of different molecular genetic diversity estimation methods will be helpful for identifying their utility as parental selection tools for plant breeders (Barrett and Kidwell 1998).

Fuentes *et al.* (2005) compared different methods of genetic diversity estimates. They showed that estimates based on RAPD data rather than AFLP efficiently represented the genetic parentage and phenotypic diversity between rice varieties. Combined diversity analysis based on phenotypic and genotypic estimates permitted a more effective separation of the progenitor set than those obtained solely by phenotypic and genealogical information. Similarly, Lu *et al.* (1996) also indicated that all PCR-based molecular markers were much more informative than RFLP. Patzak (2001) also indicated that three molecular markers (RAPD, AFLP, and ISSR) gave similar types of estimates in hop (*Humulus lupulus*). Similarly, Thormann *et al.* (1994) also showed that RAPD or RFLP estimated similar intraspecific genetic relationships in cruciferous species; however, the two marker types gave different results for interspecific genetic relationships. They concluded that RFLP data was more reliable when estimating genetic relationships of accessions from more than one species.

Barrett and Kidwell (1998) compared the pedigree and AFLP-based genetic diversity estimates (GDE_{PED} and GDE_{AFLP}) in wheat, respectively. AFLP-based genetic diversity estimates were better able to identify pairs of genotypes representing the entire range of possible genetic diversity estimates. Thus, AFLP-based genetic diversity estimates have more utility than pedigree-based estimates for identifying parental combinations with maximum allelic variation. Similarly, Lima *et al.* (2002) indicated that AFLP-based genetic similarity estimates helped to quantify the degree of genetic relationships among sugarcane varieties and AFLP-based genetic similarities were more accurate than pedigree data. Mansour *et al.* (2010) used these three marker systems to study genetic diversity and analysis of molecular variance (AMOVA) among 10 tomato cultivars. Different dendrograms constructed for the RAPD, ISSR and IRAP results individually and collectively revealed that similarity and clustering were highly dependent on the marker system used.

Dubreuil and Charcosset (1998) compared the genetic diversity estimates from isozymes and RFLP and concluded that the latter were superior because of their ability to identify the origin of a given individual and to reveal a relevant

genetic structure among populations. A summary of various studies is given in **Table 1**.

Status of genetic diversity in various crop species

Plant breeders always remain focused on the selection of plant type better suited to human needs. As a result, genotypes more uniform in growth and reproduction were selected and released for general cultivation (Donini *et al*. 2005; Fu 2006, Fu *et al*. 2006; Condon *et al*. 2008). Fu (2006) reviewed the impact of plant breeding as narrowing or widening of genetic bases and even shifting of genetic backgrounds. It was concluded that substantial allelic losses occurred due to plant breeder activity. Trethowan and Kazi (2008) indicated that genetic diversity was necessary for the rapid genetic improvement of crop species. Therefore, the status of genetic diversity in various crop species was reviewed.

1. Barley (*Hordeum vulgare*)

In the case of barley, Matus and Hayes (2002) showed low genetic diversity in elite breeding material compared with mapping populations. Similarly, genetic diversity was also found to be lower than wild cultivars (Nevo *et al*. 1986). Contrasting reports are also available showing sufficient

genetic diversity in cultivated germplasm compared to wild or land races of barley (Struss and Plieske 1998). When temporal trends of barley genetic diversity were measured, showed non-significant changes (Khlestkina *et al*. 2006; Malysheva-Otto *et al*. 2007), reported to be low (Condon *et al*. 2008) or raised (Koebner *et al*. 2003). Malysheva-Otto *et al*. (2007) showed that the impact of plant selection on diversity in barley was non-significant. The study was undertaken in 504 European barley cultivars released during the 20th century. Germplasm was categorized into four temporal groups (TG) i.e. 1900–1929 (TG1 with 19 cultivars), 1930–1949 (TG2 with 40 cultivars), 1950–1979 (237 cultivars as TG3), and 1980–2000 (TG4 consisting of 208 cultivars). TG4 was 84.3% similar to TG1 resulting in a loss of only 15.7% of alleles. TG4 contained 51 novel alleles that were absent in TG1. On the other hand, Condon *et al*. (2008) showed that plant breeder selection led to a reduction of genetic diversity and allelic losses at a few loci. A summary of some other reports are presented in **Table 2**.

2. Beans

Common bean (*Phaseolus vulgaris*) is one of the most widely grown crops in the world. Reduction of bean genetic diversity in various parts of the world both by the activities of plant breeders and during the pre-plant breeding era has

Table 2 Genetic diversity as reported in various studies of barley.

Reference	Marker/Genetic distance	Plant material	Allelic		Genetic distance	Genetic diversity
			Losses	**Gains**		
Nevo *et al*. 1986	Allozymes	509 individual 13 populations Composite cross Land races	-	-	-	Wild population were more diverse Self pollination led to a decrease in heterozygosity
Struss and Plieske 1998	15 SSR	163 barley genotype	-	-	Genetic distance (Nei and lei 1979) 0.75 wild germplasm 0.72 land races 0.70 cultivar	Sufficient genetic diversity
Matus and Hayes 2002	55 SSR	22 *Hordeum vulgare* subsp. *spontaneum* (subsp. *spontaneum*), 32 *Hordeum vulgare* subsp. *vulgare* (subsp. *vulgare*), 96 elite lines and varieties	48% 36% In elite material	14% Elite lines	Genetic distance (calculated from allelic variation) between cluster of *spontaneum* 0.84; *vulgare* 0.79; elite lines 0.42	Low diversity in elite breeding material
Kobener *et al*. 2003	21 Phenotypic 8 AFLP 21 SSR	134 Cultivars released form 1925-1995 in UK	-	-	Genetic distance between temporal groups (Reynolds *et al*. 1983; Weir and Cockerham 1984) Genetic distance (0.1) Inbreeding index (0.07) Degree of relatedness (0.04)	Systematic plant breeding did not led to decline in genetic diversity Sufficient genetic diversity
Khlestkina *et al*. 2006	28 G-SSR 13 EST-SSR	96 Cultivars released during 40 years in Austria, India and Albania	Albania (32%)	Austria (20%) India (2%)	Diversity index Austria = 1932 (0.63), 1982 (0.64) Albania = 1941 (0.72), 1994 (0.62) Indian = 1937 (0.74), 1976 (0.68)	Genetic diversity conserved in Austria and India Small reduction in Albania
Malysheva-Otto *et al*. 2007	35 SSR	504 European cultivars 1900-1929 (19 cv.) 1930-1949 (40 cv.) 1950-1979 (237 cv.) 1980-2000 (208 cv.)	0% 9% 5% 16%	0% 42% 37% 32%	Mean Nei's (1979) genetic distance in various temporal groups 0.61 (0.21-0.87) 0.60 (0-0.87) 0.56 (0-0.94) 0.55 (0-0.94)	Impact of plant breeding was non-significant on genetic diversity
Condon *et al*. 2008	70 SSR Pedigree method SNP	98 cultivars released 1958-1998	60%	-	Parental lines molecular diversity index (0.59), pedigree diversity (0.84); Elite line released during 1988-98 molecular diversity (0.24), pedigree diversity (0.39)	Decreased Plant breeder selection led to the reduction at few loci
Orabi *et al*. 2009	36 SSR	185 accession	-	-	Genetic diversity (Peakall and Smouse 2006) *Hordeum spontaneum* (0.65) *Hordeum vulgare* (0.61)	No losses Genetic diversity of land races and wild species was comparable

Abbreviations: **AFLP**, amplified fragment length polymorphism; **SSR**, simple sequence repeat; **G-SSR**, genomic simple sequence repeats; **EST-SSR**, expressed sequence tags; **SNP**, single nucleotide polymorphism

Table 3 Status of genetic diversity in common beans (*Phaseolus vulgaris* L.).

Reference	Marker	Plant material	Genetic distance	Conclusions
Sonnante *et al.* 1994	M 13 DNA finger printing (1-probe enzyme combination)	Latin American germplasm and USA cultivar	-	Domestication in both type of germplasm reduced diversity
Beebe and Ochoa 1995	RAPD	BGMV resistant lines vs. No selection	Genetic distance (Nei and Lei 1979) for BGMV resistant lines (0.16) vs. No selection (0.22)	Selection for resistance reduced genetic diversity
Metais *et al.* 2002	15SSR	45 bean lines	-	Variable genetic diversity in various bean population Lower level of genetic diversity indicated breeder intensive selection
Beebe *et al.* 2001	189AFLP	182 land races 29 wild beans	Genetic distance (Nei and Lei 1979) of 172 landraces average (0.07) Genetic distance after introgression (0.10)	Narrow genetic base needed to be expanded Introgression led to some increase in genetic diversity
Galván *et al.* 2001	16 RAPD 23ISSR	13 commercial cultivar	Genetic distance (Jaccard's coefficient) average (0.2) range (0-0.77)	Low genetic diversity
Lioi *et al.* 2001	SSR AFLP	7 Italian land races maintained by farmer	-	Considerable genetic diversity Involvement of farmer for further improvement and to preserve the genetic diversity
Singh *et al.* 2001	Review article	-	-	Genetic base was narrow, introgression recommended
Papa and Gept 2003	9AFLP	Wild vs. domesticated germplasm	Gene diversity (Nei 1978) Wild (0.17) Domesticated (0.10)	Gene flow was 3 to 4 folds higher from domesticated to wild germplasm
Sicard *et al.* 2005	8SSR 4ISSR 10cpSSR	14 *Phaseolus vulgaris* varieties 9 *P. coccineus* varieties	Genetic diversity (Peet 1974; Nei 1978) *Phaseolus vulgaris* varieties (0.75); *P. coccineus* (0.51)	Selection by farmer and heterogenous environment has maintained genetic diversity
Jose *et al.* 2009	13 RAPD	20 land races of Nilgiris	Genetic diversity (Jaccard 1908) 0.38	High genetic diversity

Abbreviations: **AFLP**, amplified fragment length polymorphism; **cp-SSR**, chloroplast single sequence repeats; **SSR**, simple sequence repeat; **RAPD**, randomly amplified polymorphic DNA

been reported (**Table 3**). Plant breeder's selection for resistance or for yield-contributed traits led to a significant reduction in diversity (Beebe and Ochoa 1995; Metais *et al.* 2002). On the other hand, losses during pre-plant breeding have also been reported such as during domestication of common beans (Sonnante *et al.* 1994). Furthermore, losses in genetic diversity during establishment of land races were also reported (Beebe *et al.* 2001). In order to expand the genetic diversity of the cultivated germplasm, interspecific hybridization was recommended (Singh *et al.* 2001). This interspecific hybridization occurred spontaneously through pollen contamination but in reverse order i.e. from cultivated to wild (Papa and Gept 2003).

3. Upland cotton (*Gossypium hirsutum* L.)

Cotton is an important fiber and oilseed crop of many continents (Khan *et al.* 2007). A number of studies have indicated low genetic diversity in this crop species (**Table 4**). Iqbal *et al.* (1997) studied the genetic diversity among Pakistani upland cotton varieties and came to the conclusion that most of the genotypes have a narrow genetic base. Similarly, Khan *et al.* (2009) also came to the same conclusion after analyzing genetic diversity in 40 Pakistani upland cotton cultivar released from 1914-2005. Rahman *et al.* (2002) showed narrow genetic diversity among elite cotton cultivars of Pakistan. Estimated genetic similarity between cotton cultivars before the *Cotton leaf curl virus* (CLCuV) epidemic was 81.5 to 93.41%. After the post-epidemic era CLCuV-resistant cultivars were developed using similar sources of resistance. Therefore, these cultivars also showed narrow genetic diversity (**Table 4**). They stressed the need to breed for high genetic diversity to serve as a buffer against a potential epidemic. Bowman *et al.* (1996) showed that genetic contribution of ancestral lines was low in modern cultivars. This genetic contribution was lost due to extensive reselection.

Van Esbroeck and Bowman (1998) identified the reason for the loss of genetic diversity in upland cotton (*Gossypium hirsutum* L.); although sufficient genetic diversity existed in cotton germplasm, a large part of this diversity was left unused because of breeders' preference for a few cultivars to be used as parents in establishment of transgressive segregation and farmers' preference for a few cultivars that occupied the major area of cultivation in USA. However, in spite of this loss modern cultivars have a broad genetic base. Khan *et al.* (2009) showed that cultivars released after 2000 contained slightly higher genetic diversity. Zhang *et al.* (2005a) studied genetic diversity among elite commercial cotton cultivars from major cottonseed companies. Genetic similarity was high within cotton cultivars from the same seed company. However, sufficient genetic diversity exits between cultivars released by different seed companies. Li *et al.* (2008) studied genetic diversity through principal component and molecular marker analysis in 71 glandless cultivars; there was higher genetic diversity in the evaluated population for both agronomic traits and molecular markers.

4. Maize and sunflower

Maize (*Zea mays* L.) and sunflower (*Helianthus annuus*) are two crops in which heterosis is being exploited on a commercial basis and thereby several commercial hybrids are available for general cultivation. Exploitation of heterosis on a commercial basis requires the development of an inbred line through selection followed by inbreeding/self pollination in open-pollinated populations.

The focus of many studies carried out in sunflower and maize was to determine whether losses of genetic diversity occurred during the development of inbred lines or whether inbred lines were as diverse as an open-pollinated population. A summary of this research is presented in **Table 5**, which indicates that allelic losses occurred in inbred lines, particularly in maize (Lu and Bernardo 2001; Liu *et al.* 2003; Reif *et al.* 2005a). Liu *et al.* (2003) analyzed the

Table 4 Genetic diversity in upland cotton (*Gossypium hirsutum* L.).

Reference	Marker	Plant material	Genetic distance	Genetic diversity
Bowman *et al.* 1996	Pedigree information cultivar released from (1970-1990)	260 cotton cultivars	Coefficient of parentage (Kempthorne 1969) 0.07. Ancestral lines only contributed 25% of the total genetic variation.	Substantial remaining genetic diversity. Stoneville 2 was most influential cultivar. Reselection resulted in significant loss of genetic information.
Iqbal *et al.* 1997	50 RAPD	22 *G. hirsutum* varieties 1 *G. arboreum*	Genetic distance (Nei and Lei 1979) average (0.23)	Low
Van Esbroeck and Bowman 1998	Pedigree information	60 cotton cultivar (grown on more than 1% area during 1987-1996)	Coefficient of parentage (Kempthorne 1969) 0.09; genetic relatedness (0.07)	High genetic diversity in germplasm Genetic vulnerability in field due to (i) farmer preference for few cultivar over large area (ii) Breeder preference for same type of parents in crossing
Rahman *et al.* 2002	50 RAPD	Cultivars pre CLCuV epidemic vs. post epidemic CLCuV	Genetic distance (Nei and Lei 1979) Cultivars pre CLCuV epidemic (0.12) vs. post epidemic CLCuV(0.10)	Both showed narrow genetic base Need to diversify germplasm to diffuse the chances of CLCuV in Pakistan.
Rungis *et al.* 2005	SSR	8 cultivars	-	SSR markers were not useful in cotton
Zhang *et al.* 2005	88 SSR	24 cultivar from various seed companies	Genetic distance (Jaccard's coefficient) Between varieties of same seed company (0.17) between seed companies (0.22)	Sufficient genetic diversity
Candida *et al.* 2006	31 SSR	53 cotton cultivars	Genetic distances (dissimilarity matrix Cruz, 2001) between cultivars (0.40)	Need for introduction of new alleles
Li *et al.* 2008	9 agronomic traits 9 RAPD 33 SSR	71 glandless cultivarss	DIST (average taxonomic distance) and DICE (Nei and Li's pairwise distance) averages were 1.78 and 0.88, respectively	Sufficient genetic diversity
Khan *et al.* 2009	34 SSR	40 Pakistani cultivars (1915-2005)	Average genetic dissimilarity (Fu *et al.* 2006) Before 2000 (0.25) vs. after 2000 (0.25) 2000 (0.20) 2001 (0.22) 2002 (0.24) 2004 (0.29) 2005 (0.25)	Over all low genetic diversity No change in genetic diversity Cultivars released during 2004 have slightly higher SSR variation

Abbreviations: **RAPD**, randomly amplified polymorphic DNA**; SSR,** simple sequence repeat

Table 5 Comparison of inbred lines, open pollinated varieties (OPVs) and land races for genetic diversity in cross-pollinated species i.e. maize and sunflower.

Reference	Marker	Plant material	Allelic		Genetic distance	Genetic diversity
			Losses	Gains		
Maize						
Lu and Bernardo 2001	SSR	8 current inbreds vs. 32 historical inbreds	35%	No	Genetic distance (Nei and Li 1979) between current (0.65) and historical inbred lines (0.67)	Losses non-significant
Warburton *et al.* 2002	85 SSR	57 CIMMYT inbred 24 CIMMYT landraces	-	Yes	Genetic distance ((Nei 1978) Land races (0.61)	High
Warburton *et al.* 2008	25 SSR	23 CIMMYT OPVs 26 CIMMYT + 1 inbred lines			OPVs (0.61) Inbred line (0.65)	
Liu *et al.* 2003	SSR	Inbred lines vs. OPVs	20%	-	-	Differential levels among inbred lines
Reif *et al.* 2005	55 SSR	5 OPVs vs.85 maize hybrids	Yes	-	-	-
Vigouroux *et al.* 2005	462 SSR	Land races vs. wild teosinte	24%	-	Genetic distance calculated of (Goudet 2001) land races (0.64) and teosinte (0.74)	12% loss of genetic diversity
le Clerc *et al.* 2005	51 SSR	133 cultivar (released during last 50 years)	-	-	Genetic distance (Nei 1978) of four periods 0.61 (1935-1975) 0.57 (1976-1985) 0.56 (1986-1995) 0.56 (1996-2003)	Narrowed 8% (bred after 1985)
Sunflower						
Lawson *et al.* 1994	RAPD	Commercial cultivar Advanced lines Wild sunflower species	-	Yes	Genetic dissimilarity Hybrid 27% dissimilar to each other Wild germplasm 38% dissimilar	High diversity and genetic differentiation among all sunflower group
Gentzbittel *et al.* 1994	181 RFLP probes	17 inbred lines	-	-	Genetic distance (Nei 1987) 0.21	Low
Zhang *et al.* 1996	81 probe enzyme	26 cultivated inbred line	-	-	-	Low
Jie *et al.* 2003	23 RAPD 10 AFLP	23 confectionary inbred line	-	-	Genetic distance Nei and Li (1979) RAPD 0.35; AFLP 0.31	High
Liu and Burke 2006	9 EST-SNP	Cultivated vs. wild sunflower	-	-	Nucleotide diversity (Rozas and Rozas 1999) Wild (0.014) vs. Cultivated (0.006)	Cultivated sunflower 60-50% less diverse
Yue *et al.* 2009	12 (TRAP)	177 inbred lines (released during 1970-2005)	-	-	Genetic distance (Nei 1978) 0.42	Substantial

Abbreviations: **EST-SNP**, expressed sequence tag-single nucleotide polymorphism; **SSR**, simple sequence repeat; **RAPD**, randomly amplified polymorphic DNA; **RFLP**, restriction fragment length polymorphism

Table 6 Genetic diversity reports in oat (*Avena sativa* L.).

Reference	Marker	Plant material	Allelic		Genetic distance	Diversity
			Losses	Gains		
Souza and Sorrells 1989	Pedigree analysis	205 North American cultivar	-	-	-	Current cultivars were broad based
Fu *et al.* 2003	30 SSR	96 Canadian oat cultivars released from 1886 to 2001			Averaged genetic distance {Dice 1945, Nei and Li 1979, Jaccard 1908}	No significant losses
			-	-	Pre-1930s (0.40)	
			44%	25%	1930s (0.46)	
			30%	30%	1940s (0.48)	
			46%	30%	1950s (0.44)	
			70%	11%	1960s (0.43)	
			56%	22%	1970s (0.40)	
			33%	31%	1980s (0.40)	
			53%	26%	1990s (0.38)	
Fu *et al.* 2005	AFLP	670 accession from 79 countries			Phi Genetic distance (Rohlf 1997) South America (0.09) West Asia (0.04) Indian subcontinent (0.03) West Asia/Europe (0.03)	Non-random distribution of genetic diversity Land races vs. non land races have similar genetic base
Nersting *et al.* 2006	7 SSR	Cultivar released after 1940 vs. land races			Shannon Weaver diversity index (Shannon and Weaver 1962)	Losses indicated
			71%	23%	Land races(0.65)	
			42%	21%	1898-20s (0.63)	
			52%	25%	1921-40s (0.64)	
			82%	18%	1941-60s (0.58)	
			83%	24%	1961-80s (0.48)	
					1981-00 (0.56)	
Li *et al.* 2007	26 SSR	Wild oat population of China and USA			Genetic diversity (Nei 1978) of Chinese (0.23) vs. USA (0.24) oat populations	Wild Chinese oat populations were genetically diverse to that of USA. Genetic diversity was not changed by environment, agronomy and herbicides
Abbas *et al.* 2008	10RAPD	10 varieties from various ecological regions			Genetic distance (Ni and Li 1979) (0.54)	High genetic diversity
Tinker *et al.* 2009	1295 DArT	182 varieties	-	-	Manhattan Genetic distance Average genetic distance within particular geographical area ranged 100-200 Between geographical area 300-600	Varieties from specific geographical area or breeding program were related with each other

Abbreviations: **AFLP**, amplified fragment length polymorphism; **SSR**, simple sequence repeat; **DArT**, diversity array technology

genetic diversity of 260 inbred lines. Tropical and subtropical inbreds possessed a greater number of alleles and greater gene diversity than their temperate counterparts. Comparison of diversity in equivalent samples of inbreds and open-pollinated landraces revealed that maize inbreds capture <80% of the alleles in the landraces, suggesting that landraces can provide additional genetic diversity for maize breeding. Similarly, Reif *et al.* (2005) studied the amount of genetic diversity transferred to an elite flint germplasm pool from adapted open-pollinated varieties (OPVs) and showed that allelic reduction occurred during the last 50 years. Lu and Reif (2001) compared current eight maize inbreds (B14, B37, B73, B84, Mo17, C103, Oh43 and H99) with 32 historical inbreds. The average number of alleles per locus was 4.9 among all 40 inbreds and 3.2 among the eight current inbreds showing a 65% decrease per locus. However, in a few cases these losses were further compensated by new alleles in inbred lines (Lu and Bernardo 2001; Warburton *et al.* 2002, 2008). These new alleles were incorporated as results of inter-specific hybridization or mutation. Therefore, allelic losses did not contribute to the reduction in genetic diversity (Lu and Bernardo 2001). On the basis of many studies, it can be concluded that genetic diversity losses did occur or sometimes they were non-significant in maize (Lu and Bernardo 2001; Warburton *et al.* 2002; Vigouroux *et al.* 2005; Warburton *et al.* 2008). Sunflower studies have indicated substantial genetic diversity in a few instances (Lawson *et al.* 1994; Jie *et al.* 2003; Yue *et al.* 2009). Studies are also available which showed a decline in genetic diversity in sunflower (Gentzbittel *et al.* 1994; Zhang *et al.* 1996). In comparison with wild sunflower, Liu and Burke (2006) showed that cultivated sunflower was 50-60% less diverse.

Therefore, inter-specific hybridization was recommended, which is already under way as indicated from many inter specific hybridization reports in sunflower (Seiler 1992; Prabakaran and Sujatha 2004; Seiler and Brother 1999; Jovanka 2004; Tavoljanskiy et al. 2004; Rauf 2008; Siniša *et al.* 2008).

5. Oats (Avena sativa)

Static genetic diversity estimates have been reported for oats (**Table 6**). Fu *et al.* (2003) showed no change in genetic diversity over years when cultivars released over the time period of 1886 to 2001 was compared. Similarly, Fu *et al.* (2005) also compared land races over non land races and found no change in genetic diversity. However, contrasting reports are also available regarding the temporal changes in genetic diversity. Nersting *et al.* (2006) compared genetic diversity of cultivars released after 1940 with land races and found a decline in genetic diversity. A static trend in one region and a decline in another shows a non-random distribution of genetic diversity which may have arisen due to variation in plant material handling, breeding methods and goals in diverse regions.

6. Rice (Oryza sativa)

Details of genetic studies carried out in rice are provided in **Table 7**. Zhu *et al.* (2000) established the benefits of using genetically diverse germplasm. When a mixture of blast disease-susceptible and -resistant varieties were grown, disease incidence was reduced by 94 and 89% increase in yield was noted in susceptible varieties. In order to determine the

Table 7 Summary of studies encompassing genetic diversity issue in rice (*Oryza sativa* L.).

Reference	Marker	Plant material	Allelic		Genetic distance	Genetic diversity
			Losses	Gains		
Zhang *et al.* 1992	3 RFLP	12 Indica 14 Japonica	-	-	-	Indica more diverse than Japonica Base substitution/ deletion led to genetic differentiation
Zhu *et al.* 2000		Genetic mixture was grown in Yunnan Province China	-	-	-	Disease susceptible varieties in mixture with resistant provided 89% more yield and 94% less blast attack.
Sun *et al.* 2001	44RFLP	122 common wild rice vs. 75 cultivated rice *Oryza sativa*	40%	-	Genetic distance (Sano and Morishima 1992) *Oryza rufipogon* (0.37) *Oryza sativa* (0.29) Chinese wild rice (0.35) vs. South Asia (0.31) and South East Asia (0.30)	Genetic diversity of cultivated rice (3/4) lower than wild one Chinese common wild rice showed the highest genetic diversity followed by South Asia and South East Asia. Domestication and evolution led to the loss of genetic diversity due to human and natural selection.
Morin *et al.* 2002	Phenotypic data	15 villages of Philippine, Vietnam and India		Yes	Genetic diversity was estimated by rate of replacement of indigenous varieties with modern cultivar Area under modern varieties increased at rate of 15% / year from 1996-1998	On-Farm genetic diversity was significantly reduced during 1996-1998 due to drought
Mantegazza *et al.* 2008	3AFLP 12SSR	135 accessions introduced from abroad or developed in Italy from 1850- 2001			Genetic distance (Sneath and Sokal 1973) 1850–1927 (0.34) 1928–1962 (0.37) 1963–1990 (0.34) 1991-2001 (0.41)	Genetic diversity increased over time
Steele *et al.* 2009	49SSR	9 Modern rice varieties vs. 12 land races of Nepal			Nei's unbiased (1979) genetic distance Land races (0.62) Client oriented breeding (0.33) Modern Check varieties (0.62)	Partial introduction of modern rice varieties did not change the rice genetic diversity
Wei *et al.* 2009	40SSR	310 Chinese cultivars 1950s -1990	7%		Nei's unbiased (1979) gene diversity 1950s (0.64) 1990s (0.62)	Non significant decrease over time

Abbreviations: **AFLP**, amplified fragment length polymorphism; **SSR**, simple sequence repeat; **RAPD**, randomly amplified polymorphic DNA; **RFLP**, Restriction fragment length polymorphism

status of genetic diversity in rice, cultivated rice germplasm was compared with wild germplasm (Sun *et al.* 2001; Steele *et al.* 2009). The former had lower diversity than the latter and allelic losses were also observed (Sun *et al.* 2001). These losses were attributed to human and natural selection in the course of evolution of modern rice. Temporal changes in rice genetic diversity were also observed by Mantegazza *et al.* (2008) in cultivars released from 1880-2001. It was shown that rice genetic diversity increased over time in Italy. This may be due to introduction of rice accessions from abroad. Steele *et al.* (2009) was also of the view that partial introduction of high-yielding rice cultivars did not harm local diversity. However, Wei *et al.* (2009) showed that genetic diversity and allelic reduction occurred over time in Chinese cultivars. Among the sub species of rice, *indica* was found to be more diverse than *japonica* (Zhang *et al.* (1992). Frequent mico-mutations in nucleotide bases may be involved in an increase of this genetic diversity.

7. Tomato

Different authors have shown high genetic diversity in land races from diverse regions (**Table 8**). Yi *et al.* (2008) indicated high genetic diversity among various land races which arose due to the diverse cultural groups in Myanmar. In comparison with commercial cultivars, Carelli *et al.* (2006) noted that land races contained high genetic diversity. However, it was also noted that this rich cultural diversity might be threatened if these land races were to be substituted by uniform and high-yielding hybrids (Yi *et al.* 2008). In order to conserve genetic diversity, land races can be used to expand the genetic diversity of commercial cultivars. Villand and Skroch (1998) compared old and new world accessions; new world accessions had higher genetic diversity

than old world accessions. The authors suggested the careful introduction of new world accessions and partially substituted with old world accessions to enhance genetic diversity.

8. Sugarcane and potato

In case of vegetatively propagated species such as sugarcane and potato, there are many studies indicating low genetic diversity in cultivated germplasm (**Table 9**). However, only a few studies have shown significant genetic diversity in wild germplasm (Lu *et al.* 1994; Nair *et al.* 1999; Lima *et al.* 2002; Nair *et al.* 2002). Lu *et al.* (1994) estimated high genetic diversity in *S. spontanum*, but lower in *S. officinarium*. Similarly, Lima *et al.* (2002) also indicated high genetic diversity in 79 cultivars produced by interspecific crosses. Therefore, in order to expand genetic diversity of vegetatively propagated material, interspecific crossing should be carried out.

9. Sorghum

In sorghum (*Sorghum bicolor*), reports on the losses of genetic diversity due to plant breeder activity have been reported (**Table 10**). For instance, Jordan *et al.* (1998) showed that genetic diversity was lowered due to development of resistant hybrids; repeated use of similar parents, linkage drag and genetic drift further aggravated the situation. Loss of genetic diversity in land races was also indicated (Casa *et al.* 2005). Land races captured 86% of the genetic diversity in wild species. However, reports from various parts of the world are also available showing the presence of high genetic diversity in germplasm (Menkir *et al.* 1997; Ghebru *et al.* 2002). Menkir *et al.* (1997) found

Table 8 Status of genetic diversity in tomato (*Lycopersicon esculentum* L.).

Reference	Marker	Plant material	Genetic distance	Diversity
Villand and Skroch 1998	41 RAPD	96 accessions Old vs. New World	-	New and Old World accessions were genetically diverse Accessions from new world were genetically diverse *L. esculentum* and its sub-species, *L. esculentum* var. *cerasiforme*, were distinct but have similar levels of diversity.
Archak *et al.* 2002	42 RAPD	27 tomato cultivars	Average genetic distance (Jaccard coefficient, 1908) (0.18)	Genetic diversity decreased during 1990s due to trends for breeding uniform fruit characteristics Genetic diversity during 1970s was high
Pawlowski *et al.* 2005	Proteomics	19 varieties of tomato	-	DNA polymorphism was low Higher protein polymorphism for wild varieties
Carelli *et al.* 2006	20 RAPD	35 Brazilian accessions Land races vs. commercial cultivar	Average genetic dissimilarity (Jaccard coefficient, 1908) within land races and commercial cultivar (0.35)	Genetic differentiation among the land races and commercial cultivar Land races were more diverse
Yi *et al.* 2008	27 SSR	87 land races	Average genetic distance (Nei 1973) (0.72)	High genetic diversity among land races due to diverse cultural groups Uniform and high yielding hybrids may threaten genetic diversity
Albrecht *et al.* 2010	SSR	*S. lycopersicoides* and *S. sitiens* population	-	Self-incompatible populations of *S. lycopersicoides* and *S. sitiens* were relatively less diverse than the wild allogamous tomato *Solanum chilense*
Mansour *et al.* 2010	IRAP, ISSR and RAPD	10 modern commercial varieties	-	All 10 varieties could be clearly differentiated in dendrograms although the resulting genetic distances and clusters differed depending on the marker system used.

Abbreviations: **RAPD**, randomly amplified polymorphic DNA; **SSR**, simple sequence repeat; **RFLP**, Restriction fragment length polymorphism **ISSR,** non anchored inter simple sequence repeats; **IRAP,** inter retrotransposons amplified polymorphism

Table 9 Genetic diversity studies in crops propagated through vegetative seed (sugarcane and potato).

Reference	Marker	Plant material	Genetic distance	Genetic diversity
Sugar cane				
Lu *et al.* 1994	RFLP	*S. officinarum* *S. spontaneum*	-	Narrow in *officinarum* High in *spontanum*
Nair *et al.* 1999 Nair *et al.* 2002	12 RAPD 25 RAPD	*S. officinarum*; *S. sinense* *S. spontaneum*; *Erianthus* spp. 28 Indian cultivars	Genetic distance was calculated using coefficient of Jaccard (1908) Pre 1960s (0.30) 1960s (0.24) 1970s (0.34) 1980s (0.28)	Narrow in *officinarum*
Jannoo *et al.* 1999	12 RFLP	53 clones 109 cultivar	Genetic distance (Dice 1945; Nei and Li 1979) between (0.43) and within (0.41) various group of cultivars Genetic distance among accessions belonging to various geographical regions Gyneology (0.44) P. New Guinea (0.43) Indo Island (0.45) Pacific (0.48)	Non random distribution Cultivated germplasm captured most of the genetic diversity
Lima *et al.* 2002	AFLP	79 cultivars (interspecific hybrid) *S. officinarum* *S. sinense* *S. barberi*	Jaccard coefficient (1908) (0.53)	High genetic diversity
Hemaprabha *et al.* 2007	18 STMS (Sequence Tags Microsatellite site)	54 Indian genetic stocks Hybrids, inbreds, mutants, somaclones	Genetic distance (Coefficient of Jaccard 1908) Commercial hybrids (0.46) Inbred lines (0.15) Soma clones (0.04)	High genetic diversity
Kawar *et al.* 2009	40 RAPD	17 Indian cultivars	Average genetic distance (Coefficient of Jaccard 1908) (0.13)	Low genetic diversity
Khan *et al.* 2009	21 RAPD	20 accessions	Genetic distance was calculated according to (Nei 1978) (0.39)	Low genetic diversity
Potato				
Elameen *et al.* 2008	10 AFLP	97 Sweet potato (*Ipomoea batatas* L.) accessions	Genetic distance (DICE coefficients, 1945) (0.29) Genetic variation within regions (0.96), between regions (0.04)	Low genetic diversity Low genetic distance between regions 13 accession capture 97% of genetic diversity
Fu *et al.* 2009	36 SSR	114 Canadian cultivar vs. 55 exotic cultivar	Average genetic dis-similarity (0.28) Genetic variation between Canadian vs. Exotic cultivars (0.06) Among vs. within countries (0.21) Existing vs. New germplasm (0.18)	Exotic germplasm slightly more diverse than Canadian germplasm Early varieties were diverse than recent one.

Abbreviations: **AFLP**, amplified fragment length polymorphism; **SSR**, simple sequence repeat; **RAPD**, randomly amplified polymorphic DNA; **RFLP**, restriction fragment length polymorphism; **STMS**, sequenced tagged microsatellite site

Table 10 Reports of genetic diversity in sorghum (*Sorghum bicolor*).

Reference	Marker	Plant material	Allelic		Genetic distance	Diversity
			Losses	Gains		
Menkir *et al.* 1997	RAPD	190 accessions	-	-	-	86% of genetic variation among the accessions 14% among races 13% of variation was attributable to geographical origin
Jordan *et al.* 1998	23 RFLP	26 grain sorghum from Australia	-	-	Average genetic distance (Nei and Li 1979) (0.14)	Narrowed due to development of resistant hybrids, repeated use of same elite parent lines, linkage drag and genetic drift
Ghebru *et al.* 2002	15 SSR	28 Eritrean land races	Eritrean vs. World Collection Total shared alleles =118 Eritrean unique = 70 World Collection unique = 23 Total alleles = 211		Genetic distance (Nei 1987) Eritrean Land races (0.14) Degree of differentiation (Reynolds *et al.* 1983) Eritrean vs. world (0.59)	High level of genetic diversity in germplasm
Casa *et al.* 2005	98 SSR	104 accessions 73 land races 31 wild type	-	Yes	Genetic diversity was calculated as (Liu and Muse 2002) Land races (0.51); Cultivated races (0.51) Wild type (0.59); Kafir (0.29); Caudatum (0.45); Durra (0.48); Guinea (0.46)	Land / cultivated races captured 86% of the total genetic diversity of wild
Ali *et al.* 2008	41 SSR	70 sorghum line	-	-	Gene diversity index (0.40)	High genetic diversity
Deu *et al.* 2010	28 SSR	Sorghum population analysis from 1976-2003 in Nigeria	10%	23%	Genetic diversity (Nei 1987) 1976 (0.60) vs. 2003 (0.62)	Farmer management preserved genetic diversity No changes in genetic diversity over time

Abbreviations: **RAPD**, randomly amplified polymorphic DNA; **RFLP**, restriction fragment length polymorphism; **SSR**, simple sequence repeat

that much of the genetic variation was concentrated in cultivated germplasm. Ghebru *et al.* (2002) also found high genetic diversity in land races. The role of the farmer in the management or preservation of genetic diversity was elucidated by Deu *et al.* (2010), who found that genetic diversity was preserved over time in farmers' field. In conclusion, sorghum genetic diversity has been reduced in cultivated germplasm. However, there are still areas or breeding programs, which have maintained high genetic diversity.

10. Wheat (*Triticum spp.*)

Wheat is an important cereal and staple crop of Asia. Wheat has been the subject of genetic diversity by many authors working in various regions. Analyses of these reports have shown that wheat genetic diversity is low in many parts of the world (Fu *et al.* 2005; Roussell *et al.* 2005; Fu *et al.* 2006; Hai *et al.* 2007; Fu and Soomers 2009). On other hand, many studies have indicated that this decline was temporal (Reif *et al.* 2005b; Christiansen *et al.* 2002; Warburton *et al.* 2006; see in detail **Table 11**). These studies showed that wheat genetic diversity was not constant during various decades of the 20th century. However, wheat genetic diversity increased after the 1990s (Reif *et al.* 2005b; Warburton *et al.* 2006). This may be due to increased breeder awareness about the issue of genetic diversity, better methodologies to estimate genetic diversity, utilization of diverse parents and better breeding methodologies in wheat. Studies have also identified some regions (Argentina, Austria, India, UK, etc.) where genetic diversity was maintained (Manifesto *et al.* 2001; Khlestkina *et al.* 2004b; Donini *et al.* 2005; Balyan *et al.* 2008). In comparison to wild or land races, cultivated germplasm showed some allelic losses. However, they were substituted by newer ones, showing an overall negligible effect on genetic diversity (**Table 11**). The decline in wheat genetic diversity occurred but was separated by spatial and temporal intervals. It is likely that wheat genetic diversity may be enhanced in coming decades due to utilization of diverse parents in developing segregating generations, wild relative for constitution of synthetic wheat. Furthermore presence of efficient and reliable

molecular marker system would help to rapidly evaluate the breeding material for genetic diversity.

PLANT INTRODUCTION

A basic tool for plant breeders is to introduce different plant species from different geographical areas into a new environment (Singh 2004). The aim of the introduction is to directly release a variety in a new area or to widen the genetic variability among the existing plant breeding stock (Veteläinen *et al.* 1996). Li *et al.* (1998) indicated that the use of introduced germplasm in breeding programs is much more important than the direct release of introduced material for cultivation. The future of plant breeding depends on the utilization and conservation of plant genetic resources and it is obligatory for plant breeders to use plant genetic resources to improve mankind's condition (Wilkes and William 1983).

Core collections and germplasm samples

To make efficient use of large germplasm collections and *ex-situ* conservation, it is necessary to have a representative sample of germplasm without losing genetic diversity from within groups of accessions defined by species, subspecies, and geographic origin. An unrepresentive core sample would result in the loss of genetic diversity and may change allele frequency due to genetic drift. When a set of a core collection has to be formed, accessions are classified into various clusters. Then selection is carried out within each cluster to constitute the core sample with the objective to maintain genetic diversity within species (Franco *et al.* 2005). Various methods have been proposed to constitute a core collection such as D, LD and NY methods (Franco *et al.* 2005). These methods provide selection criteria to determine the number of accessions from each cluster. The number of accessions that may be selected from each cluster is dependent on the allocation method. For instance, the number of accessions selected per sample in the D method will depend on the mean Gower's distance between accessions within the cluster. The logarithm of the cluster size (L

Table 11 Genetic diversity in wheat (*Triticum* spp.).

Reference	Marker	Plant material	Allelic		Genetic distance	Genetic diversity
			Losses	Gains		
Manifesto *et al.* 2001	10 SSR 4 AFLP	105 Argentine cultivar			Genetic distance (Weir 1996) <1969 (0.51) 1970-79 (0.49) 1980-89 (0.52) 1990-95 (0.50)	Maintained
Christiansen *et al.* 2002	47 SSR	75 Nordic cultivars	Yes	Yes	Genetic diversity estimates (Nei 1987) 1910s (0.34), 1920s (0.48), 1930s (0.64), 1940 (0.50), 1950s (0.53), 1960s (0.32), 1970s (0.48), 1980s (0.40), 1990s (0.50)	Increased (1900-1940) Narrowed (1941-1969) Increased (1970-1990s)
Khlestkina *et al.* 2004	24 SSR	256 Cultivated wheat (Europe-Asia) released during 50 year	34% (Europe) 40% (Asia)	116% 28%	Genetic distance (Anderson *et al.* 1993) Austria 1922-32 (0.53) vs. 1982 (0.59) Albania 1941 (0.71) vs. 1994 (0.62) India 1937 (0.72) vs. 1976 (0.72) Nepal 1937 (0.68) vs. 1971 (0.61)	Maintained
Fu *et al.* 2005	28 SSR	75 Canadian	91% 41% 41% 60% 95% 114% 63%	24% 45% 41% 40% 24% 17% 31%	Genetic diversity estimates (DICE, SMC and Jaccard) for various Canadian wheat breeding programs Introductions (0.56) CDC (Saskatoon) (0.36) CRC (Winnipeg) (0.44) ECORC (Ottawa) (0.49) SPARC (Swift Current) (0.46) LRC, LBRC, SRF (0.45) UOA (Edmonton) (0.47) APAU, SWP, REF (0.47)	Reduced
Reif *et al.* 2005	90 SSR	253 CIMMYT Cultivar Land races *T. Tauschii*	20% in Land races 30% in modern cultivar		*T. tauschii* (0.70); Land races (0.58) Modern wheat cultivar (0.58)	Narrowed (1950-1989) Enhanced (1990-1997)
Rousell *et al.* 2005	39 SSR	480 cultivars (15 Diverse European geographical area) 1840-2000	-	-	Mean diversity index (Nei 1973) was (0.65) Analysis of molecular variance Mean between geographical region variations (7.75%) Within geographical region variations (92.5%)	Non-random distribution linked to geographical area
Fu *et al.* 2006 Fu and Soomers 2009	37 e-SSR 370 SSR	cultivars (1845-2004)	0% 4% 16% 15% 20% 15%	0% 15% 20% 19% 22% 25%	Analysis of molecular variance Pre 1910 (0.28) 1910-1929 (0.34) 1930-1949 (0.27) 1950-1969 (0.29) 1970-1989 (0.27) 1990-2004 (0.26)	Reduced
Warburton *et al.* 2006	40 SSR	CIMYT improved lines 1980s Land race CIMYT improved lines 2000s	-	-	Genetic diversity (Shanon 1948 diversity indexes) Land races (4.53) 1950-1966 (4.25) 1967-1974 (4.37) 1975-1982 (4.27) 1983-1989 (4.29) 1990-1997 (4.34) 2002-2003 (4.44)	Narrowed 9.35% (1950-1980s) Increased (1990-2000s)
Donini *et al.* 2005	12 SSR	UK cultivars (1930s) UK cultivars (1990s)	NO	NO	SSR allele variation vs. state of morphological characters Early 1930-1950 (1.64) vs. (2.02) Intermediate 1960-1970 (1.79) vs. (2.36) Late 1980-1990 (2.36) vs. (3.25)	Morphological characteristics give similar picture to that of satellite markers
Hai *et al.* 2007	52 SSR	69 accessions	-	-	Average gene diversity (Nei 1978) Austria/Switzerland (0.63) Czech Republic (0.37) Spain/Portugal (0.62) France/Germany/Netherlands (0.55) Norway/Sweden (0.51) UK (0.41)	Non-random distribution linked to geographical area
Huang *et al.* 2007	42 SSR	511 wheat (Central-Northern Europe)	No	Few	UK varieties (0.54) vs. European (0.63)	Narrow (1940s) Increased (1950-1990s)
Balyan *et al.* 2008	42 SSR	134 Indian cultivar (1910-2006) Pre and Post green revolution era	0%	25%	Gene diversity Pre-Green Revolution (0.63) vs. Post-Green Revolution (0.65)	Unchanged

Table 11 (Cont.)

Reference	Marker	Plant material	Allelic		Genetic distance	Genetic diversity
			Losses	Gains		
Hysing *et al.* 2008	5 S-SAP	198 Nordic wheat cultivars (1800-2000)	-	-	Gene diversity (Nei 1973) 　　　(1910)　(1910-1969)　(1970-2003) Sweden　(0.21)　　(0.19)　　　(0.22) Norway　(0.14)　　(0.11)　　　(0.21) Denmark (0.17)　　(0.10)　　　(0.22) Final　　(0.14)　　(0.17)　　　(0.19)	Decreased (1900-1960s) Increased (1970-2003)
Ganeva *et al.* 2009	14 SSR	102 Bulgarian land races 9 Bulgarian cultivars 25 introduced	-	-	Gene diversity (Liu and Muse 2005) Bulgarian land races (0.53) Bulgarian cultivar (0.51) Introduced cultivar (0.53)	Bulgarian cultivar comprised of low genetic diversity as compared with introduced cultivar; On whole Bulgarian wheat germplasm comprised of low diversity compared to centre of domestication
Prasad *et al.* 2009	62 SSR	60 USDA cultivars	-	-	Gene diversity (Liu and Muse 2005) <1960 (0.50), 1960s (0.53), 19070s (0.41), 1980 (0.57), 1990 (0.60), 2000 (0.57)	Gradual increased since 1970s

Abbreviations: **AFLP**, amplified fragment length polymorphism; **SSR**, simple sequence repeat; **e-SSR**, expressed single sequence repeat; **SSAP**, sequence-specific amplified polymorphic

Table 12 Summary of various studies to constitute the core collections.

Reference	Method	Plant material	Core size
Diwan *et al.* 1994	Intra specific phenotypic cluster analysis	*Medicago* species 1270 accession	211 accessions
Franco *et al.* 1999 Franco *et al.* 2006	Comparison of various sampling intensities/method	500 stratified random sample 20 stratified random sample	10% sample intensity was found sufficient D method produced samples with more genetic diversity
Taba *et al.* 1998	Phenotypic diversity cluster analysis	249 maize accessions	Upper 20% of accessions representing phenotypic diversity were selected
Upadhyaya *et al.* 2001	13 quantitative traits; clustering by Ward's method	991 chick-pea accessions	Random selection of 10% of the accessions from each cluster was found sufficient to preserve genetic diversity.
Holbrook *et al.* 1993	4 morphological traits	7432 peanut accessions	10% random selection from each cluster, origin of country yielded a core representative sample of 839 accessions.
Xu *et al.* 2004	113 RFLP and 714 SSR molecular marker	236 rice accessions 125 USA cultivars 111 world collection	31 cultivar constituted a core sample accompanying 95% RFLP and 74% SSR alleles
Hao *et al.* 2006	78 SSR	340 wheat accessions	Size of sample should be more than 4% to include 70% of the variation.
de Oliveira Borba *et al.* 2009	86 SSR	242 rice accessions	10% accessions were selected to constitute a mini core sample of 24 accessions.
Pessoa-Filho *et al.* 2010	16 SSR	699 rice accessions	18% core collection contained more than 84% of the genetic variation.

method), while the product of the cluster size × the mean Gower distance (NY method), and the product of the logarithm of the cluster size × the mean Gower distance (LD method). The efficiency of the allocation method may be compared on the basis of several methods such as genetic diversity of the samples, recovery of the range of variables in the sample, and variance of the samples. This efficiency varies depending on the population in which stratified samples were drawn (Franco *et al.* 2005, 2006). In addition, molecular markers were also used to constitute the core sample (Xu *et al.* 2004).

Skinner *et al.* (1999) indicated that accessions representing the extremes could easily be added to the core collection. Furthermore, traits showing a strong relationship with yield may only be determined during future germplasm evaluation. Generally core samples, constituted by using 10% of the total plant materials, were found to be sufficient (**Table 12**).

Utilization of introduced germplasm

Plant breeders have utilized introduced germplasm to achieve various breeding objectives such as induction of early maturity, resistance to biotic and abiotic stresses, cytoplasmic male sterility source and food quality (Boubaker and Yamada 1995; Adugna 2007; Rauf and Sadaqat 2007; Rauf and Sadaqat 2008a, 2008b). Adugna (2007) reviewed

the possible utilization of introduced germplasm and indicated that germplasm was used in the improvement of disease tolerance, induction of early maturity and uncovering the high yield potential of sorghum. Ceccarelli *et al.* (1992) studied the current and future contribution of plant genetic resources and indicated that genetic erosion can be curtailed by the germplasm collection and preservation. Furthermore, Thompson and Nelson (1998) also concluded that exotic germplasm may be used to expand the genetic diversity and yield of indigenous germplasm.

Veteläinen *et al.* (1996) studied the usefulness of introduced plant germplasm of barley (*Hordeum vulgare*). The germplasm was used to study variation in agronomic traits among land races, elite cultivar and related species. The best sources for earliness were elite cultivar and landraces. Mean straw length was greatest in related wild species. Number of ears per plant was quite similar in all groups. The highest 1000-kernel weight was among landraces and the elite cultivar. Hybrids from the complex crossing between land races and elite cultivar resulted in exceeded earliness and 1000-kernel weight. It was concluded that new valuable variation was introduced in barley breeding material. Similarly, Rauf and Sadaqat (2007) evaluated introduced cultivated germplasm of sunflower in Pakistan and indicated significant genetic variation for drought tolerance in sunflower. In lentil, the introduction of ILL 4605, an early, large-seeded line, has resulted in its release as 'Man-

serha 89' for wetter areas of Pakistan. It is also now been used as a parent in breeding programs (Erskine *et al.* 1998).

Plaisted and Hoopes (1989) studied the result of several introductions in potato germplasm with the aim of widening the genetic variability in the existing germplasm in North America. Introduction from Europe during the 19th century resulted in evolution of elite potato cultivars. Similarly, utilization of wild species resulted in the evolution of many new disease resistant varieties. It was shown that unrestricted movement of potato germplasm resulted in the accelerated introduction of the plant material. However, it was concluded that only extensive screening for valuable traits would make introduced germplasm more feasible and productive.

1. Genetic diversity and germplasm introduction

Studies indicated that effect of germplasm introduction appeared both in term of increasing and decreasing genetic diversity. Mantegazza *et al.* (2008) indicated significant genetic diversity in rice gene pool and was correlated with the development of new cultivars and introduction from abroad, without substituting previous accessions. Similarly, Steele *et al.* (2009) also found that partial introduction of modern rice varieties without much disturbing the local land races increased the rice genetic diversity. Hysing *et al.* (2008) also showed that loss of plant diversity was over came by time to time introduction of foreign wheat germplasm, therefore there was over all little effect of plant selection on genetic diversity. Cui *et al.* (2000) noted that introduction of new germplasm into applied Chinese breeding was key factor for the broad genetic base of soyabean (*Glycine max*) cultivars.

Global exchange of genetic material resulted in the sharing of common genes over vast areas. For example, cereals are globally related to each other for the dwarfing genes. Reif *et al.* (2005b) showed that wheat genetic diversity has been significantly reduced from 1950–1989. This may be due to development of better selection techniques, trend for the introduction of dwarfing genes in the global germplasm. Routray *et al.* (2007) indicated that all the wheat cultivars after the introduction of high yielding dwarf wheat varieties from CIMMYT, clustered together and showed very low genetic distance within cluster while pre-green revolution indigenous varieties formed another cluster along with the landraces. The landraces had higher diversity for HMW-glutenin, glume color, awnness and grain color. Some of the landraces were resistant to yellow rust (*Puccinia striiformis*) and powdery mildew (*Blumeria graminis*). Kuleung *et al.* (2006) indicated that varieties belonging to different countries of origin grouped in the same cluster. This was attributed due to exchange germplasm exchange among breeding programs.

In summarizing the above discussion it may be concluded that introduction of plant material was beneficial when it added up or partially substituted the local germplasm in non-core areas of field crop.

2. Introduced species as a source of genetic pollution

Introduced plant species sometimes become major pests in the foreign environment. For example, *Lantana camara* (lantana or "Ham 'n Eggs") was introduced in the subcontinent for aesthetic value but it became noxious weed in the field (Raghubanshi *et al.* 2005). Similarly, *Eucalyptus* spp. were introduced to overcome the water logging in the agriculture farms and wood shortage problem. Due to its luxurious growth and freedom from diseases and insect attack, it has become threat for the native tree species in Pakistan (Altaf and Zarif 2003). Furthermore, their plantation as a shelterbelt in the agriculture was also reported to decrease the yield due to competition with crop species (Onyewotu *et al.* 1994). There are two hypotheses regarding the conversion of introduced specie to become a pest (Mitchell and Power 2003). The enemy release hypothesis states that in-

vaders' impacts result from reduced natural enemy attack. Kunwar (2003) indicated that the species may invade and thrive in foreign ecosystem due to absence of its natural enemies and allelopathic effects of competitive plant species. Therefore, introduced plants often become noxious weed in other ecosystem. Mitchell and Power (2003) indicated 84% fewer fungi and 24% fewer virus species infect each plant species in its natural range than in its native range thus supporting enemy release hypothesis.

The second hypothesis relates to the biotic resistance which argues that interactions with native species, including natural enemies limit invaders' impact. According to this hypothesis, species accumulating more pathogens in their naturalized range are less widely noxious (Mitchell and Power 2003). Many of the crop species such as sunflower, citrus, tomato and cotton have been introduced from the American continent in the subcontinent during early or mid-20th century. These crops have low biotic resistance and accumulated more pathogenicity in the diverse environment of Indian subcontinent, supporting second hypothesis. As a result, species are susceptible to large number of pest and require extra-ordinary efforts for their successful cultivation. Upland cotton was introduced from the USA in the early 20th century and is invaded by large number of pest species. On the other hand native species, *G. arboreum* is resistant to the pests (Stanton *et al.* 1992; Jindal *et al.* 2007; Nibouche *et al.* 2008; Sacks and Robinson 2009).

PLANT SELECTION

Selection is the differential reproductive rate of genotypes due to some external force. A selection pressure may be posed by natural biotic and abiotic factors collectively called as natural selection. It may also be practiced by the humans called as artificial selection. Artificial selection may further be categorized into *in vivo* and *in vitro* selection. *In vivo* is the primitive method of plant selection in which plants are mostly selected on the basis of their appearance, the phenotype, while *in vitro* selection techniques were evolve during mid of 20th century and are more targeted. *In vitro* selections are usually carried out at cellular or molecular levels (Xu and Crouch 2008). Natural selection usually leaves more heterogeneous population with broad genetic variability and adaptability while artificial selection results in more uniform population with improved economically important traits and low genetic base. A prerequisite for the selection to act upon is the presence of genetic variability in the breeding stock. Furthermore, type of genetic variability and heritability will also affect the efficiency of selection (Rauf *et al.* 2008c, 2009).

1. Domestication, the first outcome of plant selection

Primitively, man selected the plant types that were better suited to his need in an unsystematic way. Domestication was the first outcome of this selection. McCouch (2004) indicated that during the process of domestication selection for unusual phenotypes, such as large fruit or seed size, intense color, sweet flavor, or pleasing aroma was carried out. Similarly, synchronous ripening or inhibition of seed shattering was also selected to facilitate harvest. Land races originated as a result of domestication.

Epimaki *et al.* (1996) showed that domestication of common bean was achieved rapidly (provided that genetic diversity and selection intensity were high) and evolution was proceed through changes involving a few genes with large effect rather than through a gradual accumulation of changes with small effects. This hypothesis was supported by the molecular studies in other crops indicated few genes involved during domestication. Simons *et al.* (2006) indicated that the *Q* gene was responsible for the domestication of wheat; it showed free threshing character. It also pleiotropically influenced many other domestication related traits such as glume shape and tenacity, rachis fragility, spike length, plant height, and spike emergence time. Similarly,

qSH1 gene was responsible for the loss of seed shattering in rice. It encoded a BEL1-type homeobox gene which caused loss of seed shattering due to the absence of abscission layer formation (Konishi *et al*. 2006). Two genes i.e. *zfl1* and *zfl2* of major effects were identified in maize. They were known to important during domestication and produced whorled organs during flowering development. However in sunflower domestication related traits were known to control by numerous alleles in contrast to the single gene with major effects in other crops (Wills and Burke 2007).

2. Effect of domestication on genetic diversity

Several reports are available regarding the reduction of genetic diversity during the domestication (Sonnante *et al*. 1994; Hollingsworth *et al*. 2005; Reif *et al*. 2005).

Reif *et al*. (2005b) showed that loss of genetic diversity occurred during wheat domestication. The loss of genetic diversity occurred from wild species *Triticum tauschii* to the land races and from land races to elite cultivar. Similarly, Haudry *et al*. (2007) also noted that wheat genetic diversity was reduced in cultivated form by 69% in bread wheat and 84% in durum wheat during the process of domestication. Loss of genetic diversity during domestication has also been reported in other species (Hollingsworth *et al*. 2005). Hollingsworth *et al*. (2005) compared domesticated and natural populations of a fruit tree (*Inga edulis*) and showed significant loss of allelic diversity (from 39.3 to 31.3) during domestication. In cotton, Iqbal *et al*. (2001) indicated severe loss of genetic diversity due to selection pressure of domestication. Sonnante *et al*. (1994) also noted losses of genetic diversity during the process of domestication in common beans (*Phaesolus vulgaris*).

3. Effect of mass/bulk selection on genetic diversity

Lu *et al*. (2008) compared the effect of two selection methods (mass selection and half-sib family combining selection) on genetic diversity. It was shown that mean genetic distance changed slightly after mass (MS) but decreased in a greater magnitude after half sib selection in all the populations under study. Analyses on the distribution of genetic distances showed that the ranges of the genetic distance were wider after MS and most of the genetic distances in populations developed by half selection were smaller than those in both the basic populations. The number of genotypes increased after MS but decreased after HS-S3 in all the populations. Cui *et al*. (2000) also mentioned that in order to keep the broad genetic base of soybean, the population were never submitted to half or ful sib selection.

Jana and Khangura (1986) evaluated the effectiveness of bulk method for preserving genetic diversity. A decrease in genetic variability for all agronomic traits was reported after examining the early and advanced bulk population at different sites. Butrón *et al*. (2005) showed that genetic diversity was reduced in bulk population during the selection process but not significantly.

4. Recurrent selection

Labate and Lamkey (1997) showed the effect of twelve cycle of recurrent selection in two population Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic #1 (BSCB1) The BSSS and BSCB1 progenitor populations were initially genetically similar (Nei's genetic distance = 0.07). After 12 cycles of selection, they substantially diverged (Nei's distance = 0.66). Within both populations, the polymorphism level decreased from about 99 to 75%, and gene diversity decreased from about 0.6 to 0.3 between P and C12. The mean number of alleles per locus dropped from about four to less than three. Vilela *et al*. (2008) also showed that there was significant differentiation between the original and recurrent populations obtained after three cycle of selection. However, there was non-significant variation in genetic diversity between the base population and

population subjected to few cycles of recurrent selection. They also showed that loss of genetic diversity occurred when fewer plants were selected. Pereira *et al*. (2008) also came to the same conclusion when they analyzed maize population through isozyme markers.

Liu *et al*. (2006) compared wheat gene pool (*Triticum aestivum* L.) derived through recurrent selection with 30 donor parents. It was shown that there were no significant differences between gene pool and 30 parents for genetic diversities. It was further suggested that the gene pool is improved after several cycles of selection, while genetic variation is still maintained. Therefore, the gene pool is suitable for further breeding program. In *Avena sativa* L. recurrent selection reduced the genetic diversity. However, reduction in genetic diversity did not affect selection gains (DeKoeyer 2008).

Pinto *et al*. (2003) studied the effect of modified recurrent selection on genetic diversity in maize populations. Effects appeared in terms of reduction in the number and frequencies of alleles. The genetic differentiation between the synthetic population and original population increased to 77%. However, despite the high level of selection, the total gene diversity found in the synthetics was enough and allowed new cycle of reciprocal recurrent selection.

Yuan *et al*. (2008) compared the effects of two methods i.e. recurrent selection and pedigree selection on genetic diversity. Although genetic variation declined gradually (from 0.21 in C0 to 0.15 in C3) with the advance of selection cycles but the decline was not statistically significant. Breeding lines obtained from recurrent selection were more genetically diverse than lines from pedigree selection. It was suggested that base populations derived from recurrent selection could provide a wider genetic variation for selection of breeding lines with more broad genetic bases.

5. Participatory plant breeding or decentralized plant breeding

Participatory plant breeding (PPP) involves plant breeders, farmers or consumer for the development of crop varieties (Sperling *et al*. 2001). In PPP genetic variability is generated by plant breeders while selection is carried out jointly by the farmer, extension specialist and breeders. Testing, selection and seed multiplication of breeding material took place at farmer field rather than at research station (Ceccarelli and Grando 2007). The product of participatory plant breeding is improved, location-specific and heterogeneous varieties (Dawson *et al*. 2008).

Different authors indicated that decentralized breeding, specific local adaptation, and intra-varietal diversity is advantageous from an ecological point of view (Berg 1999; Dawson *et al*. 2008). Studies have showed the worth of participatory plant breeding practices for the evolution of varieties rich in allelic diversity (Joshi and Witcombe 2003; Phillips and Wolfe 2005; Dawson *et al*. 2008). Tiemens-Hulscher *et al*. (2006) compared the participatory and conventional breeding methods. It was shown that participatory plant breeding resulted in early maturing, diseases resistant and good keeping quality traits while conventional methods evolved genotype with only improved keeping quality of onion. Sthapit *et al*. (1996) involved farmer for selection in the segregating material of rice at F_5 stage. The variety evolved as a result of this selection performed much better than the products from conventional centralized breeding system. Witcombe *et al*. (2003) described the outcome of participatory plant breeding in maize. Maize variety GM-6 was evolved as result of the selection by plant breeders and farmers. The variety yielded 18% more yield at the research station and 28% more at the farmer field as compared to the control. The quality of this variety was much better than land races. It was also concluded that participatory plant breeding was much cheaper and realized variety earlier than conventional breeding methods.

Studies have showed the worth of participatory plant breeding practices for the evolution of varieties rich in

allelic diversity (Joshi and Witcombe 2003; Phillips and Wolfe 2005; Dawson *et al.* 2008). Witcombe *et al.* (1996) reviewed the long-term effect of participatory varietal selection and effect of participatory selection is to increase biodiversity, but where indigenous variability is high it can also reduce it. Patto *et al.* (2008) analysed several selection cycles for 20 years period, of a Portuguese on-farm participatory maize OPV-'Pigarro' breeding project. No significant differences in allelic richness or inbreeding coefficient (f) were detected among the selection cycles. The results showed that although an allele flow took place during the on-farm selection process but the level of genetic diversity was not significantly influenced. It was suggested that on-farm breeding projects should be taken up to preserve unique accession.

6. Participatory plant breeding and on-farm germplasm conservation

Another benefit of participatory plant breeding is on farm preserving of genetic diversity. Several author(s) have shown the worth of on-farm preserving of genetic diversity (Lioi *et al.* 2001; Bellon *et al.* 2003; Deu *et al.* 2010). Deu *et al.* (2010) showed that farmer management preserved the genetic diversity in Sorghum. Similarly, Lioi *et al.* (2005) also stressed the need to involve the farmer for further improvement of common beans and to preserve the genetic diversity. Bellon *et al.* (2003) carried out the study to determine the identification of crop populations suitable for preserving genetic diversity along with it also serve the purpose of farmer in maize (*Zea mays* L.). The 17 landraces were selected from an initial collection of 152. These populations full fill both criteria.

However, Morin *et al.* (2002) showed that on-farm genetic diversity was threatened by various environmental hazards such as drought, which significantly reduced on-farm genetic diversity during 1996-1998.

Hybridization

Hybridization is a natural phenomenon and is a source of new allelic combinations. With the discovery of flower as reproductive organ in plants, human learnt the art of controlling the hybridization. But systematic hybridization for varietal improvement only started after the formulation of Mendelian principles. Hybridization between the genotypes may be spontaneous or induced in nature. Both types of hybridization have been found difficult to achieve between the species or generic level. Therefore, extra ordinary techniques such as embryo rescue are required to hybridize the domestic crop with a very distant wild relative (Duvick 2005). Transgressive segregation as a result of hybridization leads to the evolution of improved varieties.

1. Impact of hybridization on genetic diversity

Hybridization is practiced to introduce new allelic combinations or to exploit the trangressive segregation in latter generation following crosses. In many cases, intra specific hybridization was found to lower the genetic diversity when it was attempted to exploit the trangresssive segregation (Van Esbroech and Bowman 1998; Jordan *et al.* 1998; Cui *et al.* 2000). Van Esboroech and Bowman (1998) concluded that plant breeders have lowered the genetic diversity due to preference for few cultivars to be used as parents in the establishment of trangressive generation. Cui *et al.* (2000) showed that genetic diversity of Chinese soyabean (*Glycine max*) was high due to careful selection of unrelated parents while constituting transgressive segregation.

Hybridization is also attempted to exploit the heterosis. However, exploitation of the heterosis requires rigorous self-pollination to constitute inbred line from open pollinated populations. This step also resulted in the loss of genetic diversity. Details of losses have been given in **Table 5**. Furthermore many studies have also shown the losses of

genetic diversity when few commercial hybrids were used to replace the land races or diverse germplasm (Jordan *et al.* 1998; Yi *et al.* 2008).

2. Genetic diversity as an indicative of hybrid performance and heterosis

Molecular genetic distance was able to establish phylogenetic relationships. The genetic distances may also be correlated with heterosis or yield to predict hybrid performance. A significant relationship may eliminate the need to make large number of crosses to estimate the specific (performance of parents in specific cross combination) combining ability and to pick best heterotic parents. Many studies have been conducted to estimate this relationship. For instance, Liu *et al.* (1999) showed that it is possible to classify wheat (*Triticum aestivum* L.) lines with different plant characteristics into different groups through molecular studies. It was found that these groups were of predictive value for developing superior hybrids. However, genetic distance (GD) based on RAPD markers were not significantly correlated with hybrid performance and heterosis. It appears to be impossible to predict hybrid performance from GD itself. Benchimol *et al.* (2000) also showed that RFLP-based GDs are efficient and reliable to allocate genotypes of maize populations into heterotic groups. However, this marker was poor predictor of performance of crosses between different heterotic groups. Similar results were also obtained in other species such as sunflower; durum wheat; in which it was concluded that genetic diversity was poor predictor of hybrid yield or heterosis (Fabrizius and Busch 1998; Cheres *et al.* 2000; Solomon *et al.* 2007). These results may be explained due to divergence between the parents at particular genetic loci that do not control field-level phenotypic differences (Riday *et al.* 2003). Thus EST based molecular markers may be used to estimate the genetic distance and to derive this correlation.

Marsan *et al.* (1998) also concluded that correlation between genetic distance and hybrid performance in maize was non-significant. However, the correlation between specific genetic distance calculated from AFLP data with specific combining-ability effects for yield was positive and may have a practical utility in predicting hybrid performance. Sarawat *et al.* (1993) also showed absence of correlation between the genetic distance and crosses heterosis or mean performance. However, they were of view that when genotypes with large genetic distance were crossed they produce superior *trans*-segregants.

Contrastingly, Xio *et al.* (1996) concluded that genetic distance based on the SSR and RAPD were useful for predicting yield potential and heterosis of intraspecific hybrids in rice but unable to obtain correlation in interspecific crosses.

3. Interspecific hybridization as source of new genetic diversity in cultivated germplasm

Selection for uniform plant types has exhausted intraspecific variation. Therefore, plant breeders have diverted their efforts for the introgression from wild or related species. However, this type of introgression was not achieved easily and has been limited to few crops. Reif *et al.* (2005) was of view that wheat genetic diversity has been significantly reduced from 1950–1989. However, was enhanced from 1990-1997. It was concluded that plant breeder narrowed the genetic diversity due to selection for uniform type. However, increasing awareness of loss of genetic diversity led them to the introgression from wild species. The loss of genetic diversity occurred from wild specie *Triticum tauschii* to the land races and from land races to elite cultivar. It was recommended that species *T. tauschii* may be utilized to further broaden the genetic diversity. Similarly, Maccaferri *et al.* (2003) showed that genetic diversity in modern durum wheat germplasm increased over time due to introgression from related species. Warburton *et al.* (2006) also

showed that recent efforts by the plant breeders to include synthetic wheat derived from wild species in the breeding program resulted in the significant recovery of genetic diversity. It was shown that recent wheat varieties were not statistically different from land races in diversity. However, yield, quality was significantly higher in recent germplasm. Ginkel and Ogbonnaya (2006) indicated that synthetic wheat (as a result of complex crosses between the *T. durum × Aegilops tauschii*) was crossed with modern wheat to obtain progeny having enhanced tolerance to wheat diseases, abiotic stresses such as drought, heat, waterlogging. Some of the interspecific derivatives have comparable bread wheat quality and even yielded better under stress condition. This introgression also increased wheat genetic diversity. Similar type of strategy was adopted at CIMMYT. More than 100 synthetic wheat lines were developed in the institute, the line showing resistance to the biotic and abiotic stresses were back crossed to bread wheat. Dreisigacker *et al.* (2008) showed that these backcrossed derived lines were superior in yield and contained more diversity for other agronomically important traits.

Wang *et al.* (2008) introgressed small segment of chromosome from *Zea mays* ssp. *mexicana* to cultivated maize through back crossing. Outstanding alien introgression lines were isolated which produced hybrids having 54.6% greater grain yield than that of standard check.

Gupta and Sharma (2007) exploited interspecfic hybridization as a source for widening genetic diversity in lentil. Viable hybrids were produced between *Lens culinaris* ssp. *culinaris × L. culinaris* ssp. *orientalis* and *L. culinaris* ssp. *culinaris × L. culinaris* ssp. *odomensis*. The cultivated lentil × *L. culinaris* ssp. *orientalis* crosses showed substantially higher variability for all the traits than crosses involving cultivated lentil × *L. culinaris* ssp. *odomensis*. The results showed that wild subspecies can be exploited for breeding purposes and their variation can easily be utilized to widen the genetic base of the cultivated lentil.

Zhang *et al.* (2005a) studied the genetic diversity and progress of genetic improvement in the cultivar released from 1926 to 2000. Over the past 75 year of breeding, seed yield and lint yield improved while boll size and seed index were gradually decreased. Fiber strength has been enhanced since the 1960s, which has been accompanied by steady increase in micronaire while fiber length decreased from 31.0 to 30.0 mm from 1960 to 1990. Genetic distance among cotton genotypes ranged from 0.06 to 0.38 with an average of 0.18 on the basis of 189 SSR marker alleles, indicating a substantial genetic diversity among Acala 1517 cotton germplasm. It was concluded that this genetic diversity was due to induction of diversified germplasm for the introgression which led to the continuous genetic gain in Acala cotton cultivar improvement.

Similarly, Thompson and Nelson (1998) also noted that introgression of diverse germplam lead toward greater genetic diversity and selection gains in soyabean. The introgressed lines were significantly superior in term of yield and genetic diversity.

In sunflower, Mohan and Seethram (2005) observed degree of divergence in the lines obtained from interspecific crosses. A limited divergence was observed due to rigorous back crossing to the recurrent parent. In order to keep the high level of divergence it was recommended that increased number of back crosses may be avoided and selection may be practice in BC_1F_2 generation.

4. Spontaneous hybridization as source of genetic pollution

Different studies have made the risk assessment for determining the environment safety of plants with novel traits. It was shown that inter or intra specie hybridization was important in determining the potential risk on ecosystem upon release of genetically modified plants. In sunflower, it was found that introgression of gene was likely to occur from cultivated *H. annuus* into wild *H. annuus* and from wild *H. annuus* with other annual *Helianthus* species. Ureta *et al.* (2008) estimated the hybridization rate using a crop specific isozyme marker, and a mean of 7% progenies were crop-wild hybrids. The nearest wild plants (3 m from the cultivar) showed the highest percentage (18%) of gene flow, which was found to decrease with distance increasing up to 500 m. Therefore, it was recommended that in case of release of transgenic sunflower, this interspecies exchange of genetic information should be considered (Snow 2002; Burke and Reiseberg 2003). Similarly, gene flow from transgenic and conventional crops has also been observed in other species. Zhang *et al.* (2005b) indicated the out crossing for the *tfdA* gene ranged from 10.13% at 1 m to 0.04% at 50 m while for the *Bt* gene range was 8.16% at 1 m to 0.08% at 20 m from the transgenic plants in to the conventional cotton crops. Weekes *et al.* (2007) detected gene flow in 30% of the samples (40 out of 135) at 150 m from the GM source. The gene flow from transgenic maize to nontransgenic was detected at distances up to 200 m from the transgenic source. This spontaneous hybridization may transfer genes from the crops with novel traits to wild species, which may increase the genetic diversity of recipient species, but it may threaten the balance of biodiversity in an ecosystem.

CONCLUSIONS

After examining large number of scientific reports it may be generalized that losses in plant material occurred in a specific order i.e. the highest in elite open pollinated cultivars or inbred lines. Losses of genetic diversity occurred at each step of germplasm transformation. Among various categories of germplasm, wild germplasm and land races showed the highest genetic diversity and thus can contribute toward the broadening of genetic base of cultivated germplasm and or inbred line/hybrids (**Fig. 3**).

Among evaluated plant breeding methods, plant introduction was found to add up the genetic diversity when local germplasm was partially substituted or supplemented by the introduced germplasm. Therefore, genetic diversity in many part of the world was found high due to time to time plant introduction. However, introduction of a new species in an area was also found to cause the genetic pollution.

Plant breeder's selection was found to enhance the genetic differentiation at the expense of genetic diversity. Losses in the genetic diversity were observed when plant populations were subjected to various type of plant selection i.e. domestication during the pre systematic plant breeding era and half or full sib pedigree selection during systematic plant breeding era. The systematic effect of various plant breeding selection methods on genetic diversity in descending order is: participatory plant selection > mass selection ≥ recurrent selection > bulk selection > pedigree selection.

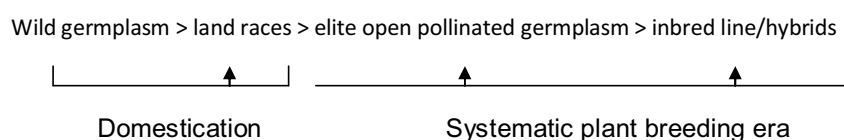Among various plant selection schemes participatory

Wild germplasm > land races > elite open pollinated germplasm > inbred line/hybrids

Domestication   Systematic plant breeding era

Fig. 3 Systematic losses in genetic diversity in various form of germplasm where > means superior in genetic diversity.

plant selection was found the most effective in generating an allelic rich and broad genetic based plant material. Many author(s) also advocated its effectiveness for conserving the genetic diversity at the farm level. Other selection methods such as recurrent, mass or bulk has also least detrimental effect on genetic diversity as compared to pedigree based selection.

Intraspecific hybridization was initially supposed to broaden the genetic diversity. However, contrary to the assumptions intraspecifc hybridization was found to lower the genetic diversity due to utilization of similar type of parents in generating trangressive segregation. Commercial hybrids when substituted the land races or diverse indigenous germplasm also lowered the genetic diversity of the area. In order to broad the genetic base of the plant material, plant breeders released the importance of interspecific hybridization which was done in many crop species with some success.

Transgenics were released as a product of biotechnology, spontaneous pollination between conventional cultivar and wild germplasm may enhance the genetic diversity but on the other hand it may raise the issue of genetic pollution.

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