Breeding: Incorporation of Exotic Germplasm

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INTRODUCTION

Exotic germplasm refers to crop varieties unadapted to a breeder's target environment, and is an important resource for crop improvement. Because genetic diversity within elite cultivars of a crop is limited compared to the variability within the species and its relatives worldwide, genes from exotic germplasm can protect the crop against new biotic and abiotic stresses, and may represent unique alleles for productivity that are absent from elite crop gene pools. Introducing substantial amounts of genetic material from exotic sources into elite crop gene pools while maintaining their productivity is difficult, however. Exotic germplasm incorporation programs require long-term commitments and appropriate breeding strategies, and may be assisted by DNA marker technologies.

CROP DOMESTICATION AND GENETIC BOTTLENECKS

Cultivars of major crops in industrialized nations represent only a small sample of the genetic variability available in those species worldwide.[1,2] Plant breeding per se often reduces genetic variation in crop species[1–3] because only superior genotypes are selected, but Darwin[4] suggested that selection by plant and animal breeders was a major cause of *increased* variation within domesticated species. Depending on circumstances, plant breeding may contribute to either increases or decreases in crop genetic variation.

Domestication of many crops involved genetic bottlenecks, initially reducing genetic diversity.[3,5] However, selection for crop adaptation to widely varying agroecological habitats and for diverse uses by farmers resulted in subsequent increases in variability. For example, bread wheat is significantly less variable than its close wild relatives because it underwent a severe genetic bottleneck during domestication.[5] Nevertheless, genetic variability exists among wheat varieties because human selection acted to preserve rare favorable variants in varieties adapted to different habitats and uses.[5] However, modern plant breeding for industrial agriculture generally results in reduced genetic variation, because uniformity of type is demanded by most farmers, commodity handlers and processors, and consumers.[2] Therefore, plant breeding per se does not necessarily reduce genetic variation. This observation provides hope that the genetic bases of modern crops can be enhanced through plant breeding.

The limited genetic variation within modern crops is a concern because it may result in widespread crop-yield and quality losses if new pathogen populations or unusual abiotic stresses occur.[2] Incorporation of new alleles from exotic germplasm that confer pathogen resistance can alleviate this genetic vulnerability.[5,6] Furthermore, improvements in crop productivity may be achieved by incorporating exotic germplasm into elite gene pools since it is highly unlikely that all favorable alleles were sampled in the ancestors of modern cultivars.

CROP ENHANCEMENTS

What is the best way to enhance crops with new alleles from exotic parents and wild species? Simmonds[1] distinguished between two general strategies: introgression and incorporation. Introgression involves backcrossing a few chromosome segments with easily identifiable effects (often disease resistances) into elite cultivars. In contrast, incorporation aims to create populations that are adapted to a breeder's target set of environments but that are also genetically distinct from elite cultivars. Incorporation requires isolating exotic populations from locally adapted populations and conducting many cycles of mild selection for adaptation while maximizing recombination. Only when exotic populations have been improved to a level of reasonably good productivity should they be crossed to elite germplasm. The aim of introgression is to disrupt elite genetic backgrounds as little as possible during the introduction of a relatively small number of exotic alleles. The objective of incorporation is to produce new breeding populations that have very high proportions of unique, exotic-derived alleles in order to broaden substantially the crop's genetic base.

EXAMPLES

Successful germplasm incorporation programs have been conducted in potato and sugarcane. In both cases,

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broad-based exotic populations were introduced to target production environments and subjected to mild selection for adaptation, disease resistance, and productivity over many generations of sexual recombination.[1] After about 20 to 30 years of selection in both crops, improved exotic populations had yields similar to local cultivars. Furthermore, crosses between local and exotic populations exhibited substantial high-parent heterosis and formed the basis for new commercial cultivars.[1]

Similarly, Goodman et al.[7] reported successful incorporation of exotic tropical maize into the narrow gene pool of agriculturally elite temperate maize. This program emphasized identifying superior exotic germplasm sources, creating selection populations by intercrossing tropical hybrids, and enhancing recombination during inbred line development by sib-mating rather than self-fertilizing. Although the tropical-derived inbreds themselves had inferior performance compared to adapted inbred lines, hybrids created from crosses between tropical-derived inbreds and temperate germplasm were agronomically competitive with commercial hybrids.

The most successful incorporation programs to date were conducted in clonally-propagated or hybrid crops because the heterosis achieved in the first generation of exotic-by-adapted crosses could be fully captured. However, many open-pollinated crops (including most forages) are not easily inbred; rather, they are managed as populations. In these crops, even though substantial heterosis often occurs in the F_1 generation of exotic-by-adapted crosses, pure F_1 hybrids cannot be created on a commercial scale.[8] However, production of semihybrids formed through population crosses could capitalize commercially on a large portion of the heterosis, and should present new opportunities for germplasm incorporation in open-pollinated crops.[8]

EXOTIC GERMPLASM IN ATYPICAL SITUATIONS

Incorporation is more difficult to implement in naturally self-fertilizing crops[9] because of two factors that hinder maintaining exotic germplasm independently from adapted populations. First, the best sources of genetic variation for many self-fertilizing crops are wild species that are entirely unadaptable to agriculture. Second, less recombination occurs during selfing than outcrossing generations. Therefore, selection within semiexotic populations created by crossing exotic and adapted germplasm is an appropriate strategy to introduce unique alleles at many loci into the narrow gene pools of self-pollinated crops, although it is not incorporation in the strict sense.

Frey and colleagues (reviewed in Refs. 9,10) extensively evaluated methods for introducing exotic germplasm into self-pollinated crop gene pools using wild and cultivated oats as a model. Their results indicated that superior transgressive segregants were obtained following a few backcrosses of wild species germplasm into cultivated oats. Another successful approach was to hybridize diverse wild and cultivated oat germplasm to form genetically broad-based populations, and to enforce outcrossing among selected early-generation lines over many cycles of recurrent selection.

Even in cross-pollinated crops, development of semiexotic populations may be required to adapt exotic germplasm sufficiently so that it can contribute to the local gene pool. For example, ‘‘conversion’’ programs to adapt exotic tropical maize and sorghum germplasm rapidly to temperate environments have been implemented to overcome photoperiod-related maturity problems.[6,7] Mild selection only for the most important adaptation characters is critical to avoid massive loss of exotic alleles from semiexotic populations before they have a chance to recombine with alleles carried on chromosomes from adapted parents.

Some attempts to incorporate exotic germplasm into elite gene pools have failed. A major difficulty is the inability to identify superior sources among the overwhelming numbers of samples stored in germplasm banks for many crops. Use of randomly chosen exotic germplasm has been unsuccessful.[7,9] Information on the breeding value of exotic germplasm sources would be most helpful[6] but phenotypic evaluations in local target environments (to which exotic germplasm is unadapted) are often worthless because beneficial alleles may not be expressed or may be masked by other genes that confer maladaptation.[1,3,7]

One approach to selecting superior exotic germplasm is to evaluate first in environments to which exotic materials are adapted. If genotype-by-environment interactions are sufficiently strong, however, there may be no relationship (or worse, a negative relationship) between the performances of exotic germplasm in their regions of origin and as breeding parents with elite germplasm in local environments. This hypothesis is testable, however, and results in maize suggest that performance within environments to which exotics are adapted sufficiently predicts breeding value in temperate environments to be useful as an initial screen for source materials.[7]

CONCLUSION

Incorporation of exotic germplasm is the best means to enhance the genetic base of modern crops substantially, but it is neither easy nor rapid. New directions for incorporation and introgression involve using DNA markers to characterize the value of specific genomic regions in

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exotic germplasm sources.[3] DNA marker analysis combined with phenotypic evaluations of exotic-by-adapted progenies permits identification of favorable alleles in exotic germplasm regardless of the effects of unfavorable alleles. Substantial gains in agronomic performance from marker-assisted backcrossing of chromosomal segments from wild tomato and rice strains into their cultivated counterparts have been reported.[3] DNA marker-assisted selection could also be used to aid exotic ‘‘conversion’’ programs by ensuring introgression of only adaptation alleles from elite into exotic germplasms. However, DNA markers alone cannot solve the primary problem of how to identify superior sources of exotic germplasm. DNA marker-based strategies may complement, but cannot replace, long-term incorporation programs based on phenotypic selection.

ARTICLES OF FURTHER INTEREST

Breeding Clones, p. 174
Breeding Hybrids, p. 186
Breeding Plants and Heterosis, p. 189
Breeding Pure Line Cultivars, p. 196
Breeding Self-Pollinated Crops Through Marker-Assisted Selection, p. 202
Breeding: Choice of Parents, p. 215
Breeding: Genotype-by-Environment Interaction, p. 218
Breeding: Recurrent Selection and Gain from Selection, p. 232
Breeding: The Backcross Method, p. 237
Crop Domestication: Fate of Genetic Diversity, p. 333
Crop Domestication: Role of Unconscious Selection, p. 340
Crop Improvement: Broadening the Genetic Base for, p. 343
Genetic Resource Conservation of Seeds, p. 499
Farmer Selection and Conservation of Crop Varieties, p. 433
Genetic Resources of Medicinal and Aromatic Plants from Brazil, p. 502
Molecular Technologies and Their Role in Maintaining and Utilizing Genetic Resources, p. 757

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