Chapter 3
Genetic Diversity and Modern Plant Breeding

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Abstract Genome sequence data provide new capabilities to characterize genetic diversity across a comprehensive range of plant germplasm including breeding materials, modern cultivars, landraces, and wild and weedy ancestors. This sequence "language" allows breeders to monitor, help identify, and select for useful diversity thereby developing new improved varieties. Although much genetic diversity in wild ancestral species was not transferred into domesticated species, surprisingly high levels of diversity have been retained during the past century, a period of intensive selection for increased productivity. Diversity in modern varieties exhibits temporal flux associated with bottlenecks due to grain quality or specific introductions of germplasm. There is no evidence over many decades in the twentieth century of a narrowing of the genetic base. Diversity has increased in some crops due to conscious sourcing of landrace diversity. Finding useful diversity to provide successful genotype by environment (G × E) interaction remains both the essential challenge for plant breeders and an assurance that new genetic diversity must continue to be sourced in order to allow continued genetic gain in a dynamic agricultural environment. Plant breeders can never afford to be complacent about stewardship and use of genetic diversity. Trends of genetic diversity

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usage should be regularly monitored in breeding programs and in commercial agriculture.

Keywords Agriculture · Conservation · Cultivar · DNA sequence · In situ · Ex situ · Gene × environment interaction · G × E · Genetic diversity · Genome · Intellectual property protection · Molecular marker · Mutation · Plant breeder · Plant variety protection · Productivity · Utility patent · Yield

3.1 Introduction

The conduct of agriculture creates a mutual codependence for humankind with domesticated animal and plant species (Harlan 1992; FAO 1997, 2010; Zeder 2006; Vaughan et al. 2007; Purugganan and Fuller 2009; Rottenberg 2013). It is vital to practice intelligent management and use of genetic diversity to sustain agricultural productivity (Stuthman 2002). Persistent narrowing of germplasm diversity would inevitably lead to a litany of undesirable consequences including reduced potential to improve crop production, increased susceptibilities to pests and diseases, reduced potential to adapt to changing weather patterns, greater instability in agricultural production, and loss of genetic resources (National Research Council 1972, 1993; FAO 1997, 2010; Brown-Guerdia et al. 2000).

Modern plant breeding has been attributed as contributing to the reduction of genetic diversity in agriculture (Vellve 1992; Clunies-Ross 1995). Most concerns arise from a focus on the initial changeover in cultivation from landraces to "modern" varieties and from comparisons using surrogate data; e.g., numbers of varieties rather than genetic diversity data per se (Meul et al. 2005). Any discussion of genetic diversity in agriculture is meaningless unless productivity gains are also considered (Fig. 3.1). Productivity gains in major US field crops are reviewed in Smith et al. (2014b).

Plant breeding contributes from 50 to 88 % of increased yield production due to genetic gain (Duvick 2005; Mackay et al. 2011; Smith et al. 2014a, b). In Iowa, the contribution of genetic gain to increased productivity was 79 % during 1930–2011 (Smith et al. 2014a). Achievement of genetic gain is dependent upon access to and effective management of genetic diversity contributing to quantity and quality of agricultural production. Future needs for increased productivity contributed by genetic gain and crop management will be very challenging to achieve. For example, the BBSRC (2011) states that: "Total wheat grain production over the next 50 years must exceed that previously produced over the last 10,000 years." It is likely that plant breeders will be called upon to contribute an even greater proportion to improved farm productivity as gains from other inputs plateau or decline. A lack of useful and well-adapted genetic diversity will undermine abilities of plant breeders and farmers to achieve these important societal goals.

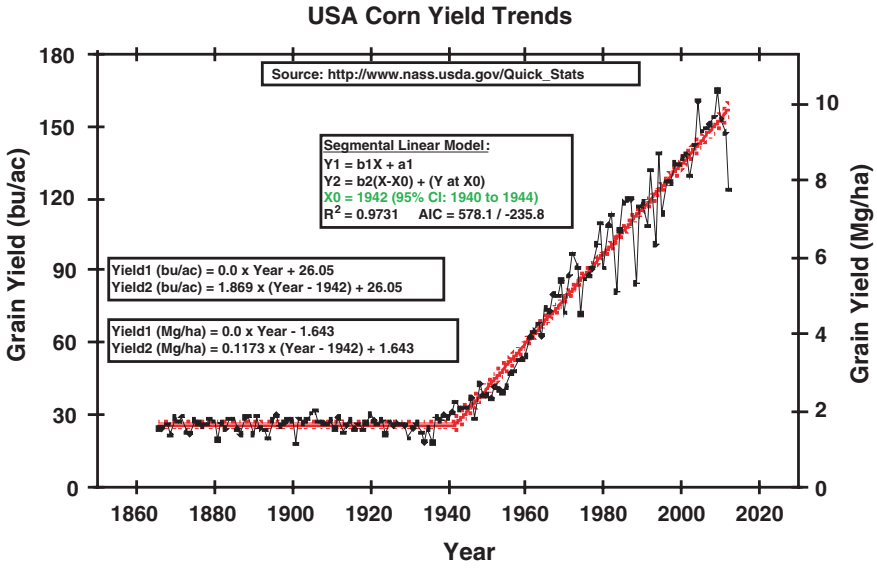


Fig. 3.1 U.S. maize yields 1865–2012 (with permission from Smith et al. 2014a)

3.2 Modern Plant Breeding

Because of the focus on genetic diversity, we adopt the definition of "modern plant breeding" or "scientific breeding" (FAO 1997) as: The act of using genetic diversity to improve the agronomic performance of plants conducted as a formal endeavor and according to scientific principles. We agree with Cooper et al. (2014) who describe modern plant breeding as an "integration of quantitative genetics, statistics, gene-to-phenotype knowledge of traits embedded within crop growth and development models"… to "advance our understanding of functional germplasm diversity." A schematic of hybrid maize breeding is presented in Fig. 3.2.

Genetic diversity changes as represented by arrays of molecular marker founder haplotypes through four generations of pedigree breeding for two representative maize chromosomes are presented in Fig. 3.3.

Diversity changes occur as a result of crosses with other parents, segregation, recombination, genetic drift, and selection by breeders. Our definition of "modern plant breeding" is broad, and we do not regard use of a specific technology as definitional of "modern." We are well aware of the debate regarding the use of genetically modified organisms (GMOs) (Gurian-Sherman 2009; Brookes and Barfoot 2014; Heinemann et al. 2013). In this respect, we recommend that definitions be based upon scientific principles. Consequently, the use of GMOs and organic methods could coexist and would not preclude the use of best principles from either fields. Bt toxin is included in many "organic approved" pesticides and was recommended for environmentally friendly pesticide use (Carson 1962).

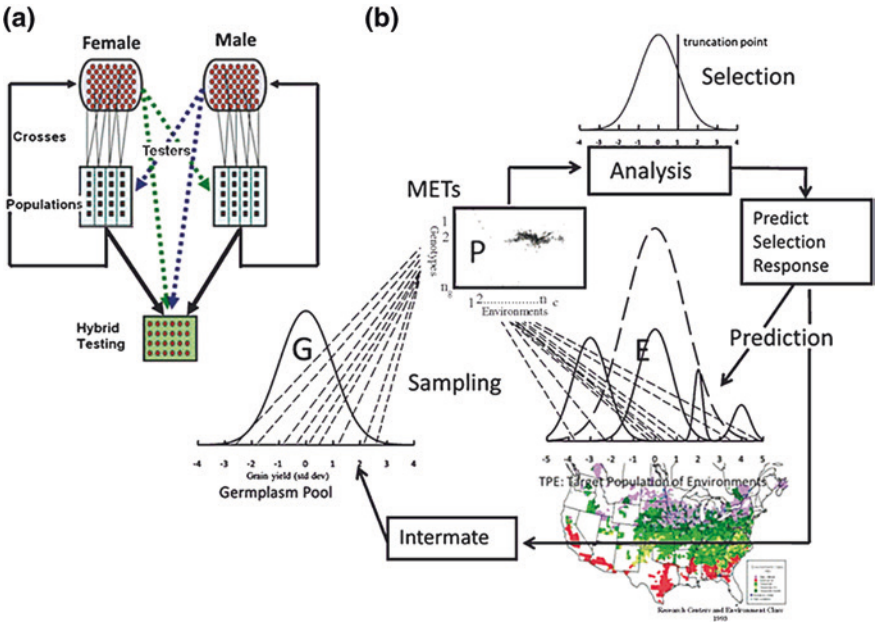
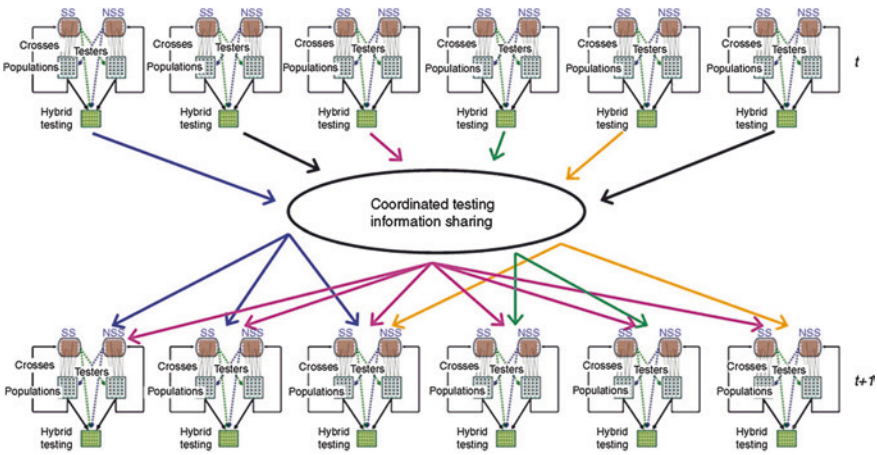


Fig. 3.2 **A** Schematic of a hybrid maize breeding program: *a* Schematic of a hybrid breeding program; *b* Schematic of the major steps undertaken within a cycle of a breeding program (by kind permission, Fig. 2 from Cooper et al. 2014). **B** Schematic of a large-scale commercial hybrid breeding program operated as a coordinated network of breeding programs. Germplasm and genetic information from experiments conducted in any cycle '*t*' are shared among breeders and breeding programs to create new inbreds and hybrids in future cycles '$t + 1$' (by kind permission, Fig. 3 from Cooper et al. 2014). **C** Use of pedigree, marker haplotypes, and phenotypic data in a breeding program: *a* germplasm universe depicting pedigree relationships between founders to modern elite inbreds: the breeding germplasm pool from which the inbreds were sampled, with the pedigree trajectory that contributed to a specific elite individual highlighted; *b* specific inbred pedigree: an extract of the highlighted pedigree that leads from founder ancestors to the highlighted elite inbred, with the founder contribution depicted for a particular 10 cM chromosome region during the pedigree history from founders to elite inbred; *c* identity-by-descent (IBD) profiles: the IBD founder haplotype diversity among a set of elite inbreds for a particular chromosome position; *d* founder haplotype frequencies: the change in frequency of alleles for two QTLs where the alleles are defined in terms of IBD to defined founder ancestors in the pedigree history (by kind permission, Fig. 13 from Cooper et al. 2014)

We regard the partitioning of yield as either "intrinsic" or "operational" (Gurian-Sherman 2009) to be a false dichotomy. The genetic basis for crop yield increase comes from either increased stress resistances or a greater relative partitioning of photosynthates to the harvested organs. Neither of these sources of yield gain could be regarded as "intrinsic" as photosynthesis per se has not increased. Further, protecting yield is as fundamentally important as creating the genetic basis for yield potential. Protecting yield from insect attack using native maize genes was considered an example of genetic gain (Duvick 2005). Protection of harvested produce from spoilage is equally important.



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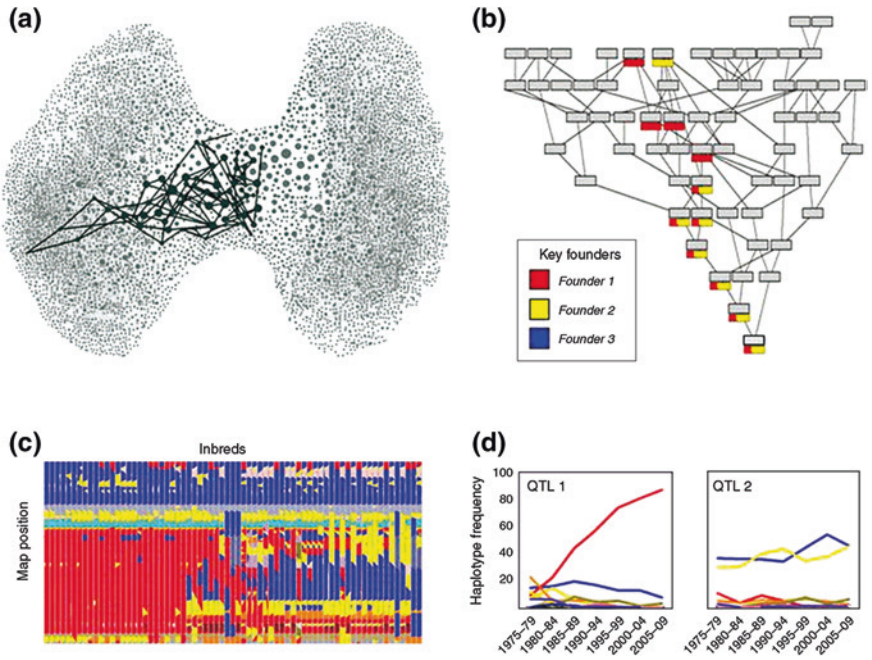

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As Charles Darwin well understood, the development of domesticated varieties provides powerful examples of evolution in progress. Each variety interacts with the environment creating selection pressures upon pest and disease organisms, especially when a variety is cultivated over a large area. Varieties that were once

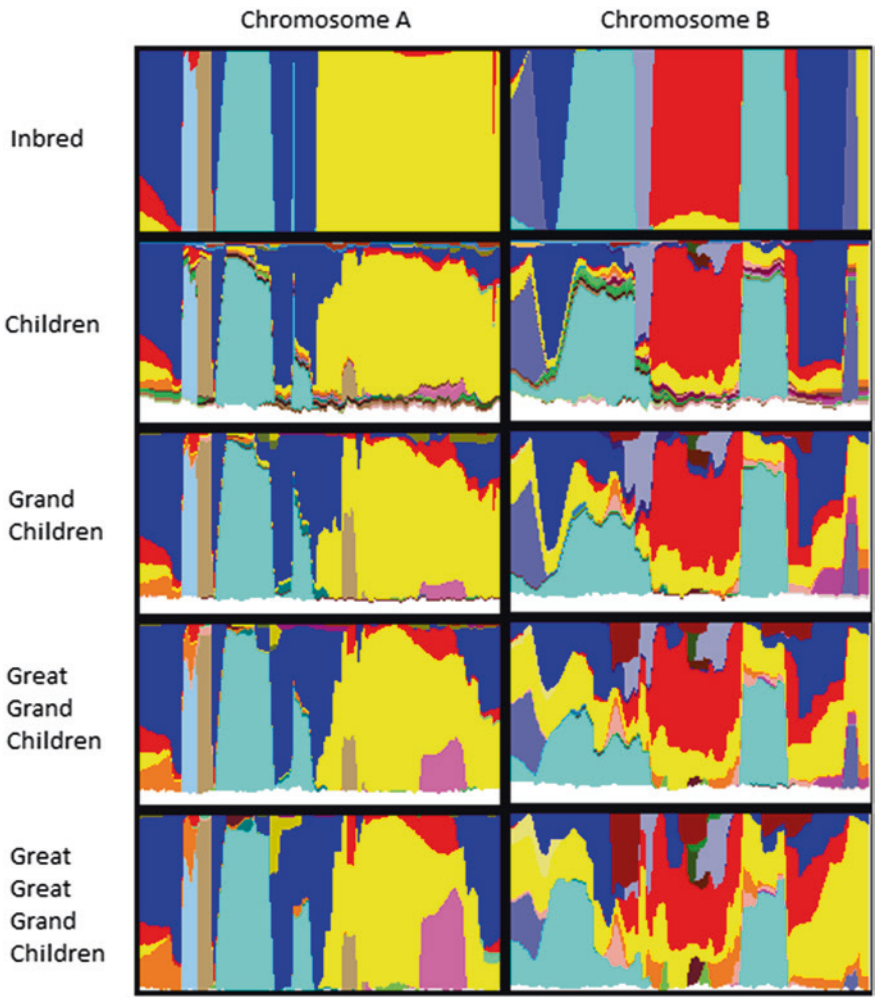

Fig. 3.3 Genetic diversity in time. The evolution of genomic constitution during the breeding process as shown by SNP-founder haplotypes coded by color from an initial parental inbred line through 4 generations of progeny; examples from 2 representative chromosomes of maize are shown. For example, on chromosome A the genomic region represented by the *yellow* haplotype becomes more diversified through the progeny as does the red region on chromosome B. The *dark gray* haplotype on chromosome B diminishes through the progeny lineage

best adapted rarely remain so for long. Varietal inadequacies are revealed by pest and disease pressures or changes in crop management. Examples include: During the 1920s–1940s maize was selected for ease of hand harvesting; however, selection then had to be reversed to adapt maize for machine harvesting. Increasing planting density using narrower rows was made possible by improved precision planting equipment and is associated with genetics conferring more upright leaf canopies. Higher plant populations put increased pressure on stalk and root

lodging which forced breeders to place more emphasis on these traits. Extreme weather events put increased pressure on stalks and the need for drought resistance. Herbicide-resistant crops facilitate no-till which makes the spring planting soil environment colder, wetter, and with increased disease carry-over forcing additional selection by breeders for "defensive" traits. Improved moisture conservation allowed maize cultivation to be feasible on land that was previously drought prone; development of drought-resistant maize hybrids has accelerated this trend. Sorghum breeders have had to source new germplasm to develop varieties that are better adapted to either dryland or irrigated conditions as farmers in the U.S. and Australia transition management practices.

3.2.1 Modern Plant Breeding and Consequences of Role Specialization

Prior to the advent of modern plant breeding farmers exercised three roles: (1) food production, (2) stewardship of genetic resources, and (3) the improvement of crop performance by agronomic practice and varietal selection. Critical changes occurred once farmers chose to use new varieties developed by plant breeders. Change may be gradual, over many decades, where farmers allow landraces to be hybridized or mixed with breeder sourced varieties (Brush 1991, 1995; Hammer et al. 1996) or can occur more swiftly during a few years or decades (Duvick 2005; Negri 2003). Landraces persist in cultivation in less favorable environments due primarily to stability of performance, consumer preference, or lack of breeding support rather than because of intrinsic abilities for high yield potential (Zeven 1998; Almekinders et al. 1994; Newton et al. 2010). Increased availability of resources and specialization of skill sets emphasize the complementary roles of farmers as producers and plant breeders as developers of varieties. Consequently, landrace genetic diversity that is not transferred into formal breeding programs will be lost unless the role of conservator is consciously taken up.

3.2.2 New Arrays of Genetic Diversity as a Result of Modern Plant Breeding

How genetic diversity is arrayed in space, and time changes when farmers transition to using newly bred varieties. Formal plant breeding systems and less formalized systems including via networks of growers and breeders facilitate international access and use of genetic diversity provided phytosanitary requirements and terms relating to access and benefit sharing are met. For example, prior to the establishment of formal maize (*Zea mays* L.) breeding programs in the U.S. the most widely used open-pollinated variety (OPV) in the central Corn Belt was

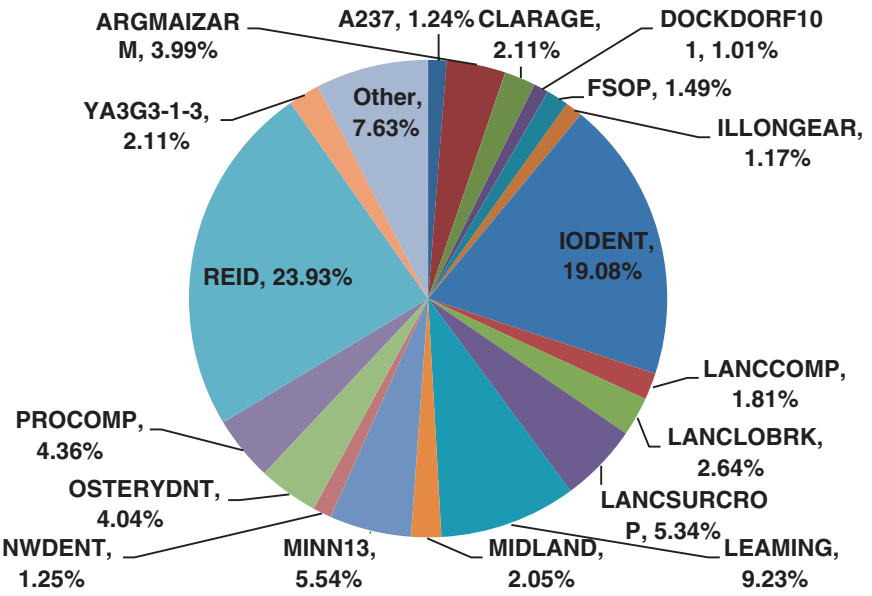

Fig. 3.4 Mean contribution by pedigree of founder genotypes to 14 Pioneer hybrids that were widely grown in the central Corn Belt of the U.S. By contrast, the landrace Reid Yellow Dent was the primary germplasm cultivated on farms prior to the advent of hybrid maize

Reid Yellow Dent (RYD). In contrast, maize farmers in this region today cultivate a broader sampling of landrace diversity. Figure 3.4 shows the mean contribution by pedigree of major founder genotypes for a set of 14 Pioneer brand hybrids that were widely cultivated in the central Corn Belt during the 2000s. The most widely grown OPV, which is grown in the central Corn Belt prior to the 1930s (RYD), now represents 24 % of diversity due to the introduction of inbred lines with pedigrees tracking to other founders. Farmers cultivate a greater diversity of founder germplasm as a result of networking among plant breeders. A typical modern variety of spring wheat released in developing countries may be derived from 45 to 50 landraces and a modern rice variety from 25 or more landraces (Morris and Heisey 1998).

Most diversity within landraces resides between individual plants. In contrast, pedigree or reciprocal recurrent selection breeding schemes partition diversity among different varieties. The inescapable biological reality is that genotype × environment (G × E) interactions condition phenotype (P). Since agroecological environments vary according to weather, maturity, and soil type, successful varieties must demonstrate genetic diversity in space (Fig. 3.5).

Genetic diversity is also arrayed in time (Figs. 3.3 and 3.6) as fresh diversity, which underpins genetic gain, is created by breeding through recombination and including diversity sourced from other geographic regions.

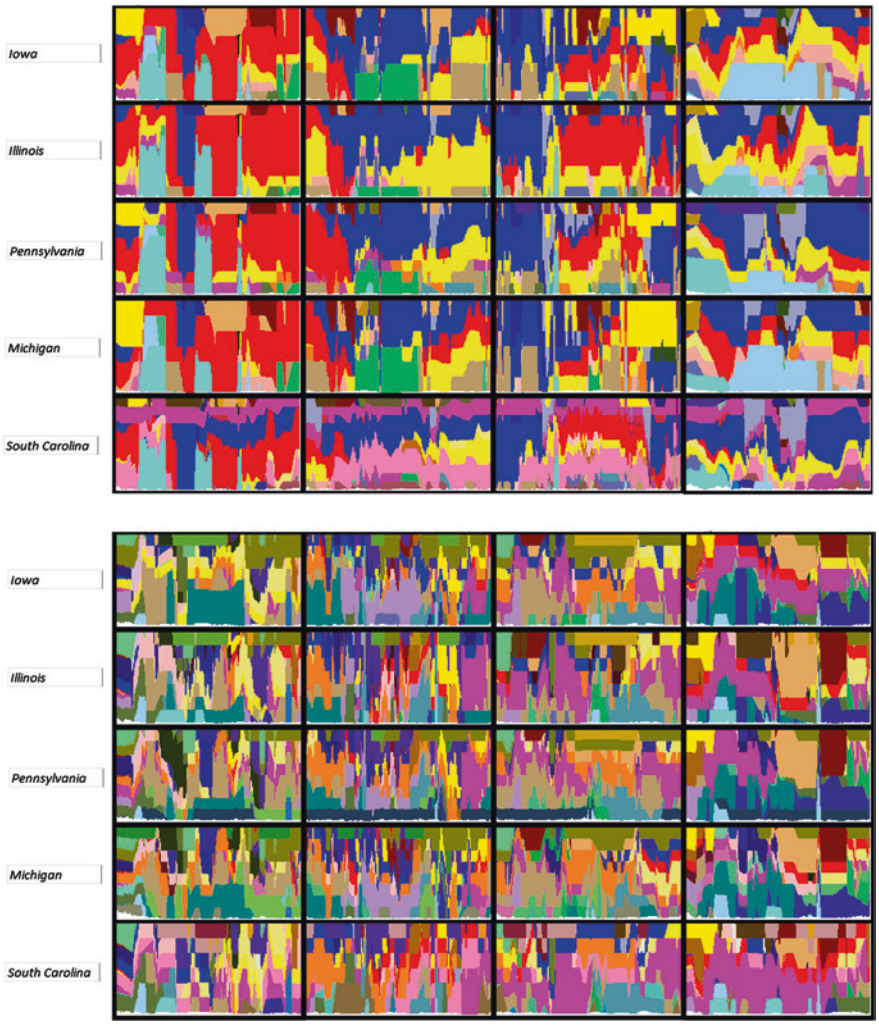

Fig. 3.5 Genetic diversity in space. Mean SNP-founder haplotype profiles for female (*upper panel*) and male (*lower panel*) parental lines of Pioneer maize hybrids that were widely cultivated during the 1990s for each of the named U.S. states. Examples from four chromosomes representing the range of diversity change are presented

3.3 Measuring Genetic Diversity

It is important to characterize and monitor genetic diversity, not only quantitatively and qualitatively, but also temporally and spatially (Morris and Heisey 1998). Comparisons of varietal names provide no diversity metric. When improved varieties are used on farms alongside traditional landraces, then diversity

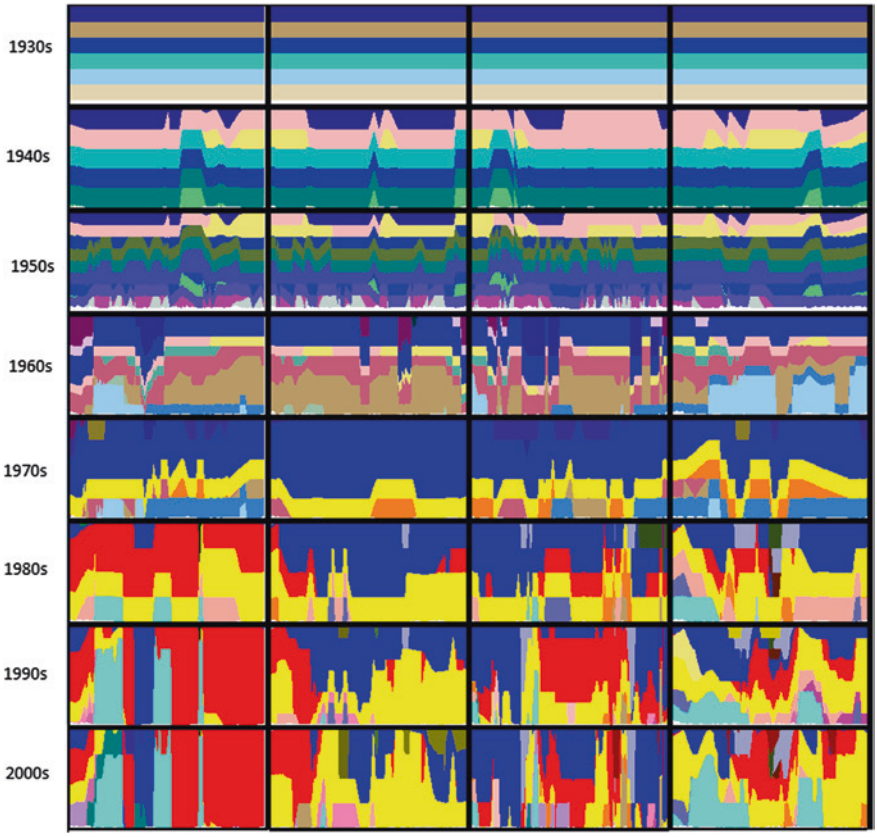

Fig. 3.6 Genetic diversity in time. Mean SNP-founder haplotype profiles for female (*upper panel*) and male (*lower panel*) parental lines of Pioneer maize hybrids that were widely cultivated during decades from the 1930s–2000s and which comprised the germplasm used to measure genetic gain (Smith et al. 2014a). Examples from 4 chromosomes representing the range of diversity change are presented

changes can be complex (Brush 1991, 1995; Bellon and Brush 1994; Louette 1995; Louette et al. 1997: Brush and Perales 2007).

An ideal parameter might be to measure diversity for agronomically important traits. However, useful genetic diversity usually remains hidden from casual observation. For example, Jack Harlan (1975) noted: "A wheat (*Triticum* spp.) I collected in a remote part of Eastern Turkey in 1948… is miserable looking…, tall, thin-stemmed, lodges badly, is susceptible to leaf rust, lacks winter hardiness yet is difficult to vernalize, and has poor baking qualities. Understandably, no-one paid any attention to it for some 15 years. Suddenly, stripe rust became serious in the northwestern states and (it) turned out to be resistant to four races of stripe rust, 35 races of common bunt, ten races of dwarf bunt and to have good tolerance

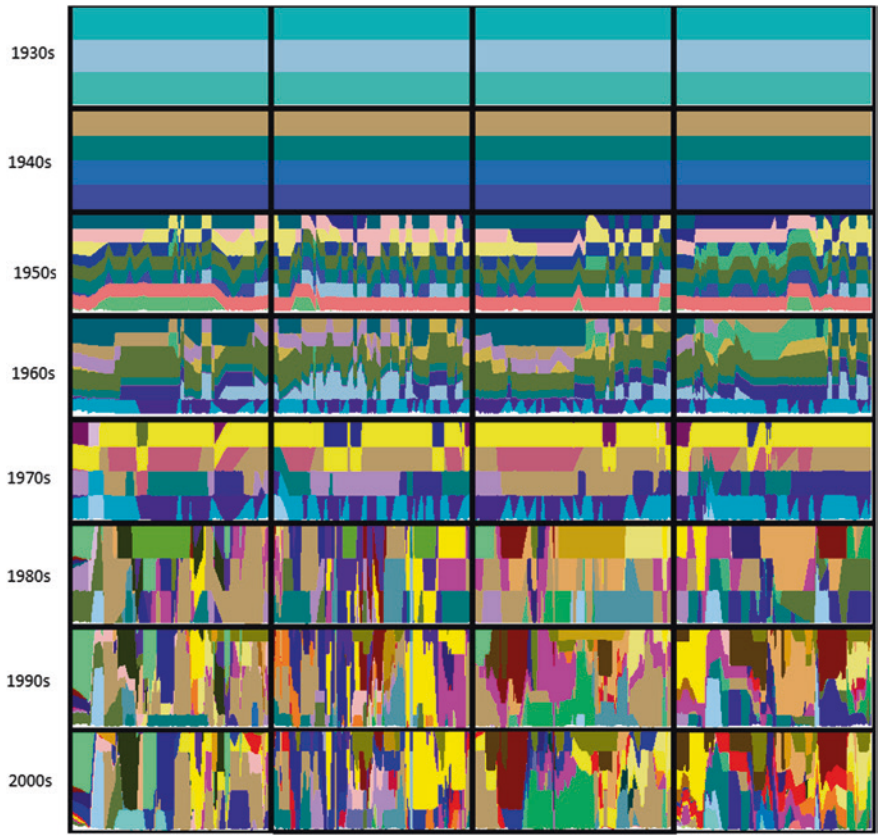

Fig. 3.6 (continued)

to flag smut and snow mould." The range and variance of genetic diversity underlying agronomic traits are important to ascertain for they determine whether sufficient progress can be made through selection. For example, ear length is a component of yield in maize yet selection of increased ear length did not result in higher yield due to negative correlations with other yield traits (Ross et al. 2006).

Other sources of data have been used to characterize genetic diversity including morphology (Dillmann et al. 1997; UPOV 2009), pedigree (Delannay et al. 1983; Cox et al. 1985), heterosis (Smith and Smith 1992; Gizlice et al. 1993), and molecular markers, (Donini et al. 2000; Kim and Ward 2000); see reviews by Rauf et al. (2010) and van de Wouw et al. (2010). Pedigree data are subject to error due to incorrect or missing data and cannot reflect selection but can reveal trends. Molecular marker technologies have evolved rapidly, from allowing 20–25 genes to be interrogated during the 1980s to today, when assays of thousands or millions of single nucleotide polymorphisms (SNPs) are routine. Molecular marker or sequence data provide the most useful means to measure genetic diversity. These

data provide a common diversity "language" encompassing wild and weedy species, domesticated landraces, and new varieties. Nonetheless, the complexities of genetic, regulatory, creation of de novo diversity (Hopkins et al. 2013), and other mechanisms (e.g., epigenetic) systems still render a comprehensive understanding of agronomic performance in terms of genetic sequence or methylation data as far from complete (De Koeyer et al. 1999; Lucas et al. 2013).

3.4 Patterns of Change in Genetic Diversity

3.4.1 Bottlenecks Where Genetic Diversity Can Be Lost in the Continuum from Crop Domestication, Through Use of Landraces, to Modern Plant Breeding

Table 3.1 presents loss of diversity during domestication 8–10,000 years ago for several plant species. For most cultivated species, approx. 65–70 % of diversity in the wild species transferred through the domesticated genepool. For soybean, the domestication process was responsible for a relatively low reduction in diversity. However, the wild species (*Glycine soja*) has unusually low levels of sequence diversity. In contrast, wild barley and wild maize (teosinte) have

Table 3.1 Estimated % genetic diversity not transferred as a result of domestication bottleneck(s) during selection from respective progenitor wild species some 8–10,000 years ago

Species	Common name	% Genetic diversity not transferred	Data source	References
Zea mays L.	Maize or corn	35	All nucleotide sites	Wright et al. (2005)
		38	Silent nucleotide sites	Tenaillon et al. (2004)
		17	Nondomestication genes	Hufford et al. (2012)
		43	SNPs in 774 gene fragments	Wright et al. (2005)
		24	Number of SSR alleles	Vigouroux et al. (2005)
		12	Genetic Diversity of SSR alleles	Vigouroux et al. (2005)
		12	SSR Gene Diversity	Matsuoka et al. (2002)
Medicago sativa	Alfalfa/Lucerne	31	All nucleotide sites	Muller et al. (2006)
		31	Silent nucleotide sites	Muller et al. (2006)

Table 3.1 (continued)

Species	Common name	% Genetic diversity not transferred	Data source	References
Helianthus annuus	Sunflower	55	All nucleotide sites	Liu and Burke (2006)
		59	Silent nucleotide sites	Liu and Burke (2006)
		27	Nucleotides	Kolkman et al. (2007)
Pennisetum	Millet	33	Silent nucleotide sites	Gaut and Clegg (1993)
Glycine	Soybean	34	All nucleotide sites	Hyten et al. (2006)
		36	Silent nucleotide sites	Hyten et al. (2006)
Hordeum	Barley	57	All nucleotide sites	Caldwell et al. (2006)
		62	Silent nucleotide sites	Kilian et al. (2006)
		20	Nucleotides	Morrell et al. (2013)
		45	Nucleotides	Glemin and Bataillon (2009)
Triticum spp.	Emmer Durum and Hexaploid bread wheat	65	All nucleotide sites	Haudry et al. (2007)
		70	Silent nucleotide sites	Haudry et al. (2007)
		84	All nucleotide sites	Haudry et al. (2007)
		69	All nucleotide sites	Haudry et al. (2007)
Avena	Oats	34		Murphy and Phillips (1993)
Oryza	Rice ssp. indica	29	SSRs	Gao and Innan (2008)
	Rice ssp. japonica	38	SSRs	Gao and Innan (2008)
Sorghum	Sorghum	34	Isozymes	Morden et al. (1990)

4× and 5× the amount of diversity, respectively (Hyten et al. 2006). Cultivated sunflower (*Helianthus annuus*) and barley (*Hordeum vulgare*) suffered higher losses of germplasm diversity (55–60 %) although more recent data for barley (Morrell et al. 2013) indicate a relatively low loss (20 %). Cultivated wheat species (*Triticum* spp.) suffered the greatest losses of diversity (65–84 %) compared to wild ancestral species.

3.4.2 Changes in Genetic Diversity from Landraces to Well-Adapted Inbred Lines and Varieties

3.4.2.1 Case Study: Soybean

The cultivated genetic base of U.S. soybean accounts for 47 % of global soy production (Wilcox 2004). Relatively few founders (17) contributed to the U.S. breeding base. However, this bottleneck was moderate for 80–87 % of nucleotide diversity in the landrace class was maintained among these founders. Nonetheless, 78 % of rare landrace alleles were lost. Another potential bottleneck occurred as elite cultivars were bred using the variety founder base. However, Hyten et al. (2006) found elite cultivars retained 83–97 % of nucleotide diversity in the founders. Nucleotide diversity among elite soybean cultivars was "similar to values reported for humans, lower than that of *Sorghum bicolor*, and an order of magnitude lower than modern maize inbreds." Hyten et al. (2006) concluded that "modern soybean breeding has minimally affected allele structure of the genome compared with the other historical bottlenecks (i.e., during initial domestication process." Hyten et al. (2006) considered that it would be unlikely to add new diversity by "randomly adding 100 new Asian landraces to the elite pool," rather it would be more effective "to introduce on a per need basis." Genetic diversity in wild *G. soja* should also be ensured by conservation.

3.4.2.2 Case Study: Maize

Vigouroux et al. (2008) examined almost the entire set of approximately 350 races of maize native to the Americas (Matsuoka et al. 2002). Landraces associated into four major groups: Highland Mexico, Northern U.S., Andean, and Tropical Lowland. Highland and tropical lowland races encompassed most diversity. Nonetheless, Northern U.S. landraces expressed 88 % of the gene diversity and 71 % of the number of alleles/locus compared to the most diverse set (Highland Mexico).

Matsuoka et al. (2002) and Liu et al. (2003) estimated that 101–206 inbred lines collectively retained 98 % of gene diversity, from 76–93 % of the number of alleles, and 73 % of the number of alleles per locus compared to landraces. The USA set (54 inbreds) retained 93–98 % of alleles present in landraces. Compared to the wild ancestor, the US inbred set retained 84 % of the genetic diversity and 67 % of the number of alleles (Matsuoka et al. 2002). In contrast, Liu et al. (2003) showed a greater reduction of diversity; inbreds had 76 % the number of alleles, 73 % the number of alleles/locus, and 98 % of overall gene diversity compared to landraces.

Liu et al. (2003) categorized 260 inbreds into three major groups; non-stiff stalk (NSS), stiff-stalk (SS), and tropicals. Tropical inbreds originated mostly from tropical lowland (66 %) and tropical highland (18 %) races. NSS and SS

originated mostly from Southern Dent (37–38 %) and Northern Flint (23–27 %) which together form the Corn Belt Dent race of maize, the most productive and globally widespread maize race. The NF and SD races are radically different in their morphology, isozymic constitution, and cytology. Doebley et al. (1988) described them as "representing the opposite ends of the spectrum of variation in maize" and Anderson and Brown (1952) considered them to be so different that "relative to the variation found within the wild grasses, they would be considered different species and possibly members of different genera."

Liu et al. (2003) concluded that tropical highland diversity was not well represented in the inbreds. Consequently, tropical highland maize and tropical inbreds could be useful candidates for broadening the diversity of the elite germplasm base. Highland races of maize showed evidence of introgression from their wild ancestor teosinte and so represent sources of both wild and cultivated exotic diversity (Hufford et al. 2013).

During the early phase of the Pioneer corn breeding program in the 1920s and 1930s, the Director of Corn Breeding, Raymond Baker, encouraged Pioneer corn breeders to source diversity from a broad base of OPVs. Considerable genetic diversity can exist within a single maize OPV. For example, results from Illinois long-term selection studies in maize that began in 1896 continue over a century later to show responsiveness to selection, including reversible responses. These results indicate high levels of complex genetic diversity contributing to oil and protein levels (Lucas et al. 2013). Lu and Bernardo (2001) compared diversity among 40 U.S. inbred lines and concluded that genetic diversity had declined at the gene level but had been maintained at the population level. We also found that genetic diversity is reducing within individual heterotic groups, but diversity overall is maintained by increased separation between heterotic groups (Figs. 3.2 and 3.7). Duvick (1984) and Morris and Heisey (1998) refer to cultivated genetic diversity being arrayed in space and in time. There is abundant evidence of temporal diversity (Figs. 3.3, 3.4, 3.6 and 3.7) reflecting the contribution of genetic gain to increase on-farm productivity (Smith et al. 2014a). There is also evidence of spatial genetic diversity (Fig. 3.5) showing that different arrays of genetic diversity are required to allow optimum phenotypic expression in different environments (Smith et al. 2006).

Romay et al. (2013) compared 2815 maize inbreds using over 680,000 SNPs. They found that: "Although all of the major private seed companies are represented within each group (consistent with the small value of divergence between companies), Pioneer germplasm is represented more in the Iodent group and more of its germplasm falls outside the three main clusters." The signature of diverse germplasm sourcing is still reflected in more recently developed germplasm (Fig. 3.4) and indicates that the U.S. maize germplasm base is broader than just Reid and Lancaster OPVs (Troyer 1999, 2004). On the other hand, there is no justification for complacency. A trend of genetic diversity being depleted by only breeding with and commercializing the best performing varieties would be a natural outcome of selection if conducted in a closed system. Plant breeders must therefore actively manage germplasm diversity to provide potential for continued

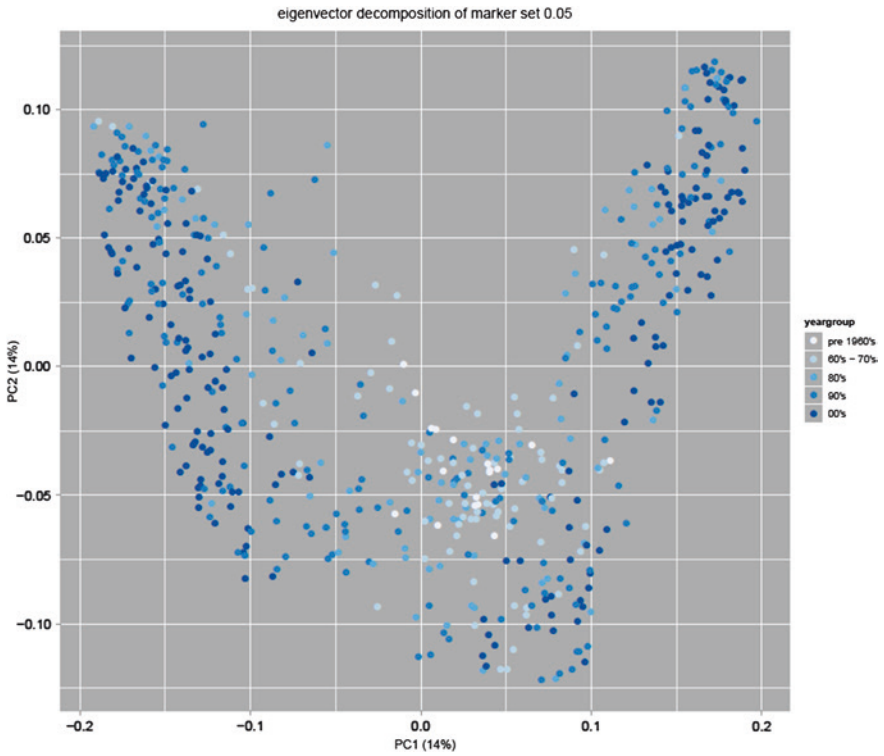

Fig. 3.7 Associations of inbred lines represented by colored dots representing different eras of breeding based upon genetic distances calculated from comparisons of SNP profiles. The pattern of association shows increasing divergence in genetic diversity between inbreds that are allocated into either female or male heterotic pools as breeding has progressed from the 1960s to the 2000s

realization of genetic gain. Furthermore, there is no reason to suppose that all useful genetic diversity present in *Zea* should reside in one race, even one with very divergent origins. Programs dedicated to evaluating exotic maize germplasm in the U.S. have proven this assertion (Lewis and Goodman 2003; GEM 2014).

3.4.3 Changes in Genetic Diversity Across Decades in Varieties Deployed in Agriculture

Diversity generally decreased during the initial transition from landraces to the first cycle of varietal breeding. During subsequent decades, there have been temporal fluctuations in diversity (Rauf et al. 2010; FAO 2010; van de Wouw et al. 2010). Fluctuations are associated with bottleneck effects due to demands for high malting, brewing, or baking qualities. Additional temporary bottlenecks

were associated with the introduction of new germplasm, e.g., semidwarf wheat and wheat-rye (*Triticum-Secale*) translocation stocks (Orabi et al. 2014). In contrast, introduction of GMO herbicide resistance did not cause a bottleneck in soybean (Sneller 2003). Some breeding programs have reversed the post-landrace trend, reaching higher levels of diversity. For example, Ren et al. (2013) observed a significant increase in wheat diversity for cultivars released during 1980–2009. Parker et al. (2002) concluded that genetic diversity in 124 Australian wheat varieties increased over time. Rauf et al. (2010) showed introduction of CIMMYT wheat lines with diverse landrace pedigrees increased diversity surpassing that of the pre-Green Revolution era by 1991–2000. Smale et al. (2002) concluded that diversity trends for spring bread wheat cultivars released after 1965 were "not consistent with the view that the genetic diversity of modern semidwarf wheat grown in the developing world has decreased over time." Orabi et al. (2014) found that during 1886–2009 diversity in European wheat varieties had declined by the 1940s as farmers moved away from cultivating landraces. However, during the 2000s, European wheat varieties reached higher levels of diversity than was exhibited by landraces. Van de Wouw et al. (2010) showed a decrease of diversity for 8 field crops from the 1950s to the 1960s with a subsequent increase in diversity. Orabi et al. (2014) credited the use by breeders of adapted germplasm from different regions, exotic germplasm, landraces, and wild relatives.

3.5 Measures to Conserve and Source Additional Genetic Diversity

The successful deployment of genetic diversity in plant breeding and agriculture to achieve sustained improvements in productivity depends upon the continued sourcing, creation, and deployment of new useful diversity. While there is evidence for de novo creation of diversity (Hopkins et al. 2013), it would be foolish to restrict access by repeatedly sourcing only widely used well-adapted varieties. Temporal fluctuations in genetic diversity reflect the dynamic nature of the agricultural environment and abilities to successfully adapt to both challenges and opportunities provided by ever-evolving weeds, pests, and diseases, unstable and unpredictable climates, changing management practices on farms, and changing consumer preferences. Primary sources of potentially useful new diversity include well-adapted varieties from adjacent regions, less immediately well-adapted or "exotic" varieties including landraces (Warburton et al. 2006), de novo generation of allelic variation in well-adapted varieties including via gene mutation or through the alteration of gene expression, crop-related wild and weedy species, and "trans-genic" diversity sourced from other genera or phyla and incorporated using molecular engineering.

3.5.1 Concerns About Genetic Uniformity; Examples Where Single-gene (or Cytoplasmic) Resistances Have Broken Down

Concerns about loss of diversity were heightened in the 1960s when a high yielding rice cultivar IR8, susceptible to the bacterial leaf blight pathogen (*Xanthomonas oryzae* pv. Oryzae) was widely planted throughout Southeast and South Asia. Outbreaks of bacterial blight cut yields by 20–50 % and as high as 80 % (American Phytopathology Society 2014). Additional concerns arose when Southern Leaf Corn Blight caused by Race T of the fungus *Bipolaris* (*Helminthosporium*) *maydis*, struck the US maize crop in 1970. In this case, uniformity was associated with a specific cytoplasm rather than the nuclear genome. Yield losses reached 50–100 % in some areas with economic losses of about 1 billion dollars (American Phytopathology Society 2014). "*Never again should a major cultivated species be molded into such uniformity that it is so universally vulnerable to attack by a pathogen, an insect, or environmental stress. Diversity must be maintained in both the genetic and cytoplasmic constitution of all important crop species.*" (Ullstrup 1972). Since maize breeders had elite inbred lines in other cytoplasms, they were able to rapidly "unmold" nuclear genomic diversity using N, C, and S cytoplasms. Similarly, soybean (*Glycine max*) variety BR16 dominated use in Brazilian agriculture until stem canker (*Diaporthe* spp.) essentially wiped it out in 1996; a single-resistance gene was incorporated and a modified version of BR16 was introduced. Soybean rust (*Puccinia pachyrhizi*) also had devastating effects and multigenic sources of particle resistance coupled with fungicides currently control the disease.

Brown (1983) reminded that diversity per se provides no guarantee of resistance to pests or diseases. For example, the American chestnut (*Castanea dentate*) was decimated by blight (*Endothia parasitica*) in two decades and the highly variable American elm (*Ulmus americana*) is very susceptible to Dutch elm disease (*Ophiostoma* spp.). Prior to the advent of plant breeding, there were attacks by the potato blight fungus (*Phytopthora infestans*) in Ireland during the 1840s and in Germany during World War I. Attacks of ergot (cased by the fungus *Claviceps purpurea*) in the Rhine valley occurred during 857 AD–1300 AD, in England during 1355, and in Russia during 1926–1927. In 1916, wheat rust (*Puccinia graminis*) caused significant yield losses to U.S. landraces. During the early 1950s, the tropical rust fungus (*Puccinia polysora*) spread across Africa on maize OPV cultivars that otherwise sequestered much genetic variability. Mercer and Perales (2010) expressed concerns that highland maize landraces could be vulnerable to loss of diversity and even potential extinction due to relatively poor performance as climates warm.

It is to be expected that farmer demand for a variety with outstanding agronomic performance will lead to its wide cultivation. FAO (1997) noted that "uniformity per se need not be dangerous, for some crop cultivars are remarkably stable." For example, for the last 40 years, Azul has been the only variety

of *Agave tequilana* permitted in the production of tequila (Valanzuela 2011). Brazilian orange (*Citrus sinensis*) production is based on few varieties (Machado et al. 2011), and use of a narrow genetic base is not restricted to humans. The Monarch butterfly (*Danaus plexippus*) feeds only on *Asclepia* spp. (milkweed), while the fastest mammal, the cheetah (*Acinonyx jubatus*), is well adapted to a predatory lifestyle, its lack of genetic diversity (Menotti-Raymond and O'Brien 1993) makes the species quite unadaptable. Overreliance upon a successful variety or reliance upon specialized behavior is a potential Achilles heel for any cultivar or species. For example, mounting selection pressures that result in pathogens overcoming varietal resistance creates a "social trap" (Morris and Heisey 1998). Biological interactions are inevitable and must be managed as integral components of plant breeding. For example, Panama disease, which caused the export banana (*Musa acuminata*) trade to be decimated at the beginning of the twentieth century, is now reappearing in Cavendish banana, the sole banana variety that is grown for export (Van der Wal and de Groot, n.d.). Outbreaks of Corn Northern Leaf Blight (*Exserohilum turcicum)* in the Alsace-Rhine valley were countered by breeding in additional resistance genes. The susceptibility of the widely sold U.S. corn hybrid B73 × Mo17 to stalk, disease, and drought was countered by development of improved varieties. B73, in particular, has been one of the most widely used parental lines and productive breeding materials in U.S. maize history with numerous improvements made by breeders to its agronomic deficiencies. Leading sunflower varieties in Argentina and a leading U.S. maize hybrid were replaced by further breeding when susceptibilities to stalk and leaf diseases were exposed as the planting environment changed. Each new variety or "genetic solution" can only be temporary as the on-farm environment is dynamic. Dynamic change requires the creative use and deployment of useful genetic diversity in breeding programs.

3.5.2 Conservation of Genetic Resources

Conservation of genetic diversity is akin to a long-term insurance policy for potential future resource use and thus a long-term public good. Conservation of plant genetic resources for food and agriculture is usually considered as occurring "on-farm" (in situ) or "off-farm" (ex situ). Ex situ gene banks are the last repository for conserving genetic diversity that otherwise would be lost as farmers transition from using landraces to cultivating varieties developed by plant breeders, including via participatory plant breeding where farmers play a more intimate role in selecting progeny. Needs to access a broad base of genetic diversity lead to the establishment of the US Plant Exploration program in 1898 (Williams 2005). Pioneering research and germplasm collection expeditions were carried out in the 1920s and 1930s by N.I. Vavilov with specific goals to better understand and thereby utilize global genetic diversity of cultivated species which included the establishment of genebanks (Vavilov Institute 2014). Additional genebanks were

established during the late 1940s–1950s in the US, Mexico (Taba et al. 2004; Williams 2005). Concerns about loss of landrace genetic diversity during the expansion of area planted to newly bred varieties during the Green Revolution lead to the establishment of additional genebanks, notably those under the auspices of the Consultative Group on International Agricultural Research (CGIAR). Globally, there are over 1300 genebanks. Of these, only 56 % accessions are stored in medium to long-term facilities, 8 % are in short-term, 10 % are in field conditions, and 25 % have no information (Scarascia-Mugnozza and Perrino 2002). Fears of loss of germplasm lead to the establishment in 2004 of the Global Crop Diversity Trust (GCDT) (www.startwithaseed.org) through a partnership with the Food and Agriculture Organization (FAO) of the United Nations (UN) and the CGIAR. Goals of the GCDT are to raise an endowment sufficient support a rational, efficient, and sustainable global system of genebanks (Raymond 2004). CGIAR collections are held as a "common responsibility of humankind" under the auspices of the FAO. These genetic resources are conserved in a multilateral system thereby recognizing the collective primary benefit of enabling access for potential further use in food and agriculture for all countries. Benefits reside in the assured ability to access a broad range of genetic diversity beyond that present in any single country or region. No single country or region, even those where crops were initially domesticated or later developed increased diversity, is or can be self-sufficient for its supply of crop genetic resources (Fowler et al. 2001; Voysest et al. 2003; Fowler and Hodgkin 2004). An alternate scenario of finding unique germplasm source in only one location of very high monetary value that could be readily realized elsewhere was acknowledged not to be concordant with the monetary worth and geographic distribution of genetic resources useful for food and agriculture (Gollin 1998; Voysest et al. 2003; Fowler and Hodgkin 2004) as witnessed by the establishment of the FAO International Treaty (FAO 2009).

Strategies to conserve germplasm ex situ have been criticized because they effectively place germplasm in cold storage and so halt further evolution of the variety in response to pests, diseases, or climate, which are under constant change. This criticism is misguided; however, for opportunities to generate new diversity occur when plant breeders access and use this germplasm, creating more new diversity by crossing and selection and at a faster rate than would otherwise have occurred even if the initial landrace diversity could have been maintained on farm. Ex situ germplasm conservation allows genetic diversity that would otherwise have been lost to be still used in plant breeding programs. Most successful plant breeding programs have to be in situ due to the effects of gene × environment interaction. The notion of in situ conservation also requires careful scrutiny. Studies of genetic diversity in farmer managed agriculture and seed supply systems indicate use of fairly sophisticated practices to maintain varietal quality and to re-invigorate existing diversity (Brush 1991, 1995; Bellon and Brush 1994; Louette 1995; Louette et al. 1997: Brush and Perales 2007). When more productive germplasm is introduced then farmers will, according to their needs, utilize that germplasm per se, or for outcrossing crops, introduce some of that "new" genetic diversity by hybridization. Thus, even if the quantitative level of genetic

diversity is maintained some of the diversity present in the native landraces is vulnerable to loss. Consequently, use of the term "conservation" in conjunction with "in situ" can be a misnomer and might better be described as "in situ crop management" or "plant breeding." Genetic diversity used on farms should be regularly monitored regardless of the source or type of germplasm (i.e., landraces, landraces with additional introduced germplasm, or varieties developed in breeding nurseries).

3.5.3 Programs to Broaden the Genetic Base in Breeding and Agriculture

There are significant challenges to evaluate exotic, including wild germplasm that is unadapted to a target production environment (TPE). Challenges include (1) deciding which of many accessions to evaluate and (2) adapting exotic germplasm by breeding with adapted germplasm to allow trait performance to be fairly tested.

Information on genetic bottlenecking helps (1) prioritize germplasm as a source of additional diversity and (2) indicate the challenges that need to be overcome to evaluate that germplasm for its potential utility. For example, maize landraces distributed in the Mexican highlands and tropical inbred lines are high priority candidates as they carry much diversity and neither has recent phylogenetic relationships with the Corn Belt Dents. For soybean, landraces would be most effectively sourced by evaluation schemes that target specific traits, whereas most additional diversity resides in wild soybean.

The conduct of germplasm introduction and evaluation programs has usually been undertaken through public or private–public partnerships. The U.S. sorghum crop is highly dependent upon recently introduced exotic germplasm. Sorghum (*S. bicolor*) was introduced into the U.S. from Africa during 1874–1908 through few, yet diverse founder cultivars (Milo, Guinea Kafir) (Klein et al. 2008). By the early 1960s, it was realized that the U.S. sorghum germplasm pool was very narrow with limited opportunities to increase adaptation to U.S. farms. A sorghum conversion program involving the USDA and Texas A&M University was initiated in 1963 to broaden the germplasm base by removing the photoperiod bottleneck. More than 840 sorghum lines with tropical germplasm were converted. A dramatic increase in marker haplotype diversity validated the introduction of new genetic diversity (Klein et al. 2008).

Dr. Major Goodman directs a program at North Carolina State University that incorporates exotic tropical maize germplasm into U.S. breeding materials. Estimated exotic contributions into new inbred lines are from 32–70 % with the best testcrosses out-yielding well-adapted check hybrids by up to 11 % (Lewis and Goodman 2003). The Genetic Enhancement of Maize (GEM) consortium comprises 17 universities, 7 USDA-ARS units, 3 international collaborators, 27 US companies, and 9 international companies. GEM utilizes germplasm from over 12

countries and has surveyed accessions from 24 maize races resulting in 190 germplasm releases (GEM 2014). Useful genetics in GEM releases include improved yield as well as resistances to insects and diseases, high protein, oil, and starch.

The UK Biotechnology and Biological Sciences Research Council (BBSRC 2011) is broadening the genetic base of wheat. Three strategies are being used: source from landrace and locally adapted varieties, make new hexaploid wheats from crossing tetraploid x diploid progenitors, and transfer small genetic segments from wild relatives into hexaploid wheat.

Van Esbroeck and Bowman (1998) cited the infrequent use of exotic germplasm in US cotton (*Gossypium hirsutum*) breeding for cultivars released during 1972–1996. They conclude that "unless methods are improved to transfer useful allelic variation from diverse to adapted germplasm without negative agronomic effects, cotton germplasm resources will remain largely under-used and the trend toward increased genetic uniformity will probably continue." A comprehensive USDA-ARS research program to broaden the genetic base of U.S. cotton was initiated (Wallace et al. 2008). Important useful germplasm releases include nematode resistance and improved fiber quality (Texas A&M 2010).

3.5.4 Generating Additional Diversity

Methods to generate additional diversity include inducing new mutants and the incorporation of specific gene sequences from other unrelated genera or phyla. Plant breeders usually draw upon diversity using the native germplasm base for their specific crop of interest to develop a variety that is well adapted to the TPE and outperforms earlier bred varieties. Targeted use of additional diversity can then be used to modify or better adapt the existing variety. Modified varieties can be developed by (1) crossing the initial variety to another variety that contains the additional diversity of interest (the donor source) and then (2) perform repeated generations of "back-crossing" using the initial (recurrent) parent while simultaneously selecting for the specific donor genes. The goal is to recover a modified variety that is as closely genetically similar to the initial variety as possible with the sole exception of the added desirable genes from the donor source germplasm. Once desired additional genes are incorporated into well-adapted varieties breeders also have the option to forgo use of donor germplasm and instead use the modified varieties as breeding parents per se (forward breeding).

3.5.4.1 Use of Induced Mutations

The fundamental cause of all genetic diversity is mutation which can be defined as "any change in nucleotide composition of the genome." Using the products of induced mutation in breeding was initiated by Stadler (1928a, b) in barley and maize using X-rays and radium. Advances in mutation breeding include the ability

to make sequence site or gene directed mutants e.g., via RNA interference, site-specific mutagenesis, use of zinc-finger nucleases, and more efficient means to identify new, including recessive alleles via the process of Targeted Induced Local Lesions IN Genomes (TILLING) and transcriptome analyses (Phillips and Rines 2009). Mutation breeding plays an increasingly important role in providing plant breeders with potentially useful sources of new genetic diversity and is particularly useful for the improvement of asexual crop species (Ishige 2009) and species with limited diversity (Shu 2009). Over 2700 new crop varieties encompassing 170 species have been developed and released to farmers including rice, wheat, barley, apples, citrus, sugar cane, and banana (Lagoda 2009). Many varieties bred using induced mutation have had significant positive economic benefits to farmers. Examples include brewing barley varieties 'Diamant' and 'Golden Promise' annually contributing $20 million annually and the Japanese pear variety 'Gold Nijesseiki' contributing $30 million annually. The Chinese rice variety 'Zhefu 802' contributed a yield increase of 10.5 % between 1980 and 1995 which is equivalent to feeding an extra 2 million people each year. A thorough review of the use of mutation breeding is provided by Shu (2009).

3.5.4.2 Use of Germplasm from Other Genera or Phyla (Transgenic)

As of July 2014 ISAAA (2014a, b) listed as present in one or more counties 31 genetically modified (GM) traits of which 8 (27 %) conferred herbicide resistance and 3 (10 %) conferred insect resistance. Twenty-seven crops were listed as having varieties that included GM traits. Seven (23 %) traits were listed as being commercially available in one or more countries. These traits comprised drought resistance, altered growth/yield, disease resistance, herbicide tolerance, insect resistance, modified product quality, and pollination control system for the production of hybrid seed. The first commercially available herbicide (glyphosate)-resistant soybean varieties were released in 1996. Maize hybrids resistant to the European Corn Borer (ECB) (*Ostrinia nubilalis*) through integration of a toxin producing gene from *Bacillus thuringiensis* completed regulatory approvals in 1996. Bt toxin had already been used as a pesticide in Europe in 1920 and is espoused as an environmentally friendly pesticide (Carson 1962).

Prior to the development of GMO approaches, maize breeders had found genotypes that were highly toxic to ECB. However, even after 7 decades of breeding with some success in developing improved tolerance (Duvick 1984, 1997), maize hybrids remained highly vulnerable to significant economic loss annually exceeding $1000 million in the 1990s (Mason et al. 1996). Hutchinson et al. (2010) estimated that $6 billion in economic benefits had accumulated over 14 years in suppressing ECB in the major US Corn Belt; an additional $1.9 billion had also accrued to non-Bt maize growers. Herbicide-resistant varieties have facilitated the more widespread use of conservation tillage, which helps protect against soil erosion and compaction and reduces fuel use thereby reducing costs and carbon emissions (Fawcett and Towery n.d; So et al. 2001; Holland 2004; Green 2012).

It is important to recognize that current transgenic approaches to achieving herbicide and insect resistance remain as chemical solutions directed by single genes using the plant as a source of energy to drive chemical manufacture. They offer the same advantages and disadvantages of any single-gene approach. They provide highly heritable and significant effects but they are liable to loose efficacy due to high selection pressure on pathogens or weeds to overcome the resistance mechanism. Transgenic approaches have also been used commercially to change oil profiles and to control pollen development. There were concerns that adding additional classes of single genes by backcrossing and transgenic modification would increase potential bottleneck effects and thereby reduce genetic diversity in commercially available varieties (Sneller 2003). However, the diversity of US cotton increased during the introduction of Bt varieties and the diversity of US soybeans was maintained as glyphosate-resistant varieties were introduced. There was an initial reduction of diversity in Indian cotton varieties with the introduction of Bt varieties. However, diversity increased as more Bt varieties became available (Carpenter 2011).

It is only very recently that single-gene approaches to agronomic traits such as drought resistance have been developed and commercially released. Even as knowledge of the complex physiological and genetic mechanisms underlying quantitative traits increases, it will still remain challenging to find single-gene or "silver-bullet" solutions either by insertion of exotic genes or though mediated expression of single native genes. To date, 100 % of the genetic potential for yield increase comes from developing new arrangements of native diversity (and possibly via some contribution of the de novo generation of diversity). To date, genetic modifications whether they be contributed by mutation breeding, changing gene expression, or through the integration of exotic germplasm via transgenic methods have served to protect or enhance quality of the existing genetic potential for yield. Such contributions can be highly significant economically, environmentally beneficial, and are in high demand by the farmer. More effective insect control makes more accessible germplasm that hitherto had been precluded from use due to its inherent limitations. Improved drought resistance and nitrogen use efficiency can contribute to a more sustainable agriculture. However, use of one approach should not preclude another including complimentary use of best practices from "organic" and other "non-organic" approaches. Plant breeders and farmers will need to use all available tools to sustainably improve productivity. Nonetheless, we anticipate that primary drivers in achieving increased yield productivity will be as a result of more efficient breeding and selection using native germplasm to further optimize genotype x environmental interactions (Smith et al. 2014a).

3.6 Intellectual Property Protection and Genetic Diversity

Seeds of self-pollinating species and vegetatively propagated plants can be readily copied. Consequently, in order to secure further investments into privately or commercially funded plant breeding, it is obligatory that new parental lines of hybrids, varieties, and other research-based products such as novel traits or breeding methods, can be eligible to be protected as intellectual property. Misappropriation also contributes to a narrowing of the genetic base and misleads farmers who wish to diversify their cultivated genetic base so as to spread maturities and to help guard against potential weather, insect, or pest-related risks associated with growing any single or narrow germplasm pool.

The most widely used form of protection is Plant Breeders' Rights (PBRs) or Plant Variety Protection (PVP). PVP was developed specifically for plant breeding under the auspices of the Union for the Protection of Cultivated Plants (UPOV) and is implemented via national or, in the case of the European Union, regional legislation. The UPOV Convention was adopted in 1961, came into force 1968 and revised in 1972, 1978, and 1991 (UPOV 2014). Briefly, PVP provides time-limited (usually 20 years) protection during which the owner has a monopoly on the sale and commercial exploitation of the variety per se. However, during that period there is an exception allowing others to breed with the protected variety and (under laws compliant with UPOV 1991) to freely commercialize the resultant progeny providing they meet the UPOV requirements for distinctness, uniformity, and stability (DUS), and they are not so similar to the initial variety as to be declared essentially derived varieties (EDVs). There may also be exceptions that allow farmers to save seed for use on their own farms; royalties may be levied for commercial scale use of farm saved seed, but this is not the case in the U.S. The U.S. initiated IPP for vegetatively propagated nontuberous species through the US Plant Patent Act of 1930 which provides PVP-style protection. The U.S. has allowed Utility Patents on biological inventions since 1980 including plant varieties per se since 1985; reinforced by the US Supreme Court (Baird 2002). Eligibility requirements for patentability of a variety include showing of DUS plus demonstration of utility, novelty, nonobviousness or inventive step, and a written description. A seed deposit completes the requirement of written description for patents on varieties per se. Additional forms of IP include trade secrets and contract law e.g., via use of bag-tag notices.

The policy goal of intellectual property protection is to increase social welfare by encouraging the development of new and useful products that otherwise would not have been created (Lence et al. 2005). The means by which PVP and patents seek to achieve net positive social welfare is to provide time-limited protection for the initial developer. PVP adds an exception allowing further breeding and commercialization in countries where the variety PVP applies. Europe does not allow utility patents on varieties per se but can allow patents on genes and associated markers, although there is intense discussion on the latter subject and the long-term situation in Europe remains unclear (EPO 2013). Whether trait

patents extend to the scope of the plant depends upon specific claims and on country or regional patent laws. The challenge, in respect of IPP and social welfare, is to provide an appropriate balance between time and level of protection in regard to quality of innovation and access to the variety or invention. Utility Patents have been criticized because, in contrast to PVP, they only allow licensed access during the period of protection. In contrast, following expiration of patent protection the previously protected object (including patented parental lines of hybrids) is placed into the public domain, whereas under UPOV such public access is not mandatory but is required by the USDA in the U.S. Consequently, European plant breeders are more reliant upon trade secrets than are US plant breeders to protect parental lines of hybrids; a practice that can have negative impact on social welfare. Furthermore, in contrast to Europe, the U.S. regularly makes available through the NPGS off-patent and off-PVP germplasm to the FAO ITPGRFA multilateral germplasm system.

IPP in respect of plant breeding exists within an environment that is continuously changing in terms of technical capabilities. For example, the effective time period of protection once afforded under PVP has been reduced as new breeding methods shorten cycle times by 2–5 years. Reduced cycle times are most dramatic for hybrids because appropriate heterotic groups for progeny can now be more readily identified. In contrast, breeding from many hybrids was precluded previously because optimum line combinations to allow expression of heterosis could not be so readily determined. Consequently, PVP now provides an even lower level of incentives to invest in more time consuming and risky breeding activities including to find, adapt, and incorporate new exotic genetic diversity. Countries that do not allow utility patents on varieties already limit the potential of commercially funded enterprises to access and utilize exotic germplasm. Meanwhile, the full potential breeders could apply to developing new adapted germplasm from exotic sources that could be supported by utility patents has possibly not yet been fully taken advantage of in the U.S. Social welfare goals of patents are increased when companies can agree to licensing terms. U.S. farmers have access to germplasm and traits developed by competing companies as a result of licensing. Transparency of patent information helps breeders license traits, or to breed traits out in order to access underlying germplasm.

IPP is often wrongly criticized as precluding commercial use of heirloom varieties when it is seed registration or certification laws that limit or preclude their use. Furthermore, it is often not IPP that acts as a barrier for access to varieties or traits but rather the needs to satisfy regulatory requirements associated with genetically modified traits. The types of IPP that countries utilize are very dependent upon their state of economic development and cultural heritage. UPOV periodically revises the PVP system to take account of new technological developments. Scope of patent claims is under constant scrutiny as the boundaries of scientific knowledge expand and so change definitions of innovation and nonobviousness. Policy measures relating to IPP are under discussion and debate within academia and by policy makers, legislatures, and courts. Ultimately each country will decide the types of IPP instruments to deploy according to its economic and cultural

needs and in the framework of global economic and trade agreements. What will be important is to monitor the degree of success contributed by different forms of IPP in achieving genetic gain and increased sustainable productivity in agriculture and to implement change as needed.

3.7 Conclusions

There is an ongoing change in plant breeding facilitated by technological advances in diverse fields such as information management, statistics, and mechanization fueled by increasing knowledge of the physiology and genetic basis of important agronomic traits. One goal remains fixed. That is to ever more effectively and efficiently find the best possible fit of G × E, including by crop management. Breeders understandably preferentially use advanced cultivars and recycle advanced breeding lines. Duvick (1984) referred to three sources of genetic reserves that are immediately available to breeders; (1) varieties on farms, (2) cultivars in advanced yield trials, and (3) cultivars in preliminary trials. Breeders are well aware that continued cycles of pedigree breeding in a closed system inevitably narrows diversity thereby reducing future potential for continued genetic gain. Looking beyond the genetic diversity present in a commercial pipeline of new varieties and their immediate ancestors, there is a staggeringly large potential of genetic diversity that remains potentially available for future use. For example, if one takes a conservative and admittedly overly simplistic view of genetic diversity and assumes there is an average diversity level among the entirety of maize races of 10 different allelic types at just 60 % (20,000) of the 32,000 protein coding genes found to date in the maize genome (Schnable et al. 2009), then it could be possible to create 10^{20000} unique genotypes. To place this number into context, approximately 2,000 two-row plots can be accommodated in 1 hectare so planting out this number of unique genotypes would require $10^{19996.7}$ ha, which is an area many orders of magnitude greater than the land area of the earth (14.8 billion hectares). Successful plant breeders must therefore balance short-term needs to deliver new varieties that meet or exceed the performance expectations while also generating and evaluating new diversity. This balance can be achieved by integrating "new" diversity from national or international breeding programs and from exotic germplasm adaptation and evaluation programs. Determining which germplasm to use from the vast array array of available diversity and developing best strategies to effectively explore and integrate that diversity into improved cultivars represent both critical challenges and opportunities for plant breeders.

The diversity of environments within and among farms and across broader eco-geographic areas provides a challenge to plant breeders; the requirement to have useful genetic diversity ready at hand or imminently accessible from more exotic sources. As a result of G × E and the need to achieve genetic gain, there is diversity in space and in time as new generations of varieties are developed to fit their individual areas of adaptation. The description of "massive

monocultures" of maize and soybean as described by Heinemann et al. (2013) is a misnomer because these varieties exhibit genetic diversity temporally and spatially. Nevertheless, we and others (Meul et al. 2005; van de Wouw et al. 2010) concur with the National Research Council (1993) that "the potential for crop vulnerability must be nationally and globally monitored."

The increasingly important and routine use of molecular marker data provides opportunities to facilitate the more effective use of genetic diversity. First, to identify genomic regions where there is a trend toward reduced diversity. Second, to identify important genomic regions for targeted selection. Third, to help identify new and potentially useful sources of genetic diversity. Stronger public funding is required to support international germplasm conservation, evaluation, and prebreeding programs. Strong public support is also needed to support breeding programs especially for regions and crops that do not fit the business model of commercially funded breeding programs.

There is arguably no higher priority or conceivably better form of social welfare or public good than to provide excellent stewardship and optimum use of genetic resources in the service of agriculture. The ample supply and availability of high quality food provides the basis for health, economic welfare, prospects for increasing global environmental sustainability, and a civilized society (Bronowski 1973). An initial application of molecular marker data was to better comprehend the domestication of cultivated varieties; a process that occurred some 8–10,000 years ago. Radically improved versions of these technologies now offer prospects to help more effectively conserve and sustainably utilize genetic diversity that resides, not only in domesticated species, but also in their wild progenitor species; genetic diversity that our ancestors did not source during the dawn of agriculture. Huge challenges are being placed upon agriculture to improve global productivity in a sustainable manner. There will be increased expectations that the more effective use of plant genetic resources can help meet these goals. There is a long-term public good in better conserving and making more accessible a broader base of wild and domesticated genetic resource diversity (McCouch et al. 2012). In terms of finance, the need is minor compared to other public expenditures. For the continued well-being of society, the need is ineluctable (Serageldin 2002; Ehrlich and Ehrlich 2013). Modern plant breeding will have an even more important role to play in the future.

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