CHAPTER FOURTEEN

Soybean

Walter R. Fehr

The cultivated soybean [*Glycine max* (L.) Merrill] is one of the major oilseed crops of the world. The crop, which originated in China, is currently grown commercially in 35 countries. Approximately 55% of the world production is in the United States, 19% in Brazil, 12% in the People's Republic of China, 5% in Argentina, and lesser amounts in other countries (Foreign Agricultural Service, 1985).

In the United States, the soybean was grown primarily as a forage crop until 1941, when the number of hectares harvested as grain first exceeded the area harvested as forage (Probst and Judd, 1973). Since that time, the area grown as a forage has declined steadily, and today, the crop is grown almost exclusively for its seed.

The soybean seed, which contains about 40% protein and 20% oil on a dry weight basis, provides approximately 60% of the world supply of vegetable protein and 30% of the oil (Foreign Agricultural Service, 1985). The majority of the seed is processed to separate the protein and oil fractions (Cowan, 1973). The protein is used primarily as a livestock feed, but also is important for various food products and industrial applications. The oil is used for margarine, shortenings, and other fat and oil products. In Asia, the soybean has been used for centuries in traditional foods as a major protein source.

TYPES OF CULTIVARS

Mode of Propagation

The soybean is a highly self-pollinated species. It has a perfect flower with the male and female organs enclosed within the corolla (Fig. 14-1). In-
Figure 14-1  Preparation and pollination of a soybean flower. (A) Flower at the stage for preparation and pollination, (B) removal of the corolla from the female flower after the calyx has been removed, (C) ring of 10 anthers and the stigma, (D) flower with pollen available, (E) pollination of the stigma, and (F) a pod 7 days after pollination with the calyx scar differentiating it from self-pollinated pods. [Photographs (A), (B), (D), (E), and (F) by C. J. Deutsch and P. A. Krumhardt, Iowa State Univ., Ames, Iowa; photograph (C) by G. I. Berkey, Ohio Agricultural Research and Development Center, Wooster, Ohio. From Hybridization of Crop Plants, p. 593, by permission of the Crop Science Society of America and American Society of Agronomy.]
sects can transmit the pollen, but the frequency of cross-pollination generally is less than 1% among fertile plants.

The relationship between vegetative and reproductive development in the soybean has been divided into three general types: indeterminate, semideterminate, and determinate. The determinacy type of a cultivar has a strong influence on the area and type of production condition in which it is grown commercially. Indeterminate cultivars begin to flower when less than half of the nodes on the main stem have developed; therefore, vegetative and reproductive development take place simultaneously for a considerable part of the life of the plant. Pod and seed development begin at the bottom of an indeterminate plant and progress toward the top as new nodes form, but all seeds reach maturity at the same time. Determinate cultivars begin to flower at or near the time when the terminal node on the main stem has developed. Pod and seed development occur at the same time throughout the length of a determinate plant. Semideterminate cultivars begin to flower when about half of the nodes on the main stem have developed, similar to indeterminate types, but terminate growth of the main stem sooner than indeterminates. Major genes at two loci control the difference in determinacy types (Bernard, 1973).

In North America, indeterminate cultivars are primarily of maturity groups OOO to IV and determinate cultivars are primarily of maturity groups V to X (Fig. 14-2). Indeterminate cultivars are well suited to the northern latitudes because they are taller and generally more consistent in production than determinate cultivars of comparable maturity. A few determinate cultivars of maturity groups II, III, and IV are grown commercially. They are often referred to as semidwarf cultivars because of their short stature, a characteristic that is associated with excellent standability (Cooper, 1981). At the southern latitudes where the growing season is longer, virtually all of the soybean production involves determinate cultivars, which are similar in height to indeterminate cultivars grown in the North. Indeterminate cultivars of maturity groups V to X have not been used because they are excessively tall and have poor standability when grown as a full-season crop, but there is some interest in the indeterminate trait for achieving greater height in late-season plantings. One indeterminate cultivar, 'Duocrop,' of maturity group VII has been released specifically for late plantings (Boerma et al., 1982). A few semideterminate cultivars have been released in recent years for northern latitudes, but none has been widely grown.

**Past and Current Cultivar Types**

Soybean cultivars grown throughout the world are pure lines or mixtures of pure lines. There have been three phases in cultivar development and
use in North America: introduction of cultivars from other countries, selection within heterogeneous plant introductions, and hybridization and selection.

*Introductions.* The first cultivars grown in North America were direct increases of germplasm introduced from other countries, commonly referred to as plant introductions. The largest portion of the acquisitions
by the U.S. Department of Agriculture (USDA) beginning in about 1898 were from China, with a large group also obtained from Japan, India, and Korea (Probst and Judd, 1973). Many of the introductions were 
landraces, which represented heterogeneous mixtures of plants that had 
evolved over many years and had been subjected to natural selection for 
adaptation to a particular environment. The characteristics of the 
landraces also were influenced by selection practiced by cultivators who 
were interested in certain plant or seed traits. Heterogeneity was main-
tained because groups of selected plants and seeds from a landrace were 
bulked together, instead of increasing the progeny of a single homo-
ygous plant. The first phase of cultivar development in North America 
consisted of evaluating the plant introductions for their agronomic char-
acteristics, increasing seed of the most desirable ones, assigning them a 
name, and releasing them for commercial use (Table 14-1). The cultivars

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Origin</th>
<th>Place</th>
<th>Date†</th>
<th>Maturity Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Midwest'</td>
<td>China</td>
<td>1901</td>
<td>IV</td>
<td></td>
</tr>
<tr>
<td>'Manchu'</td>
<td>Manchuria</td>
<td>1911</td>
<td>III</td>
<td></td>
</tr>
<tr>
<td>'Mandarin'</td>
<td>Manchuria</td>
<td>1911</td>
<td>I</td>
<td></td>
</tr>
<tr>
<td>'A. K.'</td>
<td>Manchuria</td>
<td>1912</td>
<td>III</td>
<td></td>
</tr>
<tr>
<td>'Dunfield'</td>
<td>Manchuria</td>
<td>1913</td>
<td>III</td>
<td></td>
</tr>
<tr>
<td>'Arksoy'</td>
<td>Korea</td>
<td>1914</td>
<td>V</td>
<td></td>
</tr>
<tr>
<td>'Sioux'</td>
<td>Japan</td>
<td>1929</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Originating by selection</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'Mukden'</td>
<td>Selection from introduction</td>
<td>Virginia</td>
<td>1920</td>
<td>II</td>
</tr>
<tr>
<td>'Illini'</td>
<td>Selection from 'A. K.'</td>
<td>Illinois</td>
<td>1921</td>
<td>III</td>
</tr>
<tr>
<td>'Scioto'</td>
<td>Selection from 'Manchu'</td>
<td>Ohio</td>
<td>1925</td>
<td>III</td>
</tr>
<tr>
<td>'Richland'</td>
<td>Selection from introduction</td>
<td>Virginia</td>
<td>1927</td>
<td>II</td>
</tr>
<tr>
<td>'Flambeau'</td>
<td>Selection from 'Manchu'</td>
<td>Wisconsin</td>
<td>1940</td>
<td>0</td>
</tr>
<tr>
<td>Originating by artificial hybridization</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>'Chief'</td>
<td>'Illini' × 'Manchu'</td>
<td>Illinois</td>
<td>1926</td>
<td>III</td>
</tr>
<tr>
<td>'Gibson'</td>
<td>'Midwest' × 'Dunfield'</td>
<td>Indiana</td>
<td>1930</td>
<td>IV</td>
</tr>
<tr>
<td>'Lincoln'</td>
<td>'Mandarin' × 'Manchu'</td>
<td>Illinois</td>
<td>1934</td>
<td>III</td>
</tr>
<tr>
<td>'Hawkeye'</td>
<td>'Mukden' × 'Richland'</td>
<td>Iowa</td>
<td>1938</td>
<td>II</td>
</tr>
<tr>
<td>'Adams'</td>
<td>'Dunfield' × 'Illini'</td>
<td>Iowa</td>
<td>1938</td>
<td>III</td>
</tr>
</tbody>
</table>

*These cultivars originated from direct seed increase of plant introductions, pure-line selections within heterogeneous plant introductions, and pure-line cultivars selected from populations developed by artificial hybridization. Adapted from Poehlman (1959).
†Year of introduction, selection, or hybridization.
that represented direct seed increases of plant introductions commonly were heterogeneous mixtures of homozygous plants.

Selection from Plant Introductions. The second phase of cultivar development in North America was selection of homozygous plants within heterogeneous plant introductions. A common source of desirable selections for breeders in North America was heterogeneous plant introductions that had been named and released for commercial use (Table 14-1). For example, a desirable introduction from Manchuria was named ‘Manchu,’ and its seed was made available for commercial production. Selection within ‘Manchu’ by a breeder in Ohio resulted in the maturity group III cultivar ‘Scioto,’ and selection by a breeder in Wisconsin provided the maturity group O cultivar ‘Flambeau.’ The cultivars developed by selection were considered pure lines.

Hybridization and Selection. The third phase of cultivar development began when breeders used artificial hybridization to generate new sources of genetic variability. The parents of the initial crosses commonly were introductions or selections from introductions that were being grown as commercial cultivars (Table 14-1). The hybrid populations were inbred for several generations to obtain homozygous plants, the progeny of individual plants were evaluated, and superior homogeneous lines were released as pure-line cultivars. The cultivars obtained from the initial hybridization programs were used as parents for developing new populations. This cyclic process of hybridization, inbreeding, and selection has continued up to the present.

Soybean seed currently used by farmers is of two types: pure-line cultivars or planned seed mixtures of pure-line cultivars. Pure-line cultivars currently are used for the majority of soybean production. Because the soybean is highly self-pollinated, a pure-line cultivar represents a homogeneous group of homozygous plants, and the seed harvest from a field is the same genetically as the seed that was planted.

There is a limited use of planned seed mixtures of pure-line cultivars, commonly referred to as blends. A blend is produced by growing two or more pure lines separately, mixing their seed in the desired proportion, and selling the mixture to the farmer. As a result, a blend is a heterogeneous mixture of homozygous plants. No hybridization is involved in producing a blend; therefore, it bears no relationship to a hybrid cultivar.

Hybrid cultivars are not used in soybeans. The barriers to hybrid cultivars include the relatively small amount of heterosis that is expressed, the absence of cytoplasmic-genetic male sterility or a suitable chemical gametocide, the need for insect pollination, the relatively low amount of hybrid seed that could be produced per unit of land area, and the relatively high plant population used in commercial fields.
EXTENT AND NATURE OF BREEDING PROGRAMS IN NORTH AMERICA

Cultivar development is carried out by both public and private institutions. The initial breeding programs in the United States were conducted by the USDA. USDA breeders were located throughout regions of the country that had the greatest potential for soybean production, and they developed the majority of the initial cultivars. At present, the USDA is reducing its emphasis on the development and release of soybean cultivars, and increasing its emphasis on studies related to breeding methodology and on development of germplasm that may be useful for cultivar development by state programs and the private sector. In 1985, there were 19 USDA breeders and geneticists located in 10 states.

Cultivar development is conducted by state agricultural experiment stations in those areas where the soybean is a crop of major economic importance. States with limited soybean production commonly test and release cultivars produced by institutions in other states. In 1985, there was a total of 19 breeders in 15 states who were conducting cultivar development. An additional 16 states were evaluating and releasing cultivars developed by institutions in other states.

There are four public soybean breeders in Canada. Three of them are scientists of the national research organization, Agriculture Canada, and one is a faculty member at the University of Guelph. Three of the breeders are located in Ontario, the province with the largest concentration of soybean production in Canada, and one breeder is located in Alberta.

Major involvement of the private sector in cultivar development began in the United States after passage of the Plant Variety Protection Act in 1970. The Act gave legal rights to the originator of a cultivar, which provided the incentive for investment by private companies. The number of companies involved in cultivar development grew rapidly, and today, there are more private breeders than public breeders and geneticists. In 1985, there were 62 private breeders representing 28 companies. Not only are there more private than public breeders, but private breeders devote more resources to cultivar development. Public breeders devote a major part of their resources to basic research. Private breeders are devoting the largest proportion of their resources to cultivar development for maturity groups II, III, and IV grown in the northern United States (Table 14-2). This reflects in part the heavy concentration of commercial soybean production devoted to cultivars of those maturities. Canada does not have a system of plant variety protection; as a result, investment by private companies in that country has been much less than in the United States. Only 2 of the 62 private breeders are located in Canada.

There is only limited information on the percentage of private and
Table 14-2  Percentage of Private and Public Soybean Breeders in Canada and the United States Who Are Developing Cultivars of Maturity Groups 00 to IX

<table>
<thead>
<tr>
<th>Maturity Group</th>
<th>Private Breeders</th>
<th>Public Breeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>00</td>
<td>5%</td>
<td>3%</td>
</tr>
<tr>
<td>0</td>
<td>9</td>
<td>13</td>
</tr>
<tr>
<td>I</td>
<td>18</td>
<td>50</td>
</tr>
<tr>
<td>II</td>
<td>41</td>
<td>70</td>
</tr>
<tr>
<td>III</td>
<td>45</td>
<td>67</td>
</tr>
<tr>
<td>IV</td>
<td>55</td>
<td>70</td>
</tr>
<tr>
<td>V</td>
<td>36</td>
<td>30</td>
</tr>
<tr>
<td>VI</td>
<td>36</td>
<td>20</td>
</tr>
<tr>
<td>VII</td>
<td>27</td>
<td>17</td>
</tr>
<tr>
<td>VIII</td>
<td>23</td>
<td>7</td>
</tr>
<tr>
<td>IX</td>
<td>5</td>
<td>3</td>
</tr>
</tbody>
</table>

Public cultivars grown throughout the United States. The development and adoption of private cultivars has been most rapid in the northern United States. In a survey conducted during 1984 by the Iowa Crop Improvement Association, 82% of the hectarage in Iowa was planted to private cultivars and 18% to public cultivars. In the southern United States, where the investment of the private sector has been less than in the North, public cultivars still predominate.

BREEDING OBJECTIVES FOR CULTIVAR DEVELOPMENT

Seed Yield

The highest priority in soybean cultivar development is increasing seed yield. Seed yield is a quantitative character controlled by many genes and strongly influenced by the environment. The heritability of yield is the lowest and the most variable of the major agronomic traits considered in cultivar development, with estimates ranging from 3 to 58% (Brim, 1973).

Substantial genetic improvement for seed yield has been achieved. The average rate of yield increase from several studies, as summarized by Specht and Williams (1984), has been 15.1 kg/ha per year or 0.6% per year since the 1920s. New public and private cultivars are released on a
regular basis that are superior in yield to existing cultivars, and further genetic improvement for the trait will occur in the future.

Maturity

The maturity of a soybean cultivar determines the area in which it will be most productive. Although the range in maturity among cultivars is continuous, each is assigned to one of the maturity groups from 000 to X (Fig. 14-2). The soybean is a short-day plant and its maturity is strongly influenced by its response to photoperiod. Temperature also has been shown to have an effect on the time of maturity. Although major genes for maturity have been reported, it is considered a quantitative trait in most breeding programs (Bernard, 1973). Maturity has a heritability of 75% or greater (Brim, 1973).

Lodging Resistance

The lodging resistance or standability of a cultivar is an important trait in cultivar development. It is a quantitative character with a heritability of about 55% (Brim, 1973).

The most common practice is to select for lodging resistance among indeterminate genotypes of maturity group IV or earlier for the northern latitudes and among determinate genotypes of maturity groups V or later for the southern latitudes. The exception has been the development of determinate cultivars of short stature for maturity groups II to IV (Cooper, 1981). These determinate cultivars are about 55 cm tall compared with 95 cm for indeterminate cultivars of comparable maturity. The short, determinate cultivars have exceptional lodging resistance and are particularly well suited to highly productive environments in which indeterminate cultivars exhibit excessive lodging.

Pest Resistance

All of the major diseases and nematodes of soybean are controlled primarily by genetic resistance. Consequently, only a small percentage of soybean hectarage involves the use of a fungicide or nematicide. There are many different diseases, nematodes, and insects that attack soybean, but there are relatively few that consistently cause injury of economic importance and that are given major consideration by the breeder. The pests of economic importance differ among regions. Therefore, the emphasis placed on a pest will depend on the region for which the cultivar is being
developed. A complete description of soybean diseases has been published by Sinclair (1982), and a review of methods of breeding for disease resistance has been reported by Wilcox (1983).

There are 10 diseases or nematodes for which specific or general resistance was considered essential or useful in a new cultivar by at least 10% of soybean breeders in 1985 (Table 14-3). The two pests that are most commonly considered are phytophthora rot and soybean cyst nematode.

**Phytophthora Rot.** Phytophthora rot, caused by *Phytophthora megasperma* Drechs. f. sp. *glycine*, results in injury of economic importance in much of the soybean production area of North America. The soil-borne fungus can infect the plant throughout the growing season, and may result in plant death or substantial reduction in plant growth and seed yield (Sinclair, 1982).

Genetic control of phytophthora rot is achieved by the use of major genes for resistance to specific races and by selection for general resistance. There are more than 20 physiological races of the pathogen, but relatively few are of major importance at the present time. Major genes for specific resistance are available, each of which will control some of the races, but none of which control all identified races (Wilcox, 1983). It has been a common practice to incorporate major genes for resistance into a susceptible cultivar by backcrossing. The presence of genes for resistance can be monitored readily in a backcross program by artificial

<table>
<thead>
<tr>
<th>Disease or Nematode*</th>
<th>Essential</th>
<th>Useful, but Not Essential</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytophthora rot</td>
<td>48%</td>
<td>31%</td>
</tr>
<tr>
<td>Soybean cyst nematode</td>
<td>17%</td>
<td>60%</td>
</tr>
<tr>
<td>Bacterial pustule</td>
<td>12%</td>
<td>6%</td>
</tr>
<tr>
<td>Stem canker</td>
<td>10%</td>
<td>13%</td>
</tr>
<tr>
<td>Root-knot nematodes</td>
<td>8%</td>
<td>21%</td>
</tr>
<tr>
<td>Brown stem rot</td>
<td>2%</td>
<td>27%</td>
</tr>
<tr>
<td>Bacterial blight</td>
<td>2%</td>
<td>13%</td>
</tr>
<tr>
<td>Soybean mosaic virus</td>
<td>0%</td>
<td>17%</td>
</tr>
<tr>
<td>Downy mildew</td>
<td>0%</td>
<td>15%</td>
</tr>
<tr>
<td>Charcoal rot</td>
<td>0%</td>
<td>10%</td>
</tr>
</tbody>
</table>

*Only those diseases and nematodes are listed that were considered essential or useful by 10% or more of soybean breeders.
infection of plants in the laboratory. Backcross-derived cultivars commonly are identified by the name of the susceptible recurrent parent and the year of release of the resistant version. Examples of backcross-derived cultivars currently grown are 'Century 84,' 'Corsoy 79,' and 'Williams 82.' Cultivars with major genes for resistance also are developed by hybridization, inbreeding, and selection when at least one of the parents of a cross has a major gene.

General resistance, often referred to as field resistance, is considered to be a quantitative character controlled by multiple genes. This type of resistance is desirable because it provides protection against a broad range of races, although the level of protection may not be as good against a particular race as that provided by the major genes for specific resistance. General resistance is more difficult to evaluate than specific resistance, and generally requires replicated field tests on soil infested with the pathogen. Although breeders would prefer to have an exceptionally high level of general resistance, they generally are most concerned with the elimination of lines that are excessively susceptible to the pathogen.

Soybean Cyst Nematode. The soybean cyst nematode, caused by *Heterodera glycines* Ichinohe, has been an important pest in parts of the southern United States for many years. It was not identified in most of the northern United States until the 1980s. Many breeders devote some resources to the development of resistant cultivars (Table 14-3).

There are at least five races of the soybean cyst nematode. Major genes for resistance have been reported, but no single allele confers an adequate level of protection to the known races (Wilcox, 1983). For example, three recessive and one dominant allele control resistance to race 1 of the nematode. Resistance to the nematode commonly is evaluated in the greenhouse by growing plants in infested soil brought from the field. The level of resistance is rated by the number of cysts that develop on the roots.

Seed Quality

Seed quality is a complex of characteristics that influence the marketability of seed for processing and planting. The market value of soybeans is influenced by appearance of the seed. Shrunken and discolored seed may cause a reduction in price, even though the composition of the seed may be unaffected. Seed quality also relates to the germination rate. Reduction in seed quality is caused by unfavorable weather conditions and disease. Differences among genotypes for seed quality characteristics generally are quantitatively inherited. Breeding for seed quality includes
selection for visual appearance, laboratory and field germination percentages, and disease resistance (Green and Pinnell, 1968; Aihow, 1973).

Seedling Emergence

Cultivars differ in the ability of their seeds to emerge when planted excessively deep or when soil crusting occurs due to heavy rains after planting (Fehr et al., 1973). Some of the genetic differences in seedling emergence are attributable to differential hypocotyl elongation at temperatures of about 25°C (Gilman et al., 1973). At that temperature, the hypocotyls of some cultivars do not elongate normally.

Seed Composition and Size

The value of soybeans is in the protein and oil of the seed. Nevertheless, seed composition has not been considered in marketing the crop up to the present time. This seems to be the result of frequent fluctuations in the relative market value of protein and oil. In some years, protein has the highest value and high-protein seed would be desirable, while oil is most valuable in other years and high-oil seed would be preferred. When the protein content of the seed increases, there is a proportionate decrease in the oil content, and vice versa. With the lack of any clear trend in the demand for protein or oil, there has been no reason for breeders to preferentially select for one or the other in developing cultivars for widespread use. Nevertheless, some breeders devote part of their resources to the development of high-protein seed (Table 14-4). They believe that the alternative sources of vegetable protein are more limited than for oil, and that eventually cultivars with high protein may be preferred in the world market. There currently is a limited demand for seed with above-average protein, particularly for production of tofu, a cheese-like curd for human consumption. Protein and oil content are quantitative traits with a heritability of about 65% (Brim, 1973).

Large seeds are preferred for the direct consumption of soybean as a vegetable, for certain traditional Oriental foods, and for confectionary products. Small seeds are preferred for a fermented food in Japan called natto. These relatively small markets are served by cultivars developed by a few breeding programs. Seed size is inherited as a quantitative character with a heritability of about 70% (Brim, 1973).

There has been interest in improving several factors related to seed composition that make soybeans less desirable for certain applications. Soybean seed or the protein meal obtained from it must be treated with
heat to inactivate the antinutritional factors that prevent proper digestion of the seed protein. A gene that eliminates the Kunitz trypsin inhibitor has been identified, which partially improves the digestibility of the protein (Orf and Hymowitz, 1979). There has been no market demand for seeds that lack the inhibitor, probably because it does not completely eliminate the need for heat treatment. Modification of the soybean oil to improve its stability and flavor would be desirable. Research is underway to alter the oil, primarily by reducing the percentage of linolenic acid (Hammond and Fehr, 1984).

Herbicide Tolerance

There are cultivar differences for the amount of plant injury that occurs with the application of certain herbicides. Metribuzin is currently the herbicide most widely considered by those soybean breeders who select for resistance to injury in their cultivar development programs (Table 14-4). Although most breeders do not purposefully select for metribuzin resistance, they may screen cultivars for response to the herbicide and alert farmers to those that are particularly susceptible to injury.
Iron-deficiency Chlorosis

Iron-deficiency chlorosis is characterized by yellowing of the trifoliolate leaves, when soybeans are grown on some calcareous soils with a pH of about 7.5. Cultivars differ in their ability to utilize soil iron and in their extent of yellowing when grown on the calcareous soils. The problem occurs in limited areas of several of the northern states, particularly Iowa and Minnesota. Resistance to iron chlorosis is considered a quantitative trait in breeding programs (Fehr, 1982). For breeders developing cultivars for the northern United States, most do not require resistance to iron chlorosis in all cultivars, but many devote some resources to developing resistant cultivars for use in the affected areas (Table 14-4).

STEPS IN CULTIVAR DEVELOPMENT

There are four general steps in the development of pure-line cultivars of soybean.

1. A source of genetic variability is obtained by developing segregating populations through artificial hybridization of selected parents.
2. The population is inbred by natural self-pollination to obtain pure lines. Selection may be practiced for some characteristics during the inbreeding process.
3. Pure lines are evaluated for yield and other agronomic characteristics in replicated tests over multiple locations and years.
4. Seed of a superior pure line is increased and released to farmers as a new cultivar for commercial production.

An additional step is added if the seed product to be marketed is a seed mixture or blend of pure lines. The fifth step would be the evaluation of the performance of alternative combinations of cultivars.

SOURCES OF GENETIC VARIABILITY

Types of Parents and Populations

The cultivated soybean, Glycine max (L.) Merrill, is generally considered to have evolved from the wild species G. soja (L.) Sieb. & Zucc. Both species are annual diploids with a somatic chromosome number of 2n = 40. The two species can be crossed readily to obtain fertile progeny. Other species in the genus Glycine are perennials (Table 14-5). At present, it has not been possible to transfer genes from the perennial species to G. max, although there has been some limited success in ob-
Table 14-5  Taxonomy of the Genus *Glycine* Willd

<table>
<thead>
<tr>
<th>Species</th>
<th>Chromosome Number (2n)</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. argyrea</em> Tind.</td>
<td>40</td>
<td>Australia</td>
</tr>
<tr>
<td><em>G. canescens</em> F. J. Herm.</td>
<td>40</td>
<td>Australia</td>
</tr>
<tr>
<td><em>G. clandestina</em> Wendl.</td>
<td>40</td>
<td>Australia</td>
</tr>
<tr>
<td><em>G. cyrtoloba</em> Tind.</td>
<td>40</td>
<td>Australia</td>
</tr>
<tr>
<td><em>G. falcata</em> Benth.</td>
<td>40</td>
<td>Australia</td>
</tr>
<tr>
<td><em>G. latifolia</em> (Benth.) Newell &amp; Hymowitz</td>
<td>40</td>
<td>Australia</td>
</tr>
<tr>
<td><em>G. latrobena</em> (Meissen.) Benth.</td>
<td>40,80</td>
<td>Australia, south China, South Pacific Islands, Ryukyu Islands, Taiwan</td>
</tr>
<tr>
<td><em>G. tabacina</em> (Labill.) Benth.</td>
<td>38,40,78,80</td>
<td>Australia, south China, Papua New Guinea, Taiwan, Philippines</td>
</tr>
<tr>
<td><em>G. tomentella</em> Hayata</td>
<td>38,40,78,80</td>
<td>Australia, south China, Papua New Guinea, Taiwan, Philippines</td>
</tr>
</tbody>
</table>

Subgenus *Soja* (Moenck) F. J. Herm

<table>
<thead>
<tr>
<th>Species</th>
<th>Chromosome Number (2n)</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. max</em> (L.) Merr.</td>
<td>40</td>
<td>Cultigen (worldwide)</td>
</tr>
<tr>
<td><em>G. soja</em> (L.) Sieb. &amp; Zucc.</td>
<td>40</td>
<td>China, Japan, Korea, Taiwan, USSR</td>
</tr>
</tbody>
</table>


...taining hybrid seed from crosses between *G. max* and some of the perennial species (Brown et al., 1985).

The primary germplasm that has been utilized for the development of cultivars for commercial production has been accessions of *G. max*. *G. soja* is being used as a source of genes for small seed. The wild species has many characteristics that are unacceptable in a cultivar, including prostrate growth, vining, and shattering susceptibility. Although gene transfer between the species is possible, at least two backcrosses to the cultivated species are necessary to recover segregates that have the desirable traits of the *G. max* parent (Ernl and Fehr, 1985).

Current soybean cultivars in North America were developed from a limited number of the more than 10,000 plant introductions in the U.S. germplasm collection (Specht and Williams, 1984). Despite this relatively narrow genetic base, substantial genetic improvement for yield and other traits has been and continues to be made. Since about 1970, emphasis has been placed on broadening the genetic base by increased use of plant introductions, however, the majority of parents used for artificial hybridization in a cultivar development program are current cultivars or elite experimental lines. For the populations developed by private and public breeders in 1985, 56% of the parents were cultivars, 39% were elite experimental lines, and 5% were plant introductions. Plant
introductions are seldom used because they yield less than cultivars or
elite experimental lines, and populations developed from them generally
have a lower mean yield and lower frequency of desirable lines than those
developed from elite parents (Vello et al., 1984). Plant introductions are
used extensively, however, in breeding programs as a source of genes
for special characteristics, such as pest resistance.

The type of population used for cultivar development is determined
largely by the breeding objective and the parental material available. In
1985, 79% of the populations used for cultivar development were two-
parent crosses, 7% were three-parent crosses, 4% were four-parent
crosses, 3% had more than four parents, 2% involved one backcross, 2%
were a modified backcross, and 3% had two or more backcrosses. The ex-
tensive use of two-parent crosses reflects the strong emphasis on breeding
for high seed yield by crossing two high-yielding cultivars or elite ex-
perimental lines.

Three-parent crosses and populations obtained by one backcross have
been useful for developing specialty cultivars that require a minimum
level of a quantitative trait. For example, the yield of large-seeded
specialty cultivars currently is less than that of commercial cultivars
with average seed size. Two-parent crosses of a large-seeded × small-
seeded cultivar generally do not result in progeny with adequate seed
size. A three-parent or backcross population of (large-seeded × small-
seeded) × large-seeded parents will provide the necessary large-seeded
progeny (Bravo et al., 1981).

In transferring multiple genes for a character from a relatively poor
parent, a limited number of backcrosses to the same or different elite
parents has been successful. To maintain an adequate level of the desired
trait, selection is practiced among $F_2$ plants or their progeny before each
backcross. After one or a few backcrosses, individual segregates are
evaluated for yield and other agronomic characteristics. The procedure
has been particularly successful for development of cultivars with
soybean cyst nematode resistance (Wilcox, 1983).

Complex populations developed from many parents are not routinely
used for cultivar development, but have been adopted for recurrent selec-
tion programs. Current information indicates that the complex popula-
tions are not superior for selection of high-yielding cultivars than the more
popular two-parent crosses.

Population Development by Hybridization

*Procedures for Artificial Hybridization.* The populations used for cultivar
development are obtained by artificial hybridization between suitable
parents (Fehr, 1980). The soybean has a perfect flower consisting of
a calyx, corolla, pistil, and stamen (Fig. 14-1). The calyx, consisting of five green, leaf-like sepals, envelopes the flower until about 1 day before pollination. The day before pollination occurs, the corolla begins to emerge from the sepals. The corolla includes one standard, two keel, and two wing petals that are either white or purple in current cultivars. The corolla encloses the pistil and the stamens. The pistil has a single ovary with generally two or three ovules, a style, and a stigma. The 10 stamens are in a circle around the pistil.

A flower of the female parent is at the proper stage for artificial hybridization about 1 day before it would self-pollinate. At this stage, the floral bud is plump and the petals are just beginning to emerge [Fig. 14-1(A)]. The flower is prepared for pollination by removing the calyx with a forceps. The scar that results from removal of the calyx serves to distinguish pods produced by artificial hybridization from those that develop after natural self-pollination. The petals are removed by grasping them with a forceps immediately above the calyx scar and lifting gently upward [Fig. 14-1(B)]. Removal of the corolla will expose the pistil and the ring of anthers [Fig. 14-1(C)]. It is not necessary to remove the anthers because if the flower is not pollinated after the corolla is taken off, the female becomes unreceptive before pollen from anthers of the same flower is shed.

Pollen is obtained from the male parent by removing the reproductive organs with a forceps when the anthers are mature [Fig. 14-1(D)]. In many environments, the flowers of the male parent are used immediately for pollination. In the southern United States, it is common to collect intact flowers during the morning, place them in a desiccator at about 25°C, and use the flowers in the afternoon. The anthers are gently brushed on the stigma until pollen is clearly visible on it [Fig. 14-1(E)]. A flower with profuse pollen shed may be used to pollinate several flowers, but it is most common to use only one male flower for each female flower.

After the pollination is completed, an identification tag is tied to the stem, usually below the node where the pollinated flower is located. A plastic tag strung with a copper wire commonly is used because it is not susceptible to damage by insects or moisture. The information recorded on the tag may include the male parent, the date of pollination, the node above the tag at which the pollinated flowers are located, and the initials of the worker.

If the hybridization is successful, a small pod will be visible about 7 days after pollination [Fig. 14-1(F)]. Pods produced by artificial hybridization are harvested as soon as they have reached their mature color. After the seed is dry, it can be planted whenever desired. The percentage of successful pollinations is extremely variable, being influenced by the skill of the worker and environmental conditions. An inexperienced person may achieve less than 10% success and an experienced individual
may have more than 75% success. Under favorable conditions, a skilled person usually can obtain about 75 hybrid pods per day with about two seeds per pod.

*Procedures for Natural Hybridization.* Several alleles for genetic male sterility have been identified in soybean (Graybosch and Palmer, 1985). The trait has been used to a limited extent to facilitate hybridization in populations for recurrent selection, but no cultivars have been developed from the populations (Brim and Stuber, 1973). Pollen transfer in soybean is by insects, primarily honeybees (*Apis mellifera* L.) (McGregor, 1976).

**Mutagenesis**

Attempts to use mutagenesis for the improvement of yield and other agronomic traits have not been successful. The only use of mutagenesis at the present time is to develop characteristics that are not available in the U.S. collection of plant introductions. For example, chemical mutagenesis has been used to develop genes that control unique fatty acid composition in soybean oil (Hammond and Fehr, 1984; Wilcox et al., 1984).

**BREEDING PROCEDURES**

After a source of genetic variation has been developed in a segregating population, the population is inbred by natural self-pollination to obtain pure lines that can be evaluated as potential cultivars. Two important considerations are the number of inbreeding generations that the population will be grown before pure lines are obtained and the method of managing the population during inbreeding.

The generation in which pure lines are derived from a population varies considerably among soybean breeders. For the lines evaluated in 1985 by private and public breeders, 1% were F2-derived, 20% F3-derived, 45% F4-derived, 24% F5-derived, 9% F6-derived, and 1% derived in later generations. When lines are derived in early generations, breeders generally must visually discard a higher percentage of them, due to lack of phenotypic uniformity, than when they are derived in later generations. This disadvantage of deriving lines in early generations may be offset by the opportunity to obtain lines for evaluation 1 or more years earlier than when populations are more highly inbred.

The four basic methods of managing soybean populations during inbreeding are single-seed descent, pedigree, bulk, and early-generation
testing. In 1985, 65% of the pure lines developed by soybean breeders were obtained by single-seed descent, 18% by pedigree selection, 10% by early-generation testing, 4% by the bulk method, and 3% by some combination of two of the basic methods. The extensive use of single-seed descent reflects the preference of breeders to rapidly inbreed populations as a means of reducing the number of years required to develop a cultivar.

Environments for Inbreeding

Rapid inbreeding is achieved by growing one or more generations each year in a winter nursery or greenhouse. In 1985, 94% of the soybean breeders used a winter nursery in their breeding programs. There were 38% who used a nursery in Puerto Rico, 17% in Florida, 15% in Hawaii, 13% in Belize, 11% in Chile, and 4% in other countries.

The number of generations that can be grown during the winter depends on the location of the nursery and the maturity of the population. Chile has a temperate climate in which soybeans are grown commercially from October through May, and one generation can be grown during that period. All other winter nursery locations used by breeders in North America are located in tropical or semitropical climates. Two generations can be grown in the tropical climates during the period from October through May. The ability to grow two generations during the winter in tropical locations is due to the short day lengths of about 12 hours. As a short-day plant, soybeans adapted to North America flower rapidly in response to the short photoperiod, and a mature crop can be obtained in about 85 days. The generation length can be shortened further by artificially hastening maturity by harvesting pods or spraying plants with a defoliant when the seeds are approaching full size but have not begun to turn yellow (Ciancio, 1985). Seed production in tropical climates can be increased by exposing the plants to day lengths that are extended by artificial lighting. Extended day lengths also result in the development of flowers that can be used readily for artificial hybridization, whereas flowers that develop under short days generally have self-pollinated before they are large enough to be manipulated. The use of extended photoperiods increases the length of a generation by about 15 days (Ciancio, 1985).

The effectiveness of selection in a greenhouse or winter nursery varies with the character under consideration. Selection for certain types of pest resistance is practiced in the greenhouse. Because of space limitations, it can be difficult to expose a large number of segregating populations to a pathogen and obtain seed from the resistant selections. A common use of
the greenhouse is to progeny test plants for their resistance. Most progeny tests can be conducted with young plants that can be destroyed after the results are obtained. Selection is not practiced for agronomic traits in the greenhouse because of space limitations in growing plants to maturity and because the expression of traits often is not the same as under field conditions.

Selection for most agronomic traits is possible in Chile for genotypes of maturity group III and earlier, which are adapted to its temperate environment. Although yield tests may be possible in Chile, they have not been used routinely for that purpose by breeders in North America. In the winter nurseries grown in tropical climates, selection is practiced effectively for seed size, protein and oil percentage, fatty acid composition of the oil, and growth and flowering response under short days (Cianzio, 1985). Selection for maturity, plant height, lodging resistance, and yield generally is not effective in tropical climates.

Methods of Inbreeding

Single-seed Descent. The use of single-seed descent was described by Brim (1966) who referred to it as a modified pedigree method. It is especially well-suited to inbreeding populations in tropical environments and greenhouses where selection is not possible for most important agronomic characters.

There are three procedures for implementing single-seed descent in soybean breeding. The most common procedure is to harvest one or a few pods from each plant in a population, thresh all the pods together, use a sample of the bulk to plant the next generation, and place the remainder of the sample in reserve. This multiple-seed procedure is preferred because it requires less time for harvest than the single-seed procedure, and the size of the population can remain constant during inbreeding.

For the single-seed procedure, one seed is harvested from each plant in a population, and the seeds are bulked and planted the next generation. If the breeder desires a reserve sample, a second one-seed sample must be harvested. The size of the population becomes smaller each generation because some seeds do not germinate and some plants may not produce seed. The advantage of the procedure is that each plant in the population traces to a different $F_2$ individual, and genetic variability among segregates may be larger than for the multiple-seed procedure.

The single-hill procedure is used when progeny from a plant must be maintained during inbreeding. Several seeds from a plant are sown in a hill, several seeds are harvested from the hill, the seeds are planted in a hill the next generation, and the process is repeated. The procedure is not
commonly used because it requires considerably more labor than the multiple-seed or single-seed procedures.

Selection among individual plants for characters of interest can be practiced whenever possible with single-seed descent. The amount of selection during inbreeding generally is limited because most of the generations are grown in winter nurseries where the characters of interest often are not adequately expressed.

The use of single-seed descent minimizes the number years required for cultivar development. This principle is illustrated by the description of the development of the cultivar 'Preston' (Table 14-6).

Table 14-6 Development of the Cultivar 'Preston' by the Multiple-seed Procedure of Single-seed Descent

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>The cross of Scheckinger 'S48' × Land O'Lakes 'Max' was made at the Iowa State University-University of Puerto Rico nursery at Isabela, Puerto Rico, during March. Artificial lighting was used to extend the day length to obtain flowers suitable for hybridization. The objective of the cross was to develop a new cultivar with improved yield and acceptable agronomic characteristics. The population was designated AX2357. F₁ seeds of AX2357 were planted in the field at Ames, Iowa, to obtain F₂ seeds.</td>
</tr>
<tr>
<td>1</td>
<td>F₂ seeds of AX2357 were planted during November in Puerto Rico, and the plants were grown under natural day length conditions. Three F₃ seeds from each plant were bulked.</td>
</tr>
<tr>
<td>2</td>
<td>F₃ seeds of AX2357 were planted in Puerto Rico during February under natural day length. Three F₄ seeds from each plant were bulked.</td>
</tr>
<tr>
<td>2</td>
<td>F₄ seeds of AX2357 were space planted in the field at Ames. F₄ plants were classified as early, midseason, or late maturity and were threshed individually.</td>
</tr>
<tr>
<td>3</td>
<td>F₄₉ lines of AX2357 were evaluated in two replications of single-hill plots spaced 1 by 1 m at each of two Iowa locations. About 50% of the lines with the best visual agronomic characteristics were harvested for seed yield.</td>
</tr>
<tr>
<td>4</td>
<td>Selected F₄₉ lines of AX2357 were grown in two replications of two-row plots at three Iowa locations. The line that became Preston was designated A81-257031.</td>
</tr>
</tbody>
</table>
| 5 a  | A81-257031 was evaluated for seed yield and other characters in the Uniform Soybean Test at 11 locations in nine states in the northern United States.  
  | b. Purification of the line was initiated at Ames. Forty-eight F₇ plants with uniform plant and seed traits were threshed individually. |
| 6 a  | A81-257031 was evaluated at a total of 20 locations in 12 provinces and states in Canada and the northern United States. |
Table 14-6  continued

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>b.</td>
<td>Progeny rows for each of 48 plants selected in year 5 were grown at Ames. Forty-seven progeny with uniform characteristics were harvested separately to obtain a total of about 120 kg of seed.</td>
</tr>
<tr>
<td>7</td>
<td>a. A81-257031 was evaluated in the Uniform Soybean Test at 20 locations in 12 provinces and states.</td>
</tr>
<tr>
<td>b.</td>
<td>The line was approved for release by the Iowa Agriculture and Home Economics Experiment Station, and was named ‘Preston.’</td>
</tr>
<tr>
<td>c.</td>
<td>Of the 47 progeny rows harvested in year 6, 45 were used to plant about 3 ha for breeder seed production. Two of the progeny rows from year 6 were discarded because seed with off-type hilum color was found in them. The seed from each progeny row was grown as a separate increase within the 3-ha field. The 45 progeny increases were examined for homogeneity during the growing season and all were found to be acceptable. The increases were harvested together and about 7.2 t of breeder seed was obtained. The seed was distributed to foundation seed organizations in Illinois, Iowa, and South Dakota.</td>
</tr>
<tr>
<td>8</td>
<td>The breeder seed was planted by each state to obtain foundation seed.</td>
</tr>
<tr>
<td>9</td>
<td>Foundation seed was planted by private seed producers to obtain registered seed. The registered seed was planted the following year to obtain the certified class. The registered and certified classes were used by farmers for commercial plantings.</td>
</tr>
</tbody>
</table>

Pedigree. The pedigree method is based on selection among plants and lines during inbreeding. The inability to select in winter nurseries and greenhouses for a number of important agronomic traits limits the use of the method by soybean breeders. Most breeders are not willing to extend the length of time for cultivar development by growing only one generation each year in the field to conduct visual selection. The pedigree method can be used effectively without increasing the length of cultivar development when traits can be selected effectively in winter nurseries or greenhouses, as illustrated by the development of the cultivar ‘Leflore’ (Table 14-7).

Bulk. The bulk method is conducted by growing a population of plants, harvesting all the seed in bulk, planting a sample of the bulk the next generation, and repeating the procedure until the desired level of homozygosity is achieved. The population can be grown in an environment that favors the productivity of genotypes with desirable characteristics. Populations grown on soils infested with the soybean cyst nematode increased the frequency of segregates with resistance to the pest after several gener-
Table 14-7  Evaluation of the Soybean Cultivar 'Leflore' by the Pedigree Method

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>The cross of 'Centennial' × J74-47 was made in the field at Stoneville, Mississippi. ‘Centennial’ is a highly productive cultivar of maturity group VI that is resistant to the root-knot nematode and phytophthora rot. J74-47 was a source of resistance to races 3 and 4 of the soybean cyst nematode (SCN). The objective of the cross was to develop a cultivar of maturity group VI with resistance to races 3 and 4 of SCN, and with high yield when grown on soils that are not infested with the nematode. The F₁ plants were grown during the winter in the greenhouse at Stoneville.</td>
</tr>
<tr>
<td>2</td>
<td>Approximately 1200 F₂ seeds were planted in May in individual pots in the greenhouse at Jackson, Tennessee. The soil was infested with race 4 of SCN (SCN 4). Roots were inspected 30 days after infestation, and 220 seedlings with low infection levels were transplanted to a field infested with SCN 4. F₂ plants rated as resistant were harvested individually. Ten F₂ progeny of selected F₂ plants were tested in the greenhouse at Stoneville for resistance to phytophthora rot. Four F₃ plants were harvested individually from each of 56 F₂ plants rated resistant to phytophthora rot.</td>
</tr>
<tr>
<td>3</td>
<td>F₃₄ lines were grown in a field at Stoneville that had been continuously cropped to soybeans for over 20 years to expose the plants to natural infection by phytophthora rot and other soil-borne diseases. The best one of the four lines in a family was chosen and four F₃ plants were harvested individually from the row.</td>
</tr>
<tr>
<td>4</td>
<td>Each selected F₃ plant was progeny tested in the greenhouse at Jackson for resistance to SCN 4.</td>
</tr>
<tr>
<td>5</td>
<td>F₄ lines from selected F₃ plants were grown at Stoneville in the same field used to evaluated F₃₄ lines in year 3. The best line in a family was selected and harvested in bulk. The F₄-derived line that became 'Leflore' was designated D77-6166.</td>
</tr>
<tr>
<td>6</td>
<td>D77-6166 was evaluated under greenhouse conditions for resistance to phytophthora rot at Stoneville and to races 3 and 4 of the SCN at Jackson. The line was yield tested in three replications at Stoneville and Jackson. The field at Stoneville was infested with phytophthora rot and the field at Jackson was infested with SCN 4.</td>
</tr>
<tr>
<td>7</td>
<td>D77-6166 was evaluated in replicated trials on two soil types at Stoneville, on a soil infested with SCN 4 at Jackson, and on a field infested with race 3 of SCN at Verona, Mississippi. The line was evaluated in the Uniform Soybean Test at eight locations in the southeastern United States.</td>
</tr>
<tr>
<td>8</td>
<td>a. D77-6166 was grown in the Uniform Soybean Test. b. For seed purification, 200 individual plants were harvested.</td>
</tr>
<tr>
<td>9</td>
<td>a. The line was evaluated in the Uniform Soybean Test. b. Two hundred progeny rows were grown for seed purification. Uniform rows were harvested individually, each was tested for resistance to SCN 4 in the greenhouse, and seeds of resistant rows were bulked.</td>
</tr>
</tbody>
</table>
Table 14-7  continued

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
</tr>
</thead>
</table>
| 10   | a. D77-6166 was evaluated in the Uniform Soybean Test.  
b. The line was approved for release by the Mississippi Agricultural Experiment Station and was name ‘Leflore.’  
c. The pure seed produced in year 9 was used to plant 3 ha at Stoneville to obtain breeder seed. The seed was distributed to foundation seed organizations in Arkansas, Georgia, Mississippi, and South Carolina. |
| 11   | The breeder seed was planted by each state to obtain foundation seed. |
| 12   | The breeder seed was planted by each state to obtain foundation seed. The registered seed was planted the following year to obtain the certified class. The registered and certified classes were used by farmers for commercial plantings. |

Source: Hartwig (1985); Hartwig et al. (1985).

ations of inbreeding (Hartwig et al., 1982). On the other hand, natural selection in a bulk population can cause undesirable shifts in genotypic frequency, such as increasing the proportion of late-maturing genotypes (Empig and Fehr, 1971).

The bulk method is not well suited for inbreeding populations in winter nurseries or greenhouses where the productivity of plants commonly is not the same as in their area of adaptation. Its use by soybean breeders is limited because breeders would rather rapidly inbreed a population by single-seed descent than grow only one generation each year or take the risk of obtaining undesirable genetic shifts in a population by harvesting seed in bulk in a winter nursery or greenhouse.

Early-generation Testing. The principle of early-generation testing is to evaluate a group of heterogeneous populations or lines, select those with the best performance, and inbreed the selected ones until a number of homozygous plants can be obtained from each. Less than 1% of the pure lines developed by soybean breeders in 1985 resulted from early-generation testing of heterogeneous populations. Most breeders are not confident that differences in performance among heterogeneous populations adequately predict the frequency of superior inbred lines that can be selected from them.

Selection among heterogeneous F2-derived lines accounted for 4% of the lines evaluated by soybean breeders in 1985; selection among F5-derived lines accounted for 5%. The amount of testing used to identify superior heterogeneous lines, the number of generations tested, the method of inbreeding the selected lines, and the number of pure lines
derived from each heterogeneous line is highly variable among breeders. The overall strategy is illustrated by the development of the cultivar ‘Sprite’ (Table 14-8).

Early-generation testing has not been as widely adopted as single-seed descent for several reasons. The evaluation of heterogeneous lines reduces the resources available for testing pure lines. Assessment of maturity and other agronomic traits can be more difficult in a heterogeneous

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
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<tbody>
<tr>
<td>1</td>
<td>The cross of ‘Williams’ × ‘Ransom’ was made in the field at Urbana, Illinois. ‘Williams’ is an indeterminate cultivar of maturity group III, and ‘Ransom’ is a determinate cultivar of maturity group VII. The objective of the mating was to develop a determinate cultivar of maturity group III with high yield and a high level of lodging resistance.</td>
</tr>
<tr>
<td>1</td>
<td>F₁ seeds of the single-cross population were planted during November in the USDA nursery at Mayaguez, Puerto Rico. Artificial lighting was used to extend day length for enhancement of seed production.</td>
</tr>
<tr>
<td>2</td>
<td>F₂ plants were grown at Urbana. Determinate plants of appropriate maturity were harvested individually.</td>
</tr>
<tr>
<td>3</td>
<td>Ten F₃ lines from the population were grown in unreplicated single-row plots at Urbana. Three of the lines had appropriate maturity and were harvested for assessment of seed yield. The F₃-derived line from which ‘Sprite’ originated was designated L72U-2569.</td>
</tr>
<tr>
<td>4</td>
<td>L72U-2569 was evaluated as an F₄₀ line at Urbana in a four-row plot. The center two rows were harvested for yield, and 54 F₄ plants were harvested individually from the border rows.</td>
</tr>
<tr>
<td>5</td>
<td>Fifty-four F₄₈ lines from L72U-2569 were grown at Urbana in unreplicated single-row plots. Desirable rows were harvested individually in bulk.</td>
</tr>
<tr>
<td>6</td>
<td>Thirty-four F₄₉ lines from L72U-2569 were evaluated at Urbana in four-row plots at a row spacing of 75 cm.</td>
</tr>
<tr>
<td>7</td>
<td>a. Nineteen selected F₄₉ lines from L72U-2569 were tested at Urbana in four-row plots at 75-cm row spacing and 10-row plots at 17-cm row spacing.</td>
</tr>
<tr>
<td></td>
<td>b. For seed purification, 50 individual F₁ plants were harvested from each of the 19 lines.</td>
</tr>
<tr>
<td>8</td>
<td>a. The F₄-derived line from L72U-2569 that became ‘Sprite’ was designated HW74-3384. The line was grown in the Uniform Soybean Test at nine locations in the northern United States.</td>
</tr>
<tr>
<td></td>
<td>b. Progeny from 42 of the F₁ plants harvested in year 7 were tested for yield as F₁₀ lines in unreplicated single-row plots. Thirty-seven of the lines had similar phenotype and seed yield and their seed was bulked to form the pure seed source of HW74-3384.</td>
</tr>
</tbody>
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Table 14-8  continued

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>HW74-3384 was evaluated in the Uniform Soybean Test at 26 locations.</td>
</tr>
</tbody>
</table>
| 10   | a. HW74-3384 was grown in the Uniform Soybean Test at 24 locations.  
|      | b. The line was approved for release by the Ohio Agricultural Experiment Station and was named 'Sprite.'  
|      | c. The pure seed produced in year 8 was used to obtain 2 t of breeder seed. The seed was distributed to foundation seed organizations in Illinois, Iowa, Kansas, Missouri, Ohio, and South Dakota. |
| 11   | The breeder seed was planted by each state to obtain foundation seed. |
| 12   | Foundation seed was planted by private seed producers to obtain registered seed. The registered seed was planted the following year to obtain the certified class. The registered and certified classes were used by farmers for commercial plantings. |

Source: Cooper (1985).

line than in a pure line. The replicated testing of heterogeneous lines may increase the length of time for cultivar development.

Recurrent Selection

Recurrent selection has the potential for increasing the frequency of desirable genes in a population for one or more characters. As the gene frequency is improved, the likelihood of obtaining superior segregates is enhanced. Recurrent selection has been conducted in soybean populations with and without the use of genetic male sterility. Studies have demonstrated that recurrent selection can be used in soybean to improve populations for several characters, including protein percentage of the seed, resistance to iron-deficiency chlorosis, and seed yield (Brim and Burton, 1979; Fehr, 1982). Recurrent selection for seed yield resulted in the development of the cultivar ‘Elgin’ (Table 14-9).

Although recurrent selection can be useful for population improvement, the method has not been adopted extensively for cultivar development. There is no evidence that recurrent selection for seed yield in a population will provide higher-yielding cultivars than those obtained by the traditional procedure of selection within single-cross populations formed by crossing high-yielding cultivars and experimental lines. Despite its lack of adoption for cultivar development, recurrent selection will continue to be useful for genetic improvement of quantitative characters that are not at acceptable levels in available germplasm, such as resistance to iron-deficiency chlorosis. Superior lines selected from improved populations will be useful as parents to improve cultivars for a particular quantitative trait.
Table 14-9  Development of the Cultivar ‘Elgin’ by Recurrent Selection

<table>
<thead>
<tr>
<th>Year</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Recurrent selection for seed yield was conducted in the soybean population AP6 (Fehr and Ortiz, 1975). The population was developed by intermating 40 high yielding cultivars and experimental lines of maturity groups 0 to IV for three generations to obtain the cycle 0 population. Three hundred F₁-derived lines were evaluated from the population and the 30 with the highest yield were chosen to form the cycle 1 population. The following description begins with the crossing of the 30 parents. The 30 parents were planted in January at the Iowa State University-University of Puerto Rico nursery at Isabela, Puerto Rico. Artificial lighting was used to extend the day length to obtain flowers suitable for hybridization. The parents were mated in a diallel, and at least four F₁ seeds were obtained from each of more than 300 single-cross populations.</td>
</tr>
<tr>
<td>1</td>
<td>The F₁ seeds of the single-cross populations were planted in Puerto Rico during May under artificial lights, and F₂ seed was obtained. Eight F₂ seeds of each population were planted in Puerto Rico during August without artificial lights, and 16 F₂ seeds were harvested. Eight F₂ seeds of each population were planted in Puerto Rico during November without artificial lights, and 16 F₂ seeds were harvested. Eight F₂ seeds of each population were planted in Puerto Rico during February under artificial lights. One F₁ plant was harvested from each of 300 single-cross populations to obtain F₃-derived lines for yield evaluation in Iowa.</td>
</tr>
<tr>
<td>2</td>
<td>The 300 F₃ lines were evaluated in two replications at two Iowa locations. Each plot was a single hill spaced 1 by 1 m. The lines were divided into three maturity classes (early, midseason, and late), and the 30 highest-yielding lines within each class were selected for further evaluation in year 3. The line that became ‘Elgin’ was one of the 30 lines selected in the early maturity class. The F₂₅ lines were evaluated in two replications of two-row plots at three Iowa locations. The 10 highest-yielding lines of each maturity class were selected as parents to form the cycle 2 population to continue the recurrent selection program. The line that became ‘Elgin,’ designated A79-133019, had the highest yield of the 10 parents of the early maturity class.</td>
</tr>
<tr>
<td>4 to 6</td>
<td>a. A79-133019 was evaluated in the Uniform Soybean Test at locations in Canada and the northern United States. At the end of year 6, the line was approved for release by the Iowa Agriculture and Home Economics Experiment Station and was named ‘Elgin.’ b. Breeder seed was produced in Iowa by the procedure described for the cultivar ‘Preston’ in Table 14-6. The seed was distributed to foundation seed organizations in Illinois, Iowa, Nebraska, Ohio, South Dakota, and Wisconsin.</td>
</tr>
<tr>
<td>7</td>
<td>The breeder seed was planted by each state to obtain foundation seed.</td>
</tr>
<tr>
<td>8</td>
<td>Foundation seed was planted by private seed producers to obtain registered seed. The registered seed was planted the following year to obtain the certified class. The registered and certified classes were used by farmers for commercial plantings.</td>
</tr>
</tbody>
</table>

Source: Fehr and Bahremfus (1984).
FIELD- PLOT TECHNIQUES FOR GENOTYPE EVALUATION

The pure lines developed by inbreeding must undergo extensive testing to identify those that are adequately superior to be released as a cultivar. The testing process often involves selection of the individual plants from which lines are derived, visual selection among lines before or during the initial replicated tests, and several years of replicated testing in multiple locations before the decision is made to release the line.

Selection among Plants

When a population has reached the desired level of homozygosity by whichever method of inbreeding the breeder has chosen, individual plants are selected. Selection is practiced for traits of high heritability, such as time of maturity and pest resistance. Visual selection for seed yield on an individual-plant basis is not considered to be effective, although plants that lack overall agronomic desirability generally are discarded. Although selection among plants can be useful, it may be more effective in some circumstances to hasten cultivar development by obtaining seed of individual plants in a winter nursery or greenhouse where selection for important traits is not possible.

Selection among Lines

After plants are selected from a population, their seed generally is increased and progeny tests are conducted to eliminate inferior lines before beginning replicated tests for yield. Plot size and frequency of replication are minimized to permit a large number of lines to be evaluated in a small area and at a low cost. Single-hill or single-row plots commonly are used. The single-hill plots are spaced 50 cm to 1 m apart and are planted with 10 to 12 seeds per hill. Single-row plots are 1 to 2 m long with a row spacing of 75 cm to 1 m and seeding rate of about 30 seeds per meter of row. The plots are used to classify lines for time of maturity and to discard lines for lack of uniformity, lodging susceptibility, and other undesirable traits. Visual selection for seed yield is considered effective for discarding lines that are markedly inferior, but not for identifying the highest-yielding lines.

The evaluation of lines for pest resistance may be conducted in the greenhouse or in the field. Greenhouse tests include evaluation for specific resistance to phytophthora rot and resistance to the soybean cyst nematode. Field tests for pest resistance generally are replicated because of variability in the level of infestation within a field.
First Year of Yield Evaluation

The goal of the first test for seed yield is to discard lines that do not merit extensive testing. The second and later years of yield testing are designed to identify the lines that are adequately superior to be released as a cultivar.

The emphasis in the first yield test is to evaluate a large number of lines with a limited number of locations and replications. In 1985, public breeders evaluated an average of 1600 lines in the first yield test, with a range from 80 to 12,000 lines among programs. For private breeders, the average number of lines in the first yield test was 6800, with a range from 500 to 39,000 among programs. Soybean breeders prefer to test relatively few lines from a large number of different populations, instead of large number of lines from a few populations. In 1985, public breeders tested an average of 40 lines from 40 different populations, while private breeders tested an average of 37 lines from 182 different populations. The emphasis on a large number of populations relates to the lack of any reliable method to predict the parental combinations with the greatest likelihood of providing superior progeny. A second reason is that genetic diversity can be maintained more readily from one cycle of hybridization and selection to the next when a few superior lines are selected from each of many different populations than when the same number of lines is selected from a few populations.

The number of locations used for the first yield test ranges from one to four and the number of replications at each location ranges from one to three (Table 14-10). Plot size ranges from single-hill plots to four-row plots, with the highest percentage of breeders using two-row plots (Table 14-11). Single-hill plots are planted 75 cm to 1 m apart with 10 to 12 seeds per plot. For row plots, the spacing between rows ranges from <30 cm to 1 m. In 1985, 5% of the breeders used a row spacing of <30 cm for the first yield test, 8% had 51 to 70 cm, 62% had 71 to 90 cm, and 25% had 91 to 100 cm. Row spacings of 91 to 100 cm were primarily for single-row plots, and narrower spacings were for two-row or bordered plots. The seeding rate was about 10 seeds per meter of row for row spacings of <30 cm, 26 seeds per meter for spacings of 51 to 90 cm, and 33 seeds per meter for spacings of 91 to 100 cm.

Competition between soybean genotypes in adjacent plots can bias yield test results. The extent of the bias depends on the characteristics of the genotypes being evaluated, the spacing between single-hill plots, the number of rows in a plot, and the spacing between rows within and among plots. For genotypes of maturity groups IV and earlier, intergenotypic competition can be avoided in hill plots at a spacing of 90 cm or greater (Shannon et al., 1971). In row plots, the effect of intergenotypic competition increases as row spacing between plots is nar-
Table 14-10  Percentage of Private and Public Soybean Breeders that Utilize Particular Numbers of Locations and Replications for the First and Second Years of Yield Evaluation of Experimental Lines

<table>
<thead>
<tr>
<th>Replications</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>&gt;5</th>
</tr>
</thead>
<tbody>
<tr>
<td>First Year</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>16</td>
<td>2</td>
<td>10</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>14</td>
<td>33</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second year</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>14</td>
<td>18</td>
<td>8</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>6</td>
<td>16</td>
<td>10</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

*After the second year, an average of 11 locations are used each year with three or four replications at each location.

rowed and the maturity of genotypes becomes later (Gedge et al., 1977; Hartwig et al., 1951). The effect of intergenotypic competition can be avoided completely by planting three or more rows and harvesting only the center rows.

For row plots, the length of the planted row usually is longer than the harvested length. Plots may be trimmed to the harvested length early in the season or immediately before harvest. When plots are end-trimmed early, the plants next to the blank alley at the end of the plot will be more productive than those in the center of the plot. There is a positive relationship between the extent of yield inflation and the maturity of the genotype; therefore, yield comparisons must be made among genotypes of comparable maturity or yields must be adjusted for maturity (Wilcox, 1970; Boerma et al., 1976). By removing 60 to 75 cm from the end of plots at or near maturity, the effect of the alley can be eliminated. End-trimming at maturity usually is done by hand, and the large labor requirement frequently causes breeders to complete the task early in the season, particularly for the first and second years of yield testing.
Second and Later Years of Yield Evaluation

Superior lines from the first yield test are advanced to the second year of evaluation. The number of locations for the second yield test ranges from 2 to 10 among soybean breeders, with three locations being the most common (Table 14-10). Two or three replications per location are used by 94% of the breeders. With each additional year of testing, the number of lines decreases as inferior ones are discarded.

For the second year of testing, two-row unbordered plots or four-row bordered plots are used by the majority of breeders (Table 14-11). Plots generally are from 3.1 to 6 m long. A row spacing of about 75 cm is most common, with a seeding rate of about 25 seeds per meter of row.

For the third and later years of yield evaluation, the number of locations used by soybean breeders in 1985 ranged from 4 to 20, with an average of 11. There were three or four replications per location. Four-row plots were used by the majority of breeders (Table 14-11). The plot

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**Table 14-11** Percentage of Private and Public Soybean Breeders that Utilize Particular Plot Sizes for the First, Second, and Third Year of Yield Evaluation*

<table>
<thead>
<tr>
<th>Percentage by Year</th>
<th>First</th>
<th>Second</th>
<th>Third</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plot type</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hill</td>
<td>8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1-row</td>
<td>23</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2-row</td>
<td>40</td>
<td>26</td>
<td>4</td>
</tr>
<tr>
<td>3-row</td>
<td>4</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>4-row</td>
<td>25</td>
<td>64</td>
<td>82</td>
</tr>
<tr>
<td>&gt;4-row</td>
<td>&lt;1</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td><strong>Harvested row length</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;1–2 m</td>
<td>12</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2.1–3 m</td>
<td>17</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3.1–4 m</td>
<td>12</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>4.1–5 m</td>
<td>28</td>
<td>47</td>
<td>47</td>
</tr>
<tr>
<td>5.1–6 m</td>
<td>17</td>
<td>31</td>
<td>31</td>
</tr>
<tr>
<td>&gt;6 m</td>
<td>14</td>
<td>6</td>
<td>6</td>
</tr>
</tbody>
</table>

*Plot sizes for the fourth and later years of testing are similar to those for the third year.
length, row spacing, and seeding rate were similar to those of the second yield test.

At the final stages of testing, some private companies utilize strip tests to obtain information about the performance of a potential cultivar under commercial production conditions. A single strip of each of several experimental lines and current cultivars are planted and harvested by the farmer with commercial equipment. Although the entries on an individual farm are not replicated, the yield data accumulated from many farms can be useful. The strip tests also provide a company with information about the acceptability of the line by farmers.

Public breeders in Canada and the United States cooperate in a regional testing program, referred to as the Uniform Soybean Test, which is coordinated by the USDA. Through the Uniform Soybean Test, promising lines of each maturity group are tested by all states and provinces that have commercial hectarage of cultivars of that maturity. For example, experimental lines of maturity group II developed by breeders in five states were tested together at 21 locations in 12 provinces and states during 1985. This cooperative test permits public breeders to determine the performance of lines in many different environments. An experimental line usually is evaluated in the regional test for 3 years before a decision is made to release it as a cultivar. When a superior line is identified and released as a cultivar, the originating institution provides seed to other states and provinces that are interested in growing the cultivar commercially.

Private companies conduct their own tests throughout the region in which they intend to merchandise a potential cultivar. For companies with breeding stations at several locations, each station is responsible for developing its own lines and for conducting tests in a certain geographic area. Promising lines developed by one station are tested by the other stations, similar in principle to the Uniform Soybean Test.

**Experimental Designs for Field Tests**

The experimental designs used for yield evaluation include a systematic arrangement of entries in an unreplicated test, nonrandom arrangement for replicated tests, split-plot arrangements, randomized complete-block design, and lattice designs. The choice of an arrangement or design depends on the characters being evaluated, the number of lines, the desired precision of the data, and the extent of soil heterogeneity.

*Systematic Arrangement of Lines.* Lines can be compared with check cultivars in an unreplicated test that involves a systematic arrangement of
entries. The check cultivars are placed at regular intervals within the test site, and lines are compared with the cultivars nearest to them. An unreplicated test was used by 16% of soybean breeders in 1985 for the first yield test.

Randomization is used routinely in the evaluation of lines in a replicated test. An exception is in the first yield test, when lines may be visually evaluated for agronomic desirability and only selected lines are harvested. To facilitate summarization of data, particularly when it is collected immediately before harvest, the experimental lines and check cultivars are placed in the same position within each replication. For each entry in the test, visual ratings from different replications are recorded on the same page, which facilitates summarization of information for selection. In 1985, 4% of soybean breeders used a nonrandom arrangement of entries in replicated, single-hill plots for the first yield test.

Randomized Designs. For the first yield test, 70% of soybean breeders used the randomized complete-block design and 10% used lattice designs in 1985. Beginning with the second year of testing, 84% used the randomized complete-block, 12% used lattice designs, and 4% used a split-plot arrangement. Split-plot arrangements for genotype evaluation are used for specialized tests, such as evaluation of cultivars in different row spacings, at different plant populations, or with different herbicide treatments.

Equipment for Field Operations

The likelihood of finding a superior cultivar increases with the number of experimental lines that are evaluated effectively in a breeding program. Breeders are able to evaluate thousands of plots each year by the effective use of computers and specialized field equipment.

Computers are an essential part of any modern soybean breeding program. They are used to randomize entries in a replicated test, print the field books in which to record data, print labels to identify packets of seed for planting and tags for harvest, maintain records of the parentage and characteristics of lines, and summarize field data in a manner that can be readily evaluated by the breeder.

Field preparations for the planting of breeding nurseries are carried out with the same equipment and in the same manner as for commercial production of soybeans. Pre-emergence herbicides routinely are applied before planting.

Planting of field plots is carried out primarily with tractor-powered machines (Fig. 14-3). Only small plantings, such as crossing nurseries or
Figure 14-3  Machine used to plant plots of soybean. Seeds from one envelope are poured into a divider (A), which separates them into four portions. The seeds pass to a funnel (B), which holds them until the planter reaches the beginning of the plot. The funnel is lifted and the seeds drop into a unit (C) that distributes them along the row.

space-planted F₁ seed, are sown by hand or with a planter pushed by hand. Different tractor-powered planters are available, most of which involve modification of commercial units used by farmers. Many of the original planters were designed and built by breeders. Planters now can be purchased from manufacturers of specialized field-plot equipment.
Several planter features are important for successful seed placement, adequate seed distribution, and efficient and rapid planting:

1. A planting depth of 2.5 to 5.0 cm must be controlled accurately to ensure proper seedling emergence.

2. The planting cone mounted on each unit for seed dispersion in row plots should be designed with fins that drag the seed to the outlet (Fig. 14-3).

3. A seed divider permits the planting of multiple-row plots with one packet of seed, instead of one packet for every row (Fig. 14-3).

4. To avoid marking manually the beginning and end of plots before planting, an electronic or mechanical system is available for tripping the planting units at the beginning of each plot (Clark et al., 1978).

Specialized types of planting equipment have been developed for unique plot types. For planting hill plots, the cone used for row plots is replaced by a unit that permits all the seed to drop simultaneously into a hill. Row plots that are only 1 m long can be most effectively planted with a cone that has a much smaller diameter than the one used for longer plots. To space seeds of populations from which individual plants will be harvested, commercial air-driven planters have been modified to dispense seed at desired intervals ranging from closer than 3 cm apart to greater than 30 cm.

The harvest of soybeans is accomplished in different ways depending on the number of plants in a sample and the need to maintain genetic purity of the seed. For the harvest of individual plants, each one is pulled from the soil with the root intact. They may be threshed immediately in the field or, more commonly, are tied in a bundle, stored in a dry place, and threshed at a later date with a small portable machine. When groups of plants from a plot are to be threshed together, they can be cut at the soil surface by hand with a sickle or with a mower, and carried to a machine in the field for threshing. Machines are available that will clean out entirely between samples of plants to avoid seed mixtures. For large numbers of yield test plots, self-propelled plot combines are used. The seed may be weighed directly on the combine or may be bagged and transported to the laboratory for weighing. The combines are operated by one or two persons who can harvest more than 60 plots per hour. Although the combines clean out rapidly between plots, there commonly are a few seeds that carry over from one plot to the next. The amount of seed mixture generally is less than 0.2%, and the harvested seed commonly is used to plant additional plots the next season.

The seed harvested from different plots can vary in moisture percentage. For yield comparisons, the moisture percentage of the seed from
Figure 14-4  Electronic system for recording the weight of seed from a soybean plot. The weight of a bag of seed is transferred to a data collector (N) from an electronic scale (B). The scanner (C) reads and transfers to the data collector the plot and entry number that are coded on a label attached to the harvest tag (D). A printer (E) provides a copy of the plot number, entry number, and weight recorded by the data collector. The information is transferred from the data collector to a computer for analysis.

Each plot is determined electronically at the time of weighing or the seed samples are dried naturally or artificially to a common moisture level before weighing. The weight of seed can be recorded manually in a field book or can be electronically recorded and transferred to a computer (Fig. 14-4).

Data Analysis

The availability of computers permits the breeder to summarize data in several different ways. Despite this capability, the majority of breeders use a minimum of statistical procedures for selecting lines in a cultivar development program. The primary statistic used by the breeder for selection is the mean performance of experimental lines and check cultivars
over replications at individual environments and averaged across environments. The rank of lines for yield or other characters within a test facilitates selection. The second most common statistical procedure for data evaluation is a stability analysis, which was used by 29% of soybean breeders in 1985, particularly for selection among elite lines after several years of testing. A stability analysis provides a measure of the consistency of a line’s performance over different environments. A regression adjustment of yield for time of maturity was used by 10% of breeders in 1985 to facilitate comparisons among lines of different maturities.

PROCEDURES FOR SEED PRODUCTION

Methods for Producing and Maintaining Breeder Seed

The original source of seed of a cultivar from which all commercial production originates is referred to as breeder or basic seed. The soybean breeder who develops a new cultivar generally is responsible for producing the initial quantity of pure seed. The three procedures used to produce breeder seed differ in the purity of seed that is obtained, the amount of labor required, and the number of years involved.

The simplest procedure, and the one used by 27% of soybean breeders in 1985, commonly is referred to as mass selection. A sample of seed obtained from yield tests of a new cultivar is inspected for hilum color and seed coat luster, and off-type seeds are discarded. The selected sample is planted and off-type plants are discarded for flower color, pubescence color, pod color, maturity, height, and other traits. The remaining plants are harvested in bulk to obtain breeder seed. The advantage of the procedure is that it requires only one season and a minimal amount of labor. The ability to eliminate all off-types can be difficult, however, and the uniformity of the seeds and plants often is less than for procedures that involve progeny testing.

The procedure used by 46% of soybean breeders in 1985 involves one generation of progeny testing. Individual plants with the same characteristics are harvested from a new cultivar, and a progeny row is grown from each plant. Off-type rows are discarded and the remainder are harvested together as breeder seed. The procedure requires more labor than does mass selection, but a higher level of genetic purity can be obtained.

There are 24% of soybean breeders who use two seasons of progeny testing to obtain a high level of genetic purity. Individual plants with the same characteristics are progeny tested and off-type rows are discarded. Selected progeny rows are harvested individually and the seed from each is planted in separate plots the following season. Any plot containing
off-types in the second progeny test is discarded and the remaining plots are harvested together as breeder seed. The procedure requires more time and labor than mass selection or 1 season of progeny testing, but a higher level of genetic purity can be obtained.

A procedure used by 3% of soybean breeders involves the yield evaluation of individual progeny during breeder seed production. Individual plants are selected from a new cultivar and progeny rows are grown. Progeny rows with the same visual characteristics are harvested separately. Before the progeny rows are bulked, each is evaluated in a yield test. The purpose of the yield test is to identify progeny that have acceptable visual characteristics but are genetically inferior for yield or other agronomic traits. This procedure is the most labor intensive of all procedures, but it ensures the highest level of genetic purity for both qualitative and quantitative characteristics.

Breeder seed is used to produce the foundation class of certified seed. Foundation seed of a cultivar is produced annually; therefore, breeder seed also must be available each year. Several procedures are used to produce the breeder seed of an established cultivar. Mass selection was used by 83% of soybean breeders in 1985. A field is planted with breeder seed, part or all of it is carefully rogued for off-type plants, and the rogued portion is harvested as breeder seed. If an excessive number of off-type plants are identified in any year, individual plants are harvested and progeny tested to obtain a purer source of seed. Seventeen percent of soybean breeders store part of the original pure seed produced for a cultivar. Portions of the stored seed are used periodically to maintain the genetic purity and integrity of the cultivar.

Commercial Seed Production and Marketing

In the United States, soybean seed can be sold by a cultivar name or by a brand designation. A brand can be a single pure-line cultivar or a planned seed mixture or blend of cultivars. The same pure-line cultivar is sometimes sold by different companies under their own brand designation.

Pure-line Cultivars. The developer of a soybean cultivar in the United States can control the marketing of its seed by obtaining a plant variety protection certificate. A cultivar may be protected if it is unique from any other soybean cultivar that has been developed. Plant variety protection was used by 64% of private breeders and 56% of public breeders in 1985.

Seed certification provides assurance of the genetic purity of a cultivar. It has been widely used for the production and marketing of seed of public cultivars, but is not a common practice for private cultivars. Certif-
ication was used for 19% of the private cultivars sold in the United States during 1985.

Commercial seed production with or without certification is a stepwise process of seed multiplication beginning with breeder seed. For seed certification, breeder seed is used to plant the fields from which foundation seed is obtained. Foundation seed is planted to produce the registered class. The quantities of registered seed generally are adequate to merchandise limited amounts to farmers for commercial plantings. Registered seed is planted to produce the certified class for general distribution to farmers. Certified seed of soybeans generally cannot be used to produce additional generations of certified seed.

The genetic makeup of a pure-line cultivar of soybean remains unchanged during multiple generations of seed production, and farmers commonly use the seed harvested from one year to plant their crop the following season. Maintenance of the genetic purity of a cultivar requires precautions to avoid accidental cross-pollination and seed mixtures.

Soybean seed loses its germination if stored for more than a year without temperature and humidity control. The cost of storing large quantities of soybean seed cannot be justified economically, and little if any seed for commercial planting is carried over from one season to the next.

Planned Seed Mixtures or Blends. The marketing of seed mixtures or blends of soybean cultivars in the United States began during the 1960s. The primary reason for the initial use of blends was to permit companies to market a unique seed product. Companies used public cultivars to prepare blends that were sold as a brand without disclosing the names or proportions of the cultivars that were mixed.

Research on the performance of blends indicated that some combinations of cultivars yielded more than the average of the cultivars when grown individually in pure stand; however, the yield increase generally was less than 3% (Gedge et al., 1977). Studies also indicated that, on the average, blends were more consistent in performance across environments than pure-line cultivars; however, pure lines could be found that were as consistent as a blend (Walker and Fehr, 1978).

Blends are used to a limited extent as a means of providing protection against crop damage when the highest-yielding cultivar available to the farmer is susceptible to a sporadic pest or soil problem. By mixing the high-yielding susceptible cultivar with a lower-yielding resistant one, the farmer can achieve a higher yield with the blend than with the resistant cultivar when the problem does not occur, and will obtain production from the resistant plants when the problem is expressed. Only about 30% of a resistant cultivar is needed in a mixture to obtain adequate protection against a major yield loss (Trimble and Fehr, 1983).
Data on the amount of seed sold as blends is not available. In Iowa, where blends have been as widely used as in any state, 20% of the entries in the statewide test of public and private cultivars and brands for 1985 were blends (Mason et al., 1985).

Blends are produced in two principal ways for commercial sale. The primary way is to produce seed of each component cultivar separately, mix the seed during or after it is cleaned, and sell the mixture to the farmer. The second way is to grow the blend for one or more generations of seed increase before it is sold. The second procedure is not widely used because the percentage of each component in the blend can change during seed multiplication due to intergenotypic competition (Gedge et al., 1977). For the same reason, farmers are not encouraged to save and replant blended seed.

FUTURE PROSPECTS FOR CULTIVAR DEVELOPMENT

Hybrid Cultivars

One of the most common questions asked of a soybean breeder is when will hybrid cultivars be available for commercial use. The majority of soybean breeders do not consider hybrid cultivars to be a viable economic possibility with our current technology and are not conducting any research to develop them. The primary barrier to commercial use of hybrid cultivars is the lack of an economical method of seed production. Pollen transfer by insects from male-fertile to male-sterile, female-fertile plants is limited, even when the fertile and sterile plants are grown adjacent to each other in a mixture. It would be difficult to obtain enough hybrid soybean seed from 1 ha to plant 20 ha of commercial production, whereas enough hybrid maize seed is produced on 1 ha to plant at least 150 commercial hectares. The low ratio of commercial hectares to seed production hectares would make the cost of hybrid soybean seed much more expensive than could be justified by the increase in yield due to heterosis, which averages about 13% (Weber et al., 1970).

Hybrid cultivars would be feasible if hybrid plants could be induced to produce seeds by apomixis. Apomixis results in seed production from mitotic division of maternal cells in the pistil, resulting in progeny that are genetically identical to the maternal plant. This would permit a hybrid soybean plant to be reproduced without concern for insect pollination. It may be possible with techniques developed through research in molecular biology to identify and transfer genes controlling apomixis from other species into soybean. Many years of research would be required to determine the feasibility of apomixis as a tool for commercial production of hybrid cultivars.
Doubled Haploids

It would be desirable to have the capability of obtaining homozygous lines by doubling the chromosome number of haploid segregates from a population. The technique could reduce the length of time for cultivar development and eliminate the progeny testing of plants to differentiate homozygous and heterozygous individuals. At present, no reliable method has been found to routinely produce haploid soybean plants. Future research in molecular and cellular biology may identify the barriers that are present and methods to overcome them.

Selection in Cell Culture

Research in other crop species has shown that selection among cells or tissue in culture is possible for some traits, and that individuals derived from somatic tissue in culture may have unique genetic variability. This source of genetic variability is beginning to be explored in soybean. Techniques for routine regeneration of plants from tissue culture are being developed. It is possible that selection and evaluation for pathogen resistance, herbicide reaction, and other factors in tissue culture may be possible in the future. Such techniques may identify new sources of genetic variability and increase the efficiency of cultivar development by minimizing the need for field evaluations.

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