CHAPTER SEVENTEEN

Maximizing Genetic Improvement

The objective of plant breeding is to improve genetically the performance of cultivars of a species in the most efficient manner possible. Development of an efficient strategy includes selection of an appropriate breeding method and judicious allocation of resources for population development and genotype selection. This requires a comparison of the amount of genetic improvement that can be achieved using alternative breeding methods with the resources that are available.

Plant breeders constantly are trying to identify new procedures that will improve the efficiency of cultivar development. As new ideas are suggested, the breeder must have some criteria for comparing current procedures with the efficiency of genetic improvement using the new system.

The efficiency of alternative breeding strategies can be evaluated as the amount of genetic improvement or gain realized per year. The purpose of this chapter is to review the mathematical equations that are used to compute genetic gain and utilize the equations to illustrate the principles involved in identifying an appropriate breeding strategy.

The concept of genetic gain is based on the change in the mean performance of a population that is realized with each cycle of selection. One cycle includes the establishment of a segregating population, development of genotypes for evaluation, evaluation of the genotypes, selection of the superior genotypes, and utilization of the selected genotypes as parents to form a new population for the next cycle of selection. The length of time required to complete a cycle can vary considerably; therefore, for comparison of alternative strategies, genetic gain is expressed on a yearly basis. The breeder seeks to identify the strategy that utilizes available resources to provide the greatest gain per year.

MATHEMATICAL CONSIDERATIONS

Genetic gain per cycle (G_c) was expressed by Lush (1945) as

$$G_c = h^2D$$

where h^2 is heritability in the narrow sense and D is the selection differential. Genetic gain per year (G_y) is obtained by dividing the genetic gain per cycle by the number of years (y) required to complete a cycle of selection: $G_y = G_c/y$ (Eberhart, 1972).

Heritability is the proportion of the total phenotypic variation expressed among genotypes that can be attributed to genetic differences among them. Narrow-sense heritability is the proportion of total variation attributable to additive genetic variance in the population

$$h^2 = \frac{\sigma_A^2}{\sigma_{ph}^2}$$

where σ_A^2 is the additive genetic variance and σ_{ph}^2 is the phenotypic variance.

The selection differential is the difference between the mean of genotypes selected from a population and the overall mean of the population from which they were selected. If the mean of selected genotypes is 2500 kg/ha and the mean of the population is 2200 kg/ha, the selection differential is 2500 − 2200 = 300 kg/ha. The selection differential can be expressed as

$$D = k\,\sigma_{ph}$$

where k is the selection differential expressed in standard units and σ_{ph} is the square root of the phenotypic variance.

The equation for genetic gain per cycle can be modified by substitutions for h^2 and D:

$$G_c = h^2D = \frac{\sigma_A^2}{\sigma_{ph}^2}\,k\,\sigma_{ph} = \frac{k\,\sigma_A^2}{\sigma_{ph}}$$

Phenotypic Variance

The phenotypic variance includes experimental error (σ_e^2), genotype × environment interaction (σ_{ge}^2), and the genotypic variance (σ_g^2). The square root of the phenotypic variance used in the estimation of genetic gain can be expressed as

$$\sigma_{ph} = \sqrt{\frac{\sigma_e^2}{rt} + \frac{\sigma_{ge}^2}{t} + \sigma_g^2}$$

where r is the number of replications and t is the number of environments in which the genotypes were tested. Genotype refers to an individual plant or its

progeny that is being evaluated. Environment designates locations or years in which tests are conducted.

The experimental error can be subdivided into the variance among plants within a plot (σ_w^2) and the variance from plot to plot (σ^2), expressed as

$$\sigma_e^2 = \frac{\sigma_w^2}{n} + \sigma^2$$

where n is the number of plants within a plot. The variance among plants within a plot includes variation due to environmental effects and genetic differences among plants. Environmental effects include variation in soil fertility, moisture, or any other factors that would cause genetically identical plants to perform differently. Genetic differences among plants in a plot are due to segregation within the progeny of a line or family. The variance within a plot can be subdivided into the environmental variance (σ_u^2) and the genotypic variance (σ_{wg}^2), expressed as

$$\sigma_w^2 = \sigma_u^2 + \sigma_{wg}^2$$

The equation for genetic gain per year can be summarized by substitutions for σ_{ph}.

$$G_s = \frac{k\sigma_A^2}{y\sigma_{ph}}$$

$$G_s = \frac{k\sigma_A^2}{y\sqrt{(\sigma_e^2/rt) + (\sigma_{ge}^2/t) + \sigma_g^2}}$$

$$G_s = \frac{k\sigma_A^2}{y\sqrt{\{[(\sigma_w^2/n) + \sigma^2]/rt\} + (\sigma_{ge}^2/t) + \sigma_g^2}}$$

$$G_s = \frac{k\sigma_A^2}{y\sqrt{(\{[(\sigma_u^2 + \sigma_{wg}^2)/n] + \sigma^2\}/rt) + (\sigma_{ge}^2/t) + \sigma_g^2}}$$

Parental Control

The amount of additive genetic variance is influenced by the parental control exercised in the recombination of selected individuals or families. Parental control in recurrent selection is the relationship between the plant or seed used for identifying superior genotypes (selection unit) and the plant or seed used for recombination (recombination unit).

Parental control is $^1/_2$ when the selection unit is the same as the recombination unit and only the female parent is selected, i.e., when selected female plants are pollinated by both selected and unselected males in the population. Parental

control is $^1/_2$ for recurrent phenotypic selection and modified ear-to-row selection when selection is done after pollination (Table 17-1).

Parental control is 1 when the selection unit is the same as the recombination unit and both parents are selected. Parental control is 1 for recurrent phenotypic selection before pollination, for half-sib family selection when remnant half-sib seed is used for recombination, for full-sib family selection, and for selfed families (Table 17-1).

Parental control is 2 when the selection and recombination units are not the same. Parental control is 2 for half-sib family selection when selfed seed or clones of selected genotypes are used for recombination (Table 17-1). The selection unit is half-sib seed, but the recombination unit is selfed seed or clones

Table 17-1 Methods of Intrapopulation Improvement (Improvement in Population per se)

Method	Seasons per Cycle	Parental Control (c)	σ_g^{2*}		$\sigma_{wg}^{2}\dagger$	
			σ_A^2	σ_D^2	σ_A^2	σ_D^2
Recurrent phenotype selection:						
One parent selected after flowering	1	$\frac{1}{2}$	1	1	0	0
Both parents slected before flowering	1	1	1	1	0	0
Selfed parents (clones) selected, recombined	2	1	1	1	0	0
Half-sib selection:						
Modified ear-to-row						
One parent selected	1	$\frac{1}{2}$	$\frac{1}{4}$	0	$\frac{3}{4}$	1
Both parents selected	2	1	$\frac{1}{4}$	0	$\frac{3}{4}$	1
Population as tester						
Recombination with remnant half-sib seed	2	1	$\frac{1}{4}$	0	$\frac{3}{4}$	1
Recombination with selfed seed (clones)	3	2	$\frac{1}{4}$	0	$\frac{3}{4}$	1
Inbred tester (recombined selfed seed)	3	2	$\frac{1}{4}$–$\frac{1}{2}$	0–$\frac{1}{4}$	$\frac{3}{4}$–$\frac{1}{2}$	1–$\frac{3}{4}$
Full sib	2	1	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$
Selfed progeny:						
$S_{0:1}$ lines	3	1	1	$\frac{1}{4}$‡	$\frac{1}{2}$	$\frac{1}{2}$‡
$S_{1:2}$ lines	4	1	$\frac{3}{2}$	$\frac{3}{16}$	$\frac{1}{4}$	$\frac{1}{4}$
$S_{2:3}$ lines	5	1	$\frac{7}{4}$	$\frac{7}{64}$	$\frac{1}{8}$	$\frac{1}{8}$

*σ_g^2 = Genetic variability among individuals or families.

†σ_{wg}^2 = Genetic variability within families.

‡Coefficients for σ_D^2 that are presented apply when there are two alleles at a locus, each with a frequency of 0.5 (Empig et al., 1972).

Table 17-2 Expected Genetic Gain per Cycle of Selection Under Different Intrapopulation Schemes with Noninbred Parents

Method	Expected Gain per Cycle (G_c)*
Recurrent phenotypic selection:	
Without gridding into subblocks	$\dfrac{k\ c\ \sigma_A^2}{\sqrt{\sigma_u^2 + \sigma^2 + \sigma_{AE}^2 + \sigma_{DE}^2 + \sigma_A^2 + \sigma_D^2}}$
With gridding into subblocks	$\dfrac{k\ c\ \sigma_A^2}{\sqrt{\sigma_u^2 + \sigma_{AE}^2 + \sigma_{DE}^2 + \sigma_A^2 + \sigma_D^2}}$
Modified ear-to-row†	$\dfrac{k\ c\ \frac{1}{4}\sigma_A^2}{\sqrt{\dfrac{\sigma_e^2}{rt} + \dfrac{\frac{1}{4}\sigma_{AE}^2}{t} + \frac{1}{4}\sigma_A^2}}$
Half-sib	$\dfrac{k\ c\ \frac{1}{4}\sigma_A^2}{\sqrt{\dfrac{\sigma_e^2}{rt} + \dfrac{\frac{1}{4}\sigma_{AE}^2}{t} + \frac{1}{4}\sigma_A^2}}$
Full-sib	$\dfrac{k\ c\ \frac{1}{2}\sigma_A^2}{\sqrt{\dfrac{\sigma_e^2}{rt} + \dfrac{(\frac{1}{2}\sigma_{AE}^2 + \frac{1}{4}\sigma_{DE}^2)}{t} + \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2}}$
Selfed progeny, $S_{0:1}$ lines‡	$\dfrac{k\ c\ \sigma_A^{2\prime}}{\sqrt{\dfrac{\sigma_e^2}{rt} + \dfrac{(\sigma_{AE}^{2\prime} + \frac{1}{4}\sigma_{DE}^2)}{t} + \sigma_A^{2\prime} + \frac{1}{4}\sigma_D^2}}$

*σ_u^2 is the within-plot environmental variance, σ_{AE}^2 and σ_{DE}^2 are the additive by environmental and dominance by environmental interactions, σ_A^2 and σ_D^2 are the additive and dominance variance, k is the standardized selection differential, n is the number of plants per plot, r is the number of replications per environment, t is the number of environments.

†If phenotypic selection within rows is practiced, an additional component should be added: $k\ c\ \frac{3}{4}\sigma_A^2/\sqrt{\sigma_u^2 + \frac{3}{4}\sigma_{AE}^2 + \sigma_{DE}^2 + \frac{3}{4}\sigma_A^2 + \sigma_D^2}$.

Source: Adapted from Sprague and Eberhart, 1977.

‡$\sigma_A^{2\prime}$ = additive genetic variance plus a component that is mainly a function of degree of dominance (Empig et al., 1972).

of selected genotypes. The extent of parental control, c, can be incorporated into the numerator of the prediction equation (Table 17-2).

OBTAINING VALUES FOR THE PREDICTION EQUATION

Each of the variables in the prediction equation can be estimated from appropriate experimental studies or can be extrapolated from available data. For certain applications, hypothetical values can be used to compare alternative strategies.

Genetic Variability

The phenotypic variance in the denominator contains the total genetic variance (σ_g^2) expressed among genotypes, including additive, dominance, and epistatic variance (Tables 17-2 and 17-3). The numerator of the prediction equation contains only the additive genetic variance (σ_A^2), because this is the only portion of the genetic variance that is transmitted from the parent to its offspring. Dominance and epistatic variance can be important for the performance of an individual and contribute to the total genetic variance. They are not included in the numerator because intralocus and interlocus interactions from the parent are not transmitted to its offspring (Chap. 6).

The genetic variance (σ_g^2) expressed among genotypes can be readily estimated from an analysis of variance of random genotypes evaluated in multiple environments. Breeders routinely evaluate random lines for quantitative characters, such as yield, in their first replicated test of lines from a population. Estimates of σ_g^2 obtained from evaluation of one breeding method sometimes are extrapolated to obtain estimates for other methods. For example, an estimate of σ_g^2 from an evaluation of half-sib families can be used to estimate σ_g^2 for $S_{0:1}$ or full-sib families. The estimates of σ_g^2 can be biased by the relative importance of additive and dominance variance for the types of families being studied. The variance among half-sib families is additive, whereas the variance among $S_{0:1}$ or full-sib families includes dominance (Table 17-4). The estimate of σ_g^2 equals σ_A^2 from an evaluation of half-sib families and provides a good estimate of σ_A^2 for other types of families. It may not, however, provide a good estimate of σ_g^2 for full-sib and $S_{0:1}$ families if dominance is important. For example, assume

Table 17-3 Expected Genetic Gain per Cycle of Selection for Population Cross Under Different Interpopulation Selection Schemes with Noninbred Parents*

Method	Expected gain (G_c)
Reciprocal half-sib selection†	$\dfrac{k\,c\,\frac{1}{4}\sigma^2_{A(1)}}{\sqrt{(\sigma^2_{e(1)}/rt) + (\frac{1}{4}\sigma^2_{AE(1)}/t) + \frac{1}{4}\sigma^2_{A(1)}}} + \dfrac{k\,c\,\frac{1}{4}\sigma^2_{A(2)}}{\sqrt{(\sigma^2_{e(2)}/rt) + (\frac{1}{4}\sigma^2_{AE(2)}/t) + \frac{1}{4}\sigma^2_{A(2)}}}$
Reciprocal full-sib selection	$\dfrac{k\,c\,\frac{1}{2}\sigma^2_A}{\sqrt{(\sigma^2_e/rt) + [(\frac{1}{2}\sigma^2_{AE}' + \frac{1}{4}\sigma^2_{DE}')/t] + \frac{1}{2}\sigma^2_A' + \frac{1}{4}\sigma^2_D'}}$

*Variance components are defined for the population cross and differ from the corresponding components within a population (Table 17-2) because the gene frequencies in both populations are involved.

†See Table 17-2 for definitions of the symbols in the equations. (1) refers to components in population 1 and (2) to components in population 2.

Source: Adapted from Sprague and Eberhart, 1977.

Table 17-4 Genetic Variability Among Families with Inbreeding (F) When Epistasis Is Negligible ($F = 0$ for F_2 or S_0 Plants)

Half-sib	$\frac{1 + F}{4}\sigma_A^2$
Full-sib	$\frac{1 + F}{2}\sigma_A^2 + \left(\frac{1 + F}{2}\right)^2\sigma_D^2$
Selfed	$(1 + F)\sigma_A^{2\prime} + \frac{1}{4}(1 - F)(1 + F)\sigma_D^2$

*σ_A^2 = additive genetic variance; σ_D^2 = dominance variance; $\sigma_A^{2\prime}$ = additive genetic variance plus a component that is mainly a function of degree of dominance (Empig et al., 1972).

that the true value of σ_A^2 is 40 and σ_D^2 is 10 in a population. If half-sib families are used to estimate σ_g^2, the value obtained would be $\frac{1}{4}\sigma_A = 10$. By doubling the value to estimate σ_g^2 for full-sib families, the value obtained would be 20. However, the true value for σ_g^2 among full-sib families would be $\frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2 = \frac{1}{2}(40) + \frac{1}{4}(10) = 22.5$. The estimated value based on half-sib families (20) would underestimate the true σ_g^2 (22.5) for full-sib families. The possible underestimation or overestimation of variance components should be kept in mind when extrapolating values from one type of family to another. Obtaining estimates of σ_A^2, σ_D^2, and σ_I^2 requires the use of mating designs such as the Design I and Design II that are not commonly used in cultivar development programs (Chap. 6).

The amount of genetic variance expressed among individuals or families in a population is dependent on the amount of inbreeding of the parents (Table 17-4). "Parent" refers to the plant that is selfed (S_1, S_2, S_n), crossed to another plant (full-sib family), or crossed to a tester (half-sib family). F_2 and S_o plants are assumed to have an inbreeding coefficient of $F = 0$; therefore, the inbreeding among F_2 and S_o-derived lines also is $F = 0$. A description of the derivation of inbreeding coefficients is provided by Falconer (1981).

Selection Intensity (k)

Selection intensity is the percentage of plants or families tested that are selected for recombination. The selection intensity used in the prediction equation is expressed in standard units, k. Derivation of k values is described by Falconer (1981). Values of k increase as the percentage of genotypes selected for recombination decrease (Table 17-5).

Years (y)

The number of years per cycle of selection is the time interval from the evaluation of lines of one cycle until the evaluation of lines in the next cycle. The value

Table 17-5 *k* Values for Different Selection Intensities

Selection Intensity (%)*	*k*
1	2.64
2	2.42
5	2.06
10	1.75
15	1.55
20	1.40

*Selection intensity = (number of lines selected/number of lines tested) × 100.

of *y* includes any delay between the selection of parents and their subsequent mating. If parents are selected in November but are not planted for crossing until May, the number of years per cycle may be increased.

When there is only one season per year during which lines can be evaluated, *y* will be a whole number. If lines are available for testing in December but cannot be evaluated until May, the early availability of test material in December will not reduce years per cycle. The value of *y* can only be a fraction when there is more than one season per year available for the evaluation of lines.

Plot-to-Plot (σ^2) and Within-Plot Variance (σ^2_w)

Plot-to-plot variation (σ^2) and within-plot variability (σ^2_w) are determined in sampling experiments in which two or more individual plants are measured in replicated plots. The experimental procedure commonly is referred to as subsampling. Plants can be sampled in all or some of the plots.

The derivation of σ^2 and σ^2_w can be illustrated with an experiment designed to evaluate seed weight in soybeans. Seed weight (grams per 100 seeds) of 60 $F_{4:5}$ lines of soybeans was measured on three plants in two replications in two environments. The analysis of variance based on samples taken from all plots is presented in Table 17-6. The value for σ^2_w was 2.20 and for σ^2 was 0.35.

An estimate of σ^2_w and σ^2 can be obtained by sampling plants for only part of the lines and obtaining a plot mean for all other lines. Two analyses of variance are needed, one for plants within plots and one based on plot means. To compare this procedure with sampling of all plots, single plants for 20 of 60 $F_{4:5}$ lines in the seed weight experiment were used to represent a partial sampling of lines (Table 17-7). The analysis of variance for the 20 lines provided an estimate of σ^2_w (2.16) that was similar to the value obtained by sampling all lines (2.20). To obtain an estimate of σ^2 with partial subsampling of the lines, an analysis of variance for all 60 lines based on plot means (mean of the three individual

Table 17-6 Analysis of Variance for Seed Weight (g/100 Seeds) of 60 $F_{4:5}$ Lines of Soybeans Tested in Two Replications at Two Environments, with Three Individual Plants Evaluated From All Plots

Source	Degrees of Freedom	Mean Squares		Expected Mean Squares*
Total	719	7.68		
Environments (E)	1	281.28		
Replications/E (R/E)	2	27.45		
Lines (L)	59	59.33	M_1	$\sigma_w^2 + n\sigma^2 + nr\sigma_{ge}^2 + nrt\sigma_g^2$
$E \times L$	59	4.00	M_2	$\sigma_w^2 + n\sigma^2 + nr\sigma_{ge}^2$
$(R/E) \times L$	118	3.25	M_3	$\sigma_w^2 + n\sigma^2$
Plants/plots	480	2.20	M_4	σ_w^2

*n = plants per plot = 3; r = replications = 2; t = environments = 2.

$\sigma_w^2 = M_4 = 2.20$.

$\sigma^2 = (M_3 - M_4)/n = [(\sigma_w^2 + n\sigma^2) - \sigma_w^2]/n = (3.25 - 2.20)/3 = 0.35$.

$\sigma_e^2 = M_3/n = (\sigma_w^2 + n\sigma^2)/n = 3.25/3 = 1.08$.

$\sigma_{ge}^2 = (M_2 - M_3)/nr = [(\sigma_w^2 + n\sigma^2 + nr\sigma_{ge}^2) - (\sigma_w^2 + n\sigma^2)]/nr = (4.00 - 3.25)/6 = 0.125$.

$\sigma_g^2 = (M_1 - M_2)/nrt = [(\sigma_w^2 + n\sigma^2 + nrt_{ge}^2) - (\sigma_w^2 + n\sigma^2 + nr\sigma_{ge}^2) + nrt\,\sigma_g^2)]/nrt = (59.33 - 4.00)/12 = 4.61$.

$\sigma_{ph}^2 = M_1/nrt = (\sigma_w^2 + n\sigma^2 + nr\sigma_{ge}^2 + nrt\sigma_g^2)/nrt = (\sigma_w^2/nrt) + (\sigma^2/rt) + (\sigma_{ge}^2/t) + \sigma_g^2 = 59.33/(2 \times 3 \times 2) = 4.94$.

Source: Frank, 1980.

Table 17-7 Analysis of Variance for Seed Weight (g/100 Seeds) of Random Sample of 20 of 60 $F_{4:5}$ Lines Analyzed in Table 17-6 (Three Plants Were Evaluated for All Plots of 20 Lines)

Source	Degrees of Freedom	Mean Squares		Expected Mean Squares*
Total	239	5.58		
Environments (E)	1	50.47		
Replications/E (R/E)	2	7.81		
Lines (L)	19	40.08	M_1	$\sigma_w^2 + n\sigma^2 + nr\sigma_{ge}^2 + nrt\sigma_g^2$
E × L	19	3.53	M_2	$\sigma_w^2 + n\sigma^2 + nr\sigma_{ge}^2$
(R/E)x L	38	2.29	M_3	$\sigma_w^2 + n\sigma^2$
Plants/plot	160	2.16	M_4	σ_w^2

*n = plants per plot = 3; r = replications = 2; t = environments = 2.

Source: Frank, 1980.

Table 17-8 Analysis of Variance for Seed Weight (g/100 Seeds) of 60 $F_{4:5}$ Lines of Soybeans Tested in Two Replications at Two Environments

Source	Degrees of Freedom	Mean Squares		Expected Mean Squares*
Total	239	6.23		
Environments (E)	1	94.50		
Replications/E (R/E)	2	9.37		
Lines (L)	59	19.84	M_1	$\sigma_e^2 + r\sigma_{ge}^2 + rt\sigma_g^2$
$E \times L$	59	1.33	M_2	$\sigma_e^2 + r\sigma_{ge}^2$
$(R/E) \times L$	118	1.08	M_3	σ_e^2

*$\sigma_e^2 = M_3 = 1.08$.

$\sigma_{ge}^2 = (M_2 - M_3)/r = [(\sigma_e^2 + r\sigma_{ge}^2) - \sigma_e^2]/r = (1.33 - 1.08)/2 = 0.125$.

$\sigma_g^2 = (M_1 - M_2)/rt = [(\sigma_e^2 + r\sigma_{ge}^2 + rt\sigma_g^2) - (\sigma_e^2 + r\sigma_{ge}^2)]/rt = (19.84 - 1.33)/4 = 4.63$.

Source: Frank, 1980.

plants per plot) was used to obtain an estimate of σ_e^2 (Table 17-8). The estimate of σ^2 was derived from the relationship $\sigma_e^2 = \left(\frac{\sigma_w^2}{n}\right) + \sigma^2$.

$$\sigma^2 = \sigma_e^2 - \left(\frac{\sigma_w^2}{n}\right) = 1.08 - (2.16/3) = 0.36$$

The value of 0.36 for σ^2 was similar to the 0.35 obtained from sampling plants of all the lines in all of the plots (Table 17-6).

Environmental Variance Among Plants Within Plots (σ_u^2)

The environmental variance among plants in a plot is equivalent to the plant-to-plant variation in a homogeneous inbred line or cultivar. Estimates of σ_u^2 are needed whenever selection is based on a single plant, such as for recurrent phenotypic selection or modified ear-to-row selection that includes selection within rows (Table 17-2).

Genetic Variation Among Plants Within Plots (σ_{wg}^2)

Variation among plants within plots can be due to genetic segregation. The amount of genetic variability within lines for different selection methods is presented in Table 17-1. Effective selection among plants within lines can increase the amount of genetic gain per cycle under appropriate conditions.

Genotype × Environment Interaction (σ_{ge}^2)

The genotype × environment interaction reflects the failure of genotypes to perform the same relative to each other across environments. Change in the rank

among genotypes across environments limits the effectiveness of selection of superior genotypes for recombination and reduces genetic gain per year. Methods of estimating σ^2_{ge} are described in Chap. 18.

COMPARISON OF ALTERNATIVE BREEDING METHODS

The prediction of genetic gain is useful for comparing the potential effectiveness of alternative breeding methods. Recurrent selection in an open-pollinated population of a diploid annual species, such as maize or sunflower, can be conducted by methods including recurrent phenotypic selection, half-sib selection with the population as tester, full-sib selection, and $S_{0:1}$ line selection. The breeder of a self-pollinated species would consider F_2, F_3, or more advanced generations of selfing, unless genetic male sterility was available.

The method with the greatest genetic gain for the character under selection and the resources available can be estimated by computing the predicted genetic gain. The predicted genetic gain for the methods being compared may not be realized, but the relative values for different methods provide a useful estimate of their relative effectiveness. Assume that the predicted genetic gain in yield is 100 kg/ha with $S_{0:1}$ lines and 80 kg/ha with full-sib families. The actual genetic gain realized may be only 50 percent of that predicted for both methods, but the actual gain from $S_{0:1}$ line evaluation would be expected to be greater than from full-sib selection.

There are six steps in the selection of an appropriate breeding method.

Step 1: List the alternatives available for the species being considered. The choices depend on the type of cultivar that will be developed for commercial use and the feasibility of making the required matings. A self-pollinated species that utilizes pure-line cultivars and a species that utilizes hybrid cultivars can both effectively employ $S_{0:1}$ line selection. Methods that involve tests of combining ability, such as half-sib selection with an inbred tester or reciprocal half-sib selection, would not be practical for development of improved pure-line cultivars, but do have potential for development of lines of cross-pollinated species for use in hybrid cultivars.

Step 2: Define the resources available. Resources include the number of seasons that can be utilized each year for population development, inbreeding, family development, and testing. The number of seasons available per year can markedly influence the relative genetic gain per year among methods.

The resources allocated for testing should be kept the same when comparing methods. The number of lines tested and the number of replications and environments used for evaluation are resources that can significantly influence predicted gain per year and that should be kept similar among the methods to be compared.

Step 3: Obtain estimates for the variables in the prediction equation. Methods for obtaining the estimates were discussed previously.

Step 4: Compute predicted genetic gain for the various alternatives. This step will be illustrated with a comparison of seven methods that could be used to improve a population of maize.

The following variance components will be used to compute predicted genetic gain per cycle and per year for yield (q/ha). Assume 14 plants per plot, two replications, and three environments for all replicated tests. The selection intensity will be 10 percent ($k = 1.75$) for all methods.

$\sigma_A^2 = 68$ = additive genetic variance

$\sigma_D^2 = 42$ = dominance variance

$\sigma_{AE}^2 = 70$ = additive × environment interaction

$\sigma_{DE}^2 = 42$ = dominance × environment interaction

$\sigma_e^2 = 96$ = experimental error

$\sigma^2 = 46$ = plot-to-plot environmental variance

$\sigma_w^2 = 700$ = within-plot variance

Predicted genetic gain per year will be computed for four situations.

1. One season per year in which yield evaluation and all breeding operations can be conducted. This situation will be referred to as one season.
2. Two seasons per year can be used for yield evaluation and all other breeding operations. This situation occurs in some tropical areas and will be referred to as two similar seasons.
3. Two seasons per year, one of which can be used for yield evaluation and all other breeding operations and the second of which can be used for all breeding operations, except yield evaluation. Such a situation exists when yield evaluations are possible in a temperate climate, but not in a greenhouse or a winter nursery located in the tropics. The situation will be referred to as two nonsimilar seasons.
4. Three seasons per year, in which the first can be used for yield evaluation and all other breeding operations and the second and third can be used for all breeding operations, except yield evaluation. This situation occurs when greenhouses or winter nurseries are used, and will be referred to as three seasons.

Method 1: Recurrent phenotypic selection with control of only the female parent.

$$G_c = \frac{k\, c\sigma_A^2}{\sqrt{\sigma_w^2 + \sigma_{AE}^2 + \sigma_{DE}^2 + \sigma_A^2 + \sigma_D^2}} = \frac{(1.75)(0.5)(68)}{\sqrt{700 + 70 + 42 + 68 + 42}} = 2.0$$

One season, 1 year/cycle

$G_y = G_c/y = 2.0/1 = 2.0$

Two similar seasons, 0.5 year/cycle

$G_y = G_c/y = 2.0/0.5 = 4.0$

Two nonsimilar seasons, 1 year/cycle

$G_y = G_c/y = 2.0/1 = 2.0$

Three seasons, 1 year/cycle

$G_y = G_c/y = 2.0/1 = 2.0$

Method 2: Modified ear-to-row selection with control of only the female parent and no plant selection within rows.

$$G_c = \frac{k\, c\, \frac{1}{4}\, \sigma_A^2}{\sqrt{(\sigma_e^2/rt + (\frac{1}{4}\sigma_{AE}^2/t) + \frac{1}{4}\sigma_A^2}} = \frac{(1.75)(0.5)(0.25)(68)}{\sqrt{[96/(2 \times 3)] + [(0.25)70/3] + (0.25)68}} = 2.4$$

One season, 1 year/cycle

$G_y = G_c/y = 2.4/1 = 2.4$

Two similar seasons, 0.5 year/cycle

$G_y = G_c/y = 2.4/0.5 = 4.8$

Two nonsimilar seasons, 1 year/cycle

$G_y = G_c/y = 2.4/1 = 2.4$

Three seasons, 1 year/cycle

$G_y = G_c/y = 2.4/1 = 2.4$

Method 3: Half-sib selection, population as tester, recombine remnant half-sib seed.

$$G_c = \frac{k\, c\, \frac{1}{4}\, \sigma_A^2}{\sqrt{(\sigma_e^2/rt) + (\frac{1}{4}\sigma_{AE}^2/t) + \frac{1}{4}\sigma_A^2}} = \frac{(1.75)(1)\,(0.25)(68)}{\sqrt{[96/(2 \times 3)] + [(0.25)70/3] + (0.25)68}} = 4.8$$

One season, 2 years/cycle

$G_y = G_c/y = 4.8/2 = 2.4$

Two similar seasons, 1 year/cycle

$G_y = G_c/y = 4.8/1 = 4.8$

Two nonsimilar seasons, 1 year/cycle

Method 4: Half-sib selection, population as tester, recombine selfed seed.

$$G_c = \frac{k\ c\ \frac{1}{4}\ \sigma_A^2}{\sqrt{(\sigma_e^2/rt) + (\frac{1}{4}\sigma_{AE}^2/t) + \frac{1}{4}\sigma_A^2}} =$$

$$\frac{1.75\ (2)\ (0.25)\ 68}{\sqrt{[96/(2 \times 3)] + [(0.25)70/3] + (0.25)68}} = 9.6$$

One season, 3 years/cycle

$G_y = G_c/y = 9.6/3 = 3.2$

Two similar seasons, 1.5 years/cycle

$G_y = G_c/y = 9.6/1.5 = 6.4$

Two nonsimilar seasons, 2 years/cycle

$G_y = G_c/y = 9.6/2 = 4.8$

Three seasons, 1 year/cycle

$G_y = G_c/y = 9.6/1 = 9.6$

Method 5: Full-sib selection.

$$G_c = \frac{k\ c\ \frac{1}{2}\ \sigma_A^2}{\sqrt{(\sigma_e^2/rt) + (\frac{1}{2}\sigma_{AE}^2/t) + (\frac{1}{4}\sigma_{DE}^2/t) + \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2}}$$

$$G_c = \frac{1.75\ (1)\ (0.5)\ 68}{\sqrt{[96/(2 \times 3)] + [(0.5)70/3] + [(0.25)42/3] + (0.5)68 + (0.25)42}} = 6.8$$

One season, 2 years/cycle

$G_y = G_c/y = 6.8/2 = 3.4$

Two similar seasons, 1 year/cycle

$G_y = G_c/y = 6.8/1 = 6.8$

Two nonsimilar seasons, 1 year/cycle

$G_y = G_c/y = 6.8/1 = 6.8$

Three seasons, 1 year/cycle

$G_y = G_c/y = 6.8/1 = 6.8$

Method 6: $S_{0:1}$ line evaluation, one recombination between cycles.

$$G_c = \frac{k\ c\ \sigma_A^2}{\sqrt{(\sigma_e^2/rt) + (\sigma_{AE}^2/t) + (\frac{1}{4}\sigma_{DE}^2/t) + \sigma_A^2 + \frac{1}{4}\sigma_D^2}}$$

$$G_c = \frac{1.75\ (1)\ 68}{\sqrt{[96/(2 \times 3)] + 70/3 + [(0.25)42/3] + 68 + (0.25)42}} = 10.8$$

One season, 3 years/cycle

$G_y = G_c/y = 10.8/3 = 3.6$

Two similar seasons, 1.5 years/cycle

$G_y = G_c/y = 10.8/1.5 = 7.2$

Two nonsimilar seasons, 2 years/cycle

$G_y = G_c/y = 10.8/2 = 5.4$

Three seasons, 1 year/cycle

$G_y = G_c/y = 10.8/1 = 10.8$

Method 7: $S_{1:4}$ line evaluation, three recombinations between cycles

$$G_c = \frac{k\,c\,(1 + F)\,\sigma_A^2}{\sqrt{(\sigma_e^2/rt) + [(1 + F)\sigma_{AE}^2/t] + [\frac{1}{4}(1 - F)(1 + F)\sigma_{DE}^2/t] + (1 + F)\sigma_A^2 + \frac{1}{4}(1 - F)(1 + F)\sigma_D^2}}$$

$$Gc = \frac{1.75\ (1)\ (1 + 0.875)\ 68}{\sqrt{(96/2 \times 3)} \sqrt{+ [(1 + 0.875)70/3]} \sqrt{+ [\frac{1}{4}(1 - 0.875)(1 + 0.875)42/3]} \sqrt{+ (1 + 0.875)68} \sqrt{+ \frac{1}{4}(1 - 0.875)(1 + 0.875)42} = 16.2}$$

One season, 8 years/cycle

$G_y = G_c/y = 16.2/8 = 2.0$

Two similar seasons, 4 years/cycle

$G_y = G_c/y = 16.2/4 = 4.0$

Two nonsimilar seasons, 4 years/cycle

$G_y = G_c/y = 16.2/4 = 4.0$

Three seasons, 3 years/cycle

$G_y = G_c/y = 16.2/3 = 5.4$

Step 5: Summarize computed values in a table. The values in Table 17-9 illustrate several important principles concerning the selection of a breeding method and resource allocation.

The method with the greatest gain is not the same for all situations. In our example, $S_{0:1}$ line evaluation gave the greatest gain for one season (3.6), for two similar seasons (7.2), and for three seasons (10.8), but full-sib selection gave the greatest gain for two nonsimilar seasons (6.8).

The value of utilizing more than one season per year varies with the method used and the breeding operations that can be conducted in the additional environments. In our example, one season per year had as much predicted gain as two nonsimilar seasons for recurrent phenotypic selection and modified ear-to-row selection. On the other hand, two nonsimilar seasons provided greater gain than one season for all other methods.

Table 17-9 Predicted Genetic Gain (q/ha) from Selection by Seven Methods

Method*	Gain per Cycle	Gain per Year			
		One Season	Two Similar Seasons	Two Nonsimilar Seasons	Three Seasons
1	2.0	2.0	4.0	2.0	2.0
2	2.4	2.4	4.8	2.4	2.4
3	4.8	2.4	4.8	4.8	4.8
4	9.6	3.2	6.4	4.8	9.6
5	6.8	3.4	6.8	6.8	6.8
6	10.8	3.6	7.2	5.4	10.8
7	16.2	2.0	4.0	4.0	5.4

*1, recurrent phenotypic selection; 2, modified ear-to-row; 3, half-sib, recombine remnant half-sib seed; 4, half-sib, recombine selfed seed; 5, full-sib; 6, $S_{0:1}$ line; 7, $S_{3:4}$ line.

Step 6: Determine the cost per unit of genetic gain. In our example, full-sib selection and $S_{0:1}$ line evaluation gave similar genetic gain when two similar seasons were available (Table 17-9). The cost of conducting full-sib selection includes a yield test and recombination every two seasons. The cost of genetic gain obtained from $S_{0:1}$ line evaluation, however, involves a yield test and recombination every three seasons. The

Table 17-10 Comparison of Time Required for Cultivar Development by Three Methods of Inbreeding in Self-Pollinated Species.

Year	Season	Method of Inbreeding		
		Pedigree	Early-Generation	Single-Seed Descent
1	Summer	F_2 plants selected	F_2 plants selected	F_2 plants grown
	Winter 1*			F_3 plants grown
	Winter 2			F_4 plants grown
2	Summer	$F_{2:3}$ lines selected	$F_{2:3}$ lines selected	F_5 plants selected
3	Summer	$F_{3:4}$ lines selected	Yield test of $F_{2:4}$ lines	$F_{5:6}$ lines selected
	Winter 1		F_5 plants selected	
4	Summer	$F_{4:5}$ lines selected	$F_{5:6}$ lines selected	First yield test of $F_{5:7}$ lines
5	Summer	$F_{5:6}$ lines selected	First yield test of $F_{5:7}$ lines	Second yield test
6	Summer	First yield test of $F_{5:7}$ lines	Second yield test	Third yield test

*The two winter seasons can be used for self-pollination but not for character evaluation.

cost of genetic gain obtained from $S_{0:1}$ line evaluation should be less than for full-sib selection because expensive yield tests are required less frequently.

ENHANCEMENT OF GENETIC GAIN PER YEAR IN PLANT BREEDING

The equations for predicted genetic gain were developed for populations in which some form of recurrent selection is conducted. They also are valuable, however, for comparing the efficiency of selection with conventional breeding methods (Fehr, 1976, 1978). Each of the methods available for developing cultivars has advantages and disadvantages, and the breeder must decide which method is most effective for the resources available. Cultivar development is referred to as a numbers game because the chance of finding a superior cultivar is improved by increasing the number of genotypes that are tested each year. It also can be called a time game because the amount of improvement that can be made over a period of time is influenced by the number of years required for cultivar development. For example, the production of multiple generations per year has become a common practice in the breeding of cultivars of all species. Breeding methods must be adopted that fit well into a multiple-generation system each year (Table 17-10). Pedigree selection was a popular method for inbreeding a population when only one crop was grown each year. It has been replaced in many breeding programs by single-seed descent because of the increased use of greenhouses and winter nurseries, in which visual selection is not possible.

The modern plant breeder must be willing to evaluate new resources that become available and adopt those that increase genetic gain per year at an acceptable cost. In the future, new technology will be developed in plant physiology, molecular genetics, plant pathology, and other disciplines that will aid the breeder. The concepts developed for predicting genetic gain per year in recurrent selection are valuable for evaluating the use of new technology for cultivar development programs. Each of the variables or combinations of variables in the prediction equation can be manipulated.

Years per Cycle

The production of multiple generations of a crop each year has become a fundamental part of modern plant-breeding programs. For breeders in temperate climates, one generation is grown in the field in the area for which new cultivars are being developed. Additional generations, referred to as off-season generations, are grown during the remaining months of the year in a greenhouse or growth chamber, at locations of lower latitude in the same hemisphere, or at a location in the opposite hemisphere where the crop is being grown commercially. Such off-season environments may be used for hybridization, inbreeding, and

seed increase. For some traits they also can be used for evaluation and selection. The extent to which these operations can be conducted depends on the facilities that are available, the crop that is grown, and the character that is under selection. The choice of an appropriate off-season environment is an important decision, particularly for breeders in temperate climates who must choose from the various options that are available. Each of the options have positive and negative aspects that must be considered in making the choice.

Greenhouses and Growth Chambers. Greenhouses and growth chambers are particularly well suited to crops that require limited space for each plant and to breeding operations that require relatively few plants to accomplish. Hybridization is the most common breeding operation conducted in a greenhouse. Hybrid plants also may be grown and generations may be advanced, primarily by single-seed descent. The controlled conditions are regularly used for the evaluation of pest resistance. Seed increase generally is not possible in the limited space available.

A greenhouse or growth chamber has several advantages as an off-season environment. The plants are exposed to less environmental fluctuation and fewer production hazards than occur in the field. The control of environmental conditions can be especially desirable for hybridization and screening for pest resistance. When a greenhouse is at the location where a breeder is stationed, the time, expense, and risk of transporting plant material from one location to another are eliminated. Legal restrictions on the movement of plant material are avoided. There is no possibility that pests will be accidentally moved from one location to another. The growing plants can be observed and manipulated by the breeder and staff without any travel.

Greenhouses and growth chambers have several disadvantages that limit their desirability as an off-season environment. The cost of building and maintaining the facilities can be substantial. Space is limited. Large breeding programs for certain crops require more than a hectare to grow all of their genetic material. The cost of building and operating a greenhouse or growth chamber of comparable size is prohibitive. The breeder must either limit the genetic material that is grown or use an alternative off-season environment.

Growing conditions in a greenhouse or growth chamber can cause atypical growth, even though field conditions for plant growth are duplicated as closely as possible. For example, soybean plants generally grow excessively tall in the greenhouse, which prevents adequate assessment of most agronomic characters. Certain genotypes of soybean will not consistently produce seed when planted in the greenhouse during some winter months.

Location at Low Latitudes. Locations where plants can be grown in the field throughout the year are commonly used as off-season environments. They often are referred to as winter nurseries, although some breeders use a location throughout the year. The locations commonly used by breeders in temperate climates of the United States include Florida, Arizona, Hawaii, Puerto Rico, and Mexico.

Off-season environments in low latitudes are popular because more space is available than in a greenhouse or growth chamber. They are used extensively for hybridization to form breeding populations. In crops such as maize, testcross seed may be produced to evaluate individuals for combining ability. Off-season environments in low latitudes are widely used for inbreeding of both self- and cross-pollinated species. Selection may be practiced for certain characters. Seed increases are made of genotypes for further evaluation or for production of commercial quantities of a cultivar.

The disadvantages of a location at a low latitude depend on its location and the quality of personnel available to conduct the work. It is relatively easy to underestimate the amount of work required to conduct a quality off-season nursery. It often is more difficult to grow a crop in an off-season environment at a low latitude than in a more temperate climate.

Any nursery located some distance from a breeder's station has certain inherent disadvantages. The breeder must move to the location to supervise the breeding operations or must hire qualified persons to do so. Travel to the location can be time-consuming and expensive.

Locations at low latitudes may be subject to production hazards not normally encountered in a more temperate climate. Undesirably low temperatures may occur sporadically at some locations. Crops have been destroyed by frost in Florida. Soybean hybridization is not possible during the winter when temperatures are consistently below 16°C. This has prevented hybridization during certain winter months in Florida and Puerto Rico. Pests commonly are found at a low latitude that are not of importance in a temperate climate. It may be necessary to spray a crop regularly with fungicides and insecticides to obtain satisfactory plant growth and seed quality. High temperatures and humidity during seed maturation in tropical environments can drastically reduce seed quality. The germination of soybean seed declines rapidly if seed is not harvested immediately after it is mature. This necessitates more timely harvest than is necessary in the cooler climates of high latitudes. Additional hazards that have been encountered include salt injury, bird damage, and hurricanes.

The movement of seed to locations in lower latitudes may be subject to quarantine regulations. The regulations are established to prevent the movement of pests from one area to another. They may require that seed or other plant parts be treated in a special manner before shipment, which may be time-consuming and expensive. The plant material must be inspected by authorized individuals, a process that can delay its shipment. Soybeans grown in Puerto Rico were subject to quarantine regulations after soybean rust, a disease not found in the United States, was discovered on the island. The regulation during the early 1980s required that seed shipped from the location be free of any debris, treated with a special fungicide, and inspected.

Locations in an Opposite Hemisphere. Some crops are grown commercially during different months in the northern and southern hemispheres. This makes it possible to grow two generations each year under conditions that are favorable

for many breeding operations. In the development of cultivars for the northern United States, breeding material is grown in the northern hemisphere May through October and in the southern hemisphere November through April. Conversely, breeding programs in the southern hemisphere can use the northern hemisphere as an off-season environment.

Breeding material grown in an off-season environment in another hemisphere is subject to the same conditions as the commercial crop. Land area suitable for growing the breeding material generally is not a limiting factor. Hybridization and inbreeding can be readily accomplished and evaluation of important characteristics frequently is possible. Large-scale seed increase that involves commercial equipment can be accomplished in both hemispheres.

Despite the advantages of growing breeding material in another hemisphere, this is not done as commonly as using locations in lower latitudes, for several reasons. It generally is more time-consuming and expensive for travel and shipment of plant material to another hemisphere. The time interval from harvest in one hemisphere to planting in another is often short, which can complicate preparation of material for planting. Only one crop can be grown in the off-season. At locations of low latitude, plants have a shorter generation length, which often makes it possible to obtain two generations during the off-season. Soybeans adapted to the northern United States have a 90-day generation length when grown at low latitudes; therefore, two generations can be grown during the off-season from November through May. When grown in South America, only one generation of soybean can be obtained from November through May.

Production of breeding material in another hemisphere has some of the same restraints as the use of a location at a low latitude. Proper supervision of the breeding material may be difficult. The pests common to one hemisphere may not be the same as those in another. The movement of seed may be subject to quarantine regulations.

Selection Intensity (k)

The chance of obtaining a superior segregate increases as the number of lines tested is augmented. The selection intensity associated with population improvement can increase as the number of lines tested increases.

The relationship between selection intensity and number of lines tested can be illustrated by assuming that 20 superior lines from those evaluated will be used as parents for recombination. If 100 lines are tested, the selection intensity will be 20 percent and the value of $k = 1.40$ (Table 17-5). With doubling of the number of lines tested, the selection intensity decreases to 10 percent and k increases to 1.75. Evaluation of 400 lines would result in a selection intensity of 5 percent and a k of 2.06.

Another way to illustrate the importance of number of lines tested is to assume that the selection intensity will be a constant value of 10 percent. If 100 lines are tested, the top 10 percent of the lines (10) can be used as parents. With

200 lines, the top 10 percent represents 20 parents. Use of a greater number of lines as parents may reduce the amount of inbreeding in the population (Chap. 8).

Plant breeders are constantly seeking ways to increase the number of genotypes evaluated without sacrificing the quality of the testing program. The use of computers and the mechanization of field research have increased markedly the number of genotypes that can be effectively evaluated compared with use of hand labor. These aspects of cultivar development are discussed in Chap. 19.

Parental Control (c)

Parental control can be increased from $^1/_2$ to 1 by selecting a character before female plants have been pollinated by both selected and unselected males (Table 17-1). Control of both female and male parents is preferred because the alleles passed to the next generation are from selected individuals. If only the female is controlled, only one-half of the alleles (those of the egg cells) are selected. The other half of the alleles are from unselected pollen that does not contribute to genetic gain.

The parental control can be doubled from 1 to 2 by using selfed seed or clones to recombine individuals with superior half-sib progeny, instead of using remnant half-sib seed. The alleles present in selfed seed are from only the selected individuals. The alleles in half-sib seed include alleles from the selected individual and alleles from the population when the seed was developed. Parental control of all alleles (selfed seed) is superior to parental control of only one-half of the alleles (remnant half-sib seed).

Genetic Variability (σ_A^2, σ_g^2)

The amount of additive genetic variance in a population is influenced by the (a) genetic diversity of the parents, (b) amount of inbreeding before individuals or families are evaluated, (c) type of individual or family evaluated, and (d) number of generations of recombination between cycles of selection.

Genetic Diversity of the Parents. Genetic diversity is influenced by the number of parents used to develop a population and their ancestry. In a diploid species, a single-cross population can possess only two alternative alleles at a locus, one from each parent. Each additional parent used to develop a population (three-way, double-cross) has the potential of contributing additional alleles and, therefore, additional genetic variability. This principle is especially important when developing a population in which to conduct recurrent selection for multiple cycles. The potential progress to be realized by selection is limited by the number of alleles in the base population (cycle 0). The greater the number of parents

used for recombination each cycle of selection, the greater the potential genetic variability available for selection.

Genetic diversity is a function of the ancestry of the parents. The alleles contributed by two parents with different ancestry are more likely to vary than those contributed by parents with a common background. Breeders consider the ancestry of parents when developing populations. In a recurrent selection program, the decrease in genetic variability that occurs through inbreeding can be reduced by selecting lines as parents each cycle that trace to different crosses or S_0 plants.

There is considerable debate about the value of using exotic parents for increasing the genetic diversity of a population. "Exotic" refers to any germplasm that is not highly productive in the area for which new cultivars are being developed. There is a possibility that exotic parents can contribute alleles for improvement that are not available in adapted germplasm. It also is highly likely that they will contribute many undesirable alleles to the population. As a result, an increase in genetic variability of a population developed with exotic parents generally is associated with a reduction in the population mean compared with the mean of a population developed from adapted parents. An increase in genetic variability that is due to the presence of more inferior segregates is of no value to the breeder for the selection of improved cultivars. For that reason, most breeders do not use exotic parents for populations from which they expect to obtain new cultivars in a short time. Exotic parents are sometimes used for populations that are intended for improvement by a long-term recurrent selection program.

Amount of Inbreeding Before Evaluation. Additive genetic variability is associated with the frequency of homozygous loci in a population of individuals. The effect of inbreeding (F) on the amount of σ_A^2 is described by the equations in Table 17-4. For example, the amount of σ_A^2 among selfed lines is determined by the equation $(1 + F)\,\sigma_A^2$. An F_2 population ($F = 0$) has σ_A^2 and a population of doubled haploids with no heterozygous loci ($F = 1$) has $2\sigma_A^2$. The effect of inbreeding on genetic gain is illustrated in Table 17-9. The gain per cycle for $S_{0:1}$ lines ($F = 0$) was 10.8 and for $S_{3:4}$ lines ($F = 0.875$) was 16.2.

The value of increasing σ_A^2 by inbreeding must include consideration of the time required to obtain more genotypes with a greater level of homozygosity. The importance of this principle is illustrated in Table 17-9 by the comparison of genetic gain utilizing $S_{0:1}$ or $S_{3:4}$ lines. Although genetic gain per cycle was greater with $S_{3:4}$ lines, the additional time (y) required per cycle caused the genetic gain per year to be greater for $S_{0:1}$ lines, regardless of the number of seasons per year. This principle is an important consideration in selecting an appropriate breeding strategy for cultivar improvement.

Number of Generations of Recombination Between Cycles. The amount of genetic variability in a population is associated with the number of opportunities

for recombination among members of the population. Recombination between a pair of linked genes requires that both loci be heterozygous. A crossover in the genotype $\frac{AB}{ab}$ will produce *Ab* and *aB* gametes, but a crossover in the genotypes $\frac{AB}{AB}$ or $\frac{ab}{ab}$ cannot produce the *Ab* or *aB* combinations. The probability of recombination between linked genes increases with each generation of random mating in a population. This principle is considered in determining the number of generations of intercrossing to be conducted in developing a population.

The number of generations of intercrossing can influence the genetic gain per year by increasing the number of seasons required per cycle. The types of seasons available to the breeder will be an important consideration in selecting the number of generations of intercrossing. By conducting intercrossing in a season not suited for character evaluation, the breeder may be able to add a generation of intercrossing without influencing genetic gain per year.

Within-Plot Variability (σ^2_u, σ^2_{wg}, σ^2_w)

The variability within plots (σ^2_w) is determined by environmental effects (σ^2_u) and genetic segregation (σ^2_{wg}). Their impact is a function of the number of plants that are averaged together to determine a plot mean. This can be expressed as: $\frac{\sigma^2_w}{n} = (\sigma^2_u + \sigma^2_{wg})/n$, where n is the number of plants per plot.

The value of n is 1 for individual plant selection in a population, such as for recurrent phenotypic selection. In line or family evaluation, the value of n is a function of the size of plot and the plant population used, expressed as plants per plot. The effect of increasing plants per plot can be estimated by holding σ^2_w constant and varying the value of n. For example, assume that σ^2_w equals 700.

n	$\sqrt{\sigma^2_w/n}$
1	26.5
2	18.7
3	15.3
4	13.2
5	11.8
10	8.4
20	5.9
30	4.8
40	4.2
50	3.7
60	3.4
100	2.6

The value of adding an additional plant per plot decreased as n increases. The difference between 1 and 10 plants per plot in our example was $26.5 - 8.4 = 18.1$ units. The difference between 60 and 100 plants per plot was only 0.8 units. The breeder can estimate the most efficient number of plants per plot for each of the characters to be evaluated.

Plot-to-Plot Variation (σ^2)

The estimate of σ^2 is associated with environmental differences from one plot to another. Its magnitude is influenced by the uniformity of plots within a replication. In field experiments, σ^2 is likely to increase as the amount of land area in a replication increases, because of soil heterogeneity. Possibilities for reduction of σ^2 are decreasing the number of plots per replication and decreasing the size of plots per entry.

For selection of single plants, plot-to-plot variation is not a factor if the plants within a plot or grid instead of plants in different plots are compared. For example, modified ear-to-row selection involves single plant selection within superior half-sib families. The equation for predicting genetic gain for within-plot selection does not include the plot-to-plot component (σ) in the denominator because selection is within a plot, not among plots (Table 17-2). For recurrent phenotypic selection, the plot-to-plot variance does not occur in the denominator when a population is subdivided into blocks in a grid (Table 17-2).

Experimental Error (σ_e^2)

A reduction in σ_u^2, σ_{wg}^2, and σ^2 causes a decrease in σ_e^2, because $\sigma_e^2 = (\sigma_u^2 + \sigma_{wg}^2)/n + \sigma^2$. The impact of σ_e^2 also is influenced by the number of replications (r) and environments (t) of testing, as reflected by the expression σ_e^2/rt. The relative importance of number of replications versus number of environments will be discussed in the next section.

Genotype × Environment Interaction (σ_{ge}^2)

The impact of the genotype × environment interaction can be reduced by evaluating the lines in multiple environments (t), expressed as σ_{ge}^2/t. The breeder must choose the relationship between number of replications and environments that will give the most genetic gain with the least cost.

The effect of different numbers of replications and environments can be estimated from the expression $(\sigma_e^2/rt) + (\sigma_{ge}^2/t)$. Increasing the number of environments has a greater effect than increasing replications, because t is a divisor for both σ_e^2 and σ_{ge}^2.

If the number of plots that could be grown was fixed, cost was not a factor,

and σ^2_{ge} was important, the greatest genetic gain would be realized by growing one replication at many environments. In practice, this generally is not possible, because the cost of using different environments is more than the cost of growing additional replications at an environment. Each additional replication or environment that is used will decrease the phenotypic variance, but the amount will decrease as r and t increase. The principle is the same as increasing the number of plants to reduce σ^2_w.

Indirect Selection

The efficiency of cultivar development would be improved by the identification before hybridization of parents that would produce superior progeny, of characters that would permit efficient indirect selection for yield and other desirable economic traits, and of characters that influence performance in particular environments. Consider a breeding program whose objective is to develop a cultivar with improved yield potential for an environment with high temperature and low moisture. The breeder would like to know if there are characters other than yield per se that can be used to select parents and identify the segregates that will have the desired performance. These might include leaf size and orientation, plant height, branching or tillering, length of the seed-filling period, root depth, photosynthetic rate, leaf temperature, and transpiration rate.

A quantitative character such as yield is the culmination of plant processes that begin with germination of a seed or the initiation of a vegetative propagule. The physiological processes may have a direct or indirect influence on the final yield that is obtained. Selection for variation among genotypes for physiological characters may enhance selection for yield per se.

The character of ultimate importance in a selection program can be referred to as the primary character (Falconer, 1981). The characters that influence the primary character are referred to as secondary characters. For example, yield may be considered a primary character and photosynthetic rate, length of the seed-filling period, and root depth as secondary characters.

The potential value of indirect selection for a secondary character that is quantitatively inherited was summarized by Falconer (1981) in the equation

$$\frac{CR_x}{R_x} = r_A \frac{i_y h_y}{i_x h_x}$$

where CR_x = amount of improvement in primary character obtained by indirect selection for secondary character

R_x = amount of improvement obtained by direct selection for primary character

r_A = genetic correlation between primary character (x) and secondary character (y)

i_y = selection intensity for secondary character

i_x = selection intensity for primary character

h_y = square root of narrow-sense heritability of secondary character

h_x = square root of narrow-sense heritability of primary character

The equation defines the factors that must be considered for effective indirect selection of morphological and physiological traits for improvement of characters of economic importance.

Genetic Correlation Between Characters. Selection for morphological or physiological characters is of no value if the characters' performance is not correlated with performance of the primary character. Determination of the genetic correlation between characters requires adequate evaluation of appropriate genetic material over a number of environments. Some studies on trait associations have utilized isolines, i.e., lines that are genetically similar except for genes controlling a character of interest (Qualset et al., 1965). It may be possible to create variability within a cultivar for a trait through physical rather than genetic manipulations. Pendleton and colleagues (1968) mechanically manipulated leaf angle in maize plants to investigate the relationship of this character with yield. The disadvantage of using physical manipulation is that the behavior of altered plants may not be representative of normal plant behavior.

Because isolines are often not available and physical manipulation is often not possible or desirable, initial experiments on trait associations commonly involve the evaluation of selected cultivars or experimental lines that differ for the traits of interest. A sufficient number of lines differing in the traits may be available or may be derived through hybridization and selection. The phenotypic correlations obtained from such experiments provide a preliminary indication of the association between characters. Definitive evaluation of the genetic correlation requires the use of random genotypes from segregating populations to obtain the necessary variance and covariance estimates.

Selection Intensity. Selection intensity is a ratio of the number of genotypes selected divided by the number of genotypes tested. The number of genotypes that can be evaluated for a secondary character compared with a primary character has an important influence on the effectiveness of indirect selection. Secondary characters that are more expensive and difficult to measure than the primary character are less likely to be useful than those that increase the number of genotypes that can be evaluated.

Heritability. The effectiveness of indirect selection is enhanced when the secondary character has a higher heritability than that of the primary character. The higher heritability may be associated with greater additive genetic variability, less environmental variation, less genotype × environment interaction, or lower nonadditive genetic variability. The effectiveness of indirect selection is based

Table 17-11 Plant Characters with Potential Value in Ideotype Breeding for Barley, Oat, Rice, and Wheat

Leaf Characters	Culm Characters	Inflorescence Characters
Leaf size	Number of culms	Awn length
Leaf angle	Survival of culms	Awn number
Number of leaves	Diameter of culms	Kernel number
Duration of leaves	Number of ears	Kernel weight
Thickness of leaves	Vascular bundles	
Specific leaf weight		
Stomatal frequency		
Type of Canopy	**Root Characters**	**Other**
Height of plants	Volume	Photoperiod response
Harvest index	Depth	Length of growth stages
Angle of ear		

Source: Rasmusson and Gengenbach, 1983.

on the square root of the heritabilities. As a result, the heritability of the secondary character must be considerably larger than that of the primary character to increase the ratio substantially. A heritability of 0.9 for the secondary character and 0.45 for the primary character represents a ratio of 2, but the ratio of the square root of the heritabilities is only 1.4.

Ideotype Breeding

Some plant breeders believe that a model plant type can be specified for a crop species in terms of morphological and physiological characters. This model plant type is commonly referred to as an ideotype. Rasmusson and Gengenbach (1983) have presented a list of plant characters with potential value in ideotype breeding (Table 17-11). The ideotype developed for a crop species should be subject to change as new information on plant physiology becomes available or as new methods of crop production are adopted.

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CHAPTER EIGHTEEN

Genotype × Environment Interaction

Cultivars of a crop are grown under a wide range of conditions. They are exposed to different soil types, soil fertility levels, moisture levels, temperatures, and cultural practices. All of the variables encountered in producing a crop can be described collectively as the environment.

When cultivars are compared in different environments, their performance relative to each other may not be the same. One cultivar may have the highest yield in some environments and a second cultivar may excel in others. Changes in the relative performance of genotypes across different environments are referred to as genotype × environment interaction.

TYPES OF INTERACTIONS

Every factor that is a part of the environment of a plant has the potential to cause differential performance that is associated with genotype × environment interaction. Environmental variables can be classified as either predictable or unpredictable factors (Allard and Bradshaw, 1964). Predictable factors are those that occur in a systematic manner or are under human control, such as soil type, planting date, row spacing, plant population, and rates of nutrient application. Unpredictable factors are those that fluctuate inconsistently, including rainfall, temperature, and relative humidity.

Predictable factors can be evaluated individually and collectively for their interaction with genotypes. Studies have been made of genotype × soil type, genotype × row spacing, genotype × planting date, and genotype × plant population interactions.

Unpredictable factors contribute to the interactions of genotypes with loca-

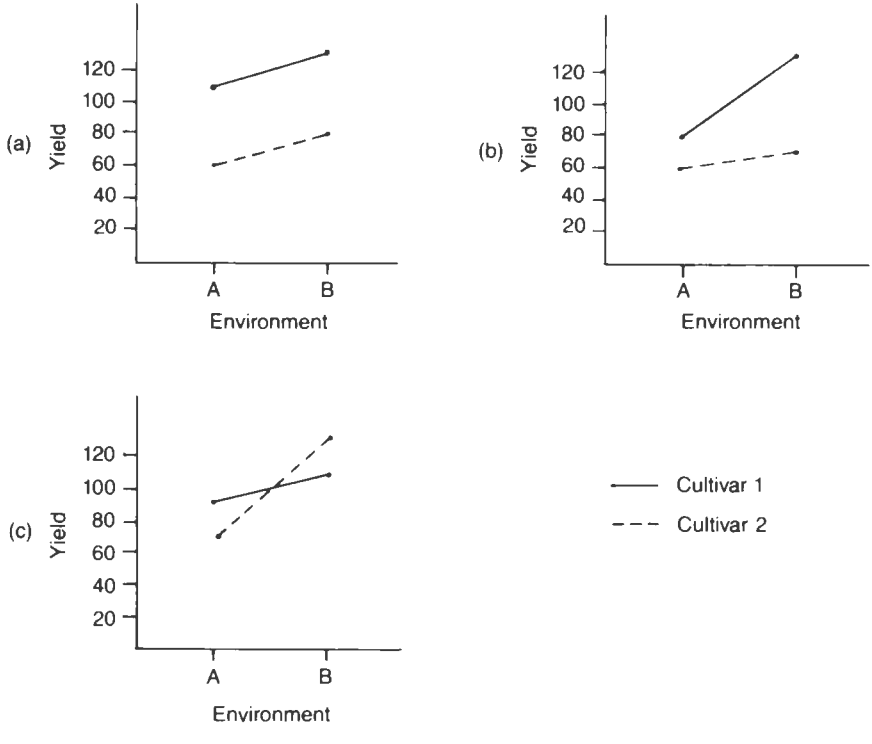
tions and years. Genotype × location, genotype × year, and genotype × location × year interactions have been evaluated in many crop species.

The relative performance of genotypes across environments determines the importance of an interaction. There is no genotype × environment interaction when the relative performance among genotypes remains constant across environments. In Fig. 18-1a, cultivar 1 has the same yield superiority over cultivar 2 across two environments. No genotype × environment interaction is present because the yield differential between the cultivars is 50 units in both environments.

Genotype × environment interactions can occur in two ways.

1. The difference among genotypes can vary without any alteration in their rank. In Fig. 18-1b, a genotype × environment interaction is present because cultivar 1 yields 20 units more than cultivar 2 in environment A and 50 units more in environment B.

Figure 18-1 The relative performance of two cultivars in two environments. (a) No genotype × environment interaction is present. (b) Genotype × environment interaction is present but does not alter genotypic ranking. (c) Genotype × environment interaction is present and alters genotypic ranking.



2. The rank among cultivars may change across environments. In Fig. 18-1c, cultivar 1 is more productive in environment A, but cultivar 2 is more productive in environment B. The change in rank between cultivars results in a genotype × environment interaction. The most important genotype × environment interaction for the plant breeder is one caused by changes in rank among genotypes.

Genotype × environment interactions are of interest to breeders for several reasons.

1. The need to develop cultivars for specific purposes is determined by an understanding of the interaction of genotypes with predictable environmental factors. Unique cultivars may be required for different row spacings, soil types, or planting dates.
2. The potential need for unique cultivars in different geographical areas requires an understanding of genotype × location interactions. The importance of this interaction can determine if division of a large geographical area into subareas is needed for testing new genotypes and obtaining data on cultivar performance for crop producers.
3. Effective allocation of resources for testing genotypes across locations and years is based on the relative importance of genotype × location, genotype × year, and genotype × location × year interactions.
4. The response of genotypes to variable productivity levels among environments provides an understanding of their stability of performance. An understanding of the environmental stability of genotypes helps in determination of their suitability for the fluctuations in growing conditions that are likely to be encountered.

ASSESSMENT OF GENOTYPE × ENVIRONMENT INTERACTIONS

Determining the importance of genotype × environment interactions requires appropriate experimental procedures. An understanding of the steps involved in the design, conduct, analysis, and interpretation of such an experiment can be useful.

Experimental Design

Objective. Planning of any experiment begins with a statement of the concept or hypothesis to be evaluated, sometimes phrased in the form of a question. Is the relative performance among genotypes different when they are grown with use of conservation tillage versus conventional tillage? Do genotypes respond differently to high and low rates of inorganic nitrogen fertilization? The breeder may have a hypothesis about the answer to the question on the basis of practical

experience. It is critical that the hypothesis should not be regarded as fact, an attitude that can bias the interpretation of the experimental results.

Genotypes for Evaluation. The genotypes chosen for an assessment of possible interactions are an important consideration in design of the experiment. Some analyses of genotype × environment interaction are not based on an experiment specifically designed for that purpose, particularly the assessment of the importance of interactions with locations and years. Instead, breeders utilize data from cultivars and experimental lines that have been evaluated over locations and years as a part of normal testing programs. The main disadvantage of such an approach is that the cultivars and experimental lines may not be a random sample of available genotypes. Estimates of genotype × environment interaction obtained with selected genotypes may be higher or lower than those that would be obtained with random individuals. The preferred procedure is to use a random sample of genotypes from those that are available for testing.

Tests must be conducted at two or more locations and years to obtain estimates of genotype × location, genotype × year, and genotype × location × year interactions (Table 18-1). The locations of testing generally are those routinely used by the breeder. Locations may be considered a fixed effect when they are not randomly chosen from all possible sites in an area. Some breeders consider them a random effect, however, because the breeder has no control over the climatic conditions that will occur at a location in any year. For the same reason, years of testing are considered random effects.

At least two replications are needed in each location and year to obtain an estimate of experimental error with which to test the significance of the interactions of interest. Any additional replications will provide a more reliable estimate of the experimental error.

An example of an experiment designed to assess genotype × environment interaction was a study of tobacco in North Carolina by Jones and colleagues (1960) (Table 18-2). They used seven cultivars that had been included in the official state trials for tobacco at five locations during each of 3 years. The seven cultivars differed for agronomic characteristics, disease resistance, and chemical composition. The five locations were those used routinely for tobacco evaluation. They had been selected to represent the tobacco production area of North Carolina and differed in soil type, elevation, and climatic conditions. The cultivars, years, and locations studied were considered representative samples of each variable and were designated as random effects.

Data Analysis

Data analysis includes the calculation of mean values, determination of the statistical significance of the sources of variation, and calculation of estimates of appropriate variance components (Snedecor and Cochran, 1980; Steel and Torrie, 1980).

Table 18-1 Analyses of Variance for Experiments in an Annual Crop with Different Numbers of Locations and Years

Sources of Variation	Degrees of Freedom	Expected Mean Squares
One location in one year:		
Replications	$r-1$	—
Genotypes	$g-1$	$\sigma_e^2 + r(\sigma_g^2 + \sigma_{gl}^2 + \sigma_{gy}^2 + \sigma_{gly})$
Error	$(r-1)(g-1)$	σ_e^2
One location in two or more years:		
Years	$y-1$	—
Replications in years	$y(r-1)$	—
Genotypes	$g-1$	$\sigma_e^2 + r(\sigma_{gy}^2 + \sigma_{gly}^2) + ry(\sigma_g^2 + \sigma_{gl}^2)$
Genotypes × years	$(g-1)(y-1)$	$\sigma_e^2 + r(\sigma_{gy}^2 + \sigma_{gly}^2)$
Error	$y(r-1)(g-1)$	σ_e^2
One year at two or more locations:		
Locations	$l-1$	—
Replications in locations	$l(r-1)$	—
Genotypes	$g-1$	$\sigma_e^2 + r(\sigma_{gl}^2 + \sigma_{gly}^2) + rl(\sigma_g^2 + \sigma_{gy}^2)$
Genotypes × locations	$(g-1)(l-1)$	$\sigma_e^2 + r(\sigma_{gl}^2 + \sigma_{gly}^2)$
Error	$l(r-1)(g-1)$	σ_e^2
Two or more locations in two or more years:		
Years	$y-1$	—
Locations	$l-1$	—
Replications in years and locations	$yl(r-1)$	—
Years × locations	$(y-1)(l-1)$	—
Genotypes	$g-1$	$\sigma_e^2 + r\sigma_{gly}^2 + ry\sigma_{gl}^2 + rl\sigma_{gy}^2 + rly\sigma_g^2$
Genotypes × years	$(g-1)(y-1)$	$\sigma_e^2 + r\sigma_{gly}^2 + rl\sigma_{gy}^2$
Genotypes × locations	$(g-1)(l-1)$	$\sigma_e^2 + r\sigma_{gly}^2 + ry\sigma_{gl}^2$
Genotypes × years × locations	$(g-1)(y-1)(l-1)$	$\sigma_e^2 + r\sigma_{gly}^2$
Error	$yl(r-1)(g-1)$	σ_e^2

Source: Johnson et al., 1955.

The sources of variation in an experiment are partitioned into main effects and their interactions (Table 18-1). The mean squares for the sources of variation are determined, and appropriate F-tests are made to assess the probability that a source of variation is significant. Components of variance can be calculated for the main effect of genotype and its interactions with years and locations. Standard errors can be computed for each component of variance.

Data Interpretation

Data interpretation includes consideration of the statistical significance of sources of variation and an assessment of the practical importance of variation observed among mean values. The genotype × location interaction measures the consistency of performance among genotypes at different locations. The consistency of performance of genotypes in different years is indicated by the genotype × year interaction. The genotype × location × year interaction measures the consistency of performance among genotypes for each combination of year and location. An experiment conducted at two locations in 2 years has four year–location combinations: year 1–location 1, year 1–location 2, year 2–location 1, and year 2–location 2. A significant genotype × location × year interaction indicates that the relative performance among genotypes was not the same for each of the year–location combinations. For all of the just mentioned interactions, an examination of mean values is necessary to determine if a significant interaction is due to a change in rank among genotypes or to changes in the differences among genotypes without variation in rank (Fig. 18-1).

The lack of any statistically significant interactions involving genotypes simplifies the nature of the testing program required for cultivar development and simplifies cultivar selection by the producer. Theoretically, the lack of a significant interaction of genotypes with locations, years, or location × year indicates that a test at one location during one year would be sufficient to identify genotypes with superior genetic potential. Cultivars with the best performance at one location in one year would also be superior at other locations in other years.

The practical implications of statistically significant genotype × environment interactions depend on the cause of the interaction. Genotype × environment interactions are not a problem for the breeder or producer if they are not due to changes in rank of performance among genotypes. Under these circumstances, a test at one location in 1 year could be used to identify superior genotypes, if genetic differences among lines were adequately expressed. The same cultivars would be superior in all locations and years, although the amount of superiority would vary. Significant genotype × environment interactions that involve changes in rank are common. In determining the practical implication of the interactions, the breeder must consider the extent of the changes in rank and their potential impact on genetic improvement. Subjective judgments often must be made; therefore, two breeders evaluating the same data may adopt different courses of action. The options available to the breeder are different for each type of interaction.

Genotype × Location. Wide fluctuations in the rank performance of genotypes at test locations suggest that it may be desirable to develop genotypes for different locations through independent selection and testing programs. The cost of establishing independent programs for different geographical areas is substantial; therefore, the decision can be difficult. Before establishing independent breeding

programs, the breeder should make a detailed examination of the environmental factors responsible for the genotype × location interaction. If the differences among locations are due to soil type or other factors that are consistent from year to year, independent programs may be appropriate. Temporary differences among locations associated with unusual climatic conditions would not justify independent programs.

Another consideration in determining the implications of genotype × location interaction is that fluctuations in rank may not preclude selection of superior genotypes for multiple locations. Assume that a group of genotypes was divided into three classes: good, intermediate, and poor. A genotype × location interaction could be caused by fluctuations in rank among genotypes within the three groups, but not among groups. Such an interaction would be unlikely to justify the establishment of breeding programs for independent locations, at least for the initial stages of testing.

Genotype × Year. An inconsistent ranking among genotypes grown in different years is in some regards more difficult to deal with than a genotype × location interaction. A breeder does not have the option of establishing independent breeding programs for different years. The primary option available is to identify genotypes that exhibit superior performance on the average across years. This involves the testing of genotypes in several years before selection of one for release as a cultivar. To reduce the length of time for genetic improvement, multiple locations in 1 year often are used as a substitute for years. The substitution is only effective when the divergence in climatic conditions among locations is comparable to differences among years.

Genotype × Year × Location. When there are fluctuations in the ranking of genotypes associated with individual location–year combinations, the breeder must identify genotypes with superior average performance over locations and years. This can be accomplished by testing over multiple locations and years. For example, an analysis of genotype × environment interaction for tobacco yield in North Carolina indicated that the mean squares for the genotype × year and genotype × location interactions were not significant (Jones et al., 1960). The rankings among cultivars were similar each year when averaged over locations (Table 18-2). Rankings of cultivars were also similar at each location when averaged over years. But the genotype × year × location interaction was significant in the experiment. The interaction seemed to be associated with specific conditions, such as rainfall pattern and disease infestation, that caused the ranking of cultivars to vary among certain year–location combinations. If the cultivar with the highest average performance over years is chosen, it would be expected to have acceptable performance the next year, but it may not be the best in that particular season. Producers often reduce the effect of fluctuations caused by genotype × year interaction by growing more than one cultivar each season.

Table 18-2 Yield per Acre and Relative Yield Ranking of Seven Tobacco Cultivars Averaged Over Five Locations for 3 Years*

	1955		1956		1957	
Cultivar	Pounds	Rank	Pounds	Rank	Pounds	Rank
C 139	2231	1	2306	1	2179	2
DB 244	1978	2	2069	2	2218	1
C 140	1830	3	1980	3	1865	3
Hicks	1701	4	1901	5	1735	5
402	1635	5	1777	7	1665	7
DB 101	1623	6	1819	6	1695	6
Va. 21	1622	7	1941	4	1809	4

*The cultivar × year interaction was not significant.

Source: Jones et al., 1960.

SELECTION OF LOCATIONS FOR TESTING

The selection of locations for the evaluation of a quantitative character is an important decision for the plant breeder, and involves a number of considerations. Locations generally are chosen that are representative of the area where a new cultivar will be grown commercially. The cost of transporting machinery and personnel may influence the distance of a location from the main research center. The availability of suitable land may be a factor when the size of the test area is large.

A primary consideration in site selection is the diversity of environments that can be obtained within a year. This is particularly important when cultivars are desired that perform well in a range of environments. A breeder will attempt to use test locations that have environments as diverse as those that would be encountered at one location in 2 or more years.

Several statistical procedures have been developed to characterize the similarity of environments encountered at different locations. They are based on the similarity in the relative performance of a group of genotypes that have been evaluated in replicated tests at all locations of interest.

Analysis of Variance

The similarity in relative performance of genotypes can be determined by the magnitude of the genotype × location interaction computed by a standard analysis of variance (Horner and Frey, 1957). The locations used for testing can be grouped into combinations of two or more. The genotype × location interactions computed for the various combinations of locations can be compared to determine the similarity or diversity of the locations involved.

The analysis of variance procedure was used by Horner and Frey (1957) to evaluate the possibility of dividing the state of Iowa into subareas for oat cultivar recommendations. Cultivar × location interactions were determined for various combinations of nine locations from which yield data were available during a 5-year period. The combinations with the lowest cultivar × location mean squares were considered the most suitable as subareas within Iowa. Horner and Frey suggested that the state could be divided into four subareas for testing.

Correlation Among Locations

Guitard (1960) used a diallel design for correlations between locations to determine the relative performance of barley cultivars over locations. The performance of the cultivars grown at one location was correlated with their performance at each of the other locations. Guitard found that by grouping locations with similar cultivar responses, he could reduce the number of locations used for yield tests from ten to five with only a small loss of information.

Cluster Analysis

Cluster analysis has been used to classify locations into groups within which genotype × location interactions are not significant. Locations are successively grouped on the basis of similarity in their interaction with a set of genotypes. At each level of clustering, an analysis of variance can be performed to test for significance of interactions. Ghaderi and colleagues (1980) used cluster analysis to investigate the interaction of genotypes of wheat at eight locations in Michigan. Although the genotype × location interaction was found to be significant over all locations, it was not significant within a cluster of the seven most similar locations. On the basis of results of cluster analysis, Barker and co-workers (1981) suggested that the performance of reed canarygrass clones grown in Iowa was representative of their performance in Minnesota and Wisconsin.

ALLOCATION OF RESOURCES

An understanding of genotype × environment interactions is useful for determining the optimum allocation of resources for testing.

An assessment of resource allocation requires data from a group of genotypes grown at two or more locations during 2 or more years. The analysis of variance provides estimates of the variance components associated with error (σ_e^2), genotype × location × year (σ_{gly}^2), genotype × location ((σ_{gl}^2), genotype × year

(σ^2_{gy}), and genotypes (σ^2_g). These can be used to compare different allocations of resources.

Variance of a Genotype Mean

The ability to identify significant differences among genotypes increases as the variance of the genotype mean decreases. Jones and colleagues (1960) used the concept of variance of a genotype mean to compare different strategies for plot allocation in tobacco trials (Table 18-2). The symbols they used have been modified in the following equation to conform to those used in this book.

$$V_{\bar{x}} = \frac{\sigma^2_e}{rly} + \frac{\sigma^2_{gly}}{ly} + \frac{\sigma^2_{gl}}{l} + \frac{\sigma^2_{gy}}{y}$$

The values for replications (r), locations (l), and years (y) were varied. The calculated variances of a genotype mean ($V_{\bar{x}}$) were compared with that obtained with their previous allocation of plots that included 2 years, five locations, and four replications. They concluded that 2 years, five locations, and three replications would be a more acceptable allocation of resources for their testing program.

Genetic Gain

Resource allocation for yield trials of maize was evaluated by Sprague and Federer (1951) by the calculation of genetic gain. The formula for genetic gain that they presented was similar in principle to the equation used in Chap. 17.

$$G_c = \frac{k\,\sigma^2_g}{\sqrt{(\sigma^2_e/rly) + (\sigma^2_{gly}/ly) + (\sigma^2_{gl}/l) + (\sigma^2_{gy}/y) + \sigma^2_g}}$$

Genetic improvement with various resource allocation procedures can be expressed in terms of gain per year (G_y) by dividing the genetic gain per cycle by the number of years required to complete a cycle of selection, $G_y = G_c/y$. Genetic gain per year is useful for evaluating resource allocation because it takes into account the length of time involved in evaluating genotypes for release as new cultivars.

Heritability

The effect of resource allocation on genetic gain can be assessed by its alteration of heritability. Heritability (h^2) can be expressed as

$$h^2 = \frac{\sigma^2_g}{(\sigma^2_e/rly) + (\sigma^2_{gly}/ly) + (\sigma^2_{gl}/l) + (\sigma^2_{gy}/y) + \sigma^2_g}$$

Rasmusson and Glass (1967) used this equation to derive heritabilities from estimates of variance components and various numbers of replications, years, and locations. The heritabilities of seven traits in two barley populations were found to vary considerably among the hypothetical testing methods.

Cost Associated with Resource Allocation

The cost associated with replications and locations is an important consideration in the allocation of resources. A fixed number of plots often is available for evaluating a genotype. In the absence of significant genotype × environment interactions, increasing the number of replications at a single location is as effective in improving gain as increasing the number of years or locations. If σ^2_{gl} and σ^2_{gly} are greater than zero, the amount of genetic improvement will be greatest with a maximum number of locations and minimum number of replications at each location. The cost of the genetic improvement generally will be increased, however, when the number of locations is increased. A compromise between the cost and the amount of genetic improvement may have to be reached.

The cost of genetic improvement was examined by Sprague and Federer (1951) for yield tests of maize. They calculated the cost per plot as a function of the number of plots per location and the cost of transportation. They indicated that cost per unit of genetic gain was least when one location was used, because transportation costs were eliminated. They also demonstrated, however, that the cost per plot decreased rapidly as the number of plots per location increased. Their cost for 25 plots at a location was less than half the cost for 100 plots at a location. The lower cost was achieved by dividing the expense for transportation among more plots. By using a sufficiently large number of plots per location, they were able to reduce the difference in cost per unit of genetic gain with varying numbers of locations.

Cost assessments may vary considerably among crops and breeding programs. The cost analysis by Sprague and Federer for maize did not apply to the situation in tobacco described by Jones and colleagues (1960) (Table 18-2). Data collection for tobacco in North Carolina was not influenced by the cost of transportation because personnel living on existing research stations provided most of the labor. As a result, the cost of a plot was essentially the same regardless of the location in which it was utilized.

Time Considerations in Resource Allocation

Genotype × year and genotype × location × year interactions often are significant for yield and other quantitative characters. Each additional year of evaluation will increase the reliability of information concerning the performance of a genotype. In terms of the statistical procedures discussed, each additional year

will reduce the theoretical variance of a genotype mean, increase the total genetic gain, and increase heritability.

There are practical limits, however, to the number of years of testing that can be conducted before a decision must be made about the genetic value of an individual. For recurrent selection programs, an increase in the number of years of testing may increase genetic gain per cycle but decrease genetic gain per year. A decision on the release of a genotype as a cultivar cannot be postponed indefinitely.

Most breeding programs attempt to save time by substituting additional locations for years of testing. The substitution is not on a one-for-one basis when the genotype × location component is less than that of genotype × year. Public breeding programs for many crops have a cooperative arrangement for testing that permits a large number of locations to be used each year at minimal cost. Private companies accomplish the same objective by establishing research stations in different geographical areas. Each station conducts tests of genotypes at several locations in a designated region.

STABILITY OF GENOTYPE PERFORMANCE

The reliability of cultivar performance across locations and years can be an important consideration in plant breeding. Some cultivars are adapted to a broad range of environmental conditions, while others are more limited in their potential distribution. There are cultivars that perform similarly regardless of the productivity level of the environment, and others whose performance is directly related to the productivity potential of the environment.

The stability of cultivar performance across environments is influenced by the genotype of individual plants and the genetic relationship among plants of the cultivar. The terms homeostasis and buffering have been used to describe the stability in performance of individual plants or groups of plants over different environments.

The terms developmental homeostasis and individual buffering have been used to describe the stability of individual plants (Allard and Bradshaw, 1964; Briggs and Knowles, 1967). It has been shown that heterozygous individuals, such as F_1 hybrids, are more stable than their homozygous parents. The stability of heterozygous individuals seems to be related to their ability to perform better under stress conditions than homozygous plants.

The terms genetic homeostasis and population buffering have been used to describe the stability of a group of plants that exceeds that of its individual members. (Allard and Bradshaw, 1964; Lerner, 1954). Heterogeneous cultivars generally have more stability on the average than do homogeneous ones.

Methods of Stability Analysis

A number of statistical procedures have been developed to enhance our understanding of genotype × environment interaction and its relationship to stability.

Analysis of Variance. The environmental stability of a group of genotypes has been evaluated with standard analysis of variance procedures. The significance of interactions involving genotypes is determined with an F-test. The relative magnitude of the genotype × location, genotype × year, and genotype × location × year variance components can be used to determine the effect of locations and years on the stability of a group of genotypes.

The relative environmental stability of different groups of genotypes has been compared with use of the analysis of variance procedure. Sprague and Federer (1951) found genotype × location and genotype × year interactions to be of greater significance in maize single-cross hybrids than in double-cross hybrids.

Pairwise Analysis of Variance. The standard analysis of variance procedure for a group of genotypes does not provide information on the environmental stability of individual genotypes. Information on individual genotypes can be obtained by conducting a combined analysis of variance for every pairwise combination of genotypes at all locations in a given year (Plaisted and Peterson, 1959). For each genotype, the mean of σ^2_{gl} estimates derived from its combination with all other genotypes can be calculated. These means provide a measure of the contribution of each genotype to the genotype × location interaction.

Regression Analysis. The environmental stability of individual genotypes has been estimated by the use of regression analysis (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966). A group of genotypes is grown over a range of environments. The mean performance of the genotypes at each environment is referred to as the environmental index. The performance of each genotype is regressed on the environmental index to obtain its mean performance over all environments, its linear response to varying environments, and an estimate of deviations from linear regression at the individual environments. A desirable genotype was described by Eberhart and Russell (1966) as one with a high mean, a regression coefficient of 1.0, and deviations from regression of 0. Such a genotype would have increased performance as the productivity of the environment improves.

Geometric Analysis. Hanson (1970) has proposed a measure of genotypic stability based on deviations from expected yield over environments. These deviations define the coordinates of a genotype within a stability space having a number of dimensions equal to the number of environments. Genotypic stability is expressed as a euclidean distance, either from a stable genotype (relative stability) or between any two genotypes (comparative stability).

Cluster Analysis. Cluster analysis also has been used to classify genotypic stability. On the basis of similarities in phenotypic responses in 16 environments, Ghaderi and colleagues (1980) arbitrarily grouped winter wheat genotypes into 10 clusters. They concluded that this method was effective in identifying groups of genotypes with various combinations of means and stabilities.

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CHAPTER NINETEEN

Field-Plot Techniques

The fundamental purpose of plant breeding is to identify genotypes with superior performance in commercial production. A large proportion of the time and expense devoted to cultivar development is in field evaluation of breeding material. The tests may involve genotypes in an initial stage of evaluation or those being given final consideration for release as new cultivars. The characters evaluated range from those that can be measured readily by visual examination to those that must be measured with appropriate instruments. The genetic potential of a genotype for some characters may be determined effectively with one or a few plants in a small plot, while for other characters extensive evaluation in larger plots may be needed.

It is the responsibility of the plant breeder to select the field-plot techniques that will provide the maximum amount of information with the resources available. The challenge is to adequately test as many genotypes as possible. The resources available to plant breeders vary; usually several alternative techniques are available for character evaluation. Plant breeders must decide which techniques will be the most effective and efficient in their particular situation.

Detailed discussions of field-plot techniques and data analysis are provided by Gomez and Gomez (1984) and LeClerg et al. (1962). An overview of the general principles will be provided in this chapter.

SOURCES OF VARIATION

The ideal way to compare genotypes would be to grow all of them in exactly the same environment and to measure their characteristics in precisely the same manner. The differences among genotypes in this ideal situation would be due only to variation in their genetic potential; therefore, the best genotype could be chosen without error. This ideal is impossible to achieve under field conditions because of lack of uniformity in the environment to which the genotypes are

exposed. Nevertheless, the use of appropriate field-plot techniques can maximize the accuracy with which genotypes are compared and selected.

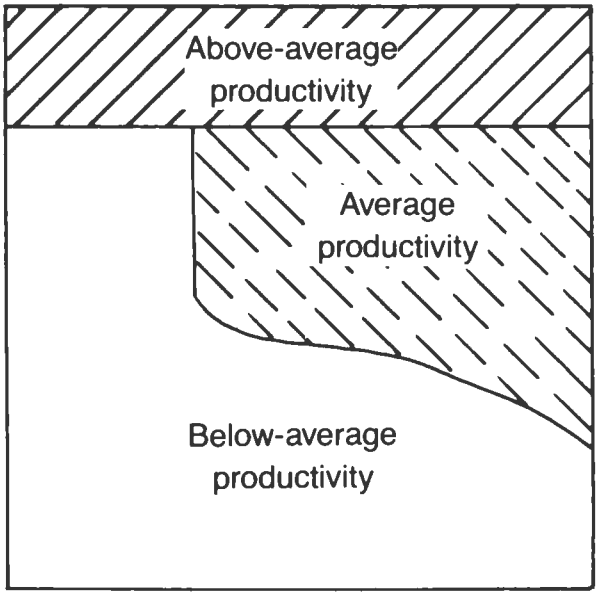
The factors that result in test conditions that are less than ideal can be referred to collectively as sources of experimental error. They include variation in the environment to which each genotype is exposed and lack of uniformity in the measurement of characters. The breeder has opportunities to minimize experimental error by carefully selecting the site to be used for field trials, the cultural practices used in crop production, the plot size and shape, and the method of data collection.

Site Selection

Variation in the productivity of the soil is commonly referred to as soil heterogeneity (Fig. 19-1). Causes of soil heterogeneity include variation in soil type, availability of plant nutrients, and soil moisture. The variation cannot be completely eliminated, but it often can be minimized by careful selection of the area in a field where plots will be grown. Soil maps are helpful for understanding the variation in soil type that is present. Soil types differ in their inherent ability to retain nutrients and moisture. Entire trials or at least an entire replication should be grown on a single soil type whenever possible.

Visual inspection of a field is important, even when a soil map is available.

Figure 19-1 Example of potential variation in soil productivity in a test area.



When a field has been identified a year in advance as a potential test site, it is useful for the breeder to look for variability in productivity of the crop grown in the area. The breeder should note variation in the terrain that may cause water to accumulate more in one place than in another. Differences in soil tillage after harvest of the previous crop may be observed that could result in nonuniformity of the area. Uneven distribution of plant or animal waste on a field should be noted as a potential contributor to variation in the availability of plant nutrients.

Before a site is chosen, information should be obtained on cultural practices that were followed in the production of previous crops, with special attention to the application of chemicals that could influence the crop that the breeder will be evaluating. The residue from herbicides applied for control of weeds in previous crops may cause damage to the crop to be tested. The following quotation from a research article by Thorne and Fehr (1970b) on soybean breeding illustrates the importance of herbicide residue:

> The strains were evaluated at Ames and Kanawha, Iowa, in 1968. . . . At Kanawha, part of the experiment was inadvertently planted in a field treated with atrazine herbicide two years before. All plots in the area were destroyed.

Previous cultural practices in a field can be especially important at research stations where crops are rotated from one field to another on a systematic basis. The research conducted on crops previously grown on a field can influence markedly the uniformity of the test site. For example, plots of oats were planted in a field at the Agronomy Research Center of Iowa State University in which soybeans had been planted the previous year. Growth of the oats varied in strips, as if nitrogen fertilizer had been applied unevenly to the field. A review of the previous soybean research revealed that the strips of oats with extra growth coincided with areas where mature soybeans had been cut and left unthreshed. The nitrogen in the soybean seeds in the strips was available to the oats the following year, and caused nonuniformity of nutrient availability in the test site.

Cultural Practices

Experimental error can be minimized by the use of uniform cultural practices for production of the crop being tested. Chemicals should be applied uniformly to the test site before, during, or after planting. Uneven soil compaction should be minimized during tillage operations. Application of supplemental water by irrigation may reduce variability in soil moisture. Weed control should be uniform; most breeders try to eliminate all weeds during the growing season to avoid experimental error caused by differential weed competition.

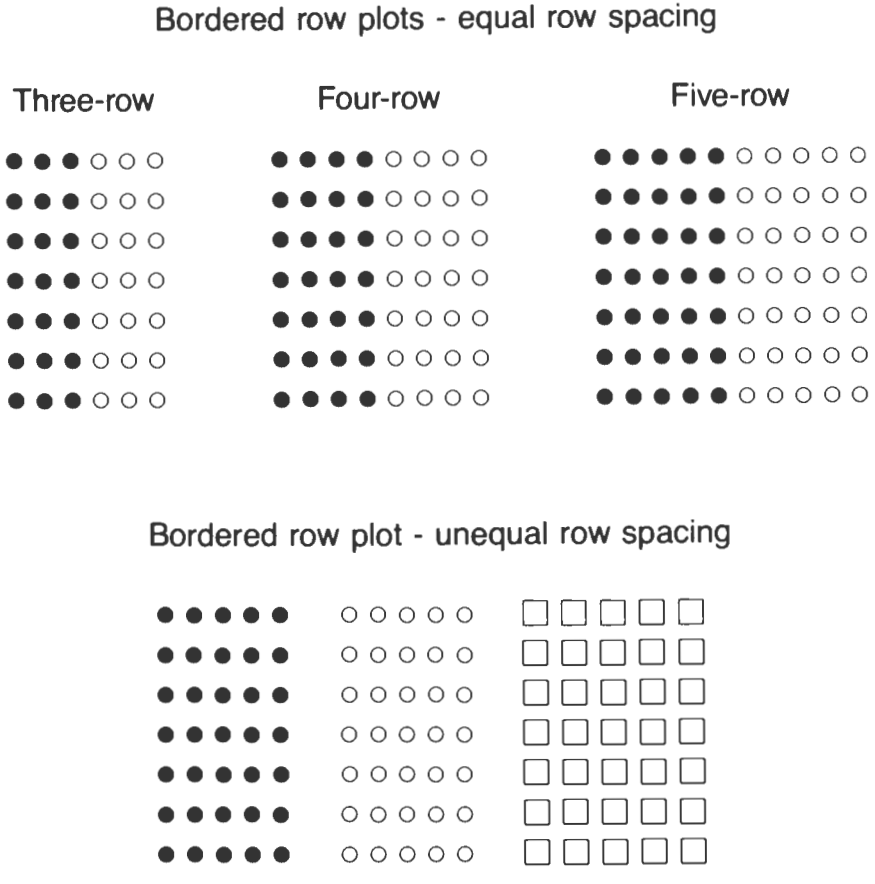
The development of equipment specifically designed for planting, managing, and harvesting research plots has permitted breeders to grow plots more efficiently. The emphasis in the design and use of any equipment must be on the uniformity with which genotypes are handled.

Plot Type

Experimental error increases whenever interplot competition causes the performance of a genotype in one plot to be altered by the performance of genotypes in adjacent plots. Interplot competition results primarily from intergenotypic competition, which is the differential ability of genotypes to compete with each other. Interplot competition is more important for the evaluation of some characters than for others. It is only through appropriate experimentation that a plot type can be identified that will provide reliable information for the character of interest.

The effects of interplot competition can be avoided by the use of plots with multiple rows in which only plants in the center rows are evaluated (Fig. 19-2). In plots with three or more rows, the outermost rows are designated as the border or guard rows. The function of the border rows is to prevent plants in adjacent

Figure 19-2 Illustration of bordered row plots with different cultivars designated as ●, ○, and □. (Courtesy of Fehr, 1978.)

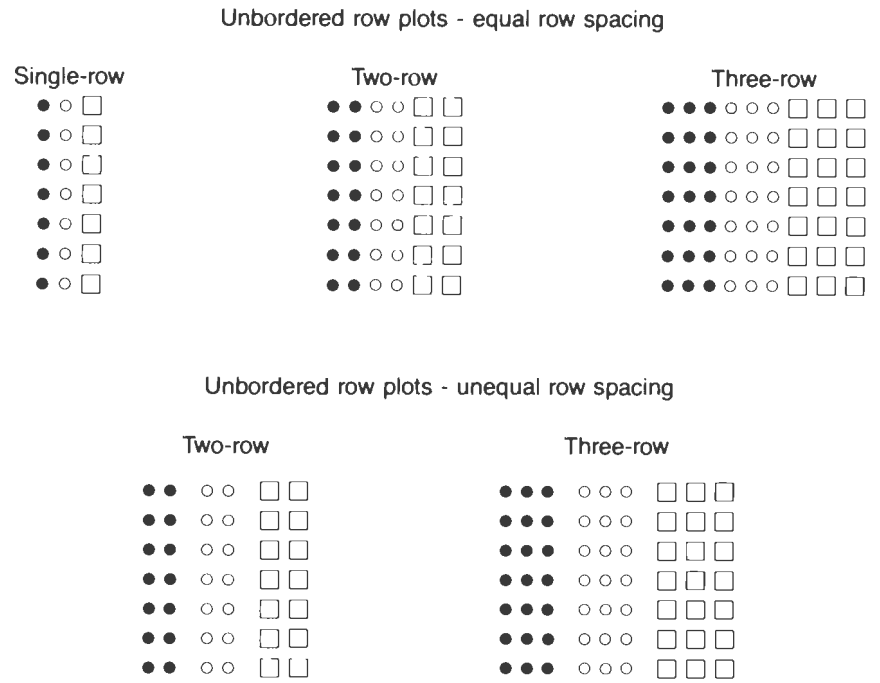


plots from influencing the performance of plants in the center of the plot. Each bordered plot can be considered a miniature field that is unaffected by neighboring fields. The spacing between plots can be greater than the within-plot spacing to facilitate the movement of equipment, particularly when narrow rows are utilized.

It would be ideal if bordered plots could be used for the evaluation of all characters that are influenced by interplot competition. That ideal is difficult to achieve when thousands of genotypes are being evaluated. Bordered plots require seed and land that do not directly provide data for a genotype. Borders take up two-thirds of the seed and land area for three-row plots and one-half for four-row plots. The cost and availability of seed and land often necessitate restriction of the use of bordered plots to the evaluation of genotypes that are being given final consideration for release as cultivars.

Interplot competition can be reduced, but not eliminated, with unbordered plots of two or more rows, all of which are used to evaluate a character (Fig. 19-3). A genotype in a single-row plot is subjected to interplot competition on both sides. Interplot competition is reduced by one-half in plots with two rows, two-thirds with three rows, three-fourths with four rows, and four-fifths with five rows. The estimated reduction of interplot competition with increasing numbers of rows is based on the fact that each row of a plot must compete on two sides. The border rows are each subjected to interplot competition on one side

Figure 19-3 Illustration of unbordered row plots with different cultivars designated as ●, ○, and □. (Courtesy of Fehr, 1978.)



but not on the other. Any rows within the two border rows are protected from interplot competition. This can be expressed as

$$\text{Reduction in interplot competition compared with single-row plot} = \frac{(\text{number of rows per plot} \times 2 \text{ sides}) - 2 \text{ sides}}{\text{number of rows per plot} \times 2 \text{ sides}}$$

$$\text{Two-row plot} = \frac{(2 \times 2) - 2}{2 \times 2} = 1/2$$

$$\text{Three-row plot} = \frac{(3 \times 2) - 2}{3 \times 2} = 2/3$$

The amount of interplot competition also can be reduced by increasing the spacing between rows of adjacent plots. Interplot competition in soybeans was evaluated with five cultivars grown in single rows spaced 100, 75, 50, and 25 cm apart (Gedge et al., 1977). The average effect of interplot competition on seed yield was 2.6 percent for the 100-cm spacing, 5.3 percent for 75 cm, 8.0 percent for 50 cm, and 17.6 percent for 25 cm.

A combination of increased row spacing between plots and a large number of rows can minimize interplot competition in unbordered plots. In the soybean example of the preceding paragraph, the average change in yield for single-row plots spaced 100 cm apart was 2.6 percent. The percentage theoretically would be reduced to 1.3 percent for two-row plots and to 0.9 percent for three-row plots. Rows within a plot are not subjected to interplot competition; therefore, the spacing between rows within a plot can be less than the spacing between adjacent plots. Figure 19-3 illustrates a two-row plot in which the spacing between plots is wide enough to minimize interplot competition and the spacing within the plot is reduced to minimize the land area required for each plot.

Some breeders plant one cultivar as a common border between one- or two-row plots. In barley, a lodging-resistant cultivar is used as a common border to prevent genotypes with lodging susceptibility from falling on genotypes in adjacent plots, thereby causing them to lodge unnaturally. The use of a common border has been evaluated as a means of eliminating intergenotypic competition between plots for seed yield and other quantitative characters. The results of the research indicate that a common border can reduce but not eliminate interplot competition (Thorne and Fehr, 1970a). The average interplot competition for seed yield among four soybean cultivars in single-row plots spaced 50 cm apart was compared with competition of the cultivars when a common border was used (Gedge et al., 1977). Interplot competition averaged 11.0 percent in single-row plots and 8.3 percent in plots with a common border.

Plot Size and Shape

The size of plots used to evaluate genotypes varies with the character being evaluated, the amount of experimental error that is considered acceptable for

measuring a character, the experimental design, and the growth characteristics of the crop. Plots vary in size from those for a single plant that is harvested by hand to those that are wide and long enough to be harvested with the same equipment used by farmers for commercial production.

Single-Plant Plots. Individual plants commonly are evaluated in segregating populations. There is no replication of the individuals, unless vegetative propagation of clones is possible. The spacing among plots varies with the crop species involved. Gardner (1961) spaced individuals 50 by 100 cm apart when selecting for yield in maize. Burton (1974) spaced plants of a population of Pensacola bahiagrass 60 by 60 cm apart when conducting recurrent phenotypic selection for forage yield. Burton and Brim (1981) used a 46 by 46 cm spacing among soybean plants for selection of oil composition in the seed.

Single-plant plots are used for the replicated evaluation of experimental lines or cultivars by the honeycomb field design (Fasoulas, 1979). The number of plants evaluated for a line is equal to the number of replications in the experiment. Fasoulas (1981) indicated that 100 single-plant plots (replications) per line would provide satisfactory results. The plots of the lines in a test are organized in a systematic manner to permit comparison of a plant of one line with adjacent plants of other lines (Fig. 19-4). The honeycomb design has not been adopted by plant breeders for replicated evaluation of lines because it requires more labor and is less amenable to mechanization than microplots or conventional row plots.

Multiple-Plant Plots. The evaluation of experimental lines or cultivars by plant breeders is usually done in plots containing two or more plants. Plot size varies from small microplots consisting of a hill or short row to a plot with one or more rows several meters in length.

Microplots. Microplots are used to minimize the amount of seed or land required to evaluate a group of lines. In an unbordered microplot, the effects of interplot competition must be considered when determining an appropriate distance among plots (Fig. 19-5). For oats, hill plots spaced about 30 by 30 cm apart have been used (Frey, 1965), while for soybeans, a spacing of about 1 by 1 m is more common (Garland and Fehr, 1981).

The number of plants in a microplot differs among crops. A planting rate of 30 seeds per hill is satisfactory in oats (Frey, 1965), while a rate of 12 seeds per hill is used for soybeans (Garland and Fehr, 1981). When short rows are used as microplots, the plant density is comparable to that of larger row plots.

There is a lack of agreement among plant breeders concerning the effectiveness of microplots for evaluation of agronomic characters, particularly seed yield. Breeders who use microplots indicate that they are useful for eliminating inferior lines during the first year of yield evaluation. Lines with acceptable performance in microplots are evaluated in conventional row plots during subsequent years of testing, to identify those that merit release as cultivars (Frey,

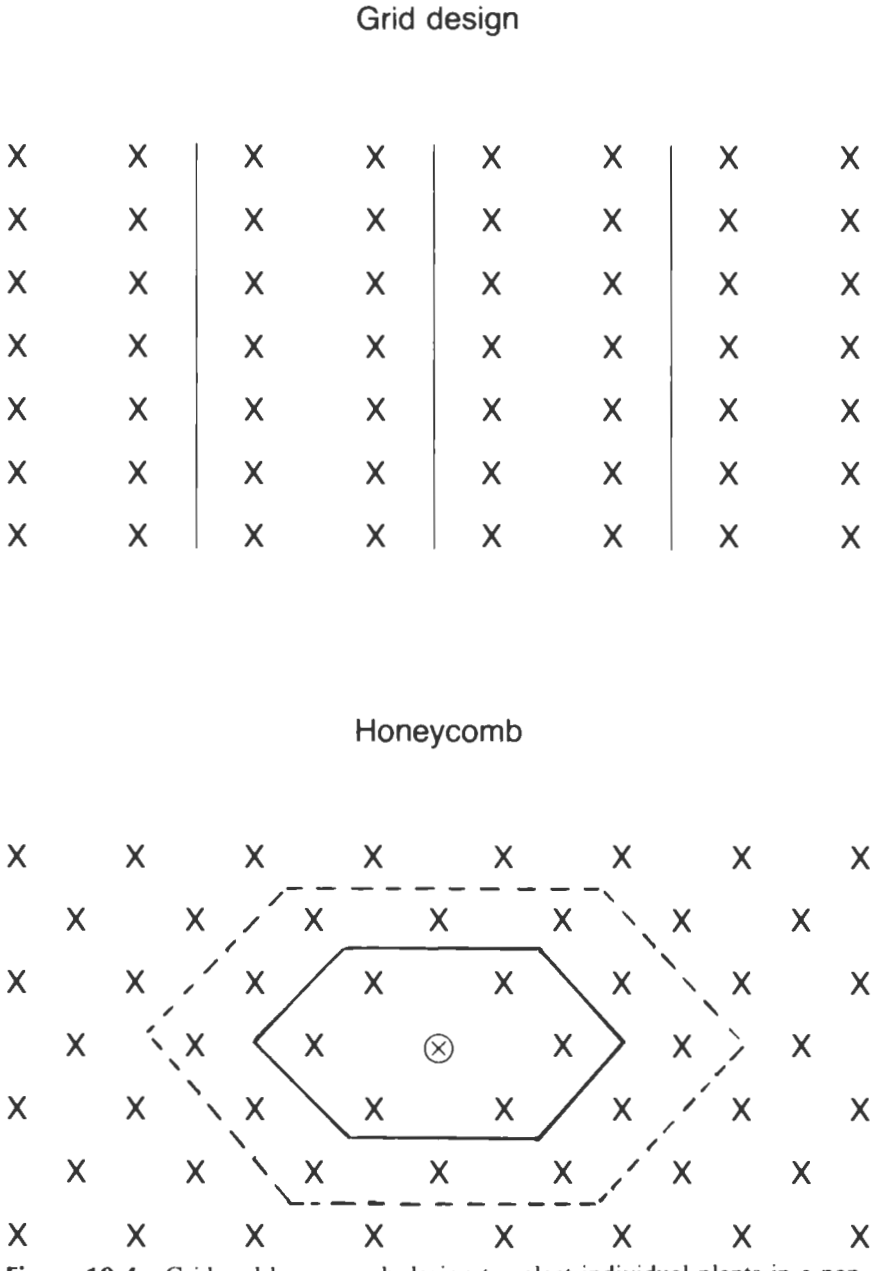


Figure 19-4 Grid and honeycomb design to select individual plants in a population. For the grid design, plants are divided into blocks and the best ones chosen from each (Gardner, 1961). For the honeycomb design, the plant at the center of the hexagon, ⊗, is compared with every other plant within the hexagon (Fasoulas, 1979). A plant is chosen only if it is superior to every other plant in the hexagon. The hexagons outlined represent two different selection intensities.

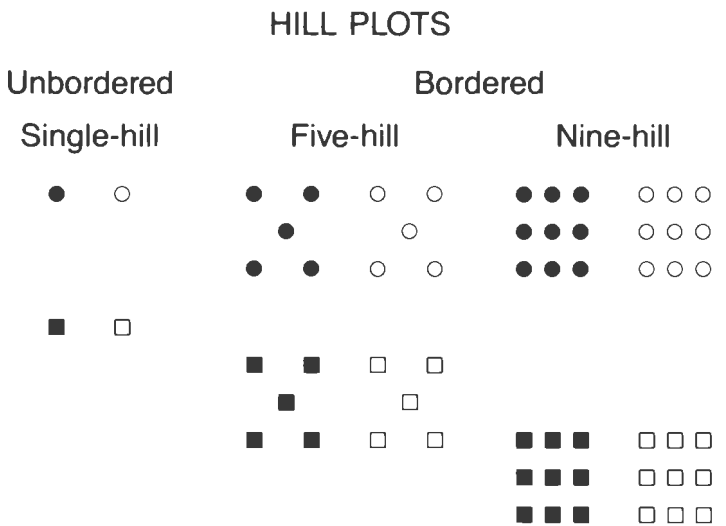


Figure 19-5 Illustration of hill plots with different cultivars designated as □, ○, ●, and ■ (Fehr, 1978).

1965; Garland and Fehr, 1981). The advantages of microplots compared with conventional row plots for the first year of yield testing are that less land is required per plot and that enough seed for replicated tests can be obtained from a single plant, which eliminates a season for seed increase. Breeders who do not use microplots are concerned about the reliability of yield data obtained from them. The coefficients of variability for microplots generally are about one and one-half to two times larger than for conventional row plots.

Row Plots. Row plots are used by virtually all plant breeders for replicated testing of genotypes. The overall plot size is determined by the number of rows, the spacing between rows, and the row length.

Single-row plots of 1 to 2 m in length are widely used for the visual evaluation of characters. Many breeders evaluate lines on the basis of their appearance in small unreplicated plots, and advance the desirable ones to replicated tests the following season. Visual selection and seed increase commonly are accomplished with the same plot.

A plot used to evaluate the yield of lines for the first time often is smaller than that employed for advanced stages of evaluation. For advanced yield tests, the breeder attempts to use a plot size that approaches or equals the dimensions considered optimal for the crop species involved. Optimum plot size is the minimum land area required to measure a character with an acceptable level of experimental error.

Optimum plot size can be determined by the use of data from a uniformity trial (Cochran, 1937). A single cultivar is planted as a solid stand, without alleys,

in an area representative of that used for yield evaluation. The cultural practices used to produce the crop are the same as those used for yield trials. The area is subdivided into small units, and the seeds or plants from each unit are harvested and weighed separately. Experimental error associated with plots of different size can be determined by making various combinations of the small units.

Optimum plot size also is determined through practical experience. The breeder often will experiment with plots of different size to find the smallest one that has an acceptable level of experimental error. Breeders often do not agree on what they consider acceptable experimental error; consequently, an optimum size for one person may not be optimum for another.

Plot width generally is determined by considerations other than the relationship of shape to experimental error. The primary factors are the number of rows required to minimize or avoid interplot competition and the width of the planting and harvesting equipment that is available. Plot width influences the percentage of land area that must be devoted to alleys between plots. Long, narrow plots require a lower percentage of alley space than do wide, short plots. This advantage is offset in bordered plots because the percentage of land area devoted to border rows decreases as the number of rows per plot increases.

Plot length provides flexibility for plot size. Before calculators and computers became readily available, row length in the United States was varied to obtain a plot size that was a fraction of an acre (one-tenth, one-twentieth, etc.) to simplify the conversion of plot yields to yields per acre. With use of computers for data summarization and analysis, this is no longer necessary.

Data Collection

The experimental error associated with the evaluation of a character is influenced by measurement errors during data collection. For characters evaluated visually, experimental error occurs whenever the data collector fails to give an identical rating to plots with an identical appearance. Reliability of the evaluation can be established readily by rating a series of plots at different times and comparing the ratings. It is essentially impossible to give visual ratings without error; therefore, the breeder must decide when the error is acceptable and when it is so large that genetic differences will be masked.

Some characters can only be evaluated efficiently with the use of an appropriate machine or instrument. Experimental error can occur because of failure to prepare a plot properly for measurement, of not obtaining a representative sample of the plot for evaluation, of using nonuniform procedures for sample preparation, and of failure of the machine or instrument to operate properly.

Preparation of a plot for data collection may begin before planting. For experimental error to be reduced, the seeds or plants of every genotype used for planting must be treated equally. If seeds or plants of genotypes to be compared

do not come from a common environment, environmental error may result. Lint yield and seedling vigor of a cotton cultivar were found to differ in plots grown from seeds obtained from different locations (Peacock and Hawkins, 1970). Seed source also has been shown to influence seed yield of soybeans (Fehr and Probst, 1971.)

In some crop species, uniformity of plant density among plots can be important in minimizing experimental error. With maize, it is a common practice to thin yield test plots to a uniform stand soon after seedling emergence. Thinning is not considered necessary with some crop species, particularly those that have the ability to branch or tiller in response to low plant density, such as barley and wheat. It also is a common practice with crops such as maize to record the number of plants per plot immediately before harvest. The yield of the plots is adjusted for plant density by an analysis of covariance, to minimize experimental error in the comparison of genotypes.

When a blank alley is used at the end of row plots, the end plants generally are more productive than those growing in the center of the plot. When end plants are harvested, yield of the plot is inflated in comparison to the yield obtained from plants growing in the center of the plot. This inflation will prevent a direct comparison of plot yields with those expected in a normal commercial planting, unless an appropriate adjustment is made for all plots. The adjustment may be made by considering the alley as part of the plot area; therefore, plot length is the distance from the center of one alley to the center of the next, instead of the distance between plants at opposite ends of a row. For example, if the length of row containing plants is 5 m and the alley is 1 m wide, the plot length for computing plot area is considered to be 6 m.

The yield inflation by end plants in a plot does not contribute to experimental error unless genotypes in a test do not respond similarly to the space in the alley. The experimental error associated with differential response of genotypes to an alley can be minimized by adjusting yields according to characteristics of the genotypes that influence this response. The end plants of soybean genotypes with late maturity give a greater yield inflation than do genotypes of early maturity. Values have been developed with which to adjust plot yields for maturity of soybean genotypes (Wilcox, 1970). More commonly, comparisons among soybean genotypes are restricted to those of similar maturity, unless plots are end-trimmed before harvest.

The only way to eliminate yield inflation by end plants is to remove the plants before harvest. This procedure, referred to as end-trimming, is a standard procedure with some crops. The end plants are removed late enough in plant development that the remaining plants in the plot cannot take advantage of the extra space. The length of row removed from each end of the plot must be long enough to include all plants that have benefited from the space provided by the alley. In soybean, 0.6 m is removed from each end of the plot (Wilcox, 1970).

The problem of a blank alley is minimized in some crops by planting the

alley with rows of a single genotype perpendicular to the test plots. The result is that the plants at the end of a plot must compete with plants in the alley, and thus their yield may not be inflated as much as is the case with a blank alley. Plants in the alley are removed immediately before the plots are harvested.

EXPERIMENTAL DESIGNS

The arrangement of genotypes in a field experiment is referred to as the experimental design. Some of the designs utilized to compare genotypes are common to research in many disciplines. Others have been developed to deal with the problem of comparing a large number of genotypes as inexpensively as possible. The experimental designs used for the initial evaluation of a large number of genotypes often differ from those used in the advanced stages of testing a few select genotypes. Alternative designs will be considered here for comparison of single plants, unreplicated genotypes in multiple-plant plots, and replicated genotypes.

Single-Plant Selection

The first evaluation step in the development of a cultivar generally is the selection of individual plants from a population. Individual plant selection also is employed in population improvement by recurrent phenotypic selection.

When single-plant selection in a population is for characters with a high heritability, the plants generally are grown in a random order and those with desirable characteristics are selected. Cultivars may be grown in adjacent plots to serve as standards with which to evaluate single plants. Date of flowering, plant height, time of maturity, and certain types of pest resistance are examples of characters for which single plants are selected without any predetermined arrangement of the individuals. They represent characteristics that are not strongly influenced by environmental variation.

Single-plant selection in a population grown in a relatively large land area can be hampered seriously by soil heterogeneity for characters with a low heritability, such as seed or plant yield. Figure 19-1 illustrates variation in soil productivity in an area where a population of plants may be grown. If plants with the highest yield are selected regardless of their location in the field, those in the area of above-average productivity will be favored. A plant with outstanding genetic potential that is located in the area with below-average productivity may be discarded. Two experimental designs are available that minimize the effect of soil heterogeneity by comparing plants that are most adjacent to each other.

Grid Design. Gardner (1961) proposed that the land area on which a population of individual plants is grown can be subdivided into blocks or grids of a limited

area (Fig. 19-4). Plants within each block are compared with each other, and the superior ones are selected. Comparisons are not made between plants from different blocks. This experimental design has been well accepted by plant breeders, particularly those conducting recurrent phenotypic selection for yield or other characters with a low heritability.

Honeycomb Design. Fasoulas (1973) developed a honeycomb design for selecting individual plants in a population (Fig. 19-4). Five aspects of the design and its implementation are unique. (a) Seeds or clones are spaced equidistantly from each other in a hexagon pattern. The name of the design was chosen because the hexagon patterns resemble a honeycomb of bees. (b) Plants are spaced far enough apart that they do not compete with adjacent individuals. At the appropriate spacing for a species, a missing plant does not influence the performance of adjacent individuals, because each plant already has sufficient space in which to develop to its full potential. (c) Homogeneous check cultivars can be included for comparison, if desired. Every plant of the check is compared with a different group of plants in the population. (d) The size of the hexagon used to select single plants determines the selection intensity in the population. The effect of soil heterogeneity is minimized because only those plants within the area of the hexagon are compared. (e) Every plant in the population is evaluated by placing it in the center of the hexagon. A plant is chosen only if it is superior to every other plant in the hexagon. By moving the hexagon, every plant is compared with a different group of plants in the population.

Comparison of the Grid and Honeycomb Designs. Both the grid and honeycomb designs reduce the problem of soil heterogeneity in the selection of characters of low heritability. In a comparison of the designs, the advantages of one are the disadvantages of the other, and vice versa.

There are three primary advantages of the grid design.

1. The spacing of plants does not have to be in a precise pattern. This facilitates the use of conventional plot equipment for planting and cultivation. Mechanized planting of the honeycomb design would require specialized equipment.
2. Selection intensity can be varied by altering the number of plants in a block and the number of plants selected. Only certain selection intensities are possible with the honeycomb design.
3. Use of a defined area for each block facilitates visual comparison of plants for selection. It is possible to compare plants within a block visually and collect data only from those with the best potential. Use of the moving hexagon for the honeycomb design makes it impractical to compare each plant with appropriate ones in its hexagon; therefore, data must be recorded for every plant, except those that are obviously inferior.

The honeycomb design has two advantages compared with the grid design.

1. Homogeneous check cultivars can be included to permit comparisons of individual plants with a standard. When one-seventh of the plants are a check, they can be arranged so that every plant in the population can be compared with a check plant. To provide adjacent plants of one check cultivar in a grid system, one-third of the area would have to be devoted to the check.
2. More than two check cultivars can be included readily in hexagons of 19 or more plants. Use of two or more check cultivars in the grid system would require that a large fraction of each block be devoted to check plants.

Unreplicated Evaluation with Multiple-Plant Plots

Plant breeders routinely conduct visual selection among lines in unreplicated plots for maturity, disease resistance, standability, and other characters of high heritability. Evaluation for yield in a single replication has been used to a limited extent to eliminate inferior lines before initiation of expensive replicated tests. With a single replication, each line is compared once with check cultivars or other lines to determine its genetic potential. A number of different arrangements are available for estimating the genetic potential of lines. One method is to compare each line with a common check cultivar (Baker and McKenzie, 1967). Figure 19-6 represents a hypothetical example of the yield of six lines in a single replication. In the figure, the yield of each line is expressed as a percentage of the yield of the check cultivar immediately adjacent to it.

Another alternative is to express the yield of each line as a percentage of the weighted average of the adjacent check plot and of the check plot two plots removed. The purpose for using a weighted average is to minimize the potential problem caused by an unusually poor yield of a check plot. In Fig. 19-6, the check cultivar adjacent to lines B and C has a much lower yield than other check cultivars. This results in an extremely high percentage for lines A and B. The weighted average of check cultivars could be computed as

$$(\tfrac{2}{3} \times \text{yield of adjacent check}) + (\tfrac{1}{3} \times \text{yield of check two plots removed}) = \text{weighted average of check cultivars}$$

The percentage yield of each line is computed as

$$\text{Line A} = \frac{59}{(\frac{2}{3} \times 55) + (\frac{1}{3} \times 39)} \times 100 = 119$$

$$\text{Line B} = \frac{70}{(\frac{2}{3} \times 39) + (\frac{1}{3} \times 55)} \times 100 = 158$$

$$\text{Line C} = \frac{53}{(\frac{2}{3} \times 39) + (\frac{1}{3} \times 48)} \times 100 = 126$$

$$\text{Line D} = \frac{51}{(\frac{2}{3} \times 48) + (\frac{1}{3} \times 39)} \times 100 = 113$$

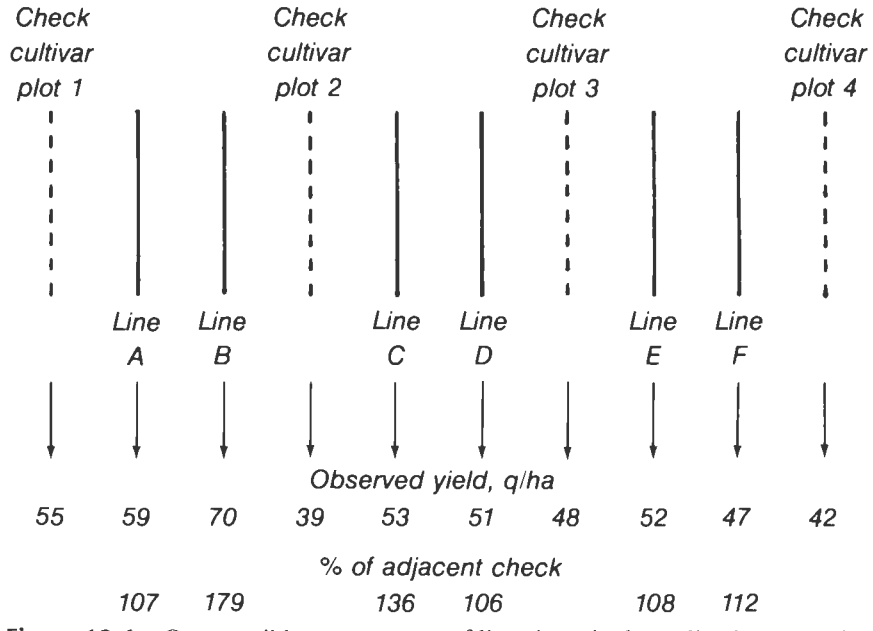


Figure 19-6 One possible arrangement of lines in a single-replication test. The performance of each line is computed as a percentage of the performance of the common check cultivar adjacent to it. Line B would be considered the superior one.

$$\text{Line E} = \frac{52}{(\frac{2}{3} \times 48) + (\frac{1}{3} \times 42)} \times 100 = 113$$

$$\text{Line F} = \frac{47}{(\frac{2}{3} \times 42) + (\frac{1}{3} \times 48)} \times 100 = 107$$

Another method used to compare genotypes in single replications is the moving mean (Mak et al., 1978; Townley-Smith and Hurd, 1973). Each genotype is compared with adjacent test genotypes, not with a check cultivar.

The disadvantage of single-replication tests is that the breeder has only one plot value with which to assess the genetic potential of a line. If by chance a line is placed on a plot of soil with above-average productivity, relative to that of plots with which the line is compared, it will seem to be genetically superior, even though it may not be. In replicated tests, the breeder will have more than one plot with which to evaluate each line. For this reason, single replications are not commonly used for yield evaluation.

Replicated Tests

Two or more independent comparisons of lines in a test provide a means of estimating whether variation in performance among lines is due to differences in genetic potential or to environmental variation. Each comparison is as rep-

lication. Replication can be accomplished by growing two or more plots of each line at one or more locations or one plot at each of two or more locations or years.

Randomization. One important consideration in the arrangement of genotypes within each replication is the degree of randomization. From a statistical viewpoint, randomization of entries is required to obtain a valid estimate of experimental error. To fulfill the requirement, each entry must have an equal chance of being assigned to any plot in a replication and an independent randomization is required for each replication.

Plant breeders understand the importance of randomization and consider it the ideal procedure for comparison of genotypes. They know that any experiment designed to estimate components of variance must be randomized. There are circumstances, however, in which plant breeders do not use complete randomization for the comparison of genotypes. Genotypes with similar characteristics may be planted next to each other to reduce interplot competition in unbordered plots. A nonrandom arrangement of genotypes among replications may be used to facilitate selection of genotypes before harvest.

Nonrandom Arrangements of Genotypes. Any discussion of nonrandom arrangements of genotypes can be misinterpreted because it may imply that randomization is not an important principle. To avoid such misinterpretation, it should be stated again that nonrandomization should only be considered when resources are not adequate to make randomization feasible. The discussion of nonrandom arrangements will include the reasons for their use, their disadvantages, and the ways procedures can be modified to permit effective randomization.

Nonrandomization Among Replications. It is common to delay replicated tests for yield until genotypes have been visually selected in unreplicated plots for characteristics such as lodging, height, and maturity. To reduce the length of time for cultivar development, the season for evaluation in unreplicated plots can be eliminated by growing genotypes in replicated plots, visually selecting those with desirable characteristics, and harvesting only the plots of selected genotypes for yield evaluation (Garland and Fehr, 1981). When visual selection is based on the performance of genotypes in all of the replications, it is necessary to evaluate each plot, summarize the data, make the selections, and identify the plots of selected genotypes that should be harvested. The length of time between plot evaluation and harvest may be only a few days when characteristics of interest are not expressed until plant maturity. If several thousand genotypes are randomized in two or more replications, summarization of data and identification of plots to be harvested can be difficult or impossible to accomplish in only a few days. The use of the same arrangement of genotypes in each replication makes the job practical.

When genotypes are in the same position within each replication, the data for plots of each genotype are recorded in adjacent columns (Fig. 19-7). Sum-

Nonrandom

		Replication		
Plot	Entry	1	2	3
1	1			
2	2			
3	3			
4	4			
5	5			
6	6			

Random

		Replication
Plot	Entry	1
1	4	
2	1	
3	6	
4	3	
5	5	
6	2	

		Replication
Plot	Entry	2
1	5	
2	4	
3	2	
4	1	
5	6	
6	3	

		Replication
Plot	Entry	3
1	2	
2	6	
3	3	
4	5	
5	1	
6	4	

Figure 19-7 Field book pages for recording the data of genotypes grown in three replications. Nonrandom arrangement of genotypes involves one page, whereas a random arrangement involves three separate sections on one or more pages.

marization of data is complete as soon as the last plot is rated. Genotypes with undesirable characteristics in one or more replications can be identified and discarded. The plots of desirable genotypes are readily identified for harvest because they are in the same position in each replication.

The disadvantages of nonrandomization relate to the fact that the same genotypes are always adjacent to each other, which can have negative effects on the comparison of genotypes.

1. In unbordered plots, intergenotypic competition can bias the performance of genotypes more seriously in a nonrandom than in a random arrangement. When a poor competitor is bordered by a good competitor, yield of the poor competitor can be reduced and that of the good competitor increased in every replication. There is no opportunity for a genotype to occur next to others with a more similar competitive ability.
2. In unbordered plots, a genotype that dies or is unusually weak in all replications can prevent the accurate evaluation of adjacent genotypes. The performance of adjacent genotypes would never be tested in replications where they were next to healthy genotypes.
3. No unbiased estimate of experimental error can be obtained.

The need to use nonrandomization of genotypes among replications can be avoided by improving the efficiency of procedures for data summarization and evaluation. An efficient procedure would include the use of a computer. Data would have to be entered rapidly into the computer, possibly by entering plot data into an electronic recorder in the field and electronically transferring the information to the computer. Computer programs would be needed to summarize the data and make selections on the basis of standards established by the breeder. Plot identification information for selected genotypes would have to be provided for harvest.

Grouping Similar Genotypes Within Replications. The evaluation of genotypes in unbordered plots can be hampered by bias from intergenotypic competition. Plant characteristics that often contribute to intergenotypic competition in a crop include such factors as differences in height and time of maturity. To reduce intergenotypic competition, genotypes with similar characteristics may be grouped within replications. The position of each genotype may be varied from one replication to the next. This procedure, sometimes referred to as restricted randomization, has the advantage of reducing the effects of intergenotypic competition in unbordered plots. The primary disadvantage is that all genotypes in a test cannot be compared with the same level of confidence. Genotypes within a group are spaced closer to each other than genotypes in different groups and are less affected by environmental variation among plots.

The use of bordered plots eliminates the need for grouping genotypes. The performance of genotypes in plots is not influenced by intergenotypic compe-

tition; therefore, randomization is practical. An increase in land, seed, and other resources will be needed for replacement of unbordered plots with bordered ones.

Experimental Designs for Replicated Tests. The arrangement of genotypes in replicated tests involves primarily the use of either the randomized complete-block design or incomplete-block designs. The Latin square is used only in special circumstances when the number of entries is small (Cochran and Cox, 1957). The honeycomb design can be used for replicated testing but is considered too difficult to implement for a large number of lines (Fasoulas, 1981).

The differences between the randomized complete-block and incomplete-block designs relate to their ability to account for environmental variation within a replication. The two types of design differ in restrictions on the size of a replication, randomization procedures, analysis of data, and comparisons among genotypes.

The terms complete-block and incomplete-block refer to the arrangement of genotypes in an experiment (Fig. 19-8). A block and a replication are equivalent in a randomized complete-block design. A block contains all of the genotypes in the test and is considered complete. Genotypes are divided into more than one block within each replication of an incomplete-block design. The blocks are considered incomplete because they contain only part of the genotypes. A number of different types of incomplete-block designs are available (Cochran and Cox, 1957). The most common types used in plant breeding are referred to as lattices. In a lattice design, a replication is divided into blocks that collectively contain all the genotypes in a test (Fig. 19-8).

The incomplete-block designs are intended to provide more control over environmental variation within a replication than is possible with the complete-block design. The ideal situation for genotype evaluation would be to test each genotype in the same plot, thus avoiding any environmental variation caused by differences in soil fertility, moisture, and other factors within a field. This is not possible, so the next best approach is to adjust the performance of each genotype according to the relative productivity of the plot in which it is evaluated. If one plot has better fertility and moisture than the average for all plots in a replication, the performance of a genotype in that plot will be adjusted downward. A genotype in a plot with lower productivity than the average will have its performance adjusted upward.

Although individual plot adjustments are not possible, the lattice designs permit the performance of a genotype to be adjusted upward or downward according to the productivity of the blocks in which it was grown. The randomized complete-block design does not divide the replication into smaller units and is not able to adjust the performance of a genotype for environmental variation within replications.

The effectiveness of the lattice design in accounting for environmental variation within replications depends on the pattern of variation. Figure 19-9 shows two replications with variation in soil productivity. The soil productivity in

Block						
	Replication 1					
1	1	2	3	4	5	6
2	7	8	9	10	11	12
3	13	14	15	16	17	18
4	19	20	21	22	23	24
5	25	26	27	28	29	30
6	31	32	33	34	35	36
7	37	38	39	40	41	42
	Replication 2					
1	7	13	19	25	31	37
2	1	14	20	26	32	38
3	2	8	21	27	33	39
4	3	9	15	28	34	40
5	4	10	16	22	35	41
6	5	11	17	23	29	42
7	6	12	18	24	30	36
	Replication 3					
1	12	17	22	28	33	38
2	2	13	24	29	35	40
3	4	9	20	25	36	42
4	6	11	16	27	32	37
5	1	7	18	23	34	39
6	3	8	14	19	30	41
7	5	10	15	21	26	31

Figure 19-8 Lattice design for an experiment with 42 entries and three replications. (Adapted from Cochran and Cox, 1957.) For a randomized complete-block design, there are no blocks within a replication and the entries are assigned at random to the 42 plots.

replication 1 increases from left to right. The blocks of the lattice design are arranged in a pattern that effectively measures the variation, as evidenced by differences in the mean for each block. The variation in soil productivity in replication 2 does not fit a consistent pattern. Much of the variation occurs within blocks, and the mean performance of the blocks is relatively similar. The lattice

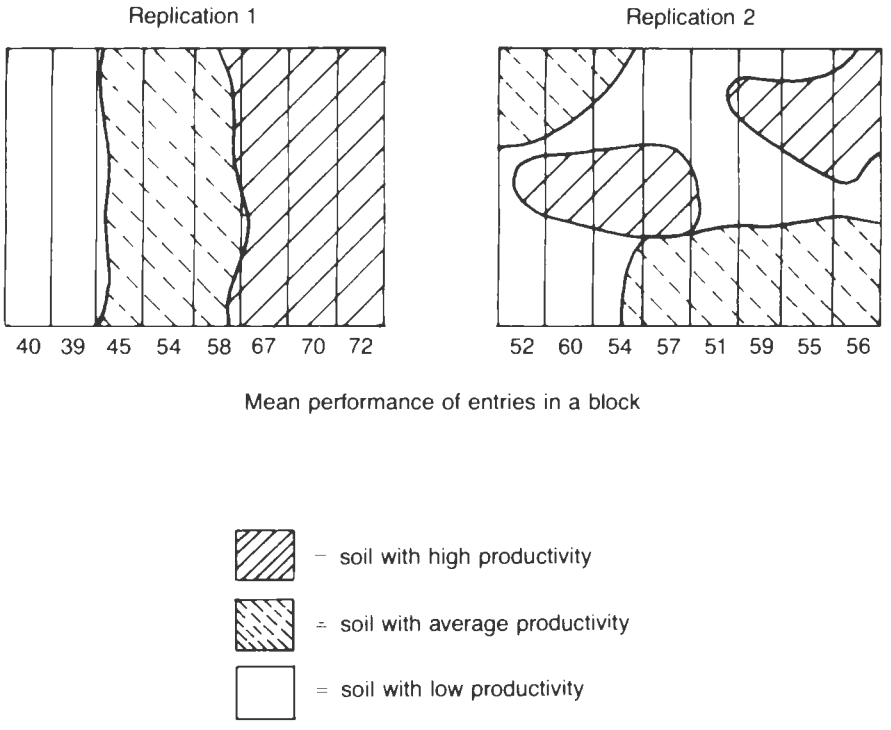


Figure 19-9 The effect of the pattern of variation in soil productivity on the effectiveness of the lattice design in accounting for environmental variation within a replication. The lattice would be more effective in replication 1 than in replication 2.

design cannot adjust for differences in productivity within a block; therefore, it would not be as effective in replication 2 as in replication 1.

The effectiveness of the lattice design compared with the randomized complete-block is expressed as relative efficiency. Relative efficiency is computed as a ratio of mean squares for experimental error of the two types of design.

$$\text{Relative efficiency} = \frac{\text{mean square for error of lattice}}{\text{mean square for error of randomized complete-block}} \times 100$$

The ratio is used to determine the number of replications that would have to be used with the randomized complete block to achieve a precision in detecting differences among the means of genotypes equal to that with a lattice design. A relative efficiency of 150 percent indicates that 50 percent more replication would have been needed with a randomized complete-block design than with a lattice.

The two types of design differ in the flexibility that is possible in a test. The randomized complete-block can accommodate any number of genotypes or replications. The lattice design requires that a specified number of genotypes and replications be included. For example, no lattice design can be used with 44, 58, or 74 genotypes. There is no restriction in a randomized complete-block for the length and width of a replication. For example, a test with 72 entries could be planted 8 plots long by 9 plots wide or 6 plots long by 12 plots wide. The shape of replication for a particular number of genotypes in a lattice is not as flexible. A test with 72 entries could be planted 8 plots long by 9 plots wide, not 6 plots long by 12 plots wide.

The randomization of an experiment and statistical analysis of data are more complex for a lattice than for a randomized complete-block. This can be important if the work is done by hand, but not if done by computer. Computer programs are available that will readily accommodate either type of design.

EQUIPMENT FOR EFFICIENT EVALUATION OF GENOTYPES

The efficient evaluation of a large number of genotypes is important for genetic improvement. Plant breeders have been actively involved in the development of equipment that permits them to evaluate more genotypes with equal or greater quality than was previously possible. The equipment ranges from simple hand devices to sophisticated computers.

Each crop has unique characteristics that influence the type of equipment used. Even for a certain crop, breeders differ as to the type of equipment they consider most desirable. Here only a small sample of available equipment will be used to illustrate how large numbers of genotypes are evaluated by plant breeders.

Preparation of Seed for Planting

The main steps involved in preparing a field experiment include packaging the seed and placing it in the proper arrangement for planting. Computers can be used to randomize entries and assign plot numbers. The computer system can print an adhesive label for each packet of seed to be packaged. The label contains the plot number, the entry number, and other information of value to the breeder. The plot and entry information also can be printed on pages used to record data in the field. The same work can be done by hand, but would require a large amount of labor and would be more subject to human error.

Seed is counted by hand or by electronic counting devices. If the number of seeds for a plot is large and precise numbers are not required, the seeds may be measured by volume.

Planting

Rapid planting of plots can be accomplished with engine-driven planters. Multiple-row plots may be planted from a single packet when each row does not require the exact same number of seeds. The seed is passed through a divider that separates the seed into a fraction for each row. The divider may be a powered spinning device or a gravity system.

The planter can move through the field without stopping. Seed for a row is placed in a container above a planting cone. When the row is to be planted, the container is lifted and the seed drops onto the planting cone. Two types of cones are used to distribute seed along the row. For one type, the base turns and carries the seed to the outlet. There it is knocked from the base by a stationary plate, falling through the outlet to the soil. This type of cone is used for relatively small seeds that do not roll easily, such as barley. The second type has fins mounted on the center cone. The seed falls onto a stationary base and is dragged by the fins to the outlet. The fins are well suited to relatively large seeds, particularly those that have a tendency to roll easily, such as maize and soybean. The length of a plot is a function of the distance traveled by the planter before all the seed has left the cone. At a constant ground speed, a cone must turn faster for short rows than for long rows. Adjustment of the speed of the cone rotation can be accomplished readily by several mechanical systems.

While the seed for one plot is being planted, the seed for the next plot is put in the container above the cone. There are a number of ways to determine when the container should be lifted to begin a plot. One way is to mark the beginning and end of each plot in the field before planting starts. When the planter reaches the beginning of a plot, the operator lifts the containers manually or electronically. The advantage of this procedure is that the location of each plot can be identified as soon as planting is complete. The second way is to use a cable extended across the field that has knobs spaced along it. The spacing between knobs is equal to the length of the plot and the alley. For plots that have rows 5 m long with a 1 m alley between them, the knobs would be spaced 6 m apart. As the planter passes by the cable, the knobs signal when the container should be lifted manually, or it activates an electronic tripping device. The cable is moved after each pass across the field. Use of the cable saves time at planting by eliminating the need to mark the start and end of plots manually.

Weed Control

Weed control is accomplished by the use of chemicals, cultivation, and hand weeding. The chemicals generally are those applied for weed control in commercial production of the crop. Cultivation equipment may be especially designed for use in research fields or may be the same equipment used commercially.

Preparation of Plots for Harvest

Trimming of plots to a constant length before harvest is done manually or with specialized equipment. Plots of small grains generally are trimmed to a constant length early in the season when the plants are about 30 cm tall. A rototiller or mower is passed along the end of each plot to kill the unwanted plants. The rototiller may be mounted on a tractor or may be a self-propelled unit that a person walks behind. Plots of soybean can be cut to a constant length with rotary mowers before seed filling begins. Two mowers are attached to a pipe so that they are separated by a distance equal to the desired plot length, and are driven perpendicular to the length of the rows.

Harvest

The most common type of harvester for the measurement of forage yield in the United States is a self-propelled flail chopper. The machine cuts the plants with a rotating flail that throws the cut portion into a collection point behind the driver. The plant material for a plot may be collected in a plastic container and weighed on a stationary scale set up in the field. To eliminate the labor required to use containers, an electronic scale can be mounted on the machine. The plant material is weighed and then it is discarded into a wagon.

The harvest of plots for their seeds is conducted with three different procedures or types of equipment. One procedure is to collect that part of the plant that bears the seed, weigh it directly, or carry it to a stationary machine for threshing. The plant part may be removed by hand or may be collected with a machine, such as a mower with a collection basket mounted behind the sickle. The harvested sample may be threshed immediately or dried for a period of time before threshing. One popular type of stationary machine is the Vogel thresher. The plants pass vertically through the machine as they are threshed. For a second type of stationary thresher, the material passes through the threshing cylinder and falls on a sieve that helps separate the seed from the plant debris. Air is used to separate the seed and the plant debris in both types of machine.

The second procedure for harvesting plots is to use a self-propelled thresher specifically designed for small plots. The plant part with the seed is gathered into the machine and passes through a threshing cylinder, then the seed and plant debris are separated by sieves and air. The seed may be placed into a bag and saved or may be weighed immediately and discarded. Seed harvested from self-propelled machines generally is more subject to mixtures than that harvested with a stationary thresher.

The third type of equipment is a commercial combine modified for the harvest of small plots. A commercial unit is used only when the amount of seed harvested

from a plot is relatively large and is not saved for planting. Modifications of the commercial combine include reduction of the number of rows harvested and the addition of equipment for weighing the seed.

Data Collection

Usually a number of characters are measured on each plot, such as height, standability, and yield. The data may be recorded in a field book, then manually entered into the computer for statistical analysis. Alternatively, the information may be recorded in an electronic data collector and transferred directly to the computer. This saves time and reduces the possibility of human error. Plot and entry designations also can be recorded on labels that can be read into the data collector by an electronic scanner.

Data Analysis

Computers facilitate the selection of lines by summarizing data in whatever manner is beneficial to the breeder. They save an extensive amount of time, minimize human error, and permit data to be summarized in a short period of time.

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