Rye

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Rye (Secale cereale L.) is important as a food grain, especially in parts of northern Europe where soils are poor and winters severe. The leading rye grain producers are U.S.S.R., Poland, West Germany, East Germany, Czechoslovakia, Hungary, Canada, and the United States. Winter and spring ryes for all purposes were seeded in the United States on about 1.4 million ha annually during the 3-year period from 1975 to 1977 with nearly two-thirds of the crop grown in Minnesota, Nebraska, North Dakota, South Dakota, and Georgia. In the North Central States, rye is grown primarily for grain and for plow-down as a green manure crop, but is also used for hay and pasture. Only 27% of the planted hectarage is harvested for grain in the United States. The grain is used for bread making, feeding livestock, and producing alcoholic beverages. Grain yields in the United States are rather low, averaging only 1,380 kg/ha. In the southern U.S. where it is grown alone or in combination with ryegrass or clovers, rye is used primarily for temporary winter grazing and also as a cover or green manure crop.

I. PARENTAL MATERIAL

Rye is an erect annual or winter annual classified in the tribe Triticeae within the grass family Gramineae. The genus Secale contains several species but only one, S. cereale L., is widely cultivated. Other rye species are
principally weedy or wild types which often occur as mixtures in other grains and grasses. Annual species, in addition to S. cereale, include S. vavilovii Grossh., S. silvestre Host., S. ancestrale Zhuk., and S. segetale Zhuk. Perennial species include S. montanum Guss., S. africanum Stapf., S. anatolicum Boiss., and S. kuprijanovii Grossh. Stutz (1972) discussed the origin of cultivated rye and gave a description of the various wild species. Evans and Scoles (1976) summarized the species situation in rye by stating that S. montanum, S. africanum, S. silvestre, and S. vavilovii differ from S. cereale by two and in the case of S. silvestre by perhaps three reciprocal translocations. Crosses between species have been successful in most instances. Price (1975) found in crosses between S. cereale x S. africanum that viable seeds were formed only when S. cereale was the female parent. He concluded the seed failure in the reciprocal cross was due to abnormal endosperm development.

Rye breeding has been enhanced over the past 50 years by induced polyploidy. Autotetraploid ryes with 28 instead of the normal 14 chromosome have been produced by colchicine. Munting (1951) reviewed the research related to the production and testing of tetraploid rye.

Some of the advantages of tetraploid rye are larger kernels, higher protein content, and better seedling emergence. Disadvantages include lower grain yield, reduced tillering, greater height, and later maturity. Another objection to tetraploid ryes is the necessity of isolation from diploid ryes to avoid formation of triploids. Triploid zygotes abort so yields are reduced in both diploids and tetraploids when grown together. Koo (1958) found that seed set in the diploid cultivars 'Emerald' and 'Imperial', when exposed to tetraploid pollen, was reduced two-thirds. In the reverse situation, the seed set of 'Tera Petkus', when exposed to diploid pollen, was one-half to two-thirds of that when isolated.

The U.S. Department of Agriculture maintains and distributes rye seed for experimental purposes from a world collection of rye. This collection contains approximately 600 entries and is stored and catalogued in Beltsville, Md.

The Food and Agricultural Organization of the United Nations (FAO) has periodically issued lists of germplasm collections including rye (Saint, 1972). Mao (1961) lists stations where plant breeding is being carried out, including the breeders and their respective crops.

Triticale breeding has created new interest in rye germplasm because rye is a parent of primary triticales. Examples of possible sources of rye germplasm are CIMMYT in Mexico and experiment stations in Germany, Canada, the United States, and other countries doing research on rye and triticale.

II. PLANT CULTURE

A. Field

Rye is the most widely adapted of the cereals because of its extreme winterhardiness and ability to grow on marginal soils. The most drought-resistant of the cereals, rye has an extensive root system and adjusts
maturity to moisture. Rye uses 20 to 30% less water per unit of dry matter formed than wheat (*Triticum* sp.) (Starzycki, 1976). Tetraploid rye cultivars are more sensitive to drought than diploids. Although rye is also able to tolerate a range of soil acidity, it does best at a pH of 6.0 to 6.5. Rye responds well to fertilizers, but care must be used to prevent excess nitrogen fertilization, which will cause the plants to lodge. The crop tillers well; normally for seed production the seeding rate is about 63 to 78 kg/ha. The culture of rye is similar to that of wheat and other cereal crops.

**B. Growth Chamber and Greenhouse**

Cultural requirements for growing rye in the greenhouse is similar to those for wheat and other small grains. Normally slightly larger pots are needed because of the extensive root system, and the plants have to be staked and tied up to prevent stem breakage. Rye is a long-day plant and extending the light period to 14 to 18 hours per day will hasten flowering. Photoperiod-insensitive types may be available; however, we are not aware of documented evidence. Temperatures in the greenhouse are not as critical as they are for the other small grains because rye will grow at lower temperatures, but it grows best at moderate temperatures. Winter, spring, and intermediate cultivars are available and differ considerably in vernalization period. The winter types require 40 to 60 days, whereas the spring types require only 10 to 12 days of cold temperatures to shift into the reproductive stage. As previously mentioned, rye tillers profusely, so individual plants can easily be split into several clones.

**III. FLORAL CHARACTERISTICS**

The rye inflorescence is a dense, terminal spike 10 to 15 cm long, more slender and nodding than wheat. The spikelets are solitary at each node and are alternately arranged on a zig-zag rachis. Each spikelet usually consists of only two fertile florets, with supernumerary florets vestigial or absent (Fig. 1). The florets are perfect, each containing three anthers and a pistil consisting of two feathery stigmas and an ovary.

Rye differs from other small grains in that it is cross-pollinated. Although pollen can and does fall into flowers of the same plant, little self-pollination takes place even when the spikes of individual plants are bagged. Leith (1925) studied over 84,000 rye flowers and concluded that self-sterility ranged from 96 to over 99% in rye. This and other evidence showed conclusively that commercially grown rye depends almost entirely upon cross-pollination for seed set and grain production. However, some inbreds selfed consecutively for 20 years or more have improved in self-fertility, perhaps as high as 20 to 40%.

The most extensive analyses of the genetics of self-incompatibility in rye have been performed by Lundquist (1954, 1956). He postulated that incompatibility is controlled by two loci, designated S and Z, each containing a multiple allelic series. A pollen grain is not inhibited unless both incompatibility loci in the stigma have alleles common to the two present in the pollen grain. If at least one of the two alleles in the pollen grain does not
have a similar matching allele in the style, the pollen is compatible and will fertilize the ovary.

Landes (1939) postulated that self-incompatibility was partially the result of inhibition of pollen tube growth. Ruebenbauer (1973) proposed a general hypothesis aimed at unraveling the genetic phenomena of self-incompatibility.

Ovule or zygote abortion also reduces seed set in open-pollinated fields. On 185 random heads from a field in Georgia, we found only 80.9% seed set. Landes (1939) found a large proportion of self-pollinated ovaries which had aborted in the early stages.

Meiotic divisions begin in the middle part of the spike and gradually proceed upwards and downwards in the spike, usually a few days before the emergence of the spike from the leaf sheath. Bennett et al. (1973) have shown that male meiosis precedes female meiosis by about 15 hours in the same floret. They found only a single megaspore mother cell per floret in wheat and rye compared with about 2,100 microspore mother cells in 'Chinese Spring' wheat and 16,000 in 'Petkus' rye. Sapra and Hughes (1975) reported an average of 42,000 pollen grains per anther in rye and 11,000 in wheat, a further indication of large anther size in rye. Pederson et al. (1961) found pollen production per unit area was 2.25 to 2.50 times greater in diploid than in tetraploid rye.

Fig. 1—Spikelet of rye, consisting of a pair of fertile florets. A) Outer or empty glume; B) Lemma with barbed awn; C) Three anthers at anthesis showing pollen grains above and threadlike, connecting filaments below; D) Feathery stigma (ovary below not visible); and E) Palea.
Wodehouse (1935) described rye pollen grains as being rather large (62 × 40 μ) and ellipsoidal with the germ pore on the side near one end. This character is rather unique among the grasses and serves to distinguish this species from others. The pollen grains of diploid rye (62.5 μ) are smaller than those of wheat (70.0 μ) (Sapra and Hughes, 1975).

The peak of rye pollen release comes at different times of day in different locations and is influenced by temperature, humidity, and sunlight. Jones and Brown (1951) observed that 'Balbo' rye in Oklahoma shed pollen from 0800 to 1200 hours with a peak between 1030 and 1100 hours. Under favorable weather, rye flowers have opened after sunrise with anthesis lasting until evening.

The first flowers to open are usually two-thirds of the way up the spike. They then open in both directions, up and down the spike, over a period of several days. The flowers usually remain open from 15 to 45 min. The lodicules swell, causing the lemma and palea of a floret to open exposing the three anthers. Brewbaker (1926) observed that rye florets open slowly at first and then more rapidly until the filaments and anthers hang out of the florets releasing large amounts of pollen carried by air currents to other plants.

Brewbaker (1926) found that unfertilized florets stayed open as long as 19 days in the greenhouse. Laube and Quadt (1959) stated that rye stigmas could be receptive for 7 days after opening of the flower. Heribert-Nilsson (1916) found rye stigmas receptive 14 days after anthesis.

D'Souza (1972) found rye stigmas (5.4 mm) to be longer than wheat stigmas (3.5 mm). He further showed that stigmas have two phases of receptivity which are dependent upon temperature and humidity. In the first phase, stigmas are receptive and seed set is good. The second phase is marked by a sudden drop in seed set. In rye at 20 C and 60% relative humidity, the first phase lasted 6 days and the second 5 days. At 30 C and 40% relative humidity, the two phases had a duration of only 3 days each. Temperature affects stigma receptivity more than humidity.

About 80% of pollen shed is viable for at least 10 hours according to D'Souza (1972) who stated that pollen tubes germinate about 3 min after coming in contact with the stigmas. High temperatures and low humidity are detrimental to pollen. Pollen storage is normally more successful at low temperatures and humidity. Gramineae pollen is an exception in that it requires storage in high humidities of 80 to 100%. Collins et al. (1973) reported that rye pollen stored in liquid air (−192 C) germinated in vitro and produced seed set in vivo.

Artificial germination of pollen from species within Gramineae has proven difficult because of the wide differences in species acceptance of the growth media. The addition of 3.5% bacto-agar to solidify a 25% sucrose and 0.02% boric acid solution was found essential for germinating rye pollen (Pfahler, 1965).

Viable pollen will travel in air currents and still be effective. Heribert-Nilsson (1916) used a wax-free (bloom-less) genetic marker and observed 54.5% natural crossing with plots separated by 50 m, 46.3% at 250 m, 29.7% at 350 m and 19.0% at 400 m.
IV. ARTIFICIAL HYBRIDIZATION AND SELF-POLLINATION

A. Equipment

Wells and Mahdawi (1953) found kraft corn tassel bags were the most convenient, dependable, and economical method for selfing single plants and for crossing paired plants. These waterproof pollen bags can be tied shut with string or stapled. It is usually necessary to support plants in the nursery with stakes to prevent plants from lodging and breaking. Rye breeders in the U.S.S.R., Poland, and other countries use cloth or heavy muslin cages to cover several plants or entire plots. Cages also can be made of wire covered with plastic film. Various sizes and weights of semitransparent paper sleeves are used for greenhouse rye breeding and are available from supply companies for corn and sorghum pollinators.

The equipment for making hand crosses includes a small pair of sharp-pointed scissors, narrow or sharp-pointed forceps, thin but high quality glassine bags, paper clips, and small tags with attached strings.

B. Preparation of the Female

Rye is cross-pollinated, and most genotypes are highly self-sterile so all that is required for hybridization is to place spikes from two different plants beneath one pollinating bag. Tapping the bags as they are raised on the supporting stake to accommodate culm elongation facilitates pollen dispersal within the bag. Normally good seed set is obtained and reciprocal crosses are obtained from one simple set-up. For critical crosses involving inheritance studies, species crosses, and self-fertile inbred lines, most workers completely emasculate rye and pollinate under controlled conditions.

At the onset of anthesis, the spikes most suitable for emasculation are those which have emerged from the leaf sheath by about one spike length. As the flowering period progresses, emerging spikes are suitable for emasculation (Bauer, 1965). The entire spike usually is emasculated by cutting across the tips of the spikelets with small, sharp scissors and removing three green anthers with forceps from each of the two primary florets (Fig. 2). Usually the left-hand column of spikes on one side of the spike is emasculated from the spike base to tip, followed by the right-hand column of florets. This method eliminates shifting the left forefinger from side to side as it is used to press outward from behind each floret tip to force the lemma and palea apart, providing easy entry for the forceps (Fig. 2). The left forefinger hooks around behind the spike for pushing on the tips of florets in the right column. Florets on the opposite side of the spike are emasculated in the same manner. After all anthers have been removed, each floret may be cut back further, just above the stigma branches. This insures stigma protrusion outside the lemma and palea, and facilitates pollination 2 to 4 days later. The florets should not be cut back if there is danger of desiccation. This entire operation is tedious and time-consuming, especially if large numbers of crosses are needed.
During the 1930's Laube and Quadt (1959) described "schnittkastration," or scissor emasculation, and it is claimed to be 90% as effective as the classical method just described. The florets are cut across about one-half of the way down from the tip with scissors just as the head emerges from the boot, or about a week before anthesis (Fig. 3). All the anthers are cut in half in this operation but the portions remaining in the florets are not removed because they dry up and do not produce viable pollen. After emasculation, the spikes must be covered to exclude foreign pollen, and tagged for easy identification. About 5 days later stigmas will protrude above the edges of the cut lemma and palea, their accessibility allowing easy pollination by the desired male parent. If conditions are favorable, good seed set should be obtained (Fig. 4).

C. Pollination

Ripe anthers are collected from male plants and placed in a petri dish or watch glass. These anthers are then placed near a warm light bulb or in sunlight for 1 to 2 min to encourage natural dehiscence of the anthers. The pollen is applied with forceps to the stigmas of the female by rubbing them with a ruptured anther. Stripping the spike between thumb and forefinger encourages anther extrusion, which makes pollen easier to collect and aids in identifying mature anthers. Spikes gathered from male parents can be laid on paper to prevent anthers from whipping in the wind and losing pollen. Two or three anthers may be enough to pollinate an entire spike; one anther will certainly suffice for several florets. In making inbred-cultivar

Fig. 2—Removing anthers from the floret during emasculation.
crosses, the flowers of the inbred lines may be emasculated in the usual manner, and when the florets open several days later a large amount of pollen may be collected by enclosing a large number of spikes of the male parent in a paper bag and applying the pollen to the emasculated flowers with a camel hair brush. Another method, which is similar to that used in barley (*Hordeum* sp.) and wheat loose smut inoculation is called the poof method. It involves collecting relatively large amounts of pollen, mixing the pollen with talc, and injecting the pollen-talc mixture into each female floret by means of a hypodermic needle attached to a small rubber bulblet. Preparing the mixture is time-consuming, but pollination is rapid (Shands, 1978).

Another method which works well for hand crossing is the approach method first described by Rosenquist (1927), especially with the improved techniques described by Curtis and Croy (1958) and McDaniel et al. (1967). The approach method involves placing an emasculated spike slightly beneath a nonemasculated or male spike and covering both spikes with a polli-

![Fig. 3 (Left)—Scissor emasculation of rye. A) Rye spike at the proper stage, and B) emasculation of the spike. Fig. 4 (Right)—Seed set in rye spike after scissor emasculation and 10 days after pollination.](image)
nation bag. Pollen from the male spike falls on the female spike, affording good opportunity for pollination. The approach method offers several advantages over hand pollination. The crosses can be set up when the emasculation is done so it will not be necessary to go back several days later. The crosses can be made up any time during the day, and many more florets can be pollinated than would be possible by hand. Important keys to successful approach crossing are the use of dialysis tubing for pollination bags and occasional thumping of the bags during the pollination period to get good pollen distribution. Hybrid seeds are often smaller with this method, but they are much more easily obtained. Rye is relatively easy to cross and, under most conditions, if self-sterility is not involved, 50 to 75% seed set can be expected.

D. Factors Affecting Efficiency

Temperatures are not critical for flowering, but 20 to 30 C are the temperatures which prevail in many rye fields at flowering time. Greenhouse temperatures in the spring may exceed 30 C, thus reducing the period of stigma receptivity and pollen effectiveness. Cooling the greenhouse below 25 C will improve seed set. Low humidity (40%) is more detrimental to stigmas than higher humidity (60%).

With many crops, altering planting dates will alter heading dates. In the United States, altering the planting date of winter rye in the field has a relatively small effect on heading date in the spring. A spread of 3 months in planting dates in Georgia changed heading dates only 11 days. Varying the planting date for material in the greenhouse generally is more effective. Also the vernalization period can be varied for different cultivars. Seed of the extreme winter-types can be vernalized by sprouting them on absorbent paper in petri dishes in a cold chamber or refrigerator at 1 to 2 C for 4 to 6 weeks before planting in the greenhouse, and thus can be matched to spring or intermediate types. The spring types can be planted about the time the winter types are removed from vernalization. Care must be taken after removing plants from vernalization because the effects can be reversed by high temperatures.

Cutting rye plants back once or twice in the vegetative stage will delay flowering. Care must be taken not to cut below the growing points and destroy or injure the reproductive meristems.

Spaced plants are best to work with in field crossing blocks, and room must be provided for staking and crossing. Planting two rows and skipping one will give some room to work around the plants. When bagging rye, space must be allowed for the continued upward growth of the spike because the rye stem continues to elongate for an extended period of time after heading.
V. NATURAL HYBRIDIZATION

Spatial isolation from other rye plants can be used for crossing blocks, increasing inbred lines, or developing synthetic populations. The disadvantage of this method is the difficulty of finding suitable isolation in frequency and distance.

Recently, rye breeders in Germany, U.S.S.R., and Poland have developed a possible way to utilize inbred lines or early generation material in the production of hybrid rye. Systems for controlled pollination based on cytoplasmic-genetic male sterility are now available (Geiger and Schnell, 1970; Gulyaeva, 1971; Klyuchko and Belousov, 1972; Kobyljanskii and Katerova, 1973; and Madej, 1976). Crossing schemes for hybrid rye are believed to be similar to those employed for the production of hybrid corn and hybrid sorghum. Several reports are available which indicate that a considerable amount of heterosis is available in rye (Pfahler, 1968a, 1968b; and Sechler and Chapman, 1967).

VI. SEED DEVELOPMENT, HARVEST, AND STORAGE

Rye seed development follows that of wheat very closely. Special care must be taken when threshing seed by machine because the pointed embryo of the seed protrudes and can easily suffer mechanical damage. Rye normally threshes free of the chaff easily and it is not necessary to use high speeds with threshing equipment. Seed viability is short-lived when rye is stored under ordinary laboratory conditions (Morey, 1976). For long-term storage, rye seed can be dried at 40 C to a moisture content of 5%, then dried at a temperature of 50 to 60 C. The seed may be safely dried to a moisture content of about 3%, but further dehydration may cause some somatic damage. For long-term storage, it is necessary to store the seed in airtight containers to retard senescence (Grzesik and Molski, 1975).

Rye does not offer the problem of a long period of afterripening dormancy as found in some crops. In Canada, Depauw (1976) studied seed dormancy or afterripening in rye and found no difference between cultivars, but did obtain a difference between years. In 1974, about 37 days of afterripening were required, but in 1975 only 1 to 7 days were required. At Tifton, Georgia, in 1977, 'Athens Abruzzi' required 21 days of afterripening to gain its full germinating capacity. Bekendam (1975) suggested the use of gibberellic acid to break dormancy of cereal seeds.

VII. TECHNIQUES FOR SPECIAL SITUATIONS

The development of homozygous lines from tissue culture of microspores of F1 plants would be a great advancement in the development of hybrid rye. Thomas and Wenzel (1975) utilizing F1 winter hybrids of S. cereale which included genes for short culm and self-fertility from S. vavilovii sug-
gested that this would be feasible, and they cultured calluses bearing pri-
mordia as well as plantlets and perfect embryos. Malepszy (1975) reported
success in culturing rye microspores into haploid callus, as well as plants
grown from the somatic callus. Despite the problems inherent in these pro-
cedures, the ability to obtain homozygous diploids immediately would be of
great advantage to breeders.

REFERENCES

Bennett, M. D., R. A. Finch, J. B. Smith, and M. K. Rao. 1973. The time and dura-


Bekendam, J. 1975. Report of the working group on the application of gibberellic
acid in routine germination testing to break dormancy of cereal seed. Seed Sci.
Technol. 3:92–93.


D'Souza, L. 1972. A comparative study of the size and receptivity of the stigma in
wheat, rye, triticale and secalotricum. Z. Pflanzenzucht. 68:73–82.


Grzesik, M., and B. Molski. 1975. The effect of temperature and dehydration of the
dried seeds on the biological properties of rye introductions. Hodowla Ros.


Heribert-Nilsson, H. 1916. Populationsanalysen und Erblichkeitsversuche. Z.
Pflanzenzucht. 4:1–44.

Jones, M. D., and J. G. Brown. 1951. Pollination cycles of some grasses in Okla-

Klyuchko, P. F., and A. A. Belousov. 1972. Genetic studies on cytoplasmic male


Koo, F. K. S. 1958. Deleterious effects from interpollination of diploid and auto-


and W. Rudorf (ed.) Handbuch Pflanzenzucht. Bd. II. Breeding of grain