43

Selection and G x E: Introduction

If only two different environments are considered, the interaction may be expressed as a genetic correlation. When so formulated the genetic aspect of the situation becomes clear and a quantitative evaluation of the efficacy of different methods of selection may be easily obtained by procedures already devised for dealing with genetic correlations. — Falconer (1952)

Version 26 June 2014

Genotype-by-environment interactions (G x E for short), wherein genotypes differentially perform across environments (LW Chapter 22), has important implications for breeding. When selecting for trait performance, care must be taken to ensure that any response obtained under the environmental conditions used for selection translate into response under the conditions of the production system. A dramatic response to selection under controlled conditions may be greatly diminished, or even vanish, when those genotypes are expressed in a different environment. Similarly, an experimentalist would like to know whether a selection response observed in the laboratory is relevant to the expected response under field/natural conditions. Depending on the circumstances, G x E can be either desirable or undesirable. In some situations a breeder wants to select for genotypes that disproportionately respond to environmental inputs such as irrigation and fertilizer. In other settings, a breeder may wish lines that are largely refractory to changes in the environment. G x E is also important in evolutionary biology, being implicitly at the heart of many discussions on adaptation, with some genotypes assumed to be more optimal in some environments than others. This is also the notion of **locally-adapted** lines or breeds.

When extensive G x E is present, a breeder has three opinions: *ignore it*, *avoid it*, or *exploit it* (Eisemann et al. 1990). If one ignores G x E when $\sigma^2_{G\times E}$ is a significant fraction of the phenotypic variance, individual selection performs poorly as heritability is low and hence the phenotype of a single individual is a poor predictor of its breeding/genotypic value (Equation 38.9). One can try to mitigate G x E effects by using family or line selection over a number of environments, which reduces the contribution of $\sigma^2_{G\times E}$ to the heritability of the family/line mean (Equation 38.10). Breeders can try to avoid the consequences of G x E by selecting for lines with wide adaptability (i.e., broad tolerance/stability over environments). Finally, the bold breeder may attempt to exploit it by developing locally-adapted lines for the environment(s) of interest. The options that are available when dealing with G x E depend upon the *predictability* of the environment. If the environment has predicable components, then G x E can potentially be exploited. Conversely, if the environment has significant unpredictable components (such as year-to-year variation), G x E cannot be exploited and instead the breeder must try to mitigate its effects (for example, by selecting for lines which are more stable over environments).

Two broad classes of models can be used to examine genotype-environment interactions. The first (which is the subject of this chapter) is the **character-state** approach, treating the environment as distribution of discrete **macroenvironments**. At one extreme these are binary (such as a high- versus a low-growth diet, or stressed versus nonstressed environments), and much of our focus in this chapter is on two-environment selection. At the other extreme, the distribution of environments is highly complex and essentially unpredictable in that each

new realization is different, such as a series of growing seasons (typically years) for a set of particular locations. Chapter 39 examines selection in these more complex environments. Implicit in this discrete treatment is that there is no natural ordering of the environmental types. However, environmental factors are often continuous or at least graded, such as the performance of the trait over a gradient of temperate, rainfall, or soil nitrogen. This notion of a **reaction norm**, the behavior of a genotype as a function of one (or more) environmental variables, forms the second broad class of models for treating G x E. Chapters 40–42 (which develops the machinery for selection on *functions* as opposed to traits) examines selection response on reaction norms. The character-state and reaction norm approaches represent two opposite ends of the spectrum in modeling the environment. The character-state is a very holistic approach, assuming that environment is a black-box with little (or no) knowledge of in the actual factors that comprise it. The reaction norm, on the other hand, is a very reductionistic approach, focusing on one (or a few) specific factors and examines how a genotype performs as we change the values of these factors (for example, weight as a function of temperature). A third aspect of G x E, namely that some genotypes may differ in their *micro*-environmental variances, has been discussed in Chapters 13 and 37.

Our introduction to selection and G x E starts with an overview of the critical features of G x E (which are examined in greater detail in LW Chapter 22). One major theme of this chapter is the connection between multi-trait selection and G x E, as performance in different environments can be considered as correlated traits. The next two sections develop this theme, first by considering the direct and correlated responses over two environments when selection occurs in only one of them. Important issues, such as which environment to select in and the consequences for mean performance and stability, are developed for two environments within this framework. We then turn to simultaneously selecting in two (or more) environments, which is accomplished by selecting between groups (such are pure lines or segregating families) where group members are scored over several environments. We conclude this chapter with an introduction to multiple-environment trails, where lines are scored over several locations and several years. This introduces the necessarily background for a more detailed treatment in Chapter 39.

SELECTION AND G x E: BASIC IDEAS

G x E is Both a Challenge and an Opportunity

The presence of G x E offers both a challenge and an opportunity. As shown in Table 38.1, any particular genotype can fall into one of four possible classes when we jointly consider its **mean performance** and its amount of G x E over some **target population of environments** (**TEP**).

Table 38.1 Possible combinations of mean performance and level of G x E for a genotype, with their implications for breeding. After Ceccarelli (1989).

		Mean Performance	
		High	Low
Amount of G x E	High	Potential for locally-adapted lines	Potential for locally-adapted lines
	Low	Ideal. Potential for widely adaptive lines	Undersirable

The ideal genotype has high mean performance and low G x E, so that it does consistently

well in all environments. The result is a **widely-adaptive** genotype/line. At the other extreme is a genotype with low mean performance and low G x E, which is undesirable, as it does poorly everywhere. Thus, when G x E is low, one or a few lines/strains may perform best over all environments in the TEP. Conversely, when G x E is high, there is usually no single widely-adaptive line/strain that does best everywhere. Rather, with high G x E, the opportunity exists to select for **locally-adapted lines**, *provided* there are predictable features of the environment. If G x E is high, but the environment is unpredictable, then the best a breeder can do is to select for lines with good mean performance and low G x E. Spatial aspects of the environment (such as location) tend to contain more predicable features than temporal aspects (such as yearly variation).

Table 38.1 distills the key questions a breeder (or evolutionary biologist modeling a trait) need to consider regarding G x E. First, is there significant G x E? If there is, one must either try to select for genotypes/lines that show stability (similar performance) over environments or else attempt to select for locally-adaptive lines. If the environment has *predictable* features (for example hot versus dry; sandy versus clay soil), then locally-adaptive lines may be feasible. However, if most of the environmental contribution to G x E is *unpredictable*, such as year-to-year variation, there is little point for a breeder (or a genotype) in trying to predict the future, unless there are a very limited number of outcomes. The reality is that the environment generally tends to have both predicable (e.g., generally wet versus generally dry locations) and unpredictable (yearly variation in rainfall within a location) features. Breeders are thus faced with two competing tasks. First, there may be different **mega-environments** (also called **agroecological environments**), collections of macroenvironments within which only modest G x E occurs. In such cases, lines can often be found (or selected) that are widely-adaptive within each mega-environment. Second, the breeder attempts to select for genotypes/lines with low G x E for unpredictable features of the environment so that their performance is relative stable. Both of these themes are explored in the next chapter.

Components of $\sigma^2_{G\times E}$: Variance Heterogeneity and Lack of Correlations

It is useful to remind the reader that there are two different sources for G x E — differences in the genetic variances across environments (**genetic heterogeneity**, often referred to as **scale effects**) and lack of perfect correlation among breeding values across environments (LW Chapter 22). For two environments, Robertson (1959) showed that the G x E interaction variance can be partitioned into theses two sources,

$$\sigma^2_{G\times E} = \frac{\left(\sigma_{A_1} - \sigma_{A_2}\right)^2}{2} + \sigma_{A_1}\,\sigma_{A_2}(1 - r_A) \tag{38.1a}$$

where $\sigma^2_{A_i}$ is the additive variance in environment i and r_A is the additive genetic correlation across environments. Cockerham (1963) and Itoh and Yamada (1990) extended Robertson's decomposition to n_e environments,

$$\sigma^2_{G\times E} = \frac{1}{n_e - 1}\sum_{j}^{n_e}\left(\sigma_{A_j} - \overline{\sigma}_A\right)^2 + \frac{2}{n_e(n_e-1)}\sum_{i<j}^{n_e}\sigma_{A_i}\sigma_{A_j}[1 - r_A(i,j)] \tag{38.1b}$$

Here $\overline{\sigma}_A$ is the average of the square root of the genetic variances over all environments, and $r_A(i,j)$ is the correlation between environments i and j. While Equation 38.1 is phrased in terms of additive genetic variances, it also holds for *genotypic* variances (with σ^2_A and r_A replaced by σ^2_G and r_G) when the focus is on a collection of pure (inbred or nearly-so) lines, as is typically the case in field trails of many crops. Hence, there can be G x E even with perfect correlations across environments ($r = 1$) and likewise even when the genetic variances are constant across environments ($\sigma_{A_j} = \overline{\sigma}_A$). With estimates of the genetic variances from

each environment in hand, the relative contributions of genetic heterogeneity versus lack of correlation can be directly accessed. For example, Cooper and DeLacy (1994) examining grain yield in 15 wheat lines over ten environments in Queensland (Australia) found that 69% of $\sigma^2_{G\times E}$ was due to lack of perfect correlation while 31% was due to heterogeneity of genetic variances across environments.

Breeders are generally more concerned about the variance in G x E generated by lack of perfect correlation across environments, as this can result in the ranking of genotypes changing over environments (this type of G x E is often called a **crossover interaction**). As we will see, however, both components (differences in variances, lack of perfect correlation across environments) enter into discussions of selection response when G x E is present.

Example 38.1. Hühn et al. (1993) examined data from the official registration trails for five crop species (Faba beans, Fodder beets, Sugar beets, oats, and winter rape) carried out in Germany from 1985-89. The correlation among line rankings (across environments for a given crop within the same year) was examined using Kendall's coefficient of concordance K, which is closely related to the Spearman rank correlation coefficient ρ. The following values were seen:

	Faba beans	Fodder Beets	Sugar Beet	Oats	Winter rape
K (mean)	0.444	0.637	0.712	0.433	0.476
K (range)	0.40-0.47	0.64-0.86	0.63-0.79	0.35-0.60	0.40-0.56
ρ (mean)	0.376	0.607	0.678	0.383	0.416
ρ (range)	0.33-0.40	0.59-0.84	0.60-0.76	0.29-0.55	0.34-0.51

For these data, the consistency of rankings across environments was only modest, especially for Oats, Faba beans, and Winter rape. The authors examined possible connections between K and variance component estimates (here σ^2_G, $\sigma^2_{G\times E}$, and σ^2_e, the line, line-by-location, and within-plot variation). By regressing the mean correlation between ranks for a given year on various ratios of variance components, they observed that K is well predicted by

$$K \simeq \left(1 + \frac{\sigma^2_{G\times E} + \sigma^2_e/n_r}{\sigma^2_G}\right)^{-1}$$

where n_r is the number of replicates per location. For these data sets it appears that most of the variation in $\sigma^2_{G\times E}$ is due to differences in correlation. However, this is a very selected set of data, namely lines submitted to official trails and have likely been selected for stability.

$G \times E$ is Context-Specific

Finally, it is important to stress that G, E, and $G \times E$ are highly *context-specific*. G x E is almost inevitable if genotypes are tested over a sufficiently large set of environments. Conversely, if genotypes are examined within a small, and appropriate chosen, set of environments, G x E may largely disappear. Thus, the mega-environment for a set of particular genotypes is often defined as that collection of environments where small amounts of $G \times E$ are displayed among the elements in this set. Defined in this fashion, a particular mega-environment is a function of a particular set of genotypes, environments, and the particular trait being scored.

RESPONSE IN TWO ENVIRONMENTS

Our discussion of selection and G x E starts with the assumption that there are only two environments of interest, which allows us to make several key points without dealing with

the further complications that arise in the more realistic situation of a large number of environments. We start with selection in only one environment, but the response is (potentially) scored in another. Thus, the focus in this section is on the response over two environments when selection occurs in only one of then. The next section examines response when selection is based on genetic groups scored over two (or more) environments.

The notion that certain genotypes perform best in specific environments was recognized by the earliest breeders, at least on an intuitive level, while the more formal discussions of the implications for G x E for applied breeding and evolution began with Wright (1939), Haldane (1946), Hammond (1947), and Lerner (1950). The modern treatment of selection and G x E traces to the critical observation by Falconer (1952) that one can treat measures of the same trait in different environments as *correlated characters*. This allows all of the machinery for direct and correlated responses and multitrait selection (Chapters 30 – 36) to be used to examine selection response across environments when G x E is present. While Falconer's initial suggestion was that this approach was viable for two environments, it works equally well for k distinct environments by treating these as a k-dimensional vector of traits and estimating the $k \times k$ $\mathbf{G}$ matrix. Thus, in those (admittedly rare) cases where we have estimates of both the genetic and phenotypic covariance matrices (for the trait measured in the k different environments), the multivariate breeder's equation and index selection theory can be directly applied. In the absence of any such estimates, are there any rules/trends that apply when selecting traits over two environments? Hammond (1947) and Jinks and Connolly (1973), as well as others to be discussed below, have suggested some informal rules in this case.

Response in a Target Environment: Hammond's Conjecture

When the breeder has two (or more) environments to choose from in which to perform selection (for example, a highly-managed controlled setting and a more natural field or production setting), the question naturally arises as to which environment should be used. In most settings, the target environment for a breeder would be the field or production setting, but there may be significant logistical advantages to working in a more controlled environment. Hammond (1947) made the interesting suggestion that selection be undertaken in the more favorable environment for a trait in order to maximum progress in the less favorable environment, an idea we will call **Hammond's conjecture**. His idea is that the favorable environment may allow for better discrimination among genotypes (due to increased genetic variance and/or reduced environment variance). Hammond's suggestion went against the common assumption that selection should be performed in the target environment (Wright 1939, Lush 1946, Nichols 1947, Kelley 1949), but raised the important idea that perhaps (at least in some cases) larger responses can result from selecting in a different environment than the target (i.e., indirect response exceeding direct response, see Chapter 30). Some plant breeders working with pure (i.e., inbred) lines also supported Hammond's notion, arguing that selection in the highest-yielding environments would produce the greatest separation between genotypes (Frey 1964, Roy and Murty 1970, Fasoulas 1973), while others noted that such favorable environmental conditions are not representative of typical environments where the majority of the crop is cultivated (Donald 1962, Hinson and Hanson 1962, Ceccarelli 1989, Simmonds 1991). This theme of direct versus indirect response will arise repeatedly throughout the chapter, and we will return on several occasions to this question of where to select.

Example 38.2. Falconer and Latyszewski (1952) and Falconer (1960) selected for growth rate in mice in two nutritional environments (this work was also discussed in Example 30.7). In one

environment, mice were housed individually and food was restricted to around 75% of normal intake, while in the other, mice were housed in groups of four to six and given unlimited food. Selection for increased weight gain was effective in both environments, although heritability was higher (0.29 to 0.20) in the restricted diet environment (although this difference was not significant). The higher heritability value arose because while the additive genetic variance was reduced in the poorer environment (by around 45%), the environmental variance was reduced even more (around 66%). Falconer suggested that this reduction in σ_e^2 may be, in part, due to rearing single versus multiple individuals.

When the restricted-diet selected individuals were grown in the unrestricted environment, they showed a significant weight gain, but when the unrestricted-selected individuals were reared in the restricted diet environment, they did not. These results are a direct contradiction to Hammond's conjecture, in that selection in the *poorer* environment gave the larger response in the target population. Further, there were other significant differences. The high-feed selected lines contained around 24% more body fat than the restricted-diet lines when both where grown in the high-feed environment. Thus, selection in the restricted diet also resulted in leaner mice, which (in many cases) would also be economically favored in a selection program.

The careful reader will note that Falconer's experiment showed an extreme *asymmetric correlated response*, with a correlated response in one direction (response in high from low-selected lines) but not in the other (no response in low from high-selected lines). Recall from Chapter 31 that while modest differences in correlated responses can occur under the infinitesimal model (provided the traits have different heritabilities), the dramatic differences seen in this experiment likely could only have arisen from allele frequency changes. Indeed, given the differences in fat content between the two lines, there was clearly selection on different pathways in high versus low lines, and hence selection on at least some different genes.

While Falconer's experiment was fairly conclusive evidence that Hammond's conjecture is not universal, there are also cases where it holds. For example, Lasslo et al. (1985) found that selection for weaning weight in Targhee sheep in a high nutritional setting results in as much improvement in growth rate under range conditions as was seen with direct selection under range conditions. Similarly, Kirigwi et al. (2004) found for wheat (*Triticum aestivum*) that selection in both high and low moisture environments resulted in comparable responses in yield in a low moisture environment. Lasslo et al. (1985) review (briefly) a number of other animal experiments, some of which support Hammond, others which are more in line with Falconer's results. Whether Hammond's conjecture holds for a particular trait from a particular genetic population under particular environmental conditions is an empirical question, but Falconer (1952) showed that significant guidance is provided from the theory of multiple trait selection.

Falconer did so by rephrasing Hammond's suggestion in terms of the conditions under-which a correlated response (change in the less favorable environment from direct selection in the more favorable one) exceeds the direct response (direct selection in the less favorable environment). Assuming equal selection intensities are possible in both environments, Equation 30.22 gives the requirement $r_A h_F / h_U > 1$ where h_F^2 and h_U^2 are the trait heritabilities in the favorable and unfavorable environments, and r_A is the genetic correlation across environments (with clones, σ_G^2 replaces σ_A^2 and broad, as opposed to narrow, sense heritability is used). If the goal is trait improvement in one environment, unless there are major differences in trait heritabilities, direct selection in the target environment is the method of choice. Even if there are major differences in h^2 across environments, we still require a high (and positive!) genetic correlation for the correlated response (selection in the non-target environ-

ment) to exceed the response from direct selection in the target environment. Of course, this ignores real-world logistical constraints which may reduce the efficiency of selection in the less-favorable environment, such as differences in selection intensity, or overall feasibility. Equation 30.22 allows these to be incorporated as well (through the ratio of the selection intensities), allowing us to compare different schemes.

Example 38.3. Different environments can, of course, be largely man-made. One example is the contrast between **low-** and **high-input** production systems. Low-input systems have very little added during production, while high-input systems often have considerable inputs such as fertilizers, pesticides, and fungicides. While high-input systems can create environments with substantially larger yields, they also result in potentially more environmental impact, can be significantly more costly, and may only be feasible in a small subset of all possible production areas. Presterl et al. (2003) and Brancourt-Hulmel et al. (2005) examined the relative efficiency of direct and correlated responses in low and high N (nitrogen) input systems in European maize and French winter wheat, respectively. Presterl et al. estimated heritabilities for grain yield in maize in high and low N systems, as well as the genetic correlation between systems, finding $r_A h_H / h_L \simeq 0.70$. Hence, correlated response in low N from direct selection for yield in high N is only 70% of the expected response from direct selection in low N. Similarly, Brancourt-Hulmel et al. found that the efficiencies of indirect selection on grain yield in wheat ranged from 0.15 to 0.99 over the pairs of environments examined. Hence, indirect selection is always beaten by direct selection with the same selection intensity. A potentially mitigating factor is lower yields in low N system, and hence the potential for stronger selection in high-N systems.

When treating the same character scored in two different environments as a correlated trait, we expect high levels of pleiotropy. Indeed, if there is no G x E, the genetic correlation between traits is one, with each allele having an identical effect in both environments. Thus, we expect that complementary pleiotropy (alleles with ++ or $--$ effects on the traits over the two environments) will be common. Of interest is the frequency of alleles with antagonistic pleiotropy, those alleles that increase the trait in one environment but decrease it in the other (i.e., $+-$ and $-+$ alleles), as such alleles reduce the genetic correlation between environments. Recall from Chapter 31 that when pleiotropic alleles are present, the correlated changes in a trait can be very unpredictable, as the genetic covariance can be quite fragile to even small changes in allele frequencies. This is especially true when antagonistic alleles are present.

Improving an Index of Mean Performance

The above discussion was concerned with response in a particular environment, and the question of interest was whether it is ever better to select in some other environment besides the targeted one. We now consider the situation where the response over *both* environments is of interest. James (1961) considered this question by examining the response for a index of weighted environmental responses,

$$H = ag_1 + g_2 \tag{38.2}$$

Here a is the weight placed on the response in environment one relative to environment two and g_i is the breeding (or genotypic) value of the trait in environment i. This is a standard index selection problem, and provided we can obtain the genetic and phenotypic correlations across environments (for example, by considering the means of a sibship split between environments or by using inbred lines), the standard machinery of index selection (Chapters 33, 34) can be used (e.g., Van Sanford et al. 1993).

Suppose we only have resources to select in one environment. Using standard results for direct and correlation responses with two traits (Equations 30.20 and 30.21), James obtained expressions for the response in the index when selection occurs in only one environment. Suppose selection occurs only in environment one, then

$$R_1 = h_1\sigma_{A_1}\overline{\imath}, \quad \text{and} \qquad CR_2 = r_A\sigma_{A_2}h_1\overline{\imath}, \tag{38.3a}$$

and the expected response in the index becomes

$$R_H(1) = aR_1 + CR_2 = h_1\sigma_{A_1}\left(a + r_A\frac{\sigma_{A_2}}{\sigma_{A_1}}\right)\overline{\imath} \tag{38.3b}$$

If we are selecting among pure lines, then ρ_G and σ^2_G replace their additive-genetic counterparts, and board-sense as opposed to narrow-sense heritability is used. Similarly, selecting only in environment two yields

$$R_H(2) = aCR_1 + R_2 = h_2\sigma_{A_1}\left(ar_A + \frac{\sigma_{A_2}}{\sigma_{A_1}}\right)\overline{\imath} \tag{38.3c}$$

Setting $v = \sigma_{A_2}/\sigma_{A_1}$, we have

$$\frac{R_H(1)}{R_H(2)} = \frac{h_1}{h_2}\left(\frac{a + r_A v}{ar_A + v}\right) \tag{38.3d}$$

as the ratio of expected responses on the index from selection in only a single environment (as obtained by James). Equation 38.3d shows that the optimal environment for selection is a function of *both* components of $\sigma^2_{G\times E}$ (heterogeneity of genetic variances v and genetic correlation across environments r_A).

As a minor aside in his paper, James noted that "exactly the same methods can be applied to selection in more than two environments", fully realizing that index selection machinery allows us to obtain the optimal index for the weighted response over any defined combinations of environments, *provided* we have estimates of $\mathbf{P}$ and $\mathbf{G}$ for the trait over these environments. It is also worth reminding the reader that the Smith-Hazel index holds even when there are different traits in the index and merit functions (Chapter 33). Thus, provided we have estimates of $\mathbf{P}$ and $\mathbf{G}$, we can obtain the optimal index for weighted response over k environments given selection only occurs in a subset $j < k$ of them.

More generally, from the theory of correlated response (Chapter 30), the expected response in environment i from selection in environment j is

$$CR_{i\,|\,j} = r_A(i,j)\sigma_{A_i}h_j\,\overline{\imath}_j \tag{38.4a}$$

Pederson and Rathjen (1983) and Cooper and DeLacy (1994) offer a further simplification of this result. Following Burdon (1977), if there is no covariance between environmental values, the expected phenotypic correlation between the same hypothetical individual measured in both environments is

$$r_P(i,j) = h_i h_j r_A(i,j) \tag{38.4b}$$

where h^2_i is the heritability measured in environment i (LW Equation 21.11). Hence,

$$r_A(i,j) = \frac{r_P(i,j)}{h_i h_j} \tag{38.4c}$$

Substituting Equation 38.4c into 38.4a, and recalling that $h_i = \sigma_{A_i}/\sigma_{z_i}$ gives

$$\begin{aligned} CR_{i\,|\,j} &= \frac{\rho_P(i,j)}{h_i h_j}\sigma_{A_i} h_j\, \overline{i}_j = \rho_P(i,j)\frac{\sigma_{A_i}}{h_i}\,\overline{i}_j \\ &= \rho_P(i,j)\sigma_{z_i}\overline{i}_j \end{aligned} \tag{38.4d}$$

as obtained by Pederson and Rathjen (1983). Equation 38.4d shows that the expected correlated response from selection in a different environment can be expressed entirely as a function of the phenotypic correlation and the phenotypic variance (Cooper and DeLacy 1994). While this may seem surprising at first, recall that the critical assumption leading to this result is that all of the cross-environment phenotypic correlation is genetic in nature.

Sensitivity and the Jinks-Connolly Rule

A second issue with selection response over two (or more) environments is whether the **sensitivity** (or its complementary measure, **stability**) of the trait (differences in performance across environments) changes following selection on that trait in a particular environment. This is an important issue in plant breeding as stability in year-to-year performance (given that each year with its unique climatic features is a new environment) is often as important as mean performance. With just two environments, sensitivity is simply the difference in the mean of a genotype in the two environments, and we use this metric here. When a trait is measured in more than two environments, a variety of stability measures (and indeed stability concepts) have been proposed and these are examined in the next chapter.

When focusing on two environments, are there somewhat general statements we can make about the response in sensitivity without knowing all the genetic details required to construct the appropriate selection indices? Jinks and Connolly (1973), Jinks and Pooni (1988), and Falconer (1989, 1990) suggested that some useful generalizations do emerge.

A nice synthesis of these suggested generalizations is given by Falconer (1990). With a slight modification of his terminology, the relationship between the effects of the environment and the direction of selection can be classified as either **antagonistic** or **synergistic G x E selection**. Antagonistic selection is in the opposite direction from the environmental effect, for example, up-selecting in an environment that has a reduced trait value and down-selecting in an environment with an increased trait value. Synergistic selection is selecting along the environment trend — up selecting in an environment that tends to increase trait value and down-selecting in an environment that decreases trait value. The G x E is inserted to avoid confusion with similar descriptions for index selection (e.g., antagonistic index selection, wherein traits are selected in the direction opposite of their genetic correlations, Chapter 30), but will generally be dropped when the context is clear.

With just two traits, the sensitivity is most easily defined as the difference in trait means across environments, and this is often rescaled to a value of one before selection. Hence, if μ^* denotes the mean after some period of selection, then the sensitivity can be scaled by

$$s^* = \frac{\mu_H^* - \mu_L^*}{\mu_H - \mu_L} \tag{38.5}$$

where μ_H and μ_L are the means in the high and low environments before selection. If s^* is less than one, then selection results in decreases sensitivity (and hence greater stability) of the trait over environments, while the converse is true when the sensitivity after selection exceeds one.

Jinks and Connolly (1973) and Jinks and Pooni (1988) made the important suggestion that *antagonistic selection reduces environmental sensitivity* (i.e., improves stability), while *synergistic selection increases sensitivity* (decreases stability), an observation that Falconer (1990)

denotes as the **Jinks-Connolly rule**. If generally correct, this is a powerful observation. A related idea is Falconer's (1989) suggestion that antagonistic selection be used to improve *mean* performance, i.e., use upward selection in a bad environment to improve an index of performance over *both* environments. A similar notion has also been proposed by plant breeders, namely selecting in a stressed environment in order to improve performance over both stressed and non-stressed environments (e.g., Johnson et al. 1968, Shabana et al. 1980). Note that this is exactly the converse of Hammond's conjecture (which is to use synergistic selection – upwards selection in the good environment). How much support is there for these suggestions?

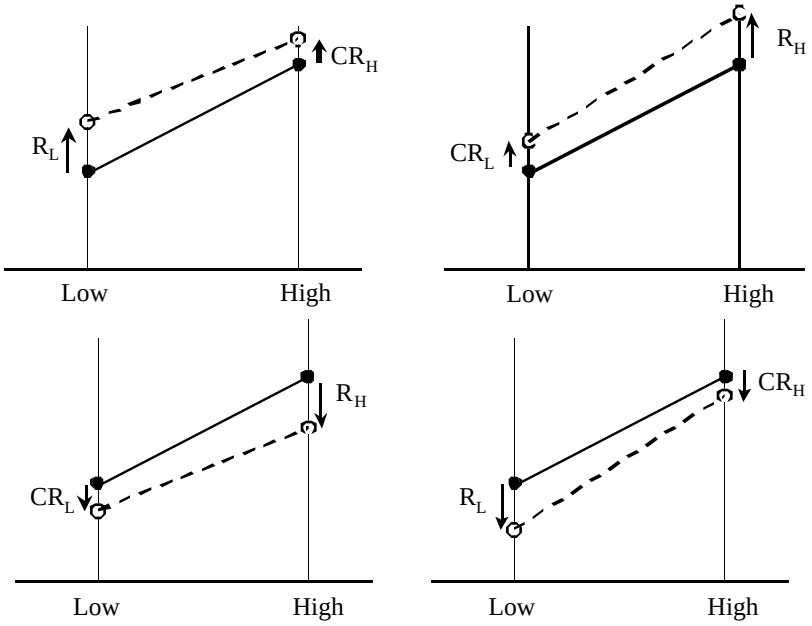

Figure 38.1. Examples of antagonistic (left) and synergistic G x E selection (right) when increasing (top) or decreasing (bottom) the overall trait mean across environments. The solid circles represent population means in a particular environment (denoted by Low and High), while the open circles are the population means following selection. The sensitivity (differences in mean values between environments) is given by the slope of the line connecting the two means, scaled to be one for the unselected populations (Equation 38.5). **Left:** Under antagonistic selection, we select *against* the environmental trend, up-selecting in the low environment (top) or down-selecting in the high environment (bottom). R and CR denote the direct and correlated responses. Notice that when $|R| > |CR|$, sensitivity is decreased (the slope of the lines connecting the means after selection is less than one). **Right:** Under synergistic selection, we select *with* the environmental trend, up-selecting in the high environment (top) or down-selecting in the low environment (bottom). Note here that when $|R| > |CR|$, sensitivity is increased (the slope of the lines connecting the means after selection is greater than one). After Falconer (1990).

Falconer (1990) reviewed the experimental literature, and found support for the Jinks-Connolly rule: in 14 of 21 cases, antagonistic selection decreased sensitivity, while synergistic selection increases it in 16 of 21 cases. Thus, while Jinks-Connolly does not hold as a *rule*, it does seem to hold as a *trend*. As to Falconer's (1989) suggestion that mean performance is best improved by antagonistic selection, it was better than synergistic selection for increasing

the mean in 8 of 13 cases, and in decreasing the mean in 6 of 8 cases. Hence, there is also some support for this approach, but Falconer (1990) later warned (as we show below) that there is no theoretical justification for his earlier suggestion. Further, the plant breeding literature shows no clear advantage to *mean* performance by selecting in the more stressed environment (e.g., Shabana et al. 1980, Zavala-García et al. 1992, Kirigwi et al. 2004).

Both of these suggestions can be easily addressed in a framework based on direct versus correlated responses. We start with sensitivity first. Figure 38.1 makes the main point: When the direct response is greater than the correlated response, the result is increased sensitivity under synergistic selection and decreased sensitivity under antagonistic selection. Hence, Jinks-Connolly rule holds when the direct response exceeds the correlated response, something we expect to happen often, but not always. More formally, if we are selecting to increase the mean, then Jinks-Connolly holds when $R_L > CR_H$ (top left of Figure 38.1), or (Equation 38.3a) when $\sigma_{A_L} > r_A\sigma_{A_H}$. If we are selecting to decrease the mean (bottom left of Figure 38.1), then Jinks-Connolly holds when $R_H > CR_L$ (considering the absolute values of responses), or when $\sigma_{A_H} > r_A\sigma_{A_L}$. Thus one condition for Jinks-Connolly to fail is a large difference in the genetic variances between environments but a strong genetic correlation between them. In terms of the Robertson-Cockerham decomposition of $\sigma^2_{G\times E}$, this implies that the first term of Equation 38.1a/b dominates the second.

While Jinks-Connolly suggests a general trend and is expected to hold more often than not, Falconer (1990) noted that a modification of this rule held in all 24 experimental cases he examined, namely that the *sensitivity is less after antagonistic selection than after synergistic selection*. Since the sensitivity is a slope, this means that the change in the numerator of Equation 38.5 is greater under antagonistic selection than under synergistic selection. When selecting to decrease a trait, this requires

$$(R_H - CR_L) - (CR_H - R_L) > 0 \tag{38.6a}$$

which rearranges to recover

$$R_H + R_L > CR_H + CR_L \tag{38.6b}$$

with this same condition holding for selection to increase a trait. Hence, for Falconer's modification to hold, the less restrictive assumption that the sum of the direct responses is greater than the sum of correlated responses must hold.

What about Falconer's (1989) suggestion that *mean performance* over the two environments is best improved by antagonistic selection? If the mean change is equally weighted in both environments, then when selecting to increase a trait, under antagonistic selection direct response occurs in the low environment, while under synergistic selection direct response occurs in the high environment. Thus, Falconer's (1989) suggestion holds when the average of the direct response in low and the correlated response in high exceeds the direct response in high and the correlated response in low,

$$R_L + CR_H > R_H + CR_L \tag{38.7a}$$

Assuming equal selection in both environments, then from Equation 38.3a, this reduces to

$$h_L\left(\sigma_{A_L} + r_A\sigma_{A_H}\right) > h_H\left(\sigma_{A_H} + r_A\sigma_{A_L}\right) \tag{38.7b}$$

Conversely, when selecting to decrease trait value, this condition becomes

$$R_H + CR_L > R_L + CR_H \tag{38.7c}$$

Note that Equations 38.7a and 38.7c are mutually exclusive, so that if antagonistic selection is better in one direction, it will be worse in the opposite direction. Thus, as Falconer (1990) pointed out, there is little theoretical justification for his earlier (1989) suggestion.

All of the above theory assumes the most basic version of the breeder's equation, in particular no changes in variances and covariances and also that responses are symmetric. We have already seen that if heritabilities are unequal, then the covariances can differentially change even under the infinitesimal model (Chapter 31), leading to asymmetric correlated responses. Likewise, when sufficient allele frequency change occurs, any initial symmetries in responses likely disappear, and no general statements can be made.

SELECTING IN TWO ENVIRONMENTS

While we have been considering the response over both environments, the careful reader will have noticed that selection was always assumed to occur in just *one* environment, allowing individual selection to be used. For example, parents may be selected in a high-performing environment, while their offspring (and hence response) are scored in both high- and low-performing environments. We now expand our analysis to allow for selection in multiple environments, for example by using between-line or between-family selection based on the performance of group members over a number of environments. Before considering this, a few comments on the cost of ignoring G x E are in order.

The Cost to Response from G x E

As a benchmark for selection when $G \times E$ is present, if environmental structure is ignored and simple mass selection used (choosing the best performing individuals based solely on their phenotypic values), then the expected response becomes

$$R = \overline{\imath}\sigma_z h_z^2 = \overline{\imath}\,\frac{\sigma_A^2}{\sigma_z} = \overline{\imath}\,\frac{\sigma_A^2}{\sqrt{\sigma_G^2 + \sigma_{G\times E}^2 + \sigma_E^2}} \tag{38.9a}$$

where σ_G^2 and σ_E^2 are the genetic and environmental variances. When $\sigma_{G\times E}^2$ is large relative to σ_A^2, the heritability is low and selection very inefficient, as an individual's phenotypic value in one environment is a poor predictor of their average breeding value over all environments. If we are selecting among clones (or pure lines) then σ_G^2 replaces σ_A^2. Setting $\sigma_{G\times E}^2$ to zero, Matheson and Cotterill (1990) note that the "cost" (loss of potential gain) of genotype-environment interaction when using standard mass selection is

$$1 - \sqrt{\frac{\sigma_G^2 + \sigma_E^2}{\sigma_G^2 + \sigma_{G\times E}^2 + \sigma_E^2}} \tag{38.9b}$$

We can improve upon response if something about the environmental structure is known. The simplest approach is stratified mass selection (Chapter 10), where the environment is assigned into blocks and individual selection occurs within each block (Equation 10.14). While this approach accounts for potential differences in the macroenvironmental values between blocks, it does not account for differences due to $G \times E$. Under either standard or stratified mass selection, selection is still based on the values of individuals (adjusted by block mean in the case of stratified selection). However, each genotype is still assessed in only a single environment.

Selecting a Group Over Several Environments

Now suppose we wish to simultaneously select across two (or more) environments. The obvious problem is that we typically cannot use the same individual to measure the trait over several environments. Instead, we must resort to measuring different individuals in each

environment, using genetic relatedness to connect them across environments. Thus, selection is based on the mean performance of individuals from a particular **genetic group** (such as a line, or half- or full-sib families) that are distributed over environments (e.g., Dickerson 1962, Scheinberg 1973, Burdon 1977). If we are using members of a group with an average coefficient of coancestry of Θ, then the correlation in breeding values between members *across* environments (say i and j) is given by $2\Theta\rho_A(i,j)$, where $\rho_A(i,j)$ is the correlation in breeding values if we were able to measure the same individual in both environments i and j (LW Chapter 22). For ease of presentation in what follows in this (and the next) chapter we often use genotype or line to refer to the genetic group.

The simplest application of this approach is a very common setting in plant breeding, where inbred lines (typically regarded as being sufficiently inbred to be considered clones, or nearly so) are measured in n_e environments, often with replication (n_r individuals from each group measured within each environment). The basic model for the value of the k-th replicate of line i in environment j is

$$z_{ijk} = \mu + G_i + E_j + GE_{ij} + \epsilon_{ijk} \tag{38.10a}$$

where G and E are the line and macro-environmental effects and ϵ the residual (the micro-environmental value that the kth replicate experiences, which are assumed to be uncorrelated and homoscedatic with constant variance σ^2_e). If the lines are still segregating, then e also includes the deviation of the genotypic value from the line mean G. The line mean for genotype i becomes

$$\begin{aligned}\overline{z}_i &= \frac{1}{n_e\, n_r}\sum_{j=1}^{n_e}\sum_{k=1}^{n_r}(\mu + G_i + E_j + GE_{ij} + \epsilon_{ijk}) \\ &= \mu + G_i + \frac{1}{n_e}\sum_{j=1}^{n_e}(E_j + GE_{ij}) + \frac{1}{n_e\, n_r}\sum_{j=1}^{n_e}\sum_{k=1}^{n_r}\epsilon_{ijk}\end{aligned} \tag{38.10b}$$

Assuming that G_i, GE_{ij}, and E_j are all uncorrelated, the variance of the line means becomes

$$\sigma^2(\,\overline{z}\,) = \sigma^2_G + \frac{\sigma^2_E + \sigma^2_{G\times E}}{n_e} + \frac{\sigma^2_e}{n_e n_r} \tag{38.10c}$$

Selecting clones with the greatest mean over environments, the expected response becomes

$$R = \overline{\imath}\,\frac{\sigma^2_G}{\sigma_{\overline{z}}} = \overline{\imath}\,\frac{\sigma^2_G}{\sqrt{\sigma^2_G + (\sigma^2_E + \sigma^2_{G\times E})/n_e + \sigma^2_e/(n_r\, n_e)}} \tag{38.10d}$$

Replication of group members reduces the contributions from $\sigma^2_{G\times E}$, σ^2_E, and σ^2_e to the variance of the line mean, which results in a higher heritability, increasing response. A common modification of Equation 38.10 is that the environmental effect is often treated as a fixed effect, and hence the data are adjusted to account for this, and the σ^2_E term disappears. One version of this is stratified mass selection, when contrasts are made within a given block. Treating E as a fixed effect is a more general way to accomplish this same goal of removing the effects of E (but not $G \times E$!). We show later (Example 38.4) how to further improve Equation 38.10d by decomposing the G x E interaction into additional effects such as location, year, and year-by-location contributions.

It is important to point out a critical assumption that leads to Equation 38.10d. Starting with Equation 38.10a, we assumed that the genotypic and G x E effects are uncorrelated and homoscedastic (variances are constant, being independent of the subscript on G and GE),

namely $G_i \sim (0, \sigma^2_G)$ and $GE_{ij} \sim (0, \sigma^2_{G\times E})$. This implies that the genetic variances are the same in each environment, as (ignoring the environment random factor E),

$$\sigma(z_{ij}, z_{ij}) = \sigma(G_i + GE_{ij}, G_i + GE_{ij}) = \sigma^2_G + \sigma^2_{G\times E}$$

Likewise, the genetic covariance between the same genotype (i) measured in two environments (j, k) is

$$\sigma(z_{ij}, z_{ik}) = \sigma(G_i + GE_{ij}, G_i + GE_{ik}) = \sigma^2_G$$

This particular covariance structure wherein the genetic variances are the same across all environments and the genetic covariances are the same across all pairs of environments is called **compound symmetry**. Obviously, this is only a very narrow view of G x E, as in general the genetic variances can change across environments and different pairs of environments can display different correlations (e.g., Equation 38.1b). Further development of selection response under more general covariance structures in covered in the next chapter (starting with Equation 39.37)

The idea is essentially the same when using half- or full-sib families, but with a little more bookkeeping (Chapter 17). Selection is based on the family means, with representive members from the chosen families randomly crossed to form the next generation. The resulting response is given by

$$R = \overline{i}\,\frac{\sigma^2_{AF}}{\sigma_{\overline{z}}} \tag{38.11a}$$

where the between-family additive genetic variance σ^2_{AF} is given below and the variance in family means $\sigma^2_{\overline{z}}$ is given by Equation 17.39a (using the definitions offered by Equations 17.11a and 17.11b). If n_r family members are measured in each of n_e environments, then setting $N = n_r\, n_e$,

$$\sigma^2_{\overline{z}} = \sigma^2_{GF} + \sigma^2_{E_c} + \frac{\sigma^2_{F\times E}}{n_e} + \frac{\sigma^2_{Gw} + \sigma^2_e}{N} \tag{38.11b}$$

where E_c is the common family environmental effect, E the remainder of the environmental effects and GF the total genetic variation accross families and $F \times E$ the family-by-environment interaction. Ignoring epistasis, the total (σ^2_{GF}) and additive (σ^2_{AF}) genetic variation across families is

$$\sigma^2_{GF} = \begin{cases} \left(1 - \frac{1}{N}\right)\frac{1}{4}\sigma^2_A & \text{half-sibs} \\ \left(1 - \frac{1}{N}\right)\left(\frac{1}{2}\sigma^2_A + \frac{1}{4}\sigma^2_D\right) & \text{full-sibs} \end{cases}, \quad \sigma^2_{AF} = \begin{cases} \left(1 - \frac{1}{N}\right)\frac{1}{4}\sigma^2_A & \text{half-sibs} \\ \left(1 - \frac{1}{N}\right)\frac{1}{2}\sigma^2_A & \text{full-sibs} \end{cases} \tag{38.11c}$$

while the genetic variation within each family (σ^2_{Gw}) and the family by environment interaction variance ($\sigma^2_{F\times E}$) are

$$\sigma^2_{Gw} = \begin{cases} \frac{3}{4}\sigma^2_A + \sigma^2_D & \text{half-sibs} \\ \frac{1}{2}\sigma^2_A + \frac{3}{4}\sigma^2_D & \text{full-sibs} \end{cases}, \qquad \sigma^2_{F\times E} = \begin{cases} \frac{1}{4}\sigma^2_{A\times E} & \text{half-sibs} \\ \frac{1}{2}\,\sigma^2_{A\times E} + \frac{1}{4}\sigma^2_{D\times E} & \text{full-sibs} \end{cases} \tag{38.11d}$$

Similar expressions can be developed for other types of families, such as S_1 and S_2 (first and second-generation selfing). While these formulae seem a bit busy, the key point to notice is that while the additive-genetic covariance is less with family selection than individual selection, so is the phenotypic variance. In particular, if G x E is significant, only part (the family x environmental component) appears in the family mean variance and this part is weighted by $1/n_e$. While the above expressions are typically not directly used, due to the

difficulty in estimating the component variances, they provide important insight into the expected response when this sort of selection scheme of evaluating the performance of the genetic group in n_e random environments is used.

Selection for Mean Performance Versus Sensitivity/Stability

When G x E is present, a breeder faces not only the question of where to perform selection, but also the issue of whether a line with wide adaptation is better than a collection of lines that are more locally adapted. If the choice is made to select for a line with good mean performance over environments, the breeder must then weight the relative importance of mean performance versus sensitivity. In subsistence agriculture, decreased sensitivity (also called **tolerance**, i.e., increased stability in performance over environments) is as important as mean performance, as farmers and their families simply cannot afford even a single bad year. Ideally, a breeder would prefer to select for lines with both high mean performance and also decreased sensitivity (improved tolerance). Unfortunately, there may be tradeoffs between these goals.

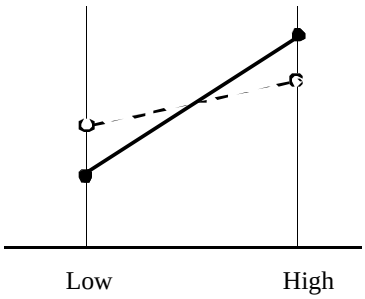

Figure 38.2. Mean performance vs. sensitivity. Both populations have the same mean performance (average value over both populations), but rather different sensitivities. The population represented by the solid circles and the solid line has greater sensitivity, so that it has a greater performance in the high environment but significantly poorer performance in the low environment relative to the low sensitivity line with the same mean performance.

Falconer's (1990) analysis of the Jinks-Connolly rule examined the effect of selection *in only a single environment* on the sensitivity of the trait. Recall Falconer's conclusion than, for two environments, sensitivity is less after antagonistic selection than after synergistic selection. Thus when the selection in a single environment is against the environmental trend (i.e., up-selecting in the poorer environment), the result is increased stability of the trait over both environments relative to the response from up-selecetion in the good environment.

Do any such general statements emerge when we allow selection to occur in *both* environments? Let μ_H and μ_L denote the means in the higher- and lower-performing environments. Mean performance is given by

$$m = \frac{\mu_H + \mu_L}{2} \tag{38.12a}$$

while sensitivity can be measured by

$$s = \mu_L - \mu_H. \tag{38.12b}$$

With this definition, s is negative, and a positive change in s ($\Delta s > 0$) corresponds to decreased sensitivity (increased stability), while a negative change corresponds to increased sensitivity. If selection occurs in only a single environment, we can ask about the *response* in

either m and s, but we are not selecting directly on either, but rather observing a correlated response from direct selection in only one environment. With selection in two environments, we can now directly selection on either m or s (or both). Rosielle and Hamblin (1981) provide some interesting insight in this case, and we follow their treatment.

Recall (e.g., Equation 38.3a) that sign of the genetic correlation r_A determines if the correlated response in one trait is in the same direction as the direct response in another. Using this simple observation, Rosielle and Hamblin's analysis follows from computing the genetic correlations for various combinations of m, s, $H = \mu_H$, and $L = \mu_L$. For example, consider the genetic correlation between sensitivity s and performance H in the high performing environment,

$$\rho_{s,H} = \frac{\sigma(s,H)}{\sigma(s)\,\sigma(H)} = \frac{\sigma(L-H,H)}{\sqrt{\sigma^2(L-H)\,\sigma^2(H)}} = \frac{\sigma(L,H)-\sigma^2(H)}{\sqrt{\sigma^4(H)+\sigma^2(H)\sigma^2(L)-2\sigma^2(H)\sigma^2(L)}} \tag{38.13a}$$

All correlations, variances and covariances refer to additive genetic variation (if outbreeding populations are considered) or total genetic variance (if selection is among pure lines). Denoting the ratio of the genetic variances for the high versus low environment by

$$\phi = \frac{\sigma^2(L)}{\sigma^2(H)}, \tag{38.13b}$$

Rosielle and Hamblin simplify Equation 38.13a to obtain

$$\rho_{s,H} = \frac{\phi\,\rho_{H,L}-1}{\sqrt{1+\phi^2-2\rho_{H,L}\phi}}. \tag{38.13c}$$

The resulting sign for the genetic correlation between sensitivity s and high performance H becomes

$$\text{sign}(\rho_{s,H}) = \text{sign}(\phi\,\rho_{H,L}-1), \tag{38.13d}$$

which is negative unless $\sigma^2(L) > \sigma^2(H)$ and $\rho_{H,L}$ is sufficiently large (such that $\phi\rho > 1$). When this correlation is negative, selection for decreased sensitivity ($\Delta s > 0$) results in a correlated response to decrease the mean performance in the high environment. Thus, unless the genetic variance is larger in the low-performing environment (which is unusual, e.g., Allen et al. 1978), selection for increased tolerance/stability results in a decreased performance in the high environment. Equivalently, selection in just the high environment to increase the mean ($\Delta H > 0$) generally results in increased sensitivity ($\Delta s < 0$), which is a restatement of the Jinks-Connolly rule.

Similarly, the genetic correlation between sensitivity and performance in the low environment is

$$r_{L,s} = \frac{\phi-\rho_{H,L}}{\sqrt{1+\phi^2-2\rho_{H,L}\phi}} \tag{38.13e}$$

so that selection on s increases the performance in the low environment when $\phi > \rho_{H,L}$, otherwise it decreases μ_L. Proceeding in exactly the same fashion, the genetic correlations between mean performance on one hand and performance in the high and low environments on the other are, respectively,

$$r_{H,m} = \frac{\phi\,\rho_{H,L}+1}{\sqrt{1+\phi^2+2\rho_{H,L}\phi}}, \quad \text{and} \quad r_{L,m} = \frac{\phi+\rho_{H,L}}{\sqrt{1+\phi^2+2\rho_{H,L}\phi}} \tag{38.14}$$

Both of which are positive unless the genetic correlation between environments is negative.

Finally, the genetic correlation between mean performance m and sensitivity s is

$$r_{s,m} = \frac{\phi^2 - 1}{\sqrt{1 + 2\phi^2 + \phi^4 - 4\rho_{H,L}^2\phi^2}} \tag{38.15}$$

which is negative unless $\phi^2 > 1$. Hence, selection on sensitivity decreases mean performance ($\Delta s > 0 \rightarrow \Delta m < 0$), and selection on mean performance decreases sensitivity ($\Delta m > 0 \rightarrow \Delta s < 0$) unless $\sigma^2(L) > \sigma^2(H)$. Rosielle and Hamblin caution not to over-interpret these two-environment results when multiple environments are considered, but their point is still well made.

We can easily incorporate joint selection on mean performance and sensitivity into a selection index. To slightly simplify matters, consider an index selecting on total performance over both environments (i.e., $2m$ in place of m) and on the sensitivity s, where a is the weight (relative to total performance) placed on sensitivity,

$$I = 2m + a \cdot s = (g_H + g_L) + a(g_L - g_H) = \begin{cases} g_H + \left(\dfrac{1+a}{1-a}\right) g_L & a \neq 1 \\ g_L & a = 1 \end{cases} \tag{38.16}$$

The last step follows by recalling we can always rescale one of the index weights to one (Chapter 33). If total performance and sensitivity are given equal weight ($a = 1$), the index reduces to the breeding (or genotypic) value g_L of performance in the low environment. Very small a corresponds to selection on total performance, while very large a corresponds to selection on sensitivity. If the genetic and phenotypic variances and covariances between low and high performance are known, then index selection theory can be used to obtain the Smith-Hazel weights for this index (Equation 33.18a).

The above results for potential tradeoffs between stability and mean performance apply in the simplest case where only two environments are considered. As one might expect, when selection potentially occurs over a number of environments, the existance of tradeoffs is much less clear. Indeed, simply defining stability can be rather problematic in such cases, as we detail in Chapter 39.

SELECTING IN MULTIPLE ENVIRONMENTS

The two-environment case served as a useful introduction to selection when G x E is present. While simple, it is an appropriate model in some settings, such as experiments using two discrete environmental treatments. It is also not an unreasonable model for many animal breeding settings, where organismal mobility and husbandry can often mitigate minor environmental variation, and the resulting contrasts are between major environmental differences such as temperate versus tropical. In situations were genotypes or lines can be replicated over locations as well as years (a common situation for many plant breeding trails), the environmental structure is considerably richer. The rest of this chapter (and much of the next) examines selection in such settings.

MET: Multiple-environment Trails

One can imagine (at least) three environmental components that can contribute to G x E. First, a location macro-environment value E_ℓ that is common to all individuals in that setting, be it a specific location/site, general geographic region, or presence/absence of a specific environmental factor. The idea is that E_ℓ is relatively predictable and hence somewhat stable, and can be a target of selection. The second is the yearly (or seasonal) component of the

environment E_y that varies from year to year (for example, average temperature or rainfall during a growing season). This is essentially an unpredictable component, and hence is not selectable. The best a breeder can do is to attempt to average out its effects by scoring genotypes over a number of seasons to access their average performance and to select for stability. Finally, a macro-environment by year interaction $E_{\ell\times y}$ may also be present, and this too is unpredictable. Thus, the G x E interaction can be decomposed into contributions for locations, years, and location x year interactions,

$$\sigma^2_{G\times E} = \sigma^2_{G\times \ell} + \sigma^2_{G\times y} + \sigma^2_{G\times y\times \ell} \tag{38.17a}$$

As mentioned, the breeder may wish to exploit G x E in predictable environments while trying to mitigate it (though selection for stability) in unpredictable environments. Note that $\sigma^2_{G\times \ell}/\sigma^2_{G\times E}$ essentially represents the potential fraction of interaction variance due to predictable environmental factors, while the remainder likely represents unpredictable features. The relative contribution of these two components informs the breeder of their options (breeding for location and/or stability).

Equation 38.17a provides the motivation for **multiple-environment trails** (or **MET**) where varieties are scored for several years over several locations (Chapter 20). The importance of Equation 38.17a is that replication can reduce the noise from $G \times E$ when trying to assess genotypes. So see this, suppose that n_r individual from a line are scored in a single environment, and the mean performance of these individuals is reported. The resulting residual error variance becomes σ^2_e/n_r. Likewise, if such replication occurs over n_ℓ locations (environments) and for n_y years per location, then the G x E and environmental variance associated with the mean performance of a line becomes (Lonnquist 1964, Comstock and Moll 1973, Patterson et al 1977, Brennan and Byth 1979, Thompson and Cunningham 1979)

$$\frac{\sigma^2_{G\times \ell}}{n_\ell} + \frac{\sigma^2_{G\times y}}{n_y} + \frac{\sigma^2_{G\times y\times \ell}}{n_\ell n_y} + \frac{\sigma^2_e}{n_\ell n_y n_r} \tag{38.17b}$$

The key feature of Equation 38.17b is that suitable replication can reduce the contribution of any particular component of $\sigma^2_{G\times E}$ to the variance of a line mean, thereby increasing the heritability of the line mean (Equation 38.4). The idea of METs is to find those lines that perform well over some target populations of environments, recognizing that while locational correlations might be reasonably stable, the unpredictability in year-to-year (and hence location-by-year) interactions implies that the breeder must select for lines that perform well over some (largely unpredictable) distribution of environments.

Example 38.4. Atlin et al. (2001) use data from six different crops to show the benefits of replication across years and locations. Estimates of line, G x E components, and residual variance were obtained from (1) Atlin and McRae (1994), (2) Cullis et al. (1996), (3) Talbot (1984), (4) Cooper and Somrith (1997), and (5) Copper et al. (1999), and were as follows:

Crop	Region	σ^2_G	$\sigma^2_{G\times\ell}$	$\sigma^2_{G\times y}$	$\sigma^2_{G\times\ell\times y}$	σ^2_e	Ref
Spring barley	Canada	62	29	18	63	174	1
Spring Oat	Canada	122	58	21	53	178	1
Wheat	Australia	23	8	9	53	87	2
Winter wheat	UK	99	7	22	113	128	3
Potatoes	UK	9780	2980	2630	14960	18790	3
Lowland rice	Thailand	198	82	18	199	178	4
Lowland rice	Thailand	60	3	49	259	440	5

Recalling Equation 38.17b, the heritability of the line means is given by

$$h^2_{\bar{z}} = \frac{\sigma^2_G}{\sigma^2_{\bar{z}}}, \quad \text{with} \quad \sigma^2_{\bar{z}} = \sigma^2_G + \frac{\sigma^2_{G\times\ell}}{n_\ell} + \frac{\sigma^2_{G\times y}}{n_y} + \frac{\sigma^2_{G\times\ell\times y}}{n_\ell\, n_y} + \frac{\sigma^2_e}{N}$$

where $N = n_r n_\ell n_y$. With increased replication, $\sigma^2_{\bar{z}}$ approaches σ^2_G, and hence the heritability of line means can be made to approach one by using sufficient replication. Using the above values, Atlin et al. (2001) calculated the estimated heritabilities under different designs (different allocation of lines over locations n_ℓ, years n_y, and replications per site n_r). The last column gives the ratio of the single-replication heritability with that for the most complete design considered here (5,5,2 = 5 replicates per location, 5 locations, 2 years per location),

	Heritability of lines means $h^2_{\bar{z}}$ as a function of (n_r, n_ℓ, n_y)				
Crop	1,1,1	1,2,1	4,1,1	5,5,2	Ratio
Spring barley	0.18	0.29	0.29	0.71	3.9
Spring Oat	0.28	0.42	0.31	0.79	2.8
Wheat	0.13	0.22	0.20	0.63	4.8
Winter wheat	0.27	0.40	0.36	0.79	2.9
Potatoes	0.20	0.32	0.28	0.72	3.6
Lowland rice	0.29	0.44	0.37	0.80	2.8
Lowland rice	0.07	0.13	0.13	0.49	7.0

For example, if we grow each line of Wheat as only a single replicate in a single location in a single year (1,1,1), the expected board-sense heritability is 0.13. However, if each line is grown as five replicates at each of five different locations over two years (5,5,2), then the heritability of the line means increases to 0.63, almost a five-fold increase in precision for choosing the best genotypes. Note that (1,1,1) corresponds to selecting between lines using a single observation, which is simply individual selection. Thus, for lowland rice, a 3 to 7 fold increase over individual selection can occur by basing selection on the means of replicated lines.

How to we treat selection under such a very complex distribution of enviroments? As always the key when G x E is present is finding the right environment(s) in which to select. While the theory of multi-trait selection provides the machinery needed, actually being able to *apply* this theory is much more problematic. For example, even if we had good estimates of the genetic correlations across locations, the genetic correlations across years at the same location are essentially unpredictable. Thus, while multi-trait selection theory provides basic ground rules, real-world selection when G x E is present requires additional approaches. One of the simplest is illustrated in Example 38.5. When the target is average performance over some region, we may be able to use data from previous years to find those locations that are most predictive of performance over the entire region. In such cases, field trails can be performed at these sites, allowing the breeder to concentrate resources. Likewise, the breeder may manipulate the environment at some locations (for example, inducing water stress through controlled irrigation) in an attempt to measure potential performance in years of environmental stress.

Example 38.5. Hamblin et al. (1980) examined the correlation between mean yield for wheat varieties (averaged over 30 sites scattered throughout an area of roughly 250,000 km^2 in the state of Western Australia) with the mean yield for particular triplets of locations. Using data

from 1973-1976, four promising triplets where chosen. The correlation between these sites and the yield data from 1969-1972 was then examined, as given in the table below, where * and ** denote 5% and 1% significance.

Location triplet	1969	1970	1971	1972	1969-72	1973-76
Beverley-Borden-Muresk	0.63	-0.07	0.94**	0.88**	0.60	0.90
Beverley-Kondinin-Wickepin	0.72	-0.26	0.98**	0.83**	0.57	0.91
Bolgart-Borden-Woogenellup	0.57	0.77*	0.94**	0.90*	0.80	0.91
Borden-Muresk-Woogenellup	0.64	0.41	0.91*	0.91*	0.72	0.94

The last two columns denote the average correlation over the four years in the validation data set (69-72) and the four years in the initial data set (73 - 76), respectively. While all four triplets appeared very promising in the intial data set (four-year correlations were all over 90%), in the validation data set two of the location triplets showed negative correlations (both in 1970), while the best triplet only had an average correlation of 0.8 over 1969-1972. Further, this best-performing triplet in the validation set (Bolgart-Borden-Woogenellup) was not the best-performing triplet in the original analysis (Borden-Muresk-Woogenellup).

Example 38.5 represents an attempt to find some structure within the G x E data, a topic we explore in great detail in Chapter 39. Another approach is to select in those environments that are the most "discriminating". The problem is that different breeders have different notions of what was meant by discriminating. One school of thought, which is essentially Hammond's Conjecture, is to select in the environments with the highest heritabilities (e.g., Frey 1964, Johnson and Frey 1967). Allen et al. (1978) suggested a modification of this approach by considering environments with the largest value of $\rho_G h$, where ρ_G was the genetic correlation with the target population (for example, mean yeild over some large region) and h the square root of the heritability (broad-sense when using inbred lines). The other school of thought is since populations are always likely to experience a stressful environment during the duration of the cultivar/line, one should select in stressed environments (e.g., Gotoh and Osanai 1959). Again we have seen this before in the idea of selecting in the worst environment. As reviewed by Allen et al. (1978), and in our previous discussions, while there are examples of improved performance in the target population by selecting in a stressed environment, there are also numerous counterexamples.

Design Trade-offs: Years Versus Location

Equation 38.17b and Example 38.4 show how replication increases the accuracy of the line mean in predicting the line genetic value. With estimates of the appropriate G x E variance components in hand, the optimal allocation of resources (i.e., a set total number of plots) can be found to maximize the heritability under these resource constraints. One important tradeoff to consider is the allocation of locations versus years. Given that genotype-by-year and genotype-by-location-by-year can comprise a considerable fraction of $\sigma^2_{G\times E}$ (Example 38.4), replication over years seems desired. However, the increased heritability due to additional replication over years does come with a price — an increase in the time between cycles of selection, and hence potential reduction of the *rate* of genetic response (Comstock and Moll 1963). As we have seen (Chapters 20-22), a single cycle of selection in some crops can take several years, so let c denote the length of a single cycle of selection with a single year of replication, so that $c + k$ is the cycle time when k additional years of replication are added. The expected rate of response per year, i.e., the rate of genetic gain, becomes

$$\Delta R = \overline{i}\frac{\sigma^2_G}{\sigma(\overline{z}_k)}\left(\frac{1}{c+k}\right)$$

where

$$\sigma^2(\overline{z}_k) = \sigma^2_G + \frac{\sigma^2_{G\times\ell}}{n_\ell} + \frac{\sigma^2_{G\times y}}{(k+1)} + \frac{\sigma^2_{G\times\ell\times y}}{(k+1)n_\ell} + \frac{\sigma^2_e}{(k+1)n_\ell\, n_r} \tag{38.18a}$$

Equation 38.18a assumes that the number of locations per year and the number of replicates per location-year combination remains constant, with only the number of years of testing ($n_y = k+1$) changing. The ratio of rate of gain for one versus k additional years of testing becomes

$$\frac{\Delta R_k}{\Delta R_1} = \left(\frac{c}{c+k}\right)\frac{\sigma(\overline{z}_1)}{\sigma(\overline{z}_k)} \tag{38.18b}$$

Comstock and Moll (1963) consider the most extreme case where $\sigma^2_{G\times y}$ dominates all other interaction terms. In this case, for one and 2 years of testing, we have

$$\sigma^2(\overline{z}_1) \simeq \sigma^2_G + \sigma^2_{G\times y}, \quad \sigma^2(\overline{z}_2) \simeq \sigma^2_G + \frac{\sigma^2_{G\times y}}{2}$$

Even if $\sigma^2_{G\times y}$ accounts for 95% of $\sigma^2_G + \sigma^2_{G\times y}$, for two years of replication $\sigma(\overline{z}_1)/\sigma(\overline{z}_2) = 1.3$. Substituting into Equation 38.18b shows that for the rate of response to be increased by replication requires a cycle time of $c \geq 3$ years. For four years of replication $\sigma(\overline{z}_1)/\sigma(\overline{z}_4) = 1.9$, requiring a cycle of at least four years for replication to increase the rate of response. Hence while replication over many years increases precision, this is often more than offset by the longer cycle time.

Several studies have examined the effects of adding additional years of testing. Compairing one to three years of testing, Cross and Helm (1986) examined maize hybrid selection, while Gellner (1989) examined spring wheat (*Triticium aestivum* L.) and oats (*Avena sativa* L.). Bowman (1998) compared the predictive results of one versus two years of testing in six crops from North Carolina (corn, cotton, oats, soybeans, wheat, and barley). Finally, Yan and Rajcan (2003) examined the prediction of soybean performance in Ontario as a function of number of years of previous testing. The rather surprising conclusion from these studies is that a single years worth of data often gives almost the same accuracy in predicting the subsequent year as does using two (or more) years of data.

Example 38.6. Using an extensive dataset on soybean yield in Ontario, Yan and Rajcan (2003) examined the effects using one, two, three, and five years worth of data in predicting yield. A partial set of their data is shown in the table below, which compares the actual performance (measured by the variance-scaled BLUP estimate of the genotype value, or t-BLUP, Yan et al. 2002) in a given year with the predicted performance based on the previous one, two, three, and five years worth of data. Prediction performance was measured by the correlation between estimates of the genotypic effects of lines in the focal year and the predicted value based on using results from previous year(s).

	Number of years of testing			
Year	1	2	3	5
2000	0.57	0.63	0.61	0.61
1999	0.57	0.57	0.57	0.65
1998	0.56	0.68	0.68	0.67
1997	0.51	0.56	0.52	0.53
1996	0.47	0.51	0.51	0.51
Average	0.54	0.59	0.58	0.59

As the above table shows, the conclusion is that using two years of data does slightly better than using a single year, but that adding additional years results in no further improvement. Yan

and Rajcan also examined another measure, the number of genotypes that can be decisively evaluated (allowing them to be judged as significantly inferior or superior, as indicated by their t-BLUP values being greater than 2 in absolute value, Yan et al. 2002). As shown below, the number of decisively evaluated genotypes increases by adding additional years.

	Number of	Number of years of testing			
Year	genotypes	1	2	3	5
2000	112	30	35	38	45
1999	112	44	50	55	55
1998	112	9	22	30	31
1997	104	33	39	38	39
1996	90	18	21	25	28

While replication over several years does not significant improve prediction ability for any given line in subsequent years, it does help the breeder in culling the least desirable, and choosing the most desirable, lines.

Design Trade-offs: Subdividing a Target Region

Another design issue is whether a target region should be further divided into subregions for selection, as opposed to selecting lines by averaging their performance over the entire region. The motivation for division into subregions follows from the basic model for G x E. We ignore year effects to make our main point. If we first ignore any potential subregions, the expected value of line i in location k becomes

$$E[z_{ik}] = \mu + G_i + \ell_k + G\ell_{ik} \tag{38.19a}$$

Now suppose that there are distinct subregions, in which case we can break up a location effect from the model given by Equation 38.19a into a subregional effect S and an effect of location nested within that subregion $\ell(S)$. Thus for line i in subregion j and the kth location nested within that subregion, we have

$$E[z_{ijk}] = \mu + G_i + S_j + \ell(S_j)_k + GS_{ij} + G\ell(S_j)_k \tag{38.19b}$$

Within a given subregion (j), the expected value of line i now becomes $G_i + GS_{ij}$, so that the numerator in the heritability of line means measured within a subregion becomes $\sigma^2_G + \sigma^2_{G\times S}$ (as opposed to just σ^2_G when subregional effects are ignored). The advantage of selecting within a subregion (as compared to selecting over the entire region) is that the component $\sigma^2_{G\times S}$ is removed from $\sigma^2_{G\times\ell}$ and now contributes to response (Comstock and Moll 1963, Atlin et al. 2000b). The tradeoff is that the number of replicates is decreased, increasing the variance of the line means (relative to the variance if all subregions are lumped). Atlin et al (2000b) considered these tradeoffs in detail, finding that subdividing a region improves response only when $\sigma^2_{G\times\ell}$ is large relative to σ^2_G and a significant fraction (they suggest at least 30%) of the $\sigma^2_{G\times\ell}$ variance is due to $\sigma^2_{G\times S}$. Atlin et al. (2000a) examined yield of using 145 random doubled-haploid barley lines tested over a total of 22 sites in Canada from 1992 and 1993. Considering Canada as a single region, $\sigma^2_G = 300$ and $\sigma^2_{G\times\ell} = 245$. Subdividing Canada into eastern versus western gave $\sigma^2_{G\times S} = 95$, so that regional effects accounted for 38% of the line by location interaction. However, based on $\sigma^2_{G\times\ell}$ and σ^2_G being of roughly equal effect, they suggest little is to be gained by selecting within each subregion.

Participatory Breeding and G x E

The notion of regional testing directly relates to a recent movement in plant breeding — **participatory breeding**, with local farmers actively involved in the selection of new lines.

The motivation for this approach was the concern that **formal plant breeding** (**FPB**), namely multiple-environment traits of new lines conducted through national and international centers, was not producing products for low-input farmers working in marginal environments. The success of FPB is clearly undeniable, but the concern was that much of its focus was for stable crops widely-adaptive to high yield environments (where most of the profit occurs), potentially at the expense of marginal farmers whose yield, while critical to them and their families, is economically quite small. Witcombe et al. (1996) make a distinction between two different types of participatory breeding. In **participatory varietal selection** (or **PVS**), the farmer helps with the selection among a set of essentially finished (i.e., fully inbred) varieties, either through input on selectively desirable traits and/or evaluation of performance in their own fields. In **participatory plant breeding** (or **PPB**), the material being worked with is still segregating (i.e., it is not yet in its stable, fully inbred, final form), and hence the selection decisions may not be as granular as those among essentially fixed lines. While participatory breeding is also motivated by the desire for conservation of local lines and a variety of social-political-economic issues, our focus here is entirely on conditions under which PPB (or PVS) may produce better results from a breeding standpoint than more traditional FPB methods. Readers wishing a more richly textured background can consult Ezyaguirre and Iwanaga (1996), as well Sperling et al. (2001) and other articles in the special issue of *Euphytica* (2001, Volume 122, issue 3) focusing on all aspects of participatory breeding.

From a strictly breeding standpoint, there are three issues when comparing PPB and FPB. The first is that the targets of selection under formal plant breeding may be different from the targets of selection desired by low-input farmers. From this standpoint, there is clearly a significant benefit from seeking input from the ultimate end-users, the farmers themselves (e.g., Ceccarelli et al. 2000). The remaining two issuses can (again) be rephrased in a direct versus correlated response framework. The target population of environments (TPE) are low-input growing situations, often under considerable stress (relative to high-input systems). Thus, PPB occurs within the TPE, while the fields at research stations typically do not, although this not be the case (for example, field trails can be made under conditions of enforced stress). Balancing this are the higher heritabilities for line means that can be obtained under FPB by using highly replicated experimental designs (e.g., Example 38.4) and greater access to more diverse genotypes (and hence a larger σ^2_G). These various tradeoffs can be placed in terms of Equation 30.22a, giving the ratio of the correlated response (FPB) to the direct response (PPB) as

$$\frac{\text{Response under FPB}}{\text{Response under PPB}} = \frac{CR_X}{R_X} = \left(\frac{\overline{i}_{FPB}}{\overline{i}_{PPB}}\right) \rho_G \left(\frac{h_{FPB}}{h_{PPB}}\right) \tag{38.19}$$

What is not included in Equation 38.19 is accounting for differences in the targets of selection desired by the farmer versus those selected for the breeder. This can be incorporated by viewing these two (potentially different) objectives as selection indices and then computing the correlated response in one given selection on the other (Chapter 33). Putting this point aside (as it can be addressed by consultation with the farmers as to the desired targets), the three terms in Equation 38.19 highlight the advantages (and disadvantages) of the two approaches (Atlin and Frey 1990, Atlin et al. 2001). Given the larger number of individuals grown, selection intensities can clearly be higher under FPB, as can the heritabilities (e.g., Example 38.4), while higher genetic correlation with the target environment is a point in favor with PPB. Let's examine these last two points (higher h^2, lower ρ_G under FPB) in more detail.

Clearly when the genetic correlation between the selection environments under FPB and the production environments under PPB is sufficiently low, differences in selection intensities and heritabilities cannot overcome this, and PPB gives a larger response. Of course, if the correlation is zero or negative, FPB has very little to offer. Thus, it remains an open empirical

question as to the correlation of yield (or some other measure of performance) in good versus poor environments. There are a few reports in the literature where the genetic correlation was computed for yield in high- versus low-yield environments, the later generated by the introduction of some agent of stress. For example, Atlin and Frey (1989) using oats in Iowa observed correlations of 0.5, 0, and 1.0 between low- and high-yield environments when the low yield was caused by stress due to low Phosphorous P, late planting, and low Nitrogen N (respectively). Thus, the full range of options is seen here – if the stress is due to low N, FPB is always preferred (as $\rho_G = 1$). If the stress is due to late planting, PPB is always preferred (as $\rho_G = 0$). If stress is due to low P, then either FPB or PPB may be preferred (as $\rho_G = 0.5$), depending on the relative strengths of selection and heritabilities under FPB vs. PPB. Ceccarelli et al. (1992) found $\rho_G = -0.12$ for barley yield under drought vs. non-drought in Syria, clearly favoring PPB. Finally, maize yield under low N stress in Mexico had a genetic correlation of 0.4 to 0.5 with yield under non-stress conditions (Lafitte and Edmeades 1994, Bänziger et al. 1977). Again, either FPB or PPB might be appropriate in these cases. The take-home message is that there is no general trend, and each case must be examined separately.

As Example 38.4 highlights, the replication over locations and (especially) years done under FPB can mitigate contributions to G x E caused by site, year, and site-by-year variation. The net result is a significantly improved heritability for the line means. Further, as Altin et al. (2001) point out, large-scale plant breeding programs likely have access to many more lines that PPB (although one might argue that the later are already more locally-adapted). As a result, σ^2_G can often be manipulated to be larger under FPB than PPB. These are the great strengths of FPB programs, and these advantages (coupled with potentially stronger selection) can overcome a modest value of ρ_G. Atlin et al. (2001) correctly argue that the success of PPB largely hinges on the ability to transport the replicated experimental design technology used by FPB to the farmer's field, as it is only by replicating across locations and years that the effects of non-predicable G x E can be accommodated. As they concisely state:

> A small, site-specific breeding program may be optimally situated to exploit local adaptation if it exists, but may lack the resources needed to evaluate genotypes with enough precision to reliably identify superior genotypes.

Clearly, both PPB and FPB work best when they borrow strenghts from the other's approach. Indeed, Atlin and Frey (1990) pointed out that by increasing replication under the stressed (i.e., marginal) environments, the heritabilities of the line means approach values near one, and (assuming equal selection intensity), Equation 38.19 simply reduces of ρ_G. Thus, when the target and selective environment are not perfectly correlated, there exists a level of replication such that direct selection in the stressed environment is expected to out-perform the correlated response from selection in the non-stressed environment. Thus, at low replication, selection under FPB can often beat PPB, but as the levels of replication under stressed environments increases, direct selection in the stressed environment should always be best.

Literature Cited

Allen, F. L., R. E. Comstock, and D. C. Rasmusson. 1978. Optimal environments for yield testing. *Crop Sci.* 18: 747–751. [38]

Atlin, G. N., K. B. McRae, and X. Lu. 2000a. Genotype X region interaction for two-row barley yeild in Canada. *Crop Sci.* 40: 1–6. [38]

Atlin, G. N., R. J. Baker, K. B. McRae, and X. Lu. 2000b. Selection response in subdivided target regions. *Crop Sci.* 40: 7–13. [38]

Atlin, G. N., M. Cooper, and Å. Bjørnstad. 2001. A comparison of formal and participatory breeding approaches using selection theory. *Euphytica* 122: 463–475. [38]

Atlin, G. N., and K. J. Frey. 1989. Breeding crop varieties for low-input agriculture. *Am. J. Alt. Agric.* 4: 53–57. [38]

Atlin, G. N., and K. J. Frey. 1990. Selecting oat lines for yield in low-productivity environments *Crop Sci.* 30: 556–561. [38]

Atlin, G. N., and K. B. McRae. 1994. Resource allocation in Maritime cereal cultivar trails. *Can. J. Plant Sci.* 74: 501–505. [38]

Bowman, D. T. 1998. Using crop performance data to select hybrids and varieties. *J. Prod. Agr.* 11: 256–259. [38]

Brancourt-Hulmel, M., E. Heumez, P. Pluchard, D. Beghin, C. Depatureaux, A. Giraud, and J. Le Gouis. 2005. Indirect versus direct selection of winter wheat for low-input or high-input levels. *Crop Sci.* 45: 1427–1431. [38]

Burton, R. D. 1977. Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. *Silvae Genetica* 26: 168–175. [38]

Brennan, P., and D. E. Byth. 1979. Genotype x environment interactions in wheat yields and selection for widely adapted wheat genotypes. *J. Agric. Sci.* 30: 221–232. [17, 38]

Ceccarelli, S. 1989. Wide adaptation: How wide? *Euphytica* 40: 197–205. [38]

Ceccarelli, S., S. Grando, and J. Hamblin. 1992. Relationship between barley grain yield measured in low- and high-yieldng environments. *Euphytica* 94: 49–58. [38]

Ceccarelli, S., S. Grando, R. Tutwiler, J. Baha, A. M. Martini, H. Salahieh, A. Goodchild, and M. Michael. 2000. A methodological study on participatory barley breeding. I. Selection phase. *Euphytica* 111: 91–104. [38]

Cockerham, C. C. 1963. Estimation of genetic variances. *In* W. D. Hanson and H. F. Robinson (eds) *Statistical genetics and plant breeding*, pp. 53–93. National Academy of Sciences-National Research Council, Publication 982, Washington, D.C. [38]

Comstock, R. E., and R. H. Moll. 1963. Genotype-environment interactions. *In* W. D. Hanson and H. F. Robinson (eds.), *Statistical genetics and plant breeding*, pp. 164–196. Natl. Acad. Sci., Natl. Res. Council Publ. No. 982, Washington, D.C. [17, 38]

Cooper, M. and I. H. DeLacy. 1994. Relationships among analytical methods used to study environmental variation and genotype-by-environment interaction in plant breeding multi-environmental experiments. *Theor. Appl. Genet.* 88: 561–572. [38]

Copper, M., and B. Somrith. 1997. Implications of genotype-by-environment interactions for yield adaptation of rainfed lowland rice: Influence of flowering date on yield variation. *In* S. Fukai, M. Copper, and J. Salisbury (eds), *Breeding strategies for rainfed lowland rice in drought-prone environments*, pp. 104-114. ACIAR Proceedings no. 77.

Cooper, M., S. Rajatasereekul, S. Immark, S. Fukai, and J. Basnayake. 1999. Rainfed lowland rice breeding strategies for northeast Thailand. I. Genotypic variation and genotype x environment interactions for grain yield. *Field Crops Res.* 64: 131–151. [38]

Cross, H. Z., and J. L. Helm. 1986. Hybrid maize selection strategies based on state yield traisl. *J. Agron. Educ.* 15: 110–113. [38]

Cullis, B. R., F. M. Thomson, J. A. Fisher, A. R. Gilmour, and R. Thompson. 1996. The analysis of the NSW wheat variety database. II. Variance component estimation. *Theor. Appl. Genet.* 92: 28–39. [38]

Dickerson, G. E. 1962. Implications of genetic-environmental interaction in animal breeding. *Anim. Prod.* 4: 47–63. [38]

Donald, C. M. 1962. In search of yield. *J. Aust. Inst. Agric. Sci.* 28: 171–178. [38]

Eisemannn, R. L., M. Cooper, and D. R. Woodruff. 1990. Beyond the analytic methodology: better interpretation and exploitation of GE interactions in plant breeding. *In* M. S. kang (Ed.) *Genotype-by-environment interactions and plant breeding*, pp. 108–117. Louisiana State University Agri. Center, Baton Rouge, LA. [38]

Eyzaguirre, P., and M. Iwanaga. 1996. *Participatory plant breeding*. Proc. Workshop on Participatory Plant Breeding, 26-29 July 1995, Wageningen, Netherlands. IPGRI, Rome, Italy. [38]

Falconer, D. S. 1952. The problem of environment and selection. *Amer. Natl.* 86: 293–298. [38]

Falconer, D. S. 1960. Selection of mice on growth on high and low planes of nutrition. *Genet. Res.* 1: 91–113. [38]

Falconer, D. S. 1989. *Introduction to quantitative genetics.* 3rd. ed. Longman. [38]

Falconer, D. S. 1990. Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. *Genet. Res.* 56: 57–70. [38]

Falconer, D. S. and M. Latyszewski. 1952. The environment in relation to selection for size in mice. *J. Genet.* 51: 67–80. [38]

Fasoulas, A. 1973. A new approach to breeding superior yielding varieties. Aristotelian Univ. of Thessaloniki, 1973 Publ. 3. Dep. of Genetics and Plant Breeding. [38]

Frey, K. J. 1964. Adaptation reaction of oat strains under stress and non-stress environments. *Crop Sci.* 4: 55–58. [38]

Gellner, J. L. 1989. Predicting superior yielding spring wheat and oat cultivars using past yield data. *Agron. J.* 81: 194–197. [38]

Gotoh, K., and S. Osanai. 1959. Efficiecy of selection for yield under different fertilizer levels in a wheat cross. *Jap. J. Breed.* 9: 173–178. [38]

Haldane, J. B. S. 1946. The interaction of nature and nurture. *Ann. Eugen.* 13: 197–205. [38]

Hamblin, J., H. M. Fisher, and H. I. Ridings. 1980. The choice of locality for plant breeding when selecting for high yield. *Euphytica* 29: 161–168. [38]

Hammond, J. 1947. Animal breeding in relation to nutrition and environmental conditions. *Biol. Rev.* 22: 195–213. [38]

Hinson, K., and D. Hansen. 1962. Competition studies in soybeans. *Crop Sci.* 2: 117–123. [38]

Hühn, M., S. Lotito, and H. P. Piepho. 1993. Relationships between genotype x environment interactions and rank orders for a set of genotypes tested in different environments. *Theor. Appl. Genet.* 86: 943–950. [38]

Itoh, Y., and Y. Yamada. 1990. Relationships between genotype x environment interaction and genetic correlation of the same trait measured in different environments. *Theor. Appl. Genet.* 80: 11–16. [38]

James, J. W. 1961. Selection in two environments. *Heredity* 16: 145–152. [38]

Jinks, J. L., and V. Connolly. 1973. Selection for specific and general response to environmental differences. *Heredity* 30: 33–40. [38]

Jinks, J. L., and H. S. Pooni. 1988. The genetic basis of environmental sensitivity. *In* B. S. Weir, E. J. Eisen, M. M. Goodman, and G. Namkoong (eds.), *Proceedings of the second international conference on quantitative genetics,* pp. 505–522. Sinauer Assocs., Sunderland, MA. [38]

Johnson, G. R., and K. J. Frey. 1967. Heritabilities of quantitative attributes of oats (*Avena* sp.) at varying levels of environmental stress. *Crop Sci.* 7: 43–46. [38]

Johnson, V. A., S. L. Shafter, and J. W. Schmidt. 1968. Regression analysis of general adaptation in hard red winter wheat (*Triticum aestivum* L.). *Crop Sci.* 8: 187–181. [38]

Kelley, R. B. 1949. *Principles and methods of animal breeding*. (2nd ed.). John Wiley and Sons, New York, N. Y. [38]

Kirigwi, F. M., M. van Ginkel, R. Trethowan, R. G. Sears, S. Rajaram, and G. M. Paulsen. 2004. Evaluation of selection strategies for wheat adaptation across water regimes. *Euphytica* 135: 361–371. [38]

Lasslo, L. L., G. E. Bradford, D. T. Torell, and B. W. Kennedy. 1985. Selection for weaning weight in Targhee sheep in two environments. I. direct response. *J. Anim. Sci.* 61: 376–386. [38]

Lerner, I. M. 1950. *Population genetics and animal improvement.* Cambridge. [38]

Lonnquist, J. H. 1964. A modification of the ear-to-row procedutre for the improvemnet of maize populations. *Crop Sci.* 4: 227-228. [17, 38]

Lush, J. L. 1945. *Animal breeding plans* (3rd ed.). Iowa State, Ames, Iowa. [38]

Nichols, J. E. 1947. *Livestock improvement in relation to heredity and environment.* (3rd ed.). Oliver and Boyd, London. [38]

Patterson, H. D., V. Silvey, M. Talbot, and S. T. C. Weatherup. 1977. Variability of yields of cereal varieties in UK trails. *J. Agric. Sci.* 89: 238–245. [17, 38]

Pederson, D. G., and A. J. Rathjen. 1981. The impact of site selection on breeding progress. *In* C. J. Driscoll (eds) *Proc. VIIIth Australian Plant Breeding Conference*, pp. 32–37, The University of Adelaide. [38]

Presterl, T., G. Seitz, M. Landbeck, E. M. Thiemt, W. Schmidt, and H. H. Geiger. 2003. Improving nitrogen-use efficiency in European miaze: estimation of quantitative genetic parameters. *Crop Sci.* 43: 1259–1265. [38]

Robertson, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* 15: 469–485. [38]

Rosielle, A. A., and J. Hamblin. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. *Crop Sci.* 21: 943–946. [38]

Roy, N. N., and B. R. Murty. 1970. A selection procedure in wheat for stress environments. *Euphytica* 19: 509–521. [38]

Scheinberg, E. 1973. The design and analysis of genetic experiments to modify genotype-environ-ment interactions. I. single pair matings and selection using one simple quantitative attribute measured in two environments. *Can. J. Genet. Cytol.* 15: 635–645. [38]

Shabana, R., T. Bailey, and K. J. Frey. 1980. Production traits of oats selected under low, medium, and high productivity. *Crop Sci.* 20: 739–744. [38]

Simmonds, N. W. 1991. Selection for local adaptation in plant breeding programme. *Theor. Appl. Genet.* 82: 363–367. [38]

Sperling, L., J. A. Ashby, M. E. Smith, E. Weltzien, and S. McGuire. 2001. A framework for analyzing participatory plant breeding approaches and results. *Euphytica* 122: 439–450. [38]

Talbot, M. 1984. Yield variability of crop varieties in the UK. *J. Agric. Sci.* 102: 315–321. [38]

Thompson, N. J., and R. B. Cunningham. 1979. Genotype x environment interactions and evaluation of cotton cultivars. *Aust. J. Agric. Res.* 30: 105–112. [17, 38]

Van Sanford, D. A., T. W. Pfeiffer, and P. L. Cornelius. 1993. Selection index based on genetic correlations among environments. *Crop Sci.* 33: 1244–1248. [38]

Witcombe, J. R. , A. Joshia, K. D. Joshia, and B. R. Sthapit. 1996. Farmer participatory crop improvement. I. Varietal selection and breeding methods and their impact on biodiversity. *Exper. Agric.* 32: 445–460. [38]

Wright. S. 1939. Genetic principles governing the rate of progress of livestock breeding. *Proc. Amer. Soc. Anim. Prod.*, 32: 18–26. [38]

Yan, W., L. A. Hunt, P. Johnson, G. Stewart, and X. Lu. 2002. On-farm strip trails vs. replicated performance trials for cultivar evaluation. *Crop Sci.* 42: 385–392. [38]

Yan, W., and I. Rajcan. 2003. Prediction of cultivar performance based on single- versus multiple-year tests in soybean. *Crop Sci.* 43: 549-–555. [38]

Zavala-García, F., P. J. Bramel-Cox, J. D. Eastin, M. D. Witt., and D. J. Andrews. 1992. Increasing the efficiency of crop selection in unpredictable environments. *Crop Sci.* 32: 51–57. [38]