Improving pearl millet for drought tolerance – Retrospect and prospects

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Abstract

Drought stress is the most important production constraint of pearl millet (Pennisetum glaucum) in sub-Sahara Africa and south Asia where it is the staple diet and cheaper source of nutritious food for more than 90 million people. A much greater necessity therefore exists for improving pearl millet for drought-prone areas to attain food security in resource-limited and fragile ecosystems. An attempt is made here to review the progress made in understanding the adaptation mechanism of pearl millet to drought situation and then to appraise how this knowledge has been used in improving drought-tolerance of pearl millet. A good amount of work has been accomplished in understanding the response of pearl millet to drought imposed at different growth stages of crop in order to understand its adaptation to drought stress. The foremost issues that have been addressed in breeding for enhanced drought tolerance in pearl millet are nature of base germplasm used, selection criterion, and representation of target environment during development, testing and evaluation of cultivars. Recent advancement in development and application of genomic tools in pearl millet is expected to improve the efficiency of breeding for improved drought tolerance. The major achievements in developing pearl millet specifically for drought conditions include identifying genetic material with built-in tolerance, developing early maturing cultivars, assigning importance to both grain and stover yields while releasing the cultivars, and identification of quantitative trait loci associated with drought tolerance. Prospects of further improvement of pearl millet for drought-prone areas are also discussed in this review.

Key words: Pearl millet, Pennisetum glaucum, drought tolerance, breeding

Introduction

Pearl millet [Pennisetum glaucum (L.) R. Br.] is the most important rainy season cereal in the drier semi-arid and arid regions of India, sub-Sahara Africa and southern America grown over 28 million ha. It is sixth most important cereal of the world after maize, rice, wheat, sorghum and barley (Yadav et al. 2012c). Pearl millet is one of the most important sources of nutritious food (Kanatti et al. 2016; Anuradha et al. 2017) and forms staple diet for more than 90 million people living in some of the most fragile ecosystems in south Asia and sub-Sahara Africa (Rai et al. 2008). The greater degree of adaptation of pearl millet to water stress and nutrient-deprived soils than other cereal crops is the primary reason of its large scale cultivation in arid and semi-arid regions. Higher tolerance levels of pearl millet to elevated temperature during reproductive stage (Gupta et al. 2015) also makes it an excellent genomic resource for isolation of candidate genes responsible for tolerance to situation arising out of global warming and climate change for accelerating further genetic improvement of other crops.

In addition, dry stover of pearl millet also provides a basis of ration for a large bovine population that is regarded as the most critical component of providing stability in the risk-prone crop-livestock farming system in water-limited regions. Its green fodder is also a rich source of protein, calcium, phosphorous and other minerals with oxalic acid within safe limits.
Improving drought tolerance of pearl millet

Cultivation of pearl millet in arid regions faces a challenging and hostile growing environment due to serious limitations imposed by climatic and edaphic conditions. The foremost among them is the extremely low precipitation and its very erratic distribution throughout the growing season that results in drought stress of different magnitude, timing, intensity and duration at one or other stages of crop. Adverse effects of drought are further exaggerated by frequent higher air temperatures, low humidity and high evaporation resulting in high water pressure deficit in pearl millet growing environments. Soils on which pearl millet is cultivated are very low in their fertility. High silt content of soils also leads to formation of soil crust that often results in poor plant stand and in severe form may often force replanting of the crop.

A good progress has been realized in the genetic and cultural improvement of pearl millet especially in India (Govila et al. 1997; Khairwal and Yadav 2005; Yadav and Rai 2013) but the situation is not so in large parts of Africa. The impact of improved technology has not been evenly realized in different pearl millet growing regions. This is primarily because most of the cultivars have been targeted for relatively favorable environmental conditions with high built-in grain yield potential. Such cultivars did not necessarily meet the requirements of farmers in the drier areas (Kelley et al. 1996; Yadav et al. 2011). In addition, development and up scaling of improved crop production technology has been a serious challenge in drought-prone regions. A much greater focus is, therefore, required for improving pearl millet for drought-prone areas in arid and drier semi-arid regions. This review summarizes results of research conducted in genetic improvement of pearl millet in drought-prone regions and further examines the prospects and approach of improving the crop for this unique but difficult production environment.

**Genetic improvement**

**Understanding adaptation to drought stress**

In view of drought being the major production constraint in pearl millet production environments, a good amount of work has been accomplished to understand pearl millet response to moisture stress occurring at different growth stages in order to understand crop adaptation to drought conditions (Yadav et al. 2012c; Yadav and Rai 2013). It has been convincingly shown that effects of drought are influenced by developmental stage of crop at which drought stress occurs. Subsequently, pearl millet research on adaptation to drought has explored the effects of drought at specific growth stages.

Drought during juvenile stage of crop causes seedling death resulting in a poor crop stand that severely reduces yield in the semi-arid regions of Indian sub-continent and Africa (Carberry et al. 1985; Soman et al. 1987). Water stress occurring after crop establishment but within the seedling phase results in prolonged seedling phase and affects the relationship between leaf formation and secondary root development (Stomph 1990). Secondary roots are formed only under adequate supply of moisture at the coleoptile node (Gregory 1983). There are reported cases of existence of genetic variability for leaf appearance rate and formation of secondary root (Stomph 1990), though there are no reports of genetic manipulation of such traits in any breeding programme. Rather, a water stress at an early stage would likely come with higher temperatures causing a deleterious effect on the seedling explaining in part early mortality. However, seedling stage tolerance to heat is extremely difficult to phenotype and virtually there has been no success in breeding for that trait.

Drought during vegetative stage of growth has little adverse effect on pearl millet productivity as there is a significant increase in number of panicles (Bidinger et al. 1987a), which has been established as a compensation mechanism for a damaged main shoot (van Oosterom et al. 2003; van Oosterom et al. 2006). This is surely what makes pearl millet so plastic and adaptable to harsh environments, as the crop can take advantage of late rain to generate new productive tillers (Siband 1983; Mahalakshmi et al. 1987). Water stress during the vegetative phase also results in delayed flowering of the main shoot (Bidinger et al. 1987a; Mahalakshmi et al. 1987). Such developmental plasticity increases the chances for escape from the most sensitive stage of growth (Henson and Mahalakshmi 1985).

Grain yield damages are maximum when drought corresponds with flowering and grain filling of crop (Lahiri and Kumar 1966; Mahalakshmi et al. 1987) owing to decrease in number of panicles per plant,
number of fertile florets per panicle and grain size (Bidinger et al. 1987a; Fussell et al. 1991). The reduction in grain size is mainly due to shortening of the period for grain filling rather than reduction in rate of grain growth (Henson et al. 1984; Bieler et al. 1993) as pearl millet has also an exceptional capacity to compensate for reduction in the supply of assimilates to the grains by mobilizing stored soluble sugars (Fussell et al. 1980). The contribution of stored assimilates to the grain growth during drought stress has, however, not been quantified (Yadav et al. 2012c). The connection between grain development and the transfer of assimilates from the leaves has been reported as central adaptation mechanism of pearl millet to terminal drought stress (Winkel and Do 1992). However, more recent evidence shows that pearl millet tolerant to terminal stress has more water available during the grain filling period, and it is this water that sustains photosynthesis for a continued carbon supply to the grain during the critical period (Vadez et al. 2013).

Breeding for improved drought tolerance

Given that pearl millet is grown in regions where rainfall is too limited for other cereals like sorghum or maize, improving drought tolerance is an important area of research in pearl millet improvement (Yadav and Rai 2013). Breeding for increased adaptation to drought remains, however, a challenging task due to uncertainty in timing, intensity and duration of water stress, and a large genotype x environment interaction under variable drought stress environments (Yadav et al. 2012c). The major issues that are relevant and have been addressed in breeding for enhanced drought tolerance are type of germplasm used, selection criterion, selection environment and representation of target environment during testing and evaluation (Vadez and Kholova 2013). The pearl millet breeding starts by carefully analyzing the stress scenarios in the target population of environment (TPE) to more specifically delimit geographical zones with more homogenous occurrence of a particular stress pattern and requiring specific breeding needs, that has been done by dividing whole pearl millet growing regions of India in three specific zones (Gupta et al. 2013).

Use of adapted germplasm: Germplasm required for enhancing performance under drought and optimum growing environments varies. Performance under drought stress is largely a result of adaptation to stress conditions rather than high yield potential, which is not expressed under stress conditions (Ceccarelli and Grando 1991). Plant breeders targeting drought environments opt for either improving adaptation of high yielding material with poor adaptation to stress conditions or to enhance adaptation of high yielding material (Bidinger et al. 1994). Enhancing adaptation to drought conditions is more difficult alternate than is enhancing yield potential because adaptation to stress conditions is much less understood, physiologically and genetically, than is yield potential (Ceccarelli et al. 1992; Yadav et al. 2012c).

Pearl millet landraces from dry areas are known to exhibit good adaptation to moisture stress (Yadav and Weltzien 2000; Yadav 2010a; Yadav 2014), regarded as a largely unexploited pool of valuable genes conditioning stress adaptation (Yadav and Manga 1999; Yadav 2014) and make very suitable base material for improving adaptation to drought. It has been shown that their yields can be improved considerably through simple mass selection (Bidinger et al. 1995; Yadav and Bidinger 2007). Breeding populations adapted to drought have also been shown as a useful source material in developing drought-adapted varieties (Yadav 2004) and deriving inbred restorer lines for hybrids (Yadav et al. 2009; Yadav et al. 2012a). Development of backcross nested association mapping populations (BCNAM) would also be an alternative for bringing back diversity in the breeding programme while maintaining essential adaptive and agronomic traits in the mode of what has been developed in sorghum or maize.

The use of elite breeding material ensures high yield potential but offers a challenge of improving adaptation. On the other land, use of landraces ensures adaptation to drought stress but require considerable improvement in productivity. Adapted landraces and high yielding elite materials have contrasting but complementary pathways to yield formation under drought stress (van Oosterom et al. 2003; van Oosterom et al. 2006) suggesting good prospects of diversifying the adapted landraces through hybridization with cautiously selected elite genetic material in order to combine the adaptive feature of landraces with higher productivity potential of elite materials (Yadav 2006; Yadav and Rai 2011; Yadav 2010). Crosses between adapted landraces and elite genetic material have been reported to have adaptation range beyond that of their parental populations as former were better able than their landrace parents to capitalize on the additional resources, and simultaneously having a better capacity than their elite parents to tolerate drought (Presterl and Weltzien 2003; Yadav 2008; Yadav and Rai 2011).
Adaptation to drought is about matching water supply to water demand by the crop (Vadez et al. 2013). Therefore, zones with specific water availabilities require specific germplasm solution, with an adequate flowering time and a canopy size that fits particular environment. Recent evidence shows that pearl millet hybrids bred for low rainfall zone had a relatively smaller canopy than hybrids that were bred for higher rainfalls (Vadez et al. 2015).

Selection environment: Choice of appropriate selection environment for improving drought tolerance continues to be a debate in plant breeding. One school of thought believes that improved varieties for drought conditions can be selected under optimum conditions (indirect approach), while other school reason that selection for drought conditions should be undertaken under target environment (direct approach) (Yadav et al. 2012c). The indirect approach recommends selection for high yield under optimum conditions assuming that cultivars selected under optimum conditions would also perform well under drought. This approach recognizes drought tolerance as an unidentified component of performance and greater emphasis is laid on yield potential (Yadav et al. 2012c). The core advantage of this approach is higher heritability of yield and component traits in optimum conditions (Ceccarelli et al. 1991; Ceccarelli 1994). Yield potential, assessed under optimum conditions, has been identified as a significant factor in pearl millet in determining the performance under drought conditions (Bidinger et al. 1987b; Fussell et al. 1991; Yadav and Bhatnagar 2001). Therefore, improving yield potential might have some spillover effects under water stress conditions. However, this approach overlooks the usually very large genotypes-by-environment interactions.

The direct approach endorses that cultivars targeted for drought conditions need to be selected, developed and evaluated in the representative target environments (Simmonds 1991; van Oosterom et al. 1995b) and this is supported by theoretical analyses (Rosielle and Hamblin 1981; Simmonds 1991). This approach does not endorse yield potential measured under optimum conditions as selection criterion (Ceccarelli and Grando 1991; Ceccarelli et al. 1992) and therefore, greater emphasis is given on yield obtained under drought conditions. There are no reports available in pearl millet comparing comparative gains in performance under drought conditions while selecting in drought and non-drought environments (Yadav et al. 2012c), though, there are several indirect inferences. For example, low correlations are commonly observed between pearl millet yields measured in stress and optimum conditions (Virk 1988; Khairwal and Singh 1999; Yadav and Bhatnagar 2001) which advocates that yields under drought and non-drought conditions are discrete genetic entities eventually suggesting that direct selection in the target drought environments would be essential to achieve higher productivity. This is further authenticated by presence of significant cross-over genotype x environment interactions observed across optimum and stress environments (Virk and Mangat 1991; van Oosterom et al. 1995a; Yadav and Weltzien 2000; Yadav 2010a). Many studies used evaluation data from drought stressed and non-stressed environments and have shown that drought tolerance and escape were major factors in determining yield performance in drought environments and high yield potential accounted only for 10-15% variation towards performance in drought environments (Yadav et al. 2011; Yadav et al. 2012c). This has underlined the significance of early maturity and evaluation and selection in drought-prone locations. Taking cognizance of these results, the All India Coordinated Research Project on Pearl Millet has carved out a distinct zone for multi-location testing and evaluation of experimental cultivars in locations receiving <400 mm of annual rainfall with the objective of identifying and releasing cultivars suitable for drought ecologies (Yadav et al. 2011; Gupta et al. 2013). There are broad indications from other crops that cultivars for drought condition need to be selected, developed and tested under target environments (Atlin and Frey 1991; Ceccarelli et al. 1992; Zavala Garcia et al. 1992). It is also very likely that the use and application of a crop modelling analysis of the stress scenarios in the target population of environment would improve a great deal the selection of representative testing sites, as previously reported for sorghum (Kholova et al. 2013).

Selection criteria: Numerous efforts have been made for identifying traits to be used as criteria in developing drought tolerant genotypes (Yadav and Rai 2013). Maximum research has concentrated on identification of physiological parameters like dehydration avoidance (Bidinger and Witcombe 1989), growth maintenance through stability of cellular membrane (Blum and Ebercon 1981), leaf gas exchange rate (Vadez and Sinclair 2001; Kholová et al. 2010), radiation reflectance (Bidinger and Witcombe 1989). Recent evidence has shown that pearl millet lines tolerant to terminal drought were those able to save water at early growth stage, therefore leaving more water available for the grain filling period (Vadez et al. 2013). This
water saving was in part related to the capacity to restrict transpiration under high VPD (Kholova et al. 2010), but also to differences in the canopy development. However, most of these have hardly found any place in conventional breeding programmes because of lack of simple techniques for selecting such characters while using large number of genotypes in breeding nurseries. Instead, morphological traits that can be measured easily have appealed most to use them selection criteria (Yadav et al. 2012c). Fanous (1967) used growth in di-mannitol solutions, seed germination, and stability of extracted chlorophyll under heat for testing drought tolerance that don’t essentially symbolize the limiting moisture conditions of the field. Early vigour that signifies a rapid development of the crop in the initial stages has been correlated with drought tolerance (Manga and Yadav 1995) claiming that crop with faster development of leaf area could intercept a greater radiation and reduce water losses by evaporation, though there are some concerns that greater transpiration from a larger leaf area will quickly exhaust soil water resources and may cause intense water shortage at growth stages more sensitive to drought (Winkel and Do 1992).

Early flowering is that most potent tool in determining yield under terminal drought conditions (Bidinger et al. 1987b; Fussell et al. 1991; van Oosterom et al. 1995b) and has been recognized as very useful selection criterion. Although its advantage is exclusively due to drought escape rather than tolerance (Yadav et al. 2012c). Earliness is also akin to lower yield potential and a potential loss of opportunity in situation of abundant rainfall. Genetic variation for earliness is abundant in pearl millet (Rai et al. 1997; Rattunde et al. 1989b; Yadav et al. 2017) and simple selection has been successful under most circumstances (Rattunde et al. 1989a). Day-length insensitive Iniadi-type landraces from western Africa represent the most widely used source of earliness (Andrews and Anand Kumar 1996) by breeders in India and Africa.

Panicle harvest index (PHI) that indicates the plants’ ability to set and fill grains under water limiting conditions is another criterion proposed for improving tolerance to terminal drought (Yadav 1994; Yadav et al. 2012c). It accounts for a large proportion of variation for yield performance under terminal drought (Fussell et al., 1991; Bidinger and Mahalakshmi 1993; Vadez et al. 2013). Yadav (1994) showed that even in a small set of inbred lines, high heritability of PHI suggests that significant gains from selection for this trait is possible under drought conditions. High tillering is another useful selection criterion in pearl millet breeding for drought-prone regions for which there is abundant variation in germplasm and elite breeding material (Appa Rao et al. 1986; Rai et al. 1997, Yadav et al. 2001, 2017).

Some mathematical models have also been used for identifying drought tolerant cultivars by comparing the change in yield measured in stress and optimum environments (Bidinger et al. 1987b; Yadav and Bhatnagar 2001). A drought response index (DRI) has been developed by Bidinger et al. (1987b) which is independent of escape and yield potential and is an effective indicator of drought tolerance. Yadav and Bhatnagar (2001) established that drought susceptibility index (DSI) of genotypes could be a valuable criterion to categorize genotypes adapted to drought stress with the condition that it must be used along with the yield performance under drought environments.

**Synergy of cultivar development and improved management**

Realized productivity under drought environments is an interactive effect of improved cultivars and improved crop management. Agronomic research has established suitable management recommendations for cropping systems, sowing time, seed rate, weed management, fertilizer application, intercropping and moisture conservation (De and Gautam 1987; Bhatnagar et al. 1998; Joshi 1997; Tetarwal and Rana 2006; Kiroiwal and Yadav 2013). Conservation of moisture through widely spaced rows and mulching both by manipulating top soil or organic means form an important recommendation in dry regions growing pearl millet (Mulumba and Lal 2008). However, implementation of agronomic recommendations especially those involving additional investment has been limited as risk of crop failures in drought-prone areas is high. Adoption of modern technologies is often restricted to use of improved varieties as seed cost can be easily recovered by farmers even with 5-10 % additional grain yield with improved varieties. However, there exists considerable scope for reducing the impact of drought through improved fertilization of crop in new cultivars.

The development and adoption of improved cultivars has resulted in the increase in the crop productivity from 458 kg ha$^{-1}$ in 1981 to 1085 kg ha$^{-1}$ in 2016 registering 137% improvement which assumes...
greater significance given that more than 90% of pearl millet is still grown as rainfed and often on marginal lands.

**Prospects of improvement**

**Broadening the genetic base**

Choice of germplasm is comparatively narrow for drought-prone arid regions primarily because only limited germplasm especially from African and other regions has been evaluated for its adaptation in arid zone. The choice of male-sterile lines having ability to produce adapted hybrids is still more limited as most of the male-sterile line development programme has taken place in better-endowed areas. This is reflected by release of only 11 cultivars for drought-prone areas as compared to 53 cultivars for better-endowed areas during last ten years in India. This explains the fact that in spite of more than 70% of pearl millet area in country under hybrid cultivation, though only 40% area is under hybrids in A1 zone. The reasons for relatively low adoption in A1 zone include challenging production system and fewer choices of cultivars in early maturity group. More germplasm needs be evaluated and identified having in-built tolerance to stress environments in order to broaden the genetic base of germplasm (Yadav et al. 2017).

**Expanding evaluation and testing in target environment**

There exists urgent need to have greater efforts to increase the testing locations of potential cultivars and germplasm in the target region. The varietal evaluation for drought-prone regions is undertaken through AICRP trials at various locations. These trials are to represent a variety of water stress conditions encountered by pearl millet in arid zone. The present average number of test locations in arid zone are very limited (11) as compared to other zones (50). Evaluation trials don’t always succeed in drought locations due to severe water stress and the yield levels in successful trials are usually not true representative of actual productivity levels in farmers’ field. The research capacity in pearl millet in water-limited environments needs to be enhanced to a great extent. The arid zone has not so far been the major priority zone in pearl millet breeding programme. For instance, by only a few (7) research organization from both public and private sector are undertaking targeted research for arid areas as compared to 35 research organizations from both public and private sector that contributed test entries annually for AICPMIP testing for last ten years. Majority of research organizations from public sector targeting arid zone allocate much lesser resources as compared to other zones. Few private-sector institutions are specifically breeding for drought-prone environments of arid regions. Given that greater challenges are involved in genetic improvement of pearl millet for drought-prone environments of arid regions, infrastructure resources appear too little to address all issues and need to be strengthened considerably.

**Engaging greater thrust on hybrids**

Two types of commercial cultivars i.e. hybrids and open-pollinated composite varieties are available in pearl millet. Most of breeding programme targeted hybrids for better-endowed environments while greater emphasis was given, at least up to 1990s for OPVs for arid areas on the presumption that genetically heterogeneous OPVs might be useful to exploit population buffering mechanism in order to provide higher and stable performance under unpredictable environments of arid and drier semi-arid areas. A large number of hybrid and OPVs in arid and drier semi-arid regions have been tested since last 15 years to generate multi-environment data in order to assess comparative advantage of each cultivar type. There are now clear evidences that hybrids yielded significantly higher grain than OPVs with yield advantage ranging from 19% to 35% with the overall advantage of hybrids over OPVs across all years being 25% (Yadav et al. 2012b). The existing seed delivery mechanism in pearl millet in India also favours hybrids but this is not so in Africa. Nonetheless, hybrids are likely to contribute than composites in augmenting crop productivity in drought-prone regions. Organizations targeting drought environments must gear their programme to strengthen hybrid development with adequate adaptation to arid zone ecosystem.

**Developing dual-purpose cultivars**

Livestock, mainly consisting of bovine and small ruminants, is an integral component of existing farming system of arid zone and play very critical role in sustenance of its economy especially during drought periods. This is reflected through a higher livestock: human ratio in arid regions (124:100) than in other parts of India (40:100). The cultivars targeted for arid regions needs to have ability to produce high grain and stover yields. This warrants the need to enhance biomass productivity of targeted cultivars, rather than harvest index. There are reported exploitable genetic differences among parental lines of hybrids for their ability to produce heterotic crosses for biomass
Targeting appropriate maturity

Given a high probability of terminal drought in arid regions, extra-early maturity (maturity up to 65 day) has been a major focus. This puts a severe restriction in yielding capacity of cultivars especially for the dry stover yield. The hybrids retaining maturing of up to 75 days have a better capacity to realize both higher grain and stover yields with good ability to avoid terminal drought (personal communication: private seed industry and farmers from western Rajasthan).

Adding value to grain and stover

Many studies on grain quality and nutrition have suggested that pearl millet grains are better choice to achieve nutritional security in the rural and urban poor population that have limited access to other sources of dietary components. Similarly, agronomic interventions have been shown to significantly improve stover yield. A good range of genetic variation and moderate to high estimates of heritability have been observed in pearl millet for quality of grain stover suggesting that there exists good opportunities to further improve both traits. Technologies have been developed for preparing various types of alternative and health food products but need to be up scaled. A greater emphasis is also needed to enhance value of both grain and stover without compromising productivity.

Complimenting with molecular breeding

Owing to inherent difficulties through conventional phenotypic selection, breeding for enhanced drought tolerance has become a priority area for molecular marker-assisted selection (Yadav et al. 2012; Serba and Yadav 2016). Efforts in this direction include development of a molecular marker-based genetic linkage map (Liu et al. 1994; Qi et al. 2004; Supriya et al. 2011; Rajaram et al. 2013), mapping of major quantitative trait loci (QTL) for terminal drought tolerance in independent populations (Bidinger et al. 2005b; Yadav et al. 2002; Yadav et al. 2004; Bidinger et al. 2007; Yadav et al. 2011b; Sharma et al. 2014; Kholová et al. 2012), genomic selection tools (Heffner et al. 2009 & 2010), genome sequencing (Varshney et al. 2017) and genotyping-by-sequencing (Sehgal et al. 2012). Progress in development and application of genomic tools in breeding pearl millet for drought tolerance have been recently reviewed with strong arguments of intensifying and applying high throughput genomic tools for improving breeding efficiency of pearl millet to minimize the impact of drought on its production (Serba and Yadav 2016).

Conclusion

There are intense challenges in pearl millet production in arid and semi-arid regions. These challenges can be translated in good opportunities of increasing the productivity of pearl millet provided the challenges are addressed in a mission mode to develop and deliver new cultivars and improved technology. There exist good prospects to enhance and stabilize the yields at higher level but this would require more concentrated efforts taking in view past experiences of pearl millet cultivation in arid zone. Involvement of all stakeholders from research, seed production and supply, technological adoption and up scaling would be principally necessary.

Declaration

The authors declare no conflict of interest.

References


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