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El Jaafari S.

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Durum wheat breeding for abiotic stresses resistance: Defining physiological traits and criteria

S. El Jaafari
Laboratoire de Biotechnologie et Amélioration des Plantes, Faculté des Sciences, Université Moulay Ismaïl, BP 4010, Béni Mhamed, 50000-Meknès, Morocco

SUMMARY – Few criteria have been developed into screening techniques that are applicable to large numbers of genotypes. To be practical, screening techniques should be inexpensive, easily performed, repeatable, and accurate for the selected trait. We have considered morphophysiological mechanisms, which contributes to avoidance of desiccation, maintenance of cell turgor, and increased tolerance to low water potentials. Research results from many sources substantiate that no single criterion is comprehensive in predicting plant resistance to stress. Selection for genotype improvement in stress resistance is possible through the use of physiological parameters: some methods have been developed into screening techniques that may be applicable to large numbers of plants in breeding programs, while others are useful only for limited selections.

Key words: Abiotic stress, resistance, screening criterion, physiological trait.

RESUME – *"Amélioration génétique du blé dur pour la résistance aux stress abiotiques : Définition de caractères physiologiques et de critères de sélection". Un nombre restreint de critères ont pu être développés en techniques de criblage applicables à un large effectif de génotypes. Pour être utilisables en sélection, ces critères doivent être précis, facilement mesurables et répétitifs et ne doivent pas être coûteux. Nous avons considéré des mécanismes morphophysiologiques qui contribuent à l'esquive de la dessiccation, au maintien de la turgescence et qui augmentent la tolérance aux potentiels hydriques bas. Les résultats des recherches soutiennent l'utilisation d'associations de critères pour prédire la résistance de la plante au stress. La sélection pour l'amélioration de la tolérance au stress est possible en utilisant des paramètres physiologiques : des méthodes ont été développées en techniques de criblage applicables à un grand nombre de plantes alors que d'autres sont utilisables seulement pour des effectifs limités.*

Mots-clés : *Stress abiotique, résistance, critère de sélection, caractère physiologique.*

Introduction

Drought, cold and heat are the main abiotic stresses affecting durum wheat yields in Mediterranean areas. Success in breeding to improve the stress resistance of crop cultivars has been limited in the past by a lack of screening techniques and a lack of knowledge of what conditions can be considered stress in crop plants (El Jaafari, 1999).

An integrated five-step breeding approach is necessary when breeding for stress environments (Ortiz-Ferrara *et al.*, 1991): (i) identifying the stress problem; (ii) developing screening techniques; (iii) identifying stress resistance traits and their association to yield; (iv) screening germplasm for suitable sources of variability of the trait; and (v) utilizing associated traits in the breeding program.

Physiologists have often suggested that the identification and selection of physiological and/or morphological traits is an effective approach to breeding for higher yield, and could be a valuable strategy for use in conjunction with normal methods of plant breeding. A range of traits has been suggested that could be utilized to increase the yield of parental germplasm or be used as indirect selection criteria, especially for improving yield under abiotic stress conditions. Genetic variation exists for many of these characters and it has been argued that they should be suitable for genetic manipulation. The manipulation of major genes controlling phenology and plant structure, e.g. genes for photoperiod sensitivity, vernalization, and reduced height, is essential to all breeding. However, except for these instances, the use of physiological traits has been largely avoided by breeders, and it has been argued that physiology has had little impact on improving yields, producing new cultivars, or developing techniques of benefit to plant breeders.

Trait identification

Establishing the importance of particular traits is very difficult and time consuming. The nature of abiotic stress (drought, heat, cold, salinity, etc.) is such that its timing and intensity is unpredictable from year to year and this also means that the physiological responses to abiotic stress are also complex and unpredictable.

In the agronomic domain, the interpretation of resistance to abiotic stress requires some estimate of the values of the modification of the trait in terms of plant production and its sustainability under environmental stress. This is an essential link between the physiological or the genetic fact and the successful application of that fact in plant breeding.

There are two general approaches to determination of physiological traits related to crop performance under abiotic stress. The first is to proceed from observed yield differences to investigation of possible physiological causes, and the second is to define an ideotype for a particular stress environment based on an understanding of physiological process. Definition of an ideotype is limited by current knowledge of the relation of particular physiological traits to yield. Several researchers have suggested trait evaluation procedures that encompass both of the approaches (Clarke, 1987; El Jaafari *et al.*, 1993).

Concurrent physiological and genetic studies could speed up the process of evaluation of physiological traits. One of the major problems in evaluation of complexly inherited physiological or morphological traits, particularly when they are difficult to measure, is the development of homozygous lines for study. Screening the large populations required can be very tedious and expensive. It is worth considering procedures to facilitate the evaluation process. Development of isogenics, whether through repeated selection of homozygous individuals or repeated backcrossing to divergent parents, is a valuable tool for physiological studies. This approach is more effective for simply-inherited traits that can be readily measured. However, due to possible linkages and epistatic or pleiotropic effects, more than one pair of parents should be used to develop the isogenics. Where it is not possible to develop isogenics, divergent selection for the trait of interest can be used to assess its effect on yield.

Trait hierarchy and the target environment

To refine the identification of the critical traits that are most likely to improve yield under abiotic stress there are several principles that can help (Richards, 1997). The first is that the degree of influence of a trait on yield depends on the time scale over which it is effective. Another principle is that the capacity of a trait to influence yield is related to the level of organisation (molecule-cell-organ-plant-crop) in which the trait is primarily expressed.

The final general rule which is important for identifying the most likely traits to improve yield is knowing the nature of the target environment. This can sometimes be difficult because abiotic stress environments are typically highly variable. The vast range of environments where durum wheat are grown and the large range of genetic variation available provides many opportunities to make genetic gain in yield under abiotic stress providing there is a thorough understanding of the crop and the environmental limitations. For a relatively determinate target stress environment and with stable genotype x environment interaction, the probability for achieving progress is high. For such conditions, it is possible to construct a physiologically valid selection index by supplementing yield with several constitutive and/or adaptative plant traits (Blum, 1993). On the other hand, when the target stress environment is indeterminate, then the physiological profile of the genotype becomes indecipherable if not totally labile for both the breeder and the forces of selection (Ceccarelli *et al.*, 1991). The present common solution for this perplexing situation is the selection for yield in different environments, which supposedly define the boundaries of the erratic target environment. Such an approach would ascribe a selective advantage to potential yield if mean yield in any of the selection environments were sufficiently high just once early enough during the selection program. The solution suggested by Blum (1993) is in attempting to pyramidize plant characteristics, which ascribe adaptation to diverse profiles of water deficit and water deficit interactions with other environmental conditions. This approach will be possible only after we learn more about the physiology and genetics of crop plant responses to stress and their interactions.

We have chosen to give examples of different traits that show substantial potential to improve yield under drought in the case of durum wheat.

Osmotic adjustment (OA)

OA is now recognised as one of the most important adaptive mechanisms to water deficits in many crops and is considered as a major component of drought tolerance mechanisms. It maintains turgor at lower water status, which, in turn, enables plants to maintain processes such as cell enlargement and stomatal opening. OA is a highly complex and integrated system of adaptation to water deficits. Sharp (1990) showed that substantial OA can be in the growing region of root at low water potential, and this is believed to be important for continued elongation of roots in drying soil.

Osmotic adjustment (OA) strongly depends on the rate of plant water stress. OA requires time, and fast reduction in plant water status does not allow time for adjustment. This is very significant when genotypes are compared for their OA capacity. However, the importance of the time and the rate of stress for the development of OA imply that OA may not be a very effective mechanism of drought resistance under conditions where the development of drought is by nature very rapid, such on very light tropical or sandy soils of very low water holding capacity (Blum, 1997).

The use of this trait as a selection criterion in drought resistance breeding has been limited due to the loss and extensive nature of physiological measurements (osmometry, thermocouple psychrometry or pressure-volume relations) which limit their practicality for screening large number of genotypes required in a breeding program.

Two methods can be used to measure genotypic differences in OA (Morgan, 1992). In the case, where fewer genotypes were measured together, OA is calculated using a derivation of osmotic potential formula (Morgan, 1992). In the case where it is necessary to sample a large number of genotypes together, a simpler but potentially less accurate approach can be used. This approach, which is suggested for routine selection in breeding programs (Morgan, 1983), is based upon the relationship between osmotic potential and relative water content.

Because cell expansion involves the accumulation of solutes to maintain turgor pressure as the whole volume increases, wheat genotypes can be selected for high OA by measuring coleoptile expansion under water stress in petri dishes (Morgan, 1988). This technique is rapid and inexpensive, and hence is suitable for routine screening of breeding populations.

Water use efficiency (WUE)

The direct gravimetric measurement of seasonal crop WUE in the field or in pots is labour intensive and data on genetic variations in WUE has been scant. Therefore, the discussion of WUE as a potential selection criterion in breeding has been largely theoretical. The recent developments in theory and application of isotope discrimination (Δ) measurement as an estimate of WUE in plants allowed the acquisition of relatively large databases on the genetic diversity for WUE in relation to plant production in different environments.

WUE is a questionable selection criterion for improving yields in water deficit environments. Plant production under drought stress depends not only on WUE but largely on the genotype's capacity to sustain transpiration (Blum, 1993). Furthermore, there may be a negative association between WUE and transpiration, such that relatively drought-resistant genotypes that sustain transpiration and maintain plant water status may present relatively low WUE as compared with susceptible ones (Mokhtari *et al.*, 1997).

The advantages of selecting for (Δ) are numerous. It is highly heritable, there is substantial genetic variation, genotypes x environment interactions are small, its measurement is non-destructive and must be measured early in the plant's life. Thus selected plants can be used for hybridisation. A drawback in its use has been the cost of the measurement.

Early vigour

Turner and Nicolas (1987) showed that grain yields of wheat were linearly related to early vigour measured as dry matter production at the five or six-leaf stages. Subsequently, Whan *et al.* (1991) confirmed in a wide range of genotypes at several locations that early growth had the potential to increase grain yields. In wheat, the early vigour was associated with greater leaf area and ground cover and probably a greater proportion of total evapotranspiration used in crop transpiration rather than soil evaporation. In wheat, early vigour was also associated with early emergence and the presence of a large coleoptile tiller. The correlation between ground cover and dry matter productions has been used to rank lines of cereals differing in early vigour using field spectroscopy (Elliot and Regan, 1993). Spectral reflectance measurement in the visible, near-infrared and mid-infrared regions has the advantages of being non-destructive, rapid, and accurate.

Water loss

The ability of a plant to survive severe water deficits depends on its ability to restrict water loss through the leaf epidermis after stomata attain minimum aperture. The non-stomatally controlled water loss through the leaf epidermis, named epidermal or residual transpiration may comprise up to 50% of total transpiration in water-stressed wheat plants during the day and 100% during the night. Epidermal transpiration, estimated gravimetrically, on excised leaves has shown promise for differentiating drought resistance among wheat cultivars (Sabour *et al.*, 1997). Several workers have reported the existence of a significant positive correlation between yield and flag water retention in durum wheat (Clarke and McCaig, 1982). Moreover it has been reported that residual transpiration is moderately heritable in durum wheat.

Waxes, mainly constituted by cerids, represent in many plants an important external coating increasing the impermeability of the cuticle. The quantity of waxes can be visually appreciated by the glaucousness or the non-glaucousness of the plant; despite reports showing that cereals glaucous lines yield more grain and dry matter than non-glaucous lines in dry environments

The efficacy of RWL for selection of durum genotypes for adaptation to dry environments was compared with visual scoring of other traits in approximately 4300 accessions from the ICARDA germplasm collection (Clarke *et al.*, 1991). The visually scored traits were glaucousness, days to heading, relative maturity, yield, flag leaf size, and leaf rolling. High RWL was negatively associated with yield, and superior agronomic score was positively associated with yield in a subsequent year. Glaucousness, leaf size, and leaf rolling showed no relationship with yield.

Root system

Cereals have evolved from a predominantly nodal to a predominantly seminal root system, particularly when grown at high densities. Seminals develop earlier and deeper, and are finer and more efficient at water uptake, have a higher resistance to water flow and tend to conserve soil water more than nodal roots.

Techniques for measuring rooting depth are unsuitable for screening large numbers of breeding lines. Most of the methods are destructive, elaborate and risky because of the possibility of uncontrollable losses during washing. Rogers and Bottomley (1987) proposed a new method using nuclear magnetic resonance in situ for non-destructive non-invasive investigation of root systems. Robertson *et al.* (1985) developed a field technique using herbicide banded into the root zone at specific depths and lateral distances from the seed rows. This method is suitable for screening large numbers of genotypes for the presence of a rapid root growth. Until now there has not been a suitable method to meet the requirements of a practical breeding programme.

Water transfer also presents intraspecific variations so that some cereal breeders have suggested to manipulate hydraulic resistance by the way of selection for long coleoptiles (which also allow the plant to emerge even though planted several centimetres deep), combined or not with a selection for vessel diameter.

Conclusion

We have discussed many morphological and physiological attributes that have or are likely to contribute to increased durum wheat yields, and yet relatively few breeding programs are currently selecting for specific physiological traits.

Many traits are measured with complex, time-consuming techniques that are unsuitable for screening large numbers of progeny in breeding programs. Consequently, most traits are evaluated in a small number of genotypes without testing in breeding populations. Some physiological techniques have been modified, and although not as accurate, they may provide a useful method for plant screening (e.g. OA in coleoptibles). Other more complicated and time-consuming techniques are only useful for screening a small number of genotypes for use as parents. Some traits can be combined in a single measurement for example, infrared thermal sensing of canopy temperatures can be used to screen for deep roots, maintenance of higher leaf water potentials, increased stomatal conductance. Use of infrared thermometry as a screening technique for drought resistance has been developed for wheat. It is based on the fact that the plant's capacity to maintain some transpiration under increasing drought stress is expressed in lowering canopy temperature. As discussed earlier, the maintenance of transpiration may be an advantage or disadvantage, depending on the stage of growth and the total seasonal distribution of water use.

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