

5 Biogeography, Local Adaptation, Vavilov, and Genetic Diversity in Soybean

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5.1 Abstract

It is the purpose of this paper to illustrate the impact of geography, climate, and humankind in shaping the present-day genetic diversity in soybean [*Glycine max* (L.) Merr.]. Examination of soybean germplasm collections around the globe reveals that an enormous phenotypic range in genetic traits exists in soybean, which is well beyond the phenotypic range observed in the wild progenitor (*Glycine soja* Seib. et Zucc.). Maturity date, seed coat color, plant height, seed size, and seed yield are noted examples of traits which have a wider phenotypic range in *G. max* than in the wild *G. soja*. The diversity found in domesticated soybean is the result of over 3,000 years of cultivation in which Chinese farmers selected more than 20,000 landraces (defined as cultivars that predate scientific breeding). The extensive range in phenotype embodied in landraces today is the result of the slow spread of soybean throughout geographically diverse Asia (China first, then Korea and Japan), the continual occurrence of natural mutations in the crop, and both conscious and unconscious selection for local adaptation. The more recent spread of soybean out of Asia in the past 250 years, coupled with modern breeding efforts of the past 70, has intensified and globalized the process of local adaptation and increased the phenotypic range in soybean beyond that of landraces. The increased range in phenotype for modern cultivars includes increases in seed yield, elevation of seed protein/oil concentration, and development, only within the past 20 years, of commercial cultivars that are sufficiently tall and adapted to be grown profitably near the equator. The phenotypic range and distribution observed in modern cultivars and antecedent landraces have clear biogeographical interpretations which relate primarily to genetic alteration of photoperiod response (a prerequisite to adaptation to diverse latitudes) and tolerance to climate extremes.

Although the phenotypic range in genetic traits has been expanded in modern soybean through global dispersal and genetic recombination, it is perhaps surprising that these factors have not had a corresponding positive impact on genetic diversity of modern breeding programs outside of China.. Genetic diversity in breeding programs is important as a concept, because it is a measure of the potential of a country to develop new and substantially improved cultivars. For the purposes of this paper, genetic diversity in breeding programs is defined, as ge-

netic variation among cultivars found within a particular country or country subregion. Empirical analysis of DNA marker and pedigree diversity in modern cultivars indicates that diversity is greatest in cultivars developed in China, less in Japan and least in North America. Phenotypic analysis of modern Chinese and North American cultivars follows the same pattern of diversity. Pedigree analyses of Latin American breeding programs, although incomplete, show that these programs are derived primarily from a subset of North American breeding stock and are, thus, likely to be less diverse than the North American breeding program. Decreased diversity of cultivars outside of China was also correlated with a reduction in the number of founding stock used to establish the breeding programs from which the cultivars arose.

Although conscious breeding choices, the high economic costs of breeding, and historical factors can be used to explain the reduced diversity in breeding programs outside of China vs. within, it is important to note that these results, obtained from modern breeding programs, are consistent with (1) Vavilov's principle of crop domestication, which states that genetic diversity will be greatest at the center of domestication (China in the case of soybean), and (2) the concept of Darwinian genetic drift which can be used to infer that genetic relatedness or uniformity will increase within breeding populations that are derived from relatively few founding members. A precaution gleaned from the observed trend in diversity is that all soybean breeding programs outside China, regardless of the phenotypic superiority of their genetic breeding materials, should be examined to determine the adequacy of genetic diversity. The impact of the transgenic glyphosate resistance on genetic diversity in soybean is assessed briefly.

5.2 A Brief History of Soybean

'More than 3,000 years ago, Chinese farmers used genetic diversity found in the wild to produce the crop species that we now know as domesticated soybean. Continued use of genetic diversity by farmers since domestication has improved the soybean crop to a remarkable degree, raising the yield of soybean over that of the original wild soybean by at least an order of magnitude, enhancing its resistance to an array of important diseases, and adapting the crop to grow in extreme climates. This transformation of soybean from wild plant to modern crop is one of the more remarkable achievements in agriculture, past or present' (Carter et al., 2004)

Not surprisingly, the technical details of this achievement are lost in antiquity. However, historical records reveal that soybean reached most of China and the Korean peninsula by the first century A.D., and was grown throughout Asia by the 15th century (Hymowitz and Newell 1980). In the 16th century, European visitors to China and Japan were introduced to soyfoods and, in 1712, Engelbert Kaempfer may have been the first Westerner to describe how to prepare food products from the soybean. Later in the 18th century, soybean was introduced throughout Europe and made its first appearance in North America. Samuel Bowen, a former seaman, brought the soybean to Savannah, Georgia, from China via London in 1765

and produced perhaps the first soy sauce in North America. This small enterprise did not persist beyond Bowen's lifetime, the technology was lost, and soybean was reintroduced to the farmer in North America in the early or mid-19th century, probably as a soil-building, green-manure legume crop. The earliest records of soybean in South America and Africa date to the late 19th or early 20th century (Paillieux 1880; D'Utra 1882; Itie 1910; Don 1911; Faura 1933; Burt-Davy 1905).

Despite the early attempts to establish soybean for soyfood production in the West, as it long had been in the East, the Western world did not fully understand the connection between the cultivation of soy and value of soy as human food. Thus, soybean was grown and valued more familiarly as a forage crop in the late 19th and early 20th centuries. Advances in chemistry led to the discovery, ca. 1915, that the soybean seed is a rich source of oil and protein. This changed soybean from forage to a cash seed crop by 1945 in the West and drastically increased hectareage to that of a major world crop. Recent medical findings which identify the health benefits of soyfoods have fostered considerable interest among western consumers so that we can say that 240 years after the Western debut of the crop, soyfoods have definitely arrived. Today, the USA, Brazil, Argentina, China and India are the major producers of soybean.

5.3 Domestication of Soybean

It is commonly believed that soybean had been domesticated from wild soybean during the Zhou dynasty in the eastern half of China by 1,100 B.C. (Hymowitz and Newell 1980; Gai 1997; Gai and Guo 2001). This estimate is derived from early references to soybean that appeared in Chinese literature (Qiu et al. 1999). At present, there are no archaeological findings to support an older origin of soybean. Poems from 600 B.C. mention the first recorded uses of soybean as food: soup made from soybean leaves and stew made from seed. The use of soybean as tofu and green vegetable were first documented around 1000 and 1550 A.D., respectively (Gai and Guo 2001), although tofu was probably in use by 0 A.D.

Although wild soybean grows commonly in eastern China (from 24–53°N lat.), Japan, Korea, and the eastern extremes of Russia, current theories suggest that soybean was domesticated in either the southern or central regions of eastern China (Wang et al. 1973; Lu 1977; Hymowitz and Newell 1980, 1981; Xu 1986; Chang 1989; Guo 1993; Zhou et al. 1998). Two recent studies illustrate the argument for eastern China as the center of origin (Carter et al. 2004). In the first study, DNA marker data were employed to compare landraces and wild soybean accessions in order to infer domestication patterns using germplasm from the southern, central, and northeastern areas of China. The premise of the study was that *G. max* would be most closely related to the *G. soja* pool from which it was domesticated. Gai et al. (1999) evaluated 200 *G. max* and 200 *G. soja* accessions for chloroplast and mitochondrial restriction fragment length polymorphism (RFLP) markers. These organellar genomes were selected rather than the nuclear

genome because their cytoplasmic nature had the presumed advantage of being uncompromised by potential cross pollination between *G. soja* and *G. max* over millennia and long after domestication. Assuming that the geographical distribution of present-day *G. soja* has not changed appreciably from that of ancient times, the marker data of Gai et al. (1999, 2000) indicated that significant differentiation of wild soybean may have occurred long before domestication of the cultivated soybean. *Glycine max* accessions from all regions of China were more closely related to southern accessions of *G. soja* from the Yangzi River valley than to *G. soja* accessions from any other region. These data support the idea that *G. max* was domesticated from southern *G. soja* types and then spread to other regions (Gai et al. 1999, 2000).

In the second study, Zhou et al. (1999) employed Vavilov's concept that the greatest genetic diversity for a species should be at the center of domestication. They evaluated 22,695 *G. max* accessions from China for 15 morphological and biochemical traits and concluded that the center of diversity for soybean resided within a corridor from southwest to northeast China which included Sichuan, Shaanxi, Shanxi, Hebei, and Shandong provinces. This corridor connected two centers of early agriculture in China, the Yellow River Valley and Yangzi River Valley. These two ancient centers have a long history of agricultural exchange (Gai and Guo 2001).

5.4 Rise of Genetic Diversity in Soybean

By the 15th century, soybean had migrated throughout Asia, following sea and land routes commonly traversed by tribes people of China, including the famous Silk Road connecting China with lands to the West, including India. Along these routes, soybean was adapted genetically by farmers to fit hundreds of diverse ethnic food cultures and varied climates alien to the new crop. During this time, genetically distinct landraces, the first cultivars, emerged in Japan, Indonesia, Vietnam, Korea, India, and China. Distinct landraces were documented by at least 1116 A.D., when Chinese authors listed soybean types that had green, brown, and black seed coats, and large and small seed (Gai and Guo 2001). By the beginning of the 20th century, at least 20,000 landraces may have been in existence in China (Chang et al. 1999). Perhaps 3,000 landraces were developed in Japan and 500 in India based on germplasm collection inventories in these countries (Carter et al, 2004).

5.5 Selection for Perceptual Distinctiveness

All studies to date indicate that DNA marker diversity is greater in *G. soja* than in *G. max*, reflecting the fact that *G. soja* is a much older species, and that *G. max* was probably domesticated from a small subset of the diversity present in *G. soja*

(Dae et al. 1995; Maughan et al. 1996; Li and Nelson 2002). Surprisingly, however, morphological genetic diversity is much greater among *G. max* accessions than in *G. soja*. The genetic ranges in seed coat color, seed size, plant height, plant yield, and maturity date, for example, are all much greater in *G. max*. The greater morphological diversity in *G. max* is likely due to a phenomenon which has been called selection for perceptual distinctiveness (Boster 1985). That is, ancient farmers saved desirable morphological mutants for seed size etc. as they harvested the crop over millennia. Such mutants would probably have been lost had they occurred in *G. soja*, and, thus, soybean production may have led naturally to increased agronomic diversity over that observed in *G. soja*. Farmers probably selected and saved mutations not only visually, but, perhaps, unconsciously as well by simply harvesting the crop. Agronomically useful mutants (e.g. disease resistance) would have had a selective advantage in the field and, therefore, would have had the opportunity to proliferate. Once soybean hectareage became significant, the sheer increase in numbers of plants grown, and related increased odds for mutation, may have played an important role as well. Mutations with neutral selective advantage, such as most DNA markers, may have been impacted less by humankind's husbandry of the soybean in ancient times. The reduced variability in DNA markers in *G. max* in comparison to *G. soja* would presumably have resulted from the genetic bottleneck created during the process of domestication (Hartl and Clark 1997). Agronomic diversity in maize (*Zea mays* (L.)) is also larger than in its wild relatives (Wilkes 1967; Brown and Goodman 1977; Sanchez and Ordaz 1987).

5.6 Biogeography, Photoperiod, and the Spread of Soybean in Asia

Biogeography is a late Victorian term which refers to the major influence that geography can exert over botany and zoology (Winchester 2003). Plate tectonic theory, and evolutionary concepts developed by Wallace and Darwin were nurtured, in part, by scientific interest in biogeography. Biogeography is still a useful concept and we invoke the word here in assessing the opportunity for geography to exert its influence and shape patterns of diversity in soybean. Although the concept of selection for perceptual distinction is critical in the analysis of morphological genetic diversity in *G. max*, it is humankind's trade and spread of soybean throughout Asia that has provided the opportunity for selection to be so effective. In this context, the authors theorize the following biogeographical interpretation of diversity in soybean, based on the biology of the soybean, especially its sensitivity to photoperiod.

We can assume that soybean was not genetically diverse at domestication (not withstanding Vavilov's principles of crop domestication) in the narrow sense that it probably lacked the genetic flexibility to be farmed successfully at latitudes that diverged more than about 2° (a few hundred kilometers) from the center of domestication. This is a surprisingly narrow zone of adaptation compared to most crops,

but holds for all individual soybean landraces and modern cultivars. This cropping restriction is brought about by the extreme sensitivity of soybean to small changes in photoperiod. For example, moving an adapted soybean genotype out of its zone 2° north could delay its maturity sufficiently to risk frost damage, while moving the same genotype south 2° would reduce plant height to a degree unacceptable for farming. Movement of soybean north or south through human migration or trade must, therefore, have been predicated on the discovery and use of rare genetic variants which extended the genetic range in photoperiod response (i.e., time of flowering and maturity) and allowed farmers to fit the life cycle of the crop to a warmer or cooler season, as the soybean gradually moved north or south. Once a soybean type was adapted to a more extreme photoperiod than was possible previously, the stage may have been set for further genetic improvements in productivity and function. It is theorized that these "first adapted" local landraces may have been sufficiently improved over later arriving, less adapted soybean types that first adapted landraces were preferred by local inhabitants. Thus, the first adapted landraces may have become a relatively isolated colony or gene pool. This initial adaptation to local conditions, especially at the edge of a soybean production region, could have preserved the genetic distinctiveness of soybean in a small area and, thereby, might have tended to preserve further genetic improvements in a colony, which would arise through subsequent mutation. This phenomenon of initial local adaptation and then isolation of colonies or gene pools would have been aided by the self-pollinating nature of soybean (>99%) which would limit outcrossing with later arriving soybean types. Outcrossing would also have been limited by the altered photoperiod response of established local landraces, by posing a temporal barrier to hybridization. That is, locally adapted and newly arriving landraces would likely not flower at the same time. In that regard, the striking contrasting photoperiod responses observed among landraces today are such that landraces developed from the northern extreme of Asia mature before landraces from the southern extreme flower, when planted adjacent to each other on the same day. (Gizlice et al. 1996). Such extremes are common in modern cultivars as well.

In the scenario outlined above, colonization, selection, and the noted hybridization barriers would lead to isolated pockets of soybean that diverged over millennia and came to carry unique and agronomically important alleles. Selecting out of stress tolerance alleles would seem likely during this process because of the extensive spread of soybean to extreme environments and climates as a result of human migration. For example, soybean production through millennia in central and southern China has exposed soybean to the long-term stresses of heat and drought, and to poor, acidic, mineral soils which restrict root growth. Production in northern China, by contrast, has subjected soybean to a much different environment that is cooler, has a shorter growing season, and more productive soils. Selection pressure induced by these conditions, in the long span of time since soybean's initial exposure to them, may have adapted soybean, aided by mankind, to tolerate drought or cold. A putative example of this phenomenon is found in the use of landraces from the northern islands of Japan (northernmost growing region for soybean landraces) as sources of cold tolerance in breeding. Cold tolerance has

been the basis for substantial yield improvement of soybean in Canada (Voldeng et al. 1997).

It should be noted that although the above scenario is attractive in explaining the derivation of the present extremes in photoperiod response in *G. max* described above, it is possible that they could have been generated through an alternate scenario involving one or a series of outcrosses with the progenitor *G. soja*, which, as a species, presumably had a wider range of photoperiod response and a more extensive geographic habitat than did *G. max* at the time of domestication. The alternate scenario for adaptation, in effect, requires multiple domestication events for *G. max*. However, the distinctiveness of nuclear DNA marker diversity in *G. soja* relative to *G. max* (i.e. very little overlap) coupled with the great difficulty in obtaining progeny that appear similar to *G. max* in F₂ populations derived from *G. max* and *G. soja* make this second scenario less likely than the first. In addition, breeding experience in North America in the 20th century has shown that natural mutations are quite common and that hundreds have been selected in the field, including maturity variants. Most experienced breeders have preserved several mutations in their careers, indicating that maturity mutants could probably be selected out easily by farmers in the centuries following domestication.

5.7 Global Adaptation of Soybean to Local Conditions in the 20th Century Through Breeding

Landraces derived from extensive dispersal of soybean in Asia and those arising from farmer selection nearer the center of domestication are collectively the reservoir of diversity that we have in soybean today. This diversity has formed the basis for modern breeding over the past 70 years. The breeding programs of Japan, China, and North America have all produced a large number of modern cultivars and have achieved their successes in relative isolation from each other (Carter et al. 1993; Cui et al. 2000a,b; Zhou et al. 2000, 2002).

The global spread of soybean, combined with extensive breeding efforts, has made the 20th century the most intense in the long history of soybean in terms of selection pressure for local adaptation to new climates, to new geographical niches and to new cropping systems involving mechanical harvest. To illustrate the large effect of modern breeding on adaptation, perhaps the best example is the development of novel cultivars which now grow commercially near the equator. Prior to the rise of modern breeding, few landraces grew closer to the equator than perhaps 20° except in Indonesia, the Philippines, Malaysia and southern India. About 1980, photoperiod response mutants were discovered by breeders in a few landraces and subsequently backcrossed into improved cultivars. This breeding process allowed soybean, after 3,000 years, to finally achieve high productivity at the equator and realize global adaptation (Carter et al. 1999). Soybean now grows on several million hectares near the equator and breeding programs in this zone are in the process of adapting soybean further to local conditions.

5.8 A Note on Hybridization and its Importance in Modern Breeding in Comparison to Farm Development of Landraces

It is important to note that adaptation of soybean to the Brazilian equator is a very rapid, efficient, organized, and scientific version of exactly the same process that led to the spread of soybean throughout the northern and southern reaches of Asia in ancient times. However, modern breeders have one essential advantage which separates them qualitatively from ancient farmers who selected out improved soybean landraces: that advantage is hybridization. Although it can be argued that genetic improvement in modern cultivars is due in part to new mutations which have occurred in soybean since its spread from Asia, most of the improvements in modern soybean trace to alleles derived from the traditional Asian landraces themselves (Carter et al. 2003). Breeding, the intentional hybridization of land races (and their derivatives), in the 20th century has made possible for the first time in the history of soybean an efficient process for accumulating into a single new cultivar the benefits from independent local adaptation events (landraces) which had been separated genetically and physically for millennia through geographical and botanical barriers. New cultivars and large scale production of soybean adapted to the equator proceeded rapidly only because of hybridization.

5.9 Genetic Diversity in Modern Cultivars Around the Globe

Pedigree analysis has shown that although more than 20,000 landraces have been preserved in germplasm collections globally, less than 2% of these have actually been used in modern breeding programs. Eighty percent of the genetic bases in China, Japan, and North America could be accounted for by only 190, 53, and 13 landraces/ancestors, respectively (Carter et al. 2003). Most landraces used in North American breeding are from China, with cultivars from the northern and southern parts of North America tracing primarily to landraces from northern and southern China, respectively. Because only a few of the many Chinese landraces became ancestors of modern breeding in North America or China, it is improbable that the ancestors for the modern North American and Asian breeding programs overlap greatly. A survey of random amplified polymorphic DNA (RAPD) markers for ancestors bears this point out, indicating that the genetic bases of Chinese and North American breeding are quite distinct (Li et al. 2001b).

Simple sequence repeat (SSR) marker analyses indicates that Japanese cultivars are strikingly different from North American and Chinese cultivars. Chinese and North American cultivars also form distinct populations (Carter et al. 2000). Northern and Southern regional distinctions in North America are also apparent based on these same analyses. Modern Japanese cultivars tend to be far less diverse for DNA markers than cultivars from China, indicating the possibility that

Japanese soybean may have experienced a genetic bottleneck when soybean was introduced from the mainland of Asia. The Midwestern and Southern breeding sub-pools of North America are also much less diverse than in China and are on a par with those in Japan.

Diversity of modern Chinese, Japanese, and North American cultivars has also been assessed through analysis of pedigrees, known as coefficient of parentage (Carter et al. 2003). Scores of 1, 0.5, 0.25, or 0 indicate a relation between cultivars of identical twins, brother and sister, half brother and sister, or no relation, respectively. The average coefficient of parentage between Chinese cultivars was near 0, that of Japanese cultivars was slightly greater (less than 0.10), but that of North American cultivars was 0.20 within the southern and midwestern regions, or near that of half brother and sister relation. This level of coefficient of parentage is sufficiently high to warrant concerns regarding long-term sustained breeding progress in North America.

Phenotypic diversity of modern Chinese and North American cultivars has been compared directly. Forty-seven Chinese and 25 North American cultivars were evaluated for 25 phenotypic traits in growth chambers (Cui et al. 2001). Both sets showed phenotypic diversity, though the Chinese cultivars were more diverse than North American cultivars for 24 of the 25 traits. Multivariate analysis of these phenotypic traits indicated that, with a few exceptions, phenotypic diversity in US cultivars was a subset of the diversity found in Chinese cultivars. Cultivars from the southern region of China were the most unique having, among other traits, the highest levels of seed protein content, thinnest leaves, and lowest leaf N and chlorophyll content (Cui et al. 2001).

To summarize the genetic diversity patterns in modern breeding programs, DNA marker and pedigree analyses of diversity in modern cultivars indicate that diversity is greatest in cultivars developed in China, less in Japan and least in North America. Phenotypic analysis of modern Chinese and North American cultivars suggests the same pattern. Pedigree analyses of Latin American soybean breeding programs, although incomplete, show that these programs are derived primarily from a subset of North American breeding stock and are, thus, likely less diverse than the North American breeding program (Vello et al. 1984). Decreased diversity of cultivars outside of China was also correlated with a reduction in the number of founding stock used to establish the breeding programs from which the cultivars arose.

Although conscious breeding choices, the high economic cost of field breeding, and human historical factors can be used to explain the reduced diversity in breeding programs outside of China vs. within, it is important to note that these results, obtained from modern breeding programs, are consistent with (1) Vavilov's principle of crop domestication which states that genetic diversity will be greatest at the center of domestication, which in this case is China (Vavilov, 1951), and (2) the concept of Darwinian genetic drift which can be used to infer that genetic relatedness will increase within breeding populations that are derived from relatively few founding members. A caution gleaned from this observed trend is that all soybean breeding programs outside China, regardless of the phenotypic superior-

ity of their genetic breeding materials, should be examined to determine the adequacy of genetic diversity.

5.10 Genetic Diversity and Distribution of Genetically Modified Soybeans

Resistance to the herbicide glyphosate is the only genetically engineered trait which has been commercially successful in soybean. This trait first appeared in commercial soybean cultivars about 1994 and since come to occupy about 80% of the approximately 32 million ha annual production in the USA and Canada (Sneller 2003). Currently, transgenic glyphosate-resistant soybean cultivars are very common in Argentina and indirect reports suggest that they are grown in Brazil as well (although it is not legal to produce glyphosate-resistant soybean in Brazil at present). Transgenic soybean is rare in Asia or India. Japan currently does not accept genetically modified soybean in the soyfood market trade. It appears that few if any *new* transgenic traits will be marketed in soybean in the USA in the near future, because of government agency regulatory costs. It is not likely, at present, that the transgenic glyphosate resistance trait will cause any major shifts in genetic diversity in soybean cultivars. Although intense selection on any one trait has the potential to create genetic bottlenecks in breeding, the owners of the glyphosate resistance trait have required in their licenses that all breeders backcross the trait into their own locally adapted breeding stocks before releasing a glyphosate-resistant cultivar. A recent study of transgenic and conventional soybean cultivars reported that the level of diversity within these two groups was similar based on coefficient of parentage analysis (Sneller 2003). This maintenance of diversity in transgenic soybean cultivars is clearly the result of the backcrossing effort.

The potential to produce glyphosate-resistant weeds by transference of the trait from new transgenic cultivars has received considerable attention in recent years in canola and other crops. In the case of soybean, the only weed which is capable of crossing with *G. max* is *G. soja*. *G. soja* grows only in Asia, transgenic soybean is rare in this region, and, thus, no immediate threat can be posed in terms of creation of super weeds or shifting genetic diversity patterns in the *G. soja*. However, one may ask what level of threat might be expected if all soybean production in China were devoted to glyphosate-resistant cultivars. Fortunately, the impact on *G. soja* as a weed problem is not likely to be large because *G. soja* is not an aggressive weed. Although it can be found in cultivated fields in Asia, it is not common. Of the more than 600 accessions of *G. soja* which exist in the USDA soybean germplasm collection, none were collected from cultivated fields, but instead on river courses, at railway stations, and at recently disturbed building sites. The senior author, although spending some months in China, noted only one *G. soja* plant in a cultivated *G. max* field.

5.11 Conclusion

Landraces developed in Asia are irreplaceable agricultural genetic resources because they *are* the sum of genetic diversity that was amassed by farmers during the long transformation of soybean from wild plant to modern crop. These landraces were selected by the human eye for perceptual distinctiveness, traded north and south throughout Asia to allow further farmer selection for local adaptation, and formed a series of isolated gene pools to develop biogeographical patterns which are present today. Many landraces were collected by plant explorers, germplasm curators, and breeders and are preserved today in extensive germplasm collections. These landraces serve as the basis for almost all modern improvements in soybean. Modern breeding expands the process of local adaptation initiated by ancient farmers in Asia to a global basis. The model for modern soybean breeding is hybridization of landraces (and their derivatives), development of large numbers of progeny, and selection of those rare recombinant progeny which have beneficial characters from both parents. Many breeding successes have been achieved in this way, including adaptation of soybean to the Brazilian equatorial region in the past 20 years. The legacy of genetic diversity resulting from the global spread of soybean has made these successes possible. Thus, dispersal and adaptation to local conditions in the 20th century as well as in ancient times, is a part of soybean's interesting genetic story.

5.12 References

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