51

Wheat

R. E. Allan USDA-SEA and Washington State University Pullman

Cultivated wheats include einkorn (2x), emmer (4x), durum (4x), and common (6x) wheats, but einkorn and emmer wheats are seldom grown today. Wild einkorn was probably domesticated in southeastern Turkey and wild emmer in the upper Jordan Valley. Evidence suggests that hexaploid common wheat (*Triticum aestivum* L. em Thell.) was domesticated outside of these regions (Harlan, 1975).

The origin of wheat is speculative, but a leading theory suggests that hexaploid wheat arose from natural hybridization involving three diploid strains. The emmer and durum wheats probably originated from natural hybridization of wild T. monococcum L., the A-genome donor, and a currently unknown B-genome donor, probably of the Sitopsis section. Hexaploid common wheat probably arose when a tetraploid type [T. turgidum L. var. dicoccoides (Körn in litt. in Schweinf.) Bowden] with the A and B genomes hybridized with T. tauschii (Coss.) Schmal., the D-genome donor.

Wheat is grown worldwide and is the most widely adapted of the cereals. It exceeds all other cereals in total area and total production. Wheat grows best between 30 and 50° N lat and 25 and 40° S lat. The crop is primarily grown under dryland or rainfed conditions with about 85% of it produced in areas where rainfall is below 900 mm annually.

Winter wheat is more extensively grown than spring wheat and is favored anywhere that fall seedings survive. The main winter wheat regions include the central and southern plains of the United States, western Europe, the Balkans, southern USSR, and China.

Spring wheat is produced in colder, drier areas that are unfavorable for winter wheat. These regions include the northern plains of the United States, the Canadian prairies, Argentina, and northern and central USSR. Spring wheat is also grown as a fall-sown crop in countries with mild winters, such as Mexico, Brazil, India, Australia, and the southwestern U.S.

Copyright © 1980 American Society of Agronomy-Crop Science Society of America, 677 S. Segoe Road, Madison, WI 53711. *Hybridization of Crop Plants.*

Wheat is used for food, feed, and industrial purposes. It is second only to rice as a food crop and serves as the chief food for about one-third of the world's population. It supplies about one-fifth of human caloric intake. It is used in a variety of products, including breads, tortillas, chapaties, crackers, cookies, cakes, crusts, confections, noodles, macaroni, bulgar, rolled flakes, many hot and cold breakfast foods, and other specialty products (Reitz, 1967). Wheat is an important livestock feed and accounts for about 10% of the grain fed to livestock. In many areas, it is used as pasture, hay, and silage. Rather small amounts of wheat are used industrially for starch, alcohol, oil, gluten, and paper products.

I. PARENTAL MATERIAL

Wheat breeders can draw from a large gene pool notable for its diversity. There are at least 23 species of *Triticum* with ploidy levels of 14, 28, and 42 chromosomes (Morris and Sears, 1967). Harlan (1975) described three subgene pools. The primary gene pool includes types that cross readily with one another. A very large secondary gene pool of about 35 species includes all species of *Aegilops, Secale, Haynaldia*, and some *Agropyrons*. Gene transfer is possible among members of the first and second pools, but special techniques may be needed. A tertiary gene pool comprised of *Hordeum vulgare* and several species of *Agropyron* and *Elymus* represents potential rather than presently useful variability.

Numerous types of wheat amphidiploids have been artificially synthesized (Morris and Sears, 1967). Species of *Triticum* hybridize with *Secale*, *Agropyron*, and *Haynaldia*. Many of these synthesized hybrids have been given names, such as Triticale, Agrotricum, and Haynaltricum. Such artificial species have potential for expanding the genetic diversity of cultivated wheat.

Several large collections of wheat germplasm exist, yet any single collection contains only a portion of the total genetic variability. An extensive and widely used collection is the USDA Wheat Collection, made up of over 34,000 accessions. Its accessions can be obtained from the Plant Genetics and Germplasm Institute, USDA, Beltsville, MD 20705. Other countries that hold large wheat stocks are the USSR, Turkey, Italy, Iran, India, Hungary, Switzerland, and East and West Germany. The Food and Agriculture Organization and the International Atomic Energy Agency have jointly listed researchers who hold stocks of wheat and its relatives. The Laboratory for Informational Sciences in Agriculture at Colorado State Univ., Ft. Collins, Colo., has compiled a wheat directory which lists several major data banks of wheat germplasm.

II. PLANT CULTURE

A. Field

Crossing nurseries are usually planted in easily accessible locations on fertile, well-drained soils where water can be provided. Manipulation of temperature and photoperiod may be possible by use of shading and supple-

WHEAT

mental light. These nurseries also facilitate manipulation of pest damage, nutrient imbalance, and other useful selective treatments. Use of wide-row spacing and within-row spacing simplifies the handling of the material during hybridization, and facilitates plant growth and development.

Environment has a greater influence on pollen production than on female receptivity. Generally, conditions that are conducive to maximum grain production benefit hybridization. Optimum pollen production of wheat occurs in a temperature range of 16 to 20 C and relative humidity of 70 to 75% (DeVries, 1971). Extremes in temperature and humidity inhibit pollen shedding and pollen viability. Temperature has more effect on pollen release than does humidity, but rainy, cloudy, windy weather and drought retard flowering. Solar radiation affects wheat pollen production, but less so than do temperature and humidity. Wheat stigmas remain most receptive at moderate temperature and humidity levels (DeVries, 1971).

Adequate supplies of water and soil nutrients during growth of the wheat plant are conducive to normal floral development and successful hybridization. Nitrogen deficiency prevents normal development of wheat flowers and kernels, and water stress subsequent to floral initiation reduces seed set and size. Rill and flood irrigation are more desirable methods than sprinkler irrigation for watering crossing blocks because they interfere less with normal pollen production and cause less lodging.

B. Growth Chamber and Greenhouse

When wheat plants are grown in greenhouses or controlled facilities, maximum production of seeds per spike is generally obtained with photoperiods of 14 to 16 hours and with mean daily radiation values above 6.3×10^6 J/m². Proper light level is particularly important 5 to 35 days before anthesis (Fischer, 1975). Temperatures ranging from 15 to 20 C during the day and 10 to 16 C at night are considered to be optimal for fertilization and subsequent kernel development (Thorne et al., 1968; Wardlaw, 1970).

Winter wheats need vernalization, but cultivars differ in length of vernalization period required. If temperatures range from 1 to 10 C, exposure for 6 to 8 weeks outdoors will vernalize most cultivars. Several methods can be used to vernalize wheat artificially, such as seeds in moist-rolled paper towels or on moist filter paper in Petri dishes in refrigerators, or in soil-filled wooden flats in cold rooms. Exposure of young wheat seedlings to 5 to 7 C for 6 to 10 weeks under 8 to 10 hours photoperiod is an effective method.

III. FLORAL CHARACTERISTICS

The inflorescence of wheat is a determinate, composite spike (Fig. 1A). Sessile spikelets are alternately arranged on opposite sides of the rachis of the main axis of the spike (Fig. 1A). Each spikelet has two bract-like empty glumes that enclose two to nine florets that are arranged alternately on a sub-axis or rachilla (Fig. 1C). The two outer parts of each floret are a flowering glume (lemma) and a thin-walled two-keeled glume (palea) (Fig. 1B). The lemma may have an awn or awnlet or may be awnless. The lemma and palea enclose the sex organs which are three stamens, a pistil, and two lodicules that regulate opening of the flower at anthesis (Fig. 1D) (Percival, 1921). Each stamen consists of a filament and an anther (Fig. 1D). The pistil consists of an ovary with two short styles and a branched feathery stigma (Fig. 1D and E). One or more of the upper florets of a spikelet usually is imperfect with either or both male and female organs nonfunctional. The basal spikelets are often entirely sterile (DeVries, 1971). Wheat spikes differ noticeably in shape, size, and density, although differences in wheat spike morphology do not usually complicate hybridization.

Although male and female floral development are closely synchronized, differentiation of the pistil generally follows that of the stamen. The stigma can remain receptive up to 13 days after anthesis, but it is most receptive from 0 to 3 days after anthesis (DeVries, 1971).

Flowering can occur anytime during daylight, but its intensity depends on variations of temperature, light, and humidity throughout the day. Flowering often is diurnal, with a large peak in the morning and a smaller one in the afternoon. Flowering generally begins midway up the spike and proceeds upward and downwards with opposite spikelets on the rachis generally undergoing synchronized flowering. The primary floret of a spikelet flowers first and is followed by the secondary, tertiary, etc. Successive florets often open on successive days (Percival, 1921). Anthers usually begin

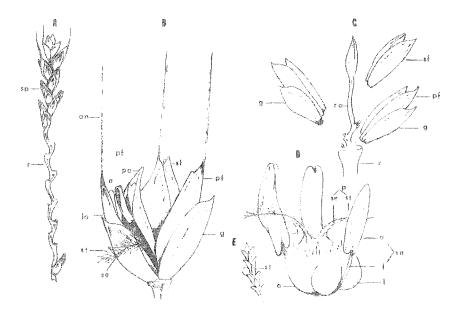


Fig. 1—Wheat spike and parts. A) Wheat spike with several spikelets (sp) removed, showing rachis (r): B) wheat spikelet showing primary (pf) and secondary (sf) florets, awn (an), lemma (la), palea (pa), anther (a), stigma (st), style (se), and glume (g); C) wheat spikelet (sp) showing sterile glumes (g), primary florets (pf), secondary florets (sf), rachilla (ra), and rachis (r); D) organs of a wheat flower including the pistil (p), stigma (st), style (se), ovary (o); stamen (sn), anther (a), filament (f); and lodicule (l); E) close-up of stigma (st) and a pollen grain.

to dehisce inside the floret, but cultivars differ in extent of anther extrusion. D'Souza (1970) found that about 5 to 7% of wheat pollen is shed on the stigma and 80% is shed outside the florets.

Wheat pollen is viable for a short time and rarely remains viable beyond 30 min in the field. The primary and secondary florets of a spikelet produce larger, and more viable pollen grains than do other florets (Ovcinnikov, 1952). Pollen on the stigma germinates readily, with pollen tube growth beginning within 15 to 120 min (DeVries, 1971).

IV. ARTIFICIAL HYBRIDIZATION OR SELF-POLLINATION

A. Equipment

Although chemical and cold treatments have been used to render stamens nonfunctional, the most reliable methods are mechanical. Tools for emasculation and pollination include a pair of smooth-jawed forceps that are 10 to 12 cm in length and a pair of scissors with sharp, close-fitting blades 30 to 40 mm long (Fig. 2A). The points of the forceps may be straight or curved depending on the user's preference, but they should fit closely together and be smoothly blunted so as not to pierce plant tissue.

Glassine bags (5 \times 17 cm) are normally used to cover the female spikes. They may be fastened by paper clips, crimp-type fasteners, or staples (Fig. 2A). Dialysis tubing, closed at one end by a staple, has proved effective. Female spikes can be wrapped in sheets of bond typing paper of at least 25% rag that have been cut diagonally and secured with clips. Such coverings stay on securely in high winds and prevent rapid desiccation of



Fig. 2—Materials and methods of emasculation. A) Items used in hybridization—1) typing paper cut for spike wrapping, 2) crimp-type fasteners, 3) soda straw, 4) tape, 5) paper tag, 6) glassine bag, 7) squeeze-type wash bottle, 8) scissors, curved and straight type forceps; B) spike being emasculated by removing anthers from top of floret; C) wheat spikes prepared for the approach method; male spike shedding pollen (ma), female spike (fe) with receptive stigmas.

female organs. Paper tags $(25 \times 45 \text{ mm})$ are used for recording cross number, pedigrees, date, and worker's initials (Fig. 2A). Color-coded tags allow rapid identification of crosses.

B. Preparation of the Female

Compared to most cereals, wheat is rather simple to hybridize. Choice of spikes for emasculation requires experience and careful observation. Emasculation should be timed 1 to 3 days before normal anthesis. This may be done by observing flowering spikes and noting the extent they have emerged beyond the flag leaf. This stage may vary due to genotype and environment. Anthers should be well developed and light green, but not yellow or cream colored. The feathery stigmas should be clearly visible and extend to about one-fourth the length of the floret. By checking spikelets about midway up the spike, the most advanced stage of floral development can be ascertained. One to three of the basal and upper spikelets may have nonfunctional flowers, therefore, they are removed with scissors or forceps. Awns are excised with scissors. All but the primary and secondary florets of the remaining spikelets are removed, as follows: the spike is grasped gently but firmly between the thumb and fingers of one hand; the thumb is lightly pressed below the tertiary floret, and the center florets are pulled downward and outward with the forceps.

Anthers can be removed from each floret by carefully inserting the forceps between the lemma and palea and spreading them. The three anthers are removed with the forceps, but care must be used not to crush them or unduly injure the feathery stigmas. With experience, the breeder can usually grasp and remove all three anthers at once. Emasculated spikes should be covered immediately by bagging or wrapping.

In another procedure, the upper one-third of each floret is cut off with scissors to expose the sex organs. Anthers are then removed with forceps from the top of the floret. This method is useful in areas where cool temperatures or high humidities minimize floral desiccation (Fig. 2B).

Scissor emasculation also can be used (Wells and Caffey, 1956). Emasculation consists of merely cutting the primary and secondary florets at an earlier stage (5 to 7 days before anthesis). The anther remnants degenerate and most do not produce viable pollen. The method is fast, but requires considerable skill and experience. Selfing may be a problem, so some way to identify the hybrid seed or plants is important.

C. Pollination

Wheat flowers usually can be pollinated 2 to 4 days after emasculation. The time varies with climatic factors and stage of stigma development when the spike was emasculated. Florets should have well-developed feathery stigmas when they are pollinated (Fig. 2C).

Spikes with suitable pollen exhibit a few freshly extruded anthers (Fig. 2C). Mature pollen can be obtained from florets of spikelets in close prox-

imity to these because alternating florets usually shed pollen on subsequent days. Anthers are removed with the forceps by entering between the lemma and palea of florets just before anthesis. If male spikes must be saved, anthers are removed from florets and quickly transported to the female in creases of the breeder's hand or in a small receptacle, such as a 35 mm plastic Petri dish. If there is no need to save the male spike, it can be rémoved and transported to the female.

Pollen can be applied several ways. The standard method is to remove the bag from the female, grasp with the forceps an anther which has just begun to shed pollen, and carefully brush it on the stigmas of the female plant. Usually one good anther can be used on three or four florets. If pollen is abundant, the breeder can repeat this process to insure better seed set.

Some breeders use a small brush to apply pollen, particularly if several spikes are to be fertilized with a single male. Several anthers are allowed to dehisce in the hand or a receptacle and the pollen is brushed on the stigmas. Residual pollen can be destroyed by placing the brush in the mouth or in alcohol.

The twirl pollination method can be used when the pollen source is plentiful (CIMMYT, 1976). This method is rapid and requires less skill than those described above. The upper one-third of each primary and secondary floret of the male spikes is removed to facilitate the extrusion of mature anthers and the release of pollen. During this operation, filaments of mature anthers usually elongate. The top of the bag covering the female flower is cut off and the male spike is inverted into the bag parallel to the female spike. The male spike is vigorously rotated by twirling its peduncle between the thumb and forefinger and the bag is resealed. The pollinating spike is often left in the inverted adjacent position for a day to provide additional pollen.

A third pollination system is the approach method (Rosenquist, 1927). The female spike is positioned slightly below the male spike and both spikes are covered with a bag. This method works well with moveable greenhouse plants. It can be used in the field by using detached male spikes or by growing male and females in closely-sown rows. Detached male spikes can be kept alive to shed pollen for 2 or more days by placing their culms in water. Such a system is used at Pullman, Wash., where one end of a plastic soda straw (Fig. 2A) is sealed with a plastic-bag sealing iron. The straw is taped to the female culm about 2 to 5 cm below the spike and is filled with water. The male spike is placed in the straw so that its midpoint is at the apex of the female spike, and their peduncles are taped together (Fig. 2C). Both spikes are covered with a glassine bag. On hot days, straws are refilled with water daily with a squeeze-type plastic wash bottle (Fig. 2A). The bags are shaken during peak anthesis periods to facilitate pollen dispersal.

The approach method has several advantages. Experienced people can be used to select pollen, the task requiring the most expertise in wheat hybridization. Lesser trained people can be used for emasculation, attaching straws, watering, etc. Because this method supplies pollen over a longer period than any other method, higher seed set can be achieved. Adverse weather affects the results less with it than with either the anther or twirl methods. The method is relatively fast, but slower than the twirl method. At Pullman, Wash., comparative studies based on 1,000 pollinations each indicated that 22% more F_1 seeds were produced by the approach method than the anther application method.

D. Factors Affecting Efficiency

Use of special nurseries or crossing blocks facilitates hybridization. Such nurseries contain parental material with genes for pest resistance, plant types, improved quality, and yield; elite lines; sterility sources; and special genetic stocks. Seeding breeding lines in wide rows 60 cm apart and spacing plants within rows 15 cm apart simplifies working with the material during hybridization and aids plant growth and development. Space planting can be done by hand or with specially designed seeders. Crossing blocks should be grown in close proximity to F_1 hybrid nurseries to facilitate back-crossing, top-crossing, and hybrid-parent comparisons.

Synchronization of flowering may be achieved by several methods. These include different seeding dates, space planting, clipping plants, and differential temperatures, photoperiods, light levels, and vernalization periods. Varying the seeding date is most effective in regions located within 30° N or S lat of the equator. It is less useful at Pullman, Wash. (46° N lat), where fall seedings made 75 days apart may flower within 5 days of one another.

Widely spaced seedings are often effective in synchronizing flowering particularly with winter wheats. Plants spaced 30 to 60 cm apart with optimum water and nutrients, have produced 50 to 100 tillers at Pullman. Single plants from these spacings have a flowering period of from 14 to 21 days. Clipping plants may be effective, especially for winter wheat. At Pullman, hybridization has been the most successful when plants that were cut back served as females. Plants should not be cut below the spike primordia or the primordia will be killed.

Growth-control facilities, including greenhouses, simplify floral synchronization. Such facilities make it possible to alter photoperiod, light level, vernalization, and temperature, all of which act individually and in various combinations to influence flowering. Increases in photoperiod (4.6 W/m^2 at plant height) at 2-hour intervals from 9 to 17 hours consistently reduced days to heading among several wheat cultivars (Levy and Peterson, 1972). Spring wheats even responded to vernalization treatment by heading 1.7 to 8.9 days earlier when vernalized 28 days. Staggered planting dates of spring wheats at transplanting time of winter wheats enables one to cross springs and winters in the greenhouse.

Temperatures 5 to 20 C above 10 C shorten heading date by 4 to 24 days. Floral initiation and heading date were shortened when light level was increased from 33 to 83 W/m² (Friend et al., 1963).

Several genetic markers available in wheat may aid in identifying hybrid plants, but very few facilitate detection of hybrid seed. In some environments, the blue-aleurone trait expresses xenia when parental selections with this gene are used as males (Suneson, 1962). The F, hybrid plants often can be identified by comparing their gross morphology to their parents. When the female parent has the recessive allele for a certain morphological trait, an F₁ plant that expresses the male's dominant phenotype confirms hybridization. Useful morphological traits include awn expression, spike type, pubescence (on glumes, ligules, nodes) and nondwarfing (coleoptile and culms). Color of anther, glume, awn, coleoptile, and culm may be useful. Generally red, purple, and black pigments are dominant to the lighter colors and usually are under single gene control. Plant disease reaction may help verify hybridization.

Because wheat is a polyploid, many traits are actually influenced by several genes rather than one or two. Phenotypic expression for certain traits in F_1 plants may vary from the expected. An experienced breeder should be able to determine which traits are reliable for his material and environment.

Three independent complementary genetic systems may act to produce lethals or partial lethals that either kill or greatly reduce the productivity of F_1 plants. These traits are hybrid necrosis, hybrid chlorosis, and grassclump dwarfness. Wheat breeders should be aware of the limitations that these genetic systems impose on wheat hybridization, and should be alert for these undesirable genotypes among their breeding lines.

Hybrid necrosis (progressive lethal necrosis) is controlled by a complementary, two-gene, multiallelic system. Hybrid chlorosis, governed by a complementary two-gene system, usually has a less drastic effect on F, plants than does hybrid necrosis and occurs less frequently. Listings of references giving genotypes of cultivars with genes for hybrid necrosis and chlorosis have been made (McIntosh, 1973).

The grass-clump dwarf trait is regulated by a rather complex genetic system involving at least four genes, possibly with multiple alleles. Frequently grass-clump plants fail to head or produce seed. Several genotypes produce dwarf plants and references with listings of the presumed grassclump genotypes are available (McIntosh, 1973). This malady can be partially alleviated by growing plants at high temperatures (McVetty et al., 1976). Seed production of dwarfed plants of certain crosses can be enhanced by using gibberellic acid in combination with high temperature (Metzger, 1978).

V. NATURAL HYBRIDIZATION

Methods for increasing natural hybridization of wheat have been developed to exploit heterosis. Breeders can use such schemes to accomplish mass hybridizations needed for recurrent selection, composite cross breeding, and production of synthetics.

The *T. timopheevii* (Zhuk.) Zhuk. var. *timopheevii* cytoplasmicsterility, genetic-fertility system is currently used in hybrid wheat programs. Adapted cultivars are converted into female cytoplasmic male steriles (A lines) by repeated backcrossing. The restorer lines (R lines) serve as pollinators possessing traits that complement those of the male-sterile females. Stable high levels of male-fertility restoration have been difficult to achieve in hybrid wheat because several genes are involved. The effectiveness of some restorer genes can usually be increased and stabilized by selfing and reselection. Certain restorer genes function less effectively in some genetic backgrounds than in others. Because of these and other restrictions, full utilization of the cytoplasmic-sterility, genetic-fertility system to achieve mass wheat hybridization has not been realized.

Genic sterility also occurs in wheat (Suneson, 1962). Various schemes have been proposed to use this form of sterility (Briggle, 1970; Gill and Anand, 1970; Driscoll, 1972).

Use of chemical hybridizing agents may eventually offer a rapid and flexible way to induce male sterility in wheat. Some reports cite positive results. Using granular ethephon (2-chloroethylphosphonic acid), Fairey and Stoskopf (1975) reported sterility levels up to 100% with no impairment of female fertility or apparent morphological or physiological abnormalities. Several chemical companies are actively researching potential chemical hybridizing agents of wheat. If a reliable chemical agent is found, wheat hybridization will be greatly simplified, compared to hybridizations by the rather cumbersome cytoplasmic-genetic and genetic schemes.

Although wheat has a perfect flower, conducive to self-pollination, cross-pollination does occur, sometimes at a rather high frequency. The extent of cross-pollination is influenced by genotypic and environmental factors. Cross-pollination levels of about 3 to 4% are common, but much higher levels have been detected for some cultivars (Heyne and Smith, 1967).

Factors that affect natural cross-pollination of wheat include distance from pollen source, pollen concentration, weather, wind direction, and floral characters. Under North Dakota conditions, Miller and Lucken (1976) found that a 1:1 (3.1:3.1 m strips) ratio of male-sterile lines to restorer lines had several advantages over a 2:1 (6.2:3.1 m strips) ratio. The 1:1 ratio produced higher quality hybrid seed and buffered the effects of adverse environment on hybrid seed set. Both ratios were equally efficient in producing hybrid seed per unit area. Any agronomic practice that improved normal wheat yields also enhanced seed production of hybrid spring wheat.

VI. SEED DEVELOPMENT, HARVEST, AND STORAGE

The success of hybridization usually can be verified within 3 to 5 days after pollination. The lemmas and paleas of fertilized florets are no longer open, and kernel development (1.0 to 2.5 mm) is discernible. Hybrid seeds usually are allowed to ripen normally and are harvested when the female plant matures. For rapid reproduction, culms with hybridized spikes can be removed and dried 10 to 14 days after pollination. Post-harvest dormancy of immature seeds may be broken with low concentrations (10 to 50 ppm) of gibberellic acid (Metzger, 1978).

Seed may be threshed several ways. They can be removed from spikes by hand, threshed out with rubbing boards, or with impeller-type head threshers. Hybrid seed packets must be properly identified. A convenient method is to fasten the crossing tag to the packet and arrange the packets in an order that catagorizes the purpose for each cross. Permanent numbers then can be assigned to indicate when and where each cross was made and to facilitate computerization for tracing the cross in subsequent generations.

VII. TECHNIQUES FOR SPECIAL SITUATIONS

Common wheat with its three genomes is genetically well buffered, which allows it to tolerate the addition and substitution of chromosomes from other species and genera. The existence of complete sets of aneuploid stocks greatly facilitates wheat chromosome engineering (Sears, 1972). Alien-addition lines are available with each of the seven chromosomes of rye and with various chromosomes of wild *Triticum (Aegilops), Agropyron,* and *Haynaldia.* Such lines have provided useful genetic information about the individual donor chromosomes and more importantly they have proven their value in gene transfers from the related species or genera to wheat, principally for their incorporation of disease and insect resistance.

The chromosomes of many of the wheat relatives also can be substituted for individual wheat chromosomes. Alien substitutions are produced by crossing alien-addition lines to a particular monosomic stock and identifying F, plants of the cross that have 20 bivalent wheat chromosomes plus a monosomic alien chromosome. Some selfed progeny of these individuals will have 20 bivalent wheat chromosomes and one bivalent alien chromosome. Such alien substitution lines are generally stable, but they almost always lack agronomic promise. Their main value has been to facilitate the exchange of a piece of alien chromosome for a piece of wheat chromosome.

Hybrid wheat plants can be successfully cloned to maximize F_2 seed return from a limited number of F_1 seeds (White, 1962). Usually four or more clones per plant may be obtained. Clones usually tiller less (about 30%) than seed stock plants and suffer slightly higher mortality rates (3 to 18%).

REFERENCES

- Briggle, L. W. 1970. A recessive gene for male sterility in hexaploid wheat. Crop Sci. 10:693–696.
- CIMMYT. 1976. The CIMMYT wheat training manual (Rev. February, 1976). Int. Maize and Wheat Improvement Ctr., Mexico 6, D.F.
- DeVries, A. Ph. 1971. Flowering biology of wheat, particularly in view of hybrid seed production—A review. Euphytica 20:152–170.
- Driscoll, C. J. 1972. XYZ system of producing hybrid wheat. Crop Sci. 12:516-517.
- D'Souza, L. 1970. Untersuchungen uber die eignung des weizens als pollenspender bei der fremdbefruchtung, verglichen mit Roggen, Triticale und Secalotricum. Z. Pflanzenzucht. 63:246–269.

Fairey, D. T., and N. C. Stoskopf. 1975. Effects of granular ethephon on male sterility in wheat. Crop Sci. 15:29-32.

Fischer, R. A. 1975. Yield potential in a dwarf spring wheat and the effect of shading. Crop Sci. 15:607–613.

- Friend, D. J. C., J. E. Fischer, and V. A. Helson. 1963. The effect of light intensity and temperature on floral initiation and inforescence development of Marquis wheat. Can. J. Bot. 41:1663-1674.
- Gill, B. S., and S. C. Anand. 1970. Genetic male sterility for hybrid seed production in wheat. Crop Sci. 10:385–386.
- Harlan, J. R. 1975. Crops and Man. Am. Soc. of Agron., Madison, Wis. 295 p.
- Heyne, E. G., and G. S. Smith. 1967. Wheat breeding. In K. S. Quisenberry (ed.) Wheat and wheat improvement. Agronomy 13:269–306. Am. Soc. of Agron., Madison, Wis.
- Levy, Jose, and M. L. Peterson. 1972. Responses of spring wheats to vernalization and photoperiod. Crop Sci. 12:487-490.
- McIntosh, R. A. 1973. A catalogue of gene symbols for wheat. p. 893-937. In E. R. Sears and L. M. S. Sears (ed.) Proc. Fourth Int. Wheat Genet. Symp., Columbia, Mo.
- McVetty, P. B. E., D. T. Canvin, and C. H. Hood. 1976. Temperature requirements for growth of grass-clump dwarf wheats and the inheritance of the trait. Crop Sci. 16:643-647.
- Metzger, R. J. 1978. Personal communication. Science and Education Administration, USDA, and Dep. of Farm Crops, Oregon State Univ., Corvallis, OR 97331.
- Miller, J. F., and K. A. Lucken. 1976. Hybrid wheat seed production methods for North Dakota. Crop Sci. 16:217–221.
- Morris, Rosalind, and E. R. Sears. 1967. The cytogenetics of wheat and its relatives. In K. S. Quisenberry (ed.) Wheat and wheat improvement. Agronomy 13:19– 87. Am. Soc. of Agron., Madison, Wis.
- Ovcinnikov, N. N. 1952. The effect of pollen from different portions of the ear upon crosses. Sel. Semenovod. (Moscow) 19(1):76-77. [Plant Breed Abstr. 22:2604-1952.]
- Percival, John. 1921. The wheat plant. Duckworth, London.
- Reitz, L. P. 1967. World distribution and importance of wheat. *In* K. S. Quisenberry (ed.) Wheat and wheat improvement. Agronomy 13:1–18. Am. Soc. of Agron., Madison, Wis.
- Rosenquist, C. E. 1927. An improved method of producing F₁ hybrid seeds of wheat and barley. J. Am. Soc. Agron. 19:968–971.
- Sears, E. R. 1972. Chromosome engineering in wheat. Stadler Symp. 4:23–38. Univ. of Missouri, Columbia, Mo.
- Suneson, C. A. 1962. Use of Pugsley's sterile wheat in cross breeding. Crop Sci. 2: 534-535.
- Thorne, G. N., M. A. Ford, and D. J. Watson. 1968. Growth, development, and yield of spring wheat in artificial climates. Ann. Bot. (N.S.) 32:425-446.
- Wardlaw, I. F. 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. Aust. J. Biol. Sci. 23:765–774.
- Wells, D. G., and H. R. Caffey. 1956. Scissor emasculation of wheat and barley. Agron. J. 48:496-499.
- White, W. J. 1962. Clonal propagation of wheat plants for the evaluation of yield. Can. J. Plant Sci. 42:571-581.