Oat improvement

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A BRIEF HISTORY OF OATS

Cultivated oats belong to the genus *Avena*, a diverse group consisting of seven to 29 diploid, tetraploid, and hexaploid species depending upon the splitting or jumping preferences of taxonomists (9,133,140). For the most part, they are annual, predominantly self-fertilizing species with disomic inheritance. The evolutionary relationships between the species are not entirely clear, but the hexaploids have three genomes, designated A, C, and D. A and C genome species exist among the known diploid species, although there is a great amount of chromosomal diversity within these two groups as well, and species can be classified into subgroups, such as $A_2$ or $A_3$, types based on chromosome pairing in interspecific hybrids (142). Three major groups of tetraploids exist. The ABB group seems to have autopoliploid origins in the $A_3$ subgroup of the diploid species, although it has strictly disomic inheritance, evidently due to genetic control of pairing between homologous chromosomes (140). A second group of tetraploids, the AAC group, seems to be amphiploid in origin, and is more closely related to the postulated progenitor species of the AACCDD hexaploids (140). The third group of tetraploids is the most unusual species in the genus: *A. macrostachya*, a perennial, tetrasomic, cross-fertilized species with some chromosomal relationship to the C genome (141, 204). There is only residual homology between the genomes of the diploids and tetraploids and those of the hexaploids, which suggests that speciation and polyplody are more ancient in *Avena* than in the well-known polyploid crop genus, *Triticum* (140). The extent of chromosomal rearrangement in *Avena* was first reported based on chromosomal pairing studies, although the conclusions of such studies were made difficult by the presence of genes that restrict chromosomal pairing to homologues (207).

More recent direct evidence of the rearrangements of the genomes among *Avena* species has come from comparisons of diploid and hexaploid oat molecular genetic linkage maps (183) and genome-specific in-situ hybridization cytogenetic techniques (39, 120). These chromosomal rearrangements have made gene transfer among ploidy levels more difficult in oats than in wheat (*Triticum aestivum* L.) (276).

The domestication of oats evidently followed those of wheat and barley (*Hordeum vulgare* L.), although all three crops have centers of diversity in the Middle East (129). Cultivated hexaploids made their first appearance on the global agricultural scene probably within the last 4,000 years (303). Before this time, oats had presumably existed as a wild, weedy species, well-adapted to cultivated wheat and barley fields in the Middle East, much like the modern *A. sterilis*. The domestication of oats most likely occurred outside of their center of diversity in northern Europe where man had migrated following the Neolithic Revolution. During this northward migration, early humans must have selected nonshrattering forms of the wild oats carried along with their wheat and barley from the Middle East, and these became the progenitors of the cultivated *A. sativa* (179). Records indicate that oats were considered at best a fodder crop and more often as a weed by ancient Egyptians, Romans, Greeks, and Israelis, whereas the cultivation of oat for food and feed was well-established in parts of northern Europe by the middle ages (179). Although evidence indicates the existence of oats in Britain before 600 BC, oats were not cultivated there to any great extent until after the Roman invasion in 43 AD and the arrival of Roman horses (171). The extent of oat cultivation in Europe paralleled the horse populations in the region, although oats were also grown as a staple crop primarily by farmers in Scotland, Wales, and Ireland from the early Middle Ages (171). Oats were often favored as a crop in marginal lands because they were adapted to soils that would not support wheat or barley well. Oats
were introduced into the Americas primarily by two
routes in the 17th and 18th centuries. Spaniards
introduced the cultivated red oat, A. byzantina (generally
a winter-type oat) to North and South America, whereas
English and German settlers introduced A. sativa (more	often a spring oat) to North America (179). These and
later introductions formed the original germplasm base of
North and South American cultivars. Similarly, oat was
introduced to Australia by English settlers. The spread of
oat into Asia occurred much earlier; records indicate the
cultivation of a domesticated oat in China in the 5th
century AD (251). Legget and Thomas (142) noted that
wild as well as cultivated oat species were introduced by
man into these areas.

Interestingly, there evidently have been
independent domesticaions at each ploidy level in the
genus Avena (107, 302). At the diploid level, an A,
genome species, A. strigosa, was domesticated from the
predecessor of A. westrit and A. kirtula in western Europe,
probably as a forage crop. At the tetraploid level, an
AABB species, A. abyssinica, was domesticated from a
progenitor of A. vaviloviana in Ethiopia. A. strigosa is
still cultivated today, particularly as forage species in
regions such as Wales, Scotland, and South America
(179), whereas A. abyssinica is at best tolerated as a
nonsnattering weed in barley fields (108, 159).
Throughout this review I will refer to the breeding and
improvement of hexaploid cultivated oats, the most
widely-grown species. Although A. byzantina and A.
sativa are often treated as separate cultivated species, they
will both be referred to as A. sativa.

It seems that the appearance of nonsnattering types
in wild Avena populations occurred with some rare
frequency, and that it is possible that more than one
founder population of domesticated hexaploid A.
contributed to our modern oat gene pool. This would
explain the observation that oats have a greater amount
of molecular genetic polymorphism than wheat (184),
another allohexaploid cereal crop from the same family,
Poaceae, which evidently underwent a more severe
 genetic bottleneck on its route to domestication.

OAT GENE POOLS AND GENETIC DIVERSITY

If sufficient genetic diversity were available within
A. sativa for traits of interest to plant breeders, there
would be no need to exploit wild species germplasm.
However, Coffman (44) has demonstrated that most of the
cultivars (winter and spring types combined) released in
the United States previous to 1970 were derived from
only seven heterogeneous land races. Frey (80) suggested
that similar situations probably existed wherever
Europeans introduced oats. Frey (80) also suggested that
two lines of evidence indicate the narrowness of the A.
sativa germplasm base in North America: first, is the
depletion of all useful crown rust resistance genes from
cultivated sources by 1960, and the second is the slow rate
of improvement in yield in the midwestern United States
until 1975. Evidence based on isozyme and molecular
genetic surveys and pedigree surveys of the North
American cultivars has suggested that, although there
seems to exist sufficient genetic diversity within the
cultivated North American gene pool to ensure continued
progress from selection for the foreseeable future, the
cultivated gene pool is simply a subsample of the great
diversity present in the hexaploid oats as a whole.
Rodgers et al. (216) examined pedigree relationships
among cultivars released in the north central United States
between 1941 and 1980 and found no trend toward
reduced genetic variation in more recent cultivars. They
suggested that extensive use of exotic germplasm (winter
oats as well as wild species) in breeding programs since
the 1960's helped maintain the variation. They examined
27 cultivars that were released between 1971 and 1980
and found that almost half had at least 25% of their
parentage from exotic types. Souza and Sorrells (247)
calculated genetic distance among North American
cultivars (both winter and spring types) based on
coefficients of parentage estimated from pedigrees. They
found that within the winter and spring oat groups,
modern oat cultivars were less closely related than older
cultivars, mainly because of intercrossing among regional
germplasm pools, and that winter oats seemed more
diverse than spring oats. In contrast to Rodgers et al.
(216), they concluded that new germplasm sources did not
have a major effect on cultivar diversity, as the diversity
of the overall (winter and spring oat) germplasm base was
little changed. O'Donoughue et al. (184) found that there
was a surprising amount of restriction fragment length
polymorphism (RFLP) among the 83 North American
cultivars that they assayed. Forty-six of 48 probes used
revealed polymorphisms across the cultivars, and 40% of
the cultivars could be distinguished from all other
cultivars based on banding patterns with a single probe.
Phillips and Murphy (199) conducted an isozyme survey of
405 accessions of North American cultivated oats and
also concluded that winter oats were more genetically
diverse than spring oats and that much mixing of the two
germplasm groups had occurred in the course of
breeding. They found extensive isozyme polymorphism
within the cultivated gene pool; all but 3\% of the accessions were distinguishable by isozyme profiles. The isozyme diversity present in a large sample of *A. sterilis* collections, however, was much greater than that present in the cultivated oats (180, 200). This finding, as well as the limited genetic variability for certain important traits, such as resistance to crown rust, have confirmed the need to evaluate and access wild hexaploid oat germplasm for the improvement of cultivated oat.

**The Primary Gene Pool - Hexaploid Species**

Legget and Thomas (142) have classified the genus into primary, secondary, and tertiary gene pools with respect to *A. sativa*, based on the system of Harlan and de Wet (109). The primary gene pool consists of all of the hexaploid oats. Ladizinsky and Zohary (133) grouped all of the hexaploid oats into a single biological species because they are interfertile. The lack of fertility barrier and the vast genetic diversity within some of the hexaploid species are the major advantage of their use as germplasm donors to oat breeding programs. McMullen et al. (169), however, found that meiotic abnormalities, such as univalents, occurred with greater frequency in *A. sativa/A. sterilis* hybrids than in intraspecific hybrids. The reduction in recombination associated with these irregularities would make it difficult to break linkages between useful and deleterious genes from *A. sterilis* during introgression. The need for and uses of the hexaploid oat species as germplasm donors to breeding programs have been reviewed by Frey (78,79,80).

Examples of the incorporation of useful traits into the *Avena sativa* gene pool from outside the species are given in Table 1. The examples are broken down by gene pools, as assigned by Legget and Thomas (142). Undoubtedly, most of the genes in the reservoir have come from the primary gene pool, because of the ease of hybridization and recovery of stable, fertile genotypes from crosses among hexaploids. For this reason and because of the massive genetic variability present in the species, *A. sterilis* has been used more than any other wild or weedy species in the genus. Frey (78) reasoned that because *A. sterilis* was the progenitor of cultivated oats (44) whereas *A. fatua* evolved as a weed from *A. sativa* or *A. sterilis*, only *A. sterilis* would represent a very divergent gene pool for exploitation by oat breeders. Nevertheless, *A. fatua* has undergone a separate evolution since its divergence from *A. sativa*, and examples of incorporation of traits from both *A. fatua* and *A. sterilis* are presented in Table 1. Other species are recognized at the hexaploid level but have not been exploited by oat breeders to any great extent. Comeau (48) found, for example, that many accessions of the hexaploid *A. orientalis* exhibited high levels of resistance to barley yellow dwarf virus (BYDV), but they have not been incorporated extensively into breeding programs yet.

*A. sterilis* has been exploited as a source of traits inherited in both qualitative and quantitative manners. Qualitatively inherited traits (controlled by single genes) have been incorporated most successfully into advanced breeding lines and cultivars because they could be introgressed into elite backgrounds with a minimum accompaniment of deleterious traits. These include genes conferring resistance to specific pathogen races of crown rust, stem rust, or powdery mildew. Incorporation of quantitatively inherited traits requires larger amounts of wild germplasm to be maintained in the resulting breeding lines, and accompanying deleterious traits are more difficult to eliminate. Nonetheless, several cultivars with high yield potentials introduced from a wild parent, such as 'Sheldon', 'Hamilton', and 'Ozark' with extensive *A. sterilis* germplasm and 'Mesa' with 50\% *A. fatua* parentage, have been released (Table 1). Other polygenic traits, such as high protein or oil content of the grain, high vegetative yield, and partial resistance to rust, have also been introduced into the cultivated oat gene pool through various methods. Cox and Frey (51) demonstrated that the genes for high protein content in *A. sterilis* were different from, and complementary to, those in *A. sativa*. Thro and Frey (282) demonstrated the same for genes for high grain oil content. These findings made it clear that *A. sterilis* possesses useful genes that do not exist in *A. sativa*, and that they can be extracted from accessions that are not necessarily superior in expression for the trait of interest compared with *A. sativa*.

Backcrossing has been used most extensively with qualitatively inherited traits to produce isogenic lines of cultivars, such as the nematode resistant isoline of 'Sol II' cultivar developed in Sweden (155) or the multilines cultivars developed by Frey, Browning, and coworkers in incorporate some quantitatively inherited traits into oats, but generally, the number of backcrosses was to limited to maintain expression of the desired trait. Recurrent selection has proved to be a technique particularly well-suited for incorporating genes from *A. sterilis* into adapted gene pools. Because linkage of undesirable characteristics of the wild species with favorable characteristics is a common problem with the use of wild species in breeding programs, methods to enhance the expression of the desired trait or traits, while reducing the linkage between favorable and unfavorable genes, are needed. Recurrent
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Selection provides such an opportunity, because the continual recombining of selected lines within the same gene pool should favor the accumulation of desired genes while allowing maximum opportunity for linkages to be broken and deleterious genes to be purged.

Two examples of successful recurrent selection programs in Iowa that have incorporated *A. sterilis* germplasm into the cultivared oat breeding pool were the high grain protein and high grain oil selection programs of Frey and his students. Careful selection of original parents for developing recurrent selection populations is critical. In the instance of the high protein recurrent selection program, Kuenzel and Frey (128) identified several matings of lines involving both *A. sterilis* and *A. sativa* germplasm in which the correlation between grain (caryopsis) protein percentage and grain yield was not
significant and was near zero. This is in contrast to the normally observed situation found in intraspecific crosses of *A. sativa*, where the correlation is strongly negative. McFerson and Frey (163) chose progeny from these matings to use as the source parents for recurrent selection programs to improve grain yield and protein yield. They completed three cycles of recurrent selection for grain yield. Moser and Frey (173) continued the program to develop Cycle 5 populations. Lines from later cycles of selection had greater yields and higher protein contents than standard checks included in the evaluation experiments (164, 173). The consequences of choosing appropriate parents and placing selection pressure on various components of grain yield were demonstrated clearly in this program. Different procedures of parental choice and recurrent selection were compared by McFerson and Frey (162). The “HP” population parents were chosen from the matings described above, in which there was no correlation between protein content and grain yield; high protein yield lines were selected only if both high grain yield and high protein content contributed to high protein yield. A second population (“HG”) was initiated with parents that had high protein yield principally due to high grain yield, and recurrent selections were made on this same basis. McFerson and Frey (162) discovered that the correlation between grain protein content and grain yield was slightly positive (0.13) in the HP population after three cycles of selection, but strongly negative in the HG population (-0.85). Thus, the original choice of both wild and adapted parents to initiate a recurrent selection program was critical and greatly affected the response to selection.

A second recurrent selection program involved incorporation of genes conferring high grain oil content from *A. sterilis* into the cultivated gene pool. Thro and Frey (282) determined that genes for high grain oil content from *A. sterilis* are complementary to those from *A. sativa*. Thus, although the oil contents of *A. sterilis* accessions were not found to be higher than those of cultivated oats, the possibility of enhancing oil content by combining the genes from the two species was raised (14). Branson and Frey (14) described a long process of “nobilizing” the *A. sterilis* germplasm to incorporate it into the cultivated gene pool. High oil *A. sterilis* accessions were mated to high oil *A. sativa* lines to combine the genes for high oil. The interspecific crosses were mated to agronomically superior *A. sativa* cultivars. F2 seeds from each three-way cross were sown in the field, and selections for agronomic adaptation and cultivated seed type were made among 8,000 individual plants in the field, keeping only about 8% of plants. These selections were then evaluated for oil content, and the 75 lines with the highest oil content were intermated. The F2 progeny of these matings were sown in the field and individual plants were culled for agronomic adaptation and cultivated type as before. Selections were made for high oil content, and the 55 lines with highest oil contents were then mated to a second group of *A. sativa* cultivars. These progeny were intermated at random to form the C0 base population in which recurrent selection was initiated. Three cycles of recurrent phenotypic selection for high oil content were completed on large populations of individual plants, with independent culling for agronomic adaptation and cultivated plant type preceding oil content evaluation. This program was continued through six cycles (224) and then through nine cycles (80) at a rate of one cycle per year. Throughout the program, oil content increased at about 1% per cycle. By Cycle 6, the mean oil content of the population was 14.2% (224) and by Cycle 9 it was 15.8% (74). In addition, individual lines from the populations had oil contents as high as 16.3% in Cycle 5 (224) and 18.2% in Cycle 9 (74). These levels of oil content compared with the highest oil content ever reported in either *Avena* species of 11.6% (17). Clearly, the combining of complementary genes from the two species resulted in such a success. The careful process of adapting the *A. sterilis* introgression lines before initiating selection no doubt was critical to the recovery of lines with high oil contents and competitive grain yields (14).

The concept of incorporation of exotic germplasm, as distinct from introgression of exotic germplasm, was developed by Simmonds (233) and is relevant to this topic. Whereas introgression refers to the use of single genes from exotic sources backcrossed into adapted breeding lines, its effect on broadening the genetic base of the locally adapted crop is minimal. Simmonds (233) argued that to truly broaden the genetic base of a local crop, breeders should practice exotic germplasm incorporation schemes. These should allow the introduction of the multiple genes necessary to improve important agronomic traits, most of which are quantitatively inherited, and would result in a true broadening of the germplasm base of the local crop. Unfortunately, but obviously, incorporation of genes for quantitatively inherited traits will require considerable and long term efforts compared with backcrossing programs. Simmonds (233) suggested that exotic germplasm be strictly isolated from locally adapted materials until it has been adapted to the local conditions, at which point it
could be introduced into the cultivar development programs. In the previous examples of recurrent selection using exotic oat germplasm, crossing of wild species germplasm to adapted materials at the start was essential to initiate the breeding process. The examples of recurrent selection, however, seem to fit better under the heading of incorporation rather than introgression, because the main goal and result was the introduction of many genes from the wild species into locally adapted breeding populations. They also relate to some of the other hallmarks of incorporation schemes identified by Simmonds (233): use of broad-based populations, quick and simple selection methods, enhanced recombination, and continuity of effort over long periods of time. Already, the results of these selection programs have provided valuable germplasm sources for cultivar development programs (80).

The utility of *A. sterilis* in the improvement of *A. sativa* has been convincingly demonstrated, but a problem with incorporating useful genes from this species is that there are more collections of *A. sterilis* available than one can reasonably handle. The USDA Small Grains collection, for example, holds 22,000 accessions of *Avena* species, about half of which are *A. sterilis* and *A. fatua* (293). Some breeders have tried to take the bull by the horns and have conducted massive screening of the wild species collections. For example, Brown and Craddock (17) evaluated over 4,000 *Avena* accessions for grain oil content; Comeau (47) evaluated 1,700 *A. sterilis* accessions for BYDV reaction, and Martens et al. (153) screened over 1,400 accessions of eight *Avena* species for resistance to stem rust. This approach has succeeded where the traits under selection could be identified rather simply. For researchers with access to the World Wide Web computer network, the USDA small grains collection can be reached at the U.S. National Plant Germplasm System homepage, “http://www.ars-grin.gov/npgs/.” The collection can be searched variably, including searches by species, geographic region, plant introduction (PI) or cereal introduction (CI) number, or by value of a particular trait of interest. Of greatest interest to plant breeders is the ability to search the USDA collection according to specific trait criteria. For accessions that have been evaluated for specific characteristics, such as a disease reaction, grain quality characters (e.g., oil or protein content), or morphological characters such (e.g., panicle length), the data have been entered into the database along with other information about the collections, including where and when they were collected. For example, if one is interested in all accessions that have a crown rust reaction score of less than 4 and a protein content greater than 19%, one can search the small grains collection for all *Avena* accessions (or just those of a single species) that satisfy the criteria by using the query page at “http://www.ars-grin.gov/cgi-bin/npgs/html DESC_FORM.P766.” The results of the search will be rendered nearly instantaneously, and the PI’s or CI’s of interest can be requested from the germplasm bank by electronic mail.

On the other hand, screening germplasm banks for favorable yield genes or genes conditioning other useful traits in a quantitative manner would be an overwhelming proposition. Murphy and Frey (178) developed lines expected to have 12.5% *A. sterilis* germplasm from randomly chosen collections and compared the yields of these lines to those developed from intraspecific crossings. They concluded that introgressing genes from randomly chosen *A. sterilis* accessions was a poor approach to improving yields of cultivated oats. At the time of their study “there was no established positive criterion for selecting potentially useful *A. sterilis* parents... Clearly, we need to develop methods to efficiently identify potentially superior wild parents among the myriads.” (178). Based on these results, and those of previous studies (Table 1), it seemed that genes for yield could be extracted from the wild species, but that breeders lacked some empirical method with which to choose accessions from the germplasm collections for testing. Phillips et al. (200) addressed this issue by genotyping more than 1,000 accessions of *A. sterilis* from the USDA collection by using 23 isozyme systems. Using multivariate analysis, they were able to group the accessions into six major clusters, which only partly corresponded to geographic boundaries. They noted that Turkey seemed to be a center of genetic diversity for *A. sterilis*, and this was confirmed when Hunter et al. (117) surveyed a recently collected sample of *A. sterilis* germplasm from Turkey. In addition, Phillips and Murphy (199) studied isozyme variation in 405 oat accessions representing the North American gene pool. After comparing the patterns of variation in the two species, Murphy and Phillips (180) proposed three strategies to sample *A. sterilis* germplasm for use in cultivated oat breeding programs. The first strategy was to sample from Turkish accessions, because Turkey was found to contain more *A. sterilis* genetic diversity than any other country. Second was selecting equal numbers of accessions from each of the six clusters defined by Phillips et al. (200). Phillips and Murphy (198) developed an example of a proposed core collection based on this strategy. A third strategy was selecting accessions that
possessed isozymic banding patterns absent in the *A. sativa* collections but present at intermediate to high frequencies in some of the *A. sterilis* clusters. These strategies are not mutually exclusive and could be combined. Murphy and Phillips (180) proposed that *A. sterilis* accessions (selected on the basis of these methods) be crossed and backcrossed to at least two different *A. sativa* parents to develop progenies for agronomic evaluation. An additional advantage to having the isozymic clustering information is that, having identified superior accessions for the traits of interest, one could resample from clusters found to contain the trait at higher frequencies. In addition, one could use these strategies just as well to sample accessions to screen for qualitative traits when resources are limited. To compare the patterns of diversity revealed by isozymes with those revealed by DNA markers, Beer et al. (10) used 48 RFLP probes to survey the genetic variation in a subsample of 177 of the *A. sterilis* accessions surveyed by Phillips et al. (200). They found that both isozymes and RFLPs revealed similar broad patterns of variation in the accessions, but that the correlation between genetic distance measures based on isozymes and those based on RFLPs was low (r = 0.27). Thus, where possible, breeders should select accessions based on similarity clusters developed from DNA marker information in addition to those developed based on isozyme data.

**The Secondary Gene Pool - AACC Genome Tetraploid Species**

According to Legget and Thomas (142), the secondary gene pool consists of two species, *A. marocanna* (also called *A. magna*) and *A. murphyi*. The genomes of both species were classified as AACC. Thus, these species have two genomes potentially homologous with the cultivated hexaploid species. Pentaploid F1 hybrids from crosses between these tetraploids and the cultivated species are completely self-sterile, but occasional seeds are produced when pollinated with either parental species (132, 278). Sufficient pairing between the genomes of *A. sativa* and these two species suggested that transference of genes from the tetraploid to hexaploid species via recombination is a possibility. By backcrossing these hybrids to the hexaploid species for several generations, lines with restored fertility and segregating for both cultivated and wild species traits were observed (132, 278). The high protein content and large grain size of *A. marocanna* were introduced to the hexaploid gene pool in this fashion (131, 278).

Rothman (221) described the development of a synthetic hexaploid to transfer crown rust resistance from *A. marocanna* to the cultivated hexaploid oats. Rothman (220) crossed a crown rust resistant tetraploid *A. marocanna* accession to an accession of the diploid species, *A. longiglumis*. The triploid hybrid was fertile, but by doubling its chromosome number with colchicine, a fertile hexaploid was developed. Rothman (221) found no barriers to the transfer of crown rust resistance from this synthetic hexaploid to the cultivated hexaploids.

Ladizinsky and Fainstein (132) and Ladizinsky (130) suggested a more radical approach to developing oats with the high protein contents and large grain sizes of *A. marocanna* and *A. murphyi*. Rather than attempting to introgress those traits into cultivated hexaploids, they suggested that the nonshattering trait from the domesticated hexaploid be introgressed into the tetraploids. This would allow domestication of the tetraploids directly as a new crop. Ladizinsky (130) suggested that these tetraploids, high protein oats might thrive under warm conditions to which *A. sativa* is poorly adapted. In addition, the unique grain quality of these tetraploids might lend itself to some special purpose, analogous to the use of tetraploid wheats for pasta rather than bread, for which hexaploid wheats are used. Ladizinsky (130) developed fertile tetraploid oats with the “domesticated syndrome” (nonshattering spikelets, lack of awns, and glabrous, yellow lemma) from both *A. marocanna* and *A. murphyi*. In both instances, pentaploid hybrids between the tetraploid and *A. sativa* parents were backcrossed to the tetraploids to produce BC1F1 plants differing in chromosome number. Upon selfing, some fertile BC1F2 plants with 2n = 28 and the domesticated syndrome were produced. The domesticated tetraploids from *A. marocanna* had protein contents superior to their domesticated parents, whereas those from *A. murphyi* did not; however, Ladizinsky and Fainstein (132) reported recovering domesticated tetraploids of both species with protein contents higher than that of the *A. sativa* parent.

**The Tertiary Gene Pool - Diploid Species, AABB and Autotetraploid Tetraploid Species**

Legget and Thomas (142) defined the tertiary gene pool as those *Avena* species that do not readily hybridize with *A. sativa* and often require embryo rescue to produce an F1 hybrid, which then cannot be backcrossed to the *A. sativa* without the use of colchicine to double the chromosome number of the hybrid. Such species include the AABB tetraploids, such as *A. barbata*; the autotetraploid *A. macrostachya*; the A genome diploids such as *A. strigosa*; and the C genome diploids such as *A.
ventricosa. For examples of gene introgression from the tertiary gene pool, see Table 1.

Introgression of useful genes from the tertiary gene pool generally begins with the production of alien chromosome addition or substitution lines. Chromosome addition lines have been developed from crosses between A. sativa and A. barbata, A. striigosa, and A. hirtula (276). Hybrids between A. sativa and the diploid species can be developed more easily if an autotetraploid line can be synthesized from the diploid species and used as a parent in the interspecific cross. Dyck and Rajathidy (57) used this method to develop a pentaploid interspecific hybrid between A. striigosa and A. sativa, which was backcrossed to A. sativa for several generations to develop a disomic addition line. A disomic addition line containing a chromosome pair introduced from A. barbata was used to introgress powdery mildew resistance into the A. sativa background (279). But, the line was not sufficiently stable to produce a cultivar, because the two A. barbata chromosomes did not always pair at meiosis (279).

Thomas (276) concluded that “Although there are no difficulties in producing alien chromosome addition lines in A. sativa, their instability leading to addition decay precludes their development as commercial cultivars. These lines provide useful material, however, to start further procedures of chromosome manipulation to effect gene transfers.”

Chromosome substitution lines have also been developed involving chromosomes from A. striigosa (carrying a rust resistance gene) (231) and A. barbata (carrying the gene for powdery mildew resistance mentioned previously) (277). Thomas (276) concluded that “In general, the substitution lines were superior to the chromosome addition lines, being more stable and fertile. However, the inclusion of a whole chromosome does have the disadvantage that it introduces genes other than the desired ones and this often has a deleterious effect on the development of the substitution line.” Therefore, methods to incorporate only small parts of alien chromosomes with desired genes were developed.

One effect of irradiation is to break chromosomes and produce translocations by rejoicing of the resulting chromosome pieces. Therefore, the disomic addition line developed with a chromosome from A. barbata that conferred powdery mildew resistance described previously (279) was subjected to irradiation by Aung and Thomas (4). They recovered a line with part of the A. barbata chromosome that carried the resistance gene translocated onto part of an A. sativa chromosome (4, 5). The translocation behaved normally in meiosis in the original background, but was not transmitted normally when backcrossed into certain other backgrounds (5).

Brown et al. (22) introduced a gene for stem rust resistance into A. sativa from A. barbata using a similar technique of inducing translocations. Sharma and Forsberg (232) used this method on a monosomic substitution line containing a chromosome introduced from A. striigosa via a derived tetraploid from the cross of a rust-resistant A. striigosa line to a susceptible genotype of tetraploid A. abyssinica. They recovered a stable, crown rust resistant line from a rare intergeneric recombination between the A. striigosa chromosome and one of the A. sativa chromosomes. A slightly different approach was used by Forsberg and Shands (70, 71) who developed a crown rust-resistant 6x amphiploid from a cross between A. abyssinica x A. striigosa. After crossing this amphiploid to A. sativa, developing monosomic substitution lines, and treating them with radiation, they recovered stable, rust-resistant, euploid progeny used in the pedigree of such cultivars as ‘Centennial’ (68), ‘Horizon’ (67), ‘Bay’, ‘Belle’, and ‘Dane’ (66). The major limitation to this method is that the translocation involves deletion of part of the A. sativa genome; the usefulness of cultivars carrying a translocation depends upon their ability to tolerate the loss of this chromosomal region (276).

Another approach to incorporating genes from the tertiary gene pool into A. sativa is to promote recombination between the A. sativa and alien chromosomes. There are two barriers to recombination between the cultivated and alien chromosomes. First is that the homology between the chromosomes of A. sativa and those of species in the tertiary gene pool is only residual. There is now clear evidence based on the arrangement of RFLP maps in A. striigosa and A. sativa that the chromosomes in A. sativa are considerably rearranged with respect to those in A. striigosa (183). The second barrier to recombination is a mechanism that restricts pairing to homologous chromosomes of the same genome (93, 206). Although not much can be done to circumvent the first barrier, Rajathidy and Thomas (206) discovered that a particular genotype of the diploid species A. longigermus, ‘Cw 57’; causes increased pairing between chromosomes of different genomes when incorporated into amphiploids. The effect of this genotype is much like that exploited to incorporate alien germplasm into wheat by deleting chromosome 5B carrying the Ph gene, allowing pairing of and recombination between homoeologous cultivated wheat and alien species chromosomes (214).
Thomas et al. (280) used Cw 57 to promote incorporation of a powdery mildew resistance gene into *A. sativa*. They began with a ditelocentric addition line that carried a fragment with the powdery mildew resistance gene introduced from *A. barbata*. This line was crossed to an octan amphiploid derived from the cross of *A. longiglumis* Cw57 and *A. sativa*. After backcrossing this F1 hybrid to *A. sativa* twice, a line was found to have 2n = 42 chromosomes, regular meiosis, and powdery mildew resistance, suggesting that the gene for resistance had been incorporated into the *A. sativa* genome via recombination. Although some additional germplasm was undoubtedly introduced from *A. longiglumis* during the recombination, Thomas (276) suggested that the residual, undesirable variation introduced could be removed by making additional backcrosses to *A. sativa*.

An extension of the tertiary gene pool of oats to beyond the *Avena* genus has recently been reported by Matzke (156). In a series of crosses between *A. sativa* and pearl millet (*Pennisetum americanum* L.) and maize (*Zea mays* L.), Matzke (156) recovered haploids with more than 21 chromosomes. Although most of these plants were not fertile even after treatment with colchicine, progeny of one fertile euploid (2n = 42) plant from an oat x maize hybridization exhibited unexpected variation and new characteristics. Matzke (156) suggested that this due to incorporation of genes from maize into the oat genome.

In summary, it seems that extensive genetic variation still remains within the adapted breeding stocks of oat breeders; however, some useful traits, such as disease resistances, are lacking in the cultivated gene pool and must be incorporated from other species. The hexaploid wild species, particularly *A. sterilis*, seem to be extremely valuable sources of useful genes for oat breeders. The hexaploid *Avenas* are interfertile, and extensive exploitation of simply inherited traits introgressed from *A. sterilis* to *A. sativa* has been relatively simple. Incorporation of unique genes for more complexly inherited traits from *A. sterilis* is more difficult and has been more rarely documented, but is feasible. When genes for specific traits cannot be identified in the primary gene pool of cultivated oats, introgression from the secondary and tertiary gene pools is possible, although considerably more difficult.

**HISTORICAL APPROACHES TO OAT BREEDING**

Moore-Colyer (171), tracing the history of oats in the British Isles, noted that the first recognition that locally produced varieties were distinguishable for particular qualities probably occurred in the period between 1500-1700 AD. By the nineteenth century, a great number of local varieties were recognized and classified. According to Coffman et al. (45), the mass selection technique was the first systematic method used for oat improvement in both England and Germany, and resulted in a multitude of land races in those regions. The ‘Potato Oat’ variety was, for many years, considered the benchmark variety in England, and may have been the first pure-line oat variety developed, because it was selected from a single plant in 1788 (171). H.J. Nilsson in Sweden employed mass selection in oats beginning in 1886 (124); however, after detailed investigation, he realized that the method did not provide the desired improvements and began making single-plant selections from heterogeneous populations. In Minnesota, W.M. Hays began systematic pure-line selection and progeny testing in oats in 1888 (250). Eventually, this method exhausted much of the useful variation available in the land races, and oat breeders shifted to making artificial hybridizations to generate variability for selection and to combine favorable attributes of different varieties. Shireff, in England, may have been the first oat hybridizer, beginning in the 1860’s (45). The Gartons breeding farm in England began producing commercial oat varieties from hybridizations made in the 1880’s (45); in the United States, the first variety developed from hybridization was ‘Pringle’s Progress,’ first distributed in 1875; and in 1909, Nilsson-Ehle began hybridizing oats as a primary method of developing populations in the Swedish breeding program (250, 45). Oat breeders in the United States, however, were slower to adopt hybridization methods than those in Europe, and hybridization, as a rule, did not become part of U.S. oat breeding programs until around 1925-1930 (45, 256). Stanton (250) reviewed the history and current status of oat breeding up to the time of his writing in 1936. At that time, 73% of the improved oat varieties grown commercially in the United States and Canada were pure-line selections from heterogeneous varieties originally introduced primarily from Europe. Breeders in North America were just then beginning to move thoroughly exploit hybridization techniques to increase variability in breeding populations. European oat breeders, on the other hand, had already shifted to nearly exclusive use of hybridization techniques in their breeding programs; Stanton (250) reported that 64% of the cultivars from overseas were derived from hybridization.
GENETIC IMPROVEMENT IN OATS

Several studies have attempted to assess the amount of genetic improvement for grain yield and other important agronomic traits in oats brought about by plant breeding efforts. Browning et al. (24) estimated a total increase of only 15% in cultivars developed between 1930 and 1960 and adapted to Iowa. Improvements in test weight, lodging resistance, and disease resistance were also noted, however. Langer et al. (135) studied genetic improvement in oat lines and cultivars developed between 1930 and 1973 and concluded that grain yields increased only 9% during this period, and that most of the improvement occurred in the 1930’s. Rodgers et al. (216) estimated genetic improvement in early-maturity and midseason-maturity lines and cultivars adapted to Iowa and released between 1941 and 1980. Grain yields of early-maturing lines increased only 16% between 1941 and 1976, but a burst of improvement (another 18%) occurred between 1976 and 1980. Similar, but less dramatic, improvements were found in the midseason-maturity group. Lynch and Frey (145) examined cultivars adapted to Iowa and released over a nearly eighty-year period. They concluded that improvement for grain yield was not dramatic and could only be detected in a dry, stressful environment. Also, they found that postanthesis leaf senescence was slower in more modern cultivars, which may have contributed to their superiority in the stress environment and that significant gains in harvest index were associated with grain yield improvement. Higher rates of gain were reported by Wyche and Stuthman (298), who investigated genetic improvements in Minnesota-adapted cultivars released between 1923 and 1979 and reported a 0.8% per year gain for grain yield. They also reported that more recent cultivars had improved lodging resistance, harvest index, and grain protein yield. Lawes (136) also reported a total yield gain of 30% from 50 years of European oat breeding. Congruent with the results of Lynch and Frey (145), Lawes (136) found significant increases in harvest index in newer varieties, but, in contrast, found that the yield advantage of newer cultivars was greatest in high-yield, nonstress environments. Peltonen-Sainio and Karjalainen (193) and Rekunen (212) reported that modern Finnish oat cultivars yielded, on average, 35% higher than land races. Rekunen (212) also found that Finnish cultivars developed between 1921 and 1982 achieved a 20% shortening of straw, reduction in lodging by 50%, and reduced hull content by two percentage points, whereas no improvements in test weight, protein content, or yellow dwarf virus resistance were observed. Mac Key (147) reported that Swedish oat cultivar grain yields were increased by 20% before 1920 by using pureline selection breeding from land races. No further grain yield gains were achieved until the 1970’s. Livingston and Elwinger (144) estimated the genetic gain for winter hardiness in North American winter oats by using historical data (1935-1992) from the Uniform Winter Oat Hardiness Nursery. Significant gains from breeding were observed, with the largest gains occurring before 1970.

Stuthman (256) discussed alternative philosophies of oat breeding, and the change in dominant philosophy over time. One approach to oat breeding that has been traditionally popular is “defect elimination” (55), a defensive strategy that concentrates on correcting the negative aspects of elite cultivars, such as disease susceptibilities. An offensive strategy of breeding for increased yield was not widely followed among oat breeders until the 1970’s. Stuthman (256) suggests that Donald’s (55) paper on crop ideotypes stimulated interest in pursuing offensive approaches to oat breeding, be they direct yield selection or ideotype breeding, in combination with defensive approaches. This increased emphasis on yield improvements in the 1970’s may have been primarily responsible for the increased rates of gain in yield observed in Rodgers et al.’s (216) study.

GENETICS OF AGRONOMIC TRAITS IN OATS

The genetics of many traits in oats have recently been reviewed by Marshall and Shaner (152). They noted that “The most important complicating factor is the polymerism associated with the allopolyploid condition of tetraploid and hexaploid oat plants.” As mentioned previously, A. sativa possesses three distinct genomes acquired through its segmental allopolyploid evolution (206). This implies that the genome contains genetic duplication (and triplication!), which has been confirmed by the observations that oat can tolerate some chromosome loss (207) and that multiple, unlinked loci controlling discrete traits have frequently been reported in oat (152). DNA probes used to detect AFLP loci map to two or three loci on different chromosomes (183). Compared with the alternative of hexacomplex inheritance, however, disomic inheritance with gene duplications simplifies inheritance and breeding methodology in oat considerably. For the most part, the methods used in oat breeding do not differ greatly from those used in other diploid or disomic self-pollinating crops, such as wheat, barley, or soybean (Glycine max L.).
Marshall and Shaner (152) reviewed numerous simply-inherited traits in oats, many of which are not of great interest to oat breeders. Some traits, however, such as rust resistances, dwarfness, photoperiod insensitivity, and naked seed are controlled by discrete factors and are of considerable interest in breeding programs.

Many important agronomic traits, such as grain yield, test weight (volume weight of grain), maturity, and plant height are inherited in a quantitative manner and are strongly influenced by the environment. The manipulation of these traits requires more extensive testing and larger population sizes to recover genotypes with improved combinations of desired genes. Several studies have been conducted to estimate the heritability of grain yield in oats and the relative importance of additive and nonadditive genetic variances for grain yield. The results of these studies have considerable bearing on breeding methods for oats because, for example, the relative importance of additive genetic variance for grain yield determinates, in large part, the probability of success of such methods as early generation selection for yield. Most studies of genetic variances for yield were conducted on early generation materials (generally F1 to F3) that permit the expression of dominance variance. The necessarily limited seed supplies of F1 hybrids and the inability to replicate F2 individuals, however, can confound interpretation of these studies. Escour et al. (60) reported high estimates of nonadditive genetic variance, and nil estimates of additive genetic variance and narrow-sense heritability for grain yield. They suggested that early generation selection for grain yield would likely be unsuccessful and that selection only be practiced in later generations when additive genetic variances would be higher and replication of progenies could be used to reduce environmental variances. Petr and Frey (197) estimated a broad-sense heritability of 0.53 for yield in the F2, but noted that dominance was in the overdominance range. Thus, dominance could have severely biased this estimate upward. Hatcher and McDaniel (110) found F1 high parent heterosis for grain yield. Rosielle and Frey (218) found that dominance variance was greater than additive variance, and that overdominant gene action for yield existed in the populations they tested. Because they estimated genetic parameters in populations in linkage disequilibrium, however, it was not clear if the seeming overdominance was due to truly overdominant gene action or to linkage of partially dominant genes. Stuthman and Stucker (263) developed near-homozygous lines from a diatell cross, which enabled them to estimate additive and additive by additive epistatic genetic variances in the absence of dominance effects. They found that additive and additive by additive epistatic variances were very similar in magnitude, and that epistasis reduced the correlations between parental and offspring yields. They concluded that the importance of epistasis for yield in oats was great enough to reduce the probability of success from early generation selection for yield, and make schemes such as single seed descent more appealing for oat breeding. In contrast to the preceding results, Kolb et al. (127) reported that additive gene effects for grain yield accounted for nearly 50% of the variation in F3 populations from a diallel mating, whereas specific combining ability (nonadditive) effects contributed only half as much. Summarizing these findings, Marshall and Shaner (152) concluded that nonadditive gene effects, including dominance, were usually more important than additive gene effects for yield in oats.

Given that sufficient dominant gene action exists in oats to produce high parent heterosis with some frequency, the possibility of developing hybrid oat cultivars might be appealing. McDaniel (160) reported a male sterility gene in oats, but it acted as a nuclear recessive gene, therefore it could not be used in the commercial production of hybrid oats. Even if a cytoplasmic male sterility(restorer) system could be developed in oats, Brown and Patterson (20) concluded that pollen dispersal of oats is not adequate for commercial-scale hybrid production. Therefore, oat cultivar development programs are aimed at producing inbred, highly homozygous cultivars. The relatively low narrow-sense heritabilities and relatively high importance of epistasis reported for grain yield suggest reduced gains from early generation selection. Thus, most oat breeding programs are designed to select for only highly heritable traits (such as rust resistance) in early generations and to defer selection for grain yield and other low heritability traits to later generations. Variation among lines due to additive by additive epistasis will be maximized in highly inbred lines, and at least a portion of the favorable epistatic interactions fixed in selected lines will be transmitted to progeny following hybridization. The importance of epistasis in the evolution of disomic polyploids was discussed by Mac Key (146), who suggested that dysomy is a mechanism to maintain allelic interactions in the form of epistatic interactions among homoeologous loci under autogamy, and that these interactions are critical to the evolutionary success of self-fertilizing polyploids.
SELECTION FOR YIELD COMPONENTS AND IDEOTYPES

As described above, selection for yield in early generations does not seem to be a promising strategy in oats. Thus, attempts were made to identify yield components that could be easily identified in early generations and that correlate well with grain yield in later generations. A brief review of the salient points of indirect selection are relevant here. The correlated response in trait Y due to selection for trait X can be predicted as: \( \Delta Y = \hat{h}_x \hat{h}_y r_{xy} \sigma_{xy} \) (where \( \hat{h}_x \) is the standardized selection intensity; \( \hat{h}_y \) and \( \hat{h}_y \) are the square roots of the heritabilities of traits X and Y, respectively; \( r_{xy} \) is the additive genetic correlation between traits X and Y; and \( \sigma_{xy} \) is the square root of the phenotypic variance of trait Y) (61). This can be compared with direct selection for trait Y, predicted to give the following response: \( \Delta Y = \hat{h}_y^2 \sigma_{xy} \) (61). Therefore, response to indirect selection for trait X will be expected to produce a greater response than direct selection for Y only if the inequality \( \hat{h}_x r_{xy} > \hat{h}_y \) holds true. It should be emphasized that the additive genetic correlation, not the phenotypic correlation, between the traits is involved in these equations. Even if the two traits are highly phenotypically correlated, it does not necessarily imply that they have a high additive genetic correlation. In addition, all of these genetic parameters are population-specific, and inferences about the efficacy of indirect selection from populations in which the traits were measured to the populations in a breeders' program should not be made unless it can be assumed that the populations are genetically similar. Finally, note that these equations do not take into account time or economic investments required to measure the two traits. Even if indirect selection is found to be theoretically more efficient, it should not be practiced unless the gain in response offsets any additional expenditures of time and/or money required to measure the second trait.

Chandranamuttu and Frey (36) reported yield gains of 5.6% per cycle resulting from mass selection on panicle weight in a bulk population of highly inbred lines. The genotypic correlation between panicle weight and grain yield was positive but not significant. Geiselmuller and Frey (94) reported similar yield gains from indirect mass selection on panicle weight in a bulk inbred population. They found that selection for panicle weight was the most effective indirect selection method for improving grain yield and gave results similar to those from direct selection. Panicle weight had a higher genotypic correlation with grain yield in this study, although the magnitude of the correlation was influenced by environment. These results do not imply that early generation indirect selection for grain yield will work because these selection studies were performed in populations of inbred lines, in which both additive and dominant by additive epistatic interaction effects important for grain yield would have been fixed, genetic variation among lines would have been maximized, and the genetic correlation between traits would have been greater than that found in early generations. Chapko and Brinkman (37) used selection for panicle weight in the F5 generation of three biparental breeding populations and measured response to selection in the F6 and F7 generations. They found that selection for high panicle weight did not identify lines with higher grain yields, but in some populations, selection against low panicle weight could have been used to eliminate poorly yielding lines. The phenotypic correlation between panicle weight in the F5 and grain yield in later generations was significant in only one population. They concluded that direct visual selection would probably be about as effective as, and much simpler than, selection for panicle weight. Brown and Patterson (20) concluded that "some moderately useful characteristics have been identified, but none of them provides a dependable substitute for actual yield testing under field conditions."

Grafixus (96) defined a geometric model of oat yield as the product of three yield components: number of panicles per unit area, number of kernels per panicle, and kernel weight. He suggested that yield could be improved only via improvement of the yield components; therefore, breeders should devise breeding strategies to improve the components of yield. Grafixus (97) interpreted the presence of epistasis for yield as evidence of the importance of interactions among yield components. Grafixus (96), therefore, predicted the failure of selection for yield per se without taking into account the components of yield: "Matings of high yielding selections that are as different in respect to the components of yield...will not tend to concentrate the genes for yield but will tend to maintain a population with a gene frequency near 0.5." Similar ideas led Donald (55) to propose "ideotypes" or idealized models of cereal crops, that would be developed based on knowledge of the physiology of yield and would provide a morphological and physiological target for which breeders could select. Peltonen-Sainio (192) has recently proposed an ideotype of oats consisting of numerous traits to be increased, decreased, or maintained at a present level. This was justified "Because using grain yield as a selection criterion in young generations is unreasonable."
(192) as previously discussed.

Griffis (98) found that the components of oat yield compete for similar pools of resources, resulting in negative correlations between the yield components. Griffis and Okoli (100) found in barley that the yield components compensated for one another, and that the optimum model (analogous to the ideotype) continuously changed as yield increases were attained, as environments changed, and as populations changed. Thus, the genetic and physiological parameters that are used to develop ideotypes are constantly changing as breeders make selections and introduce new sources of germplasm, and differ from one environment to another. Furthermore, many of the ideotype characters (such as leaf area index, root mass, or area of vascular tissue) suggested by Pettonen-Sainio (192) can be more difficult to measure than is yield. It is not clear if ideotype breeding strategies would improve the efficiency of breeding efforts or would make breeding more costly, time consuming, and less effective. Stuthman (256) concluded that, whereas ideotype breeding in oats remains largely untested, direct selection for yield has resulted in dramatic increases in yield. In a sense, direct selection for yield, although simpler than ideotype selection, takes into account all of the complex character interactions that determine yield, and avoids the reductionism inherent in model development. One wonders, what progress would occur from ideotype breeding if the model is wrong and the theoretical ideal is not the biological ideal, which as Griffis and Okoli (100) have shown, can easily happen.

OAT BREEDING METHODS

Popular oat breeding methods include backcrossing, bulk breeding, pedigree selection, single-seed descent, multiline breeding, and recurrent selection. These methods have been reviewed by Brown and Forsberg (18), Forsberg and Shands (72), and Brown and Patterson (20) and will be discussed only briefly here.

Parental Selection

The first step in initiating populations for selection is to choose parents to combine via hybridizations. It has often been observed that a line's performance is not a valuable indicator of its breeding value for complex traits, such as yield. In fact, Murphy (176) stated that "The selection of parents, in self-pollinated species, is largely a matter of guesswork," a conclusion with which Stuthman and Stucker (263) agreed. The reason for this may be the importance of epistatic gene action for yield in oats. Nonetheless, there are really no indicators other than line performance that can be used to select parents, so this is what most breeders rely on. In addition, for many simply-inherited traits, line performance is a useful indicator of breeding value, and parents are often chosen on the basis of having complimentary desirable traits. Often, more than two parents are required to combine all of the desirable traits into a single breeding population (72). Brown and Patterson (20) reviewed the pedigrees and breeding methods used to develop North American cultivars between 1961 and 1985 and concluded that bi-parental crosses were the most commonly used crosses in the development of cultivars, although multi-parental crosses were also used with some frequency.

Parents can be chosen from within a breeder's own populations or from lines or cultivars developed by other breeders. The United States Department of Agriculture (USDA) organizes several cooperative uniform nurseries in the United States, in which breeders from different states contribute lines for testing to a common set of entries and also carry out replicated yield testing of the set in their own environment. This provides breeders an opportunity to see how their own lines perform over a wide geographic area and how the advanced lines from other programs perform in their own environment. Traditionally, any lines entered into the uniform nurseries have been available for use as parents in hybridizations by cooperators. Several such uniform nurseries are conducted in Canada, and the Quaker Oats Company of the United States has organized a Quaker Oats South American Oat Nursery (72). Much germplasm exchange among breeders occurs on an informal basis, however. Finally, one can search the germplasm banks, such as the U.S. National Small Grains Germplasm Facility, operated by the USDA and mentioned previously, for A. sativa parents as well as those of wild species.

Hybridization

The details of oat hybridization have been reviewed by Brown (15). Briefly, oats can be hybridized in the field, greenhouse, or growth chamber, and hybridization success is dependent upon conditions favorable to oat plant growth and development. Two main methods are used for pollinating, manual pollination and the approach method. In both methods, female parents are emasculated by hand, a task that is time-consuming and must be performed with some care. Manual hybridization is accomplished by tapping a mature anther of the male parent against emasculated flowers of the female parent and covering the pollinated panicles with
glassine bags. The approach method, described by McDaniel et al. (161), involves enclosing the emasculated (female) panicle with a panicle from the male parent inside the same bag or plastic tube and allowing pollinations to occur over several days. The approach method is often more convenient when more than a single seed is required from each hybridization, as in recurrent selection or when making crosses among noninbred parents. In either instance, because only one seed can be produced from a single floret, the number of seeds produced per cross is limited by the number of florets that can be emasculated. This prevents the easy production of large numbers of hybrid seeds, as can be readily achieved in crops such as maize or tobacco (Nicotiana tabacum L.).

**Backcross Method**

Backcrossing is most often used to introgress a single, simply-inherited trait into the background of an elite, agronomically adapted line or cultivar. An unadapted parent with a trait of interest (the donor parent) is crossed to an elite parent (the recurrent parent), repeated backcrossings of the progeny to the recurrent parent are performed, and selection for the trait of interest is practiced in each generation. Ultimately, one hopes to recover a line that has the trait of interest from the donor parent but is equivalent to the recurrent parent in all other traits. Often, the trait to be introgressed is a disease-resistance gene, as when crown rust resistance genes were backcrossed into the cultivar ‘Clinton’ to produce the cultivars ‘Clinton 60’, ‘Clinton 64’, and ‘Clinton 64’ (20). Backcrossing is also used in the development of multilines, to be discussed later under the topic of breeding for resistance to crown rust. Backcrossing for only one or two generations is also used to develop segregating populations with higher gene frequencies from one parent, as was used in the development of ‘Tippecanoe’ and ‘Tyler’ cultivars (20).

Advantages of the backcross method include the introduction of useful genes from unadapted sources into cultivar-quality lines. A major disadvantage is that backcrossing requires many generations to recover most of the recurrent parent genotype, and in that time, cultivars superior to the recurrent parent can also be developed through on-going, regular cultivar-development programs.

**Bulk Breeding Method**

Breeding populations can be advanced through selfing generations in bulk by simply planting all of the progeny from a single cross in the same plot, harvesting in bulk, and replanting the progeny in the following season. This can be continued until the progenies are reasonably homozygous, for example, to the F6 generation, and selection of individual panicles from the bulk population can then be used to initiate pure lines for further testing and selection. The population will be subject to natural selection during the period that it is maintained in bulk, and mass selection can also be practiced on the population to reduce the number of inferior progenies. Frey and Caldwell (89) suggested that yield testing of bulk progeny families could be used to identify populations with a high proportion of good-yielding lines, but Brown and Patterson (20) indicated that there was disagreement on this point. Finally, bulk breeding can be practiced for a few generations, and before the population reaches homozygosity, lines can be extracted and developed by using a pedigree method for the last generations of inbreeding.

The major advantage of the bulk method is that it is extremely simple to use, and requires minimal record-keeping, planting, harvesting, or land resources. The major disadvantage is that selection cannot be practiced with great efficiency within bulk populations. The breeder may end up with many poor lines in late generations with this method. In addition, the natural selection that cannot be avoided in bulk populations may favor late, lodging-susceptible plants at the expense of more desirable genotypes that perform better in pure stands (20, 256).

**Pedigree Method**

Brown and Patterson (20) stated that the pedigree breeding method was the most widely used method in oat breeding. The fact that most oat breeding programs involve some degree of selection for resistances to diseases, such as crown and stem rust, and that these resistances can be identified in early generations very effectively by using the pedigree method is a major reason for its popularity. Selection generally begins on individual F2 plants grown in the field, often under epiphytotic conditions. Superior plants are harvested, and all of the seeds from a single plant are grown in one or two rows in the following season. Selection is practiced among and within rows and single panicles are harvested and maintained separately in each generation, until the desired level of inbreeding has been achieved. Lines are derived most often from single plants at the F4 or later generations (20). A detailed example of the use of the pedigree method in the development of the cultivar ‘Dal’ was given by Brown and Forsberg (18).
When resources allow, some breeders can advance two generations per year via pedigree selection by using off-season nurseries. Breeders in the north central United States can plant off-season nurseries in regions such as Chile or New Zealand, which have summer temperatures and photoperiods similar to those in the northern United States. Burrows introduced a gene for photoperiod insensitivity, Di-1, into his Ottawa, Canada oat breeding program, which allowed him to use off-season nurseries with short day photoperiods, such as in southern California, United States, in the development of 'Donald' and 'AC Lotta' cultivars (29, 30, 32).

The major advantage of this method is that lines inferior for particular traits can be eliminated in very early generations, and resources can be concentrated on evaluating greater numbers of better lines in later generations. On the other hand, as has already been discussed, high yielding lines cannot be identified in early generations, so selection will be successful only for traits with high heritabilities. Stuthman (254) suggested that if intense selection is placed on these high heritability traits in early generations, then variability for yield may be greatly reduced in later generations, slowing genetic gain for yield. A major disadvantage of the method is that it requires more record-keeping, more manual labor, and more field space than any of the other breeding methods. Mechanization of planting panicle-rows and computerized record-keeping can alleviate these problems to some extent.

Single-Seed Descent

Cisar et al. (43) and Brown and Forsberg (18) described a simple, inexpensive method for conducting modified single-seed descent in oats. This involves planting 120 or so F2 seeds from a single population together in a 15-cm diameter pot filled with 10 cm of sand covered with 2-3 cm of potting soil in the greenhouse. Clearly, these conditions are quite stressful to the plants, but only one seed per F2 plant is needed to advance to the next generation, and this requirement can be met under these conditions. In addition, the stress tends to speed up the life-cycle of the plants, which allows rapid generation advance. The plants are bulk-harvested and the seeds are resown under similar conditions. Two or three generations of single-seed descent can be accomplished in an off-season greenhouse this way. Thus, one can make a cross in the winter greenhouse, increase F1 plants in the summer field, and have F4 or F5 plants developed through single-seed descent in the field the following summer. At that point, selection among individual inbred plants can be practiced in the field and panicle-derived lines can be evaluated in nursery rows or hill plots in the following season. A detailed example of the use of single-seed descent in the development of 'Ogle', the most widely adapted oat cultivar developed in the United States, was presented by Brown and Forsberg (18).

The simple and extremely rapid development of inbred progenies is the major advantage of this method. Disadvantages include the possibility of natural selection acting against favorable genotypes during the stress of the process. Cisar et al. (43) investigated this possibility, and although they found some evidence that genetic variability was reduced from higher density plantings during single-seed descent, the mean grain yields, plant heights, and maturities were not affected by the single-seed descent method.

Recurrent Selection

Recurrent selection has been less popular with oat breeders mainly because of the difficulty in making the many crosses required; however, several examples of recurrent selection in oats indicate that the method is a useful complement to other breeding methods. Stuthman et al. (257) reviewed their experience with recurrent selection for high yield in a population developed from 12 inbred parents in 1968. To date, seven cycles of recurrent selection have been conducted (256), and the results through cycle 5 have been presented by Pomeranke and Stuthman (205) and Stuthman et al. (257). This method involves combining 21 selected parent lines each generation to make 63 crosses, advancing ten lines of each cross via single-seed descent to produce 630 total F4-derived F6 (F4:6) lines. Replicated yield tests of the lines were performed in one location for one year, and the best line in each of the best 21 crosses was selected to develop a new cycle population (255). Each cycle required three years to complete. Note that the extensive inbreeding achieved before yield-testing allowed fixation of epistatic combinations. Five cycles of selection produced a total grain yield gain of 40%, an average of 2.5% per year increase (205); however, lines in later populations tended to be taller and later because of the positive correlations of these traits with grain yield. These undesirable, correlated changes have prevented any of the recurrent selection lines from being released as cultivars directly, but they have been extremely useful as parental lines in the University of Minnesota breeding program (256). To correct some of these deficiencies, Stuthman "opened up" the closed population by also mating the parents of the fourth cycle to two agronomically elite cultivars, selecting
the best progeny lines for intermating, and initiating a new population for recurrent selection (256, 257).

Frey et al. (91) developed a method for conducting one cycle of recurrent selection per year in spring oats. The yearly cycle begins in the fall greenhouse (August to December), when crosses are made among selected parent lines to develop 50 progeny seeds. In the spring greenhouse (December to March), the 50 progeny are increased and harvested individually to form 50:1 lines. These lines are sown during the summer (March to August) in the field and evaluated for the trait of interest to allow selections to be made and new parents chosen for the next cycle.

Frey’s program at Iowa State University utilized the method extensively to develop populations selected for high levels of particular traits. Examples of recurrent selection programs to increase the grain protein yield and grain oil content have been presented previously. In addition, recurrent selection programs have been conducted to increase test weight and grain yield (125), grain b-glucan content, and grain yield and adaptation (74).

A major advantage of the recurrent selection method is the enhanced opportunity it provides for recombination during the selection process. As mentioned before, this is critical to promote the breaking of linkages between favorable and unfavorable genes introduced from wild relatives or other exotic germplasm. It also provides opportunities to make dramatic genetic gains rather quickly in the trait under selection. On the other hand, it has the disadvantage that extensive crossing among parents is required to develop each cycle. Also, the gains made in the trait under selection may be offset by correlated changes in other traits. This can be avoided to some extent by making selections based on a multiple trait index, but the rate of gain for any individual trait will be slowed. In addition to its use as an applied breeding method, recurrent selection provides excellent material with which to investigate the genetics of, and the correlations among, important traits, because it involves closed breeding populations and precisely defined selection criteria and intensities.

Field Evaluations

Yield evaluations are most often conducted by using 4-row plots of minimum size 1 x 3 m². Replicated testing in multiple locations and years is critical for identifying high-yielding lines; however, extensive testing of breeding lines is resource-intensive. Therefore, breeders attempt to eliminate as many inferior lines as possible before advancing materials to multi-environment yield tests. Selections can be made visually on highly heritable traits, such as disease resistance, during early generations by using the pedigree breeding method. Breeders who use bulk or single-seed descent methods can also evaluate their unselected, late-generation lines in unreplicated breeding nurseries to eliminate poorly adapted or disease susceptible lines. The University of Illinois program has had good success with the use of augmented designs (62) to evaluate yield potential of unreplicated experimental lines in yield trial-sized plots (20). On the other hand, short single-row plots are often used for nursery evaluations, because these plots can be planted with great ease by using seed-tray type planting machines. Various methods are used to induce epiphytotic conditions in nurseries to permit disease screenings. Late planting of nurseries is a simple but effective way to induce infection of plants by large pathogen populations. Artificial inoculations of susceptible spreader-rows planted at regular intervals in the nursery can also be performed.

Hill plots have also been used as an inexpensive alternative to evaluate large numbers of experimental lines for yield and disease resistance. Frey (76) proposed the use of hill plots, each planted with 20-30 seeds and spaced 30 cm apart on a grid for yield evaluations. The plots can be easily planted by hand with jab planters or by machine into small field areas. Frey (76) reported genetic correlations between hill plots and large 4-row plots of 0.98 for grain yield and 0.96 for both plant height and heading date. Pomeranz and Stuthman (205) reported highly significant phenotypic correlations of 0.85 for grain yield, 0.81 for seed weight, and 0.69 for seed number between hill plots and row plots. Because hill plots require fewer seeds per entry and numerous plots can be planted with ease in a small area, they have been used in all of the recurrent selection programs at Iowa State University and the University of Minnesota.

**Breeding Objectives**

The objectives of any oat breeding program should be determined primarily by the role of oats in the farmer’s cropping system and by the end-use of the oats. The importance of various traits in a cultivar will be determined by whether the oats are to be used on-farm or marketed off the farm and by other purposes the oats will serve. On the other hand, some traits are of primary importance irrespective of the particular use of the crop. Virtually all oat breeding programs are aimed at
improving grain yield, test weight, lodging resistance, disease resistance, and grain protein yield; however, the value of other traits is determined by the end-use of the oats, and some traits valuable for oat millers may be less desirable for on-farm use. For example, an ideal oat cultivar for oat millers might possess high grain percentage, low grain oil content, high grain protein content, and high grain β-glucan content. In comparison, a farmer who intends to use the oats on-farm might prefer a cultivar with high grain oil percentage, low β-glucan content, high protein content, hull-less kernels, high straw yield, high forage yield and quality, grazing tolerance, and good companion cropping ability with forage legumes. Thus, although some breeding objectives are common to different end-use goals, breeders may be forced to bifurcate their programs to meet multiple breeding objectives.

**Crown Rust Resistance**

Crown rust, incited by *Puccinia coronata*, is considered to be the most damaging oat disease on a worldwide basis (105). Crown rust can reduce grain yields and quality, forage yields and quality, and promote lodging (187). Up to 30% yield losses due to crown rust on susceptible varieties have been reported (59, 87). Seed weight, grain percentage, and protein yield are also reduced by crown rust (240, 241, 248).

The original approach to breeding for resistance to crown rust was to identify and incorporate single genes that provided complete resistance to rust. Most of these types of genes used in the United States were derived from the introduced land races and varieties, such as 'Victoria', 'Bond', 'Landhafer', and 'Ascencio' (45). It was soon realized, however, that the effectiveness of these genes generally did not last longer than 5 years after they were released in pure-line cultivars (24). These single-gene races were rapidly "overcome" by new races of the pathogen that evolved under the selection pressure exerted by large acreage of resistant hosts. Harder and Haber (105) noted that the virulence patterns of rust populations tended to be relatively stable over time within a given geographic area, but the virulence of the population can shift dramatically when a single gene for resistance is widely distributed. This occurred in the United States during the 1940's when most oat cultivars possessed rust resistance derived from 'Bond' and again in the 1950's when resistance from 'Landhafer' was widely distributed. In both instances, races that were virulent to those genotypes evolved and became predominant in the rust population (87). The manner of evolution of new virulences in rust populations is still debated. Buckthorn (*Rhamna cathartica* L.) is an alternate host for *Puccinia coronata* and which the pathogen can reproduce sexually, in contrast to the limitation of asexual reproduction on oats. Sexual reproduction on buckthorn helps to create and maintain phenotypic diversity for crown rust virulence (42); however, Simons et al. (239), Simons (237) and Harder and Haber (105) concluded that sexual recombination on *Rhamna* was not a critical factor in the evolution of new races. Dinoor et al. (54) suggested that sexual recombination may be important, but that mutation was a potentially powerful force driving evolution of new virulences. In addition, asexual variation and hybridization between different forms of specialized *Puccinia* could be important factors, although the latter has not yet been proved to occur in nature (54).

Regardless of the manner in which it occurs, the evolution of virulence in *Puccinia* populations was rapid enough that by the 1960's, all of the rust resistance genes derived from the *A. sativa* land races were rendered useless (80). Murphy et al. (177) reported that *A. sterilis* was a valuable source of unique genes for crown rust resistance, and the effort from that time on was to introgress genes from *A. sterilis* into cultivated oats. In addition, genes for rust resistance were identified in the secondary and tertiary gene pools and introduced into breeding programs (see Table 1). Unfortunately, the resistance genes from *A. sterilis* have proved no more durable than those from *A. sativa*. Chong and Kolmer (42) found that the frequency of virulence to resistance genes derived from *A. sterilis* such as *Pc38* and *Pc39* increased rapidly in *P. coronata* populations in regions of Canada where cultivars possessing the genes were grown on a wide scale in the 1980's. As before, effectiveness of the resistance genes was limited to only about five years. Frequencies of virulence to genes not used in commercial cultivars, on the other hand, remained at low levels (42).

Recognizing that the durability of single-gene resistance was limited, no matter what source they were derived from, oat breeders began to search for ways to improve the durability of genetic resistance to crown rust. One such method is through "gene deployment," wherein breeders in different regions agree to release cultivars with different sets of resistance genes, which should put disruptive, rather than directional, selection pressure on the pathogen population (87). Another approach, "gene pyramiding," is to combine multiple race-specific resistance genes into a single line. The genes *Pc38* and *Pc39* derived from *A. sterilis* were combined into a single genotype by researchers at Winnipeg, Canada and
released as a gene combination in the cultivars 'Dumont', 'Riel', and 'Robert' (168). In addition to Pc38 and Pc39, 'Dumont' possesses at least one other gene for crown rust resistance (41). 'Steele' and 'Valley' cultivars were developed in North Dakota, United States, with the Pc38/Pc39 gene combination (168); however, simultaneous virulence to both Pc38 and Pc39 became frequent in Canadian rust populations after the release of cultivars with the gene combination (42).

Another approach to increasing the durability of resistance to crown rust is the development of multiline cultivars. Jensen (122) first proposed multiline varieties as a mixture of different but agronomically uniform pure lines. Such a variety would combine the favorable agronomic aspects of a uniform cultivar with greater stability across different environments and pathogen populations. Frey et al. (84, 85, 88) and Frey & Browning (82, 83) developed and released the first multiline varieties of oats, a series of cultivars named 'E66' through 'E77' and 'M68' through 'M73', by backcrossing rust resistance genes from both A. sativa and A. sterilis with resistances to various spectra of races into a common, agronomically superior recurrent parent. The resulting isogenic lines were combined by mixing seed to form the multiline cultivars. Frey (77) described the features of multilines that affect the usefulness and durability of their resistance. One is that multiline varieties delay the build up of inoculum during the course of epiphytotic by "spore trapping," in which spores with particular virulence genes may reproduce on some isolines in the variety, but many spores will fall on resistant isoline hosts. This reduces the amount of diseased tissue over time and, consequently, reduces the amount of yield and quality damage suffered by the variety. Multilines theoretically should also maintain their levels of resistance longer than pure-line varieties because they exert stabilizing, rather than directional, selection on the pathogen populations (77). Although this claim would be difficult to verify experimentally, Frey (77) noted that the resistance of the original multiline varieties had not decreased 13 years after their release. The major difficulty in developing multiline cultivars is the extensive backcrossing required, which tends to restrict the yield potential of the variety to that of the recurrent parent. After five generations of backcrossing, the recurrent parent might be agronomically inferior to newly released cultivars developed by "offensive" breeding schemes.

Yet another approach to developing oat cultivars with durable rust resistance is the use of any one of various forms of partial resistance. Stuthman (256) discussed the strategy developed by Moore, who selected breeding lines with intermediate reactions to rust in a buckthorn nursery in Minnesota. In this way, Moore selected for two characteristics of durable resistance: generalized resistance, that is, resistance to a broad spectrum of races produced by the alternate hosts (239) and partial rather than complete resistance by selecting for intermediate types. These characteristics are not the same because broad-spectrum resistance is not necessarily partial resistance, and partial resistance is not necessarily race nonspecific. But, the two characteristics often occur together (hence the frequent use of the terms interchangeably) and in combination they theoretically provide more durable resistance than race-specific, complete resistance, because selection pressure on the rust population is reduced and not directional (236). In addition, partial resistance is usually considered to be polygenically inherited, whereas complete resistance is often considered to be mono- or oligo-genically inherited; although there are exceptions to both (13, 236). In any event, Stuthman (256) noted that 'Portage', a variety identified as partially resistant in the buckthorn nursery has maintained its partial resistance from its release in 1960 to the present, testifying to its durability.

Various forms of partial resistance have been described, and it is not entirely clear if they are manifestations of different mechanisms of resistance; however, all have the potential to decrease damage from crown rust in a durable fashion. Terms such as "moderate resistance," "early telia," "slow rusting," and "tolerance" have been applied to various phenomena associated with partial resistance (236). Early telia refers to the effect of some oat genotypes on Puccinia, in which the pathogen enters the telial phase of its life cycle more quickly than on other genotypes. Because the telia (unlike uredia) can infect only the alternate host and not oats, this type of resistance tends to slow the growth of the pathogen population on oats. Slow rusting refers to reduced rate of pathogen buildup in certain varieties. Tolerance refers to genotypes that achieve more of their yield potential under heavy rusting compared with other varieties.

Simons (236) suggested that partial resistance is most clearly expressed in the field, and evaluations should only be conducted in the field. Brake and Irwin (13), however, have suggested that evaluation of genotypes according to uredia density on particular leaves of young greenhouse-grown plants could also be used to identify partially resistant genotypes. Because the heritabilities of partial resistance traits are generally low (236), large numbers of progenies must be screened to identify
superior types. The use of a buckthorn nursery is one way to accomplish this. Simons (236) suggested that hill-plot evaluations could be useful for screening large numbers of progeny for partial resistance in the field. Because identification of partially resistant lines can be difficult based on just disease phenotypes, measurement of tolerance traits is a more reliable alternative (236). By using split-plot experiments in which one whole plot was inoculated with crown rust and the other was maintained rust-free, Simons (234) was able to estimate tolerances for grain yield and 200-kernel weight of many lines grown in hill plots. Tolerance ratios were calculated by dividing the trait measured in the rust-laden plots by the trait measured in the rust-free plots. Simons (234) concluded that tolerance ratios for 200-kernel weight were reliable and simple estimates of tolerance. Heritabilities of yield and kernel weight tolerance ratios were large enough to allow progress from selection for tolerance in either trait (235); however, tolerance is, in some instances, negatively associated with yield potential (237), therefore, breeders should not ignore yield potential when selecting for tolerance. Other component traits of partial resistance, such as hyphal growth rate, time from infection to sporulation, and spores per pustule, have been described (237), and they could also be used for selection for tolerance. But, such traits are not easily measured on large numbers of progeny, and their utility in breeding programs is limited.

Simons (236) suggested that partial resistance need not be used alone and could be combined with single-gene types of complete resistance. If this is to be done, the breeder should be aware that the effects of major genes will mask those of minor genes, leading to eventual elimination of minor genes from the breeding population, which has been termed the "Verticillia effect" (50, 236). By maintaining genes with minor effects on resistance separately from those with major effects in some breeding populations, this effect can be avoided.

Barley Yellow Dwarf Virus Tolerance

Barley yellow dwarf virus (BYDV) is probably the second most damaging disease of oats worldwide. Good estimates of yield reductions caused by this disease are difficult to obtain, but have ranged between 20% and 50% in Australian and New Zealand studies reviewed by Johnstone (123). The epidemiology of this disease is quite complex and not well-understood, because it involves different strains of the virus, multiple insect vectors that can move over long distances, and many wild and cultivated host species that can potentially act as reservoirs of inoculum (111, 123, 203). The most important vectors of the disease for oats are the aphid species Rhopalosiphum padi L., R. maidis Fitch, Macrosiphum avenae Fab., Schizaphis graminum Rondani, and Metopolophium dirhodum Walker (105). Jedlinski et al. (19) and Skaria et al. (243) found that field tolerance (reduced symptoms) was associated with lower virus titer levels, suggesting that mechanisms of true resistance exist in oats, but Burnett et al. (28) concluded that this may not be universally true.

Tolerance is normally assessed by visual scoring of germplasm under field infection. Burnett et al. (28) suggested that disease expression in the field could be improved by space planting, late planting, planting aphid trap crops early in disease nursery, rearing infective aphids in the greenhouse to use for artificial infestations, and replication of entries. Comeau (47, 48) screened extensive collections of many species of Avena for tolerance to BYDV and identified many useful sources of tolerance, particularly in A. sterilis and A. occidentalis. Sources of tolerance have also been identified within A. sativa, and germplasm lines with superior tolerance have been developed through breeding at the University of Illinois (19, 26). Burnett et al. (28) cited a number of cultivars with good tolerance to the virus.

Brown and Poehlman (21) reported that tolerance to BYDV behaved as a quantitative character with a broad-sense heritability ranging from 23% to 51%, with higher heritabilities found in crosses of tolerant by susceptible lines compared with susceptible by susceptible crosses. Landry et al. (134) studied the heritability of BYDV tolerance in crosses of resistant A. sterilis and A. sativavines to a common susceptible A. sativa line. They reported broad-sense heritabilities ranging from 88% to 98%, and suggested that 2 to 4 genes controlled tolerance to BYDV in these populations. Gourma et al. (95) reported heritability estimates ranging from 50% to 90%. Bultenberger et al. (7) achieved a 20% improvement in the mean BYDV tolerance score from two cycles of recurrent phenotypic selection in a population developed from winter oat by spring oat crosses. Gourma et al. (95) investigated the strategy of selecting against BYDV susceptible F2 plants in the greenhouse with artificial aphid inoculations. They found the method to be moderately successful in eliminating susceptible types from tolerant by susceptible crosses but not effective in tolerant by tolerant populations. Thus, with good field techniques, it seems that improvement of BYDV tolerance is feasible in most oat breeding programs. Harder and Haber (105), however, cautioned that visual
evaluations of tolerance can be misleading. In addition, the correlation of BYDV tolerance with yield potential is not known. Another potential difficulty that has not been investigated is strain-specificity for tolerance or resistance to BYDV. This could be problematic, given the genetic variation detected among isolates of the virus.

**Resistance to Other Diseases**

Other diseases, such as stem rust, powdery mildew, nematodes, and smuts are important in particular regions. Breeding for resistance to such diseases has been reviewed by Forsberg and Shands (72) and Ohm and Shaner (187).

**Lodging Resistance**

Lodging in oats can cause serious losses in grain yield and test weights of oats (194, 182). The increased use of intensive management practices, such as fertilization and irrigation, on oats has increased opportunities for lodging (148). Difficulties of breeding for improved lodging resistance include: low heritability, difficulty in measuring the trait because of high environmental influences, tendency to underestimate lodging severity in small plots, and the difficulty of combining lodging resistance with high yield (148). Correlations of various characters with lodging resistance have been measured in an attempt to provide breeders with easily measured traits that can be used to select for lodging resistance. At best, peduncle and internode diameters were reasonably well correlated with estimated lodging resistance \( r = 0.63 \) (11). Two indirect methods of estimating lodging resistance have been used: the “snap test” described by Marshall (148) and the “cLr” method developed by Grafius and Brown (99). The snap test is performed by grasping a group of panicles, pulling the plants back about 45°, and noting the resistance and resiliency of the straw as they are released. The cLr method involves measuring the number of links on a chain hung from the panicle that a stem will support. Although the snap test requires considerable experience, Marshall (148) suggested that it is the most useful measure of lodging resistance available to breeders because it can be used in years when lodging does not occur. It is rapid and simple, and it has good correlation to observed lodging when such does occur.

Interest in the use of dwarfing genes to improve lodging resistance in oats has increased recently. Two qualitative genes of primary interest have been identified, Dw-6 and Dw-7. Dw-6 was reported by Brown et al. (23) and has been used in many breeding programs around the world (148). The Dw-6 must be combined with a peduncle extender gene \((pl-1)\) to ensure that the panicles will emerge fully from the boot (30). The Dw-7 gene lacks this problem and has been released in parental lines such as ‘Penline 116’ and ‘NC2469-3’ (149, 151). The use of semidwarf varieties is attractive for producers who grow oats primarily for marketing off-farm, but not for farmers who rely on the straw produced by oats for animal bedding on-farm. In the latter instance, straw yields should be given some consideration in addition to grain yields and lodging resistance.

**Protein Content**

The oat grain has a nutritionally superior amino acid profile compared with wheat, rye (Secale cereale L.), or barley because it contains higher levels of all of the “essential” amino acids (291). The superior amino acid profile of oats seems to be constant over varying levels of total protein content (75). Therefore, an important breeding objective has been for increased protein content to improve the feed value of oat grain for animals and also the nutritional quality of the grain for humans. The correlation between protein content and grain yield was often reported to be negative (118, 249). Two observations in particular have made clear a physiological basis of the negative correlation. One is that varieties that differ in protein content (percentage of protein in the grain) do not necessarily differ in absolute amount of protein in the grain. Cataldo et al. (34) observed that the difference in protein content between a “high” protein cultivar and a “low” protein cultivar was not amount of protein, but rather the amount of carbohydrate in the grain. The low protein cultivar had higher amounts of carbohydrate in the grain, leading to higher grain yields, but also to lower protein percentages even though the amount of protein was the same in high and low protein cultivars. A second observation was that grain protein percentage was higher in shattering vs. nonshattering progeny of an interspecific cross of A. sativa x A. fatua (210). Earlier termination of carbohydrate deposition in the shattered grains may have promoted higher protein content at the expense of higher grain yield.

For this reason, it is clear that both grain yield and protein percentage should be considered during selection (72). One manner in which this is accomplished is by basing selection on protein yield rather than content. McFerson and Frey (162) demonstrated that selection on the basis of gross protein yield was successful in improving yield without a reduction in protein content. Forsberg and Shands (72) suggested that “concurrent
reciprocal selection" could achieve the goal by selecting in two different gene pools. Both grain yield and protein content were used as selection criteria, but their relative weights were reversed in the two gene pools. It was proposed that crosses among the two gene pools would produce lines superior for both traits. Several agronomically competitive high protein cultivars have been released in the United States, including 'Dal', 'Olee', 'Goodland', 'Spear', 'Preston', and 'Prost' (72).

Another approach for improving protein concentration in oats is through the use of *A. sterilis* parents as donors of high protein genes. Cox and Frey (49) demonstrated that genes for high protein yield from *A. sterilis* were complementary to those already found in *A. sativa*, leading to high protein content transgressive segregants from matings of *A. sativa* and *A. sterilis*. Ohm and Patterson (186) reported low, nonsignificant correlations between protein percentage and grain yield in one set of *A. sativa* x *A. sterilis* matings. Twig and Ohm (118), when screening many lines from such an interspecific cross in which the correlation between protein content and grain yield was negative, still found some lines with both high protein content and seed yield. Also, as discussed previously, Kuenzel and Frey (128) identified particular interspecific crosses in which the correlation between grain yield and protein content was not negative, and progeny from these matings were used in a recurrent selection program. Thus, the incorporation of genes for high protein content from *A. sterilis* has helped breeders overcome the often negative correlations between favorable traits.

**Milling Quality**

Milling quality refers to the value of the oat grain to millers producing food for human consumption. These include physical factors, such as kernel weight, size, shape, and grain percentage and also biochemical factors such as protein, oil, and β-glucan contents of the groats. Milling yield is the mass of whole oat grain required to produce a particular mass of rolled oats, such that low values of milling yield are desired by oat millers. Both test weight and grain percentage are valuable indicators of milling yield, because they have significant negative correlations with milling yield (i.e., higher test weight is correlated with a favorable lower milling yield), and they can be assessed easily by using only small amounts of seed from experimental breeding lines.

**Test Weight**

Test weight is the standard indicator of grain quality because of the ease and speed of grading oats in the marketplace (69). Test weight has broad sense heritability in the range of 60% - 90% across many different populations (191, 202, 294). Test weight seems to be controlled primarily by additive gene action with lesser contributions from epistatic gene action (201, 202). Both positive and negative correlations between grain yield and test weight have been reported (191, 202, 246). Thus, the possibility of simultaneously improving test weight and grain yield exists. Klein et al. (125) found that test weight could be increased by using recurrent selection, but that yield was decreased unless both test weight and yield were selected for by using an index, which resulted in the simultaneous improvement of both traits.

Forsberg and Reeves (69) noted that the following traits influenced test weight: kernel and grain size and shape, grain density, hull thickness and length, grain percentage, the presence of awns, and disease resistances. As differences in some of these traits, such as kernel size and shape, disease resistance, and the presence of awns, can be easily scored visually, they can be used as indirect selection criteria for test weight in early generations. They suggested that direct measurement of test weight be delayed until later generations when sufficient seed is available to obtain accurate estimates.

**Grain Percentage**

Grain percentage is an important indicator of grain quality but has been used less extensively by breeders and grain marketers mainly because rapid, accurate measures of grain percentage are not available. Reasonably quick and reliable estimates of grain percentage, however, can be made using small samples (as few as 15 to 25) of primary kernels (294). Estimates of broad-sense heritability of grain percentage have been reported to range from 20% to 92% in different populations (258, 294, 295). Forsberg and Reeves (69) reviewed the literature on relationship between grain percentage and grain yield, which frequently has been reported as nonsignificant but also positive in some studies and negative in others. Bunch and Forsberg (27), who found a negative relationship between the two traits, concluded that stringent selection for grain percentage should not be used in early generations to avoid eliminating high-yielding genotypes.

**β-glucan Content**

Cultivars with high levels of β-glucan in the grain are of interest to millers because of the desirable effects of
b-glucan on human health. Welch (290) summarized the results of 37 studies on the effect of oats in human diets, and concluded that there was strong evidence for efficacy of oats in lowering plasma cholesterol levels. Furthermore, the oat soluble-fiber fraction, which consists primarily of b-glucan, seemed to be responsible for the effect. Amran and Graham (2), Peterson (196), Lim et al. (143), and Welch and Toney (292) have reported significant differences among genotypes for b-glucan content. Brunner and Freed (26), Peterson (196), and Lim et al. (143) found significant genotype-by-environment interactions for b-glucan content. Brunner and Freed (25) reported broad-sense heritability estimates for b-glucan content of 41% and 54% in two single-cross populations. Holthaus et al. (114) reported a broad-sense heritability estimate of 55% in a large, diverse sample of midwestern U.S. breeding lines and cultivars. Additive gene effects seemed to be most important for the trait (114). Positive correlations between b-glucan content and grain yield have been found (26, 114), but negative correlations were also reported in some environments (26). Frey (74) recently completed three cycles of recurrent phenotypic selection for high b-glucan content, and preliminary (unreplicated) results indicate good success.

The major difficulty in selecting for increased b-glucan content is the evaluation of the trait itself. Rather complex, expensive, and time-consuming chemical methods have traditionally been used to estimate b-glucan content (143, 292). Although reliable, such methods preclude the routine screening of large numbers of breeding lines, especially in early generations. Evaluation of b-glucan may not be feasible until late generations, after selection for other traits has eliminated most undesirable lines from the population. On the other hand, it may be feasible to use the much more rapid method of near-infrared spectrophotometry combined with minimal lab chemistry to screen larger numbers of genotypes on a regular basis. Another advantage of near-infrared spectrophotometry is that b-glucan, oil, and protein contents can all be analyzed simultaneously.

Although increased b-glucan contents may be valuable for milling oats for human consumption, they lower the metabolizable energy for animal feed. b-glucan has been implicated in reduced weight gain in poultry when oats were incorporated into their diets (35). Thus, breeders interested in developing varieties specifically for animal feeding might be interested in selecting for lower b-glucan content.

On-Farm Uses of Oats

Oats have many on-farm uses, such as a source of animal feed, fodder, and bedding. The utility of oat cultivars for on-farm use depends on their ability to fulfill some need created by farm animals. Breeders should attempt to determine which roles oats could serve on-farm that might provide growers with some benefit not supplied by other crop species. Some possible on-farm uses of oats and traits that could be modified through breeding to meet those goals are sketched here. Special-purpose cultivars might be developed, or more multipurpose cultivars might be envisaged to provide growers flexibility.

Forage Yield and Quality

Oats can be used in a variety of ways to produce forage. In mild climates where winter oats can be grown, oats are sown in the autumn and can serve as a source of forage for grazing cattle. In the spring, they can continue to be grazed or they can be allowed to mature and produce grain. In colder climates, spring oats can serve as a source of forage only in the spring and summer months. Another option is to harvest green oats, while the grain is in the milk or early dough stage or before, and use this material for hay or silage. This can be followed by planting a second crop, such as soybeans. Or the oats can be sown as a “companion crop” with forage legumes to help establish pastures and harvested either for grain or for forage. Oat cultivars that produce both high forage yields and high grain yields may be preferred by growers because they could choose to use the oats for either type of feed, depending upon the changing needs of their animals during the growing season. Marshall et al. (150) reviewed the cultural practices for grazing oat and for harvesting oat for hay or silage. They concluded that, in some instances, the feed value of the green oats produced as forage is greater than that of the oat grain that could be produced on the same land. Even where oats are harvested for grain the straw can be fed as forage to ruminants; however, the nutritional quality of the straw is very low. Burrows (30) suggested developing oat cultivars that maintain green stems even when the grain has matured and dried down. These could be harvested at grain maturity but before the stems have fully ripened and be ensiled or be dried and threshed to obtain grain and more nutritious straw for feed.

A few studies have investigated differences among oat genotypes for forage yield and quality. Anderson and Kaufman (3) and Stuthman and Marten (219) suggested that late-maturing cultivars could be used for either grain or forage production. Chapko et al. (38) also found that tall, late genotypes provided best forage yields, but they and Stuthman and Marten (259) found no association
between grain yield and forage yield, suggesting that dual-purpose cultivars could be developed, but that selection for grain yield alone would not ensure high forage yields. Forage quality can be measured via in vitro digestible dry matter, acid detergent fiber, neutral detergent fiber, and crude protein. A high-quality forage should have high digestibility and protein and low fiber components. Stuthman and Marten (259) evaluated forage quality of oats harvested at heading and two weeks later (dough stage). They found that differences among genotypes in quality components were greater at the early harvest stage, and that differences in quality among genotypes were not repeatable between years. They suggested that breeding for forage quality would not likely be successful. Chapko et al. (38), on the other hand, evaluated forage quality at very early heading and found highly repeatable differences among genotypes. They attributed the difference between their finding and that of Stuthman and Marten (259) to the difference in harvest times, as forage quality is reduced after heading (40) and differences among genotypes might be eliminated. Forage quality was negatively associated with forage yield in both studies, suggesting that developing cultivars with both good forage yield and quality will be difficult. Researchers in Wisconsin, however, released ‘Ensiler’, an oat cultivar with good forage yield and quality (266). Taylor et al. (274) suggested the use of an oat mutant expressing giantism (very tall, late-maturing, and leafy) conferred by a single recessive gene, gi-3, in breeding high forage-yielding oat cultivars.

Oats are the most commonly used companion crops to establish forage legumes in the north central United States (275). The benefits of using an oat companion crop include reduced soil erosion and improved weed control (150). Intercropping oats and forage legumes can increase the economic return from the land compared with growing either crop alone because the different species have complementary rather than competitive growth habits and requirements. For example, legumes can rely on biological nitrogen fixation and will not necessarily compete with oats for nitrogen. Also, oats utilize sunlight more efficiently in early spring but may be harvested and removed from competition with the legume later in the season when the legume requires greater resources. Trenbath (284) fully reviewed the physiological advantages of intercrops. Care must be taken, however, to choose oat cultivars that will not out compete the legume and reduce its yield or persistence or oats that will lodge and damage the legume underneath (275). Few studies have investigated variation among oat genotypes for companion cropping performance. Flanagan and Washko (65) compared the effects of one barley and six oat cultivars intercropped with four different legume species. They observed that cultivars that allowed greater light penetration were associated with higher populations of red clover and smaller losses in red clover and alfalfa. The number of tillers, plant height, and grain plus straw yields of each variety were correlated with light penetration. Collister and Kramer (46) compared the effects of seven oat varieties on the stands and yields of overseeded red clover. Some oat varieties decreased red clover stands and yields more than others, and the decrease was correlated with height, but not grain yield, of oats. Nielsen et al. (181) combined five oat and five alfalfa cultivars in factorial combinations to measure interference of the two crops with each other. In general, the presence of alfalfa either reduced or increased the grain yields of oats, depending upon environment, whereas oats tended to decrease alfalfa forage yields to a greater or lesser extent across environments. They found that specific combinations of oats and alfalfa caused reductions in oat grain yield or alfalfa yield. Therefore, oat and alfalfa cultivars exhibited interactions for intercropping performance. Under such conditions, improvements in companion cropping ability of oats may be specific to particular varieties of the legume species. Cooperation between forage breeders and oat breeders would greatly improve the chances of developing improved intercropping variety combinations. To date, several cultivars have been developed specifically for companion cropping with forage legumes, including ‘Preston’, ‘Starter’, and ‘Pal’ oats from Minnesota. (260, 262, 264). These cultivars tend to be short-statured, early-maturing, and lodging-resistant.

Oil Content

Edible oil provides more than twice as much dietary energy per unit of weight as carbohydrates or protein (291). Oat grains have the highest oil content and, consequently, the highest gross energy value of any temperate small grain crop species; however, the presence of the fibrous hull of the grain reduces the metabolizable energy of oat grain to less than that of wheat, barley, or maize (289). Gullard (103) suggested that improvements in the feeding value of oats could be accomplished by either reducing the hull percentage of the grain or by increasing the oil content of the grain.

Great oil content has a high heritability and can be assayed reliably by using nuclear magnetic resonance or near infra-red spectrophotometry methods (20).
Heritability and stability of the trait was high enough to permit progress from selections based on oil content in greenhouse-grown plants (225). The relationship between oat oil and other seed quality and agronomic characteristics has been studied extensively. Phenotypic correlations between oil content and yield have generally been reported as nonsignificant (16, 73, 103); however, Schipper and Frey (227) reported that selection for increased oil content was associated with decreases in grain yield, groat yield, test weight, and groat percentage. They suggested that a restricted selection index should be used to select for high oil content while maintaining favorable levels of other agronomic traits. Phenotypic correlations between oil content and protein contents have been reported as negative (16) and as nonsignificant (73, 103). Youngs and Forsberg (299) found that phenotypic correlations between oil and protein contents were generally nonsignificant, but varied across environments. Schipper and Frey (226) reported that selection for increased groat oil content had no effect on groat protein content, whereas selection for increased groat protein yield resulted in increased groat oil content. An example of recurrent selection for increased oil content by using A. sativa and A. sterilis germplasm has been presented previously.

Frey and Hammond (90) suggested that oats with 17% oat oil content and favorable levels of grain yield could compete economically as an oilseed crop. Bjornstad et al. (12) suggested that such a crop could be particularly useful in Scandinavia because of a paucity of productive oil crops in that region. Oat oil has a very favorable fatty acid profile for human nutrition, high in linoleic acid and low in linolenic acid. In addition, the proportions of linolenic and palmitic acids are negatively phenotypically correlated with total oil content. Schipper et al. (128) reported that the ratio of unsaturated to saturated fatty acids increased over cycles of selection for high oil content. Thus, high oil oats could improve on-farm uses of oats and also provide new markets for oat products; however, high oil content oats would not be favorable to marketers interested in promoting oats as part of a low fat, high fiber diet. In addition, high groat oil may make some types of milling more difficult (30). Thus, for the purposes of producing milling-quality oats, breeders may wish to select for low oil.

Hull-less Oats

As mentioned previously, the major factor contributing to the low feeding value of oat grain is the non-nutritious fibrous hull. This limits the use of whole oats primarily to horse, cow, and sheep diets. Whole oats are unpalatable to pigs. Feed value of the grains can be improved by dehulling the oats, but this is not always an economically feasible procedure (52). Thus, breeders can attempt to improve feeding value of oats by reducing the hull percentage of the grain, or, more drastically, by breeding oats that have groats that thresh free of the hulls, as occurs with naked-seeded or hull-less oats. Cudderford (52) concluded that naked oats are superior to other cereals (wheat, barley, or maize) as an animal feed.

Burrows (30) reviewed the breeding of naked oats with emphasis on the Ottawa, Canada program, and Valentine (285) reviewed the topic emphasizing naked oats in the United Kingdom. The genetics of the naked-seeded trait are rather simple, with one major and up to three minor genes postulated for the trait (30). Thus, incorporating the naked-seeded trait along with other desirable agronomic and grain quality characteristics in a single oat genotype should not prove especially problematic. Burrows (30) and Valentine (285) described the development of several hull-less cultivars, each more recent one improved over previous varieties in terms of more complete expression of the hull-less trait, higher groat yields and lodging resistance. The major obstacle to the wide-spread acceptance of hull-less oats no longer seems to be genetics but the absence of widespread market recognition of hull-less oats. This, however, should not prevent farmers from growing hull-less oats for use directly on the farm as an excellent animal feed. By combining high oil contents with the hull-less trait, oats could become a superior high-energy feed for farm animals.

Burrows (30) proposed that hull-less oats could also improve the ability of growers to market oats off-farm because the density of the grain is increased dramatically compared with the lighter hulled oats. This could facilitate less expensive long-distance shipping of oats from production areas to food oat mills. Weaver (288) suggested that oat milling companies would accept hull-less oats and would even prefer them if supply could be guaranteed. Thus, hull-less oats could be equally useful on-farm and off-farm, and this is an example of new markets being developed because of progress from plant breeding.

BIOTECHNOLOGICAL APPROACHES TO OAT IMPROVEMENT

Two potential applications of molecular and cellular biology to oat improvement will be briefly
discussed here. The first is the development of transgenic oats, and the second is the use of molecular markers in oat breeding.

**Transgenic Oats**

Somers et al. (244) reported the first recovery of stably transformed, fertile oat plants using microprojectile bombardment. They found, however, that the frequency of male sterile plants regenerated from tissue culture was quite high and suggested that this was due to somaclonal variation induced by tissue culture rather than the transformation process itself. Torbert et al. (283) recovered higher frequencies of fertile transgenic oats by using an antibiotic resistance gene as a selectable marker for transgenic cells in culture rather than the herbicide resistance gene used by Somers et al. (244). Cytogenetic variation of oats regenerated from tissue culture has been reported (157) and variation for agronomic traits of regenerated oats tends to be undesirable (53). This suggests that even after all of the difficulties associated with identifying and cloning genes of agronomic utility and developing transgenic constructs have been overcome, tissue culture-induced variation may remain a major difficulty with the development of transgenic oat crops. The transgene may be introgressed into elite cultivar backgrounds rather easily via backcrossing, however, because the presence of the transgene in a plant generally can be easily assayed using the transgene clone as a DNA probe, or by assaying expression of a selectable marker included on the transgene construct. A further difficulty with transgenic plants that has been observed in many species is the unexpected loss or reduction of expression of transgenes in some regenerated plants (64). Finally, the coexistence of the cultivated oat and problematic, weedy oat species (*A. sterilis* and *A. f Warnich*), with which cultivated oats are interfertile, in many production areas presents a further complication in the release of transgenic oats. Transgenes in cultivated oats might escape into wild oat populations by natural hybridization. If the transgene confers herbicide resistance, the resulting hybrids and some of their offspring might present an increased pest problem in cereal production fields.

Transgenic oats may provide a new source of resistance to BYDV. Miller and Young (170) reviewed the potential of, and progress toward, genetically engineered resistance to BYDV. They outlined many strategies of transgenic viral resistance, being attempted in oats or in other plant species. Such methods include the use of sense or anti-sense versions of viral coat protein genes, ribozyme genes, or immunoglobulin antibody genes as transgenes to inhibit the replication or movement of viruses in a variety of ways. The possibility of transferring natural resistance genes from barley (the Yr7 gene) (28) or wild relatives of wheat via transformation also exists. Indirect methods of BYDV resistance achieved by inhibiting aphid feeding through expression of aphid pheromone or insecticide genes are possible in theory but are not immediately applicable.

Another potential use of transgenes in oats is to provide new mechanisms of resistance to fungal pathogens, such as *P. coronata*. Chitinases, endogenous plant enzymes that exhibit antifungal activity, could be used to construct transgenic rust resistant oats. Transformed tobacco plants containing chitinase transgenes have exhibited inconsistent levels of fungal resistance, depending on the transgenes and the pathogens studied (101). While some endogenous oat chitinases are induced following inoculation with incompatible (avirulent) races of *Puccinia* (63), expression of exogenous chitinase transgenes might provide resistance to previously compatible (virulent) races of *P. coronata*. Chitinases differ for the range of fungal species which they inhibit (101). Therefore, a range of plant and bacterial chitinases might have to be tested to identify one that will inhibit *P. coronata*. Genes coding for other antifungal compounds, such as lectins, might also be a source of transgenes to develop rust-resistant oats (222).

In addition, co-expression of more than one transgene with anti-fungal activity might provide greater protection against disease than single transgenes. Zhu et al. (301) observed that transformed tobacco plants co-expressing a rice chitinase and an alfalfa glucanase exhibited greater resistance to a fungal pathogen than plants expressing either of the transgenes individually. It seems that at least some chitinases are involved in plant development (101, 222); therefore, expression of exogenous chitinases in transgenic oats may have unexpected and unfavorable effects on plant growth and agronomic performance.

**Molecular Markers**

The study of genetics of oats has lagged behind that of other cereal crops, such as wheat and barley. Marshall and Shaner (152) recently reviewed the state of classical oat genetics and noted that whereas some linkages between genes have been reported in oats, the linkage relationships of most genes are unknown, and few genes have been assigned to chromosomes. As an example, at least 56 genes for crown rust resistance in hexaploid oats have been named, but few allelism tests have been performed among these genes, and their
specific chromosomal locations in the genome is virtually unknown. With the recent development of an extensive linkage map of diploid and hexaploid oats based on molecular markers (183, 185, 208), it seems that the state of the art in oat genetics is bound to improve in the next few years. Linkage maps based on DNA polymorphisms can aid greatly in the elucidation of genome organization of genes affecting traits of interest and can be used to select for such traits based on genotypic data.

Genome mapping in allohexaploids such as oat can be complex because of the detection of multiple loci on different chromosomes by individual probes (245). For this reason, the first published molecular linkage maps of oats were based on crosses among A genome diploids (185, 208). Mapping in oats is also complicated by the relatively large nuclear genome of the species. Although hexaploid oats have 21 pairs of chromosomes, the hexaploid map developed by O'Donoghue et al. (183) has 38 linkage groups and numerous unlinked markers. This suggests that markers have not yet been isolated for large portions of the genome, despite the use of 361 markers to construct the map. By comparing the hexaploid map to the diploid maps, O'Donoghue et al. (185) illustrated that extensive genomic rearrangements had occurred between the diploid and hexaploid A genomes. This complicates assignment of linkage groups to homoeologous sets (121).

Linkages between restriction fragment length polymorphism (RFLP) markers and genes for crown rust resistance in A. sativa have been reported (33, 217). Linkages between polyolase chain reaction (PCR)-based markers and genes conferring stem rust resistance (195) and daylength insensitivity (296) have also been reported. Storage protein loci have been shown to be linked to both stem rust and crown rust loci (41, 209). In some instances, understanding of the genomic organization of these genes has been aided by use of molecular markers. Rooney et al. (217), for example, used RFLP markers to determine that crown rust resistance genes, PC 91 and PC 92, mapped to different linkage groups. By using monosomic lines and RFLPs, they identified the specific chromosome that carried one of the genes. The genomic organization of genes for rust resistance in maize has proved to be of great interest because of the existence of clusters of tightly linked resistance genes that likely evolved slightly different race-specificities after descending from a common ancestor gene by tandem-duplication and/or unequal meiotic crossing-over (223). RFLP markers have been used effectively to investigate the mechanisms of meiotic instability, variation of recombination frequencies, and the evolution of new race-specificities in these complex resistance loci (116, 213, 265). Similar types of rust resistance gene organization might be found in oats, as examples of linkages between rust resistance genes in hexaploid oats have been reported (41, 152), while Gregory and Wise (102) reported linkages between crown rust resistance genes in diploid oats, and Rayapati et al. (208) and Wise et al. (297) suggested that a cluster of rust resistance genes exists in diploid oats. As discussed previously, crown rust resistance genes have been introduced from A. strigosa into hexaploid oat cultivars. It is possible that whole or partial clusters of resistance genes have been transferred from A. strigosa to A. sativa. Detection of linkages between molecular markers and genes of interest in populations that have been used to develop marker linkage maps will provide greater insight into the genomic organization of oats.

Molecular markers can also be used to identify genomic regions associated with genes affecting quantitative traits, known as quantitative trait loci (QTLs). Edwards et al. (28) used 17 isozyme markers distributed over eight of ten chromosomes to detect a minimum number of agronomically important QTLs and their relative effects and mode of gene action in a maize population. Paterson et al. (190) reported the first use of a complete RFLP-based linkage map to resolve quantitative traits into Mendelian factors by mapping QTLs affecting fruit traits in tomato (Lycopersicon esculentum L.). Dudley (56) reviewed the theory regarding detection and manipulation of QTLs in crop species. The first use of an extensive molecular linkage map to investigate QTLs in oats was made recently by Sirpongwiwat et al. (242). They located QTLs affecting grain yield, straw yield, test weight, plant height, and days to heading in a recombinant inbred population derived from the same cross of a winter oat cultivar and a spring oat cultivar that was used to develop the linkage map published by O'Donoghue et al. (185). Holland et al. (113) used the same map and populations to identify vernalization-sensitive and insensitive QTLs affecting days to heading and plant height.

Lee (139) recently reviewed the use of DNA markers in plant breeding programs. Even if genes of interest have not yet been identified and mapped, markers can be used for various purposes by plant breeders. One use of markers is to obtain estimates of genetic diversity and relatedness in breeding populations and germplasm resources. The uses of isozymes and RFLPs to assess the relative amounts of variation and genetic relatedness of cultivated oat breeding populations and wild species collections have been discussed previously. One possible application of such data is to choose parents for breeding
crosses based on genetic divergence estimates made from marker data, under the assumption that more genetically divergent parents should produce more variable progeny populations. Moser and Lee (175), however, attempted to use marker-based genetic distances to predict heterosis and magnitude of genetic variance for several traits in crosses among a small sample of parents without success. Once genes affecting traits of interest have been mapped using molecular markers, plant breeders have available the use of the markers themselves as aids to selection. Use of markers could greatly facilitate introgression via backcrossing of useful genes from exotic germplasm or wild species into elite lines by allowing selection for the desired gene and against undesired genes from the donor parent in individual plants in each generation. Hospital et al. (155) and Opanshaw et al. (189) have shown that marker-assisted backcrossing should theoretically require fewer generations to recover the recurrent parent genotype with the donor gene of interest. Such an approach could greatly aid in the development of multiligne cultivars and in pyramiding disease resistance genes.

The current potential of markers to improve selection efficiency for polygenic traits seems lower than that of single-gene traits, mainly because of the economic limitations of collecting genotypic data on large numbers of progeny. Lee (139), however, has suggested that this will most likely change as DNA technologies become faster and less expensive. Stuber (253) has reported good success with the use of molecular markers in maize breeding, but Stromberg et al. (252) reported that early generation marker-assisted selection was not effective in maize. Sorrells (245) suggested that a major advantage of the use of markers to identify individual genes affecting quantitative traits is that favorable alleles in exotic germplasm can be identified independently of the effects of the deleterious genes also carried by the exotic germplasm. The masking of useful genes in exotic and wild species germplasm by the overwhelming effects of unfavorable genes at the phenotypic level is a great obstacle to the use of exotic germplasm in oat and many other crops. Tanksley and Nelson (273) have outlined a method termed "advanced backcross QTL analysis" in which BC2 or BC3 generations developed from elite cultivated by exotic matings are analyzed with markers in order to locate favorable QTL alleles introduced from the exotic parent. They suggested that this method is more suitable for identifying useful alleles from exotic germplasm compared to traditional QTL analyses in F2, recombinant inbred, or BC1 generations because favorable alleles from the exotic germplasm will be better expressed in the genetic background of the elite parent. Tanksley et al. (272) used this method to identify many favorable QTL alleles from a wild tomato (L. pimpinellifolium) parent backcrossed into an elite cultivated tomato parent. Thus, despite the fact that the wild parent was phenotypically quite poor, it did possess genes useful to tomato breeders, a situation not unlike that found in A. sativa and A. sterilis.

The development of marker linkage maps has also greatly aided the study of genomic similarities between oats and other grass species. Jelien et al. (121) reported that some molecular markers developed in wheat could identify homoeologous regions in the oat genome. Van Deynze et al. (286) developed a "consensus" linkage map of chromosome 1 of Triticaceae species, based on comparisons of linkage maps in several Triticum species and barley and rye. Homoeology exists between this consensus map and large regions of linkage group A from the diploid A genome oat map developed by O'Donoughue et al. (185). Van Deynze et al. (287) then compared the complete A genome diploid oat map to wheat, rice (Oryza sativa L.), and maize maps. A surprising amount of genome conservation between oats and the other species was found, and large homoeologous regions with conserved map order were discovered in comparisons of the oat linkage groups with those of the other species. Linkage groups A and D were highly conserved with respect to the other species, while other linkage groups exhibited many examples of genomic rearrangements with respect to wheat, rice, and maize. O'Donoughue et al. (183) have also shown that the hexaploid oat map is considerably rearranged with respect to the A genome diploid map, which was predicted by Rajhathy and Thomas (207) based on chromosome pairing analysis of hybrids between diploid and hexaploid oats. It seems, therefore, that whereas genome rearrangements have occurred to a greater extent in the evolution of Avena compared with related grass genera, there are, nonetheless, genomic regions that have maintained some organizational integrity throughout millions of years of evolution. Rayapati et al. (209) reported that genes for resistance to P. coronata and genes encoding seed storage proteins were localized to the same linkage group in diploid oats, and noted that this physical linkage of seed storage proteins and disease resistance loci was also reported in rye, barley, wheat, and maize. Chong et al. (41) observed a tighter linkage between seed storage protein and rust resistance genes in hexaploid oat. Yu et al. (300) suggested that the position of crown rust resistance loci in diploid and hexaploid oats was similar
to the positions of disease resistance loci in barley and maize. Van Deynze et al. (287) proposed that map locations of three independent regions affecting vernalization response or time to flowering were conserved among oat, wheat, rice, and maize. If this pattern is universal, the study of genome relationships between oat and other Gramineae may be a great benefit to oat breeders, as much understanding of genes of interest derived from better-studied crops, such as wheat, barley, maize, and rice will be transferrable to oats. Van Deynze et al. (286) suggested that oat workers would gain the most from such comparative studies. For example, isolation of genes of interest to oat breeders could be more easily performed in rice, with its small, well-characterized genome and the gene clone obtained in rice could be used to isolate its homologues in oats. Similarly, maize, with its extensive collection of transposon-tagged mutant genes, could provide a source of heterologous probes for oat genes. In addition, localization of QTLs affecting agronomically important traits in wheat or rice could provide oat geneticists with a head start by indicating which regions of the oat genome are likely to contain such QTLs.

CONCLUSIONS

Oats are an excellent multipurpose crop suitable to production of food and feed grains, and forage and bedding for animals. Oat grain quality is excellent, with the best amino acid profile of any of the cereals for human or animal nutrition; however, whole oat grain quality is inferior to many other cereals because of the presence of the fibrous hull, which provides little nutrition. Oats can be used on-farm for livestock or the grain can be marketed off-farm to oat millers if the grain quality is sufficient. Although oat consumption by humans is increasing, world production has been decreasing, particularly for the past twenty years (112). In some areas, the decrease has been quite drastic, as in the United States, which recorded the lowest oat production in 1995 since records were kept beginning in the 1800s. As oat acreage has decreased, funding has followed suit, and consequently, there are fewer oat breeding programs in the United States in 1996 compared with twenty years ago. Thus, the next millennium will not lack for challenges for oat breeders who will be, in a sense, competing with breeders of other, better-funded, and more widely grown crops. Oat breeders may be forced to direct their cultivar development programs toward multiple specialty or "niche" markets or farming systems, which may dilute the impact of plant breeding even further. Breeders should be aware of the current and potential ways in which oats can be grown, used, and marketed profitably in their regions and to provide farmers with the types of cultivars needed for those purposes. Promising avenues of research and cultivar development abound, with hull-less oats becoming more widely accepted, the availability of modern molecular genetic tools, and information trickling down from plant geneticists working with other grass species. One might hope that modern genetics will allow oat workers to close some of the knowledge gap that exists between oats and other species, such as wheat, barley, maize, and rice. The possibility also exists, however, that increases in funding for fewer, better-studied crops will simply widen the gap further: this will be another of the many challenges that must be overcome by oat breeders and geneticists in the future to maintain the viability of the oat crop.

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