Oat

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The cultivated oat (*Avena sativa* L. and *Avena byzantina* C. Koch) is an annual grass that ranks fifth among cereal grains in world production. Oats are grown on every continent, but their production is of far greater importance in the Northern Hemisphere. The areas of greatest production are in the North Central U.S., the Prairie Provinces in Canada, Western Russia, countries of Northwest Europe, and the British Isles. Of the cereal grains, oats contain the highest quality and quantity of protein and although approximately 90% of the oat crop is used for livestock feed, oats also provide an important source of human food. Prepared foods include rolled oats and dry breakfast cereals.

I. PARENTAL MATERIAL

The origin of cultivated oats is uncertain. Evidence indicates that various species of oats persisted as a mixture in wheat and barley used by several civilizations in areas surrounding and to the north of the Mediterranean Sea before being cultivated as a crop.

The genus *Avena* forms a polyploid series of diploids, tetraploids, and hexaploids with a basic chromosome number of seven. Rajhathy and Thomas (1974) have classified *Avena* into 19 taxonomic species of which 10 are diploid (2n = 14), five are tetraploid (2n = 28), and four are hexaploid (2n = 42). They have further divided the 19 taxa into 11 genome groups each representing a biological species, of which seven are diploid, three are tetraploid, and one is hexaploid. Taxa of the same biological species (same genomes) are cross compatible and produce fertile F₁ hybrids. Crosses between different biological species may exhibit varying amounts of cross-incompatibility and sterility in the F₁ hybrids.
Wild and cultivated species occur in each of the three ploidy levels, but most cultivated oats belong to the hexaploid group. Wild species possess certain desirable traits, such as disease resistance, and gene transfers between wild and cultivated species within the same biological species are usually accomplished with little difficulty. For example, all hexaploid wild and cultivated species are cross-compatible and produce fertile F₁ hybrids. Consequently, gene transfers between cultivated hexaploid species *A. sativa* and *A. byzantina* and the wild hexaploid species *A. fatua* and *A. sterilis* are common in most oat breeding programs. Gene transfers from the diploid and tetraploid wild or cultivated species into the gene pool of cultivated hexaploid oats are complicated by varying degrees of cross-incompatibility and sterility. However, considerable progress has been made in recent years and some transfers have been made, e.g., Aung and Thomas (1976) and Sharma and Forsberg (1977). The oat breeder needs to have a clear understanding of species relationships and the genomic structure of the ployploids of *Avena* to identify suitable pathways for accomplishing gene transfers from the lower ploidy species to the hexaploid species. For a more complete review of the current state of knowledge of species relationships and genomic structure of *Avena*, the reader is referred to Rajhathy and Thomas (1974) and Baum (1977).

Comprehensive germplasm collections of wild and cultivated species of *Avena* are maintained and distributed by the Plant Genetics and Germplasm Institute, Science and Education Administration, U.S. Department of Agriculture, Beltsville, Md., and by the Canada Department of Agriculture, Ottawa, Ontario.

II. PLANT CULTURE

A. Field

Environmental conditions that provide healthy and vigorous oat plants also provide optimum material for making crosses. Most soil types provide a suitable medium for growing oats, provided adequate nutrient, pH, and moisture levels exist. Although the requirements for added nitrogen depend especially upon soil type and previous cropping, some supplemental nitrogen is usually needed. Light-colored, low organic matter soils have a low capacity to supply nitrogen; the deep, dark-colored, high organic matter soils have a high capacity to supply nitrogen. Nitrogen fertilization rates of 32 to 45 kg/ha on dark-colored and 67 to 90 kg/ha on light-colored soils are usually adequate for optimum growth of oats.

Lime, phosphorus, and potassium needs should be determined by soil tests. Most soil fertility specialists consider a pH of 6 or above, Bray P, of 56 kg/ha, and an exchangeable K test of 336 kg/ha to be adequate for oats. The need for supplemental application of secondary and micronutrients varies greatly from region to region, and one should be alert for deficiency symptoms.

Oats respond favorably to cool, moist conditions and bright, sunny days. Field-grown oats intended for crossing should be watered when moisture stress is evident. Supplemental water will be beneficial even in the
relatively humid oat growing regions, particularly during any extended dry period. Conditions that are favorable for growth of oats are also quite favorable for disease and insect development on the crop, and it is often desirable to use fungicides and insecticides to protect susceptible parents that are to be used for crossing. Birds, which can cause severe damage to field-grown oats, must also be controlled when present in damaging numbers.

B. Growth Chamber and Greenhouse

Optimum conditions for greenhouse and growth chamber hybridization are similar to those for field hybridization. Fertility, moisture, light, and temperature should be maintained so that vigorous plants are available. Adequate light level is an essential requirement for successful crossing in greenhouses and growth chambers. Supplemental light must be available for extending the photoperiod and increasing light level. This is particularly important in the northern latitudes where many cloudy days occur during the short-day winter months.

In Illinois, excellent seed set has been obtained in greenhouses using metal halide lights and a 12 to 13-hour photoperiod. The lights are usually left on during the entire day even on clear days. Temperature is maintained at 25 to 30 °C during the day and 20 to 25 °C during the night. Light level at bench level under the halide lights approximates 900 μE sec⁻¹ m⁻².

Material for greenhouse crossing can be grown in pots, in soil beds, in nutrient solutions, or using any other method that provides vigorous plants. Plants grown in pots can be moved about for convenience when crossing. Four to five plants can be grown in a 15 cm pot provided adequate light, moisture, and fertility are provided.

III. FLORAL CHARACTERISTICS

All cultivated and wild species of oats are predominately self-pollinating and outcrossing seldom exceeds 0.5%.

The inflorescence of oats is an open panicle consisting of a main axis, which is a continuation of the stem, and lateral axillary branches that arise from alternate sides of nodes of the main axis (Fig. 1; Bonnett, 1966). Branches arising from the main axis are designated first order branches while those arising from the lateral branches are designated second or third order branches. The main axis and each of the lateral branches terminate in a single spikelet. The number of spikelets per panicle may vary from approximately 20 to 30 depending on genotype and on growing conditions.

The oat spikelet consists of several florets enclosed in two empty glumes with the tip of one glume extending slightly above the other (Fig. 2). Usually only the two basal florets of each spikelet are fertile (Fig. 3), but occasionally the lower three will be fertile. The florets are arranged alternately upon a central axis, the rachilla. Oat flowers are perfect and each is enclosed by two chaff-like bracts, the lemma and palea. The palea is located on the side of the floral axis next to the rachilla. Each flower contains three
stamens, a pistil, and two lodicules. The lodicules, located between the base of the pistil and the lemma, swell at anthesis causing the flower to open. After anthesis, the lodicules collapse.

Natural anthesis usually occurs in the field in the afternoon, but the exact time of opening varies with environmental conditions and locations. Misonoo (1936) in Japan found that temperature variation was the primary factor that determined time of day for natural anthesis. On some days, natural anthesis did not occur, while on most days it occurred in the afternoon after the temperature had reached its maximum and had begun to decline. Coffman (1937) reported that natural anthesis usually reached its maximum in the field between 1500 and 1600 hours in Virginia, Iowa, and Idaho. Hadden (1952) observed that anthesis usually began at approximately 1530 hours in South Carolina and lasted for about 1 hour. On warm days (32 to 38 C) in Idaho, Coffman and Stevens (1951) found that natural anthesis was delayed until late afternoon. Natural anthesis usually occurs under field conditions in Illinois between 1400 and 1600 hours, but the author has seen it delayed to as late as 2000 hours on hot days.

Misonoo (1936) observed that anthesis occurs in oat flowers in the order of emergence from the sheath. Primary florets open first, but at times the primary and secondary florets open on the same day. Florets on an individual panicle bloom over a period of 8 to 9 days (Brown and Shands,

Fig. 1.—Oat panicle.
Fig. 2—Oat spikelet showing ventral (underlapping and longer) and dorsal empty glumes.

Fig. 3—Side view of a spikelet showing dorsal (shorter, overlapping) glume, primary floret, secondary floret, and ventral (longer, underlapping) glume.
1956; Misonoo, 1936). Usually only one or two florets of a panicle bloom on the first day, but on large panicles as many as 10 to 13 florets near the middle of the panicle may bloom on one particular day.

Individual stigmas are usually receptive 1 day before natural anthesis and remain receptive for as long as 3 to 5 days. Length of receptivity is shorter under conditions of high temperature. Excessive mutilation of flower parts during emasculation contributes to floral dessication and more rapid loss of receptivity (Brown and Shands, 1956).

Pollen of oats is most abundant and of highest quality just prior to and during natural anthesis. Suitable pollen for effective crossing can usually be found in individual florets 1 to 2 hours before the flower opens during natural anthesis. Anthers dehisce most of their pollen just before or during opening of the floret, and one can seldom find usable pollen in a floret that has opened. Brown and Shands (1956) found that some oat pollen viability was maintained for several hours up to several days by storage at temperatures of 4 or 11°C. However, their results were somewhat variable and anthers tended to dehisce prior to use, thereby limiting the availability of usable pollen.

IV. ARTIFICIAL HYBRIDIZATION AND SELF-POLLINATION

a. Equipment

The equipment for making oat hybridizations consists of a small pair of sharp pointed scissors, narrow or sharp-pointed forceps, thin glassine bags, paper clips or staples, and small tags with attached strings (Fig. 4). Forceps and scissors are readily available in hospital supply houses or department stores. Forceps are the most important item of equipment. Some hybridists use sharp pointed forceps with curved ends while others prefer

![Image](Fig. 4—Equipment for making oat hybridizations: tag and paper clip, alternative sizes of glassine bags, alternative types of forceps, and scissors.)
straight ends (Fig. 4). Sometimes the tip 0.5 to 1 cm of each prong is ground or filed to a more or less flat edge to minimize damage to the glumes, lemma, and palea.

Glassine bags for protecting emasculated florets can be of various sizes depending to a large extent on preference of the breeder (Fig. 4). Many breeders use a bag that is just large enough to cover the emasculated florets and long enough to be secured to the culm of the female plant. A bag 3 × 15 cm or smaller will usually cover the emasculated florets on a single panicle.

B. Preparation of the Female

Frey and Caldwell (1961) suggested that the optimum time to emasculate oats is when the anthers have obtained full size, but are not yet ready to dehisce. Natural pollination begins in the uppermost florets and proceeds according to the order of emergence from the boot. Florets in individual spikelets will usually flower within 1 to 3 days after emerging from the boot, with the exact time being somewhat dependent on environmental conditions (Fig. 5). Anthers in florets near the tip of the panicle and at the ends of longer lateral branches are more mature than those below or, in the case of
lateral branches, those to the inside or on shorter branches. Anthers in the primary floret are more mature than those in the secondary floret of the same spikelet. Because of the above considerations, the hybridist can locate a primary floret containing anthers near maturity and be assured that those below have not dehisced and are good candidates for emasculation. Withered, empty anthers from natural anthesis the previous day are usually apparent the following morning, hanging from between the glumes of a closed spikelet, and these anthers provide an excellent benchmark below which florets can be selected for emasculation.

Emasculation can be started at any point on the panicle, but most hybridists emasculate florets near the top. Five to eight primary florets are usually emasculated on each panicle, but more can be emasculated on large panicles particularly if florets near the center of the panicle are ready for emasculation or if both primary and secondary florets are used. Hadden (1952) and Zillinsky (1955) found that secondary florets produce as many successful crosses as primary florets, but they are not as easy to use because of their smaller size and later stage of development. The most important consideration in making emasculations is to be sure that anthers are removed before they have dehisced any pollen. Although the more mature florets are easier to emasculate, they are more subject to accidental selfing during the emasculation process. A panicle with spikelets near the top in approximate stage for emasculation is shown in Fig. 5.

Although florets can be emasculated at any time of day that natural anthesis is not in progress, most hybridists emasculate in the morning to avoid the period of natural anthesis which occurs in the afternoon. The risk of accidental selfing during emasculation increases as the period of natural anthesis is approached; however, I have successfully emasculated and pollinated florets simultaneously. When using this method, emasculations must be made very near the period of natural anthesis to have usable pollen, and only a few (three to five) florets can be used on each panicle. While this method is convenient and useful, it should not be used by inexperienced workers or for genetic or other studies where an occasional self cannot be tolerated.

Each hybridist develops, through practice, an individual technique for manipulation of floral parts during emasculation. The spikelet is held near the base and usually between the thumb and index finger of one hand with the ventral (underlapping and longest) outer glume facing the hybridist (Fig. 6). The ventral glume is easy to identify because its tip extends slightly above the tip of the dorsal glume. Using the index finger instead of forefinger leaves the forefinger free to manipulate the floral parts. The outer glumes are separated with forceps held between the thumb, forefinger, and index finger of the other hand, resting the hand holding the forceps on the index finger of the hand holding the spikelet. The exposed secondary floret can be removed by snipping it with the forceps. The palea is separated from the lemma by inserting the tip of one prong of the forceps between the palea and lemma and pulling forward on the palea to expose the three anthers of the primary floret (Fig. 6). With practice, the hybridist will discover that the forefinger of the hand holding the spikelet will be extremely useful in separating first the glumes, lemma, and palea by applying light pressure on the
dorsal glume. The forefinger is used to hold the floral parts open once they have been separated. The three anthers are extracted from the floret cavity with the forceps using care to avoid breaking any ripe anthers that are present and to avoid damage to the two stigma branches. The floral parts are replaced in their original positions. A slight rotation of the spikelet helps in tucking the edges of the ventral glume inside the edges of the dorsal glume.

The palea is usually subjected to less bending or creasing, especially by inexperienced workers, if the secondary floret is not removed until after the primary floret has been emasculated. In this case, the palea is pulled out and down and held by the forefinger against the secondary floret while the anthers in the primary floret are being removed. After the palea is pushed back into its original position, the secondary floret is snipped off with the forceps or pulled out and down breaking the rachilla attachment.

Several authors (Brown and Shands, 1956; Coffman, 1937; Zillinsky, 1955) have emphasized that care should be exercised to avoid mutilation of flower parts. However, my more recent experiences and the results reported by McDaniel et al. (1967, 1969) suggest that a reasonable amount of mutilation can be tolerated with little detrimental effect on seed set, particularly when other conditions are favorable.

The emasculated florets are covered with a glassine bag to exclude outside pollen. The bag should be just wide enough to cover the emasculated spikelets and long enough to be folded and secured with a paper clip or staple (Fig. 7). When securing the bag, the paper clip should not be extended across the culm because it will often cause the culm to break at that point. Coffman (1956) reported that bagging was detrimental to seed set during hot weather, but it is doubtful that this is very important under most conditions. When crossing in the field, panicles may need to be supported by a stake, but this is usually not necessary if a small bag is used. Bagging of emasculated florets is sometimes omitted if a small bag is used. Bagging of emasculated florets is sometimes omitted if a small bag is used. Bagging of emasculated florets is sometimes omitted if a small bag is used. Bagging of emasculated florets is sometimes omitted if a small bag is used. Bagging of emasculated florets is sometimes omitted if a small bag is used. Bagging of emasculated florets is sometimes omitted if a small bag is used.

Fig. 6—Floret opened for emasculation. Note position of fingers on one hand holding spikelet and the other holding forceps.
The emasculated panicle should be labelled with a tag designating the female parent and date of emasculation (Fig. 7). A small tag attached on the main panicle axis just below the last emasculated floret can indicate that all florets above that point have been emasculated. A small length of yarn can also serve the same purpose. When this method is used, only the unemasculated spikelets that interfere with bagging need to be removed, but any spikelets above this point that had pollinated naturally prior to emasculation should be removed so that only emasculated florets are under the bag.

C. Pollination

Ideal environmental conditions for making successful pollinations are clear days and moderate to low temperatures. High temperatures (30 C and above) reduce the availability of usable pollen, and contribute to floral desiccation and loss of stigma receptivity (Brown and Shands, 1956). High temperatures on days between emasculation and pollination cause reduced seed set, particularly in cases where 3 or 4 days elapse between emasculation and pollination.

Fig. 7—Emasculated florets bagged to exclude outside pollen.
Brown and Shands (1956) reported that the optimum time between emasculation and pollination was 1 to 3 days. Hadden (1952) reported excellent results from emasculations made in the morning and pollinated on the afternoon of the same day. I also have experienced some excellent results when making pollinations immediately after emasculation. If emasculations and pollinations are to be made simultaneously or even on the same day, more mature and fewer florets need to be selected on each panicle, and it should be recognized that this will increase the probability of natural selfs. Brown and Shands (1956) suggested that selfing can be reduced to a minimum by emasculation 1 or more days previous to natural anthesis and then allowing 2 to 3 days between emasculation and pollination. Usually the more mature stigmas begin to dehydrate and lose receptivity if more than 3 days elapse between emasculation and pollination. If a large number of florets have been emasculated on an individual panicle, it may be desirable to pollinate them over a period of 2 to 3 days due to differences in maturity and receptivity of the females.

Most pollinations of oats are made between 1300 and 1600 hours, but the best time will vary from day to day. The important consideration is to make sure that pollinations are made when usable and viable pollen is available. This optimum period for good pollen usually begins 1 to 2 hours prior to natural anthesis and extends until natural anthesis has occurred. The problem of poor pollen quality on very hot days can sometimes be overcome by waiting until the temperature drops so that the time of hand pollination more nearly approximates that of natural flowering. However, the hybridist must be careful that pollination is not delayed to the point where natural anthesis has occurred such that all sources of viable pollen are eliminated for that day’s crossing. Even the most experienced hybridist has to determine the optimum period each day through trial and error by examining anthers in the most mature florets that have not pollinated.

Anthers with usable pollen will be yellow, plump, and should dehisce within 1 min when removed from the floret and placed on the hand. Anthers can be collected from primary or secondary florets. Several florets with suitable pollen often will be found on the same panicle so that the hybridist can find a sufficient number of mature anthers on a single panicle for pollinating all the emasculated florets on one or more panicles. Within a panicle, those spikelets immediately below those with withered anthers from the previous day of natural anthesis are the most likely to be in the proper stage for use as pollen sources.

Anthers can be moved from one location to another by transporting entire panicles, individual spikelets, or anthers that have been removed from panicles on intact plants. Anthers that have been removed from florets should be used almost immediately. The anthers used for making pollinations are held in the crease of the palm, on the back of the hand between the thumb and forefinger, or on the wrist at the base of the thumb. When making pollinations, the lemma and palea of each emasculated floret are separated in the same way as for emasculation, and a mature anther held between the prongs of the forceps is gently tapped against the inside of the lemma to be sure the anther opens and spreads pollen on the stigma hairs.
The used anther may be left in the floret or in some cases it can be used to pollinate additional florets. The palea and glumes are returned to their original position. When all emasculated florets on a panicle have been pollinated, the tag is labeled with the male parent and date of pollination, and the glassine bag is replaced to prevent outcrossing.

The approach method is an alternative procedure for pollination of oats. It initially had good success in wheat and barley, but poor success in oats (Rosenquest, 1927). Curtis and Croy (1958) refined the method and found it quite satisfactory for making oat crosses in Oklahoma. McDaniel et al. (1967) further refined the technique and have used it with excellent success for making oat crosses in Texas. These workers found that approach crossing offers several important advantages over the conventional method. Crosses can be made at any time of day and many more florets can be pollinated than would be possible by hand. Even very young florets can be emasculated because the male parent sheds pollen over several days, providing pollen when the stigmas become receptive. More than one cross can be made under the same bag by bagging one or two panicles of the same male with several different female parents. Labor is reduced because it is not necessary to return to florets to apply pollen. Their seed set percentage was much higher with the approach method of crossing than with the conventional method.

With the approach method, each spikelet used as a female is prepared by removing the secondary floret and anthers of the primary floret. After emasculation, the upper portion of each spikelet is removed by clipping straight across the glumes, lemma, and palea just above the stigma (Fig. 8). The clipped spikelets remain erect so that pollen from the male parent falls directly onto the stigmas. Panicles used for male parents require little preparation except that heavy awns, if present, are removed to facilitate bagging.

In the greenhouse, pots containing the male and female parents are placed together so that the lowest floret on the male parent is just above the uppermost floret on the female parent. Blocks, pots, or other devices can be used to adjust the height of the parent panicles to the desired level. Panicles from both parents are enclosed in a bag. McDaniel et al. (1967) used a bag approximately 35 cm in length made from 2.9 cm cellulose dialyzing tubing.

Approach crossing can also be used to cross greenhouse-grown plants with field-grown plants (McDaniel et al., 1967). They cut culms of field-grown plants that were in the appropriate stage for use as male parents, and placed them in test tubes of water attached to stakes positioned near the female parents. The top of each test tube was then placed below the emasculated female panicle and the length of detached male culm was cut so that its panicle was just above the female. A pollinating bag was placed over both panicles and drawn over the open end of the test tube. The evaporation and transpiration were thought to add humidity to the atmosphere under the bag, providing a more favorable environment for seed set.

Even the experienced hybridist will encounter considerable variation in seed set from time to time. Although technique and environmental conditions influence success, pollen quality at time of making pollinations appears to be the major determining factor. An experienced hybridist working in near optimum conditions should expect 25% or more of the pollinated florets to set seeds in the field, 50% or more in the greenhouse.
D. Factors Affecting Efficiency

Field nurseries for crossing usually are made in rows, although they can be made by any method that will provide vigorous plants. Two to three plantings of one row 2 to 3 m long will provide plenty of material for crossing. Parental rows should be sufficiently far apart to allow space for working. Single rows 60 cm apart or paired rows with 30 cm between members of the pair and 60 cm between pairs provides sufficient space for most workers. Some breeders space plant or plant thin populations in the row to stimulate tillering and provide more crossing material for parents that are in small supply. Rows in the crossing nursery are sometimes arranged so that parents to be crossed with each other are adjacent.

Flowering date can be altered by varying planting dates. Low planting rates or even space planting will stimulate tillering and provide more usable male and female florets over a longer period of time. Clipping of plants in the late tillering or preboot stages to a height of 15 cm also will delay flowering and stimulate additional tillering.

Oats for crossing grown in the greenhouse can be handled most efficiently in pots. Two to three plantings of several pots of each parent made at 5- to 7-day intervals will usually provide ample material for crossing, and

Fig. 8—Spikelets clipped in preparation for approach crossing.
will extend the crossing period to accommodate the maturity ranges of most parents. More dates or more pots per date may be required where certain parents are to be used for a large number of crosses.

V. NATURAL HYBRIDIZATION

To date there has been no report of a reliable and efficient way of producing natural hybrids in oats. Cytoplasmic male sterility has not been reported. Although several cases of varying degrees of male sterility have been attributed to genetic causes or to pollen control chemicals, none has provided a suitable method for making hybrids. Lafever and Patterson (1964) suggested the possible use of a male-sterile nullisomic as the female parent to produce a fertile F1 monosomic, but they obtained only 11.7% natural cross-pollination by using the method.

VI. SEED DEVELOPMENT, HARVEST, AND STORAGE

The reader is referred to Bonnett (1961) for an excellent treatment of all aspects of seed development in oats. Brown and Shands (1957) examined the time sequences involved in pollen tube growth, fertilization, and early development of the seed. Pollen germinated and tubes had entered the style 5 min after pollination. The male generative nuclei were near the egg nucleus and polar nuclei within 30 min, and male gametes had entered the egg after 4 hours. The fertilized egg was in prophase 13.5 hours after pollination and a two-celled proembryo was observed 19 hours after pollination.

Examination of the pistil of pollinated florets 2 or 3 days after pollination will distinguish between successful and unsuccessful hybridization. If fertilization has occurred, the floret will be closed, the stigma wilted, and the ovary noticeably enlarged.

Crossed seed harvested as soon as 12 to 14 days after fertilization will usually provide viable seed, but such seed will be small and poorly filled. After 25 to 30 days, seed will be fully mature, large, and plump. Oat genotypes exhibit varying degrees of seed dormancy, and chilling often is required to break this dormancy when crossed seed are to be planted soon after harvest. Wild oats usually exhibit a high level of seed dormancy.

Schwendiman and Shands (1943) found that dormancy in oats could be overcome by germinating at continuous low temperatures between 8 and 12 C for 10 to 14 days or by prechilling moistened seed for 4 days at 4 C and then placing them at 22 C for 6 days. Removing the hulls also increased the rate and total percentage germination. I have obtained excellent germination of freshly harvested seed by placing them between wet germination blotters or paper towels at 18 C for 7 days prior to planting in the field or greenhouse.

REFERENCES