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 F_1, 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.

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

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

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 F_1 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 F_1 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.
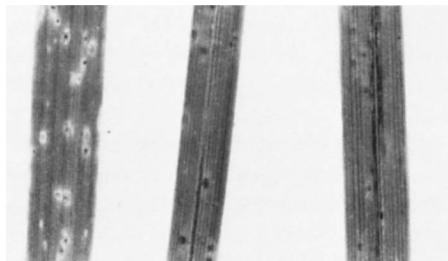
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