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Storage root formation, dry matter synthesis, accumulation and genetics in sweetpotato

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Abstract

Sweetpotato is a relatively drought tolerant crop providing the highest dry matter content for human consumption. High dry matter content is the main characteristic preferred by consumers and processors of sweetpotato. There is a continued need to develop and release new and high yielding sweetpotato varieties possessing high dry matter content. The objective of this paper is to review important aspects in the breeding of the crop to achieve high storage root yield and increased dry matter content. The paper highlights development and synthesis processes of dry matter of sweetpotato storage root, gene actions and correlation between traits associated with dry matter accumulation, breeding of sweetpotato for high dry matter content, approaches to screening of clones with high dry matter content and effects of genotype by environment interaction on yield and dry matter content.

Keywords: Dry matter, storage root, sweetpotato.
Abbreviations: AMMI -Additive main effects and multiplicative interactions, ASV-AMMI stability value, CV-Coefficient of variation, ESTs-Expressed sequence tags, G×E-Genotype by environment interactions, GGE-Genotype main effect plus genotype by environment interactions, SSR-Simple sequence repeat, QTL-Quantitative trait loci.

Introduction

Sweetpotato (*Ipomoea batatas* [L.] Lam.); 2n=6x=90) is one of the valuable crops producing the highest root dry matter content for human consumption. It provides comparatively high calorie at 152 MJ ha^{-1} day^{-1}. Other crops such as cassava, wheat, rice and maize provide 121, 135, 151, and 159 MJ ha^{-1} day^{-1} calories, respectively (Horton and Fano, 1985; Scott et al., 2000). Starch is the main component constituting 70% of the dry weight of sweetpotato (Woolfe, 1992). Slafer and Savin (1994) and Mwanga et al. (2007) reported high dry matter content as an important characteristic of a good sweetpotato variety. Storage roots with high starch and low hexoses contents are important characteristics preferred by the sweetpotato industry (Slafer and Savin, 1994). High starch and low soluble sugar contents decrease the cost of sweetpotato processing due to the absence of oxidation reactions (McKibbin et al., 2006). Oxidation reaction is mainly favoured by high content of hexoses such as glucose and fructose. This reaction leads to the development of brown and dark colours and bitter taste after drying or frying. Such change of colour is associated with Maillard reaction (Dale and Bradshaw, 2003). Li, (2008) reported that the high dry matter content of the root significantly reduces industrial processing cost because of low oil absorption. Sweetpotato is an important raw material to manufacture different products such as noodles, vermicelli, jell, amylophosphate, soluble and refined starch, and alcohol drinks (Loebenstein and Thottappilly, 2009; Woolfe, 1992). Currently the crop is targeted as an important source for biofuel production because of its ability to provide high amount of starch biomass which can be fermented and converted into ethanol (Loebenstein and Thottappilly, 2009; Cervantes-Flores et al., 2010). The use of sweetpotato as a raw material for the biofuel and processing industries requires varieties with a dry matter content that is above 35% of the flesh weight (Gruneberg et al., 2009). High dry matter content is the main characteristic preferred by consumers and processors of sweetpotato. For instance in sub-Sahara Africa, small-scale farmers prefer sweetpotato varieties that have a high dry matter content (Mwanga et al., 2007; Cervantes-Flores et al., 2010). Also high dry matter content, low fibre, and good taste are the most preferred traits of the crop by women farmers' (Gruneberg et al., 2009; Mwanga et al., 2010). A dry matter content >25% is an important component for acceptability of a new sweetpotato variety by farmers (Shumbusha et al., 2010). Recently the orange fleshed sweetpotato varieties with high β-carotene are being promoted in the sub-Sahara Africa to improve vitamin A nutrition of the poor. However, these varieties are reportedly possessing low dry matter content, a challenge towards their adoption and wide-scale production by farmers. Therefore, these varieties should carry increased β-carotene and dry matter to promote their adoption and large-scale production (Cervantes-Flores et al., 2010; Mwanga et al., 2010). The sustainability and expansion of sweetpotato production depend on the availability of varieties that meet end-users preferences. Consequently, a sweetpotato breeding programme should incorporate valuable traits such as high dry matter content and farmers-preferred traits before the release of elite clones. The development of a new variety of sweetpotato with high dry matter content requires efficient methods of crossing, selection of clones from recombined parents and evaluation of the effects of genetic by environment interactions. This permits the release of end-users preferred varieties at the target production environment.

The objective of this paper is to review important aspects in the breeding of the crop to achieve high storage root yield and increased dry matter content. The paper highlighted mechanisms of root formation and dry matter synthesis, methods to screen for high dry matter content, and genotype by environment interaction on root yield and dry matter content in the sweetpotato.

Development of storage root and dry matter synthesis in sweetpotato

The formation of sweetpotato storage roots is a complex process involving various steps such as stopping of root elongation, initiation of first and second vascular cambia, development of anomalous and interstitial cambia, increasing of radial growth, cell proliferation and expansion, and massive accumulation of starch and proteins (Desai, 2008; Ravi et al., 2009). Typically, a storage root has to stop an elongation growth but continues a radial growth (Desai, 2008). The initiation of storage root starts with a thickening of stellar structure of an adventitious root followed by a formation of a circular primary vascular cambium and other several cambia in sub-apical regions of thickening root (Ravi and Indira, 1999). The cambia are meristematic tissues which undergo many mitotic cell divisions resulting into the formation of starch storage tissues, growth of storage root and suppression of stele lignification. All these processes are controlled by endogenous phytohormones and its expression are controlled by different genes (Ravi et al., 2009).

Cytokinines are the main phytohormones involved in the root formation. Zeatin riboside, trans-zeatin riboside and 9-glycosyl-N-62-isopentenyl adenosine were identified to be responsible for the initiation of cambia tissues (Tanaka et al., 2005; Wang et al., 2005). These cytokinines and others such as isopentenyladenine and dihydrozeatin riboside were proven to play a pivotal role in the initiation and proliferation of cambia tissues of storage root (Desai, 2008). Ku et al. (2008) reported that abscisic acid stimulates the cell division of cambial meristematic tissues by interacting with other cytokinines and resulting in the growth of storage root.

Storage root growth takes place at cellular level and involves the expansion in size by increasing the cell number, size and weight by accumulation of photosynthesis products (Desai, 2008; Ravi et al., 2009). The accumulation of dry matter is associated with the ability of root to attract photo-assimilated products from photosynthetic organs. The photosynthesized sucrose is moved from leaves through the stem, towards underground parts including storage roots (Li, 2008). Sucrose is split into hexoses which are transformed to glucose-1 phosphate, which is then used to synthesise starch in the amyloplasts. Reactions of starch synthesis are mainly catalysed by ADP-glucose pyrophosphorylase and starch synthase (Li, 2008; Nakatani and Komeichi, 1992).

Studies of molecular mechanisms of synthesis and accumulation of dry matter revealed that products expressed by knotted-like homeobox (KNOXI), MADS-box and polyamine genes play an important role in the formation of sweetpotato storage root (Chen et al., 2003; Ku et al., 2008; Tanaka et al., 2008). Products expressed by KNOXI genes were identified in initial and growing sweetpotato storage roots (Tanaka et al., 2008). It was observed that an up regulated of KNOXI genes expression is associated with the reduction of lateral roots development (Scanlon et al., 2002). Whereas, the down regulation of these genes is linked with an increase of the number of lateral roots. Products of KNOXI genes were identified to regulate the cytokinine level in the storage roots of sweetpotato and a high expression of KNOXI genes was associated with a high synthesis of cytokinines (Chen et al., 2003; Tanaka et al., 2008). The concentration of trans-zeatin riboside content in the growing sweetpotato storage roots was identified to be correlated with the level of expression of KNOXI genes. This observation suggested an active involvement of products of KNOXI genes in the formation of storage roots of sweetpotato (Tanaka et al., 2008). Products of MADS-box genes were identified to stimulate the production of phytohormones such as jasmonic acid and cytokinines which participate in the initiation and development of sweetpotato storage roots (Ku et al., 2008). Spermidine and other products coded by polyamine genes were identified to play an important role of pathway signal transduction, protein kinase activation and transcription factors that increase genes expression during storage root formation and growth (Kasukabe et al., 2006). Also, many genes products were identified to be involved in the dry matter synthesis. The expression of genes coding for these products was identified to be extremely highly influenced by genetic effects and not by factors such as water deficit (Ravi and Indira, 1999; Ravi et al., 2009), soil and air temperature (Li, 2008) and physiology and age of seedling (Caldiz et al., 1996). However, there are many other aspects of storage root and dry matter synthesis that need to be further investigated and understood.

Gene actions and correlation between traits

Important traits in crops are controlled by quantitative genes which have different actions (Mitra, 2001). Gene effects are described by gene actions which can be additive, dominant or epistatic (Acquaah, 2007). The expression of a trait is dependent to genotype, environment and genotype by environment (G×E) interactions (Cheema and Sadaqat, 2004). Therefore, the gene actions need a particular analysis in each case study involving various genotypes and environments through appropriate genetic designs (Acquaah, 2007). Various gene actions have been identified and described in different studies on sweetpotato. Miller, (1939) found that white skin, green stem and white flesh are dominant to red skin, red stem and yellow flesh of sweetpotato. Ma (2009) observed that the inheritance of β-carotene is controlled by additive gene effects. The additive gene effects were identified in the inheritance of dry matter and β-carotene content (Chiona, 2009). Hariprakash (2011) found the continuous and overlapping characters of vine, storage root, dry matter and cooking qualities of sweetpotato. More than five genes were suggested to be involved in the β-carotene synthesis and in combination with other genes to determine the flesh colour of storage roots of sweetpotato. Heterosis was observed for the size and number of roots per plant, indicating dominance gene action or intra-allelic interaction between alleles of the same gene (Gasura et al., 2010). These findings emphasised the quantitative nature of many sweetpotato traits and indicate that several plant characteristics associated with yield are controlled by more than two genes acting and interacting in complex model. Therefore, the combination of two or more quantitative traits in one cultivar requires knowledge of the gene actions and correlation between traits to improve selection response.

Traits can be positively or negatively correlated or not correlated (Acquaah, 2007). The existence of positive correlation between traits implies that selection of one trait positively influences the other requiring simultaneous selection. While negative correlations between traits suggest that selection of one trait causes an obligatory decrease of the other trait. The absence of correlation indicates that each trait

can be selected and improved independently (Acquaah, 2007). However, the complete absence of correlation between traits is a rare case in plant breeding. For example, the breeding for orange fresh sweetpotato with a high β-carotene, iron and zinc contents is challenged by a strong negative genetic correlation with dry matter content (Gruneberg et al., 2009; Ma et al., 2009; Vimala and Hariprakash, 2011). This negative association of dry matter and β-carotene content was attributed to a competition between the starch and the β-carotene because both are synthesised in plastids (Cervantes-Flores et al., 2008). Ma-Teresa et al. (1994) observed a negative correlation between root dry matter content and root yield. A negative correlation was also noted between dry matter and soluble sugar contents of sweetpotato (Gruneberg et al., 2009). However, the correlation between dry matter and drought tolerance in sweetpotato is poorly documented.

Breeding of sweetpotato

Sweetpotato breeding has been slower than that of several other staple crops because of the inherent nature of the crop including polyploidy, poor flowering and seed set, self- and cross-incompatibility, heterozygosity and large chromosome number. Often, flowering dates are different between sweetpotato genotypes which in turn may be influenced by environmental conditions (Jones et al., 1986). Its hexaploidy (Jones and Deonier, 1965; Vimala and Hariprakash, 2011) and the irregular meiotic division of sweetpotato (Ting and Kehr, 1953; Jones and Deonier, 1965; Maluf et al., 1983) have negatively affected breeding progress. In addition, self- or cross- incompatibility between genotypes remain the major challenge to sweetpotato breeders (Martin, 1965). Thus, a successful breeding program has to overcome these challenges to achieve greater selection efficiency.

Several techniques and controlled environmental conditions have improved the flowering and seed production of sweetpotato (Jones, 1980). Techniques including physiological shocks, grafting, girdling and chemical treatment help to improve the flowering of sweetpotato (Jones et al., 1986). Miller (1939) revealed fertilization of ovule and seed production are temperature, humidity and light dependent. At low temperature, fertilisation is low because of poor pollen germination and reduced pollen tube growth. Flower and seed production is enhanced under tropical than temperate climates. Jones et al. (1986) indicated that seed production is reduced when the crop shows lush and high vegetative growth. The authors pinpointed that adequate plant canopy air circulation improves seed set. All these findings have an important implication on sweetpotato breeding. Sweetpotato breeding programmes often have a common overall objective but differ in specific objectives. The overall objective of most sweetpotato breeding programmes is to improve quality and quantity of sweetpotato production through breeding (Jones et al., 1986; Kapinga and Carey, 2003). But the specific objectives vary depending on various needs. Many breeding programmes focus on the development of new varieties with enhanced quality such as improved β-carotene, anthocyanin and iron contents, and high yield, dry matter and biomass production (Jones et al., 1986; Fuglie, 2007; Gruneberg et al., 2009; Mwanga et al., 2010). Also, most breeding programmes aim to devolve new clones with high yield and combined resistance to abiotic and biotic stresses, and other characteristics that enhance acceptability by end users (Kapinga and Carey, 2003; Loebenstein and Thottappilly, 2009) Therefore, it is necessary to define the breeding objectives which guide the choice of potential parents and ensuing breeding method. Adequate genetic variation is important to identify valuable genes. Therefore, characterisation of available germplasm and identification of potential parents is the first step in most breeding programmes (Mitra, 2001; Shumbusha et al., 2010). Globally there are recognized institutions such as Vegetable Breeding Laboratory of Charleston and Louisiana sweetpotato research center in USA, Asian Vegetable Research and Development Center (AVRDC) in China, Genetic Resources Unit of the International Institute for Tropical Agriculture (IITA) at Ibadan/Nigeria and the International Potato Centre (CIP) in Peru to acquire valuable genetic resources of sweetpotato for breeding (Villareal and Lo, 1983; Iwanaga, 1988; Tjintokohadi and Mok, 2001). Likewise, local landraces should be properly collected and efficiently phenotyped to identify useful genes for characteristics of interest.

Breeding for high dry matter content

High dry matter content is one of the main aims in sweetpotato breeding programmes. Dry matter content varies due to a number of factors such as variety, location, climate, incidence of pests and diseases, cultural practices and soil types (Jones et al., 1986; Manrique and Hermann, 2000; Shumbusha et al., 2010; Vimala and Hariprakash, 2011). The narrow sense heritability estimates of dry matter content were reported to vary from 0.65 to 0.92. In addition, transgressive segregation for dry matter content has been indicated in sweetpotato progenies (Cervantes-Flores et al., 2008). Most genetic studies and the existence of several enzymes involved in starch biosynthesis indicate that dry matter content show quantitative inheritance (Cervantes-Flores et al., 2008). Jones, (1986) reported that the value and acceptability of a new sweetpotato variety depends on presence of relevant traits in suitable genetic combination. Therefore, characteristics that meet the farmers', consumers' and market preferences have to be considered in the selection process of new cultivars.

Selection for high dry matter content

Morphological markers

Screening for high dry matter content can be direct or indirect depending on the correlation between dry matter content and other traits (Acquaah, 2007). In the direct approach the screening is mainly based on the weight of dry root mass (Ma et al., 2009; Vimala and Hariprakash, 2011). To determine dry matter content, precise quantity of fresh weight of root is excised and dried to a constant weight. Then, the dry matter content is determined as a ratio of dry weight and initial fresh weight (Shumbusha et al., 2010). In the indirect approach, clones with a high dry matter can be selected by quantifying the starch continent of the root. This method is based on a highly positive correlation between dry matter and starch content (Cervantes-Flores et al., 2010; Ma et al., 2009). Because of genotypic variance and genotype by environment interaction, it was suggested that dry matter and starch content may be improved with a high selection efficiency in the earlier breeding stages (Grüneberg et al., 2005).

Molecular markers

Molecular or DNA markers are alternative tools that can be used in the screening for high dry matter content (Cervantes-Flores et al., 2010; Cervantes-Flores et al., 2011). Molecular markers have showed important potential to improve the

efficiency and precision of conventional breeding techniques (Acquaah, 2007). The large number of quantitative trait loci (QTLs) mapping studies for diverse crops species have provided an abundance of DNA marker-trait associations. The principles of molecular marker development consist of population development, QTL mapping, QTL validation, marker validation and marker-assisted selection (Collard and Mackill, 2008). If available, molecular markers are useful for selection of traits with low heritability (Collard and Mackill, 2008; Gupta et al., 1999). Molecular markers are used to monitor the variation of DNA sequence between and among species and to identify the genetic variability and presence of genes associated with valuable traits (Korzun, 2003). They could help to identify multiple alleles in the analysis of plant genome and genetic similarities between individuals (Buteler et al., 1999). Different molecular markers such as simple sequence repeats (SSRs) also known as microsatellites genetic markers, restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), sequence tagged sites (STS), amplified fragment length polymorphisms (AFLPs), single nucleotide polymorphisms (SNPs) were proposed in genetic and breeding studies (Acquaah, 2007; Gupta et al., 2009; Korzun, 2003). Mackill and Ni (2001) and Gupta et al. (1999) reported that the reliability, quantity and quality of DNA required, technical procedure for marker assay, level of polymorphism and cost are the main considerations for the use of molecular markers in a breeding programme. The most widely used molecular markers are SSRs because they are highly reliable, co-dominant in inheritance, relatively simple and cheap, and generally high polymorphic (Collard and Mackill, 2008; Gupta et al., 1999). The disadvantages of SSRs markers are that they require polyacrylamide gel electrophoresis and give generally the information of a single locus per assay. These problems have been handled by developing SSR markers that present large size differences for detection in agarose gels and multiplexing several markers in a single reaction (Collard and Mackill, 2008; Korzun, 2003). Molecular markers have been applied in the characterization of genetic variation, quantitative trait mapping and molecular marker assisted selection. The application of molecular tools in breeding has resulted in a new field of molecular breeding (Acquaah, 2007). The basis of molecular breeding involves the utilization of molecular marker fingerprints to improve the selection efficiency of breeding programs (Collard and Mackill, 2008; Eathington et al., 2007). This molecular breeding programme requires standard plant breeding procedures such as field trials, crosses, collection of phenotypic data and their analysis, analysis and interpretation of genotypic data, joint analysis of genotypic and phenotypic data, and decision making using molecular marker information. This process improves the genetic gain of a selection program (Eathington et al., 2007). In sweet potatoes quantitative trait loci (QTL) are identified showing associations with dry-matter, starch and β-carotene content. This was developed via mapping population generated from crosses between varieties with white-fleshed and high dry-matter content and orange-fleshed and low dry-matter content. The analysis of parental maps constructed using a population of 240 clones revealed the presence of 13 QTLs for storage root dry matter content, 12 QTLs for starch content and 8 QTLs for β-carotene content (Cervantes-Flores et al., 2011). Fourteen molecular markers associated with root dry matter content of sweetpotato were selected from 903 markers generated with four AFLP primers. The application of these markers revealed the phenotypic grouping without error (Labonte et al., 2002). Fifty seven sweetpotato genotypes with high dry matter content and resistant to sweetpotato virus disease (SPVD) were characterized using four SSR markers. The total number of alleles was 395, with an average of 4 alleles per locus. However, there were not specific groups in relation to SPVD resistance, dry matter content and geographic location. This high level of genetic diversity shows the broad genetic base for sweetpotato breeding (Tairo et al., 2012). RAPD markers for sweetpotato were developed and used to produce genetic fingerprints of six clonal cultivars and to estimate genetic distances between these cultivars. The analysis of patterns generated by this study has resulted in the classification of cultivars into groups based on similarities and the identification of primers which gave greatest discrimination among the cultivars (Connolly et al., 1994). RFLPs and RAPDs were used to evaluate phylogenetic relationships, genetic diversity and relationships of sweetpotato genotypes. The results from these studies have showed the importance of molecular tools to evaluate the genetic diversity and to identify the taxonomic and evolutionary relationships of *Ipomoea* species (Jarret and Austin, 1994; Jarret et al., 1992). Karuri et al. (2010) used morphological and SSR markers to evaluate genetic diversity of 89 sweetpotato genotypes. Accordingly, the comparison between morphological and molecular data revealed a low correlation (r = -0.05) between the two data sets. However, both methods showed a high degree of variation among the genotypes (Karuri et al., 2010). Mcharo and Labonte (2010) developed the molecular markers associated with β-carotene of sweetpotato using multivariate selection of AFLP markers in F_1 half-sib population and their parents. Veasey et al. (2008) studied the genetic diversity in Brazilian sweetpotato landraces using microsatellite markers. Each pair of primer generated between three and ten clearly scorable polymorphic fragments. This study revealed a high genetic and intra-varietal diversity. However, there was not a significant difference among the sampled sites. This observation was attributed to the outcrossing mating system of sweetpotato, selection of different varieties and their maintenance within household plots, and extensive exchange system of planting materials between farmer communities. Zhangying et al. (2011) characterized and developed expressed sequence tags (ESTs) derived SSR markers in cultivated sweetpotato. This study showed the frequency, type and distribution of sweetpotato EST-SSRs and demonstrated successful development of EST-SSR markers in cultivated sweetpotato. These EST-SSR markers could be useful for qualitative and quantitative trait mapping, marker-assisted selection, evolution and genetic diversity studies in cultivated sweetpotato and related *Ipomoea* species (Zhangying et al., 2011). The efficiency of results from these studies revealed the importance of use of molecular markers in conventional breeding programme and their potential to screen sweetpotato clones with high dry matter content.

Genotype by environment (G×E) interaction and yield stability

Crop growth and production are a result of interactions of its genetic potential and environment. Crops perform well in environments in which they are adapted (Acquaah, 2007). The performance of genotypes is quantified in terms of a wide and specific adaptability and yield stability (Abidin et al., 2005). The wide adaptability is generally attributed to genotypes performing well over large areas and presenting high mean yields across different environments. A variety has a specific adaptability when it ranks among the highest yielding genotypes at only some locations. The stability

which can be static or dynamic is the ability of a genotype to perform consistently across a wide range of environments (Acquaah, 2007). Knowledge on the types of genotype by environment (G×E) interactions is very important before release to decide if a new variety has wide or specific adaptation (Grüneberg et al., 2005; Manrique and Hermann, 2000). The G×E interaction are differential genotypic expression across multiple environments (Acquaah, 2007). It complicates the comparison of the performance of genotypes across environments when a high number of genotypes and locations are involved and quite often delays the selection process of a breeding programme (Caliskan et al., 2007). Prior to release of a new variety, genotypes of high yield potential are evaluated at different locations and several years to identify their G×E interaction and yield stability (Acquaah, 2007). Therefore, breeders need robust biometrical methods to estimates phenotypic stability and to analyse G×E interactions (Bacusmo et al., 1988; Becker and Leon, 1988).

Methods to evaluate G×E and yield stability

There are various methods to estimate the phenotypic stability and to analyse the G×E interactions (Bacusmo et al., 1988; Caliskan et al., 2007). These methods are classified into two main groups of univariate stability statistics and multivariate methods (Becker and Leon, 1988). The univariate stability statistics can be parametric by using a variance of a genotype across environments (Shukla, 1972), ecovalence, regression coefficient (Finlay and Wilkinson, 1963; Russell and Eberhart, 1966; Shukla, 1972), deviation mean squares, or coefficient of determination to identify the stability of genotypes (Becker and Leon, 1988). It can also be nonparametric when it is based on rank orders of genotypes using mean or variance ranks (Becker and Leon, 1988). Multivariate methods of analysis of G×E interactions consist of a wide range of methods including multivariate analysis of variance (MANOVA), cluster analysis, principal component analysis, additive main effects and multiplicative interactions (AMMI), GGE-bioplot, geometrical methods and stochastic dominance (Becker and Leon, 1988; Gauch and Zobel, 1996; Purchase, 1997; Yan, 2001). Both univariate stability statistics and multivariate methods are based mainly on the analysis of variance, regression methods, or principal component analysis.

G×E interaction and yield stability on sweetpotato

Sweetpotato is very sensitive to environmental changes (Bacusmo et al., 1988; Carpena et al., 1980). Grunerberd et al. (2005) observed variations in the yield and stability in the multi-environmental trials of different genotypes of sweetpotato. A significant G×E interaction was found for the mean storage root weight and storage root yield. However, the contribution of genotype main effects to the total variability was bigger than the environment and G×E interaction effects (Caliskan et al., 2007). The analysis of combined and AMMI analysis of total storage root yield of sweetpotato genotypes revealed high significant effects of genotype, environment and G×E interactions. The genotype mean effects explained 67.9% of the total variation whereas environment and G×E interactions explained 21.0% and 10.4% respectively of total variation (Caliskan et al., 2007). Genotype, environment and G×E interaction effects for average storage roots were significant in combined and AMMI analysis. The genotype mean effects explained 49.5% of the total variation and G×E interactions explained 23.5% (Caliskan et al., 2007). Manrique and Hermann (2000) found that β-carotene content in roots increases with altitude. However, they did not find a high yielding variety with sufficient stability for total root yield. The G×E analysis with regression, AMMI and cluster analysis methods revealed that the G×E interactions for yield traits were larger than genetic variation. However, the G×E interactions for nutritional traits of sweetpotato were small (Grüneberg et al., 2005). Although the presence of significant G×E interactions for wide and specific yield stability and quality of sweetpotato has been reported (Caliskan et al., 2007; Manrique and Hermann, 2000; Ngeve, 1993), it has been observed that it is difficult to get a variety with wide stability together with high yield and good performance (Affleck et al., 2008). Breeders and agronomists have to carry out multi-environmental trials to identify the stability and G×E interactions of a new cultivar before its release (Grüneberg et al., 2005). However, multi-environmental trials are very difficult to conduct because of cost of labor and lack of seed or planting materials. Vermeer (1990) and Affleck et al. (2008) suggested that identification of low number of best environments that have ability for differentiating genotypes can reduce the cost of the breeding programme. In this regard, the use of at least one favourable and one unfavourable environment in the early stage of selection of sweetpotato was proposed to increase beneficial alleles in the breeding materials (Grüneberg et al., 2005). This also requires an appropriate method to quantify the stability across a range of environments. The comparison of Eberhart and Russell's (1966), Tai's (1971) and biplot approaches in studies of G×E interactions and yield stability of root crops concluded that the biplot analysis presents advantages compared to other methods (Affleck et al., 2008). Caliskan et al., (2007) and Hermann (2005) suggested that the additive main effects and multiplicative interaction (AMMI) approach is the best to evaluate the G×E interactions and stability of sweetpotato genotypes in the multi-locational trials. In the investigation of G×E interactions and stability analysis of sweetpotato geneotypes, Caliskan et al. (2007) observed a significant correlation between at least one parameter of Eberhart and Russell's, Tai's, and Shukla's methods. The Eberhart and Russell's (1966) and Tai (1971) stability parameters provided similar ranking patterns of genotypes. However, these genotypes were not stable for total storage root yield. It was also found that ranking correlation based on the AMMI stability value (ASV) and coefficient of variation (CV) was similar for average storage root weight and total storage root (Caliskan et al., 2007). This indicates that the AMMI model provides similar information of genotype stability as Eberhart and Russell's, Tai's, and Shukla's methods. Highly significant ranking correlations were found among the deviations from regression, ASV, CV and stability variances (Adugna and Labuschagne, 2002). This revealed a close similarity and effectiveness between univariate and multivariate methods to determine genotype stability and G×E interactions. Studies to determine the stability of sweetpotato genotypes in the multilocational trials have revealed that Eberhart and Russell (1966), Tai (1971), Shukla (1972) methods tended to give the same results (Bacusmo et al., 1988). Ngeve (1993) using the regression method with Eberhart and Russell (1966) and Shukla (1972) approaches to analyse G×E interactions in sweetpotato found irregularity in identifying stable genotypes. Causes of this irregularity were attributed to the use of various regression parameters which interpret stability in different ways. Because of various methods to estimate the G×E interactions and yield stability, most breeders use more than one method to get accurate results (Bacusmo et al., 1988; Caliskan et al., 2007). However, the choice of a

suitable method depends on the intended purpose and required outcome.

Conclusion

High dry matter of storage root of sweetpotato is an important characteristic for consumers and processors. Dry matter content above 25% is an important factor for farmers to adopt a new variety of sweetpotato. For industrial use of sweetpotato varieties with a dry matter content that is above 30% of fresh root weight is required. These standards necessitate serious consideration of dry matter content in any breeding programme aiming to develop a new variety of sweetpotato. The development of new variety with high dry matter content requires efficient methods of crossing and screening and evaluating the effects of G×E interaction on the yield and dry matter content of storage root as summarised in this paper.

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