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.

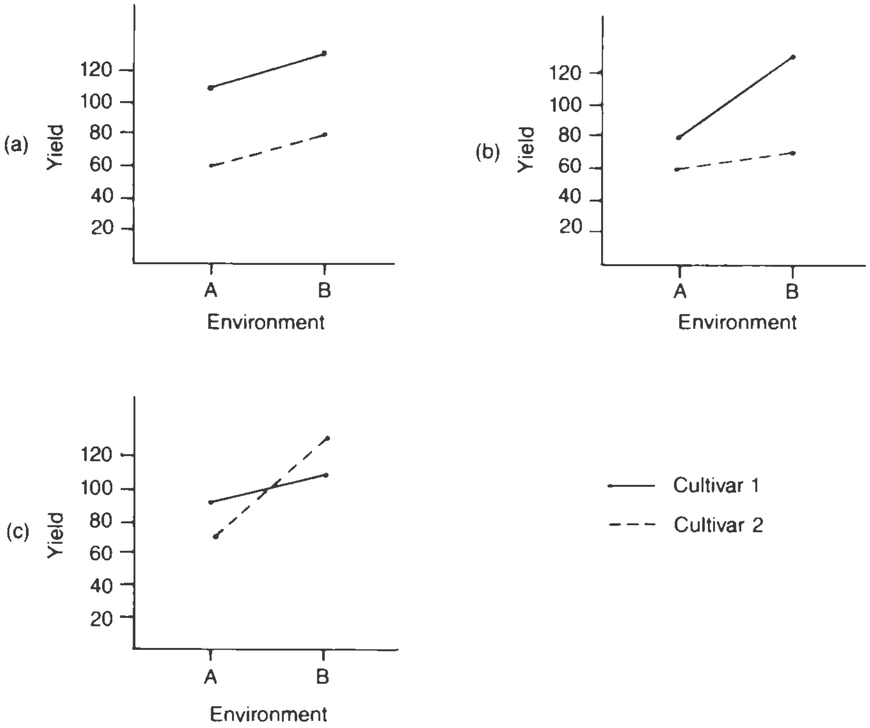
Unpredictable factors contribute to the interactions of genotypes with locations and years. Genotype × location, genotype × year, and genotype × location × year interactions have been evaluated in many crop species.

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	$g-1$	$\sigma_e^2 + r(\sigma_g^2 + \sigma_{gl}^2 + \sigma_{gy}^2 + \sigma_{gly}^2)$
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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