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Choice of selection environment for improving crop yields in saline areas

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Abstract Spatial variability in salt-affected fields is normally very high. Thus, most salinity affected lands are actually comprised of many micro-environments, ranging from low to high salinity in the same field. The evidence on testing genotypes across a broad range of salinity levels shows that the genotype-by-salinity level interaction is commonly large. Thus, breeding for saline areas can be compared to what has been known as breeding for 'wide adaptation'. The target environments both for breeding for saline soils or for wide adaptation are actually a population of many possible environments, for which there exists a significant component of genotype-by-environment (G × E) interaction. Thus it is possible to study the merit of potential strategies for breeding for salinity tolerance using the tools that have been developed for the study of breeding for wide adaptation. The evidence from selection and breeding experiments for wide adaptation seems to favour testing on a representative subset of environments, including stress and non-stress locations; but the choice of these locations is complicated by the multidimensional nature of G × E. However, in the case of salt stress, the crop-yield response functions to salinity are well known. This paper presents an attempt to systematise the choice of the optimum environment(s) to select for improved yield under saline soil conditions, based on the three-piece linear equation presented by Maas and Hoffman (1977) and the theory of direct and indirect responses to selection. It is proposed that three saline levels should be enough to make a valid estimation of the suitability of a number of selection strategies. A worked example with data from a set of grain sorghum inbred lines tested on ten saline levels shows that the same selection strategies would be chosen using the information from the ten saline levels as that obtained using the two extremes and one intermediate level.

Key words Salinity · Wide adaptation · Genotype × environment interaction

Introduction

A practical problem when breeding crops for environments prone to abiotic stresses is the choice of an optimum selection environment (or environments). This must be guided mainly by maximising the expectation of genetic gain in the target environment, and by sensible resource allocation during the testing process.

The variability in salinity-affected fields is normally very high, both spatially and temporally (Hajrasuliha et al. 1980; Richards and Dennett 1980; Richards et al. 1987). Spatial variation occurs horizontally and vertically on very small scales. The variable nature of saline fields is often intensified by irrigation (Shainberg and Shalhevet 1984). Thus, most salinity affected lands are actually comprised of many micro-environments, ranging from low to high salinity in the same field, and crop yields in these fields are patchy, responding to salinity 'on the spot'.

Many experiments in which sets of genotypes have been tested across a broad range of salinity levels (as can be encountered in natural fields) have been carried out for a wide variety of crops. The results from these experiments, either on artificial or natural substrates, have shown that the genotype-by-salinity level interaction is usually large and significant (Ayers et al. 1952; Shannon and Francois 1978; Azhar and McNeilly 1988; Kelman and Qualset 1991; among others). This interaction is commonly of the crossover type, i.e. the genotypic ranking varies across salinity levels.

Thus, breeding for saline areas can be compared to what has been known as breeding for 'wide adaptation'. This is the name that has been traditionally assigned to a

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plant-breeding philosophy aimed at obtaining genotypes showing superiority over a range of environmental conditions.

The ways of reaching this goal, and even its mere feasibility, have been controversial issues for a long time (Romagosa and Fox 1993). When confronted with this type of situation, the plant breeder must decide whether to work over the whole target environment, or subdivide it into more homogeneous sub-environments. This decision depends mainly upon the relative sizes of the genotype × year and genotype × location interactions (Austin 1993). Unfortunately, this choice does not exist when working in areas with saline soils, since, as mentioned above, the highly variable conditions occur concurrently in the same field.

The target environments for breeding for saline soils or for wide adaptation are actually a population of many possible environments, for which there exists a large and significant component of genotype-by-environment (G × E) interaction. Thus it is possible to study the merit of potential strategies for breeding for salinity tolerance using the tools that have been developed for the study of breeding for wide adaptation.

The objective of the present study is to explore the application of this approach, taking into account the peculiarities of crop response functions to salinity. I illustrate the method for choosing an optimum selection strategy with an example from a grain sorghum improvement program.

Background on breeding for variable conditions

Calhoun et al. (1994) summarised the three strategies that have been proposed to address the issue of choice of selection environment for the situations described in the previous section: (1) make selections in an stressful environment; (2) select under optimum growing conditions; and (3) use a combination of both approaches, i.e. select materials that perform well under both stress and non-stress conditions. The main drawback of the third alternative is that resources during selection must be at least duplicated to allow for testing under stress and non-stress conditions, and so its advantage must be large enough to justify its adoption.

The theoretical pros and cons for these three alternatives have been extensively dealt with in many studies (Johnson and Frey 1967; Allen et al. 1978; Hamblin et al. 1980; Blum 1988; Falconer 1990; Zavala-García et al. 1991), mainly in relation to drought or unidentified environmental stresses (though they also apply to salinity stress) and will not be discussed further here. The only general conclusion arising from these studies is that the choice of an optimum selection strategy must be based on a knowledge of the magnitude of G × E interaction and of the heritability (h^2) within the acceptable agronomic range likely to occur in the target environments.

The experimental evidence on the benefit of options (1) and (2) is diverse. Atlin and Frey (1990) mentioned numerous examples where authors have favoured selection either under stress or non-stress conditions, for a wide variety of abiotic stresses. Falconer (1990) reviewed 21 selection experiments considering two contrasting environments in very diverse organisms. He found that antagonistic selection (i.e., selection against the environment, such as selection for higher yield in a yield-depressing environment, like a saline treatment) changed the mean across the two environments considered in the desired direction in a significantly higher number of cases than did synergistic selection (i.e., selection for a trait in the same direction that it is altered by the environment). Also, he demonstrated how synergistic selection always produced an increase in sensitivity (i.e. the difference between the good and the bad environment, or, in this case, salinity tolerance) larger than antagonistic selection. Thus, it seems that if only one environment had to be chosen, selection for a trait in a stress environment would not only produce more tolerant material, but would also have a higher probability of increasing the overall mean across environments for that trait.

In the context of breeding for salinity tolerance, the evidence is not conclusive. Richards (1983) compared several simulated selection strategies for barley production in saline areas, concluding that the best strategy was to select for yield under non-saline conditions, that is option (1). This conclusion was based on the large variability present in saline soils, which resulted in most of the yield being derived from the least-saline areas in a field. This is a very attractive hypothesis, as it would be possible to delay testing under saline conditions during a breeding program until the very late stages, when there remain only a few advanced genotypes, already selected for high-yield potential and any other desirable agronomic traits. Some selection experiments on production under saline conditions indirectly support this hypothesis (Rawson et al. 1988; Kapulnik et al. 1989), while others seem in conflict with it (Johnson et al. 1992). Nevertheless, there are few examples of studies directly approaching this question in a systematic way, as did Kelman and Qualset (1991). The findings by these authors supported Richards's hypothesis, but their study focused on a different situation than that treated here, as in their environment the salinity was not originally in the soil but was brought in by irrigation water of poor quality.

With respect to option (3) Jinks and Connolly (1973), studying the fungus *Shizophyllum commune*, pointed out that, to achieve a desirable average growth rate across a range of environments, selection must be based on average performance in two or more contrasting environments within that range. Most works with field crops, mainly in relation to unidentified abiotic environmental stresses, have arrived at a similar conclusion. Hamblin et al. (1980) found that combinations of two or (preferably) three locations predicted the overall behaviour of wheat genotypes across 26 locations much better than did any one location. Rosielle and Hamblin (1981) suggested the use of information from both stress and non-stress environments for improving yield gain, and Zavala-García et al. (1991) found that selection criteria involving yield combinations from stress, intermediate, and non-stress environments produced better selections than did any single environment, in a situation where water was the main limiting factor. These findings make sense from the point of view of population genetics, as selection of an organism in a particular environment would lead to adaptations to those specific conditions, shrinking the niche for the species, thus limiting its competitiveness in different situations (Tigerstedt 1994).

The conclusion arising from the studies reviewed above is that, when separate selection for distinct environments is not possible, the option most likely to maximise genetic gain for wide adaptation is a combination of selection environments; that is, option (3). Obviously, the more environments used, the better will be the results obtained. However, as testing resources are limited, a sensible compromise seems likely to be a combination of a non-stress location, and at least one stress environment (within the range of the target environment), between which there is significant G × E interaction (of the crossover type).

There are other considerations which should be given attention when choosing a selection strategy. The recognition of the high variability of crop yields on naturally saline soils has prevented their use by plant breeders to perform selection and testing trials (Shannon and Qualset 1984; Blum 1988). Thus, in a vast majority of cases, selection trials are done on artificial systems, ranging from Petri dishes to artificially saline soils. Another point is the possible existence of adaptive mechanisms of salinity tolerance. The genes responsible for these potential mechanisms, which would be expressed preferentially under saline conditions, would not be selected for if selection is performed only in the absence of stress. Finally, another important aspect is focusing the work on an acceptable range of yield. Selection for survival at very high saline levels has been carried out for a number of crops, with some success (Dewey 1962; Kingsbury and Epstein 1984, among others). However, screening for whole-plant survival may depress the growth potential of the selections, since some physiological mechanisms which enhance survival may depress growth (Munns 1993), and hence yield potential. Selection for survival may be a valuable tool for identifying donors of salinity tolerance, but its use as a selection criterion in a breeding program should be accompanied, in my opinion, by an examination of the selections under non-stress conditions to avoid loss of desirable agronomic traits.

There are several possible explanations for the disagreement among the various studies about the choice of selection environments. In addition to the relative magnitudes of heritabilities and genetic variances between environments, and the magnitude and type of G × E interaction present, the variability of the shape of the response functions to the environmental factors responsible for G × E interactions makes it difficult to arrive at any generalisations. Some studies dealing with two environments, e.g. Falconer (1990), assumed a linear relationship between the measured variables and the environmental variables considered over the range of environments studied. But this is a risky assumption to make unless the environmental factors influencing the G × E interaction are known and the response functions to those factors are well established. Generally, G × E interaction is caused by various unidentified factors, including weather, soil, and management variables (Nor and Cady 1979; Gorman et al. 1989), and in most studies dealing with breeding for wide adaptation it is difficult to single out those environmental factors which account for significant portions of the G × E variance. Thus, the response of genotypes across a range of environments is often non-linear, and the nature of the G × E interaction is better studied using multivariate techniques (Saaed and Francis 1984; Zobel et al. 1988).

The experimental approaches to identify test environments for wide adaptation must rely on having data from a representative sample of all possible environments. In most cases, this data must be very extensive, due to the multidimensional nature of the G × E interaction and, as Hamblin et al. (1980) pointed out, by the time this is available it is likely that the siting of breeding facilities will have already been determined for other reasons. Nevertheless, in the case of irrigated, high-input, saline environments, the G × E interaction present is likely to be caused by different genotypic responses to salinity. This assumption is less likely to hold for dryland agriculture, where salinity fertility and salinity humidity interactions may be of importance. The knowledge of crop response-functions to salinity can help the breeder to calculate and identify the minimum number of test location necessary for the prediction of the response across all possible environments.

A systematic procedure for choosing environments for breeding for saline areas

The response functions of crop yields to soil salinity have been fitted by various regression equations. Popular among them is a three-piece linear response model proposed by Maas and Hoffman (1977):

$$Y_s = Y_{\max} \qquad (0 \leq EC_e \leq a) \qquad (1)$$

$$Y_s = Y_{\max} - b(EC_e - a) \qquad (a \leq EC_e \leq EC_0) \qquad (2)$$

$$Y_s = 0 \qquad (EC_e > EC_0) \qquad (3)$$

where Y_s is the relative yield: $Y_{\max}$ is the potential yield, not affected by salinity; a represents the threshold, i.e. the maximum allowable salinity without yield reduction; b is the slope, the absolute yield decrease per unit increase in salinity beyond the threshold; and EC_e is a measure of the electrical conductivity of the soil saturated extract.

Based on this equation, I propose the following method to systematise the choice of the optimum selection environment(s): the minimum number of points needed to define Maas and Hoffman's response function are three: one below the threshold level (hereafter low salinity, or LS), to estimate maximum yield; and two in the sloping part of the function, one at an intermediate level (IS), and one at a high level (HS). I recommend that LS represents the lowest salinity level possible at each situation; HS be close to the maximum salinity level producing a positive economic return; and IS be the midpoint between LS and HS. The slope, b, can be calculated following the equation

$$b_{(EC_{LS}<a)} = (Y_{IS} - Y_{HS})/(EC_{HS} - EC_{IS}). \tag{4}$$

Once b is known, a is calculated by substituting all the known parameters in (2). In the case where LS is placed to the right of a, b can be better estimated after classic linear regression, using the information from the three saline levels to fit the following equation:

$$Y_{s,(EC_{LS}>a)} = Y_{\max} - (bEC_e). \tag{5}$$

In this case, a can not be estimated, and $Y_{\max}$ is probably overestimated.

Falconer (1989) suggested that yield in low- and high-production environments could be considered as separate traits, not necessarily maximised by identical sets of alleles. Under these circumstances, the problem of choosing the best productivity level for selecting genotypes for use at a range of productivity levels is reduced to a comparison of the magnitude of selection responses (direct or indirect) estimated for each level (or group of levels) tested. By calculating the selection responses in the three environments (LS, IS, and HS), it is possible to evaluate the effect of a number of selection strategies (selection at any single environment, or combination of environments) on the parameters $Y_{\max}$, a, and b of the response function (see Fig. 1). Then it is possible to calculate the desirability index (D), proposed by Hernández et al. (1993), for the interval LS-HS, to use as a yardstick to compare selection strategies. D_s is the average yield value for the average genotype in a given interval of environmental conditions, and is calculated by dividing the area under the function [obtained by integration of equation (1) for the LS-HS interval] by the distance between the two salinity levels chosen. Thus, the following equations can be derived.

$$D_{s,(EC_{LS}<a)}$$

$$= \left[\left(\int_{EC_{LS}}^{a} \mathrm{eq}(1)d(EC_e)\right) + \left(\int_{a}^{EC_{HS}} eq(2)d(EC_e)\right)\right] \Big/ (EC_{HS} - EC_{LS}) = Y_{\max}$$

$$- b[(EC_{HS} - a)^2/2(EC_{HS} - EC_{LS})] \tag{6}$$

for cases in which EC_{LS} is below a, and

$$D_{s,(EC_{LS}>a)} = \left[\int_{EC_{LS}}^{EC_{HS}} \mathrm{eq}(5)d(EC_e)\right] \Big/ (EC_{HS} - EC_{LS})$$

$$= Y_{\max} - b[(EC_{HS} + EC_{LS})/2] \tag{7}$$

for cases in which EC_{LS} is above a.

The calculation would stop here if the probability of occurrence for each salinity level in the target environment is similar. As this is not likely to be the case, it would then be necessary to: (1) divide the target environment into salinity classes, and estimate the proportion of the total area in each salinity class, (2) calculate mean gains for each selection strategy and salinity class, (3) multiply the calculated mean gains by the proportion of land in each salinity class, and (4) total these products for each selection strategy. The total obtained would be an estimate of the genetic gain attainable after each selection strategy for the target environment of interest.

Obviously, the first part of this analysis demands the evaluation of a set of genotypes (ideally a breeding population with the potential for salinity tolerance) in three environments, followed by the calculation of genetic, environmental and genotypic variances, genetic correlations, heritabilities, and direct and indirect responses to selection (Falconer 1989). The choice of the three environments could be guided by the yield response functions to salinity which have been already published for most crops (Francois and Maas 1994).

The second part of the analysis calls for a detailed mapping of soil salinity in the target area. This may be done by means of devices such as on electromagnetic sensor, which provides fast and reliable measurements of soil salinity (Díaz and Herrero 1992).

A worked example: grain sorghum

I illustrate this approach with data from a set of trials carried out with 12 grain sorghum inbred lines at the Aula Dei Experimental Station, in Zaragoza, Spain. Details of these trials can be found in Igartua et al. (1995). The trials were carried out over 3 years, using a triple line source sprinkler system (Aragüés et al. 1992).

Table 1 Grain yield means, genetic variances, heritabilities, and genotypic correlation coefficients for all selection environments

Treatment	Mean	σ_g^2	h^2	r_g				
				Mean	LS	IS	HS	LIS
	kg ha^{-1}							
Mean (10)	3206	166 161	0.569					
LS	5025	359 786	0.552	0.40				
IS	3276	162 821	0.446	0.94	0.00			
HS	1386	316 978	0.863	0.93	0.14	1.02		
LIS		131 082	0.408	0.86	0.83	0.56	0.69	
LHS		192 916	0.628	0.87	0.77	0.66	0.74	0.94

With this system, the inbreds were exposed to a linear salinity gradient divided in ten treatments, which ranged from an EC of water applied (EC_w) of 2.1 dSm^{-1} at the lowest salinity treatment (LS), to 11.6 dSm^{-1} at the highest level (HS). The LS and HS environments were chosen for this analysis along with the average of the two intermediate treatments (IS, $EC_w = 7$).

Soil-salinity measurements made with the electromagnetic sensor could not be acceptably converted to soil saturation extracts EC units. Instead, I used the salinity of the water applied for the calculations. Thus, the second part of the analysis (calculating selection responses for actual saline areas) could not be performed, as available maps of soil salinity were expressed in EC_e units. This drawback, and the fact that the sample is probably too small to provide reliable estimates of genetic parameters, prevents an extrapolation of the conclusions to other situations. Nevertheless, the example is valid for the purpose of illustration.

Five selection strategies were considered: selection in the LS, IS or HS environments, and selection for the average yield from the LS-IS (LIS) or the LS-HS (LHS) environments.

The genetic variances, broad-sense heritabilities, and genotypic and environmental correlations for these treatments, along with the results for the overall mean across the total of ten salinity treatments, are shown in Table 1. The h^2 was maximum for the HS treatment, and not for the non-stress treatment (LS). As there was a single replicate per year, the genotype-by-year interaction could not be estimated. The residual term in the analyses of variance for each treatment (data not shown) comprised both the error variance and the genotype-by-year interaction. Thus, it is possible that this interaction term was greater for the LS and the IS than for the HS treatments (HS probably being less dependent on other environmental factors, due to an overriding effect of salinity).

All genotypic correlations between the IS and HS saline treatments and the overall mean across the ten treatments were close to +1, while correlations of IS and HS with LS were close to 0. This is an indication of different mechanisms (and possibly, genes) governing yield under saline and non-saline conditions, for this set of materials. Genotypic correlation coefficients for LIS and LHS were intermediate, but closer to those of the saline treatments.

Table 2 shows the expected responses to selection, calculated for all test environments, after Falconer (1989). Also reported are the estimated responses across the ten saline treatments, for all test environments (column labelled 'Mean'), and the responses to selection that would result from testing in the ten saline treatments (line labelled 'Mean'). As expected from the genotypic correlations, the predicted response in the most-saline environments after selection in the LS treatment is very low, and vice versa. Selecting jointly in a saline and a non-saline treatment (LIS and LHS) is predicted to result in intermediate gains across all treatments.

Table 3 reports the estimated parameters for the functions resulting from yield evaluation in LS, IS and HS, and for the functions derived for five different selection strategies. Also included are the parameters for the equation that would result from selecting on the overall mean across the ten treatments. Column 'D_s' shows the values of the desirability index. All selection methods increase the EC at which the yield becomes zero (Table 3), except selection in LS. Selection in IS or HS alone increases the salinity tolerance, as *a* increases, and *b* decreases. D_s is highest for HS, as was expected from its notably greater h^2; next is LHS, and the lowest gain occurs when selection was simulated in LS. The best strategies appear to be either selecting in HS, or jointly in LS and HS. The choice between the two is not evident, but it seems sensible to choose LHS, as selection in HS may compromise the gain in yield potential.

The predicted gains for the whole range of salinity levels presented in Table 3 have been calculated with the data from three treatments. Figure 1 shows the functions for the original data, and for the predicted responses after selection in LS and HS. The comparison of these values with the same predicted responses, but calculated for the actual mean-yield for the ten treatments, presented in Table 2 (column labelled 'Mean'), is one way of assessing how well the 'reduced' approach of using just three treatments condenses the information of the ten treatments. The only appreciable difference for these two values occurs for the LS treatment; however,

Table 2 Direct and indirect responses to selection for several selection strategies (10% selection differential, $i = 1.755$)

Selection criteria	Predicted response			
	Mean	LS	IS	HS
	$kg ha^{-1}$			
Mean	541	322	447	618
LS	216	785	2	103
IS	449	3	474	676
HS	618	138	674	921
LIS	393	560	254	434
LHS	495	646	369	579

Table 3 Estimated parameters for the response functions resulting from applying diverse selection strategies, and average yield (Di) and predicted response to selection (Pred. R) for the interval between the LS and HS environments using those functions

Selection criteria	$EC_{y=0}$	a	Y_{max}	b	D_i	Pred. R
	dSm^{-1}		$kg ha^{-1}$			
None	15.0	2.74	5025	411	3322	0
LS	14.6	Non-est.	6688	389	3545	223
IS	17.2	3.52	5028	367	3761	439
HS	18.1	3.60	5163	357	3956	634
LIS	16.1	Non-est.	6398	372	3662	340
LHS	16.5	Non-est.	6470	365	3777	455
Mean	17.0	2.65	5566	374	3766	444

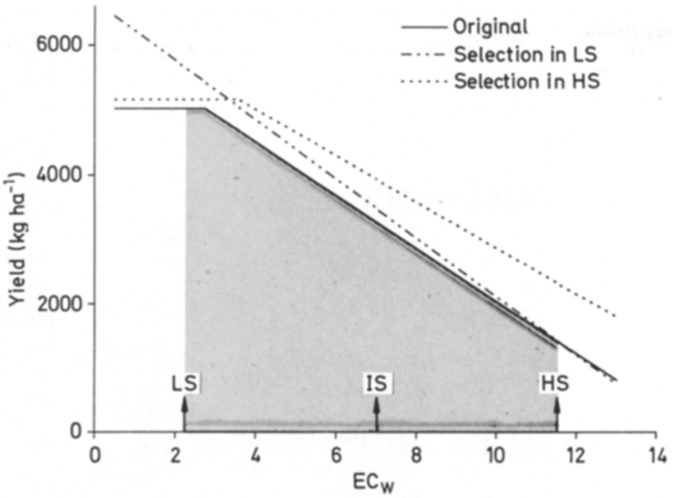

Fig. 1 Grain-yield response functions estimated with data from treatments LS, IS, and HS, for the original data, and for predicted selection responses at LS and HS. The *shaded area* is used in the calculation of the desirability index, D_s

the predicted mean response to selection in LS is always the least. The ranking of the predicted responses did not vary with either method of calculation, thus validating the use of the three treatments as a model of the whole range of saline levels in the gradient.

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