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Developing drought-resilient crops for improving productivity of drought-prone ecologies

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Abstract

Limitation of water is major abiotic factor affecting crop productivity in different parts of world. Climate change is likely to make drought stress even more severe in the future, particularly in semi-arid and arid tropics. Therefore, development of crops with better adaptation to water stress is very critical to have sustainable crop production. An attempt is made here to assess different approaches undertaken to enhance crop performance under water-limited conditions. Improving drought tolerance during reproductive phase is often a high priority in crop breeding programmes targeting drought-prone areas. Empirical approach followed in different crops to enhance drought tolerance has mainly addressed the issue of environment for selection and of criteria for improving drought adaptation. Using evaluation data from drought stressed and non-stressed environments, many studies highlighted importance of evaluation and selection in drought-prone locations. Most physiological research has concentrated on the identification of parameters that have found little place in regular breeding programmes owing to the lack of simple and easy techniques for selecting such characters on a large scale. Use of adapted germplasm has played a pivotal role in developing drought tolerant crops. The introgression of elite genetic material into drought-adapted germplasm has also been established as an effective approach to enhance performance under drought without compromising performance under stress-free environments. Molecular breeding is fast emerging as a supplement approach to enhance drought adaptation at a faster rate with greater precision. Efforts in this direction started with the development of a molecular marker-based genetic linkage maps in major food crops followed by identification of quantitative trait loci (QTL) determining yield under drought environments. Further success would depend upon development of repeatable, low-cost, high throughput phenotyping procedures that reliably characterize genetic variation for drought tolerance and its component traits.

Key words: Adaptation, climate-resilience, drought, genetic improvement, selection criterion

Introduction

Limitation of water is one of the major abiotic factors affecting crop productivity in different parts of world. Climate change is likely to make water stress even more severe in the future, particularly in semi-arid and arid tropics. Therefore, dvelopment of crops with better adaptation to water stress is very critical to have sustainable and equitable food production. This article deals with the research efforts that have gone into the understanding of adaptation to drought and breeding for drought tolerance. The cases are primarily drawn from pearl millet (*Pennisetum glaucum* L. R. Br.) and maize (*Zea mays* L.), crops that are largely grown under rainfed ecology and which are naturally subjected to different degree of water stress during their growth period. However, some examples from other crops have also been taken.

Nature and effects of drought

A great deal of work has been done on understanding the response of crops to moisture stress at various growth stages with a view to understanding crops adaptation to drought stress conditions. Severe moisture stress during emergence and the early seedling phase causes seedling death which results in poor crop establishment [1]. Stress occurring after crop establishment but within the seedling phase has little effect on grain yield provided it is relieved at the later stages.

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Water stress during vegetative growth might have differential effects in various crops. Prolonged stress during vegetative phase adversely affects growth rate which eventually affects biomass accumulation in many cereal crops. However, in high tillering crops like pearl millet, stress during vegetative stage has little adverse effect on grain yield as stress has been shown to increase the number of panicles per plant [2]. The apparent excess production of tillers provides potential compensation for a damaged main shoot or primary tillers [3]. High tillering and asynchrony of tillering contribute to adaptation to drought stress during the vegetative growth phase [4].

Grain yield losses are highest when drought stress coincides with the most sensitive stages of crop growth. It has been conclusively established that water stress during flowering and grain filling stages is most damaging. Grain yield and its components are drastically reduced when drought occurs during this stage [5]. Yield reduction is both due to decrease in number of grains and grain size. The reduction in grain size is mainly due to a shortening of the grain filling period rather than to a reduction in grain growth rate [6].

Developing drought resilient crops

Improving drought tolerance during reproductive phase is a priority in crop breeding programmes targeting rainfed areas. Breeding for increased adaptation to drought is, however, a challenging task due to various complexities associated with drought adaptation mechanism; uncertainty in timing, intensity and duration of stress; and a large genotype x environment interaction. Empirical approach has been followed in different crops to enhance drought tolerance. Recently, molecular breeding is becoming an important option to improve drought tolerance with greater precision and efficiency.

Empirical breeding

Empirical breeding for drought tolerance has mainly addressed the issue of environment for selection and of criteria for improving drought adaptation.

Selection environment

Choosing an appropriate selection environment to improve productivity under drought has been a subject of the major debate in plant breeding, and several theoretical and empirical studies have been reported. Some believe that cultivars targeted for drought conditions can be identified under non-drought conditions (indirect approach) while others think that selection for drought environments should be undertaken under drought stress (direct approach).

The indirect approach involves selection for high yield potential under non-stress conditions with the assumption that genotypes selected under optimum conditions would also perform well under drought. In this approach, drought resistance is an unidentified component of performance over different environments and more emphasis is laid on yield potential. The main advantage of this approach is that yield potential and its components have higher heritability in optimum conditions than that under stress conditions [7]. Since yield potential has been reported to be a significant factor in determining the yield under moisture stress [5], improvement in yield potential may have some spill over effects under water stress conditions.

The direct approach recommends that varieties for drought-prone areas must be selected, developed and tested in the target drought environments. Theoretical analyses also indicate that selection for stress environments should be done in stress environments [8-9]. In this approach, improvement of yield under moisture stress requires dissociation from yield potential under optimum conditions as a major selection criterion [10-11] and the emphasis is placed on drought adaptation and yield under drought.

Many studies have compared relative gains in performance under drought conditions through selection in drought vis-à-vis non-drought environments. Low correlations are often reported between yields measured in stress and optimum conditions which indicate that yield performance under drought and non-drought conditions are separate genetic entities and direct selection for yield performance in the target drought environments would be required to make greater gains in productivity. This is further substantiated by existence of significant cross-over genotype x environment interactions observed across optimum and stress environments [12]. Using evaluation data from drought stressed and non-stressed environments, many studies showed that drought tolerance and escape were major determinants of performance in drought environments [5, 13]. On the other hand, high yield potential accounted for 10-15% variation towards performance under drought. This has highlighted the importance of evaluation and selection in drought-prone locations and early maturity and suggested for *in-situ* breeding for drought environments.

Alternatively, simple and efficient screening techniques might be employed for evaluating large number of genotypes under managed drought conditions. Field screening for response to stage-specific drought can be carried out by withholding irrigation to impose water stress during the rain-free seasons to study the effects of drought stress and to identify whole plant traits associated with adaptation to a particular stress. Drought resistance is then determined on the basis of genotype performance in the stressed treatment after accounting for differences due to escape and yield potential among genotypes. However, off-season drought screening may not necessarily give results similar to naturally occurring stress, as fluctuations in atmospheric conditions or changes in phenology due to different day lengths may alter the results. Additional limitation of artificially created screening techniques is that they are unable to expose the test material to all the combinations of stress the crop might subsequently experience given that drought stress occurs in a wide range of combinations based on variability in timing, severity and duration of drought. This necessitates selecting in the target environments that are highly prone to terminal drought. There are extensive evidences that cultivars for stress environments should be selected, developed and tested under target environments [11, 14-15].

Selection criteria

Several efforts have been made to identify traits that can be used as selection criteria in breeding drought resistant genotypes. Most research has concentrated on the identification of physiological parameters like dehydration tolerance, dehydration avoidance, growth maintenance through stability of cellular membrane, osmotic adjustment, desiccation and heat tolerance, leaf gas exchange rate and radiation reflectance [16-17]. However, most of these have hardly found any place in routine breeding programmes, particularly in developing countries, owing to the lack of simple and easy techniques for selecting such characters on a large scale. On the other hand, morphological characters that can be measured easily appeal most to plant breeders for use as selection criteria. Rapid growth during initial stage is one such trait. Early flowering, the most important factor determining yield under terminal water stress is recognized as another selection criterion, although its advantage is due to drought escape rather than due to drought tolerance. Genetic variability for earliness is widely available in most of crops and simple selection has been successful under most circumstances. However, value of earliness as a selection criterion is significant only if drought predictably occurs towards the end of the growing season. Short reproductive cycle, ability to fill and set grains under receding moisture conditions, leaf rolling and stay green [26] are other phenotypic traits being used as criteria.

Some studies have also used mathematical models to identify crop cultivars that are productive in stressful marginal environments by comparing the change in seed yield between stress and non-stress (optimum) environments [8, 18-19].

Yield improvement under drought

Use of adapted germplasm: The base material required for a successful breeding programme may differ for the drought and more favourable environments. Success in drought environments is often much more a consequence of adaptation to environmental stresses than it is of yield potential *per se*, which is not effectively expressed under severe stress. Plant breeders focusing on drought environments are faced with the choice of trying to improve either the adaptation of high yielding, but poorly adapted germplasm, or the yield potential of already adapted germplasm, often in the form of local landraces. Improving adaptation to marginal environments is the more difficult alternative than is improving yield potential, as adaptation is much less well understood, physiologically and genetically.

The breeding material should provide a good starting point for the programme, i.e., high productivity under drought conditions, as well as sufficient genetic variation to allow for gains from selection. Traditional landraces that evolved in dry areas as a result of natural and human selection over centuries usually exhibit good adaptation to drought and other naturally occurring stresses and represent a largely untapped reservoir of useful genes for adaptation to stress environments.

Genetic introgression of drought-adapted germplasm

The traditional cultivars and landraces possess good levels of drought adaptation but fail to capitalize on yield-enhancing conditions. On the other hand, elite genetic material has a greater yield potential expressed under better endowed conditions but lacks adaptation to severe drought stress conditions [20-21]. Thus, these two contrasting groups of genetic materials have differential pathways to yield formation under drought stress [3].

Several attempts have been made in this direction through hybridization of selected landraces and elite materials. Crosses between these two materials had enhanced adaptation range, beyond that of their parental populations as they were better able than their landrace parents to capitalize on the additional resources of good growing seasons, and simultaneously having a better capacity than their elite parents to tolerate drought which suggests that the hybridization between landraces and exotic populations breaks up gene complexes of two contrasting groups of genetic material and is effective in combining drought tolerance and high productivity [22, 23].

Hybrids for drought ecology

It is generally argued that hybrids are more suitable for better endowed environments. The adoption and impact of hybrids in pearl millet and maize in rainfed ecology in India is an evidence that hybrids are better cultivar type to make use of limited water resources. A large number of pearl millet hybrids and open-pollinated varieties (OPVs) have been tested under severe drought environments and it has been explicitly showed that hybrids provided 25% higher grain than OPVs [24].

Molecular breeding

Because of intrinsic difficulties in breeding for drought adaptation by conventional phenotypic selection, molecular breeding is fast emerging as a supplement approach to enhance drought adaptation at a faster rate with greater precision. Efforts in this direction started with the development of a molecular marker-based genetic linkage maps in major food crops followed by identification of quantitative trait loci (QTL) determining yield under drought environments and thus preparing a road map for marker-assisted selection. The identified QTL are now being transferred to a wide range of crops and there is increasing evidence that genotypes with drought tolerant QTL have improved performance under water-limiting conditions. Comparison of hybrids with and without such QTL showed that QTL-based hybrids were significantly higher yielding in a series of terminal drought stress environments [25].

The way forward

Majority of arable acreage would continue to be rainfed during rainy season where moisture availability is seldom adequate and field crops would always be prone to face intermittent drought at critical growth stages. Climate change effects pose further challenges to drought ecology. Several climate modelling studies suggested heavy and concentrated rainfall within limited days causing water-logging for short periods and leaving severe dry days in rest of the season in majority of the Asian regions. Using weather data from past 110 years (1901-2011), it has been indicated that though there is no significant change in total rainfall, but in recent years the number of rainy days have reduced significantly, which resulted in episode of extremes of moisture availability [26]. Such changes are already being felt in a number of real and recognizable ways in different regions, in terms of shifting seasons, and higher frequency of extreme weather events, such as drought and water logging.

In view of burgeoning population, there will be a greater competition for water among agriculture, industry and domestic sectors. Enhancing crop productivity with limited quantity of water is becoming a global necessity. Genetic interventions to increase tolerance to water stress are more important than ever before. Further success would depend upon development of repeatable, low-cost, high throughput phenotyping procedures that reliably characterize genetic variation for drought resistance and its component traits.

Several new techniques offer a great opportunity of accelerating the line development process. Molecular markers tagged with genomic regions controlling yield and yield-related traits under water-limited conditions have opened up new opportunity for integrating conventional breeding and molecular biology. Association mapping has enabled dissection of complex traits. Genome wide association studies using nested association mapping populations would help to probe deeper into the genetic architecture of key agronomic traits that contribute to yield under drought conditions.

Genetic approach needs to be supplemented with other management strategies particularly water conserving techniques such as drip irrigation, sprinkler irrigation, mulching and zero tillage in order to maximize gains in productivity under water stress.

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