PRINCIPLES OF CULTIVAR DEVELOPMENT

VOLUME 1

Theory and Technique

Walter R. Fehr

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To my wife Elinor, whose numerous contributions to this book and to my life have been of immeasurable value.

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Preface

The development of superior cultivars of plant species is a challenge that tests the ingenuity, patience, and persistence of an individual. Ingenuity is based on an appreciation of the scientific principles of genetics, agronomy, horticulture, statistics, physiology, and many other disciplines that are an essential part of plant breeding. It involves the ability to evaluate an array of alternative methods for cultivar development, assess the resources that are available, and develop a strategy that is efficient and effective. Patience is required to undertake the development of a cultivar, a process that commonly requires 10 years or more. Persistence is essential in dealing with the numerous obstacles that must be confronted, particularly uncontrollable fluctuations in the weather.

As a university professor, it has been my privilege to teach young women and men who have the ingenuity, patience, and persistence required to be a plant breeder. One of my responsibilities has been to help students understand how cultivar development actually is carried out, sometimes referred to as the nuts and bolts of plant breeding. My colleagues generously shared their experiences with me, which made it possible to develop a set of class notes for distribution to the students. Those class notes became the foundation for this book.

The purpose of the book is to provide some assistance in the decision-making process that every plant breeder encounters. There are not any plant breeding programs that are identical in all respects. Each breeder is faced with unique circumstances for which an appropriate strategy of cultivar development must be developed. The plant species, resources available, expectations of the employer, and demands of the marketplace are a few of the factors that contribute to the circumstances that are encountered. To develop an effective strategy of cultivar development, the breeder must be able to understand the alternative methods that could be used and evaluate the genetic improvement that could be realized from each method. This book is intended to describe in detail the alternative breeding methods and to provide guidelines for the evaluation of their advantages and disadvantages under different circumstances.

The selection and application of plant breeding methods for the genetic improvement of a crop species depends on such factors as the types of cultivars that are grown commercially, the type of parental germplasm available, and the objectives of cultivar improvement. To help students and other interested people understand how plant breeders develop an appropriate strategy of genetic improvement, Volume 2 of *Principles of Cultivar Development* was prepared. In that volume, successful plant breeders describe the step-by-step process of cultivar development for the crop series with which they work, discuss alternative procedures that are available for each step of the process, and provide examples of those methods that have been used most successfully.

There is considerable emphasis in current plant research on the role of cellular and molecular biology in genetic improvement of plant species. The results of the research undoubtedly will improve procedures for cultivar development in the future. The emphasis in this book has been placed on techniques that actually have been used to develop cultivars, however, instead of on future possibilities that have yet to be widely adopted by plant breeders. Future opportunities for the improvement of plant breeding methods are addressed by the authors of individual crop species in Volume 2 of *Principles of Cultivar Development*.

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WALTER R. FEHR

Contents

CHAPTER THIRTY-FIVE

Hybrid Seed Production

Hybrid seed is used for the commercial production of a number of crops. Each of these crops must meet four requirements for the successful production and use of hybrid seed. (a) Heterosis is exhibited by the F_1 progeny of crosses between the parents. (b) Fertile pollen can be eliminated from the female parent. (c) Pollen from the male parent is effectively transported to the female parent. (d) Hybrid seed can be produced reliably and economically.

REQUIREMENTS FOR HYBRID SEED PRODUCTION

Heterosis

Heterosis (hybrid vigor) is present when the performance of the F_1 progeny of a cross exceeds that of the parents. The F_1 progeny can be compared with the mean performance of the parents, referred to as mid-parent heterosis, or to the performance of the best parent, referred to as high-parent heterosis (Chap. 9). To justify the use of hybrid seed, high-parent heterosis must be present.

The production of hybrid seed is more expensive than the multiplication of pure-line or open-pollinated cultivars. The performance of the hybrid must sufficiently exceed the performance of other types of cultivars available for the species to offset the added cost of hybrid seed production. For example, sunflower can be produced commercially as open-pollinated cultivars or as hybrids. Hybrids are used in the United States because there is adequate high-parent heterosis present and the hybrids yield more than open-pollinated cultivars.

Elimination of Fertile Pollen from the Female Parent

The two methods for eliminating fertile pollen from the female parent are artificial emasculation and use of male sterility. Artificial emasculation of male-fertile females can be accomplished by manually removing the anthers or by special treatment of the anthers. Manual removal of the anthers is done on a commercial scale for a few crops, such as maize. Chemical or physical treatment of the anthers to make them male-sterile has been tried experimentally, but is not used currently for commercial hybrid seed production.

The types of male sterility available in crop plants are genetic and cytoplasmic-genetic. Systems for utilizing genetic male sterility have been proposed, but none has been adopted at present. The proposed systems are discussed in Chap. 5. Only cytoplasmic-genetic sterility currently is used to produce hybrid seed commercially.

Transfer of Pollen from the Male to the Female Parent

Large-scale production of hybrid seed requires effective pollen transfer from the male to the female parent by wind or insects. Manual pollination is feasible only for crops, such as tomato and petunia, in which performance or demand for the hybrid justifies the cost of the labor required to produce it.

Wind is an effective mode of pollen transport in grass species, such as maize and sorghum. Insect pollination is effective for producing hybrid seed of sunflower if special precautions are taken to ensure that adequate numbers of the appropriate pollen vector are available. Insect pollination of alfalfa has had only limited success in hybrid seed production, because male-fertile plants are preferred by the insects more than male-sterile plants of the female parent. The insect preference results in limited seed set on the male-sterile plants.

Reliable and Economical Hybrid Seed Production

Hybrid seed is feasible for commercial production of a crop when it can be produced reliably and at a cost consistent with performance of the hybrid. The cost of production is related to the amount of quality seed obtained per hectare from the female parent and the amount of seed required to plant each hectare of commercial production.

Yield and quality of seed from the female parent are important considerations in hybrid seed production. In the early years of hybrid maize, yield of the inbred lines was too low to permit reliable and economical production of single-cross hybrids. Double-cross or three-way-cross hybrids were used because the female parent for commercial hybrid seed production was a productive single cross. Today, single-cross maize hybrids are used commercially because breeders have improved the yield of inbred lines sufficiently to permit their use as female parents for commercial hybrid seed production.

Male parents must provide an adequate supply of fertile pollen to pollinate the female parent. Pollen production is a consideration in the development of inbred lines to be used as male parents in hybrid combinations.

The amount of hybrid seed produced per hectare and the amount of seed used per hectare of commercial production are major factors in determining the economic feasibility of hybrid seed. The principle can be illustrated with the following ratio: Number of units of hybrid seed produced per hectare:number of units of seed required to plant a hectare of commercial production.

The economic feasibility for the commercial use of hybrid seed is greatest when the ratio is the largest. For example, the ratio for soybean would be about 20:1, compared with 240:1 for maize. The ratio for soybean assumes that the ratio of the female-to-male rows in a hybrid seed field would be about 1:1, the number of units of hybrid seed per hectare of the female rows would be 40, and that two units of seed would be required to plant 1 hectare of commercial production. For maize, 1 hectare produces about 120 units of hybrid seed and only 0.5 of a unit is needed to plant a hectare. This means that the cost of producing 1 hectare of hybrid soybean seed must be divided among only 20 hectares, but the cost of producing a hectare of hybrid maize would be divided among 240 hectares. It would be much more difficult to make hybrid soybeans economically feasible than it has been for maize.

TYPES OF HYBRID SEED

The type of hybrid produced is a function of the number of parents involved and the relationship among the parents. Some types of hybrids are used in many species, while others are only used in a few. In the following discussion of types of hybrids, the letter P followed by a number (P1, P2, P3, and P4) will be used to designate parents. When two parents in a cross are closely related, commonly referred to as sister lines, one of them will be designated with a P and a number, and the other will have the same designation with an asterisk added to it (P1*).

The degree of relationship between sister lines is not well defined. They may be closely related when P1* is derived from a backcross program in which P1 was the recurrent parent. P1* and P1 may not be as closely related when they trace to different S_0 plants from the same breeding population. Sister lines may result from two or more plant selections from within a line derived in the S_0, S_1, S_2, or a later generation of inbreeding.

Single Cross

A single-cross hybrid is produced by mating two parents, P1 × P2. When cytoplasmic-genetic male sterility is used, the essential aspects of the cytoplasmic and genetic makeup of the parents are

$$\mathrm{P1}(S\,rfrf) \times \mathrm{P2}(RfRf) \rightarrow \mathrm{hybrid}(S\,Rfrf)$$

S designates the cytoplasm that results in male sterility of the parent when the recessive nonrestorer (*rfrf*) alleles are present in the nucleus. Plants with S cytoplasm are male-fertile when a dominant restorer allele (*Rf*) is present in the nucleus. Plants with normal (N) cytoplasm are male-fertile, regardless if the nuclear alleles are *rfrf* or *Rf*__. In the single cross above, P1 is male-sterile, while P2 and the hybrid are male-fertile. The cytoplasm of the parent with the dominant restorer alleles can be either S or N.

Seed production of a single-cross hybrid and its parents by manual or chemical emasculation requires three separate and isolated plantings: P1 alone, P2 alone, and the P1 × P2 cross. Four separate plantings are required when male stertility is used: A line × B line cross to obtain seed of P1, B line of P1 alone, R line (P2) alone, and the P1 × P2 cross. The cytoplasmic and genetic makeup for the A line of a parent is S*rfrf*, for the B line is N*rfrf*, and for the R line is *RfRf*.

Modified Single Cross

A modified single-cross hybrid is obtained from the cross (P1* × P1) × P2. The P1* × P1 cross provides a female parent that produces more seed than either P1* or P1 alone. The production of a modified single-cross hybrid and its parents by emasculation requires five separate plantings: P1* alone, P1 alone, P2 alone, the P1* × P1 cross, and the (P1* × P1) × P2 cross.

For the production of a modified single-cross hybrid by the use of male sterility, the cytoplasmic and genetic makeup of the parents and the hybrid is

$$[\mathrm{P1}^*(\mathrm{S}\mathit{rfrf}) \times \mathrm{P1}(\mathrm{N}\mathit{rfrf})] \times \mathrm{P2}(\mathit{RfRf}) \rightarrow \mathrm{hybrid}(\mathrm{S}\mathit{Rfrf})$$

P1* is male-sterile and P1, P2, and the hybrid are male-fertile. Six separate plantings are needed for production of seed of the parents and the hybrid: A line × B line cross to obtain P1*, B line of P1* alone, P1 alone, P2 alone, the P1* × P1 cross, and the (P1* × P1) × P2 cross.

Double Modified Single Cross

The mating used to produce a double modified single-cross hybrid is (P1* × P1) × (P2* × P2). P1* and P1 are closely related lines, as are P2* and P2. The P1* × P1 cross used as a female produces more seed than does either P1* or P1 independently. More pollen production is obtained from the P2* × P2 cross than from either P2* or P2 alone. There are seven separate plantings for the production of the hybrid and its parents by emasculation: P1* alone, P1 alone, P2* alone, P2 alone, and the P1* × P1 cross, the P2* × P2 cross, and the (P1* × P1) × (P2* × P2) cross. The procedure for producing the double modified single cross with cytoplasmic-genetic male sterility is the same as that described for the double cross.

Three-Way Cross

A three-way-cross hybrid is obtained from the mating (P1 × P2) × P3. The female parent is a single-cross hybrid and the male is a third parent. Seed production of the hybrid and its parents by emasculation involves five plantings: P1 alone, P2 alone, P3 alone, the P1 × P2 cross, and the (P1 × P2) × P3 cross.

The cytoplasmic and genetic constitution of the parents and the hybrid with the use of male sterility is

$$[\mathrm{P1}(S\,rfrf) \times \mathrm{P2}(N\,rfrf)] \times \mathrm{P3}(RfRf) \rightarrow \mathrm{hybrid}(S\,Rfrf)$$

P1 is male-sterile and P2, P3, and the hybrid are male-fertile. Production of seed for the parents and hybrid requires six separate plantings: A line × B line cross to obtain P1, B line of P1 alone, P2 alone, P3 alone, the P1 × P2 cross, and the (P1 × P2) × P3 cross.

Modified Three-Way Cross

A modified three-way hybrid is produced from the cross (P1 × P2) × (P3* × P3). The female parent is a single-cross hybrid and the male is the cross between two closely related lines. When emasculation is used, seven separate plantings are required to obtain seed of the parents and the hybrid: P1 alone, P2 alone, P3* alone, P3 alone, the P1 × P2 cross, the P3* × P3 cross, and the (P1 × P2) × (P3* × P3) cross.

For production of a modified three-way-cross hybrid by the use of male sterility, the cytoplasmic and genetic makeup of the parents is

$$[\mathrm{P1}(S\,rfrf) \times \mathrm{P2}(N\,rfrf)] \times [\mathrm{P3^*}(S\,rfrf) \times \mathrm{P3}(RfRf)] \rightarrow \text{hybrid: } 1/2\ S\,Rfrf\text{(male-fertile) and } 1/2\,S\,rfrf\text{(male-sterile)}$$

P1 and P3* are male-sterile and P2 and P3 are male-fertile. Half of the hybrid plants are male-sterile and half are male-fertile. Nine separate plantings are required to produce seed of the parents and the hybrid: A line × B line cross to obtain P1, B line of P1 alone, P2 alone, A line × B line cross to obtain P3*, B line of P3* alone, P3 alone, the P1 × P2 cross, the P3* × P3 cross, and the (P1 × P2) × (P3* × P3) cross.

Double Cross

The mating (P1 × P2) × (P3 × P4) produces a double-cross hybrid. The female and male parents are single crosses, which provide greater seed and pollen production in the hybrid seed field than do inbred parents. Seven plantings are required to produce seed of the parents and the hybrid by emasculation: P1 alone, P2 alone, P3 alone, P4 alone, the P1 × P2 cross, the P3 × P4 cross, and the (P1 × P2) × (P3 × P4) mating.

When male sterility is used to produce the hybrid, the cytoplasmic and genetic makeup of the parents and the hybrid is

$$[\mathrm{P1}(S\mathit{rfrf}) \times \mathrm{P2}(\mathrm{N}\mathit{rfrf})] \times [\mathrm{P3}(S\mathit{rfrf}) \times \mathrm{P4}(\mathit{RfRf})] \rightarrow \text{hybrid: } 1/2\ S\mathit{Rfrf}(\text{male-fertile}) \text{ and } 1/2\ S\mathit{rfrf}(\text{male-sterile})$$

P1 and P3 are male-sterile and P2 and P4 are male-fertile. The hybrid contains male-fertile and male-sterile individuals in a 1:1 ratio. Production of the hybrid and its parents involves nine separate plantings: A line × B line cross to obtain P1, B line of P1 alone, P2 alone, A line × B line cross to obtain P3, B line of P3 alone, P4 alone, the P1 × P2 cross, the P3 × P4 cross, and the (P1 × P2) × (P3 × P4) cross.

Advantages and Disadvantages of the Hybrid Types

Types of hybrids can be compared by considering their rankings with respect to productivity and uniformity in a commercial field, the cost of hybrid seed production, and the number of different plantings required for hybrid seed production.

Productivity. The rank of the hybrid types from the most to the least productive in a commercial field is single cross, modified single cross, double modified single cross, three-way cross, modified three-way cross, and the double cross. The greater productivity of the single cross makes it the preferred hybrid type and the one most widely used for crops in the United States.

Uniformity. The uniformity of plants in a commercial field may be an advantage in obtaining uniform seeds or fruits for marketing and in facilitating harvesting. A single-cross hybrid produced from two inbred parents is the most uniform, because all of the plants are genetically alike. A double-cross hybrid involves genetic segregation of the alleles from four parents and is, on the average, the least uniform of the hybrid types. The rank order of hybrids from the most to the least uniform is single cross, modified single cross, double modified single cross, three-way cross, modified three-way cross, and double cross.

Cost of Hybrid Seed Production. The cost of large-scale production of a hybrid is related to the relative quantity and quality of seed obtained from different types of female parents and the quantity of pollen provided by different types of male parents. Inbred parents have the smallest production of seed and pollen, parents that are the cross between related parents are more productive, and single-cross parents are the most productive. As a result, the single-cross hybrid is the most expensive to produce because both parents are inbreds, and the double-

Table 35-1 Number of Separate Plantings Required to Produce Different Hybrid Types and Their Parents

Hybrid Type	Manual or Chemical Emasculation	Cytoplasmic-Genetic Male Sterility
Single	3	4
Modified single	5	6
Three-way	5	6
Double modified single	7	9
Modified three-way	7	9
Double	7	9

cross hybrid is the least expensive because both parents are single crosses. The rank of hybrid types from the most to the least expensive to produce is single cross, modified single cross, double modified single cross, three-way cross, modified three-way cross, and double cross.

Number of Different Plantings. The production of seed of each parent and of the hybrid itself requires separate plantings that are properly isolated to maintain genetic purity (Table 35-1). The number of different plantings needed depends on the hybrid type that is produced and the use of manual or chemical emasculation or of cytoplasmic-genetic male sterility. The complexity of producing a hybrid increases as the number of separate plantings increases. Separate operations must be conducted for roguing, harvesting, drying, storage, cleaning, inventory, and distribution of each planting.

PRODUCTION OF PARENT SEED

The production of adequate quantities of parent seed is an important part of hybrid seed production. The difficulty of the task increases with the number of lines in the hybrid, particularly when cytoplasmic-genetic male sterility is involved.

The primary objective in producing the parents is to obtain high-quality seed with a high level of genetic purity. Maintenance of genetic purity in species with a high degree of cross-pollination involves elimination of undesired pollen by hand pollination or by isolated plantings. Removal of variation in a parent due to mutation or relic heterozygosity also is a consideration.

Production of seed of an inbred parent has two phases, maintenance of small quantities of pure seed and preparation of larger quantities of seed for use in hybrid seed fields. In many public and private organizations, the breeder is responsible for maintaining pure seed and a separate department handles the preparation of large quantities of parent seed.

Obtaining and Maintaining Pure Seed of an Inbred Line

Pure seed of an inbred line can be obtained by self-pollination or by sib mating.

Self-pollination with progeny testing: The procedure that has the best probability of providing pure seed involves self-pollination and progeny testing. Its primary disadvantages are that repeated generations of self-pollination may reduce the vigor of the line to an undesirable level, and the cost and time required may be greater than for sib mating. The procedure is as follows:

Season 1: Plants within a new inbred line are self-pollinated. Those plants with uniform characteristics are harvested individually, the seed of each is examined, and the ones with similar appearance are retained.

Season 2: A progeny row is grown for each plant retained in season 1. Plants are self-pollinated within each row, and the rows with uniform characteristics are retained. Self-pollinated plants are harvested individually, and their seed is examined for uniform appearance. Part of the seed from each selected plant is saved for progeny testing in season 3, and a similar quantity from each plant is bulked to form the source of pure seed of the inbred.

Season 3: In season 3 and subsequent seasons, pure seed is produced by progeny testing in the manner described for season 2.

Sib mating: The use of plant-to-plant crosses to maintain an inbred line has the advantage of maintaining a higher level of vigor and productivity and of being less expensive than self-pollination and progeny testing. The disadvantage is that the level of genetic purity may be less because selection is based on individual plants rather than on a progeny test.

Season 1: Plants are selected for uniformity before pollination. Selected plants are mated to each other by hand or in isolation. At harvest, plants with uniform characteristics are retained and their seed is bulked. Part of the seed is used for further increase of the inbred, and part is used for continued maintenance of the inbred.

Season 2: The procedure used in season 1 is repeated in season 2 and all subsequent generations to produce breeder seed of the inbred.

Self-pollination and sib mating may be used in alternation to combine the advantages of both procedures. Regardless of the system used, a sample of pure seed first prepared for the parent should be put in storage to retain its viability. The seed can be used periodically as a pure source of the parent free from any genetic change that could occur through multiple generations of self-pollination, sib mating, or both.

Producing Large Quantities of a Parent

Generally it is not practical to produce large quantities of a parent by any form of hand pollination. The parents are planted in isolation, and the seed is produced by open-pollination. Off-type plants are rogued from the fields. Special care is taken to avoid mixtures with other seed lots during harvesting, transport, cleaning, and bagging (Wright, 1980).

Producing Seed of a Male-Sterile Parent

Large quantities of seed of an A line are produced in isolation. The A line (female) is grown in alternating rows with the B line (male) and the seed is obtained by open-pollination. Seed harvested from the A line is used for hybrid seed production, and seed harvested from the B line is used for further production of A line seed.

The male-fertile parents in a hybrid, either N *rfrf* or *RfRf*, are produced in large quantities by growing each in isolation and allowing open-pollination to occur.

PRODUCTION OF HYBRID SEED

Hybrid seed production requires special care to maintain genetic purity and obtain large quantities of high-quality seed. The general principles involved in hybrid seed production were reviewed by Wright (1980).

Field Selection

A field in which seed is produced should be properly isolated from sources of contaminating pollen, including other cultivars and related weed species. The cultural practices used to produce the crop should be those consistent with obtaining high yields, including proper fertilization, weed control, and pest management.

Optimizing Seed Set

Obtaining maximum seed set requires management of the parents to ensure simultaneous flowering and adequate pollen shed. Adequate numbers of the appropriate pollen vector must be provided for insect-pollinated species.

Roguing

Off-type plants in the female and male parents must be removed before they shed pollen.

Artificial Emasculation

Production of hybrid seed for commercial use by artificial emasculation is used only for maize and some high-value horticultural crops. The female parent must be emasculated before pollen shed occurs.

Harvesting

Production of high-quality seed requires harvest at the proper moisture level with suitable equipment. All equipment and storage facilities must be properly cleaned to avoid mixing of seed. Gentle handling of the seed is required to prevent seed damage.

Seed Drying

Some crops are harvested at moisture levels higher than are suitable for seed storage. The seed must be dried at the proper temperature as soon as possible after harvest to prevent loss of germination and vigor.

Seed Conditioning

The steps required to prepare hybrid seed for marketing vary among species. The steps may include cleaning, sizing, treatment of the seed with a fungicide, insecticide, or inoculant, and bagging.

Quality Control

Maintaining genetic purity of hybrid seed involves field and seed inspections. Samples of hybrid seed may be grown in an off-season nursery to determine the frequency of off-type plants. The germination percentage for hybrid seed is always determined before it is sold. Determinations also are made on the amount of weed seed and foreign material.

Storage

Hybrid seed should be stored in facilities that maintain high germination. Temperature and humidity control are important when seed is to be stored for more than 1 year.

Marketing

The merchandising of hybrid seed generally is carried out by a specialized department of a company or organization. Farmers are informed about the available seed through an array of promotional activities.

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