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Stress tolerance indices based on yield, phenology and biomass partitioning: A review

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ABSTRACT

Breeding for water stress tolerance is very difficult as the stress conditions created in experimental set up and actual field conditions, invariably, have poor correspondence. 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. 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. 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. 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 yield based indices to regression based as well as crop model based approaches that have been used to understand crop response to water stress.

Key words: Abiotic stress, Biomass partitioning, Crop model, Phenolgy, Stress tolerance indices.

The challenges of ensuring food security and combating the implications of climate change on food production systems have injected a new urgency into accelerating the rates of genetic gain in breeding programs. The high yielding varieties and improved management have resulted in an average increase in food production globally, to the tune of 32 million tons per year (Dhillon *et al.* 2012). However, in light of the recent Declaration of the World Summit on Food Security (FAO 2009) target of 70% more food by 2050 requires an annual increase of 44 million tonnes in the global food production. This amounts to about 30 years of sustained increase over historical increases in food production, to the tune of 38%. The predicted scale of sustained increase in global food production is a great challenge, even under favourable environments, in light of the fact that climate change is denting our efforts of achieving targeted goals through improved cultivars and better agronomy.

Breeding for water stress tolerance is very difficult as the stress conditions created in experimental set up and actual field conditions, invariably, have poor correspondence. In fact the translation of greenhouse and laboratory observations to myriad of diverse patterns and processes observed in the field is a huge challenge, even in case of experiments where seemingly fair amount of control is expected (Poorter *et al.* 2016). Even in case of experiments where similar traits are studied under different screening systems, the correspondence is not fairly straightforward. 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. One major problem that is encountered by researchers while dealing with the yield data is that yield under stress per se as well as yield differences under non-stress and stress conditions (Y_p-Y_d) cannot effectively discriminate the genotypes into tolerant and susceptible as well cannot account for the range of response exhibited by genotypes under stress. Historically the plant breeding programmes have mainly focussed on selecting genotypes that exhibit higher yield under yield non-stress conditions followed by testing under stress conditions of various severities (mild/severe) and applying stress at various stages (early season, intermittent and terminal stress) on the assumption is that a genotype with high yield potential will perform comparably well under most environments (Blum 2005). There are evidences that higher yield potential

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under non-stress conditions may correspondingly comp arable under mild stress but a lower yield and higher resilience under severe stress may be desirable (Panthuwan *et al.* 2002).

In the field experiments usually the classification of genotypes is based on the premise that the tolerance and susceptibility response are quite distinguishable. However, invariably, the genotypic responses are never so distinct and extreme, but overlapping. Moreover, differential genotypic responses in form of varied degrees of resilience and productivity are a result of different underlying physiological and biochemical mechanisms. As outlined by Fernandez (1992) and Thiry *et al*. (2016) the genotypic response under stress and non-stress conditions can be broadly grouped into following four classes (Fig 2).

Class A: The class A represents those genotypes that express uniform superiority in both stress and non- stress condition. These genotypes are very rare and have both resilience and productivity.

Class B: The class B genotypes that express good performance only in non-stress and not under stress conditions. These genotypes have high productivity under non-stress conditions but do not possess resilience to stress.

Class C: The class C genotypes that exhibit higher yield only under stress i.e, they possess resilience but not productivity; and.

Class D: The class D genotypes that express poor yield performance in both environments and lack both productivity and resilience.

DROUGHT STRESS INDICES

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.

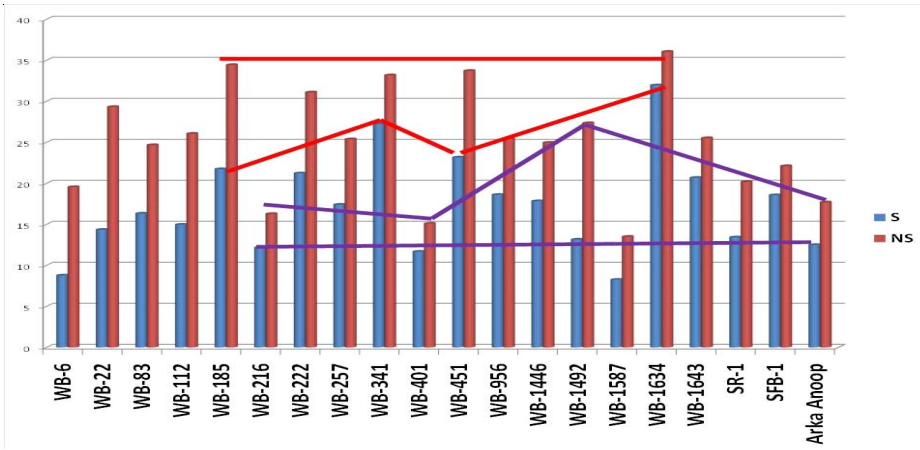


Fig 1: Response of common bean genotypes based on yield *per se* to water stress (S=stress, NS=non-stress environments).

Fig 1: Presents some of the typical responses that are encountered while handling yield data from stress experiments. The bean genotypes WB-185, WB-341, WB-451 and WB-1634 (marked with red line) have almost comparable yields in non-stress conditions but have different yield responses under stress conditions. Similarly the genotypes WB-216, WB-401, WB-1492, SR-1 and Arka Anoop (marked with purple) have almost comparable yields in stress conditions but have different yield responses under non-stress conditions.

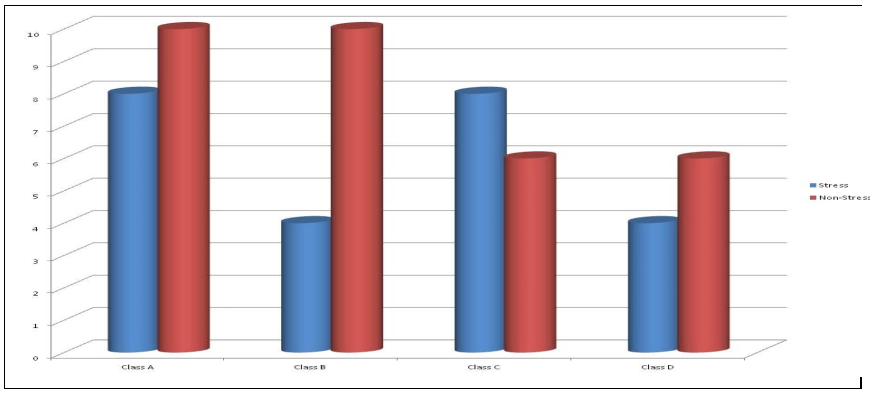


Fig 2: The four types of genotypic response to abiotic stress observed in field experiments (Modified from Thiry *et al*, 2016).

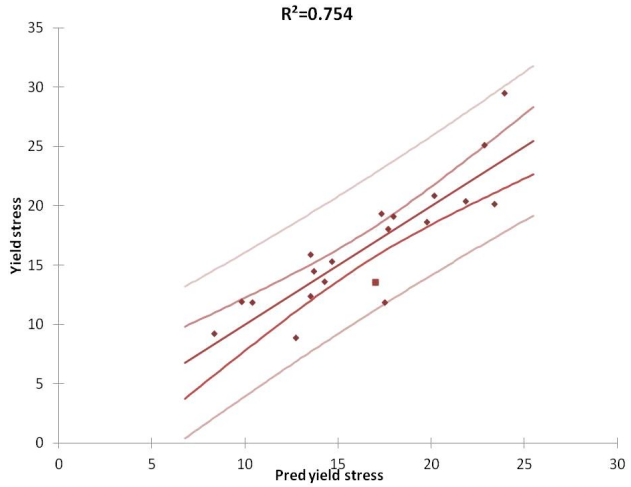


Fig 3: Regression of common bean yield under stress with pre dicted yield under stress based on Bidinger's model (1987).

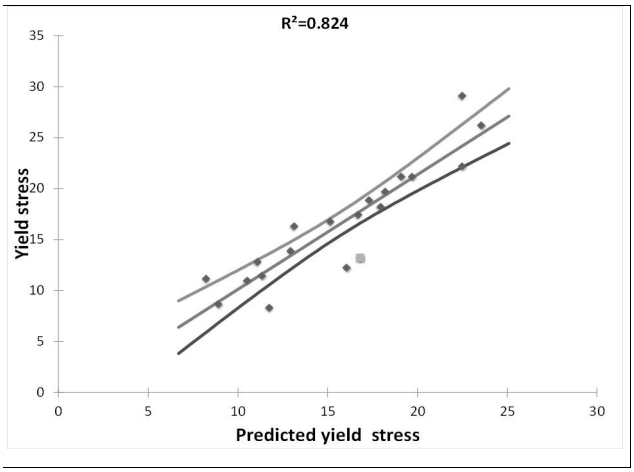


Fig 4: Proposed modification in regression of yield under stress with predicted yield under stress based on Bidinger's model (1987).

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). 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 (Mohammadi *et al.* 2011). 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: Recently, Thiry *et al.* (2016) 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. They could combine the five indices into two groups namely class 1 and class 2; class 1 discriminates the tolerant from the susceptible, and class 2 distinguishes the tolerant with high mean yield. They could experimentally establish the comparative advantage of combining index scores to develop two new indices RCI (based on index scores of SSI and TOL) and PCI (based on index scores of MP, GMP and STI) in a core set of 294 wheat genotypes over the indices per se.

In order to overcome the ambiguity regarding the reliable genotypic response to stress conditions using the yield per se and the five stress indices (SSI, TOL, MP, GMP and STI), two new indices defined as resilience and production capacity indices (Thiry *et al*. 2016) were used. Thiry *et al.* (2016) outlined the discriminatory power of the resilience capacity index (RCI) in terms of the yield decrease of the genotypes under stress within a population, compared with yield potential (non-stress) conditions; and the production capacity index (PCI) in terms of the mean production of the genotypes under both stressed and non-stressed conditions within a population. They emphasised that the combined use of the five indices (SSI, TOL, MP, GMP and STI), and both new indices (RCI and PCI) are highly effective in understanding the basis of any yield limitations under stress.

Thiry *et al*. (2016) 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. The new index combines 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 index scores are then easily combined to elucidate differential genotypic response in terms of adaptability stress and/ or non-stress environments. A high regression coefficient value has been reported using such an index with stress yield in wheat (Thiry *et al.* 2016) and common bean (Sofi *et al.* 2017a).

Regression based indices: Regression analysis is a mathematical description of the relationship between independent variables and the dependent variable. Bidinger *et al*. (1987) 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.

Mid-season stress is defined by the regression equation

$$Y\hat{}s = a + b1\ (Yc) + b2(bl) + b3(bl2)$$

Terminal stress is defined by the regression equation

$$Y\hat{}s = a + b1(Yc) + b2\ (bl)$$

Where Y^s is the regression estimate of the stress yield, Ys is the measured stress yield, Yc is the non-stress control yield, bl the days to flowering under non-stress, a is the intercept and b1 and b2 the regression coefficients. The drought index is then given by

$$DRI = (Ys - Y\hat{}_s)/\ S.\ E.\ (Y\hat{}_s)$$

where S.E. indicates the standard error.

In this method, only on the cultivars with index value of less than -1.3 (susceptible) or more than +1.3 (tolerant) are considered. These represent the upper and lower 10% of the normal distribution of the index. The magnitude of the index indicates the degree of the response. Using the similar approach as used by Bidinger *et al*. (1987), Slim and Saxena (1993) proposed another DRI to describe the response of individual genotypes to drought conditions

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

Index	Formula	Reference
Stress susceptibility index (SSI)	$\{1-(Y_S / Y_{NS})\}/ \{1-(X_S / X_{NS}\}$	Fisher and Maurer (1978)
Tolerance index (TOL)	$Y_{NS} - Y_S$	Rosielle and Hamblin 1981
Mean productivity (MP)	$(Y_S + Y_{NS}) / 2$	Rosielle and Hamblin (1981)
Geometric mean productivity (GMP)	$\sqrt{(Y_{NS} \times Y_S)}$	Fernandez (1992)
Stress Tolerance Index (STI)	$(Y_S \times Y_{NS}) / X^2_{NS}$	Fernandez (1992)
Harmonic mean (HM)	$(2^* Y_S X Y_{NS})/ Y_S + Y_{NS}$	Jafari *et al.* (2009)
Yield reduction (YR)	$1-(Y_S /Y_{NS})$	Choukan *et al.* (2006)
Yield stability index (YSI)	Y_S / Y_{NS}	Bouslama and Schapaugh (1984)
Yield index (YI)	Y_S / X_S	Gavuzi *et al.* (1997)
Mean productivity index	$(Y_{NS} - Y_S)/2$	Rosielle and Hamblin (1981)
Relative efficiency index (REI)	$(Y_S \times Y_{NS}) / (X_S \times X_{NS})$	Ramirez and Kelly (1998)
Mean relative performance (MRP)	$(Y_S / X_S) + (Y_{NS} / X_{NS})$	Ramirez and Kelly (1998)
Drought index (DI)	$(Y_S - X_S)/ SE (X_S)$	Bidinger *et al.* (1987)
Drought Resistance index (DRI)	$(Y_S / Y_{NS})/ (X_S / X_{NS})$	Fisher and Maurer (1978)
Drought yield index (DYI)	$(Y_{NS}/ Y_S) / (G_{NS}/G_S)$	Raman *et al.* (2012)
Schnieders Stress Susceptibility Index	$\{1-(Y_S/ Y_{NS})\}- \{1- X_S/ X_{NS}\}$	Schnieder *et al.* ((1997)
Sensitivity drought index (SDI)	$(Y_{NS} - Y_S)/ Y_{NS}$	Farshadfar and Javadina (2011)
Modified stress tolerance index-I (MSTI-I)	$\{(Y_{NS})^2/ (X_{NS})^2\} \times STI$	Farshadfar and Shukla (2003)
Modified stress tolerance index-II (MSTI-II)	$\{(Y_S)^2/ (X_S)^2\} \times STI$	Farshadfar and Shukla (2003)
Coefficient of regression (b)	$Y_{ij} \times Y_j / Y^2$	Bansal and Sinha (1991)
Superiority index (SI)	$\sum_{(j-1)} \{(X\ ij - Mij)^2\}/4$	Lin and Binns (1988)
Relative drought index (RDI)	$(Y_{S\text{-}} / Y_{NS}) / (X_{S\text{-}} / X_{NS})$	Fischer and Wood (1979)
Golden mean (Gm)	$(Y_{NS\text{-}} + Y_{S\text{-}}) / (Y_{NS\text{-}} - Y_{S\text{-}})$	Moradi *et al.* (2012)
Abiotic stress tolerance index (ATI)	$\{(Y_{NS\text{-}} - Y_{S\text{-}}) / (X_{NS\text{-}} - X_{S\text{-}})\} \times \sqrt{Y_{NS}} - \times YS$	Moosavi *et al.*. (2008)
Stress susceptibility percentage index (SSPI)	$\{(Y_{NS\text{-}} - Y_{S\text{-}}) / 2 . Y_{NS}\} \times 100$	Moosavi *et al.*. (2008)
Stress/non-stress productivity index (SNPI)	$\{\sqrt[3]{(Y_{NS\text{-}} + Y_{S\text{-}}) / (Y_{NS\text{-}} - Y_{S\text{-}})}\} \times \sqrt[3]{(Y_{NS\text{-}} \times Y_{S\text{-}})}$	Moosavi *et al.*. (2008)
Relative decrease in yield (RDY)	$\{100 - (Y_S /100)\} \times Y_{NS}$	Faeshadfar and Elyasi (2012)
Drought tolerance efficiency (DTE)	$(Y_{S\text{-}} / Y_{NS}) \times 100$	Fischer and Wood ((1981)
Drought resistance index	$Ys \times (Y_S/Y_{NS}) / XS$	Lan (1998)

Where Y_S and Y_{NS} are mean yields of genotypes under stress and non-stress conditions respectively and X_S and X_{NS} are mean of yield of all genotypes under stress and non-stress conditions. Y_{ES} is the regression estimate of yield under stress, SE is the standard error. G_{NS} and G_S are the geometric mean across genotypes for non-stress and stress conditions respectively.

and fitted multiple regression of stressed grain yield on unstressed grain yield and days to flowering by using the regression equation:

$$Y^{\wedge}_0 = a - b(F) + C(Y_i)$$

where, Y^0 is the regression estimate of yield under drought, Yi is the yield potential, F is the number of days to flowering under non-stress, b and C are the regression coefficients and a is the intercept. The drought response index is then given by

$$DRI = (Y_0 - Y^{\wedge}_0) / S{:}E\ Y^{\wedge}_0$$

Where, S.E indicates the standard error

Similarly, Karamanos and Papatheohari (1999) developed a regression based index taking water potential index instead of days to flowering. It was based on the premise that high potential yields are invariably associated with low adaptability (Laing and Fischer 1977). Alternatively, a high potential yield with a low slope would be biologically less feasible; although the opposite combination is possible (Fischer and Maurer, 1978). The relative adaptability to drought in the regression model is:

$$b_N = b/a$$

where b_N was designated as relative adaptability to drought (RAD) by Karamanos and Papatheohari (1999). As per the model, b_N will take its lowest values for an "ideal" cultivar (i.e., exhibiting high a and low b) and its highest ones for the most undesirable genotypes (low a and high b). In these regressions, the intercept represents the "potential" yield at no stress conditions and the slope represents the "adaptability" of each genotype.

Drought response index as proposed by Bidinger *et al*. (1982, 1987) has been used by a number of workers to identify stress tolerant genotypes in case of rice (Xangsayasane *et al.* 2014), wheat (Mohammadi *et al.* 2012; Amiri *et al*. 2013; Munjal and Dhanda 2016), maize (Sabaghnia and Janmohammadi 2014), sunflower (Safavi *et al.* 2013), chickpea (Kashiwagi *et al.* 2013) and common bean (Polania *et al.* 2016).

A modification of Bidinger *et al*. (1987) incorporates more number of explanatory variables into the model. The modified regression equation can be expended to incorporate more number of variables. In our analysis we incorporated relative water content (RWC) and canopy temperature depression (CTD), two important physiological traits for water stress tolerance. Our results showed that the value of regression coefficient increased from 0.754 to 0.824 (Fig 3). However, despite the temptation of increasing the number of explanatory variables in view of increased value of R-square, the focus should be laid more on the adjusted R-square (a value usually lower than R-square value that removes the bias on account of estimation from sample).

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). 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) 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) 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) used various phenology based biomass

Table 2: Various stress screening indices based on index scores

Index	Formula	Reference
Yield susceptibility score index (YSSI)	(STI s + SSI s)/2	Thiry *et al.* 2016
Yield production score index (YPSI)	{(MP s + SSI s)/2 – (SSI s + TOL s)/2}	Thiry *et al.* 2016

Where, STI s, SSI s, MP s, TOL s are the index scores of Stress tolerance index, stress susceptibility index, mean productivity and Tolerance index respectively.

Table 3: 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 = Biomass/DM	Measures daily growth rate of biomass accumulated during entire life cycle.
Economic growth rate (EGR)	EGR= Seed yield/DM	Measures the daily growth rate of the economic product *viz.* Seed yield
Seed growth rate (SGR)	SGR = 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.

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.

The phenology based indices namely DSF, BGR, EGR, SGR and RSS have been used to understand the stress response in terms of biomass partitioning in relation to phonological stages. Ramirez Vallejo and Kelly (1998) used these indices in common bean and found that the indices were positively correlated with seeds per pod and seed number while as there was no clear relationship with seed yield and seed number under stress. Among physiological parameters, the indices were positively correlated with relative water content and stomatal conductance but negatively correlated with moisture retention capacity and water content. Sofi *et al.* (2017b) also used these indices in common bean and reported that all the indices except DSF were positively correlated with seed yield under stress conditions. Similar observations were made in cauliflower for curd yield under water stress in terms of relative sink strength (Kage *et al.* 2004). Genotypes with a high relative growth rate (RGR) in any given environment are more likely to be able to respond to stress better than genotypes with a lower RGR for the same stress level. However, such genotypes when grown in optimum environments need appropriately matching sink strength to be able to have higher economic yields. Such a phenomenon, in which certain genotypes that fail to convert photoassimilates into economic yield, has been designated as "***lazy pod syndrome***" in common bean (Beebe *et al.* 2009). Under severe water stress, the carbon assimilation may diminish and stored reserves remobilised to seed resulting in a sustained seed growth rate (SGR) with a decrease in days to seed fill (DSF) that may result in smaller seeds. In case of crops like groundnut and cotton, the phenological plasticity under water stress operates by decreasing the number of smaller pods and bolls respectively (Turner *et al.* 1986).

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. Recently, various crop models such as CROPWAT, AQUAPRO and PHENOLOGY MMS have been developed that can predict the performance of crop based on various parameters including phenology and evapotranspiration. Such approaches not only help to identify genotypes that give better yields under stress as well as possess yield stability, but also delineate different adaptive mechanisms such as escape, avoidance and tolerance. These approaches can be used in different situations based on screening systems as well as data sets available to facilitate breeding programme aimed at genetic enhancement for stress resilience.

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