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Breeding for drought tolerance in vegetables

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Abstract : Drought or moisture stress is one of the most significant environmental stresses causing huge loss to the agriculture worldwide. Vegetables are more sensitive to drought as compare to many other crops. Improving yield under drought is a major goal of plant breeding. An understanding of genetic basis of drought tolerance is a pre-requisite for plant breeders to evolve superior genotype through conventional breeding methodology. Drought is often accompanied by relatively high temperatures, which promote evapotranspiration and affects photosynthetic kinetics, thus intensifying the effects of drought and further reducing crop yields. Traditionally, plant breeders have addressed the problem of environmental stress by selecting for suitability of performance over a series of environmental conditions using extensive testing and biometrical approaches. Progress requires the introduction of traits that reduce the gap between yield potential and actual yield in drought-prone environments. An attempt has been made in this review to compile the scattered information on concepts, genetics, and traditional breeding approaches of drought tolerance with suitable illustrations. A comprehensive list of genes responsible for drought and examples of species and genotypes of vegetables with drought tolerance has also been provided.

Introduction

Moisture stress is one of the greatest environmental factors in reducing yield in the arid and semi-arid tropics. From agricultural point of view, its working definition would be the inadequacy of water availability, including precipitation and soil moisture storage capacity, in quantity and distribution during the life cycle of a crop plant that restricts the expression of full genetic potential of the plant (Sinha, 1986). The ability of a plant to produce its economic product with minimum loss under water deficit environment in relation to the water-constraint-free management is referred as drought tolerance (Mitra, 2001). In other words, drought can be described as a climatic hazard which implies the absence or very low level of rainfall for a period of time, long enough to cause moisture depletion in soil with a decline of water potential in plant tissues. Drought is often accompanied by relatively high temperatures, which promote evapotranspiration and affects photosynthetic kinetics, thus intensifying the effects of drought and further reducing crop yields (Mir *et al.,* 2012). Drought stress is the major abiotic stress for many Indian states *viz.* Rajasthan, parts of Gujarat, Haryana and Andhra Pradesh (Mitra, 2001). About two thirds of the geographic area of India receives low rainfall (less than 1000 mm), which is also characterized by uneven and erratic distributions. Out of net sown area of 140 million hectares about 68 % is reported to be vulnerable to drought conditions and about 50 % of such vulnerable area is classified as 'severe', where frequency of drought is almost regular (http://www.dsc.nrsc.gov.in/). Being succulent in nature, most of the vegetable crops are sensitive to drought stress, particularly during flowering to seed development stage. Moreover, the legume vegetables, for instance cowpea, vegetable pea, Indian beans etc., grown in arid and semi-arid regions are generally affected by drought at the reproductive stage. Cullis (1991) opined that a perceptive of how the interaction of physico-chemical environment reduces plant development and yield will pave the ways for a combination of breeding methods for plant modification to improve tolerance against environmental stresses. Drought stress modifies photosynthetic rate, relative water content, leaf water potential, and stomatal conductance. Ultimately, it destabilizes the membrane structure and permeability, protein structure and function, leading to cell death (Bhardwaj and Yadav, 2012).

Several physiological and biochemical processes essential for plant growth and development are significantly affected by drought stress, and plant develops various defense mechanisms against moisture stress at the molecular, cellular and whole plant levels.

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An understanding of genetic basis of drought tolerance in vegetables is a pre-requisite for plant breeders to evolve superior genotype by adopting conventional breeding methodology. In view of the fact that there is no single mechanism by which stress can be alleviated, this paper shall concentrate on water stress, mainly in terms of drought. Attempt has been made to discuss the concept of drought tolerance, the adaptive mechanisms, traits conferring drought tolerance, and their use in conventional/traditional breeding activities for vegetable improvement.

The concept and mechanism of drought tolerance

Drought is a sustained period of time without significant rainfall (Linsley *et al.*, 1959). Whereas, Quizenberry (1982) suggested that such rainfall deficit does not constitute drought in a crop production system until the water scarcity begins to limit the growth and development of crop plants.

At genetic level, the adaptive mechanisms by which plants survive drought, collectively referred to drought tolerance (Jones *et al.*, 1980), can be grouped into three categories, *viz*. drought escape, drought avoidance and drought tolerance (Fig. 1) (Leonardis *et al.* 2012). However, crop plants make use of more than one mechanism at a time to tolerate drought (Gaff, 1980).

1. Drought escape: The ability of a crop plant to complete its life cycle before development of serious soil and plant water deficits is called as drought escape. This mechanism involves rapid phenological development *i.e.* early flowering and maturity, variation in duration of growth period depending on the extent of water scarcity. For instance, in cow pea early erect cultivars, such as ‘Ein El Gazal’ and ‘Melakh’, have performed well when the rainfall season was short but distinct due to their ability to escape late-season drought (Hall, 2004).

2. Drought avoidance: It refers to the ability of a crop to endure periods without significant rainfall even as maintaining a high plant status at high plant water potential, *i.e.*, dehydration postponement or drought avoidance (Krammer, 1980). In other way, drought avoidance is the ability of plants to maintain relatively high tissue water potential despite a shortage of soil-moisture. Improving the mechanisms of water uptake, storing in plant cell and reducing water loss confer drought avoidance. Drought avoidance mechanisms are associated with physiological whole-plant mechanisms such as canopy tolerance and leaf area reduction (which decrease radiation, adsorption and transpiration), stomatal closure and cuticular wax formation, and adjustments of sink-source relationships through altering root depth and density, root hair development and root hydraulic conductance (Beard and Sifers 1997; Rivero *et al.* 2007).

3. Drought tolerance: The ability of a crop to endure moisture deficits at low tissue water potential or dehydration tolerance (Levitt, 1972). Under drought condition, plants survive through a balancing act between maintenance of turgor with reduction of water loss (Begg and Turner, 1976). Drought tolerance mechanisms are balancing of turgor through osmotic adjustment (solute accumulation in cell), increase in elasticity in cell but decrease in cell size and desiccation tolerance by protoplasmic tolerance (Ugherughe, 1986). In an *in-vitro* study of tomato, cv. PS-10 showed low osmotic potential at all polyethylene glycol (PEG), treatments and thus it turned to be a better drought tolerant cultivar than Roma while cv. Peto and Nora showed average drought tolerance (Aazami *et al.*, 2010).

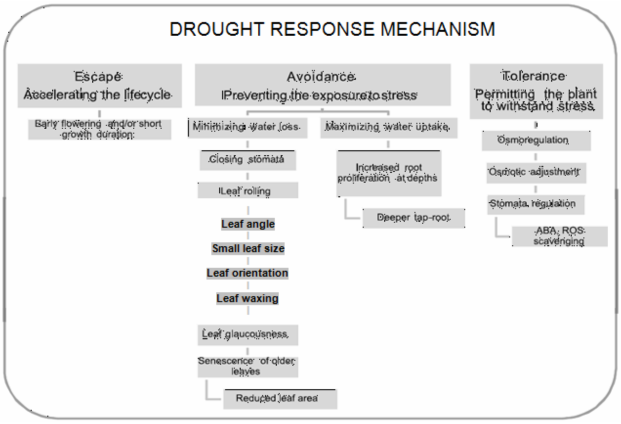

Fig. 1: Response mechanism of drought stress (modified from Leonardis *et al.*, 2012)

Most of drought adaptations have disadvantages as the genotypes of short duration are less productive compared to that of normal duration. The drought tolerance mechanisms conferred by reducing water loss (such as stomatal closure and reduced leaf area) usually result in reduction of assimilation of carbon dioxide (Mitra, 2001). Drought tolerance can be increased through osmotic adjustment by maintaining plant turgor, but the increased solute concentration responsible for osmotic adjustment may have detrimental effect in addition to energy requirement for osmotic regulation (Turner, 1979). Therefore, crop adaptations to drought may be established through a balance between escape, avoidance and tolerance while maintaining adequate productivity.

Genetic mechanism for drought tolerance

Drought tolerance is a complex character, expression of which depends on accomplishment and interaction of various morphological traits *viz.* earliness, reduced leaf area, leaf molding, wax content, efficient rooting system, stability in yield and number of branches; physiological traits *i.e.* transpiration, water-use efficiency, stomatal activity and osmotic adjustment and biochemical traits *i.e.* accumulation of proline, polyamine, trehalose etc., increasing of nitrate reductase activity and storage of carbohydrate. Very little is known about the genetic mechanisms that have room for these characters.

The identification, inheritance and action of genes responsible for morphological and physiological traits in some crops have been reported. Root characters are inherited polygenically (Ekanayake *et al.*, 1985) where the dominant alleles govern long and more numbers of roots while, thick root tip is governed by recessive alleles (Gaff, 1980). Leaf molding (Turner, 1979) and osmotic adjustment (O'Toole and Moya, 1978) have revealed monogenic inheritance. In cowpea, drought tolerance is reported to be governed by a single dominant gene (Mai Kodomi *et al.*, 1999). Besides morphological and physiological changes, biochemical changes involving biosynthesis of compatible solute is another way to impart drought. Under drought stress, plants tends to maintain water content by accumulating various compatible solutes that are non-toxic and do not interfere with plant processes. This includes fructan, trehalose, polyols, glycine betaine, proline and polyamines (Mitra, 2001). The various genes responsible for different enzymes involved in biosynthesis of these solutes have been recognized and cloned from different organisms *i.e.* bacteria, yeast, human and plants. Many stress related genes (Table 1) have been isolated and characterized in the last two decades in a variety of crop species.

Among the horticultural traits, although number of pods per plant had shown good narrow sense heritability and genetic advance under drought, yet leaf water potential appeared to be better indicator for selection criteria owning to higher heritability under drought stress in okra (Ben-Ahmad *et al.*, 2006, Naveed *et al.*, 2009). Thus, chances to find stress tolerant material in segregating populations having high heritability and genetic advance may be higher. Rauf and Sadaqat (2008) reported significant positive relationship of physiological traits with yield in sunflower. Similarly in wheat studies on narrow-sense heritability for excised leaf water losses, relative water content and biomass concluded that high genetic advance for relative water content and excised leaf water loss may be used for direct selection (Farshadfar *et al.*, 2001).

Ahmad *et al.* (2009) found that in cotton additive, dominance and interactions were involved for agronomic (plant height, number of monopodial branches per plant, number of sympodial branches per plant, number of bolls per plant, boll weight, ginning out-turn), fiber quality (staple length, fiber strength, fiber fineness) and physiological traits (relative water content & excised leaf water loss) under drought stress environments.

Screening for drought tolerance

The diversity among the genotypes may serve as primary source for screening against drought stress. Drought tolerance is the interactive result of diverse morphological, physiological and biochemical traits and thus, these components could be used as strong selection criteria to screen out appropriate plant ideotype. Implications of developing an effective screening procedure for drought tolerance have been realized utilizing different procedures (Table 2). Traditionally, plant breeders have addressed the problem of environmental stress by selecting for suitability of performance over a series of environmental conditions using extensive testing and biometrical approaches (Blum, 1988).

Water stress, mostly at critical period of growth may drastically reduce productivity and quality of vegetables (Table 3). Singh and Sarkar (1991) stated that a combination of different traits of direct relevance, rather than a single trait, should be used as selection criteria for drought stress. A corresponding experiment including 46 sugar beet genotypes representing different genetic backgrounds grown in drought and irrigated conditions led to similar results (Ober *et al.*, 2004). Sugar beet genotypes with high yielding capacity when irrigated also tended to perform well under drought and vice versa.

At seedling stage *in vitro* application of PEG is commonly used to stimulate osmotic stress effects in petridishes to control water potential in seed germination. A culture medium supplemented with PEG resulted in highest proline accumulation in tomato cv. Roma (Aazami *et al.*, 2010). A drought tolerant tomato line (IIHR-2274) was identified (Chavan, 2007) on the basis of number of fruits under different moisture stress regime *i.e.* imposing drought after two weeks of transplanting to 11 genotypes with two treatments [depth of irrigation (IW)/ cumulative pan evaporation (CPE) ratio of 0.40 and 1.20] at different phenological stages *viz.* 45, 75 days after transplanting and at harvesting stage (Fig. 2). The quantity of water to be irrigated

Table 1. Genes conferring drought tolerance and their salient features

Genes	Function	Mechanism of action	References
DREBs/CBFs; ABF3	Stress induced transcription factors	Enhanced expression of downstream stress related genes confers drought/cold/salt tolerance. Constitutively overexpression can lead to stunting growth	Oh *et al.* (2005), Ito *et al.* (2006)
SNAC1	Stress induced transcription factor	SNAC1 expression reduces water loss increasing stomatal sensitivity to ABA	Hu *et al.* (2006)
OsCDPK7	Stress induced Ca-dependent protein kinase	Enhanced expression of stress responsive genes	Saijo *et al.* (2000)
Farnesyl-transferase *(ERA1)*	Negative-regulator of ABA sensing	Down-regulation of farnesyltransferase enhances the plant's response to ABA and drought tolerance reducing stomatal conductance	Wang *et al.* (2005)
Mn-SOD	Mn-superoxide dismutase	Overexpression improves stress tolerance also in field conditions	McKersie *et al.* (1996)
AVP1	Vacuolar H^+ - pyrophosphatase	Overexpression facilitate auxin fluxes leading to increased root growth	Gaxiola *et al.* (2001), Park *et al.* (2005)
HVA1; OsLEA3	Stress induced LEA proteins	Over-accumulation of LEA increases drought tolerance also in field conditions	Bahieldin *et al.* (2005), Xiao *et al.* (2007)
ERECTA	A putative leucine-rich repeat receptor-like kinase is a major contributor to a locus for D on Arabidopsis chromosome 2	ERECTA acts as a regulator of transpiration efficiency with effects on stomatal density, epidermal cell expansion, mesophyll cell proliferation and cell–cell contact	Masle *et al.* (2005)
otsA and *otsB*	Escherichia coli trehalose biosynthetic genes	Increased trehalose accumulation correlates with higher soluble carbohydrate levels, elevated photosynthetic capacity and increased tolerance to photo-oxidative damage	Garg *et al.* (2002)
P5CS	d-Pyrroline-5-carboxylate synthetase	Enhanced accumulation of proline leads to increased osmotolerance	Kavi Kishor *et al.* (1995), Zhu *et al.* (1998)
mtlD	Mannitol-1-phosphate dehydrogenase	Mannitol accumulation leads to increased osmotolerance	Abebe *et al.* (2003)
GF14l	14-3-3 protein	Lines overexpressing GF14l have a ''stay green'' phenotype, improved water stress tolerance and higher photosynthetic rates under water deficit conditions	Yan *et al.* (2004)
NADP-Me	NADP-malic enzyme	The overexpression decreased stomatal conductance and improves WUE	Laporte *et al.* (2002)
AREB	bZIP transcription factor in tomato	Overexpression increasing dehydrin expression.	Hsieh *et al.* (2010)
cupida	Leaf necrosis in tomato	Overwilting or stomatal defect	Anonymous (2006)
dehydrin	Increased distances from dehydrins activated by abscisic acid in tomato	Probably the dehydrins protect membranes during stresses. Dehydrins are upregulated by abscisic acid.	Weiss and Cortines (2010)
Chloroplast drought-induced stress protein	Thiol-disulfide exchange intermediate activity in potato	Preservation of the thiol: disulfide redox potential of chloroplastic proteins during water deficit.	Anonymous (2006)
CDSP 32	Thiol-disulfide exchange intermediate activity in potato	Preserve chloroplastic structures against oxidative injury upon drought.	Anonymous (2006)
CDSP 34	Increases in CDSP 34 transcript and protein abundances were also observed in potato plants subjected to high illumination.	The CDSP 34 protein is proposed to play a structural role in stabilizing stromal lamellae thylakoids upon osmotic or oxidative stress.	Beyly *et al.* (1998)
Wilty	Dominant TGRC gene in tomato	Leaves overwilt when drought stressed. Wilting under field or greenhouse conditions; marginal leaf narcrosis.	Anonymous (2006)
Wilty dwarf	Recessive TGRC gene in tomato	Grayish-green, droopy leaves; stunted plants; leaves droop when drought stressed.	Anonymous (2006)
Water stress-induced *ER5* protein	Stress induced CaLEA6 (for *Capsicum annuum* LEA) is 709 bp long with an open reading frame encoding 164 amino acids	Predicted to produce a highly hydrophobic, but cytoplasmic, protein.	Kim *et al.* (2005)
Abscicic acid stress ripening 2	Putative DNA binding and chaperon like activity	A member of the Asr gene family. It is induced by abiotic stress such as water and is expressed in the leaf phloem companion cells.	Giombini *et al.* (2009)

Modified from Cattivelli *et al.* (2008)

Table 2. Screening procedure for drought tolerance

S. No.	Instruments/ techniques used	Screening for the purpose of	References
1	Infrared thermometry	Efficient water uptake	Blum *et al.*, 1982
2	Banding herbicide metribuzin at a certain depth of soil, and use of iodine-131 and hydroponic culture under stress of 15 bar	Root growth	Robertson *et al.*, 1985; Ugherughe, 1986
3	Adaptation of psychometric procedure	Evaluation of osmotic	Morgan, 1980; 1983
4	Diffusion porometry technique	Leaf water conductance	Gay, 1986
5	Mini-rhizotron technique	Root penetration, distribution and density in the field	Bohm, 1974
6	Infrared aerial photography	Dehydration postponement	Blum *et al.*, 1978
7	Carbon isotope discrimination	Increased water-use efficiency	Farquhar and Richards, 1984
8	Drought index measurement	Total yield and number of fruits	Clarke *et al.*, 1984; Ndunguru *et al.*, 1995
9	Visual scoring or measurement	Maturity, leaf molding, leaf length, angle, orientation, root morphology and other morphological characters	Mitra, 2001

Table 3: Critical stages of drought stress and its impact on vegetable crops

Vegetable crops	Critical period for watering	Impact of water stress
Tomato	Early flowering, fruit set, and enlargement	Flower shedding, lack of fertilization, reduced fruit size, fruit splitting, puffiness and development of calcium deficient disorder *i.e.* blossom end rot (BER), poor seed viability
Brinjal	Flowering and fruit development	Reduces yield with poor colour development in fruits, poor seed viability
Chilli and Capsicum	Flowering and fruit set	Shedding of flowers and young fruits, reduction in dry matter production and nutrient uptake, poor seed viability
Potato	Tuberization and tuber enlargement	Poor tuber growth and yield, splitting, internal brown spot
Okra	Flowering and pod development	Considerable yield loss, development of fibres, high infestation of mites, poor seed viability
Cauliflower, cabbage and broccoli	Head/ curd formation and enlargement	Tip burning and splitting of head in cabbage; browning and buttoning in cauliflower
Carrot, radish and turnip	Root enlargement	Distorted, rough and poor growth of roots, strong and pungent odour in carrot, accumulation of harmful nitrates in roots
Onion	Bulb formation and enlargement	Splitting and doubling of bulb, poor storage life
Cucumber	Flowering as well as throughout fruit development	Deformed and non-viable pollen grains, bitterness and deformity in fruits, poor seed viability
Melons	Flowering and evenly throughout fruit development	Poor fruit quality in muskmelon due to decrease in TSS, reducing sugar and ascorbic acid, increase nitrate content in watermelon fruit, poor seed viability
Summer squash	Bud development and flowering	Deformed and non-viable pollen grains, misshapen fruits
Leafy vegetables	Throughout growth and development of plant	Toughness of leaves, poor foliage growth, accumulation of nitrates
Asparagus	Spear production and fern (foliage) development	Reduce spear quality through reduced spear size and increased fibre content, leading to tougher, lower grade spears.
Lettuce	Consistently throughout development	Toughness of leaves, poor plant growth, tip burning
Vegetable pea	Flowering and pod filling	Reduction in root nodulation and plant growth, poor pod filling, poor seed viability
Lima bean	Pollination and pod development	Leaf color takes on a slight grayish cast, blossom drop, poor seed viability
Snap bean	Flowering and pod enlargement	Blossoms drop with inadequate moisture levels and pods fail to fill, poor seed viability
Sweet corn	Silking, tasseling and ear development	Crop may tassel and shed pollen before silks on ears are ready for pollination, lack of pollination may result in missing rows of kernels, reduced yields, or even eliminate ear production, poor seed viability
Sweet potato	Root enlargement	Reduced root enlargement with poor yield, growth crack

Modified from Bahadur *et al.* (2011)

through furrow was measured with the help of V-notch installed at plot head. Accordingly the measured quantity of water was applied to the plots as per the irrigation schedules. It was applied based on IW/CPE ratio, where in IW was maintained constantly at 50 mm. Soon after reaching the particular ratio based on the CPE, irrigation was given to particular treatment. In 0.40 IW/CPE ratio treatment crop was irrigated for every 125 mm of CPE where as in 1.20 IW/CPE ratio irrigation was given for every 41.66 mm of CPE.

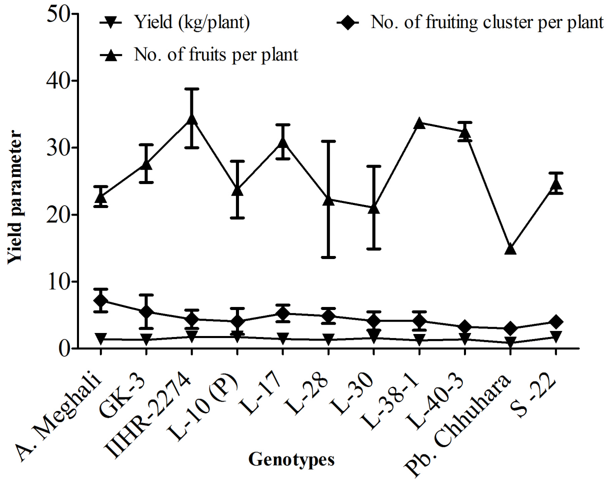

Fig. 2. Yield contributing traits influenced by irrigation levels in tomato

Sources of drought stress tolerant vegetables

Potential sources of drought tolerance species and genotypes of major vegetable crops have been identified in many of the vegetable crops (Table 4). In tomato, water stresses during vegetative growth and later stages have been identified among accessions of the wild species *Solanum chilense* and *S. pennellii* (Rai *et al.*, 2011). The physiological basis of drought tolerance in *S. chilense* was attributed to its deep vigorous root system, similar to those reported for cultivar Red Rock (Stoner, 1972) and a few accessions of *S. pimpinellifolium* (Rana and Kalloo 1989). In contrast to these, the drought tolerant accession LA716 (*S. pennellii*) has a limited and shallow root system and the basis for its drought tolerance is largely due to the ability to conserve moisture in succulent leaves during periods of inadequate moisture. LA716 has also been characterized as having a greater water use efficiency (WUE) under drought stress than *S. esculentum,* as measured by g dry weight (DW) produced per kilogram of water consumed (Martin and Thorstenson, 1988). A high WUE in this accession was attributed to smaller leaf conductance due to fewer and smaller stomata, longer trichomes, lower chlorophyll content and Rubisco activity per unit leaf area, and larger mesophyll cell surface exposed to intercellular air space (Martin *et al.*, 1999). In tomato, most of the commercial cultivars are sensitive to drought stress throughout the ontogeny of the plant, yet genotypic variation for drought tolerance exists within the cultivated (Wudiri and Henderson 1985) and related wild species such as *S. cheesmanii, L. chilense, S. pennellii, S. pimpinellifolium,* and *S. esculentum* var. *cerasiforme* (Pillay and Beyl, 1990). Evaluation of 150 lines of cultivated and wild species of tomato under water-deficit conditions identified a few *S. esculentum* genotypes and a few accessions of *S. pimpinellifolium* and *S. chilense* with drought tolerance attributes (Rana and Kalloo, 1990).

A potential source of drought stress-tolerant traits in *Phaseolus vulgaris* has been reported through interspecific hybridization with *P. acutifolius* (Lazcano-Ferrat and Louatt, 1999). *P. acutifolius* possesses both morphological and physiological characteristics that enable it to complete well its life cycle and yield under hot arid conditions. However, progress in the development of tolerant lines is slow due to the lack of simple traits associated with drought tolerance. Therefore, it is important to identify the characteristic traits associated with pod setting, the number of pods reaching maturity, and the seed yield with the purpose to use as a marker to screen germplasm with drought tolerance (Omae *et al.*, 2005). Trehalose played a role in drought tolerance of rhizobia/legume symbioses, particularly in common beans. Nodulated plants that accumulate only small amounts of trehalose were poor drought-tolerant, whereas those accumulating higher concentrations were more tolerant to drought stress (Farlas-Rodriquez *et al.*, 1998).

Significant differences were observed between genotypes (Table 4). Alpha, Bintje, *Solanum acaule, S. demissum* and *S. stenotonum* were significantly more drought tolerant compared with the other potato genotypes. High levels of drought tolerance were also reported for *S. acaule* and *S. demissum in vitro* and in greenhouse pot trials (Arvin and Donnelly, 2008).

Approaches for drought stress resilience

To develop a drought tolerance variety, the breeding methodology to be applied is the same as for other traits improvement programmes *viz.* bulk and pedigree method could be used for self-pollinated crops and recurrent selection for cross-pollinated crops. Conversely, if transfer of few drought tolerance traits to a high-yielding genotype is the aim, then back cross method is adopted. In contrast, biparental mating (half sib and full sib) maintains the broad genetic base in addition to provides the possibility to evolve the desired genotype of drought tolerance (Yunus and Paroda, 1982). Development and adaptation to drought tolerance in a plant is the result of overall expression of many traits in a specific environment. In view of the fact that many adaptative traits are effective only for certain aspects of drought tolerance and over a limited range of moisture stress, there is no single trait that plant breeders can use to improve productivity of a given crop under drought stress. Hence, alternative potential systematic approach

Table 4. Drought tolerant species and genotypes of vegetables

Sl. No.	Vegetable Crops	Drought tolerant genotypes/species	References
1	Tomato	*S. habrochaites* (EC- 520061), *S. pennelli* (IIHR 14-1, IIHR 146-2, IIHR 383, IIHR 553 , IIHR 555, K-14, EC-130042, EC-104395, Sel-28), *S. pimpinellifoloium* (PI-205009, EC- 65992, PanAmerican), *S. esculentum* var. *cerasiforme, S. hirsutum, S. cheesmanii, S. chilense, S. habrochaites, S. sitiens*	Rai *et al.* (2011)
		Arka Vikas, RF- 4A	Singh (2010)
		L. pennellii (LA0716), *L. chilense* (LA1958, LA1959, LA1972), *S. sitiens* (LA1974, LA2876, LA2877, LA2878, LA2885), *S. pimpinellifolium* (LA1579)	Razdan and Mattoo (2007) Symonds *et al.* (2010)
2	Brinjal	*S. microcarpon, S. gilo S. macrosperma, S. integrifolium,* Bundelkhand Deshi	Rai *et al.* (2011)
		S. sodomaeum (syn. S. linneanum)	Toppino *et al.* (2009)
		SM- 1, SM- 19, SM- 30, VioletteRound, Supreme	Kumar and Singh (2006)
3	Chilli	*C. chinense*, *C. baccatum* var. *pendulum*, *C. eximium*	
		Arka Lohit, IIHR - Sel.-132	Singh (2010)
4	Potato	*S. acaule*, *S. demissum* and *S. stenotonum,* Alpha, Bintje	Arvin and Donnelly (2008)
		S.ajanhuiri, S.curtilobum, S.xjuzepczukii Kufri Sheetman	Ross (1986)
		Solanum chacoense, Kufri Sindhuri	Pandey *et al.* (2007)
5	Okra	*A. caillei, A. rugosus, A. tuberosus*	Charrler (1984).
6	Onion	*Allium fistulosum, A. munzii,* Arka Kalyan, MST 42, MST 46	Singh (2010)
7	French bean	*P. acutifolius*	Kavar *et al.* (2011)
8	Water melon	*Citrullus colocynthis (L.) Schrad.*	Dane *et al.* (2007)
9	Cucumber	INGR-98018 (AHC-13)	Rai *et al.* (2008)
10	Winter Squash	*Cucurbita maxima*	Chigumira and Grubben (2004)
11	*Cucumis Spp.*	*Cucumis melo var. momordica* VRSM- 58, INGR-98015 (AHS-10), INGR-98016 (AHS-82), CU 159, CU 196	Rai *et al.* (2008), Kusvuran (2012), Pandey *et al.* (2011)
		Cucumis pubescens, INGR-98013 (AHK-119)	
		Cucumis melo var. *callosus,* AHK- 200, SKY/DR/RS-101	
		Cucumis melo var. chat, Arya	
		Cucumis melo, SC- 15	
12	Cassava	CE-54, CE-534, CI-260, CI-308, CI-848, 129, 7, 16, TP White, Narukku-3, Ci-4, Ci-60, Ci-17, Ci-80	Singh (2010)
13	Sweet potato	VLS6, IGSP 10, IGSP 14, Sree Bhadra	Singh (2010)

is to pyramid a number of traits in one genotype which can be helpful for the improvement for its drought tolerance. Some of the key traits for breeding for drought tolerance [*e.g.* phenology, rapid establishment, early vigor, root density and depths, low and high temperature tolerance, ^{13}C discritunation (a measure of the extent to which photosynthesis is maintained while stomatal conductance decreases), root conductance, osmoregulation, low stomatal conductance, leaf posture, reflectance and duration, and sugar accumulation in stems to support later growth of yield components] are important traits for breeding point of view. However, priority should be given to those traits which can maintain stability of yield in addition to overall yield, because traits for higher yield may, in fact, decrease yield stability *e.g.* longer growth period (Parry *et al.*, 2005). Therefore, for the evolvement of an improved drought tolerant high yielding variety, it is necessary that the variety should have short life span (drought escape), well-developed root system, high stomatal tolerance, high water use efficiency (drought avoidance), and increased and stabilized yield during water stress period (drought tolerance). Although a number of crop cultivars tolerant to drought stress have been developed through this method, this approach has been partly successful because it requires large investments in land, labor and capital to screen a large number of progenies and variability in stress occurrence in the target environment (Athar and Ashraf, 2009). For drought tolerance, three breeding approaches have been proposed. The first approach is to breed for high yield under optimum (irrigated) condition where the maximum genetic potential of yield is expected to be realized in optimum condition with a high positive association for performance in optimum and stress conditions (Johnson and Frey, 1967). The basic philosophy of this approach is that where a genotype performs better under optimum level will also yield comparatively well in drought stress condition. Genotype × environment (G × E) interaction may restrict the performance of high-yielding genotype under drought condition, therefore, the second approach, *i.e.* to breed under actual drought condition has been recommended (Hurd, 1971). However, the relative expression of optimum genetic potential in the two extreme conditions may not always fit good for most of the traits. The desired goal to develop high yielding drought-tolerant genotype may be achieved through simultaneous selection in non-stress environment for yield and in drought condition for stability. Moreover, the major drawback of second approach is that the intensity of drought is vastly variable from year to year and as a consequence environmental selection pressure on breeding materials changes drastically from generation to generation. This situation is compounded with lower heritability and makes the breeding activities slower and complicated (Roy and Murty, 1970).

An alternative strategy to the above two approaches would be to improve drought tolerance in high yielding genotypes through integration of breeding methods based on morphological and physiological mechanisms of drought tolerance. Improving the yield potential of an already tolerant genotype may be a more promising approach, provided there is genetic diversity in such material (Bidinger *et al.*, 1995). Evolving a high-yielding potential variety along with drought stress through conventional breeding is usually carried out either through stability analysis to evaluate the response of the components of yield to stress (Fischer and Sanchez, 1979) or by incorporating traits that contribute directly, or indirectly, to yield stability (Sadras and Connor, 1993). Utilization of available genetic variation at inter-specific, intra-specific and intra-varietal levels is of prime importance for selection and breeding for enhanced tolerance to any kind of stress (Ashraf and Sharif, 1998; Serraj *et al.*, 2005). Several selection indices based on anatomic, physiological and biochemical criteria for breeding drought tolerant varieties are being employed *e.g.*, seed yield, harvest index, shoot fresh and dry weight, leaf water potential, osmotic adjustment, accumulation of compatible solutes, water use efficiency, stomatal conductance, chlorophyll fluorescence (Ashraf *et al.*, 2007; Neumann, 2008) and therefore strategy for developing elite material against drought is basically inclined towards the physiogenetic approach.

Physiogenetic approach

The degree of drought stress severity can be seen on plants by symptoms and effects on physiological metabolisms and yield. Many symptoms of drought stress are clear such as leaf rolling (Kadioglu *et al.*, 2012), molding, yellowing (chlorosis), browning and wilting. At the physiological level, drought stress alters the complete physiology and metabolism of plants. The physiologically relevant indicators of drought effects are the water content and the water potential of plant tissues (Jones, 2007). Which in turn, depend on the relative fluxes of water through the plant within the soil-plant-atmosphere continuum. The physiogenetic approach basically depends upon the hypothesis that yield and drought tolerance are different traits governed by different genes and gene systems (Turner, 1986). Some of the researchers argue that if yield and drought are to be handled independently, the degree of independence for any individual tolerance mechanism must be evaluated (Blum *et al.*, 1983). A physiological approach has an advantage over empirical breeding for yield *per se* because it increases the probability of crosses resulting in additive gene action for stress adaptation, provided that the germplasm is characterized more thoroughly than for yield alone (Reynolds and Trethowan, 2007). Consequently, even a negative correlation between yield and drought tolerance can be exploited, since potential yield is never realized under drought (Danquah and Blay, 1999). To maximize the impact of specific traits, breeding strategies requires a detailed knowledge of the environment where the crop is grown, genotype × environment interactions and fine tuning the genotypes suited for local environments, *e.g.*, in drought environments, osmotic adjustment, accumulation and remobilization of stem reserves, superior photosynthesis, heat- and desiccation-tolerant enzymes, etc. are important physiological traits (Mir *et al.*, 2012). Water stress significantly decreases leaf chlorophyll concentrations, plant growth, fruit yield but increases membrane permeability in eggplant grown to the fruiting stage. The severe water stress treatment reduces the fruit yield by 66% compared to control although, high water stress can lower nutrient levels in the leaves (Kirnak *et al.*, 2001).

In tomato, polyphenols play a significant physiological role in water-stress tolerance, and moderate water stress can induce shikimate pathway. Therefore, greater synthesis of phenolic compounds and the presence of flavonoids would be key in the protection against damage caused by water stress (Sánchez-Rodríguez *et al.*, 2011).

Relationship between carbon accumulation and the transpired water volume and the associationship between harvest index and post-anthesis water use imply that yield is strongly dependent on biomass accumulation after anthesis in water-limited environments (Passioura, 1977; Tanner and Sinclair, 1983). Moreover, the contribution of pre-anthesis assimilate can be significant to yield under drought stress condition (Blum *et al.*, 1983; Turner and Nicholas, 1988). In sunflower, pre-anthesis assimilate played an important role in seed filling under water stress condition where the stems were seems to be the foremost reserve structures (Sadras *et al.*, 1993). Furthermore, accumulation of solutes within cells resulting in osmotic adjustment lowers the osmotic potential and helps maintain turgor pressure of shoots and roots under water stress environment. This results to turgor-driven processes *i.e.* stomata opening and expansion of growth to continue at reduced rates to gradually lower potentials (Ludlow, 1987). Seed yield is also contributed by osmotic adjustments by increasing the amount of water transpired and by minimizing the reduction in harvest index (Ludlow *et al.*, 1990). This attribute confers adaptation to drought stress, and there is some evidence that a minor gene may be influencing the expression of osmotic adjustment (Basnayake *et al.*, 1995). Physiological traits relevant for the responses to water deficits and/or modified by water deficits span a wide range of vital processes (Table 5). The different crop developmental stages show different sensitivity to drought stress.

Grafting tools for drought tolerance breeding

The stionic effect (effect of root stock on scion and vice versa) has been used for various prospects of biotic and abiotic tolerant breeding programme for a long time. Several effective rootstocks have been mentioned and are used in breeding programs (Schwarz *et al.,* 2010). Sanders and Markhart (1992) reported that the osmotic potential of dehydrated scions of grafted bean (*Phaseolus vulgaris* L.) plants was determined by the rootstocks, while the osmotic potential of non-stressed scions was governed by the shoot. Drought tolerance provided by either the rootstock or the scion resulted in enhanced nitrogen fixation in soybean (Serraj and Sinclair, 1996). Experimental results did not confirm the advantage of eggplants when used as a rootstock for tomato (Abadelhafeez *et al.*, 1975). Grafted mini-watermelons onto a commercial rootstock (PS 1313: *Cucurbita maxima* Duchesne × *Cucurbita moschata* Duchesne) revealed a more than 60% higher marketable yield when grown under conditions of deficit irrigation compared with ungrafted melons (Rouphael *et al.*, 2008). In tomato, ungrafted cv. Zarina and grafted cv. Josefina × Zarina again registered the highest differences for these ratios, and therefore appear to present a greater capacity to eliminate reactive oxygen species.Grafted plants achieve greater tolerance to water stress apparently by developing a better antioxidant system, which in turn leads to better overall plant development. When shoots were of the drought tolerant genotype, Zarina, the changes in antioxidant enzyme activities were large and consistent. However, when shoots were of the drought sensitive genotype Josefina, the antioxidant enzyme activities were more limited and the oxidative stress was evident. Therefore, grafting on specific rootstocks more adapted to water stress conditions may be a tool to improve crop quality under artificially imposed mild water stress (Sánchez-Rodríguez *et al.*, 2012). Thus, selective stocks and scion can be effectively used for improving the antioxidant response in tomato under water stress.

Mutation breeding for drought stress

Ronde and Spreeth (2007) used γ-irradiation to obtain a high frequency of gene mutation and chromosomal alterations. Irradiation dosages between 0 and 300 Gy were applied in order to determine the optimal irradiation dose of 180 Gy. Mature plants of M1-M4 generation were screened in a rain-out shelter and physiological traits for drought stress were identified. Roots of mature plants were also assessed and the variation observed could be correlated with drought tolerance. Six mutant cowpea lines were included in a physiological screening experiment that was conducted on greenhouse plants (Ronde and Spreeth, 2007). The results demonstrated that the mutant line 217 performed very well in terms of relative water content, free proline concentration and yield. Two Cuban tomato varieties (INCA 9-1 and Amalia) were irradiated by ^{60}Co γ-rays at doses of 300 and 500 Gy (Gonzalez *et al.*, 2005). Selection was made for genotypes of high yield, large fruit, disease tolerance and fruit quality. In M6 generation, evaluation was conducted under water stress conditions for (Fig. 3) 60 plants of each of the best mutant lines, four of them from INCA 9-1 variety and three from Amalia variety.

Due to the environmental uncertainties especially drought stress faced by crop, the primary objective will be to optimize confined management practices to reduce severe stress as far as possible and, in particular, to intensify the search for genotypes/ lines which show higher resilience in the face of a given environmental stress. There is a need for evaluating how combination of traits influences plant water status and growth which may usefully bridge physiology and breeding into the integrated programme of crop improvement for drought management. The growing threat of dwindling water resources demands germplasm that carry drought tolerance and water-use efficiency. Research must combine the latest genomics resources including quantitative genetics, genomics along with physiological and biochemical understandings of the interactions between crop plant genotypes and the growing environment for better management of drought stress.

Table 5. Response of physiological traits to drought conditions

Plant traits	Effects relevant for yield	Modulation under stress	References
Stomatal conductance/leaf temperature	More/less rapid water consumption. Leaf temperature reflects the evaporation and hence is a function of stomatal conductance	Stomatal tolerance increases under stress	Jones (1999), Lawlor and Cornic (2002)
Photosynthetic capacity	Modulation of concentration of Calvin cycle enzymes and elements of the light reactions	Reduction under stress	Lawlor and Cornic (2002)
Timing of phenological phases	Early/late flowering. Maturity and growth duration, synchrony of silk emergence and anthesis, reduced grain number	Wheat and barley advanced flowering, rice delayed, maize asynchrony	Slafer *et al.* (2005), Richards (2006)
Anthesis-silking interval (ASI) in maize	ASI is negatively associated with yield in drought conditions	Drought stress at flowering causes a delay in silk emergence relative to anthesis	Bolanos and Edmeades (1993), Edmeades *et al.* (2000)
Starch availability during ovary/embryo development	A reduced starch availability leads to abortion, reduced grain number	Inhibition of photosynthetic activity reduces starch availability	Boyer and Westgate (2004)
Partitioning and stem reserve utilization	Lower/higher remobilization of reserves from stems for grain-filling, effecting kernel weight	Compensation of reduced current leaf photosynthesis by increased remobilization	Blum (1988), Slafer *et al.* (2005)
Stay green	Delayed senescence	-	Rajcan and Tollenaar (1999)
Single plant leaf area	Plant size and related productivity	Reduced under stress (wilting, senescence, abscission)	Walter and Shurr (2005)
Rooting depth	Higher/lower tapping of soil water resources	Reduced total mass but increased root/shoot ratio, growth into wet soil layers, re-growth on stress release	Hoad *et al.* (2001), Sharp *et al.* (2004)
Cuticular tolerance and surface roughness	Higher or lower water loss, modification of boundary layer and reflectance	-	Kerstiens (1996)
Photosynthetic pathway	C3/C4/CAM, higher WUE and greater heat tolerance of C4 and CAM	-	Cushman (2001)
Osmotic adjustment	Accumulation of solutes: ions, sugars, poly-sugars, amino acids, glycinebetaine	Slow response to water potential	Serraj and Sinclair (2002)
Membrane composition	Increased membrane stability and changes in aquaporine function	Regulation in response to water potential changes	Tyerman *et al.* (2002)
Antioxidative defense	Protection against active oxygen species	Acclimation of defence systems	Reddy *et al.* (2004)
Accumulation of stress-related proteins	Involved in the protection of cellular structure and protein activities	Accumulated under stress	Ramanjulu and Bartels (2002), Cattivelli *et al.* (2002)

Source: Adopted from Cattivelli *et al.* (2008).

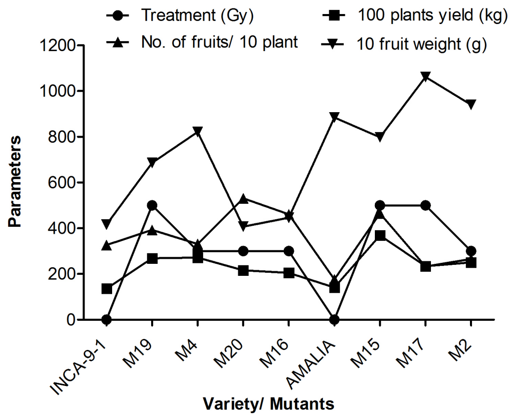

Fig. 3. Performance of variety and their mutant lines under drought conditions in tomato

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