PRINCIPLES OF CULTIVAR DEVELOPMENT

VOLUME 1

Theory and Technique

Walter R. Fehr

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with the assistance of
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Library of Congress Cataloging-in-Publication Data

Fehr, W. R. (Walter R.), 1939–
Principles of cultivar development.

Includes bibliographies and indexes.
Contents v.1. Theory and technique
v.2. Crop species/Walter R. Fehr, editor.
1. Plant-breeding. 2. Field crops—Breeding.
3. Field crops—Varieties. I. Title.
SB123.F44 1987 631.5'3 86-33344
ISBN 0-9635989-0-2 (v.1) (previously published by
Macmillan Publishing Company, ISBN 0-07-020345-8)
ISBN 0-07-020344-X (v.2)

Reprinted 1993

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

Credits

The author wishes to thank the following publishers for permission to adapt or reproduce material in *Principles of Cultivar Development*, Vol. 1.

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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*.

ACKNOWLEDGMENTS

This book was made possible by the generous support of many people, only a few of whom will be mentioned. Sincere appreciation is expressed to my wife Elinor, who typed the manuscripts for the book, drafted all the figures, and assisted in indexing and proofreading. Thanks are extended to Holly Jessen, who reviewed each chapter, made valuable revisions and additions, and assisted in indexing and proofreading. The technical support of the publication editors, Sarah Greene and Gregory Payne, is gratefully acknowledged. My thanks to Cal Qualset who reviewed the manuscripts for all the chapters, and to all of the students and colleagues who reviewed individual chapters.

WALTER R. FEHR

Contents

CHAPTER THIRTY-ONE

Development of Self-Pollinated Cultivars

The self-pollinated cultivars grown by farmers throughout the world range from landraces that are heterogeneous mixtures developed by mass selection in natural populations to homogeneous genotypes developed by inbreeding and selection within populations formed by artificial hybridization or artificial mutagenesis. The origin of cultivars and their method of development can be reviewed by observing the stepwise process that occurs when a crop is introduced for commercial production into a country where it was not previously grown.

CROP INTRODUCTION

The first step in production of a new crop is to introduce cultivars from countries where they are currently grown. Cultivars may be heterogeneous if they originate from geographical areas where the crop has been grown for a long time, if farmers use their own seed to plant the crop each season, and if a high degree of uniformity is not required for commercial production. A higher degree of homogeneity generally would be present if the introduced cultivars had been developed by a plant breeder.

Introduced cultivars with adequate uniformity are evaluated for productivity, quality, and other characters considered important. The best ones can be released to farmers under the name used in the country from which they originated, or with another suitable designation.

SELECTION WITHIN HETEROGENEOUS CULTIVARS

Introduced cultivars that have good performance but are too heterogeneous can be subjected to individual plant selection followed by progeny testing. If plants

in the heterogeneous cultivars are homozygous, a series of homogeneous lines with different characteristics may be identified. Homogeneous lines with desirable performance can be released for use by farmers.

HYBRIDIZATION OR ARTIFICIAL MUTAGENESIS

After the genetic variability of germplasm from other countries has been exploited, the breeder must produce additional variability for the development of cultivars superior to those available. The development of a self-pollinated cultivar by use of hybridization or artificial mutagenesis involves four steps: (a) formation of a segregating population, (b) inbreeding the population by self-pollination to an adequate level of homozygosity, (c) evaluation of homogeneous lines and selection of the superior ones, and (d) preparation of seed stocks for commercial distribution of the cultivar.

Population Formation

The two ways of forming a segregating population are by hybridization and artificial mutagenesis. Both ways have been used to develop self-pollinated cultivars. Hybridization, however, is much more widely used than mutagenesis. A discussion of the relative merits of hybridization and mutagenesis is provided in Chap. 20.

The populations developed by hybridization include two-parent, three-parent, four-parent, and more complex crosses (Chap. 12). Backcrossing is used to form a segregating population and to transfer characters from one cultivar to another (Chaps. 12 and 28). Populations improved by recurrent selection can be used to develop self-pollinated cultivars (Chaps. 15 and 16).

Self-Pollination to an Adequate Level of Homozygosity

Two of the major decisions that must be made by the breeder are the number of generations of inbreeding that will be conducted in a population before plants are selected for evaluation as potential new cultivars and the method of managing the population during inbreeding. The variation in strategies used by breeders to develop cultivars reflects the array of alternatives that can be considered in making the decisions.

Number of Inbreeding Generations. A self-pollinated cultivar is developed by selecting an individual plant, evaluating the bulk progeny as a breeding line, and releasing the superior line as a cultivar. Cultivars of self-pollinated species

are derived as early as the F_2 and and as late as the F_{11} generation. The generation in which a cultivar is derived refers to the generation of inbreeding of the single plant from which the cultivar originated. The generation in which cultivars are derived is dependent on the degree of uniformity required within a cultivar, the number of generations of self-pollination required to obtain an adequate number of lines with that level of uniformity, and the time required to develop and release a cultivar.

The level of uniformity required in a cultivar is determined by the breeder, seed regulatory agencies, farmers, and the consumer. The breeder must be confident that the genetic makeup of a cultivar will not change during multiple generations of seed production. A line derived in early generations that contains genotypes with differential competitive ability may undergo significant genetic changes during successive generations due to intergenotypic competition, in the same manner as a planned seed mixture of cultivars (Chap. 32).

Seed regulatory agencies, including plant variety protection and seed certification, have requirements for uniformity that must be considered (Chap. 36). Those agencies often are concerned about variability for qualitative characters, such as hilum and pubescence color of soybean and seed color of oat. A breeder may choose to discard heterogeneous lines before evaluation or may evaluate heterogeneous lines and purify any superior ones before their release as a cultivar.

Farmers may have preferences for uniformity of certain characteristics, particularly those that influence the harvestability and marketability of the crop. Uneven maturation or height of a crop can influence the effectiveness of mechanical harvest. There are, however, qualitative characteristics for which uniformity may not be important to the farmer. For example, hilum color of soybean seed is not a factor in marketing, and farmers generally are unconcerned about heterogeneity for the trait.

After the required level of uniformity has been determined, it is necessary to establish the number of selfing generations required to obtain a sufficient number of lines for evaluation that have adequate uniformity. The percentage of homozygous individuals in a population increases with each generation of self-pollination. It may be possible to obtain uniform lines from F_2 plants, but the percentage of such lines would be less than the percentage from later generations of inbreeding. Breeders who develop cultivars derived from F_2 and F_3 plants must grow a larger number of progenies to obtain a given number of uniform lines than breeders who delay selection until later generations.

The generation in which lines are derived from a population can influence the time required to develop and release a cultivar. If a breeder can grow only one generation a year, each generation of selfing that takes place before lines are derived adds one additional year to the length of cultivar development. However, for annual species the ability to grow populations in off-season nurseries and greenhouses often permits an increase in the number of generations of inbreeding without increasing the time required for cultivar development.

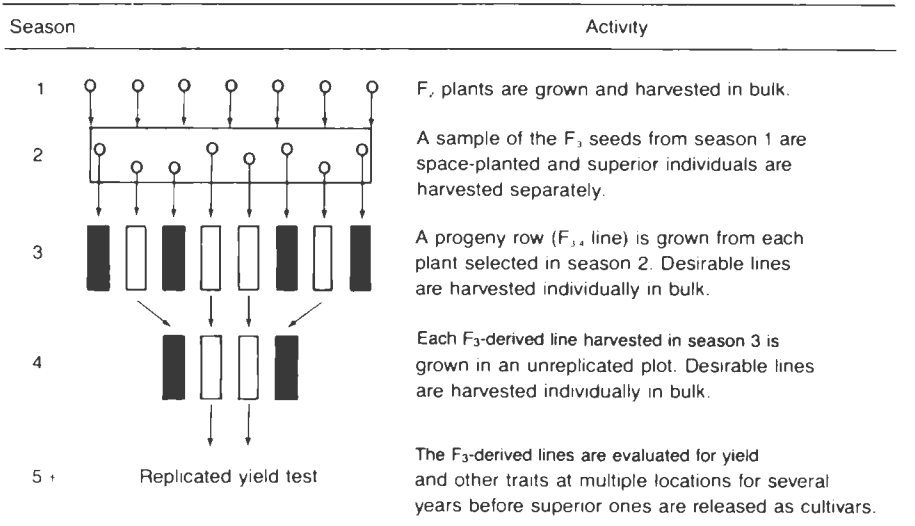

Figure 31-1 Outline of a procedure used by Ohio State University, Wooster, to develop by the bulk method winter wheat cultivars derived from F_3 plants. Dark rectangles represent discarded lines.

Methods of Inbreeding. The basic methods of managing a population during inbreeding include pedigree, bulk, single-seed descent, early-generation testing, and mass selection. These methods are used individually and in various combinations by breeders of self-pollinated species for the development of improved cultivars. Examples of methods currently in use are given in the following descriptions and in Figs. 31-1 and 31-2.

Outline of Procedure Used at Iowa State University, Ames, to Develop by the Multiple-Seed Procedure of Single-Seed Descent Soybean Cultivars Derived from F_4 Plants.

Season 1: Two-hundred fifty F_2 seeds of a population are planted about November 1 in Puerto Rico under natural day length conditions. After about 90 days, one three-seeded pod is harvested from each plant and the pods are threshed in bulk. Two-hundred fifty seeds are used for season 2 and the remainder are kept as a reserve.

Season 2: Two-hundred fifty F_3 seeds are planted about February 1 in Puerto Rico under natural day length conditions. After about 90 days, one three-seeded pod is harvested from each plant and the pods are threshed in bulk. Two-hundred fifty seeds are used for season 3 and the remainder are kept as a reserve.

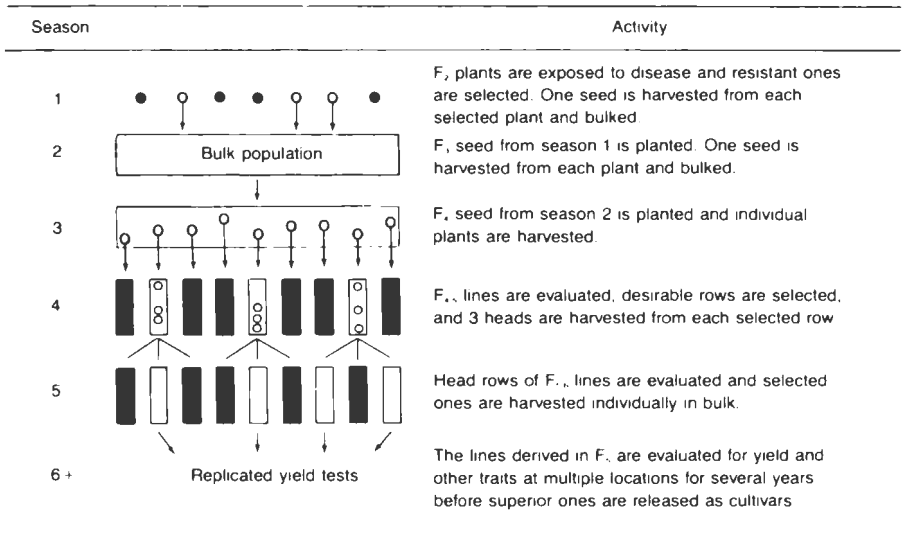

Figure 31-2 Outline of a procedure used by the University of Minnesota, St. Paul, to develop by mass selection, single-seed descent, and pedigree selection spring wheat cultivars derived from F_5 plants. Dark circles and rectangles represent discarded plants or lines.

Season 3: Two-hundred fifty F_4 seeds are planted in May in the northern United States, and individual plants are harvested.

Season 4+: The lines derived in F_4 are evaluated for yield and other traits at multiple locations for several years before superior ones are released as cultivars.

Outline of Procedure Used by Ohio State University, Wooster, to Develop by Early-Generation Testing Soybean Cultivars Derived from F_4 Plants.

Season 1: F_2 plants are grown, and desirable ones are harvested individually.

Season 2: Progeny of each plant harvested in season 1 ($F_{2:3}$ lines) are evaluated for yield in an unreplicated plot.

Season 3: The highest yielding lines in season 2 are evaluated for yield as $F_{2:4}$ lines in replicated plots. Individual F_4 plants are harvested from the border rows of a plot of each line.

Season 4+: Progeny from individual F_4 plants (F_4-derived lines) harvested from the superior $F_{2:4}$ lines in season 3 are evaluated for yield and other traits at multiple locations for several years before superior ones are released as cultivars.

Outline of Procedure Used by the University of Wisconsin, Madison, to Develop by Pedigree Selection Oat and Spring Wheat Cultivars Derived from F_5 Plants.

Season 1: F_2 plants are grown, and desirable ones are harvested individually.
Season 2: A progeny row ($F_{2:3}$ line) is grown from each plant selected in season 1. Five or six plants are harvested individually from selected rows.
Season 3: A progeny row ($F_{3:4}$ line) is grown from each plant harvested in season 2. Five or six plants are harvested individually from selected rows.
Season 4: A progeny row ($F_{4:5}$ line) is grown from each plant harvested in season 3. Five or six plants are harvested individually from selected rows.
Season 5: A progeny row ($F_{5:6}$ line) is grown from each plant harvested in season 4. Desirable rows are harvested individually in bulk.
Season 6+: The lines derived in F_5 are evaluated for yield and other traits at multiple locations for several years before superior ones are released as cultivars.

Outline of Procedure Used by Oklahoma State University, Stillwater, to Develop Winter Wheat Cultivars Derived from F_2 Plants.

Season 1: F_2 plants of a population are grown, and desirable ones are harvested individually.
Season 2: $F_{2:3}$ lines are evaluated in unreplicated plots and the most desirable ones are harvested individually in bulk.
Season 3: $F_{2:4}$ lines are evaluated in unreplicated plots and selected ones are harvested individually in bulk.
Season 4+: The lines derived in F_2 are tested for yield and other traits at multiple locations for several years before superior ones are released as cultivars.

Outline of Procedure Used by Virginia Polytechnic Institute and State University, Blacksburg, to Develop by Mass Selection with Self-Pollination and the Bulk Method Barley Cultivars Derived from F_5 Plants.

Season 1: F_2 plants are grown, desirable individuals are selected, and selected plants are threshed together in bulk.
Season 2: A sample of F_3 seed from season 1 is planted. Desirable individuals are selected and threshed together in bulk.
Season 3: A sample of F_4 seed from season 2 is planted. Desirable individuals are selected and threshed together in bulk.
Season 4: A sample of F_5 seed from season 3 is planted. Desirable individuals are harvested individually.
Season 5: A progeny row ($F_{5:6}$) is grown for each plant selected in season 4. The superior ones are harvested individually in bulk.

Season 6+: The lines derived in F_5 are evaluated for yield and other traits at multiple locations for several years before superior ones are released as cultivars.

Outline of Procedure Used by the University of Minnesota, St. Paul, to Develop by Pedigree Selection Oat Cultivars Derived from F_3 Plants.

Season 1: F_2 plants of a population are exposed to disease, and desirable plants are harvested individually.

Season 2: $F_{2:3}$ lines are evaluated in unreplicated plots, and five panicles are harvested from each selected row. The remainder of the row is harvested in bulk and the seed analyzed for protein content. Panicles are retained from rows with adequate protein composition.

Season 3: A progeny row ($F_{3:4}$ line) is grown from each panicle selected in season 2. Superior lines are harvested individually in bulk.

Season 4+: F_3-derived lines are evaluated for yield and other traits in multiple locations and years before superior ones are released as cultivars.

The method chosen to manage a population is strongly influenced by the length of time a breeder is willing to spend in the development of a new cultivar and the suitability of available environments for selection and replicated testing. The pedigree method and mass selection with self-pollination can only be used in environments where selection for the characters of interest is possible. The bulk method is not suited to environments in which natural selection is likely to favor undesirable genotypes. The replicated testing phase of the early-generation method must be done in environments where characters can be measured appropriately. Only single-seed descent can be used in any environment, regardless of its suitability for artificial or natural selection.

Breeders often vary the method of inbreeding to maximize the use of available environments. This flexibility was emphasized by Harrington (1937) when he proposed the use of the mass-pedigree method of inbreeding. He had found that selection in the F_2 generation for straw strength, resistance to some diseases, plant height, earliness, and shattering resistance was largely ineffective in dry seasons. The effectiveness of selection in later generations also was reduced under these conditions, although to a lesser extent. Utilization of the typical pedigree method proved expensive and thus constituted a large loss of resources in dry seasons. The strict use of mass selection, however, resulted in smaller gains during favorable years than use of the pedigree method. A modified method was developed to overcome the limitations imposed by the frequent occurrence of dry seasons.

> The modifications consisted in selecting for desirability in one or more important characters when circumstances were favorable. A wet season or a combination of long straw and high winds sometimes presented an excellent opportunity for selection for resistance to lodging as well as for several other characters. Such opportunities were taken advantage of, whether they occurred when a cross was in F_2 or in any

later segregating generation. Again, if a satisfactory disease epidemic occurred naturally, or was induced artificially, selection for resistance was made in the mass plats, irrespective of the generation they were in. In very dry or hot seasons, selection for drought and heat resistance was carried on.

These modifications led to the introduction of the progeny test as a further feature of the method and owing to this feature the process was called the "Mass-Pedigree Method." The plan is to go on with individual plant progeny tests whenever the circumstances have particularly favored selection in the preceding year. [Harrington, 1937]

The mass-pedigree method is just one of several possible combinations of inbreeding methods. The procedure outlined in Fig. 31-2 includes mass selection with self-pollination, single-seed descent, and pedigree selection. By fitting the inbreeding method to the environment, it may be possible for the breeder to practice selection in some generations without increasing the length of time for cultivar development.

Selection of a method for inbreeding a population can have an impact on the genetic improvement per year realized from a breeding program. Many of the concepts for maximizing genetic gain that are associated with methods of recurrent selection apply equally well to methods of inbreeding. A breeder will consider those concepts when planning an appropriate strategy for inbreeding (Chap. 17).

Evaluation of Lines

The evaluation of homogeneous lines in replicated tests is a major aspect of any breeding program. The breeder must decide if a line will have the desired performance for quantitative characters over a range of environments. The number of locations and years of replicated testing that are conducted before a homogeneous line is released as a cultivar generally is not influenced by the method of inbreeding used. The primary difference among methods is the division of resources between tests conducted during inbreeding and those available for the evaluation of homogeneous lines. Every breeder has a fixed amount of resources available to carry out all phases of selection and testing; therefore, resources expended during the inbreeding program will reduce those available for evaluation of homogeneous lines in replicated tests.

The most obvious division of testing resources is for early-generation testing. Heterogeneous lines or populations are evaluated in replicated tests, and the inferior ones are discarded. Every plot used to evaluate a heterogeneous line or population reduces by one the number available to evaluate homogeneous lines. Therefore, the number of homogeneous lines that can be evaluated with early-generation testing is less than with the other methods of inbreeding. The division of resources between the two phases of testing is a major decision for the breeder. Those who use the method believe that use of testing resources in early gener-

ations is worthwhile to improve the sample of homogeneous lines available in later generations of selection.

Pedigree selection does not utilize resources for replicated testing per se, but an extensive amount of time and land is needed for evaluation during inbreeding. The time and land used for selection during inbreeding could be spent instead to evaluate more homogeneous lines in a replicated testing program. Breeders who use the pedigree method are willing to expend resources during inbreeding so that the homogeneous lines entered into replicated tests are superior to a group of random lines for highly heritable characters.

The mass selection, bulk, and single-seed descent methods do not involve any progeny testing during inbreeding. As a result, more resources are available for replicated testing of homogeneous lines than for the early-generation testing or pedigree methods. Homogeneous lines obtained from mass selection, bulk, or single-seed descent generally are evaluated during one season for the same highly heritable characters considered in pedigree selection, and the superior ones are entered into replicated tests.

The emphasis in the first season of replicated testing is to evaluate as many lines as possible in a limited number of locations and replications per location. In the following seasons, the number of lines is progressively decreased and the number of locations is progressively increased. The plot size and type also may be changed during the different testing phases (Chap. 19).

Preparation of Breeder Seed

When a new cultivar is developed, the breeder prepares a seed sample that is used for increasing seed of the cultivar for distribution to farmers. The sample commonly is referred to as breeder seed because the breeder generally is responsible for producing and maintaining it. It also is called basic seed because it represents the genetic basis of the cultivar from which all subsequent seed is produced. The breeder seed is used to produce foundation seed. The foundation seed and subsequent generations of production generally are produced on a large scale by persons other than the breeder (Fig. 31-3).

The preparation of breeder seed generally begins before the decision to release a line has been made, which requires extra effort by the breeder because seed of lines not released must be discarded. However, simultaneous line evaluation and breeder seed production reduces the length of time required to have seed of a new cultivar available to farmers. The following procedure has been used by the soybean breeding project at Iowa State University. After 2 years of testing in Iowa, about 1 percent of the lines first entered in the yield evaluation program have been selected. During the third to fifth years, the lines are evaluated extensively in states of similar latitude. If a line is selected for release, breeder seed is available for immediate production of foundation seed.

Some breeders prefer to begin the preparation of breeder seed the first or

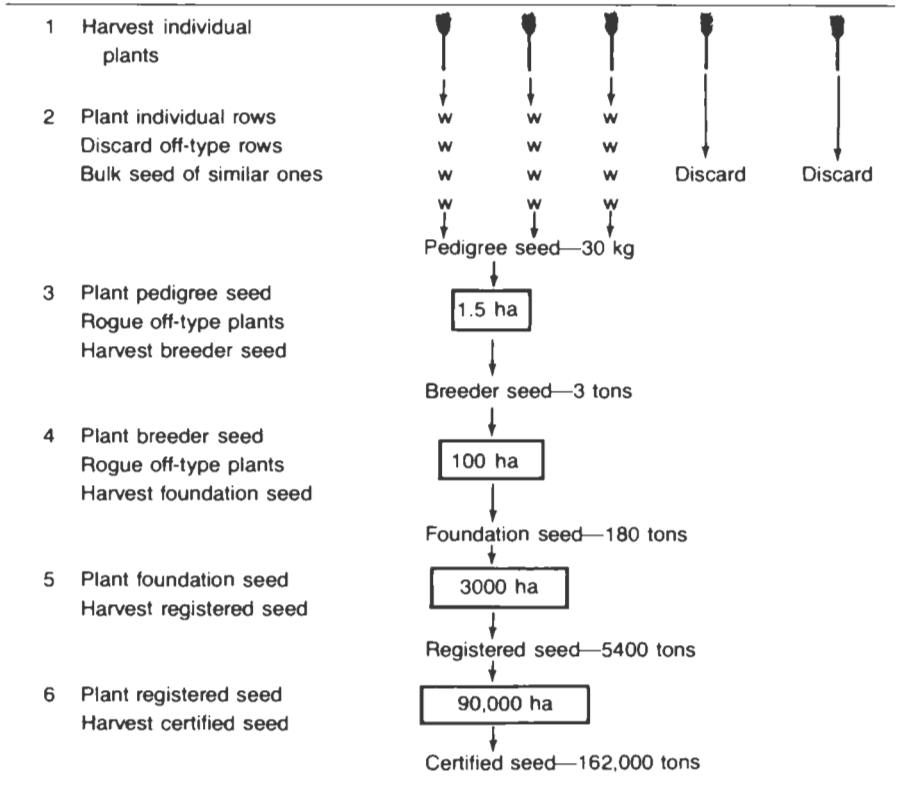

Figure 31-3 Illustration of a procedure for purification and seed increase of a new cultivar. The kilograms, tons, and hectares indicated are approximate quantities that could be produced for each seed class. (Courtesy of Fehr, 1978.)

Line Evaluation	*Seed Multiplication*
First year	—
Second year	—
Third year	Single plants harvested
Fourth year	Progeny rows grown
Fifth year—Decision to release is made	Progeny rows increased and bulked to form breeder seed

second year a line is tested. This reduces the time required to make large quantities of seed available to farmers, but increases the cost of seed stock preparation because many more lines must be handled.

The seed used to develop breeder seed can be derived from yield tests in which mechanical mixing is minimized or from a seed sample of the line that was retained in storage. Some breeders put a seed sample of each line in storage when replicated tests begin. The seed from storage is used to produce breeder seed of a line chosen to be a cultivar, instead of seed obtained from replicated tests.

Initial Production of Breeder Seed. The two alternatives for the initial production of breeder seed are mass selection and progeny testing.

Mass Selection. For mass selection, a sample of seed with uniform characters is planted, off-type plants are removed before harvest, and the remaining plants are harvested in bulk to obtain breeder seed. The advantages of the procedure are that breeder seed can be produced in one season and that the procedure requires much less time and expense than the use of progeny testing. The disadvantage is that a high degree of uniformity is difficult or impossible to achieve. Individual off-type plants are more difficult to identify than a group of off-type plants in a progeny row, particularly for quantitative characters. Heterozygous and homozygous plants cannot be distinguished for characters controlled by dominant alleles.

Progeny Testing. The use of progeny testing provides the greatest assurance of achieving a high degree of uniformity in the breeder seed. Steps are as follows:

Season 1: A sample of seed with uniform characteristics is planted. Plants with similar phenotypic characteristics, such as flowering date, color of plant parts, and leaf size and shape, are selected and threshed individually. The seed from each plant is inspected, and plants with similar seed characteristics are retained.

Season 2: Plants from season 1 are progeny tested for important characteristics, such as pest resistance and agronomic traits. Rows that are segregating for any important characteristic or that are dissimilar from the majority of the other rows are discarded. Each selected row is harvested separately. The seed from each row is inspected for uniform characteristics.

Season 3: Seed from each row in season 2 is grown in a separate increase block, and the plants are inspected for uniformity. Blocks that are not uniform are discarded. The selected blocks are harvested in bulk and properly mixed to obtain breeder seed.

The second progeny test in season 3 frequently is omitted—uniform families in season 2 are harvested together in bulk and properly mixed to obtain breeder seed. Elimination of the second progeny test in season 3 reduces the number of

seasons and the expense required, but does not ensure the same level of genetic purity.

The number of progenies that are evaluated and mixed together to produce breeder seed varies widely among breeders. Some are satisfied to use only a few progenies, while others prefer to maintain possible heterogeneity for nonvisual characters by including the progenies of 100 or more plants.

The advantage of progeny testing is that a high degree of uniformity can be achieved in the breeder seed. The disadvantages are that two or more seasons are required and much more time and expense are involved than with the use of single-plant selection.

Repeated Production of Breeder Seed. Several procedures are used to provide an adequate supply of breeder seed each year for established cultivars.

1. A quantity of breeder seed is put in storage when the cultivar is first released. When the supply of seed in storage becomes inadequate, a new supply is developed by the progeny-testing procedure. This method is effective if adequate storage facilities are available to maintain the required seed supplies.
2. Breeder seed is produced each season by progeny testing. The method is effective in providing pure seed each year, but can require considerable time and expense when a large number of cultivars are involved.
3. Part of a foundation seed field is designated for use in obtaining breeder seed. The area is rogued rigorously for off-type plants and harvested separately from the remainder of the field. The procedure is continued until the frequency of off-types that cannot be identified on a single-plant basis becomes too high, at which time the cultivar is purified by progeny testing. The method provides a supply of breeder seed of adequate genetic purity at a lower cost than alternative 2, but the genetic purity for all characters may be less.

Examples of Breeder Seed Preparation. Mass selection is used to obtain breeder seed of winter wheat and oat by the University of Wisconsin, Madison. Seed obtained from yield tests of a potential new cultivar are sown in a plot 3 m × 25 m. Off-type plants are rogued for maturity and height, and the plot is harvested in bulk as breeder seed.

Progeny testing for one year is used to obtain breeder seed of spring wheat by the University of Minnesota, St. Paul. Five-hundred heads are harvested individually from a potential new cultivar. A progeny row is grown from each head, and rows with uniform characteristics are harvested in bulk as breeder seed.

The Foundation Seed Organization of the University of Nebraska maintains breeder seed of wheat by marking out an area in a foundation seed field, roguing

the area carefully, and harvesting the rogued area separately from the remainder of the field.

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