Breeding for stress tolerance: Drought as a case study

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SUMMARY

Drought is an important climatic phenomenon which after soil infertility ranks as the second most severe limitation in the production of crops under rainfed, low input agriculture. Breeding of genotypes with greater drought tolerance is the best strategy for maintaining and/or increasing crop production in such systems. This paper reviews the concept of drought tolerance and discusses approaches that may be adapted to breed varieties of crops with tolerance to drought. What remains to be done is for breeders to use the available genetic variability with respect to mechanisms that aid the plant in adapting to drought in their breeding programmes. It is concluded that biotechnologies will prove quick and stable markers for identifying genes that confer drought resistance.

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RÉSUMÉ

DANQUAH, E. Y. & BLAY, E. T.: *La reproduction pour la tolérance à la tension: La sécheresse en tant qu' étude de cas.* La sècheresse est un phenomène climatique important qui, après l'infertilité de sol, occupe la deuxième ordre dans le classement des limitations les plus sévères de la production des cultures sous la culture pluviale et la faible facteur d'intrants. La reproduction de génotypes de plus grande tolérance à la sècheresse est la meilleure stratégie pour soutenir et/ou augmenter la production des cultures sous ces systèmes. Cet article réexamine cette idée de la tolérance à la sècheresse et discute les démarches à suivre pour reproduire les variétés de cultures ayant la tolérance à la sècheresse. Ce qui reste à faire est que les phytogénéticiens doivent utiliser la variabilité génétique qui existe à l'égard de mécanismes qui aident la plante à l'adaptation à la sècheresse en leurs programmes de reproduction. La conclusion est tirée que les biotechnologies ferons preuves d'être les indicateurs rapides et stables pour l'identification de gènes qui accordent la résistance à la sècheresse.

Introduction

Levitt (1972) defines biological stress as any environmental factor capable of inducing a potentially injurious strain on living organisms. The environmental factors that determine productivity of crop plants are water availability, temperature, light, and the chemical and physical properties of the soil. Other localized stresses such as air pollutants, wind, and hail exact a minor toll. Cardwell (1982) observed that the main factor responsible for the difference between the potential and actual yield of crops is environmental stress.

Breeding genotypes with greater tolerance to adverse environmental conditions offers considerable promise for maintaining and/or increasing crop production on arid and semi-arid lands, in areas with problem soils, and in marginal agricultural areas throughout the world. This is especially true in developing countries where low incomes usually prevent the use of more direct approaches for altering stress conditions such as provision of irrigation water, or the use of soil amendments.

Traditionally, breeders have addressed the problem of environmental stress, normally by selecting for suitability of performance over a wide range of environments, using extensive testing and biometrical approaches (Blum, 1988). An understanding of how the interaction of chemical and physical environments reduces plant development and yield will open the door to a combination of breeding, physiological and biotechnological approaches to plant modification in a comprehensive strategy for improving resistance to environmental stresses (Cullis, 1991). However, due to the environmental uncertainties being faced in crop production, the goal will be to optimize local management practices to reduce extreme stress as far as possible and, in particular, to intensify the search for genotypes which will show higher resilience in the face of a given stress.

Water supply and temperature are the most ubiquitous sources of environmental stress. Since there is no single mechanism by which stress can be alleviated, this paper shall concentrate on water stress, mainly in terms of drought. It first discusses the concept of drought tolerance and reviews the adaptive mechanisms and traits that seem to confer drought tolerance, and their use in breeding programmes as well as limitations to breeding for drought tolerance. An example of how biotechnological approaches have been used in breeding for drought tolerance in maize is also reported. The paper concludes by stressing the need for breeding crop varieties with tolerance to drought in moisture-stressed environments, and suggesting an integrative, multidisciplinary approach in breeding for drought tolerance.

The concept of drought tolerance

Linsley, Kohler & Paulhus (1959) defined drought as a sustained period of time without significant rainfall. However, such rainfall deficit does not constitute drought in a crop production system until the water shortage begins to limit the growth and development of crop plants (Quizenberry, 1982). The adaptive mechanisms by which plants survive drought, collectively referred to as drought resistance (Jones, Osmond & Turner, 1980), may be conveniently divided into three primary categories (May & Milthorpe, 1962; Turner, 1979; 1986a):

1. *Drought escape.* The ability of a crop plant to complete its life cycle before serious soil and plant water deficits develop.
2. *Drought tolerance at high plant water potential.* The ability of a crop to endure periods without significant rainfall whilst maintaining a high plant status, i. e., dehydration postponement (Krammer, 1980) or drought avoidance (Levitt, 1972).
3. *Drought tolerance at low tissue water potential.* The ability of a crop to endure rainfall deficits at low tissue water status, i.e., dehydration tolerance (Levitt, 1972).

Breeding approaches for drought tolerance and yield

Breeding of high-yielding varieties for environments with moisture deficits is usually carried out either through stability analysis to evaluate the response of the components of yield to stress (Fischer & Maurer, 1978; Fischer & Sanchez, 1979) or by incorporating traits that contribute directly, or indirectly, to yield stability (Ludlow & Muchow, 1990; Sadras, Connor & Whitefield, 1993). The following are some of the approaches that can be adopted in trying to develop varieties suitable for drought. In practice, however, breeders are always restricted in the choice of the breeding approaches they can adopt by the limited resources at their disposal (Simmonds, 1979).

Adaptation to a specific environment

One approach is to develop varieties that are specifically adapted to moisture-deficit environments. This approach is most useful in environments where plants must complete their life cycle on soil moisture stored during the previous season (Quinzenberry, 1982). Hurd (1976) indicated that varieties selected for high yields in optimal moisture conditions would not necessarily have high yields when grown in moisture-stressed conditions. He believes that a superior variety for an environment with moisture stress must be selected and evaluated under that environment.

Hurd (1976) showed in wheat that the variety that has the greatest root development when grown in non-stressed environment does not necessarily have the most developed root system in a moisture-stressed environment. Cotton varieties that had the highest water-use efficiency in an optimal environment did not have the highest efficiency under moisture-stressed conditions.

The use of this approach may present several problems. Considering the variability in amount and temporal distribution of available moisture, from year to year, a variety developed through this approach may be unable to respond to years of above-normal precipitation (Quizenberry, 1982). This variability in precipitation also changes the breeder's environmental selection index from year to year (Ludlow & Muchow, 1990). Therefore, the breeder must attempt to compensate for this moisture variability by increasing the number of testing locations and by increasing population size (Hurd, 1976). The disadvantage is that it makes the whole process slow and more expensive. If below-normal precipitation occurs, the yield and yield components of the selections may be too small to be effectively separated by the available statistical techniques. Heritabilities for yield and its components will be extremely low, thereby reducing the effectiveness of selection (Johnson & Frey, 1967). Varieties developed by this method have a narrow adaptation and show high genotype-by-environment interaction (Blum, 1988).

Adaptation to a variable environment

Another breeding approach is to develop varieties that are adapted to a broad range of environmental conditions. This approach is the most appropriate when plants receive precipitation during the growing season or in a more optimal growing climate where periodic droughts may occur. The assumption is that drought is an unidentifiable component of stability in yield performance (Quizenberry, 1982). Finlay & Wilkinson (1963) used linear regression to identify and describe the environmental responses of a range of different wheat and barley genotypes. The identified genotypes which were able to produce high mean yield over all the test environments. Allard & Bradshaw (1964) and Easton & Clements (1973) used regression analysis to contrast overall population responses with cultivar responses in a bid to link drought resistance to stress severity. Their work provided a relatively reliable method of quantifying stress severity in the absence of sophisticated instrumentation, and simultaneously related stress severity to yield response for each increment of stress observed (Sojka, 1985).

A major drawback with the biometrical approach is that the precision and accuracy of the techniques depends upon the researcher's capacity to ensure that all other factors affecting the experiment are uniform across all varieties and stress treatment (Blum, 1988). The environment is taken as a unique random occurrence of events, the biological effects of which are integrated into one statistical parameter of stability in yield performance over changing environments.

A physiogenetic approach

A physiogenetic approach combines the use of optimal and moisture-stressed environments. It is based on the assumption that yield and drought resistance are different traits controlled by different genes and gene systems (Turner, 1986a). The breeder selects for yield and quality in an optimal moisture environment. Blum *et al.* (1983) argue that if yield and drought are to be handled independently, then the degree of independence for any individual resistance mechanism must be evaluated. Thus, even a negative association between yield and drought resistance can be exploited, since potential yield is never realized under drought. Most breeding studies so far tended to the line of the physiogenic approach, usually with various modifications.

Important putative traits in breeding for drought tolerance

Plant breeders (Blum *et al.*, 1983) and crop physiologists (Biginger *et al*., 1982) believe that better adaptation and high-yielding genotypes could be bred more efficiently if attributes that improve yield under water-limited conditions could be identified and used as selection criteria. However, only those traits that either benefit one of the components of yield or contribute to the determinants of survival should be pursued (Passioura, 1977). Many traits have been proposed for improving the performance of drought-affected crops (Turner, 1986a, b; Ludlow & Muchow, 1990). However, this paper shall restrict coverage to traits for which genetic variation has been demonstrated and which have been shown to contribute either directly, or indirectly, to grain yield.

Genotypic variation in growth duration

Genotypic variation in growth duration is an important means of matching seasonal transpiration with water supply, thus maximizing water transpired. Early flowering tends to bring about higher and greater stability than later flowering, if it does not rain during the latter half of the growing season (Ludlow & Muchow, 1990). The development of short season varieties provides benefit where rainfall is reasonably predictable, but in unpredictable environments, potentially transpirable water may be left in the soil in better years, and yield is sacrificed.

Developmental plasticity

Developmental plasticity is the mechanism whereby the duration of growth varies depending on the extent of water deficit. Drought-induced early maturity may be advantageous in dry years and because it is a facultative response, the plant is still able to respond to longer seasons and produce higher yields during wetter years. Sinclair *et al*. (1987) found that the developmental plasticity of cowpea and mung bean contributed to their superior performance over soybean in water-limited environments. Developmental plasticity ensures that all the available water is transpired.

Mobilization of pre-anthesis assimilate to grain

The relation betweeen carbon accumulation and the amount of water transpired (Tanner & Sinclair, 1983), and the correlation between harvest index and post-anthesis water use (Passioura, 1977) suggest that grain yield is strongly dependent on biomass accumulation after anthesis in water-limited environments. However, Blum *et al*. (1983) and Turner & Nicholas (1988) have shown that the contribution to yield of pre-anthesis assimilate can be significant under drought. Sadras *et al*. (1993) reported that in the sunflower, pre-anthesis assimilate plays an important role in seed filling under stress. The stems are the major reserve structures.

Osmotic adjustment

Osmotic adjustment results from the accumulation of solutes within cells, which lowers the osmotic potential and helps maintain turgor of shoots and roots as plants are water stressed. This allows turgor-driven processes such as stomatal opening and expansion of growth to continue at reduced rates to progressively lower potentials (Turner, Begg & Tonnet, 1978; Turner, 1986a, b; Ludlow, 1987). Osmotic adjustments contribute to grain yield by increasing the amount of water transpired and by minimizing the reduction in harvest index (Ludlow, Santamaria & Fukai, 1990). It has been widely proposed that this attribute confers adaptation to water stress, and there is some evidence that a minor gene may be influencing the expression of osmotic adjustment (Basnayake *et al*., 1995).

Carbon isotope discrimination and transpiration efficiency

Genetic variation in water use efficiency (WUE) has been detected in crop species (Virgona *et al*., 1988), but breeding for improved WUE has been constrained by the difficulties in making measurements of WUE on many plants under field conditions. Selection criteria and methods are needed that are efficient and can be used, at least indirectly, to select genotypes with high WUE from large populations in the field. Theory has predicted an association between WUE and leaf discrimination against ^{13}C that could be used in indirect selection for WUE in C_3 plants.

Several studies have provided empirical evidence supporting this theory (Farquhar & Richards, 1984; Hubick, Shorter & Farquhar, 1986; Wright, Hubick & Farquhar 1988; Virgona *et al.*, 1988). Carbon isotope discrimination is based on the fact that ^{13}C is assimilated less rapidly than ^{12}C, and the ratio of ^{13}C to ^{12}C seems to be associated with the severity of drought (Farquhar *et al.*, 1988; Condon, Richards & Farquhar, 1987; Condon & Richards, 1990), and this seems to be associated with yields in genotypes in which they have been measured (Farquhar *et al.*, 1988; Condon *et al.*, 1987; Ngugi, 1991). Carbon isotope discrimination should, therefore, be useful for indirectly selecting genotypes with water use efficiency (Ismail & Hall, 1992).

Other putative traits

Several other traits, which shall only be mentioned, have been suggested for use in breeding programmes. These include tolerance to high temperature, high leaf reflectance, leaf movements, photoperiod sensitivity, rooting depth and density, and root hydraulic conductance (Summerfield, Huxley & Steel, 1974; Passioura, 1977; Ebercon, Blum & Jordan, 1977; Ludlow & Bjorkman, 1985; Richards, 1987; O'toole & Bland, 1988).

Biotechnological approaches

The yield loss under drought has been difficult to measure and has shown low heritability resulting in inefficient selection. While the anthesis-silking interval in maize is correlated with yield under drought stress (Bolanos & Edmeades, 1996; Pons *et al.*, 1995; Agrama & Mounssa, 1996; Ribaut *et al.*, 1996), selection under drought stress requires 2 or 3 months without rain as well as adequate irrigation infrastructure to control levels of stress. Owing to these difficulties, the use of marker-assisted selection (MAS) for improving drought tolerance cannot be overemphasized (Bartels *et al.*, 1996). This requires a segregating population which can be synthesized from a cross of two lines clearly contrasting in the expression of the drought tolerance traits. Restriction fragment length polymorphisms (RFLPs) genetic linkage maps can then be obtained to identify segments responsible for the expression of these traits. These traits are under polygenic control and the identified genomic segments are called quantitative trait loci (QTL).

Successful application of QTL mapping through MAS in plant breeding depends on the precision of both the detection of the QTL and the estimation of their effects and positions on the chromosomes. Results of work at CIMMYT are very encouraging. As the first step towards using molecular markers in CIMMYT's maize-breeding programme, RFLPs have been used to understand the genetic basis of one major component of drought tolerance, anthesis-silking interval. In their maize programme, two QTLs with major effects have been detected and can explain more than 50 per cent of the genetic difference between parental lines from widely different germplasm background. None of the QTLs alone had prominent effects on drought tolerance, thus suggesting that the trait is a typical quantitative trait (Hoisington *et al.*, 1996). Without epistatic effects, the accumulation of these QTLs would be expected to provide considerable improvement in the trait in any background. Most of the QTLs detected were consistent in their effects over locations and years. It is expected that the application of MAS to improve the anthesis-silking interval in maize should be more successful in the short term.

Conclusion

The economic advantages associated with crop varieties that have superior performance under moisture stress are numerous. Many mechanisms which aid the plant in adapting to drought have been identified. What remains for the breeder is to exploit genetic variability with respect to these mechanisms in developing crop varieties that will produce satisfactory yields in the event of drought. However, the exploitation of these adaptive mechanisms in breeding programmes depends on the resources available to a given group of breeders. For instance, breeders in the developing countries prefer breeding varieties with wide adaptation through the statistical approach of regression analysis, since it provides substantial information concerning the stability of genotypes across changing environments, and spreads costs of the breeding programmes over large areas.

The system also requires less instrumentation which is appropriate for resource-limited breeders and makes it suitable for the few breeders who have to cater for large areas. The advent of molecular techniques has allowed the development of dense genome maps for most of the important crops. It is hoped that QTLs will play a major role in identifying, isolating, and incorporating genes that confer drought resistance on crops like maize, sorghum, and millet which are grown in drought-stressed environments in low-input agriculture.

Advances in breeding for drought tolerance will demand an integrative, multidisciplinary approach (involving plant physiologists, biotechnologists, socio-economists, and breeders) in which the skills of the plant breeder to identify well-characterized germplasm are of paramount importance. National scientists and staff of international research centres have a vital role to play in identifying objectives and in exploiting appropriate technology to address the problem of poor yields of crops in moisture-stressed environments.

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