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Challenges Associated with Crop Breeding for Adaptation to Drought-Prone Environments

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Abstract

Crop production is the main source of food, and drought is among the most important crop production constraints in the world, particularly in sub-Saharan Africa. The use of improved cultivars can at least partly ameliorate the calamities of drought stress, and considerable investments and efforts have been made worldwide to develop drought tolerant crop cultivars. A number of improved cultivars of different crops have also been released for production in different countries. As related to the situation under normal environments, it is yet hardly possible to say that these investments and efforts have modernized the production under drought-prone environments as a whole and boosted the actual productivity as desired. Therefore, the limitations and strategic implications of past experiences made to develop drought tolerant crop cultivars needs to be synthesized in order to formulate better strategies and approaches. In this review article, the scope and impacts of drought, approaches to breeding for drought tolerance and the associated challenges and ways out of the challenges have been discussed. We believe that this review will enhance the efforts underway to meaningfully adopt plant breeding for improving crop production in the face of the changing climate.

Keywords: Adaptation to drought, drought-prone environments, drought tolerance

Introduction

Crop production has a significant share of the total contribution of agriculture as a whole (FAO, 1995). The productivity of agriculture as a sector in general and that of crop production in particular has, however, been very low in most parts of the developing world compared to population growth (Bunders *et al.*, 1996). The full genetic potential of crop plants is rarely attained particularly in tropical and sub-tropical Africa, where limitations imposed by abiotic and biotic stresses are severe (Kramer, 1980; Buddenhagen and Richards, 1988). Generally, abiotic stresses cause more economic losses to crop plants than the biotic ones (Slater *et al.*, 2003). Of these, drought followed by low nutrient stress may be among the most important abiotic stresses with worldwide distribution constraining the productivity of crops more than any other environmental factors (Singh, 2002; Cattivelli *et al.*, 2008). Some estimates show that losses from drought alone may exceed the losses from all other causes put together (Kramer, 1980).

Drought is defined in different ways by agriculturalists (Njoroge *et al.*, 1997), meteorologists (Turner and Kramer, 1980; Sinha, 1987) and hydrologists (Sinha, 1987).To an agriculturalist, drought is explained in terms of moisture requirements by crop plants, as inadequate moisture level to meet the physiological requirement and to the realization of the full genetic yield potential. To a meteorologist, drought may be said to occur when less than 75% of the normal rainfall is received over several consecutive months. To a hydrologist, drought may also be considered as the failure of surface and underground water supplies as a result of rain shortage, excessive run-off and/or overuse of the land.

Drought tolerance may also be defined in different ways by different disciplines of biology (Sinha, 1987). A molecular biologist may explain it in terms of survival of individual cells or unicellular organisms through osmo-regulation of water stress. A biochemist may consider it as tolerance of biochemical reactions such as protein synthesis to water deficit. A plant physiologist may define drought tolerance as maintenance of growth during water stress and its accelerated resumption on termination of water stress. Similarly, an agronomist may explain it as stability in yield performance of a crop or a variety in water-deficient environments. A number of workers also defined drought tolerance in terms of the difference in yield performance between stressed and non-stressed environments (Rosielle and Hamblin, 1981; Fernandez, 1992). Definitions by molecular biologists, biochemists and physiologists are based on plant survival while agronomists relate drought tolerance rather to productivity and economic yield. Thus, rainfall, soil water storage capacity, potential evapo-transpiration and crop phenology and developmental stages must all be considered when assessing the impact of drought on crop production (Kramer, 1980; Njoroge *et al.*, 1997).

In addition to the agronomic moisture conservation methods like tie ridging, breeding for more productive crop cultivars is one of the sound strategies in increasing crop yields in drought-prone environments. This is because better environmental manipulation with moisture-conserving agronomic practices alone may not lead to better yields from inferior genotypes unless they are integrated with crop genotypes that are capable of efficiently exploiting the limited moisture conserved (Buddenhagen and Rechards, 1988; Singh, 2002). Furthermore, once drought tolerant cultivars become available, their adoption by the resource-poor farmers in the dry areas should be rapid because their use may not necessarily involve additional costs apart from the initial seed cost, and the existing cropping systems and soil and water management practices may not necessarily be affected. Experience also shows that seed-based technologies are easier to transfer to farmers than more complex knowledge based agronomic practices (Edmeades *et al.*, 1998).

Improving adaptation to drought is considered as the genetic modifications in the structures or functions of crop plants to improve the ability to survive and reproduce under drought (Kramer, 1980). It is generally believed that better breeding efforts and investments have been made under drought-prone environments to improve drought tolerance for over half a century (Srivastava, 1987; Cattivelli *et al.*, 2008). Despite the assumptions and logical expectations, however, it is hardly possible to say that, in relation to the situations under non-stressed areas, these efforts have modernized the production of crops in drought-prone environments and boosted the productivity as desired. Therefore, the limitations and strategic implications of past experiences made to develop drought tolerant crop cultivars needs to be synthesized in order to formulate better strategies and approaches in the future. The main purpose of this paper is to review the efforts made, the technical difficulties associated with breeding crop cultivars for drought tolerance as causes of limited breeding success, and draw lessons useful to design future breeding strategies to be followed for improving adaptation of crop cultivars to drought-prone environments. It is believed that this review will enhance the efforts underway to meaningfully adopt plant breeding for improving crop production in the face of the changing climate.

Scope and impacts of drought

It is estimated that about 26% of the arable land worldwide is in the drought-prone areas (Singh, 2002). At regional levels, FAO (1995) made assessments on the relative proportion of drylands based on length of growing season. With this criterion, areas with a growing season of less than 75 days have been categorized as 'arid drylands', while those with 75 to 119 days are classified as 'semi-arid drylands'. Africa, with a total dryland (arid and semi-arid) area of 25% excluding South Africa, has the second largest proportion of dry lands in the world preceded only by Central America with 28%. In sub-Saharan Africa, 40% of the total land area is predominantly arid or semi-arid (Leisinger and Schmitt, 1995). In Ethiopia, for instance, the area coverage under drought-prone zones accounts for 55%, and nearly 40% of the population lives in these zones (EMA, 1988).

The impact of drought is very severe particularly in Africa where it is aggravated by ecological imbalance (nutrient exhaustion, soil erosion, depletion of water resources, over exploitation of natural vegetation and environmental catastrophes), fragile and destructive agricultural production and excessive population growth (Leisinger and Schmitt, 1995). The continent is the most liable to potential risks of environmental degradation and desertification (Kumar and Rowland, 1993). The situation is expected to be rather worsening with time due to further environmental degradation by the increasing population pressure. For instance, about 4 million ha of forest lands are annually cleared in sub-Saharan Africa alone (McWilliam, 1986). Not all drought result in failures of crop production depending on the ability of nations to adjust to the situation and technologies and alternatives available. It is evident that the impact of drought is even worst in developing countries in general and

Africa in particular as agriculture is very subsistent, and the economic potentials of the farmers cannot permit shouldering the risk. Most of the major famines in Africa, of course, aggravated by civil war, were mainly due to drought whereas an equivalent drought in the developed nations might not have resulted in famine at all as the economy can easily absorb the shocks (Ceccarelli *et al*., 2004).

Reports indicate that relatively recent droughts alone affected hundreds of millions of people in Africa including Ethiopia (Leisinger and Schmitt, 1995). Food production growth in sub-Saharan Africa is only around 1.5% while the population is currently growing by around 3% annually, and an increase of 4-5% in food production, which is more than twice the increases in the recent decades, is necessary in order to reduce poverty and adequately feed the ever-increasing population (Quinones *et al*., 1997). The wider scope and the tremendous negative impacts of drought in developing countries show that food security is totally unsustainable without increases in yield in marginal environments, especially drought-prone areas, as 80% of agriculture worldwide is rain-fed (Lorieux, 2005) and a significant portion of the rain-fed production is in drought-prone areas (Singh, 2002).

Mechanism of drought tolerance in crop plants

Drought is considered as a multidimensional stress affecting plant cellular process, growth, development and economic yield formation through alteration in metabolism and gene expression (Abdelmula, 1999; Singh, 2002). The effect of drought is particularly critical at flowering because of reduced pollen viability and poor stigma receptivity and seed formation (Poehlman and Sleper, 1996). Crop plants have drought tolerance mechanisms which, broadly speaking, involve physiological or biochemical responses that minimize tissue dehydration or allow metabolism despite dehydration or mechanisms of pre-adaptation to future stress (Aspinall, 1980). Drought tolerance in crops comprises of three important mechanisms, namely: drought escape; dehydration avoidance; and dehydration tolerance.

Drought escape is the situation whereby a variety may perform well in a drought environment simply by completing its life cycle before the period of drought. Short growth duration is advantageous in environments with terminal drought stress but late flowering plants may also escape or recover from early drought stress (Singh, 2002). Some scientists do not consider drought escape as a "true" tolerance mechanism (Poehlman and Sleper, 1996) may be because an otherwise drought susceptible cultivar may also perform under drought environment simply due to lack of coincidence between the active growing season of the cultivar and the drought period (Singh, 2002).

Dehydration avoidance refers to the ability of plants to retain a relatively higher level of hydration under conditions of soil or atmospheric water stress (Singh, 2002). The important features include deep root system (increased water uptake), stomatal closure, leaf rolling and waxy substance on the leaf surface (reduced water loss) and osmotic adjustment to lower the osmotic potential (Poehlman and Sleper, 1996; Singh, 2002). In some cases, the deposition of wax cover within and over the cuticle may affect leaf reflectance which in turn may affect net radiation and leaf temperature (Singh, 2002). In other cases, the concentration of abscisic acid may increase in response to drought. Water stress is somehow sensed by roots which then begin to synthesis abscisic acid and this is transported *via* xylem from roots to leaves and somehow affects stomatal closure, reduction in leaf expansion and promotion of root growth (Singh, 2002).

The mechanism of dehydration tolerance comprises stabilities in membrane, protein and chlorophyll and membrane repair and cell elasticity (Singh, 2002). It is normally a general trend that when cells loose turgor and dehydrate, there is reduced chemical activity of water, increased concentration of solutes and macromolecules, and alteration in cellular membrane (Singh, 2002). The ability of some plants to continue metabolizing at low leaf water potential, and to maintain growth and development despite dehydration of the tissue, or recover after release from drought stress conditions is a drought tolerance mechanism (Poehlman and Sleper, 1996). Examples of different mechanisms of drought tolerance in different crops are summarized on Table 1.

Breeding philosophies for drought tolerance

Efforts have been made to establish baseline information as a prerequisite for breeding drought tolerant crop cultivars. The genetic controls of traits related to drought tolerance have been found to be complicated, ranging from oligogenic for characteristics like leaf waxy bloom and abscisic acid and proline accumulation to polygenic for most of the other characters (Poehlman and Sleper, 1996; Singh, 2002) with both additive and dominant gene effects (Singh, 2002).

Estimates of heritability and genetic gains from selection are available for only some attributes of drought tolerance, and there are inconsistencies among reports on their magnitude. Some researchers believe that heritability and genetic variance usually decrease under abiotic stresses and, hence, the expected genetic gains from selection are lower under stressed than under non-stressed environments (Rosielle and Harblin, 1981; Hawtin, 1982; Simmonds, 1991; Banziger and Edmeades, 1997; Singh, 2002). There are also other group of reports indicating that there is no interrelationship between the type of the environment (yield level) and the magnitude of heritability in respective crops they studied (Ceccarelli and Grando, 1996).

The magnitude of heritability, according to the latter, is rather affected by the nature of the genetic material under consideration than it is affected by the environmental factors. The level of association between grain yield and its components is also usually lower under drought stressed than non-stressed conditions (Singh, 2002). Fortunately, the existence of genetic variation for drought tolerance has been demonstrated in landraces, cultivated varieties and wild relatives of many crops (Poehlman and Sleper, 1996; Singh, 2002). Landraces (Ceccarelli, 1994) and wild relatives (ICAR, 1993; Poehlman and Sleper, 1996; Singh, 2002) have already proved extremely useful in breeding for drought tolerance. That the significant portions of the centers of origin and the primary and secondary centers of diversity are located in drought-prone areas in the developing countries of the world (BANRC, 1993; Poehlmand and Sleper, 1996) could also be considered as a noble opportunity to be exploited. Nevertheless, the task would not be easy as the utilization of the wealth of genetic sources of drought tolerance has been constrained by undesirable linkages, while the probability of recovering genes for tolerance is very low in cultivated varieties (Singh, 2002). Due, may be, to these and other complexities, there is no one breeding philosophy commonly followed, and breeders follow different approaches in crop breeding for drought tolerance.

Table 1. Summary of various mechanisms of drought tolerance and the component traits in a few sample crops

Mechanism of drought tolerance	Means of drought tolerance	Component traits	Example (s)	References
Drought escape	Completing life cycle before the on-set of drought	Early maturity	Wheat, Haricot bean	Poehlman and Sleper, 1996; Tilahun *et al*., 2004
	Better reproductive synchrony	Short anthesis-silking (ASI) interval	Maize	Banziger *et al*., 1998; Sari-Gorla *et al*., 2004
Dehydration avoidance	Reduced transpiration	Stomatal sensitivity	Cotton	Singh, 2002
		Reduced leaf angle and rolling	Rice, Haricot bean	Singh, 2002; Tilahun *et al*., 2004
	Osmotic adjustment	Stomatal closure	Maize, wheat	Poehlman and Sleper, 1996; Dass *et al*., 1997
		Waxy membrane	Wheat	
		Proline accumulation	Barley, Brassica, maize	Aspinall, 1980; Dass *et al*., 1997; Singh, 2002
		High leaf sugar content	Maize	Aspinall, 1980; Dass *et al*., 1997
	Increased water uptake	Increased root depth	Sorghum, rice, oat, wheat, maize, Haricot bean, Rape seed	Richards and Thurling, 1978; Poehlman and Sleper, 1996; Singh, 2002; Tilahun *et al*., 2004
		Increased root xylem diameter	Wheat	Singh, 2002
Dehydration tolerance	Recovery after stress	Seedling survival	Maize, sorghum	Poehlman and Sleper, 1996
	Plant growth	Early vigor under stress	Wheat, sorghum, Haricot bean	Poehlman and Sleper, 1996; Singh, 2002; Tilahun *et al*., 2004
	Staygreen	Low leaf senescence at grain filling	maize	Dass *et al*., 1997

Defect removal vis-à-vis recombination breeding

Defect removal, as described by Donald (1968), involves elimination of specific limiting traits. Breeding efforts to remove defects should not go far away from the areas of past success but rather they should build on the past successes. The conversion of the otherwise well adapted varieties for simply inherited traits like leaf waxy bloom and abscisic acid and proline accumulation into their tolerant versions through incorporation of missing desirable genes using the backcross technique. On the other hand, recombination breeding may involve a series of (multiple) crossing or (transgressive) recombination in order to bring different desirable traits from two best parents into a single genetic background.

Defect removal may be the best strategy whenever it is the possibility not only in terms of time saving but also in terms of effectiveness and efficiency as one of the parents is already adapted but this method is less common for breeding drought tolerant varieties because drought tolerance is not only polygenic but also conditioned by multiple traits (Singh, 2002). Then again, the application of recombination breeding may also need the best parents to pre-exist for best-is-by-best recombination. If best parents do not pre-exist, starting breeding works just from the scratch to develop such parents for drought tolerance may take a longer time and/or ultimately show lesser probability of success to generate good results.

Defect removal breeding usually results in the genotype of the adapted parent except for the gene being transferred whereas recombination breeding results in a new genotype with equal contribution of chromosome from both parents with complementary characters.

Direct vis-à-vis indirect selection environments

The concept of direct and indirect selection environments was first suggested by Falconer (1960) and later used in several investigations related to the determination of optimum selection environments in crops (Ceccarelli, 1989; Ceccarelli and Grando, 1996; Banziger and Edmeades, 1997; Banziger *et al.*, 1997; Banziger and Lafitte, 1997). Direct selection may refer to a kind of selection made directly under the target production environment or under simulated condition as the target environment. Indirect selection, conversely, refers to selection made under distinctly different environment from the actual target production environment, but still to improve productivity under the latter; for example, selection under good moisture level to improve productivity under drought condition.

To determine the efficiency of selection under favourable environments for improving performance under unfavourable target environments, the procedure assumes a character measured in two different environments not as one but as two characters with genetic correlation between them since the physiological mechanisms and the genes required for high performance may be different. If the genetic correlation between them is high, then performances in two different environments represent nearly the same character, determined nearly by the same set of genes. If it is low, however, the characters are likely to differ to a great extent, and high performance requires a different set of genes (Falconer, 1989). The mathematical details of determining efficiencies of direct and indirect selection environments are presented elsewhere (Gemechu Keneni *et al.*, 2001). It is still debatable whether selection under more favourable condition is likely to result in better yields than if selection were done under stress condition (Rosielle and Harblin, 1981; Hawtin, 1982). There is a tendency of preference among breeders to work under favourable condition at the expense of the unfavourable ones because heritability and genetic variance usually decrease under stressed condition and the expected genetic gains from selection are, therefore, less than that at under favourable conditions (Rosielle and Harblin, 1981; Simmonds, 1991; Banziger and Edmeades, 1997; Singh, 2002).

Possibilities to forecast the performance of genotypes under one condition on the basis of that obtained under another can assist breeders in allocation of the scarce resources, and to decide whether to develop varieties for wide or specific adaptation and in recommending their final release. However, many studies claimed to have proved the concept that cultivars selected under favourable environments also suit to the unfavourable ones including drought-prone environments does not have sufficient scientific background (Ceccarelli, 1989; Ceccarelli and Grando, 1996; Banziger and Edmeades, 1997; Banziger *et al.*, 1997; Banziger and Lafitte, 1997). Many of such varieties developed under potential conditions have also failed to succeed under drought (Ceccarelli, 1989; Reijntjes *et al.*, 1992; Ceccarelli and Grando, 1996) because it is practically impossible to collect together genes responsible for superior performance in all environments into a single genotype (Annicchiarico, 2002).

There are also some reports with compromising ideas as far as the concept of direct and indirect selection environments are considered. The use of “intermediate” environments as primary selection sites was suggested as a good alternative over either selection at high or low yielding environments (Allen *et al.*, 1978), but there is no clear criterion to determine the intermediateness of a given environment. Testing of varieties under both stressed and non-stressed conditions could be one of the stable options to create alternative varieties that suit both conditions, but the cost of germplasm evaluation would obviously be greatly increased.

Empirical vis-à-vis analytical breeding approaches

Selection applied on one character to improve another character is termed as indirect selection (analytical or reductionist approach), whereas selection for the ultimate product like grain yield is called direct selection (the so-called "empirical or traditional" approach). Reports from studies to establish the comparative yield advantages from empirical and analytical methods of selection do not appear to follow a simple trend as there are conflicting results.

The analytical approach emanates from the concept that heritability and genetic variance of grain yield are typically lower under stress *versus* non-stress conditions (Rosielle and Hamblin, 1981). As a result, direct selection for yield *per se* is often not sufficiently effective as yield is a complicated character more polygenic than its components (Lawes *et al.*, 1983). The use of secondary traits positively associated with grain yield and that are genetically variable and highly heritable is advisable under such conditions (Edmeades *et al.*, 1997; Edmeades *et al.*, 1998) when yield is the ultimate expression of these traits. Despite lower heritability and genetic variance of grain yield under stress, it is assumed that heritability and genetic variation of some secondary traits may remain high and at the same time the traits may maintain good level of favourable correlation with grain yield (Bolanos and Edmeades, 1996; Banziger and Lafitte, 1997). Nevertheless, most of the recent reports confirm that it is not sufficient for a breeder to identify secondary traits as determinants of grain yield but the relative efficiency of indirect selection for these determinants over selection for grain yield *per se* must be systematically quantified (Banziger and Edmeades, 1997; Banziger and Lafitte, 1997; Banziger *et al.*, 1997) as shown in Wricke and Weber (1986) and Gemechu Keneni and Mussa Jarso (2002). The genetic expression of different traits and the extent and pattern of their relationship with grain yield may also vary with changes in the environment (Rosielle and Harblin, 1981; Hawtin, 1982; Lawes *et al.*, 1983; Singh, 2002; Simmonds, 1991; Banziger and Edmeades, 1997; Banziger and Lafitte, 1997), and some traits may become more influential to grain yield than others with changes in intensity and timing of drought stress (Richards, 1987; Edmeades *et al.*, 1998).

The empirical approach, on the other hand, is based on the concept that direct selection for grain yield has been a very successful approach to be considered as the only dependable route to improve yields under drought (Richards, 1987). However, direct selection for grain yield may not be possible in the early stages of segregating materials in breeding nurseries where the breeder is forced to select individual plants on the basis of their phenotypic performance for yield attributes (Singh, 2002).

The ideotype breeding approach

The concept of ideotype breeding was first suggested by Donald (1968). An ideotype may be defined as a hypothetical plant frame or architecture described in terms of characters that can exploit available resources efficiently to produce maximum economic yield (Chahal and Gosal, 2002). Selection in this case is totally based on yield components (Smith, 1987; Singh, 2002). However, the desirability of a trait may be environment specific, and a common ideotype may not suit all environments (Saxsena and Sinha, 1987) as the genetic expression of different traits and the extent and pattern of their relationship with grain yield normally vary with changes in the environment (Lawes *et al.*, 1983). Some traits may become more influential to grain yield than others with changes in intensity of stress as stated above (Richards, 1987). The traits to be considered in the ideotype breeding approach are generally morphological, physiological, biochemical, anatomical, phenological or their combinations (Singh, 2002). While the theory of ideotype breeding itself is attractive, the required characterization of "model" components for the target environment has been difficult to achieve as different genotypes may give the same yield through different yield component pathways (Smith, 1987).

The concept of "component optimization"

This approach supplements the analytical approach which assumes that indirect improvement of a yield-contributing trait would result in a higher yield. Each component trait, for a given level of expression, must compete and compromise with all the other traits sharing photosyntates which has only a "constant capacity". In relation to the analytical approach which deals with a single or a few components of a complex system, the component optimization approach rather deals with the holistic plant system. According to this concept, superior cultivars are required to have favourably balanced level of combination of component traits that maximize the system functioning for optimal use of the growth factors (Wallace and Yan, 1998). This concept recognizes that optimal combination of component traits exists for different environments. Even though the concept is theoretically appealing, particularly for breeding in predictable environments with minimal temporal and spatial variability, the optimum combination of the component traits will shift with changes in the level of growth resources and with alteration in genetically and physiologically established optimal level of even one of the traits (Wallace and Yan, 1998). For instance, cultivars constituted for terminal drought may not be tolerant when the drought stress comes early in the growing season or when it comes in the middle of the season (Ceccarelli *et al.*, 2004).

Challenges associated with breeding for drought tolerance

Breeding efforts to combine better adaptation under drought-prone environments with reasonable yield and other desirable traits have been underway for long periods of time (Srivastava, 1987, Cattivelli *et al.*, 2008). Extensive efforts were made by different actors including those under the Consultative Group for International Agricultural Research and by the National Agricultural Research Systems. Some authors rather believe that better efforts were made under drought stress than they were under non-stressed environments (Richards, 1987). The cultivars released in different countries for drought-tolerance, mostly of the escaping types, are too many to be listed but it is yet hardly possible to say that these efforts have resulted in varietal breakthrough as such, and boosted productivity under drought-prone environments as desired because of technical difficulties encountered in making major advances. The difficulties associated with breeding crop cultivars for drought tolerance as compared to breeding for optimal conditions are discussed in the following sub-sections (Table 2).

Complexity of the problem

Drought is a complicated phenomenon which is technically difficult to exhaustively address for many reasons. First, multitude of causes like the amount and the distribution of rainfall, soil water storage capacity, potential evapo-transpiration and crop phenological and development stages contribute to the occurrence of drought (Njoroge *et al.*, 1997). Second, drought seldom occurs alone in isolation from other environmental stresses. It is associated with many other biotic and abiotic stresses like temperature extremes, diseases and low nutrient deficiencies (Ceccarelli *et al.*, 2004). Crops exposed to drought will, at the same time, be faced with other biotic and abiotic stresses that modify the response to moisture stress resulting in temporal variability of grain yields per location (Ceccarelli *et al.*, 2004). One of the major challenges to the plant breeder is, therefore, to develop cultivars that tolerate not only drought as such but also along with multiple associated biotic and abiotic stresses. While developing drought tolerant cultivars itself is sufficient to complicate the task of plant breeding, it is rather worsened by the interaction with the associated stresses (Ceccarelli *et al.*, 2004). Third, drought-prone areas are also characterized with low-input agricultural production owned by resource-poor farmers (de Boef *et al.*, 1996; Ceccarelli *et al.*, 2004). Once drought occurs on marginal areas of the resource-poor farmers, where not only environmental fluctuations are great but also the economic potential of the farmers is unlikely to absorb the shocks, the consequence will be very severe. And fourth, not only the physical environment but also the price ratios between external inputs and farm outputs may not allow the use of the required level of purchased inputs, especially agro-chemicals to control the associated biotic and nutrient deficiency stresses (de Boef *et al.*, 1996).

Inconsistency in pattern of drought scenarios

Drought does not mostly follow a consistent pattern of occurrence, and there is high temporal and spatial variability (Srivastava, 1987; Leisinger and Schmitt, 1995) in terms of severity, timing and duration of stress (Ceccarelli *et al.*, 2004). Evidences show that rainfall distribution can more adversely influence crop productivity than the total amount received in the growing season (Frere *et al.*, 1987). Rainfall distribution pattern may follow different scenarios, but the most important ones in parts of Africa include early, intermittent, terminal and a sort of continuous drought throughout the growing season (Tilahun *et al.*, 2004). Therefore, cultivars successful in one dry year may fail in another, or cultivars tolerant to terminal drought may not be tolerant to intermediate drought, or to drought occurring in early season (Ceccarelli *et al.*, 2004). That is may be why some scientists like Ceccarelli *et al.* (2004) considered drought as a "moving target" that is difficult to address through breeding for neither specific nor wide adaptation.

High genotype by environment interaction

Genotype by environment interaction effects are greater under stressed environments relative to the non-stressed ones (Rosielle and Hamblin, 1981; Buddenhagen and Richards, 1988; Singh, 2002). The tropical and sub-tropical regions of the world, where abiotic stresses particularly drought is a common phenomenon, are characterized by great geographical diversity, resulting in a high level of environmental variation (de Boef *et al.*, 1996). Among the unique features of countries like Ethiopia is the high spatial and temporal variation in environmental factors (EMA, 1988). In situations with high environmental variation, the differential response of genotypes to varying environments, will be high (Falconer, 1989; van Oosterom *et al.*, 1993) including at quantitative trait loci (QTL) levels (Hayes *et al.*, 1993; Ceccarelli, 1997; Mussa and Gemechu, 2003).

High level of genotype by environment interaction hinders progress in breeding programs and complicates the task of plant breeding as a whole (Ceccarelli and Grando, 1996). Genotype by environment interaction effects is not heritable and, hence, the higher the interaction effects, the lesser will be the level of success from selection. When genotypes perform consistently across environments, breeders are able to effectively evaluate germplasm with a minimum cost in a few environments for ultimate use across wider geographic area. However, with high genotype by environment interaction, genotypes selected for superior performance under one set of conditions may perform poorly under different environmental conditions (Romagosa *et al.*, 1996; Ceccarelli, 1997; Singh, 2002).

Table 2. Comparison of breeding crop cultivars for drought stressed and non-stressed conditions

Parameter of Comparison	Non-stressed Environments	Stressed environments	Reference(s)
Risks and uncertainties	More predictable	Less predictable	Singh, 2002
Achievements (genetic gain from selection)	Dramatic	Gradual and steady	Rosielle and Hamblin, 1981; Buddenhagen and Richards, 1988; Singh, 2002
Genotype x environment interaction	Low	High	Campbell and Lafever, 1980; Fox and Rosielle, 1982; Yau *et al*., 1991; van Oosterom *et al*., 1993
More appropriate breeding approach	Wide adaptation/ centralized breeding	Specific adaptation/ decentralized breeding	de Boef *et al*., 1996; Ceccarelli *et al*., 2004
Complexity of target production problems	Lower	Higher	Njoroge *et al*., 1997; Ceccarelli *et al*., 2004
Impact of plant breeding	A "panacea"	Just a means of coping	Singh, 2000; Annicchiarico, 2002
Breeding priority	High yields (yield maximization)	Yields stability (risk minimization)	Richards, 1987; Coffman and Smith, 1991; Ceccarelli *et al*., 2004
Preferred cultivars	Commercial cultivars (highly uniform)	Improved natural population or landraces (genetically diverse)	Agrios, 1978; Simmonds, 1979; de Boef *et al*., 1996; Singh, 2002
Risk of genetic vulnerability (if genetically uniform cultivars are used)	Lower	Higher	Agrios, 1978; Simmonds, 1979; de Boef *et al*., 1996; Singh, 2002
Breeding versus management	Environment better being altered to fit the cultivars	Cultivars better adapted to fit the environment	Coffman and Smith, 1991; Ceccarelli *et al*., 2004
Parents in Hybridization	Breeders should focus on a few parents of early success story	Breeders should not depend on a few parents	Russel, 1978; Singh, 2002

Genotype by environment interaction is particularly important when the environments for which breeding is targeted are completely different from the environments where selection and evaluation are made (van Oosterom *et al.*, 1993). Evidence of change in rank order for performance of genotypes across different environments and years, or the existence of a cross-over type of interaction is believed to be an indicator of significant genotype by environment interaction (Ceccarelli and Grando, 1996; Ceccarelli, 1997).

High risk of genetic vulnerability

Basically, plant breeding as a science seems to evolve towards genetic uniformity. The current technical innovations in breeding procedures like plant tissue and pollen cultures, for instance, aid the efficient development of genetically uniform cultivars (Snape, 1989; Zhang, 1989). Varietal uniformity offers substantial economic advantages to growers, processors, packers and consumers under non-stressed condition in developed countries. Breeding, variety registration and seed certification procedures in the tropics are also influenced by experiences from breeding in temperate areas despite the fact that both production (for mechanization) and utilization (for consumers' preference) aspects demand uniformity in temperate areas (Banziger *et al.*, 1998).

Crop production characterized by genetic diversity under abiotic stress is normally stable as compared to those characterized by genetic uniformity (Simmonds, 1979; de Boef *et al.*, 1996), even though there is no as such new plant breeding techniques encouraging genetic diversity. It is well established that narrow genetic base of the cultivated varieties is the direct cause of genetic vulnerability, and the susceptibility of cultivars to drought (in this case) (Singh, 2002), in risky environments (Agrios, 1978; Simmonds, 1979; de Boef *et al.*, 1996; Singh, 2002). Normally, natural populations may suffer from natural calamities but they are still genetically more flexible to adapt themselves or to evolve with the calamities while commercial cultivars are genetically uniform that their population is less flexible to do so (Simmonds, 1979; de Boef *et al.*, 1996). Natural population has either low genotype by environment interaction, enabling it to perform under both stressful and optimal conditions or, in a mixed population, genotype substitution may occur, such that plants which fail to produce under one set of conditions yield well under different conditions (de Boef *et al.*, 1996). One good example of genetic vulnerability due to the use of narrow genetic base in drought areas is the failures of hybrid maize as compared to traditional cultivars in Zimbabwe in response to dry years in the mid 1980's (Reijntjes *et al.*, 1992).

Low genetic gain from selection

We should not anticipate dramatic results from breeding efforts in drought-prone areas, but only small gradual changes should be expected (Buddenhagen and Richards, 1988). The development of suitable genotypes to marginal areas in general and drought-prone environments in particular may not provide the required productivity levels as lower genetic gains expected from selection under such circumstances (Rosielle and Hamblin, 1981; Buddenhagen and Richards, 1988; Singh, 2002) may limit yield improvements. Generally, plant breeding is not a "panacea", and initiatives like the Green Revolution technologies were not as useful under dryland conditions as they were under non-stressed ones (Singh, 2000; Annicchiarico, 2002). As the number of population is growing at an alarming rate in developing countries where drought is the main production constraint, it is obvious that there is a continued and steadily increasing demand for food in many countries, and plant breeders also aspire to meet this demand (de Boef *et al.*, 1996). However, the level of genetic gain from crop improvement under marginal conditions in general and drought in particular put at risk the desire to double or triple productivity in order to feed the increasing population (Woldeyesus and Chilot, 2002).

Limited knowledge of genetic and physiological bases of drought tolerance

A better understanding of the genetic and physiological bases of crop adaptation under drought-prone condition is of particular importance as baseline information to breeders. The generation of baseline information related to the genetic and physiological bases of drought tolerance in crop cultivars has received increasing attention during the last tens of decades. A number of conference proceedings, review and journal articles and books have been presented more on the basic aspects. The genetic possibilities for the improvement of tolerance to drought in crops have been shown by a number of authors (reviews by Srivastava *et al.*, 1987; Poehlman and Sleper, 1996; Singh, 2002) including at molecular level (Sari-Gorla *et al.*, 2004). A number of stress physiologists have also claimed to have investigated physiological and biochemical basis of drought tolerance (reviews by Turner and Kramer, 1980; Srivastava *et al.*, 1987, Tilahun *et al.*, 2004). Nevertheless, such efforts generated only piecemeal of information that do not give full insight into the whole-plant processes and functioning systems as a single entity (Wallace and Yan, 1998). For instance, even though it is well known that the effects of drought on crop growth and development may be revealed at both cellular and plant levels (Sinha, 1987; Singh, 2002), the relationship between cellular effects of drought and those observed at plant level are not clearly established (Singh, 2002).

Overcoming the challenges of breeding for drought tolerance

Classification of drought-prone environments for cultivar development

The genetic developments of stable genotypes that perform consistently across all sets of drought-prone environments seem to be a sound strategy in terms of practical feasibility and cost. However, this concept is bound by some technical limitations with the current state of knowledge. First, there is no way breeders can identify stable genotypes from among the segregating materials or germplasm in the nursery just from the scratch as it is only after certain genotypes are selected and tested in multiple environments (spatially and temporally) that sufficient data could be available for stability analysis. Even if that were possible, it may also be difficult to develop varieties universally suitable across highly diversified environmental conditions. What the breeder could feasibly do under such conditions, with still all the limitations and uncertainties, is to first group the test environments into fairly similar categories.

The environment for which breeding is undertaken should be clearly defined and systematically classified into similar categories to reduce the magnitude of genotype by environment interaction within a "tolerance range" for stability analysis, and thereby increase gains from breeding efforts (Collaku *et al.*, 2002). When the genotype by environment interaction is a cross-over type, it means that the environments are distinctly different, and they do not represent one another in terms of variety generation (van Oosterom *et al.*, 1993). Grouping of the test environments into fairly similar categories should be made with a representative number of "test cultivars" having relatively better stability for performance across drought-prone environments. This is because it is not only the degree of diversity between the test environments that influences the magnitude of genotype by environment interaction but also the confounding effects from the diversity in the test genotypes (Simmonds, 1979; Cleveland, 2001). In cases of high genotype by environment interaction with representative number of stable cultivars, to the extent that it causes rank order changes among the genotypes, there is no scientific base to select varieties under one environment to indirectly improve productivity under another (Ceccarelli and Grando, 1996).

Classification of drought-prone environments should mainly be based on crop biological responses, climatic data and edaphic factors. The main climatic factor in environmental classification is amount and distribution of rainfall, even though altitude and temperature may also be considered. Alternatively cluster analysis can be used based on the similarity of crop biological responses, climatic data and edaphic factors (Campbell and Lafever, 1980; Fox and Rosielle, 1982; Yau *et al.*, 1991; van Oosterom *et al.*, 1993). The schematic presentation of one possible environmental classification strategy appropriate where low, moderate and high genotype by environment interaction prevails is given in Figure 1. The detailed mathematical aspect is beyond the scope of this review paper.

Fitting the growing period of the crop genotypes to the probable period of moisture availability under different scenarios through genetic manipulation is absolutely essential. For terminal stress, for instance, developing crop cultivars for earliness or cultivars that can complete their lifecycle before the on-set of terminal moisture stress could be one option. Cultivars with high water use efficiency at the early stage of development and those that can fairly distribute throughout their lifecycle can also be targeted. Cultivars that can continue with growing and yielding only with residual moisture at the later stage could also be considered in case of terminal moisture stress. With early drought where rainfall is sufficient at the later stages of crop growth, selection may be based on modest moisture requirement for early establishment and vegetative growth and high requirement at the reproductive stage. Similarly, where rainfall is intermittent or low throughout the growth period, cultivars with fast recovery from wilting after drought or those with minimal moisture requirement throughout their lifecycle may be required. On the other hand, growing crop cultivars out of their niches could cause over exploitation of water resources and yet result in yield penalty.

Maintaining broad genetic base in cultivars

The reduction of genetic diversity at intra-varietal level is considered as the most important cause of genetic vulnerability. A number of authors suggested that the practice of deliberately leaving some variability in varieties has biological advantages in that it offers more stability, and hence, protection against climatic fluctuations (Simmonds, 1979; BANRC, 1993; de Boef *et al.*, 1996; Singh, 2002) due to better buffering effects (Simmonds, 1979; BANRC, 1993). Currently, the habit of pushing varieties for release under stress environments to a state of extreme uniformity by modern plant breeding has been criticized (Simmonds, 1979; de Boef *et al.*, 1996; Singh, 2002). It is rather believed that uniformity is not biologically necessary or even desired while diversity can, at least sometimes, enhance performance and stability (Simmonds, 1979). Several other reports also indicated the dangers inherent in the increasing use of uniform cultivars under stress, and suggested that emphasis should be given to the maintenance of diversity in some planned fashion (Simmonds, 1979; de Boef *et al.*, 1996; Singh, 2002).

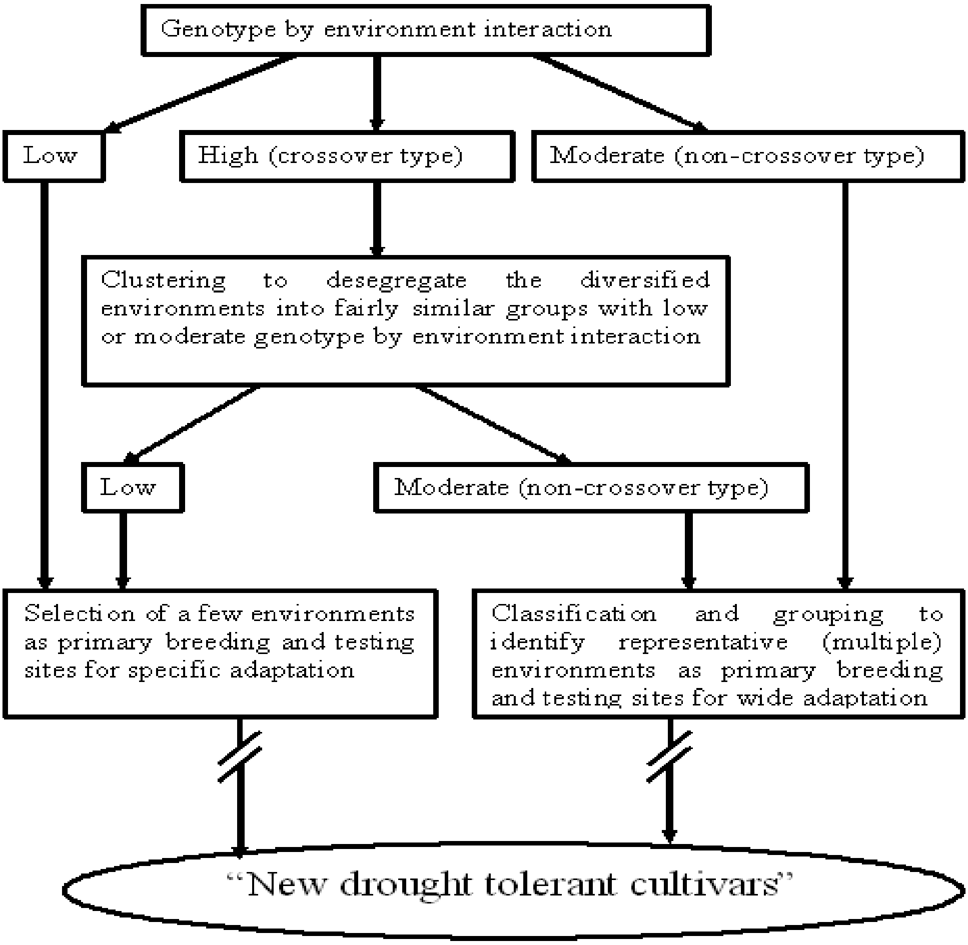

Figure 1. Schematic presentation of one possible environmental classification strategy appropriate where low, moderate and high genotype by environment interaction prevail (the broken points of the bottom arrows stand for a series of yield trials and variety release procedures)

A wide range of breeding strategies may be employed to maintain variability within crop cultivars and minimize the consequent risks of genetic vulnerability. Variability may be maintained by stopping purification, while there is still some residual heterogeneity left or by mixing late generation lines selected after homogeneity (Simmonds, 1979). Varieties developed through mass selection would have considerable genetic variation because several similar looking plants which are variable for quantitative traits are selected and bulked (Singh, 2002). The use of multiline varieties in self-pollinated crops, each pure line component of the multiline having different tolerance genes, may be expected to tolerate diseases and insect pests attack and environmental fluctuation better than their pure line components, and reduce the severity of losses since one or a few of the component lines is expected to become vulnerable at a time (Simmonds, 1979; Welish, 1981; BANRC, 1993; Singh, 2002).

It is a comparative advantage that abiotic stresses including drought do not co-evolve with cultivars of crop plants as it is the case for biotic stresses, and there is less probability that tolerance being broken after the wide spread of cultivars. It should be borne in mind during the constitution of multi lines that plants morphologically look alike can be quite different genetically, and the reverse may also be true (de Boef *et al.*, 1996). Successful examples of multiline varieties were reported from different countries (Simmonds, 1979; Frey, 1982; Singh, 2002) with a merit of stress-determined modification through withdrawal of susceptible components and replacement with new tolerant lines (Wolfe and Barrett, 1977). A recent work in Kenya clearly showed that deliberately maintaining some level of variation in varieties turned out to be an important prerequisite for high grain yield in sorghum grown under drought stress (Haussmann, 2000). The dangers of genetic uniformity can also be avoided if plant breeders use different sources of genes (inter-parental diversity) in their breeding materials, and it would certainly be dangerous to rely too much on any one individual source of tolerance to stresses in developing future varieties (Russel, 1978; Singh, 2002).

Decentralized breeding for specific adaptation

The breeding objectives for drought-prone areas must quite be different from those in the non-stressed areas. This emanates from differences in the objectives and priorities of crop production in the two areas. The objective of crop production in the potential areas is to increase production and productivity through the use of yield-increasing technologies like high-yielding varieties and agro-chemicals (de Boef *et al.*, 1996). Then again, there is no doubt that reasonable yields with fewer risks are preferable than high yields with high risks to the resource-poor farmers living under highly vulnerable condition, and risk aversion, rather than yield maximization, must be the top priority. In such areas, a process in which cultivars are adapted to fit the environment instead of the environment being altered to fit the cultivars is crucial for the development of sustainable agriculture (Coffman and Smith, 1991; Ceccarelli *et al.*, 2004).

Traits of interest to the resource-poor farmers in the marginal areas include yield stability and tolerance to stresses and low dependence on the external inputs (de Boef *et al.*, 1996). Farmers achieve these by deliberately creating genetic diversity at intra-varietal and/or inter-specific levels (Weltzien and Fischbeck, 1990; Broerse and Visser, 1996; de Boef *et al.*, 1996). Breeding activities to address this group of farmers should, therefore, build on farmers' practices to complement them and not to substitute their practices (Bunders *et al.*, 1996). Landraces have already proved extremely useful in breeding programs conducted for marginal areas including the drought-prone ones (Ceccarelli, 1994). In the marginal areas where problems of diseases, insects and environmental fluctuations and, hence risks are great, specific adaptation to local circumstances, rather than broad adaptation, ensures varieties that are more closely situated to the physical environment, producer's needs and enhance genetic diversity in a given area (de Boef *et al.*, 1996; Ceccarelli *et al.*, 2004). This is partly because unfavourable environments are more variable (both temporally and spatially) than the favourable ones (Ceccarelli *et al.*, 2004), and there is more cross-over type of genotype by environment interaction under unfavourable environments than there is under the favourable ones (Ceccarelli and Grando, 1996; Ceccarelli, 1997).

Effective screening and selection techniques

The efficiency of techniques of screening and selection is highly essential for the success of a plant breeding program. Procedure that can discard undesirable germplasm in early generations adds efficiency and cost effectiveness to the variety improvement efforts (Srivastava, 1987). As no one set of selection procedures fits all arid and semi-arid areas, the available techniques for each situation must be evaluated to select the best and to develop the most appropriate one (Smith, 1987; Srivastava, 1987; Ceccarelli *et al.*, 2004). There is a need to develop screening methodologies that result in high precision and consistent progress from selection. The efficiency of breeding under uncontrolled field condition *versus* controlled field condition, the critical stages of exposure of crops to the drought stress under different scenarios and the interaction of drought with other stresses like low soil fertility levels should also be taken into consideration in formulation of efficient techniques. Recently, the use of QTL based marker-assisted selection has also shown promise in a number of crops (Sari-Gorla *et al.*, 2004; Lorieux, 2005).

Use of modern biotechnological tools

Conventional plant breeding approaches have tried to address the problems associated with drought but, unlike the non-stressed environments, the conventional approaches failed to meet their expectations under drought conditions (Richards, 1987). As food security is still totally unsustainable without yield increases in marginal environments (Lorieux, 2005), agricultural researchers as a whole are historically confronted with the challenge of bridging the radically widening gap between the demand and supply for food and feed. The recent advances in biotechnology, defined as a wide array of technologies that include techniques that use living organisms or substances from these organisms to make or modify a biological product for specific uses, enabled breeders to move desirable genes from different parents into a single genotype including from distantly related wild species with more precession. Even if biotechnological tools should not be viewed as a sole technological “magic-bullets” for a quick-fix of problems related to drought as it was initially thought to be (Poehlmand and Sleper, 1996), it is hoped that they should help further understanding of the scientific bases of drought tolerance in crop cultivar development and, together with conventional breeding approach in the identification of desired genes in related and unrelated species and efficiently incorporate these genes into the cultivars of interest (Poehlmand and Sleper, 1996; Singh, 2002). There are some model achievements of biotechnological tools in breeding for drought tolerance. These tools have been utilized in DNA fingerprinting in identification of cultivars, marker assisted selection and to a limited level for genetic modification in breeding for drought tolerance (Bunders *et al.*, 1996; Banziger *et al.*, 1998; Singh, 2002). A few practical examples for advanced-level use of biotechnology for drought tolerance breeding are given on Table 3.

Table 3. Examples of the application of biotechnological tools in crop cultivar development for drought tolerance

Crop	Biotechnological tools used	Achievements	References
Maize	DNA fingerprinting of populations and parental lines	Several populations and lines have been characterized	Banziger *et al*., 1998
	Mapping QTL for ASI and use of MAS	Drought tolerant populations or lines developed	Beck *et al*., 1996; Banziger *et al*., 1998; Sari-Gorla *et al*., 2004
Tobacco	Transformation by transferring the gene encoding protein production isolated from soybean	Drought tolerant tobacco cultivar	Singh, 2002
	Transformation for a transgene *osm* (osmoregulatory gene from bacteria)	Drought tolerance increased as a result of increased osmotin accumulation	Slater *et al*., 2003
Tobacco, rice, soybean	Transformation for a transgene *Moth bean P5CS*	Drought tolerance increased as a result of increased proline accumulation	
Rice	Transformation for a transgene *betA*	Drought tolerant rice cultivar	
Rape seed	Transformation for a transgene *cox*	Drought tolerant rape seed cultivar	

Conclusions

Drought is among the real challenges to agricultural researchers and development workers in general and to plant breeders in particular. Past efforts towards development of drought tolerant crop cultivars, in addition to the generation of considerable baseline scientific information, had only limited success in terms of crop varietal breakthrough relative to the achievements made under non-stressed environments. Among the major reasons for this are the various technical challenges inherently associated with breeding for drought tolerance.

It is undeniable that breeders have specific strategies and approaches to breeding crop cultivars for drought tolerance. Even then, there are methodological components that need to be refined and optimized with time in terms of both biological procedures (breeding philosophies and detailed procedures) and the physical components (optimum selection and test environments) under specific situations.

Overall, strengthening concerted efforts would be indispensable as much remains the subject of future investigation in understanding genetic and physiological bases underlying drought tolerances in a holistic manner at physiological, biochemical and molecular levels, concerted efforts to better understand the phenomenon at whole-plant level must be continued with more collaboration among different disciplines. Particularly the efforts of physiologists to understand plant responses to drought, efforts of plant breeders to beneficially change responses of plants to water stress and agro-climatologists to characterize the test environments should be balanced and integrated.

In conclusion, the current methods and approaches need a systematic refinement and optimization under specific situations in a holistic and integrated manner by best reconciling optimal plant and environment related factors that contribute to breeding efficiency. Some methodologies could be centrally formulated at conceptual level at least for the most important crops and under the most important scenarios in the dry areas and then utilized under specific situations after specific amendments are made. We believe that the technical problems and the solutions raised and discussed here in this paper worth considering in developing drought tolerant cultivars.

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