

Chapter 2

Breeding for Stress-Tolerance or Resource-Use Efficiency?

Roberto Fritsche-Neto and Júlio César DoVale

Abstract In plant breeding programs, it is not entirely clear whether the goal is to improve resource-use efficiency or the tolerance to low resource availability. The aim of this chapter was to verify the relationship between breeding for a tolerance to low levels of soil nutrients and for nutrient-use efficiency. The relationship between nutritional efficiency and the tolerance to nutritional stress was estimated by the Spearman ranking correlation between maize genotypes for the traits related to nitrogen, phosphorus and water-use efficiency and phenotypic plasticity indices. The lack of relationship between the traits, in both magnitude and significance, indicates that these traits are controlled by different gene groups. Consequently, simultaneous selection for both nutrient-use efficiency and tolerance to nutritional stress is possible if the mechanisms that confer efficiency and tolerance are not competitive.

Keywords Plant breeding · Abiotic stress

2.1 Introduction

To meet the rising worldwide demand for food, there are some options, such as further exploration of planting in dry seasons, that often leads to lower yields, increased productivity, and the expansion of cultivation areas, an alternative that

R. Fritsche-Neto (✉) · J. C. DoVale
Department of Plant Science, Federal University of Viçosa,
Viçosa, Minas Gerais, Brazil
e-mail: roberto.neto@ufv.br

J. C. DoVale
e-mail: julio.vale@ufv.br

ensures greater food production and is still viable in some emerging countries, including Brazil. Within this context, a significant fraction of cultivation can be performed in marginal areas, which tend to have low fertility (Giaveno et al. 2007).

When water availability and soil nutrients are limiting to plant growth and development, there is a reduction of metabolism, biomass, and the surface areas of various plant organs, thus affecting the productivity (Sultenfuss and Doyle 1999). Considering this fact, several plant breeding programs have emerged, and other lines of research have been directed at improving conditions for abiotic stresses. Thus, two breeding strategies can be considered: tolerance to a low availability of water and nutrients and resource-use efficiency.

2.2 Tolerance and Efficiency as Responses to Abiotic Stress

The literal meaning of the word “stress” is coercion, that is, force in one direction. The term, in Physics, is used to denote the tension produced within a body by the action of an external force. Biologically, stress is considered as a significant deviation from the ideal conditions in which plants are grown, preventing them from expressing their full genetic potential for growth, development, and reproduction (Rehman et al. 2005). According to Larcher (2006), in principle, the change-induced responses at all functional levels of the organism are reversible (elastic deformation) but may become permanent (plastic deformation) (Fig. 2.1).

It has been observed that brief exposure to stress does not exceed the tolerance limit and causes only temporary changes in the plant, whereas prolonged exposure results in permanent changes. Thus, after recovery, the dry matter returns to the original rate (angle of inclination α). However, in the case of chronic stress, the growth rate is reduced at a continuous angle ($\beta < \alpha$), and the loss in productivity is significantly higher.

Abiotic stress may trigger a series of responses in plants that include changes in gene expression and cellular metabolism. The duration, severity, and frequency with which a stress is imposed, and the affected organs and tissues, developmental stage, and genotype also influence plant responses to stress. Consequently, a combination of different conditions can cause different plants responses to the same type of stress (Fig. 2.2).

For the efficient improvement of this process, it is essential to identify the responses that promote or maintain the growth and development of plants during the stress period (Bray et al. 2000).

The tolerance to a particular stress is quite variable but is related to the plant's ability to withstand adverse conditions, survive, and reproduce successfully. Agronomically, Miti et al. (2010) defined tolerance as the reduction in yield under stress conditions compared to the yield under the optimal condition of cultivation.

The use efficiency (UE) of water or nutrients is defined as the ratio between the yield per unit of resource available to the plant (Moll et al. 1982). In studies with plants in early stages, the yield is usually replaced by the mass of shoot dry weight

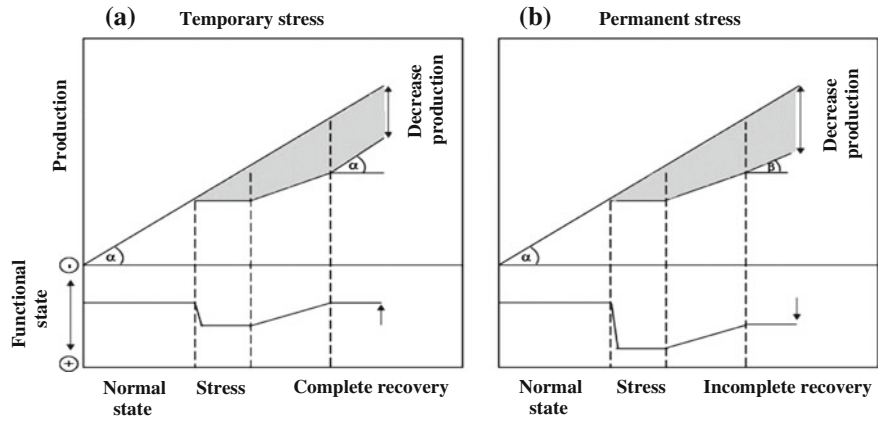


Fig. 2.1 Effect of environmental stress on productivity. **a** Temporary stress and **b** Permanent stress. *Source* Adapted from Larcher (2006)

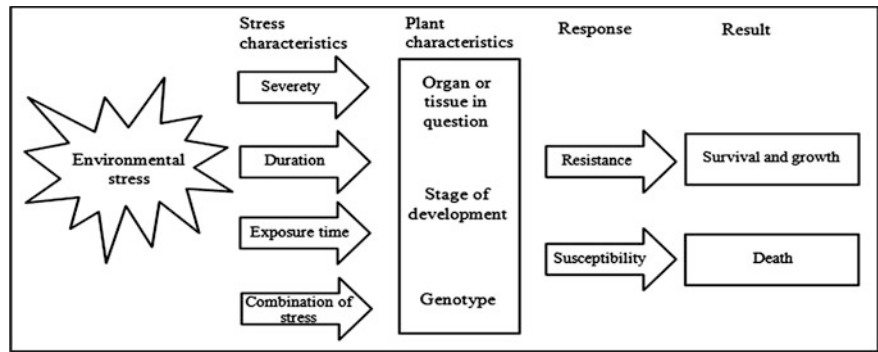


Fig. 2.2 Plant responses in accordance with the characteristics of environmental stress. *Source* Bray et al. (2000)

to estimate the UE (Maia et al. 2011; Fritsche-Neto 2011). Thus, particular genotypes will be considered as efficient when producing well with the minimum availability of the resource (Good et al. 2004).

The UE consists of the acquisition efficiency (AE) and utilization efficiency (UtE). The AE is defined as the ability of a given genotype to absorb certain nutrients or soil water, whereas the UtE refers to the ability of this genotype to produce biomass or grain using the resource that has been absorbed. For Hirel et al. (2007), genotypes more efficient in the use these resources can be achieved by increasing the AE and UtE.

In cases of tolerance and efficiency, plants use physiological mechanisms, and sometimes, anatomic mechanisms to avoid the effect of stress and rapidly recover (Zheng et al. 2000). As a result, three main strategies have been recognized that

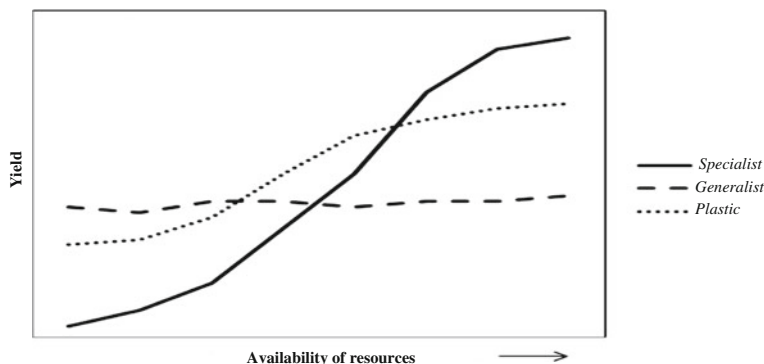


Fig. 2.3 Classification and behavior of plants based on their response to heterogeneity in resource availability

plants use to cope with stress: (i) *specialization*, the genotype is adapted to the specific environment; (ii) *generalization*, the genotype has moderate suitability in most environments; and (iii) *phenotypic plasticity*, signals from the environment interact with the genotype and stimulate the production of alternative phenotypes (Fig. 2.3).

The farmer wants cultivars that produce a satisfactory yield when subjected to stress conditions but that have a high productivity under ideal growing conditions. However, considering the concepts stated above, from a physiological point of view, the simultaneous improvement of abiotic stress tolerance and resource-use efficiency is contradictory. Furthermore, there is some confusion between these terms in many reports published and also in the objectives of research.

According to Bradshaw (2006), phenotypic plasticity is high when compared to the yield stability. Thus, low plasticity (or high stability) is not always a desirable characteristic because tolerant genotypes generally have moderate productivity, even under ideal growing conditions (Cruz et al. 2004), which is important in marginal areas and under cultivation with permanent stress. Thus, these genotype “generalists” exhibit superior productivity in environments with low resource availability. However, when the environmental conditions are not limiting, there is no significant increase in productivity, which is a disadvantage.

Given this fact, most of the improvement programs are aimed at increasing the UE or in obtaining genotypes with high phenotypic plasticity. Thus, when the plants are subjected to limiting conditions, they would use fewer resources to produce satisfactory results but show high yields when the conditions are ideal.

The genetic control of both stress tolerance and resource-use efficiency is quantitative and involves many loci distributed in different regions of the genome in cultivated species (Wu et al. 2011). Quantifying and understanding the genetic relationship between these two strategies for improvement in plant selection is the key in the implementation of programs to improve and increase the effectiveness of the approach.

Table 2.1 Spearman correlation estimates between the plasticity index of shoot dry weight mass (iSDW), length lateral roots (iL_{LAT}), axial roots (iL_{AXI}) and ratio shoot/root (iRSR) to the acquisition efficiency (AE) and utilization efficiency (UtE) at high (HN) and low nitrogen (LN) and high (AP) and low phosphorus (LP) in 15 tropical maize inbred lines

Trait	AE _{LN}	AE _{HN}	UtE _{LN}	UtE _{HN}	AE _{LP}	AE _{HP}	UtE _{LP}	UtE _{HP}
iSDW	−0.11 ^a	0.18 ^a	0.28 ^a	0.49 ^a	0.22 ^a	0.15 ^a	0.04 ^a	−0.23 ^a
iL _{LAT}	0.28 ^a	0.41 ^a	−0.25 ^a	−0.27 ^a	0.28 ^a	−0.20 ^a	0.02 ^a	0.08 ^a
iL _{AXI}	0.50 ^a	0.11 ^a	−0.14 ^a	0.07 ^a	0.42 ^a	0.26 ^a	0.12 ^a	0.11 ^a
iRSR	−0.23 ^a	0.05 ^a	0.37 ^a	−0.35 ^a	−0.28 ^a	−0.40 ^a	−0.06 ^a	0.00 ^a

^a Not significant at $p < 0.05$ % by the t test

Source Adapted from Maia (2011)

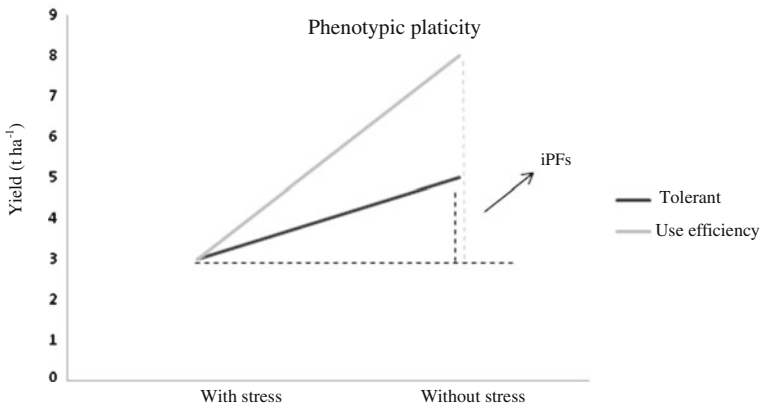


Fig. 2.4 Phenotypic plasticity indexes (iPFs) of two hypothetical genotypes, which demonstrate contrasting behaviors in relation to stress (with stress and without stress)

2.3 Results Observed

Seeking to quantify the possible relationship between improvements in stress tolerance and nutrient efficiency in corn, Maia et al. (2011) evaluated strains in two experiments conducted in a greenhouse under conditions of contrasting nitrogen (N) and phosphorus (P). The relationship between the nutritional efficiency and tolerance to the respective nutrients was estimated using the *Spearman* correlation between the rank of the lineages selected for traits related to UE of N and P or the rate of phenotypic plasticity (Valladares et al. 2000) (Table 2.1).

There is a lack of correlation among the traits, both for significance and magnitude, indicating that they are controlled by different gene groups. Therefore, mechanisms that provide an efficient use of resources and stress tolerance and are not competitive will allow the simultaneous selection for both traits. However, one must consider that most of the observed correlations were negative. With the increase in effective size, the coefficients would have a greater magnitude, and its effects, most likely, would be significant.

Table 2.2 Means of the plasticity index and water-use efficiency (WUE) for five strains of tropical maize

Maize lines	Plasticity index	WUE
13	0.60	1.465
9	0.59	1.535
12	0.57	1.43
3	0.46	1.405
7	0.44	1.335

Source Adapted from Coutinho (2011)

In another study, Wu et al. (2011) observed differences in the performance of 189 maize lines under contrasting conditions of N on the agronomic UE of this nutrient and the index of tolerance to a low soil N. The authors concluded that there is genetic variability for both the N-use efficiency and tolerance to this stress.

The physiological point of view predicts that the genotypes with higher resource-use efficiencies are not the most tolerant to the shortage of that resource. Thus, considering the rate of phenotypic plasticity, genotypes are classified as tolerant when they have the lowest values of this index, that is, the lower range of productivity between environments with and without stress. Genotypes with higher values for the index of plasticity, in turn, are considered efficient in resource usage or more efficiently adaptive to changes in growing conditions. For these genotypes, there are considerable increases in productivity with small increases in resource availability (Fig. 2.4).

A study that supports this evidence was conducted by Coutinho (2011) in the selection among 14 tropical maize inbred lines that contrasted with the parents for water-use efficiency (WUE). According to the author, the lines that showed the lowest rates were those with less WUE plasticity, whereas the lines that showed higher rates were those with more WUE plasticity (Table 2.2).

It is believed that, in most cases, genotypes that are efficient under nutritional stress and water stress should be sought, i.e., those that respond positively to the addition of features that enhance productivity. However, other factors, such as restrictive cultivation, temperature, content of aluminum, and salinity, should also be considered when selecting more tolerant genotypes.

Finally, we emphasize the need of additional studies for better understanding of the relationship between resource-use efficiency and stress tolerance to increase the efficiency of breeding programs for plants growing under conditions of abiotic stress.

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