

Review Article

Volume 3 Issue 1 - August 2018

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Breeding Sweet potato [*Ipomoeaebatatas* (L.) Lam] For Low Moisture Stress Tolerance



Tariku Simion*

South Agricultural Research Institute, Ethopia

Submission: June 06, 2018; Published: August 16, 2018

*Corresponding author: Tariku Simion, South Agricultural Research Institute, Ethopia, Email: trk2011smn@gmail.com

Abstract

Sweet potato is important sources of carbohydrates, vitamins A and C, fiber, iron, potassium, and protein, Sweet potato is also used as animal feed. Increasing recognition of the great potential of the sweet potato crop as a nutritious food for humans and animals has resulted in intensified research efforts to enhance production and consumption. Sweet potato is sensitive to water deficits particularly during the establishment period including vine development and storage root initiation. However, drought is often a major environmental constraint for sweet potato production in areas where it is grown under rain fed conditions. Different cultivars may respond differently to limited quantities of soil water. Selection for good cultivar performance under drought conditions is thus considered to be of major importance.

Keywords: Stress; Dehydration; Avoidance and Tolerance

Introduction

More than 70 percent of potential yield loses in agriculture worldwide is attributed to adverse environmental factors of which water scarcity represents the most severe constraint [1]. Agriculture is the largest consumer of water in the world and in the drier areas of the world which include South Africa. The use of water for agriculture can exceed 90 percent of consumption. Global warming is also predicted to affect most severely developing countries where agricultural systems are most vulnerable to climatic conditions and where small increases in temperature are very detrimental to productivity. The Food and Agricultural Organization of the United Nations estimates that by 2025 approximately 480 million people in Africa could be living in areas with very scarce water, and that as climatic conditions deteriorate, 600,000 km2 currently classed as moderately constrained will become severely limited [2]. It is thus essential to improve water use efficiency in agriculture. This will require an integrated approach to water resources management to encourage an efficient and equitable use of the resource, and to ensure sustainability. The improvement of crop with increased tolerance to drought is therefore, an important strategy to meet global food demands with less water. Sweet potato is an important food, feed and vegetable crop in most tropical developing countries. The crop is ranked fifth economically after rice, wheat, maize, and cassava, sixth in dry matter production, seventh in digestible energy production, and ninth in protein production in the developing countries [3]. World production is about 131 million tones/ year, on approximately 9 million ha with mean estimated yields of 13.7 tones /ha [2]. About 97% of the world production is found in the developing countries. The crop is widely grown in Africa, Asia, and Latin America, with

China accounting for 52% of the crop grown on approximately 4.7 million ha [2]. In sub-Saharan Africa (SSA), sweet potato is the most widely grown root crop and about 9.9 million tons of storage roots are produced on an estimated 2.1 million ha [2].

Sweet potato is important sources of carbohydrates, vitamins A and C, fiber, iron, potassium, and protein [4]. Sweet potato is also used as animal feed. Increasing recognition of the great potential of the sweet potato crop as a nutritious food for humans and animals has resulted in intensified research efforts to enhance production and consumption [4,5]. Sweet potato is especially important in developing countries because it is a highly adaptable crop that generates large amounts of food per unit area and unit time during relatively short rainy periods, giving it an advantage over major staples [6]. Sweet potato also has flexible planting and harvesting times, tolerates high temperatures and low fertility soils. It is drought tolerant and easy to propagate. Sweet potato is sensitive to water deficits particularly during the establishment period including vine development and storage root initiation. However, drought is often a major environmental constraint for sweet potato production in areas where it is grown under rain fed conditions. Different cultivars may respond differently to limited quantities of soil water. Selection for good cultivar performance under drought conditions is thus considered to be of major importance. Despite its importance, there have been few genetic studies on sweet potato, probably due to its self- incompatibility and high level of cross-incompatibility, polyploidy level (hexaploid), and large chromosome number (2n=6X=90) [7]. The Ipomoea series batatas contain sweet potato and 13-14 other taxa. Nearly 26,000 accessions of Ipomoea species are maintained at various gene banks in the world, and 8,000 accessions are sweet potato cultivars or breeding lines [8]. The objective of this paper is to review the effort that has been made to improve sweet potato for low moisture stress tolerance.

Origin and Distribution of Sweet Potato

Sweet potato [Ipomoeaebatatas (L.) Lam] is a perennial plant cultivated as annual crop. It is dicotyledonous and belongs to morning glory family Convolvulaceae. Principally, sweet potato is grown for its storage roots for food security and income generation [9]. Sweet potato (Ipomoea batatas) originated from Central America where it was found growing in the wild spreading across the Pacific from Central America and transported to warmer regions of Asia and Africa by Spanish and Portuguese traders [10]. Sweet potato is grown in more than 100 countries in tropical, subtropical and temperate climates [10]. It ranks as the world's seventh most important crop with an estimated annual production of approximately 121.52 million tons on 9.2 million ha with an estimated average yield of 13.2t/ ha (FAO, 2005). Sweet potato was domesticated in either South America or Central America more than 5000 years ago. Ancient sweet potato is grouped into three distinct clusters: Kumara, Camote and Batata [11]. These three groups form the two gene pools in the modern sweet potato. The gene pools are; the Carribean and Central America (Northern) gene pool comprising batata and camote and northwestern South American (Southern) gene pool comprising Kumara [11]. Batata and Camote also dominate in the New Guinea and Eastern Pacific gene pool. Thus, since its domestication, sweet potato has been cultivated in two widely separate areas; tropical America and Southwest Pacific (Polynesia). Therefore, sweet potato is believed to have moved from its center of diversity (America) to caves of Peru then to pacific Polynesia and South East Asia possibly by seafarers before Columbus at around 1200-1300 AD [11]. Today sweet potato is cultivated in 117 countries in tropical and subtropics. Asia is the highest producer followed by Africa and the Americas. In addition, the inhabitants of the Pacific islands are among the largest per capita consumers of sweet potato in the world today [12].

Sweet potato is also referred to as batata, camote, boniato, batata doce, apichu, or kumara in Latin America. It was botanically described in 1753 by Linnaeus as Convolvulus batatas, but Lamarck, in 1791, re-classified the crop into the genus Ipomoea based on the stigma shape and the surface of the pollen grains. Hence, the crop belongs to the family of Convolvulaceae, genus Ipomoea and species batatas. Therefore, the botanical name of sweet potato was changed to *Ipomoea batatas* (L.) Lam. The storage organ of sweet potato is a root. The center of diversity of the wild relatives of I. batatas is within the Americas, except I. littoralis, found in Australia and Asia. Sweet potato thrives well in sandy-loam and clay loam soils, which must be well drained because of the plant sensitivity to long-lasting excessive moisture in the soil [13]. It is very sensitive to alkaline and saline conditions which influence growth. Soil pH between 5.6 and 6.6

is very good for production [14]. China is the largest producer of sweet potato with 80% of annual world supply (FAO, 2008). It is the third most important root and tuber crop in Sub-Saharan Africa. Africa produces 11.6 million tons annually with Nigeria being the largest producer followed by Uganda and Tanzania.

Drought Stress and Drought Tolerance

The term 'drought' was defined by as a meteorological occurrence characterized by below normal rainfall [15]. The phenomena of drought stress are on the other hand defined as a period of insufficient rain which causes injury to crop and leads to a phenomenal reduction in economic yield. It is usually associated with non-availability or exhaustion of water in the root zone. Drought can be permanent, periodic, or random, occurring early, late, or in the middle of the crop season. Drought can also be cumulative or specific and short. Drought tolerance is defined as the relative yield of a genotype compared to other genotypes subjected to the same drought stress [16]. Drought remains a challenge for researchers due to complexity of factors affecting crop response to drought [16]. According to Ekanayake a genotype is drought resistant when it produces an economic crop within the limits of its production potential under conditions of limited water availability [17]. Drought resistance and its components are almost constantly being redefined [18]. A genotype can be drought resistant due to the mechanisms of drought escape, drought tolerance, drought avoidance, and drought recovery [19]. These mechanisms are not mutually exclusive and provide the crop with the ability to resist drought at any given period during its growth cycle. Escape mechanisms allow the crop to complete the drought sensitive growth stages during periods of adequate moisture or to complete the cycle prior to an onset of a drought [17]. Avoidance is the ability to endure drought or exclusion of a stress by maintaining high water potentials of the plant through higher levels of water absorption due to better distributed and larger root system and reducing the water loss by stomata control. Tolerance is the ability to survive an internal stress due to dehydration tolerance or avoidance mechanisms [17].

Mechanisms of Drought Tolerance

When a genotype yields better than another under a severe strain of drought, it is relatively more drought resistant. The strain of drought is developed when crop demand for water is not met by the supply, and plant water status is reduced. Plants can resist drought by either dehydration avoidance or by dehydration tolerance. Drought resistance in terms of the physiology involved interacts with the magnitude and the timing of the stress. There are several mechanisms through which plants exhibit resistance or tolerance to drought as described by Blum [18].

Dehydration Avoidance and Tolerance

Dehydration avoidance is defined as the plant capacity to sustain high plant water status or cellular hydration under the effect of drought. Hence, by this mechanism, the plant avoids being stressed because plant functions are relatively unexposed to tissue dehydration. Crop plants avoid dehydration by enhanced capture of soil moisture, by limited crop water loss, and by retaining cellular hydration despite the reduction in plant water potential [19]. Dehydration tolerance is defined as the relative capacity to sustain or conserve plant function in a dehydrated state. This is sometimes seen as the second defense line after dehydration avoidance. Dehydration tolerance as an effective drought-resistance mechanism in crop plants is rare. It exists in the seed embryo, but once germinated the plant loses its tolerance. Extreme desiccation tolerance is known in resurrection plants and some attempts are made in various laboratories to use this tolerance for improving crop plants. Dehydration tolerance, like freezing tolerance, requires that the plant enter a quiescent or a dormant state [18].

Enhanced Capture of Soil Moisture

Deep soil moisture is available and a long root to reach this moisture is simply as effective as a long rope in a deep well. Genetic variation exists in potential root length (maximum root length measured under non-stress and non-restrictive soil conditions [18]. However, when plants are exposed to a drying soil, root morphology and growth can change to the extent that the potential root length, whether it is short or long, becomes irrelevant. In cereals, for example, drying, hard topsoil resists the penetration and establishment of adventitious (crown) roots while existing roots receive all transient assimilates and grow deeper [20].

Reduced plant size and leaf area

Reduced plant size leaf area is a major mechanism for moderating water use and reducing injury under drought stress. Often, crop cultivars breed for water-limited environments by selection for yield under stress have a constitutively reduced leaf area. The radioactive energy load on the canopy (net radiation), of which only a fraction is used for photosynthesis, is dissipated mainly by transpiration. A reduction in transpiration can be achieved by reducing net radiation by way of reflection, namely increasing crop albedo. Various plant surface structures allow an increase in albedo.

Water Use Efficiency

Epicuticular wax or plant glaucousness reduces cuticular conductance and reflects incoming radiation at the ultraviolet (UV) and 400–700 nm wavelengths to the extent that leaf temperature and transpiration are reduced without a reduction in stomata conductance. This is expressed in greater water use efficiency (WUE) for the glaucous genotype. Reduced leaf chlorophyll content expressed in yellowish or pallid green shade of color is indicative of reduced antenna complexes at the Photosystem II reaction center. This reduces photosynthetically active radiation absorption and subsequently water use. Such varieties were found adapted to dry and cold conditions [21]. However, at the same time, these reflective properties that are

beneficial under drought stress were often associated with reduced photosynthesis and yield potential. Programmed moderated crop water use has become an important agronomic practice in maximizing crop production in dry land environments that are largely based on stored soil moisture use.

Osmotic Adjustment

An increasing number of reports also provide evidence on the association between high rate of osmotic adjustment and sustained yield or biomass under water-limited conditions across different cultivars of crop plants. Since osmotic adjustment helps to maintain higher leaf relative water content at low leaf water potential, it is evident that osmotic adjustment helps to sustain growth while the plant is meeting transpiration demand by reducing its low leaf water potential. 'Osmotic adjustment sustained turgid maintenance and hence the yield-forming processes during moderate and severe water stress'.

Drought screening methods and parameters

According to International Rice Research Institute (IRRI) several field and laboratory screening methods have been used successfully to screen for drought resistance, including line-source sprinkler irrigation, rainout shelters, and measurement of drought susceptibility [22]. It is however, important to use a simple and easily repeatable method when screening for drought tolerance in target environment. The most obvious means to select for improved drought tolerance is to withhold water or reduce irrigation and compare the response of various genotypes through several parameters. The major parameters that have been successfully used in estimating the level of drought tolerance in plants include.

Chlorophyll fluorescence

There is generally a decrease in the rate of photosynthesis during drought stress which results in an increase in abscisic acid concentration leading to stomata closure to reduce water loss that may affect yield. Abscisic acid major role is the stomata adjustment and its accumulation are known to induce gene expression. Severe drought leads to stomata closure which leads to yield reduction.

Relative Water content

Relative water content is one of the parameters used to estimate the level of drought tolerance in plants. This determines leaf water status in plants and is a component to consider the ability of a plant that maintains tolerance during drought. It is measured in terms of fresh weight and dry weight.

Leaf Area

The leaf area maintains water balance and it is responsible for the light energy that can be absorbed to provide chemical energy and is determined by stem phonology, morphology, leaf size and emergence [23].

Canopy Temperature

Canopy temperature is measured using an infrared thermometer. A lower canopy temperature is an indication that a plant has capacity to take up soil moisture content and maintain better water status [24].

Dry Matter Content

The dry matter content and the moisture can be used as an index to determine stress in crops. Both are a good indicator of drought resistance because of its high sensitivity and irritability [23].

Yield

The yield of cultivars can be compared after undergoing stress conditions. It is an indicator while selecting because there must be a correlation between a resistant cultivar and the yield.

Breeding for Drought Tolerance

Sources of drought tolerance

Development of drought tolerant varieties through conventional breeding requires making crosses. The choice of the right parent increases the number of promising recombinant genotypes among the best families. Good parents should have good combining ability and good performance for all traits. Parents with drought tolerant characteristics are selected from genotypes that have evolved under drought conditions. Crosses are made to ensure good recombination of genes responsible for drought tolerance. Genotypes with large root volume, deeper root growth, early maturity, small foliage, thick leaves and trichomes, low canopy temperature, are crossed with drought susceptible parents and the gene frequency increased through recurrent selection, backcross, three-way crosses or modified double crosses. Sometimes wild relatives are used as the source of drought tolerance genes in various crops. The International Potato Center is enhancing the drought tolerance using indigenous germplasm from the Andes. Further, and its collaborators have also identified drought tolerant sweet potato lines. However, cross-pollination barriers and absence of suitable donors for drought traits has hindered progress in screening for tolerance in sweet potato [25].

Drought evaluation and screening methods

Different experimental methods have been developed for evaluating drought stress. These include; field experimentation, pot experiments, chamber house experiments, nutrient solution experiments, rain out shelters, rhizotomy experiments, and petri dish experiments. These types of experimentation methods enable some level of drought simulation depending on how they are designed and they all have limitations. It is difficult to quantify roots, and ensure homogeneity in soil properties, and soil moisture as well as day and night soil temperature in field experiments.

Identification of drought related genes

Genes responsible for drought tolerance have been identified through various ways. These include studying the anabolic and catabolic pathways for metabolites that accumulate in drought stressed plants; these metabolites include proline, glycine, betaine, trehalas, and ABA [26]. They also involve studying drought response regulatory gene expression and the changes in protein synthesis under drought stress in plants. Mapping QTL for drought tolerance, using segregating populations as well as studying and isolating natural or artificial drought tolerance directed mutants and transgenic plants, may also lead to identification of drought tolerance genes. Increased drought tolerance is dependent on finding the most appropriate alleles of drought tolerance genes and pyramiding them [25]. This is done by screening the population with standardized phenotyping protocols followed by detailed genetic analysis for the best performing materials in segregating progenies [25]. These segregates perform well because of either positive allele at a number of QTL of small effect, or positive alleles at one or two major genes (QTL of large effect) [25]. In general, a few QTL of large effect are of greater interest and useful for a crop breeding program than many QTL with smaller effects. This is because they can accurately be used as screening markers for the trait [25].

Sweet Potato Breeding

Mating designs are important in the breeding of any crop as they are used to evaluate parents and develop F1 recombinant crosses that form the base population for selection. They also help to generate synthetic populations and provide information for estimating gene action and genetic gains. In sweet potato, mating designs such as polycross, diallel, or North Carolina design I may be used [27]. The diallel mating design is used to study the polygenic action. Its analysis is based on general combining ability and specific combining ability General combining ability and specific combining ability enable distinguishing between the average performance of parents and their crosses, respectively. The general combining ability indicates the relative value of the population in terms of frequency of favorable genes and identifies superior parents for use in intra-population breeding programs. On the other hand, the specific combining ability indicates the predominant direction of the deviations due to dominance in a population. After making crosses in sweet potato breeding, visual selection that eliminates genotypes that do not meet the lowest acceptable values for each trait is done. This is followed by index selection for yield and nutritional quality based on the desired genetic gain. Further, the remaining clones are selected against pests and diseases done by visual selection. The last 100-200 clones enter late breeding stages but are also used as parental materials for the next cycle of recombination and selection. Each sweet potato seedling is potentially a new variety [27]. The seedlings are clonally propagated, whereby; about 40-60 cuttings per plant are produced under rapid multiplication. The breeder may reduce the selection cycles from five years to about a year or two and get the best genotype for tolerance to abiotic and biotic factors using accelerated breeding scheme.

Breeding of sweet potato is also carried out through random polycross and hand pollination. In the polycross method, crossing blocks are installed and allowed to be naturally open pollinated by insects [25]. 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. On the other hand, hand pollination is commonly applied to insure cross combinations of different characteristics in the hybrid seeds through a highly demanding practice [25]. When using hand pollination, the commonly used matting designs in the sweet potato breeding are diallel and North Carolina [27]. Breeding for drought tolerance is complicated because of a negative correlation between some stress adaptive traits and a crop yield observed that the use of yield components as the unique indicators for drought tolerance is not enough. Physiological, morphological and biochemical characters that may show the drought tolerance were proposed through greenhouse and laboratory studies. However, some varieties selected under greenhouse and laboratory conditions did not show the drought tolerance under field condition [25].

This indicates that the expression of genes for drought resistance is strongly affected by environmental conditions [25]. 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. 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. Sexual reproduction of sweet potato generates genetic variability are selected for further selection. Mass selection method was first suggested because most important traits of sweet potato are quantitative.

Ekanayake 1990 proposed two stages in the approach to screen sweet potato for drought tolerance. Firstly, genotypes must be evaluated under screening nursery using yield and pulling resistance as selection criteria. Secondly, selected genotypes must 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 favorable traits. Selection and breeding for varieties that perform very well under drought condition is a key factor to improve the production of sweet potato. Identification and characterization of genes have a positive effect on the genetic engineering for tolerance to drought stress. 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 [29]. 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. These plants have showed enhanced tolerance to multiple environmental stresses including a high temperature compared to non-transgenic plants [30]. 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 [31-35].

Conclusion

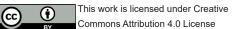
Drought stress is one of yield limiting factors in sweet potato production causing an annual yield loss estimated at 25%. It is associated with adverse changes at morphological, physiological, biochemical and molecular levels among genotypes [36]. These changes are useful indicators in the selection 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 [37,38].

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