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Review

Physiological mechanisms and conventional breeding of sweet potato (*Ipomoea batatas* (L.) Lam.) to drought-tolerance

Rukundo Placide[1,2]*, Hussein Shimelis[1], Mark Laing[1] and Daphrose Gahakwa[2]

[1]African Centre for Crop Improvement, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, Pietermaritzburg, South Africa.
[2]Rwanda Agriculture Board (RAB), P. O. Box 5016, Kigali-Rwanda.

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The paper is aimed at highlighting the physiological mechanisms associated with breeding of sweet potato towards drought tolerance. It describes important aspects including: the effects of drought stress, mechanisms of adaptation of crops to drought stress, drought stress on sweet potato, inheritance of drought tolerance, methods of screening and breeding of sweet potato for drought tolerance. The literature summarized in this paper may serve as important guideline in sweet potato breeding towards drought-tolerance.

Key words: Breeding, drought-tolerance, genetics, physiology, sweet potato.

INTRODUCTION

Sweet potato (*Ipomoea batatas* (L.) Lam.) is an important crop worldwide which is cultivated in more than 110 countries on an estimated area of 8.5 million ha. The annual global production of sweet potato is estimated at 106.5 million metric tons of which 15% is from East and Central Africa. Nine African countries namely Uganda, Nigeria, Tanzania, Angola, Burundi, Mozambique, Madagascar, Rwanda and Ethiopia are among the top 15 sweet potato producers in the world (Table 1). The other six are China, Indonesia, Viet Nam, India, USA and Japan (FAOSTAT, 2010).

Sweet potato is a cheap source of β-carotene, polyphenolic components, carbohydrates and other nutrients. The orange flesh sweet potato varieties are an important source of β-carotene which is the major provitamin A carotenoid (Chassy et al., 2008) while the purple fleshed sweet potato varieties are rich in anthocyanins and other polyphenolic components (Teow et al., 2007; Steed and Truong, 2008). The level of β-carotene and anthocyanin in sweet potato is as high as in carrot juice, pumpkin, Vaccinium species such as blueberry, cranberry and bilberry, and red cabbage (Woolfe, 1992; Steed and Truong, 2008). The sweet potato storage roots are a major source of energy due to their high carbohydrate content which ranges between 80 to 90% of their dry weight. These carbohydrates consist mainly of starch, sugars and a low quantity of pectin, hemicelluloses, and cellulose (Lebot, 2009). Sweet potato is also a source of vitamins C and B6, mineral salts and fibres (Woolfe, 1992; Chassy et al., 2008). Due to its high nutritional value, sweet potato has multiple uses.

Sweet potato is grown mainly for food, with 50% of production in Asia and 85% in Africa (Scott and Ewell, 1993). Sweet potato consumption per capita per year is estimated to be 112 kg in Africa, 16 kg in Asia 18 kg, in

*Corresponding author. E-mail: rukundoplacide@yahoo.fr. Tel: +250786112423 / +27783930397.

Table 1. The major fifteen sweet potato producing countries with total production and productivity.

S/N	Country	Total production (tonnes)	Productivity (tonnes/ha)
1	China	81175660	22.037
2	Uganda	2838000	4.577
3	Nigeria	2703500	2.896
4	Indonesia	2051050	11.327
5	United Republic of Tanzania	1400000	2.917
6	Viet Nam	1317060	8.716
7	India	1094700	9.207
8	United States of America	1081590	22.863
9	Angola	986563	5.796
10	Burundi	966343	6.903
11	Mozambique	920000	7.077
12	Madagascar	919127	7.125
13	Japan	863600	21.753
14	Rwanda	840072	7.488
15	Ethiopia	736349	9.013

Source: (FAOSTAT, 2010).

Oceania, 2 kg in America, < 0.5 kg in Europe, 147 kg in Rwanda, 120 kg in Burundi and 88 kg in Uganda (Chassy et al., 2008; FAOSTAT, 2010). It is consumed in different forms. Consumption pattern varies within countries by regions and by income of the population group. Humans can consume sweet potato roots, young leaves and the tips of stems as vegetables. Most rural poor consumes boiled or baked sweet potato roots, while people with more economic means tend to eat sweet potato roots as fried chips or as a snack food (Woolfe, 1992). In many rural areas, sweet potato is mostly used as food and feed by small-scale farmers.

The roots, by-product of roots and vines of sweet potato are commonly used as feed for cattle, pigs, goat, sheep and rabbit (Woolfe, 1992). In 2007, about half of all sweet potato production in the world was used for animal feed (Lebot, 2009). For this purpose, it is used as a raw material or ingredient in the feed processing industries (Gupta et al., 2009). Studies have shown that sweet potato is a valuable forage containing nutrients that can support acceptable growth of livestock (Kariuki et al., 1998; Aregheore, 2004; Gupta et al., 2009). Therefore, the mixture of sweet potato forage with poor quality fodder has been suggested to sustain the growth of livestock and to increase the availability of animal products for human consumption (Aregheore, 2004).

In spite of the economic value of sweet potato, its production is limited by drought stress in many tropical regions (Lebot, 2009). The yield reduction due to drought stress was estimated at 60% (Van Heerden and Laurie, 2008). Under field experiment, it was observed that drought stress for 20 days during the critical growing stage decreased yield by 15 to 39% of sweet potato (Gong and Wang, 1990). Moreover, insect pests and viral diseases were reported to be very severe in drought conditions (Fuglie, 2007). Irrigation agriculture is an ideal and practical solution to overcome drought in crop production. However, farmers do not have access to irrigation water and infrastructures. Moreover, allocation of clean water for irrigation is a big challenge because of exponential increase of population and the current global climate change.

Therefore, the sustainable solution to improve sweet potato production is to develop and deploy drought tolerance varieties. Breeding for drought tolerance requires knowledge on the physiological mechanisms involved in drought tolerance and the genetic control of yield and its components (Subbarao et al., 2005). Molecular breeding techniques may improve the response of selection to drought tolerance. However, their efficiency greatly depends on the availability of linked physiological and morphological traits (Subbarao et al., 2005). Further, it has been observed that the degree of expression of physiological and phenotypic traits varies depending on severity of drought stress and genotypes (Yang et al., 1991). Therefore, the objective of this paper is to review the physiological mechanisms and breeding for drought-tolerance in sweet potato. The review may assist to design breeding strategies of sweet potato for drought-tolerance.

EFFECTS OF DROUGHT STRESS

Drought is an extended period of dry weather characterized by a shortage of water supply to plants (Acquaah, 2007). In drought conditions, a water potential (Ψw) of soil becomes negative because of a concentration increase of soil solutes. The movement of cell water is determined by the water potential gradient

($\Delta\Psi w$) that acts as a driving force for transport through a permeable cell membrane (Taiz and Zeiger, 2006). A plant can continue to absorb water only if its Ψw is lower than of the soil. Drought stress requires changes in plant cells and tissues to adapt to drought stress condition and continue to acquire little available water of soil (Bartels and Sunkar, 2005). Symptoms of drought stress start when crop has used between 50 and 80% of extractable soil moisture (Acquaah, 2007) and the failure of plant to absorb the remaining soil water has severe consequence.

Water plays a crucial role in the life of plant and its availability is a main factor that determines the plant population in the environment (Coley et al., 2009). Water is the main constituent of plant tissues but its quantity varies within plant tissues and plants species. The water content was estimated at 80 to 95% in masses of growing tissues, 85 to 95% in vegetative tissues, 35 to 75% in wood with dead cells, and at 5 to 15% in dried seeds (Taiz and Zeiger, 2006).The distribution of plant species in the environment is associated with their tolerance to environmental stresses (Brenes et al., 2009). It was observed that the most widespread plant species are drought tolerant (Baltzer et al., 2008; Brenes et al., 2009). A low temperature was suspected to be the main limiting factor of life in the Antarctic environment. However, it was found that the water deficit is the major life threatening cause with a positive correlation observed between the soil moisture and the abundance of organisms in this environment (Kennedy, 1993).

Drought is the primary abiotic stress that affects crop production and food availability globally. In many developing countries, agriculture depends on rainfall which in many cases does not meet the crop need (Ober, 2008). The limited occurrence, amount, and uneven distribution of rain affect growth and productivity of crops. Eventually this causes famines in many semi-arid countries (Acquaah, 2007). Drought can cause the biggest loss in crop production compared to other isolated biotic or abiotic stress factors (Boyer, 1982; Ober, 2008). It affects crop production by reducing the genetic potential of a plant (Mitra, 2001). Consequently, it is responsible of the difference between the mean yield and the yield potential of a crop and the cause of the yield instability in time (Sorrells et al., 2000).

Drought induces physiological, biochemical and molecular changes that have consequences on crop growth and productivity (Reddy et al., 2004). The drought osmotic stress causes the removal of water from the cytoplasm to the extracellular space and cell dehydration (Bartels and Sunkar, 2005). Water deficit affects the photosynthesis ability of plants by changing the content and components of chlorophyll, reducing the net CO_2 uptake by leaves and by decreasing activities of enzymes in the Calvin cycle (Becana et al., 1998; Cornic, 2000; Gong et al., 2005; Lawlor and Tezara, 2009). The osmotic stress of water deficit inhibits strongly the growth of leaves and stem of plants. This has negative effects on the yield potential of the crop (Westgate and Boyer, 1985). However, the degree of growth inhibition and yield reduction depends on the duration and intensity of drought stress and the genotypes of crop species (Monakhova and Chernyad'ev, 2002; Bartels and Sunkar, 2005).

The major cause of reduction of photosynthesis ability and growth under drought stress is the disequilibrium between the production of reactive oxygen species (ROS) and their scavenging systems (Becana et al., 1998). Plants under abiotic stress generate ROS that cause oxidative reactions (Lin et al., 2006a). The main ROS are hydrogen peroxide (H_2O_2) and superoxide (O_2^-). These ROS are routinely produced in different cellular reactions catalysed by various enzymes such as lipoxygenase, peroxidase, NADPH oxidase and xanthine oxidase, but the main source of these molecules is the Fenton and Haber-Weiss reactions (Blokhina et al., 2003; Debarry et al., 2005; Lin et al., 2006b). The ROS damage lipids, carbohydrates and proteins of cell membrane and cell nucleic acids (Zhang and Kirkham, 1996; Sairam et al., 1997; Fu and Huang, 2001; Blokhina et al., 2003). When a plant is under a serious stress condition; there is an accumulation of ROS because scavenging and repairing mechanisms of ROS damages are surpassed (Lin et al., 2006b). Therefore, a crop genotype must have efficient mechanisms of defence against ROS to survive a severe drought osmotic stress and adapt to drought condition.

MECHANISMS OF ADAPTATION TO DROUGHT STRESS

Crop genotypes can withhold the drought stress by dehydration tolerance, dehydration avoidance or drought escape (Ludlow, 1989; Yue et al., 2006). It was observe that a genotype can use all or two of these strategies. However, a molecular study with 245 SSR markers has revealed that dehydration tolerance and dehydration avoidance have distinct genetic bases (Yue et al., 2006). Mechanisms involved in drought stress adaptation are outlined thus.

Dehydration tolerance

Dehydration tolerance involves the desiccation tolerance, osmotic adjustment and antioxidant capacity. This strategy involves the resurrection and survival of genotypes after extended and extreme internal water deficit. These genotypes can be still alive when there is 95% of leaf water loss (Scott et al., 2000). Dehydration tolerance enables the plants to survive a long and strong periods of water deficit and regrow when rain falls. It allows also plants to maintain metabolic activities for longer and to translocate more stored assimilates to the storage tissues (Fukai and Cooper, 1995). Accumulation of compatible solutes is one of biochemical processes that result the dehydration tolerance (McCue and Hanson, 1990). It was reported that compatible solutes play an adaptive role by osmotic adjustment and protection of cellular compounds (Hare et al., 1998; Ain-Lhout et al., 2001). The compatibles solutes are mainly nitrogen containing molecules such as amino acids and polyamines, and hydroxyl compounds. Types of these compatible solutes and levels of their accumulation vary with plant species (McCue and Hanson, 1990). The compatible solutes work together with antioxidants which intervene to eliminate ROS and to repair damages of ROS.

Crop plants produce different antioxidants that have abilities to scavenge ROS. Antioxidants have small molecular mass such as ascorbic acid, glutathione, tocopherols, phenolic compounds, ROS-interacting enzymes such as superoxide dismutase (SOD), ascorbate peroxidise (APX) and catalase (CAT) (Blokhina et al., 2003; Brosché et al., 2010). These molecules play an important role to control the equilibrium between the production and the elimination of free radicals. Moreover, they work in cohesive network reactions and use mainly redox reactions (Lin et al., 2006b). Crop varieties that are drought resistant or tolerant express a high quantity of antioxidants than sensitive varieties (Herbinger et al., 2002; Lin et al., 2006b). Indeed, the quality and the quantity of these molecules are crop species dependent and their expression is affected by environmental conditions (Herbinger et al., 2002; Blokhina et al., 2003; Lin et al., 2006b). Therefore, understanding the expression and mechanisms of these molecules and their function models can assist to identify and develop drought tolerant crop varieties.

Dehydration avoidance

Dehydration avoidance consists of minimizing the water loss and maximizing the water absorption under water deficit conditions. This model is mainly observed on succulent and C3 crop species (Yue et al., 2006). Water loss can be minimized by reducing the light absorbance through leaf rolling, stomata closing, dense trichome layer that increases the reflectance, steep leaf angles, decrease of leaf area and canopy through reduced growth or shedding of leaves (Ehleringer and Cooper, 1992; Larcher, 2000; Chaves et al., 2003). It was observed that perennial and deciduous crop plants reduce their foliage in drought seasons. Plants that are always green present sometimes thick leaves with solid cuticle, highly sclerophyllous and reduced size leaves (Lebreton et al., 1995; Sanguineti et al., 1999; Sorrells et al., 2000; Ain-Lhout et al., 2001; Taiz and Zeiger, 2006). The water uptake is maximised by the increase of the capacity of root system (Jackson et al., 2000). Root characteristics such as thickness, depth, length and density have been associated with drought avoidance in rice (Ekanayake et al., 1985). All these characteristics of roots and leaves observed in the strategy of dehydration avoidance have effects on the effective water use and control of evapotranspiration.

Drought escape

The strategy of drought escapeis based on a short life cycle and developmental plasticity (Yue et al., 2006). Genotypes grow and reproduce before an appearance of a drought season (Passioura, 1996; Richards, 1996; Mitra, 2001; Mckay et al., 2003). In the drought escape, it was suggested that a genotype must have a high metabolic activity and rapid growth to support the plant to complete its life cycle before the most intense period of drought. However, the selection based on the phenology has revealed that the selection of both high photosynthetic activities and rapid growth can only be achieved under a well-watered environment (Sherrard and Maherali, 2006). Therefore, the strong correlation of development duration and metabolic activities to promote the drought escape is not necessary under drought condition.

CONSEQUENCES OF ADAPTATION MECHANISMS TO DROUGHT STRESS

Adaptation mechanisms to drought stress may incriminate crop growth and productivity (Larcher, 2000). For instance, crop varieties of short life cycle can escape a drought period but they produce low yield (Acquaah, 2007). Mechanisms of dehydration avoidance such as a stomatal closure and decrease of leaf area reduce assimilation of light and CO_2 necessary for photosynthesis and consequently lowers biomass production (Cornic, 2000; Larcher, 2000; Lawlor and Tezara, 2009). Dehydration tolerance with the accumulation of compatible solutes, the synthesis of antioxidants and the process of ROS scavenging depletes assimilates and energy. Consequently, these mechanisms reduce the ability of crop genotypes to synthesize organic end-products (Mitra, 2001). Thus, the development of a drought tolerant sweet potato variety needs to balance all drought tolerance mechanisms without sacrificing the crop productivity (Passioura, 1996; Richards, 1996; Mitra, 2001; Mckay et al., 2003).

DROUGHT STRESS ON SWEET POTATO

Sweet potato has unique characteristics of drought tolerance compared to the widely grown crop species.

The root system of sweet potato has a big surface that allows easy access to available soil water (Loebenstein and Thottappilly, 2009). It is very rich in antioxidants such as vitamin C, carotenoids and polyphenolic substances (Blokhina et al., 2003; Lin et al., 2006b), which are powerful to scavenge hydroxyl and peroxyl radicals and to control oxidation of lipid and protein of cell membrane. They are also chelators of metals and inhibitors of Fenton and Haber-Weiss reactions, which are the principal sources of free radicals (Debarry et al., 2005). However, sweet potato is negatively affected by drought stress.

In sweet potato, it was observed that the water deficit reduces the number of leaves and tubers, the size and composition of roots and vines, and the gain of dry weight of shoot and roots (Bourke, 1989; Pardales et al., 2000). In the pot experiment to screen 15 sweet potato varieties for drought tolerance, Sarawasti et al. (2004) observed that biomass and morphological traits such a main stem length, internode diameter and length, leaf area and number decreased in response to drought stress. Zhang el al. (2004) observed that soluble sugar and total amino acid increased as the loss of leaf water increased; but the potassium content decreased significantly. Sweet potato cells grown under an induced drought osmotic stress condition had a reduced growth, an induction of plasmolysis, an increase of amino acid pool and sucrose and starch accumulation (Wang et al., 1999). It was suggested that the accumulation of starch and the plasmolysis process decrease significantly the cell cytoplasm. Consequently, a small quantity of compatible solutes is enough to adjust an osmotic pressure induced by a water deficit (Wang et al., 1999). The drought condition was found to reduce the ability of sweet potato to eliminate ROS and this reduction varies from one variety to another (Herbinger et al., 2002; Blokhina et al., 2003; Lin et al., 2006b).

Germplasm collections from water limited regions showed distinctive leaf morphology compared to collections from environments with high rainfall. Moreover, the local landraces were found drought tolerant than introduced varieties under limited water tropical regions (Carey et al., 1997). Indira and Kabeerathumma (1988) observed that sweet potato is sensitive to water shortage especially during establishment, vine development and storage initiation. It was revealed that the shortage of water during critical periods of growth causes irreversible consequences on yield (Lin et al., 2006a). Anselmo et al., (1998) reported that drought is the main production constraint of sweet potato in the region where agriculture is rainfall dependent. According to Ekanayake (1990) a variety is drought tolerant when it produces an economic crop yield under limited water availability. Drought tolerance was associated to vine availability for planting after prolonged dry season (Gruneberg et al., 2009). Drought stress causes physiological changes of sweet potato. Van Heerden and Laurie (2008) reported that drought causes a stomatol closure which reduces CO_2 uptake, photosynthesis and plant growth and yield. It was suggested that drought stress affect the metabolism of carbon and nitrogen (Haimeirong and Kubota, 2003). The effects of osmotic stress induced by polyethylene glycol on sweet potato seedlings were investigated by measuring changes in relative water content, malondialdehyde and proline contents and superoxide dismutase activity. A highly positive correlation between relative water content and drought resistance (r = 0. 783), a highly negative correlation between malondialdehyde contents and drought resistance (r= 0. 848), a highly positive correlation between superoxide dismutase activity and drought resistance (r= 0. 777) were observed. However, the proline contents in leaves did not reveal any relation with sweet potato drought resistance (Zhang et al., 2001). Under filed trial, Niu et al. (1996) observed that leaf relative water content and catalase activity are best indicators of drought tolerance. Chowdhhury and Naskar (1993) found the positive correlation between relative water content of leaves and yield of sweet potato under water stress condition.

Soil water content is the main factor that determines the formation and growth of root tubers of sweet potato (Bourke, 1989). In field trials, it was observed that drought stress for 20 days in part of the growing period decreased the storage root yield by 15 to 39% (Gong and Wang, 1990).The constant soil humidity was proved to reduce adventitious roots (Pardales et al., 2000). In the water logging condition, the plants do not develop effective roots because underground parts of plant do not have enough oxygen to carry out metabolic reactions. Consequently, there is a rotting of storage roots. Inversely, the prolonged drought condition reduces the formation and growth of roots and dry matter accumulation (Bourke, 1989; Pardales et al., 2000). Therefore, a balanced level of water availability is necessary for good production of sweet potato.

METHODS OF SCREENING FOR DROUGHT

Drought-tolerance studies can be carried out under field or controlled environmental conditions (Acquaah, 2007). Field trials are carried out under a natural condition which is a real environment of a plant but this environment presents some limitations of fluctuation of water availability caused by unpredictable rainfall. Moreover, environmental factors such as temperature, air humidity and light are variable. Therefore, field screening for drought tolerance is complicated by unpredictable environmental conditions (Lafitte et al., 2004). The rainout shelter and in vitro techniques were proposed to overcome the limitations of selection for drought tolerance under field condition (Acquaah, 2007). The rainout shelter is a mobile infrastructure that protects genotypes under experiment from rain. This method permits to control the uniformity of water supply to plants (Blum, 2002). The in vitro approach consists on growing cells or tissues of plant or plantlets on a defined drought stressing culture media under an aseptic and controlled environment (Wang et al., 1999; Ahloowalia et al., 2004). The in vitro technique provides precise results but the working environment differs from the natural environment of crops. Therefore, the combination of *in vitro* screening with selection under the natural condition or under the rainout shelter could improve the quality of results.

Drought tolerance can be identified by quantifying phenological, morphological, physiological and biochemical characteristics and using molecular tools (Blum, 2002). Phenological and morphological characteristics are the most used in breeding for drought tolerance. In these approaches data collection consists of measurement of plant growth (size of roots, stem and leaf area, accumulation of fresh and dry biomasses), growth stage (days to flowering and maturity), senescence, leaf rolling and yield loss (Spitters and Schaapendonk, 1990; Cheema and Sadaqat, 2004). The water content and water potential of the crops are indicators of drought tolerant varieties. A variety that maintains its internal water status under a drought stress is considered as drought tolerant (Acquaah, 2007). Drought tolerance is also determined by quantifying plant biochemical products such as compatible solutes, chlorophyll, antioxidants and other proteins produced by plants as responses to drought stress (Wang et al., 1999; Reddy et al., 2004; Kasukabe et al., 2006). Diffusion porometry for leaf water conductance, root penetration, distribution and density in the field and infrared aerial photography for dehydration are used commonly in studies for drought tolerance (Mitra, 2001).

Molecular tools to select for drought tolerance have been developed (Srisuwan et al., 2006; Acquaah, 2007). The basis of this molecular approach is the progress of genomics, transcriptomics, metabolomics and proteomics. Among these tools, DNA molecular markers based on the hybridization, polymerase chain reaction and DNA sequence are the most commonly used (Tuberosa and Salvi, 2006; Michael et al., 2008). Simple sequence repeats (SSRs) or microsatellites genetic markers are commonly used in sweet potato studies. They have been used in genetic characterization of sweet potato germplasm (Buteler et al., 1999; Veasey et al., 2008; Karuri et al., 2010) and analysis of paternity in polyploidy sweet potato (Buteler et al., 2002). Other molecular markers such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), sequence tagged sites (STS), amplified fragment length polymorphisms (AFLPs), single nucleotide polymorphisms (SNPs) were also proposed in genetic and breeding studies (Acquaah, 2007). However, the utilisation of molecular approach in a plant breeding requires a well-equipped laboratory and trained personnel (Srisuwan et al., 2006).

INHERITANCE OF DROUGHT TOLERANCE

Drought tolerance is reportedly a complex trait because of the heterogeneity of drought stress in time and space, and unpredictable characteristics of drought stress (Sorrells et al., 2000). The drought tolerance involves actions and interactions of various biochemical, morphological and physiological mechanisms that are controlled by products expressed by different genes (Mitra, 2001; Acquaah, 2007). Moreover, it is difficult to study isolated single gene and to understand its role of drought tolerance in crop plants (Mitra, 2001). Both qualitative and quantitative inheritances were found in traits associated with drought tolerance. Ekanayake et al. (1985) observed that root characteristics are controlled by a qualitative inheritance under a drought condition. Leaf rolling, osmotic adjustment and number of roots were identified to be qualitative traits (Mitra, 2001). Study on water deficit mediator genes indicated that crop species vary in symptoms and reactions to water deficit (Sorrells et al., 2000). The genes responsible for earliness of stem reserves, leaf persistence and dwarfing were identified to be associated with drought tolerance (Foulkes et al., 2007). In rice and cowpea a drought resistance gene linked with genes for plant height and pigmentation was reportedly pleiotropic on a root system (Morgan, 1995; Mitra, 2001; Agbicodo et al., 2009). Other proposed candidate genes that are involved in drought tolerance are genes coding for dehidrin proteins that protect cellular components under dehydration condition (Shinozaki and Yamaguchi-Shinozaki, 2007), proteins controlling the equilibrium and damages of ROS (Foyer and Noctor, 2005), proteins involving in the osmotic adjustment and plant morphology (Moinuddin et al., 2005; Ober, 2008) and enzymes involving in the accumulation of compatible solutes (Mitra, 2001). Indeed, drought tolerance involves many genes which code for products working in a highly coordinated network.

BREEDING OF SWEET POTATO FOR DROUGHT TOLERANCE

Breeding of sweet potato is carried out through random polycross and hand pollination (Gruneberg et al., 2009). In the polycross method, crossing blocks are installed and allowed to be naturally open pollinated by insects (Nyquist and Santini, 2007). This method is very useful to generate a genetic diversity in a sweet potato population but it is not efficient in genetic studies because the source of pollen is unknown. Therefore, the hand pollination method was proposed to overcome this problem (Acquaah, 2007). The hand pollination is carried out in four main steps of preventing insect pollination before doing hand pollination, hand pollination, preventing insect pollination after hand pollination and labelling (Jones and Deonier, 1965; Jones et al., 1986).This method is commonly applied to insure cross combinations of different characteristics in the hybrid seeds through a highly demanding practice (Jones et al., 1986; Wilson et al., 1989; Gruneberg et al., 2009). When using hand pollination the commonly used matting designs in the sweet potato breeding are diallel and North Carolina ((Mihovilovich et al., 2000; Mwanga et al., 2002; Chiona, 2009; Gasura et al., 2010).

Breeding for drought tolerance is complicated because of a negative correlation between some stress adaptive traits and a crop yield (Chapin et al., 1993). Zehui (1996) observed that the use of yield components as the unique indicators for drought tolerance is not sufficient. Physiological, morphological and biochemical characters that may show the drought tolerance were proposed through greenhouse and laboratory studies (Blum, 2002). However, some varieties selected under greenhouse and laboratory conditions did not show the drought tolerance under field condition (Sorrells et al., 2000).This indicates that the expression of genes for drought resistance is strongly affected by environmental conditions (Cheema and Sadaqat, 2004).

Knowledge of environmental effects on the expression of genes leads to breeders to adopt new methods to develop drought tolerant varieties. Efforts of breeders are oriented on the development of varieties that can produce in an environment where the rainfall is irregular in the distribution and quantity. This is because crops must have a minimum level of water to sustain growth (Acquaah, 2007). Zehui (1996) suggested that it is necessary to explore all morphological, biochemical and physiological characters associated to drought tolerance under screening process. Also it was suggested that selection should be carried out in environments in which a new crop variety will be released and grown (Cheema and Sadaqat, 2004; Abidin et al., 2005; Mwanga et al., 2007).

Sexual reproduction of sweet potato generates genetic variability in which valuable colones are selected for further selection. Mass selection method was first suggested because most important traits of sweet potato are quantitative. After the population improvement through recurrent selection method was adopted (Carey et al., 1992). Ekanayake (1990) proposed two stages in the approach to screen sweet potato for drought tolerance. Firstly, genotypes have to be evaluated under screening nursery using yield and pulling resistance as selection criteria. Secondly, selected genotypes have to be evaluated under drought conditions in a field for physiological traits, water use efficiency and yield. Genotypes identified as drought tolerant could be used as progenitors for combining with others favourable traits. Selection and breeding for varieties that perform very well under drought condition is a key factor to improve the production of sweet potato. Studying sweet potato varieties for 70 days under drought condition, Hou et al. (1999) observed a significant difference in a survival rate which was associated with drought resistance. However, the authors did not found a correlation between drought resistance and above ground growth. The evaluation of drought resistance of 50 genotypes revealed a yield range from 0.76 to 73.85 g per plant and 17 genotypes were identified to be drought resistant (Ding et al., 1997). Anselmo et al. (1998) investigated the drought tolerance of clones of high yielding cultivars and their progenies from open pollination in the Philippine for two years in dry season. Based on yield, the authors found that some clones and open pollinated progenies were drought tolerant.

Identification and characterisation of genes have a positive effect on the genetic engineering for tolerance to drought stress (Acquaah, 2007). Genetic engineers have tried to develop transgenic plants resistant to drought by using isolated genes. Genes coding for sperimidine synthase were used to improve environmental stress of sweet potato. These transgenic plants have revealed a tolerance to drought, salt, chilling and heat stresses (Kasukabe et al., 2006). Transgenic plants of sweet potato containing the gene from Spinaciaoleracea encoding the betaine aldehyde dehydrogenase revealed an increased glycine betaine accumulation and betaine aldehyde dehydrogenase activity. These plants have showed the tolerance to multiple environmental stresses with high ability of protection against cell damage, strong photosynthetic activity, reduced production of ROS and increased activity of free radical scavenging enzymes (Fan et al., 2012). A transgenic potato plants with the genes of Cu / Zn superoxide dismutase and ascorbate peroxidase were developed. These plants have showed enhanced tolerance to multiple environmental stresses including a high temperature compared to non-transgenic plants (Tang et al., 2006). Even though genetic engineering revealed promising results, its progress is limited by a shortage of successful screening methods and multidisciplinary approach and genotype by environment interactions (Mitra, 2001).

CONCLUSION

Drought stress is one of yield limiting factors in sweet potato production causing an annual yield loss estimated at 25%. It is associated with adverse changes at morphological, physiological, biochemical and molecular levels among genotypes. These changes are useful indicators in the selection and breeding of drought-tolerant genotypes in sweet potato. Further, breeding of sweet potato for drought-tolerance requires understanding effects of drought stress, presence of genetic diversity, efficient crossing and selection methods that lead to identification and development of potential clonal cultivars. The present paper reviewed various physiological responses to drought stress and patterns of drought tolerance that may assist in breeding of sweet potato for drought-tolerance.

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