

To produce wheat-barley cross, embryo is excised from immature barley endosperm (A) and is replaced by frail hybrid embryo (B) produced by hand pollination. The endosperm serves as nurse tissue for the hybrid (C). About 70 percent of the embryo cultures may give rise to plants (D), but of 270 plants obtained by this process at Davis, only 20 were true wheat \times barley hybrids (E, center; spike at left is wheat; right, barley).

A major factor limiting the rate of progress in plant breeding has been low heritability. This occurs frequently in complex traits such as yield and quality, which are controlled by a large number of genes and are environmentally unstable. Plant breeders and physiologists are cooperating in an effort to overcome this problem by breaking a complex character down to components, and ultimately to the actual molecules that mediate the expression of the character. By selecting for the components of a character or for its underlying molecular constitution, breeders hope to reduce complexity and environmental impact, allowing for faster progress.

Areas currently being explored for application of this approach are yield, quality, salt and drought tolerance, water-logging tolerance, chilling tolerance, disease and insect resistance, and self-incompatibility phenotypes (which are used in F_1 hybrid production). For example, in processing tomatoes the major component of yield is volume of finished product (sauce, paste, catsup) per unit of cultivated area. In breeding for harvest yield alone, much of the progress observed results from increased water content, which must, in turn, be eliminated by the processor. The solution has been to maintain or increase the economic yield of processing tomatoes (solids) while decreasing water content. The alternative character used by breeders as a selective criterion is sugar (soluble solids) concentration, which is negatively correlated with water content. By combining this character with additional selection for gross yield, uniform maturity, thick skin, and firm flesh, it has been possible to make more rapid progress in improving this crop than in the past.

Another approach to solving the problem of low heritability, recently developed at the University of California, is the use of electrophoretic variation as an alternative selection

criterion in tomatoes.

One strength of cellular and molecular genetic approaches is the possibility of performing selection with chemicals or physical conditions on extremely large populations of haploid individuals in a small space and over a short time. Numerous schemes have been devised to select desirable genetic variation with respect to nutrition, stress tolerance, herbicide resistance, and disease resistance. Until now, variant cells selected *in vitro* have only rarely been translated into functionally equivalent whole plants. Recent studies show that it may be possible to circumvent some of the problems associated with selection of cultured cells by substituting whole plants. For example, chemicals have been used to screen barley seedlings exhibiting increased nutritional value. Other experiments have shown that pollen can be responsive to selection *in vivo*, opening up the possibility for screening large populations of haploid individuals.

Plant breeding has brought about drastic changes in plant architecture or genetic makeup, revolutionizing production and marketing methods. Recent examples include determinate growth habit for mechanical harvesting, disease-resistant cultivars, and hybrid varieties. New ideas are constantly emerging, such as techniques to permit the selection of plants with multiple tolerance genes ("horizontal" resistance) as opposed to often unstable single gene ("vertical") resistance. Dwarf fruit trees are being developed that will produce more with lower management and harvesting costs.

Although genetic engineering for crop improvement holds great promise, plant breeding and other aspects of whole plant genetics are also becoming increasingly sophisticated. Advances in breeding technology guarantee that plant breeders will continue to make valuable contributions to agriculture.



Wheat-barley hybrids

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Some crop plants have simple inherited characters that would be desirable if transferred to another crop. Our current work on transfer of resistance to the barley yellow dwarf virus (BYDV) from barley to wheat is an example of a simple modification to the embryo culture method that produced hybrid plants from two difficult-to-hybridize species.

BYDV is an aphid-transmitted virus that occurs on many grasses, including forage grasses and cereal grains. Discovered in Cali-

fornia in 1951, BYDV causes serious yield losses in barley, wheat, and oats. Resistance to BYDV was found only in barley from Ethiopia and was subsequently transferred to several California barley varieties. A single gene, *Yd2*, in barley confers resistance. An extensive search among wheats from around the world failed to find a resistant variety, so it appeared necessary to transfer *Yd2* from barley to wheat.

The wheat × barley hybrid is very difficult to make because the two species are not closely related. Barley has 7 pairs of chromosomes, and bread wheat has 21 pairs. When pollen from barley is applied to wheat, fertilization can take place, but at a very low frequency. The resulting embryos abort unless excised and cultured on a sterile growth medium; even then few embryos survive (less than 1 percent).

In the early 1970s Anthon Kruse, working in Denmark, discovered a simple embryo rescue technique. He placed the hybrid embryo on immature endosperm excised from the developing seed of one of the parent species. The endosperm serves as a nurse tissue for the hybrid. Australian workers found that barley endosperm was the best nurse tissue and reported that about 70 percent of the cultured hybrid embryos produced plants.

We adopted these techniques at Davis in a program that will transfer to wheat the *Yd2* gene, which is on barley chromosome 3. Even with the method described, it is difficult to produce the hybrid plant. In two years, more than 50,000 individual wheat ovaries were pollinated by barley, and of those, only about 440 showed embryo development. These were excised and transferred to nurse tissue on sterile culture medium. About 270 plants were obtained, but only 20 were true wheat × barley hybrids.

The hybrid plants were completely male-sterile but did produce seeds when pollinated with wheat. These seeds, called backcross F₁, produced plants that had the 7 chromosomes of barley and 21 wheat chromosome pairs. We have backcrossed and self-pollinated several more generations and now have wheat-like plants with 44 chromosomes—all of the wheat chromosomes (42) and one chromosome pair from barley.

Seven types of wheat plants have individual barley chromosomes, one type for each of the 7 barley chromosomes. Our task now is to identify the wheat plant with barley chromosome 3. We can then expose those plants to BYDV to see if the *Yd2* gene functions in wheat. The next step will be to induce recombination of a wheat chromosome with the barley chromosome, so that we eventually have a wheat plant with 21 pairs of chromosomes with the *Yd2* gene incorporated direct-

ly into a wheat chromosome. Techniques are already available for this step, but the key to success in making the difficult hybrid was the rescue of the hybrid embryos with the endosperm nurse tissue.

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Induced chromosome pairing

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Success in hybridizing wild with cultivated species ultimately depends on the ability of the alien chromosomes to pair and recombine with the chromosomes of the crop species at meiosis. In bread wheat, pairing and thus recombination normally occur only between identical or homologous chromosomes and not, unfortunately, between a wheat chromosome and an alien chromosome. However, increasing knowledge of the components of the genetic system controlling pairing has made it possible to manipulate them to achieve pairing between nonhomologous chromosomes. A major advantage of such induced pairing is that it usually occurs between closely related but not homologous chromosomes—termed homoeologues. Recombination of genetic material between homoeologues is likely to result in genetically more balanced chromosomes than if recombination were between unrelated chromosomes.

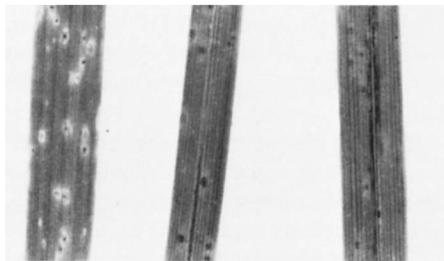
Two approaches can be used to transfer genes from related species into wheat. There are diploid species (with 14 chromosomes) related to wheat (42 chromosomes) that modify the chromosome pairing control system of wheat so that pairing between homoeologous

chromosomes can occur. One approach employs hybrids between such species and wheat. When an alien set of chromosomes is present in the hybrid along with the donor chromosome carrying the desired trait, the chances of pairing between the donor and wheat chromosomes are enhanced. The second approach manipulates dosages of genes known to regulate chromosome pairing in wheat.

A recent successful example of the first approach involves the wild diploid species *Aegilops speltoides*, which is native to the Middle East. This species has a genotype capable of inducing pairing between homoeologues in hybrids with bread wheat. It also possesses resistance to the leaf rust fungus *Puccinia recondita*. Following initial hybridization between the susceptible wheat cultivar Pitic 62 and resistant *Ae. speltoides* plants, the hybrids were backcrossed to Pitic 62 for several generations. The F₁ and first backcross plants were male sterile, but by the third backcross, pollen fertility was substantially restored in the derivative lines. When progeny of the third and fourth backcrosses were screened for resistance to the fungus, resistant plants were found. Observations of chromosomes at meiosis in resistant plants of the fourth backcross revealed some 42-chromosome plants with normal wheat-like meiosis. Thus, the required portion of an *Ae. speltoides* chromosome conferring resistance had been translocated to a wheat chromosome.

The exchange occurred in plants of the F₁ generation following initial hybridization through homoeologous chromosome pairing permitted by the interaction of the *Ae. speltoides* genotype with the wheat genotype. The desired exchange was only one of many that may have occurred. Backcrossing and screening were necessary to exclude unwanted exchanges and retain plants with wheat characteristics and resistance. After the first backcross, some of the *Ae. speltoides* chromosomes were lost, since they had no pairing partner at meiosis. Normal meiosis returned to the derivatives as backcrossing continued.

This technique is efficient, because in one step it incorporates resistance and provides an opportunity for the recombination of homoeologous chromosomes. From these recombinants, backcrossing and screening select any plants that possess the desired portion of the alien chromosome translocated to wheat without interfering with normal chromosome pairing and fertility once the wheat background is restored.



Reactions to leaf rust on leaves of (from left): susceptible Pitic 62 wheat cultivar; susceptible derivative; resistant derivative.

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