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Screening of yield traits and new score indices for improving resilience and productivity in crops under moisture stress: A review

Asmat Ara, PA Sofi and ZA Dar

Abstract

Yield has been the primary breeding objective in production breeding and has been improved by targeting yield per se as well as yield components based on correlated response. Direct selection for yield under stress holds promise but is slow on account of complexity of yield. Screening based on yield suffers from low heritability. Selection for drought tolerance typically involves evaluating genotypes for either high yield potential or stable performance under drought stress. Breeding for drought tolerance is very difficult as the stress conditions created in experimental set up and actual field conditions, invariably, have poor correspondence. Plant physiology approaches provide general outlines of plant responses, identifying stress tolerance-related traits or elite cultivars. The new selection method based on water stress indices could help breeders and researchers by defining clear and strong criteria to identify genotypes with high resilience and high productivity and provide a clear visualization of contrasts in terms of grain yield production under stress. A major drawback of using these indices has been lack of correspondence in rankings across indices and their failure to discriminate overlapping responses in terms of yield under stress. There has been substantial effort on part of scientists to develop and validate different indices based on yield per se, index scores, regression analysis as well as various model based approaches. The major focus has been on identifying variables such as phenology, physiological traits, biomass partitioning or other parameters that influence crop performance under stress. The paper appraises the approaches from physiological parameters to yield based indices as well as regression based approaches that have been used to understand crop response to water stress.

Keywords: Drought, indices, physiology, yield

Introduction

Plants have had to cope with periodic and unpredictable environmental stresses during growth and development because of their early migration from aquatic environments to the land. Surviving such stresses over a long evolutionary scale led them to acquire mechanisms by which they can sensitively perceive incoming stresses and regulate their physiology accordingly (Zhang *et al.*, 2006) [44]. In recent years, interest in crop response to environmental stresses has greatly increased because severe losses may result from heat, cold, drought and high concentrations of toxic mineral elements (Blum, 1996) [3]. Drought is one of the most damaging abiotic stresses affecting agriculture. It is an important abiotic factor affecting the yield and yield stability of food cereals and this stress acts simultaneously on many traits leading to a decrease in yield (Aebe *et al.*, 2003; Sebnem., 2012) [1, 32]. Drought stress occurs at different times in the growing season, and with different intensity, while its effects on crops are modified by soil type and fertility (Rao, 2001) [28]. To survive under drought stress, various mechanisms play a role in providing drought tolerance, and their importance depends on growing stage at which the drought occurs.

Plants use various mechanisms to cope with drought stress. These may be classified into three groups: drought escape, drought avoidance and drought tolerance (Turner *et al.* 2001) [37]. Drought escape allows the plant to complete its life cycle during the period of sufficient water supply before the onset of drought. Normally the life cycle is shorter and plants set some seeds instead of complete crop failure. The second mechanism, drought avoidance, involves strategies which help the plant maintain high water status during periods of stress, either by efficient water absorption from roots or by reducing evapotranspiration from aerial parts. The third mechanism, drought tolerance, allows the plant to maintain turgor and continue metabolism even at low water potential e.g. by protoplasmic tolerance or synthesis of osmoprotectants, osmolytes or compatible solutes (Nguyen *et al.* 1997) [22].

A widely accepted equation for grain yield (Y) under water-limited conditions is a function of three components, namely the amount of water transpired (T), water-use efficiency (WUE) and harvest index (HI) (Turner *et al.* 2001) ^[37]. Maintenance of optimum transpiration, leading to increased WUE, is one of the strategies to improve yield. Secondary traits have been reported to be associated with the likelihood of increasing or maintaining T during drought. These traits are phenology, photoperiod sensitivity, developmental plasticity, leaf area maintenance, heat tolerance, osmotic adjustment, early vigour, rooting depth and rooting density. Additionally, transpiration efficiency and leaf reflectance are the other two traits related to WUE (Purcell and Specht 2004) ^[26]. Significant progress in breeding for drought resistance cannot be made unless the stress is imposed year after year to allow direct selection for yield. For this reason, a field with poor moisture-holding capacity, soil uniformity and a reasonable drought each year is important, but is unfortunately very difficult to achieve (Pathan *et al.* 2007) ^[27]. In order to enable high throughput and reliable gravimetric measurements of water relation traits and water use in soybean, it is also important to include modern facilities such as a rainout shelter in a breeding program. By using a rainout shelter with a movable roof, researchers at the National Center for Plant Gene Research (NCPGR) in Wuhan, China, have succeeded in dissecting the genetics of complex traits such as drought resistance (Pennisi, 2008) ^[25]. The plant-wise drought treatment strategy developed at the NCPGR provides a useful method for independent evaluation of the individual components of drought resistance (Yue *et al.* 2006) ^[43]. In addition, current advances, such as automated plant phenotyping platforms to study the plant responses to soil water deficit under controlled conditions (Granier *et al.* 2006) ^[9], an automated rotating lysimeter system for evapotranspiration and plant growth measurements (Lazarovitch *et al.* 2006) ^[17], non-destructive measurement of plant water status over time using portable unilateral nuclear magnetic resonance (Capitani *et al.* 2009) ^[6], and other precision equipments to quantify plant water use should be exploited. Screening of genotypes in such controlled facilities has the advantage of quantifying the morpho-physiological traits that influence drought adaptation, which in turn will complement yield selection criteria. Overall, root traits show strong potential for improvement of drought resistance through breeding. However, it would be extremely difficult to perform selection based on measuring the root phenotype. Instead, molecular tagging will facilitate breeding for root-related traits. The candidate gene approach is another alternative methodology, which involves choosing a candidate gene for root traits from public data, obtaining primer sequences to amplify the gene, uncovering polymorphisms, developing a convenient procedure for large-scale genotyping, identifying a population for association studies, carrying out an association study of the candidate gene with trait phenotype and finally verifying the uncovered associations. This approach was successful in finding candidate genes associated with root number in rice under low moisture conditions (Vinod *et al.* 2006) ^[38]. Understanding the physiological mechanisms and genetic regulation of root adaptation to drought will help to identify specific genes and metabolic pathways for either gene-based marker selection or genetic engineering to develop better root-related traits.

Shoot-related traits

1. Stomatal conductance. One of the shoot-related physiological traits that may affect drought tolerance is

the decline in whole-plant water use during a soil water deficit event. As a soil water deficit develops, plants undergo a transition from the water-saturated phase, in which whole-plant water use is not dependent on the soil water content, to a second phase where water use is directly related to the availability of soil water (Sinclair and Ludlow, 1986) ^[33]. This transition is associated with a reduction in the average stomatal conductance, and can occur at different soil water contents in different species (Earl, 2003) ^[7]. Stomatal conductance is a key variable influencing leaf gas and water vapour exchange. It was shown that drought stress decreases relative leaf expansion rate, stomatal conductance and leaf turgor, whereas it increases the content of ABA in the leaf and xylem (Liu *et al.* 2003) ^[18]. Further research is needed to establish the physiological and biochemical basis for stomatal closure during intermittent drought conditions as well as mild soil water deficits, particularly under field conditions.

2. Epidermal conductance. A second shoot-related physiological trait which may help identify cultivars with increased drought tolerance and prolonged crop survival during severe water stress is low leaf epidermal conductance (ge). Total leaf conductance to water vapour is the sum of the stomatal and cuticular diffusive pathways acting in parallel (van Gardingen and Grace 1992) ^[38]. When the stomata are open, cuticular conductance is generally a negligible fraction of total conductance. However, in water-stressed or dark-adapted leaves in which the stomata tend to be closed, the cuticular component of leaf epidermal conductance may exceed the stomatal conductance (Boyer *et al.* 1997) ^[4]. Under severe water deficit when stomatal closure is maximal, ge (the sum of cuticular conductance and any residual stomatal conductance) determines the rate of water loss from leaf tissues and therefore the rate of progression toward critically low (injurious) leaf water content. Selection for lower epidermal conductance could allow improved survival of leaves under intermittent water stress, so that sufficient leaf area remains available for growth after the stress is relieved (Paje *et al.* 1988) ^[24]. A significant negative correlation ($r = -0.74$) was reported between ge and WUE under drought, which again supports the hypothesis that lower epidermal conductance is a desirable trait for drought resistance (Hufstetler *et al.* 2007) ^[11].

3. Leaf pubescence density: Leaf pubescence is a common feature of xerophytic plants, as well as some crop plants including soybean. Generally, leaf pubescence density increases reflectance from the leaf, resulting in lower leaf temperatures under high irradiance. Leaf pubescence density is an important adaptive trait for soybean under water stressed conditions. Densely pubescent lines had increased vegetative vigour, greater root density and deeper root extension (Garay and Wilhelm 1983) ^[8]. Reduced leaf temperature, restricted transpiration water loss and enhanced photosynthesis due to lower radiation penetration into the canopy were also reported to be associated with the dense pubescence trait.

4. Osmotic adjustment: Osmotic adjustment (OA) is defined as the active accumulation of solutes that occurs in plant tissues in response to an increasing water deficit.

OA is considered a useful measure because it provides a means for maintaining cell turgor when tissue water potential declines. OA has been shown to maintain stomatal conductance and photosynthesis at lower water potentials, delayed leaf senescence and death, reduced flower abortion, improved root growth and increased water extraction from the soil as water deficit develops (Turner *et al.* 2001) [37].

Accumulating solutes is a wide spread plant response to environmental stresses such as drought, while carbohydrates are used for energy and maintaining metabolism under water deficit conditions (Khalid *et al.*, 2010) [16]. Proline is one of the most common compatible osmolytes in drought stressed plants. Proline has an important role in conferring osmotolerance (Mittler *et al.*, 2004) [19]. Compatible solutes are over produced under drought stress for facilitate osmotic adjustment (Hasegawa *et al.*, 2000 and Shao *et al.*, 2005) [15, 35]. These compounds accumulated in high amounts mainly in cytoplasm of stressed cells without interfering with macromolecules and behaved as osmoprotectants (Yancey, 1994) [42]. Also proline has a key role in stabilizing cellular proteins and membranes in high concentrations of osmoticum (Yancey, 1994) [42]. In the same orientation Vendruscolo *et al.* (2007) [40] reported that proline accumulation in stressed plants is a tolerance mechanism against oxidative stress and it is the main strategy of plants to avoid harmful effects of drought stress.

Cross talk- signalling response through interaction

When stress signalling pathways are examined in the laboratory, they are usually considered in isolation from other stresses to simplify interpretation. In nature, however, the plant encounters stress combinations concurrently or separated temporally and must present an integrated response to them. In the case of phytochrome signalling, the two pathways leading to red-light-induced *CHS* and *CAB* gene expression negatively regulate flux through one another. Seemingly separate abiotic stress signalling pathways are also likely to interact in a similar manner. In addition, several abiotic stress pathways share common elements that are potential “nodes” for cross-talk (Fig 1). Cross-talk can also occur between pathways in different organs of the plant when a systemic signal such as hydrogen peroxide moves from a stimulated cell into another tissue to elicit a response.

Genetic engineering for drought resistance

In response to stress, plants activate a number of defence mechanisms that function to increase tolerance to adverse conditions. A large array of genes is activated and consequently a number of proteins are produced to contribute to the metabolic pathways that lead synergistically to the enhancement of stress tolerance (Fig 2). The application of this emerging understanding to the genetic engineering of food crops has already led to examples of improved drought tolerance and increased yield under drought (Hu *et al.* 2006) [10]. Introduction of the *SNAC1* and *ZmNF-YB2* TFs into rice and maize, respectively, enhanced the drought tolerance of transgenic plants as demonstrated by field studies. Transgenic rice overexpressing the *SNAC1* gene had 22–34 higher seed setting in the field than the negative control under severe drought stress conditions at the reproductive stage. *SNAC1* transgenic rice plants are drought tolerant not only due to the increased expression of genes encoding proteins functioning

in the production of osmolytes, detoxification and redox homeostasis, and in protection of macromolecules, but also because of the increased stomatal closure in transgenic leaves which prevents water loss from the plant (Hu *et al.* 2006) [10]. Transgenic canola was generated using a farnesyltransferase (*ERA1*) antisense construct driven by a drought-inducible *rd29A* promoter. The developed transgenic canola plants showed increased ABA sensitivity, a significant decrease in stomatal conductance and decreased transpiration when tested under drought conditions (Wang *et al.* 2005) [41]. Recently, transgenic tobacco was engineered to overexpress an isopentenyl transferase gene (*IPT*) from *Agrobacterium tumefaciens* driven by the *SARK* promoter, which was isolated from bean *Phaseolus vulgaris* and was shown to be induced by both drought stress and maturation. The transgenic plants showed improved drought tolerance by maintaining high water content and photosynthetic activity (Rivero *et al.* 2007) [27].

Screening Indices for resilience and biomass partitioning under drought

Drought stress indices are quantitative measures that characterize water stress response by yield data from one or several environments based on timing, duration and intensity of stress. Such an index is more readily useable than raw yield data. Since drought resistance is a yield based trait, selection could vary depending on which index is chosen by the breeder. Where differential yield reduction ($Y_p - Y_d$) due to stress has been used as a basis for selecting cultivars with resistance to water stress, the strategy can be counterproductive because of the likelihood of selecting low yielding cultivars with a small yield differential.

Seed yield based indices: A predominantly held premise by many workers is that selection based on yield under both non-stress and stress conditions is more efficient especially under unpredictable rain-fed conditions with various yearly drought scenarios (Farshadfar *et al.* 2001; Moosavi *et al.* 2008; Mohammadi, *et al.* 2010) [12, 21, 20]. In light of this premise, many drought tolerance indices have been proposed (Table 1) for screening drought tolerant genotypes based on mathematical relationship between yields under stress and non-stress conditions aimed at identification of stable, high yielding, drought tolerant genotypes.

A major drawback of using these indices has been lack of correspondence in rankings across indices and their failure to discriminate overlapping responses in terms of yield under stress. Moreover, there have been contrasting reports about their discriminatory powers in identifying optimally yielding genotypes. The differential rankings of genotypes through different indices, across all crops, suggest that the indices *per se* are potential indicators of different biological responses to drought. Although all these indices are mathematical derivations of the same yield data, selection based on a combination of different indices may provide a more useful criterion for improving water stress adaptation of common bean. However, there are not yet any accurate screening index that can be used in breeding programmes to select genotypes for abiotic stress adaptation and high yield in both stress and non-stress environments.

Index score based indices

Thiry *et al.* (2016) [36] suggested a new way of combining indices in terms of their abilities to classify genotypes into susceptible and tolerant. The method so devised focuses on

resilience and productivity and uses index scores to build the regression equations for elucidating genotypic response. Thiry *et al.*, (2016) ^[36] divided these five indices into two classes *viz.*, Class 1 (SSI and TOL) and Class 2 (MP, GMP and STI) based on the premise that the first class tends to identify genotypes based on resilience and productivity respectively. They proposed two new indices that combine the discriminatory power of the score indices. These score indices have been classified within two new scales called resilience capacity index (RCI) and production capacity index (PCI). The scoring scale for each index is based on deriving the range from minimum and maximum values from original index.. This range is further divided into ten parts and each part has a score from 1 to 10 in a way that each part represents 10%, 20%, or 100% of the range value. Additionally, the value of TOL and SSI are inverted, so a high value obtained with the original equation will receive a lower score in all case that allows the two classes of indices to have the same scale, where a high score will always mean a 'good' genotype and a lower score a poor genotype (Thiry *et al.*, 2016) ^[36]. The index scores can then be easily combined and test them against yield under stress and non-stress conditions to elucidate differential genotypic response in terms of adaptability stress and/ or non-stress environments.

Regression based indices

Regression analysis is a mathematical description of the relationship between independent variables and the dependent variable. Bidinger *et al.* (1987) ^[2] developed a drought response index (DRI) based on a regression model to quantify the part of the variation associated with tolerance / susceptibility and to identify traits linked to tolerance. In order to fit the regression equations, all the genotypes should be tested together for yield under stress and non-stress conditions. In order to develop the DRI, a two-step regression approach is used for analysis.

Initially the stress yield is regressed on potential (Non-stress) yield and drought escape (days to flowering measured under

non-stress conditions) over all cultivars (initial regression). Where this regression is significant, the estimated stress yield for each cultivar by this regression is then calculated. The actual measured yield under stress is then regressed on this estimated yield across all cultivars (second regression). Any cultivar that expresses a positive deviation from this regression line can be defined as drought resistant, independently of the effect of potential yield or growth duration on its yield under stress.

Phenology based indices

The final economic yield achieved by plants indicates their efficiency to translate their accumulated biomass into yield. In common bean, the biomass is translocated from stems onto pods and finally into seeds and genotypic differences have been established for resource remobilisation traits in response to drought stress (Sofi and Iram Saba, 2016) ^[34]. Growth and developmental phases correspond to phenological events, and consequently the timing of photoassimilate partitioning is largely determined by phenology. There can be substantial and stable differences between species and varieties in the patterns of dry matter allocation (de Dorlodot *et al.* 2007) ^[5] and these differences can be clearly related to crop performance. Certain varieties allocate more of its dry matter to growth of deep roots whereas another may give more priority to producing an extensive but shallow root system. Rosales-Serna *et al.* (2004) ^[29] found that larger values for plant biomass accumulation were observed across well watered treatments at the basal plant phytomers in all cultivars. Ramirez Vallejo and Kelly (1998) ^[31] used various phenology based biomass accumulation and partitioning indices in common bean to elucidate response to water stress and reported that, the differential correlations between phenological, biomass and partitioning traits and the indices for yield and drought susceptibility would suggest that the most effective approach in breeding for drought tolerance (Table 2).

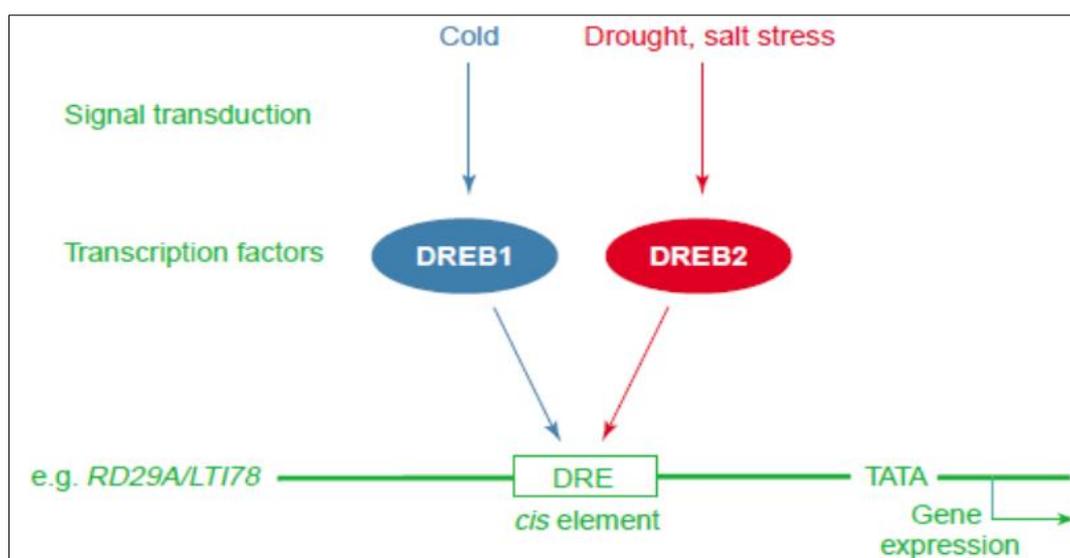


Fig 1: The DREB1 and DREB2 transcription factors, key components in cross-talk between cold and drought signalling in Arabidopsis

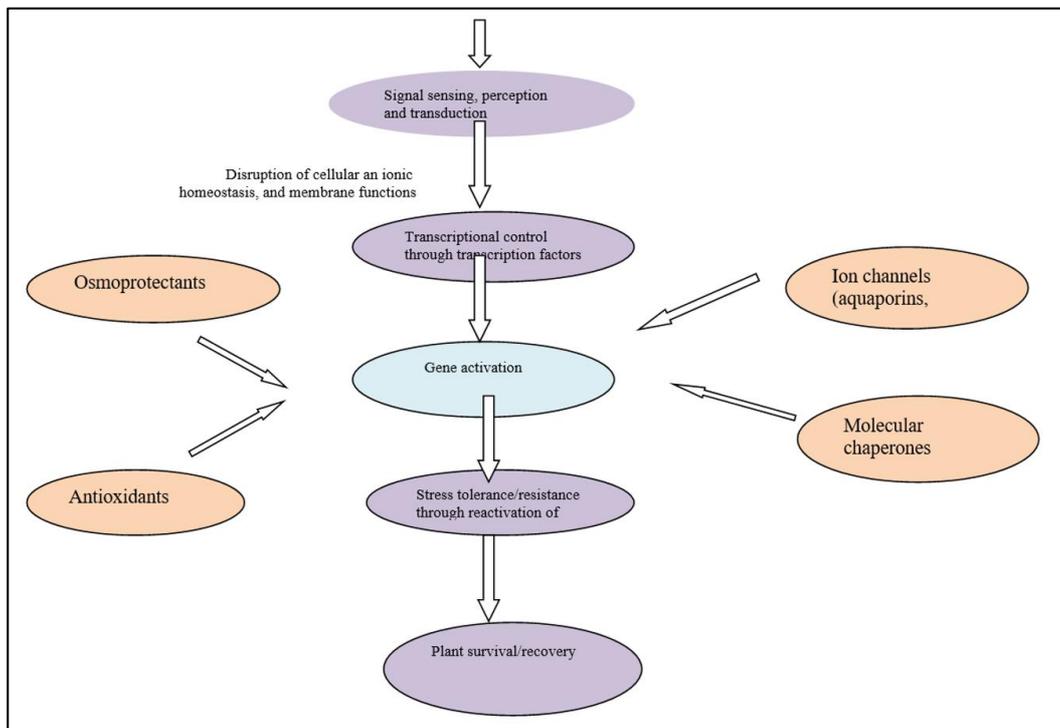


Fig 2: Activation of different molecules and pathways under moisture stress

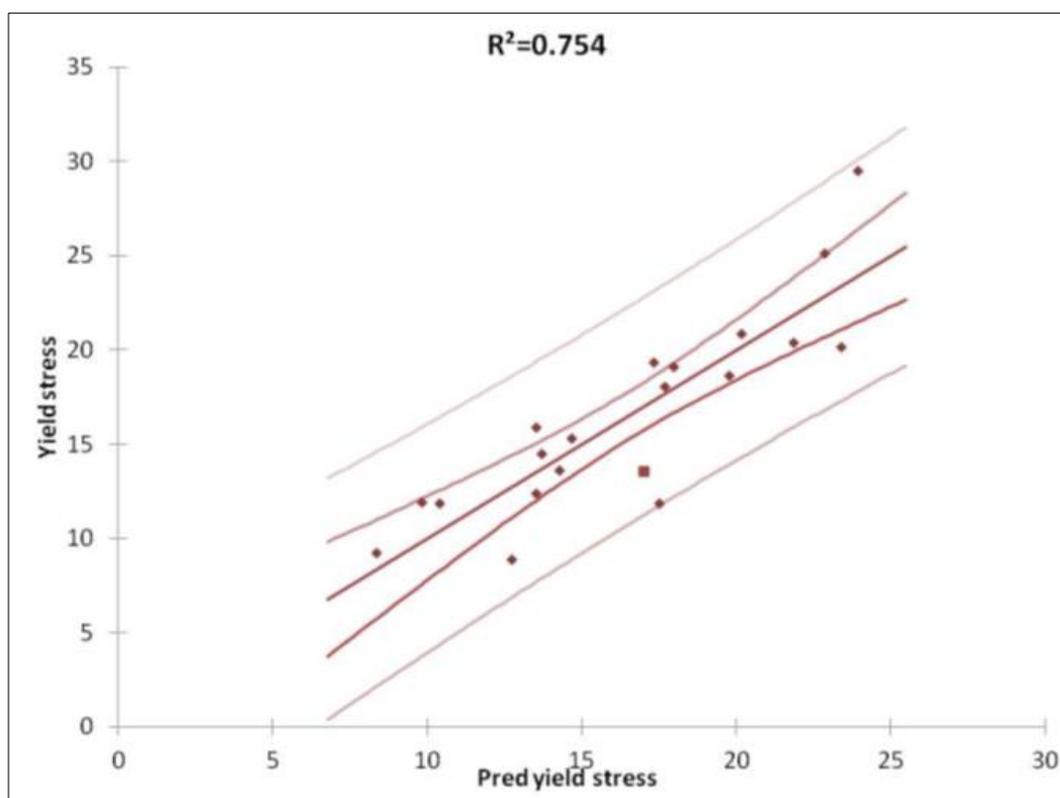


Fig 3: Regression of common bean yield under stress with predicted yield under stress based on Bidinger's model (1987).

Table 1: Various stress screening indices based on seed yield.

| Index | Formula | Reference |
|-----------------------------------|---|--|
| Stress susceptibility index (SSI) | $\{1 - (YS / YNS)\} / \{1 - (XS / XNS)\}$ | (Fisher and Maurer, 1978) ^[14] |
| Tolerance index (TOL) | $YNS - YS$ | (Rosielle and Hamblin, 1981) ^[45] |
| Mean productivity (MP) | $(YS - YNS) / 2$ | (Rosielle and Hamblin, 1981) ^[45] |
| Geometric mean productivity (GMP) | $\sqrt{(YNS \times YS)}$ | (Fernandez, 1992) ^[13] |
| Stress Tolerance Index (STI) | $YS \times YNS / X2NS$ | (Fernandez, 1992) ^[13] |

Where YS and YNS are mean yields of genotypes under stress and non-stress conditions respectively and XS and XNS are mean of yield of all genotypes under stress and non-stress conditions.

Table 2: Various stress screening indices based on phenology

| Index | Formula | Relevance |
|------------------------------|-------------------------------|---|
| Days of seed fill (DSF) | $DSF = DM - DF$ | Measures the time period that is used by plant to accumulate and remobilise photosynthates after flowering |
| Biomass growth rate (BGR) | $BGR = \text{Biomass}/DM$ | Measures daily growth rate of biomass accumulated during entire life cycle. |
| Economic growth rate (EGR) | $EGR = \text{Seed yield}/DM$ | Measures the daily growth rate of the economic product viz. Seed yield |
| Seed growth rate (SGR) | $SGR = \text{Seed yield}/DSF$ | Measures the growth rate of seed biomass post fertilisation |
| Relative sink strength (RSS) | $RSS = SGR/BGR$ | Measures the relative growth rate of economic product vis-a-vis total biomass accumulated during life cycle |

Conclusion

Plant breeders, by and large, focus on grain yield as a target trait for genetic enhancement for water stress. Using yield *per se* or yield reductions under stress is invariably misleading and warrants use of certain indices based on either simple mathematical relationships of stress and non-stress yields, relating yields under stress with phenology, using multiple regression where stress yields can be explained on the basis of various explanatory variables ranging from phenology to physiology based on their established influence on yield under stress.

Integration of genomics, proteomics and systems biology platforms will undoubtedly lead to the discovery of novel candidate genes and pathways involved in drought resistance. Transgenic approaches have been shown to be powerful tools to help understand and manipulate the responses of plants to stress, but this can be achieved only when studied by precise physiological and biochemical investigation of transgenic plants under stress conditions. Moreover, to ensure that the responses of the transgenic plants to water stress treatments are comparable with those in field conditions, the plants should be subjected to the same or comparable drought regime that crops experience in the field.

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