CAPITALIZING ON COMPLEMENTARY GENE ACTION IN ALFALFA

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Complementary gene action, including both allelic and non-allelic interactions especially among linkats, appears to be important for maximizing forage yields of alfalfa (Bingham et al. 1994) and has been effectively exploited through hybrid breeding in several crops. In alfalfa, cultivars have been developed as synthetic populations by phenotypic selection of several to many genotypes followed by intermating to produce enough seed for testing and then additional generations of intermating to produce enough seed for sale. This is an efficient breeding scheme for production of cultivar seed, but it does not capitalize on complementary gene action. This has become apparent in the lack of improvement for forage yield during the last century of alfalfa breeding (Holland and Bingham 1994).

In the early 1990s, we began to investigate the use of molecular markers for studying the relationship among genetic diversity, heterozygosity, and forage yield in alfalfa. The working hypothesis was that progenies from intermating genetically diverse parents would have more complementary gene action and higher forage yields; and thus, marker information could be useful for selecting seed parents. The first experiment on this idea was conducted by Kidwell et al. (1994b and 1994c) and utilized the excellent isogenic diploid and tetraploid materials developed by E.T. Bingham. The result was quite striking: genetic diversity of the parents, as determined by molecular markers, was significantly correlated with forage yield of single cross progenies, but only at the tetraploid level. This was attributed to higher levels of heterozygosity, and thus greater complementary gene action, at the tetraploid versus the diploid level.

Our desire to exploit these findings in cultivar development lead to a collaboration with ABI Alfalfa and an experiment involving synthetic populations. Kidwell et al. (1999) screened a set of 93 genotypes with molecular markers and selected sets ranging from 2 to 24 genotypes based on maximizing genetic diversity or genetic similarity. These genotypes were intermated within sets to produce seed and the progenies were evaluated for forage yield. The result was somewhat disappointing, but perhaps predictable: there were no significant differences in forage yield between progenies of genetically diverse parents and progenies of genetically similar parents. A likely explanation for this result is that cultivated alfalfa populations are approaching linkage equilibrium, thus making it difficult to select genotypes from these populations that maximize complementary gene action. The experiment did provide some interesting results relating parent number to average diversity or similarity level and to variation for forage yield. Essentially, it emphasized the need to produce progenies from a small number of parents (preferably two) to generate sufficient genetic distinction to make gain from selection.

The results of these experiments lead me to recognize the need for fixing complementary gene action as much as is practically possible in genotypes to be evaluated and ultimately in the product for sale. Synthetic populations are too heterogeneous to recognize any slight genetic advantage that one may have over another. However, progenies from single cross hybrids are much more homogenous and provide a practical means to fix all forms of gene action that contribute to forage yield. Of course, hybrids from inbreds provide that highest level of fidelity and fixation of gene action, and I believe inbreeding is worth pursuing in alfalfa, not only for its value in producing uniform hybrids but also for general genetic improvement. However, inbred improvement is a long process and in the meantime much progress can be made using non-inbred or slightly inbred genotypes as parents to evaluate hybrids.

A few years ago, we began an experiment involving population improvement based on hybrid performance. Assuming that cultivated alfalfa germplasm is approaching linkage equilibrium, we decided to create a genetically distinct population that may contain a high frequency of genes complementary to those in current alfalfa cultivars. This population was constructed by crossing the Falcata and Peruvian germplasm sources analyzed by Kidwell et al. (1994a). These were the only truly distinct populations among the nine seminal sources of North American alfalfa cultivars analyzed in that study. The F1s between these sources were intermated for several generations to help break up linkages. Individual genotypes from this population are now being evaluated for forage yield as testcross progenies derived by hybridization to two male-sterile clones from different alfalfa cultivars. We will intermate the parents having the best testcross performance and continue with the next cycle of selection. The goal is to determine if progress can be made for hybrid performance and to develop a unique population enriched for genes complementing those in alfalfa cultivars.

The commercial deployment of genetically improved hybrids will be a challenge. However, at least one system has been developed for producing commercial quantities of seed, as indicated by Dairyland's recent release of the first hybrid alfalfa cultivar. Other systems have been considered and could be developed for commercial use. The main limitation has been production of inbred parental seed and sufficient intermating among parents planted in different rows. The use of populations as parents for hybrid seed production solves the first problem. Although this would sacrifice the high degree of genetic fidelity achieved by using inbred parents, the intermating of two populations enriched for complementary gene action would theoretically be an improvement over synthetic populations. As a solution to the second problem, Brummer (1999) advocated the development of semi-hybrids by producing open-pollinated seed on mix-planted parent populations and accepting the lower percentage of hybridity in the harvested seed. Brummer and others (Rosellini et al. 2001) also have recognized the value of genetically engineered male-sterility, especially when linked to herbicide resistance. Development of this system would allow the selection of plants setting only hybrid seed or of hybrid plants in forage production fields. It is difficult to predict which hybrid seed production systems will predominate in the future, but surely these systems will be refined and utilized if rapid gain from selection based on hybrid performance can be demonstrated.

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