Early-season Soil Moisture Deficit Reduces Sweetpotato Storage Root Initiation and Development

Bandara Gajanayake¹ and K. Raja Reddy^{2,4}

Department of Plant and Soil Sciences, 117 Dorman Hall, Box 9555, Mississippi State University, Mississippi State, MS 39762

Mark W. Shankle² and Ramon A. Arancibia³

Pontotoc Ridge-Flatwoods Branch Experiment Station, North Mississippi Research and Extension Center, Mississippi State University, 8320, Highway 15 South, Pontotoc, MS 38863

Additional index words. adventitious root, development, growth, soil moisture, storage root

Abstract. Sweetpotato [*Ipomoea batatas* (L.) Lam.] storage root formation is a complex developmental process. Little quantitative information is available on storage root initiation in response to a wide range of soil moisture levels. This study aimed to quantify the effects of different levels of soil moisture on sweetpotato storage root initiation and to develop functional relationships for crop modeling. Five levels of soil moisture, 0.256, 0.216, 0.164, 0.107, and 0.058 m³·m⁻³ soil, were maintained using sensor-based soil moisture monitoring and semiautomated programmed irrigation. Two commercial sweetpotato cultivars, Beauregard and Evangeline, were grown in pots under greenhouse conditions and treatments were imposed from transplanting to 50 days. Identification of storage roots was based on anatomical, using cross-sections of adventitious roots, and visual features harvested at 5-day intervals from 14 to 50 days after transplanting (DAT). Recorded time-series storage root numbers exhibited sigmoidal responses at all soil moisture levels in both cultivars. Time to 50% storage root initiation and maximum storage root numbers were estimated from those curves. Rate of storage root development was determined as a reciprocal of time to 50% storage root formation data. Time to 50% storage root initiation declined quadratically from 0.05 to 0.15 m³·m⁻³ soil moisture and increased slightly at the higher soil moisture levels in both the cultivars. Cultivars differed in time to 50% storage root initiation and the storage root developmental rate. Soil moisture optima for storage root initiation were 0.168 and 0.199 m³·m⁻³ soil, equivalent to 63% and 75% field capacity for cultivars Beauregard and Evangeline, respectively. The data and the inferences derived from the functional algorithms developed in this study could be used to advise growers to schedule irrigation more precisely, make planting decisions based on available soil moisture, and to develop sweetpotato crop models for field applications.

Sweetpotato is an important root crop grown in tropical and subtropical regions and ranks as the seventh major food crop produced annually worldwide (Bovell-Benjamin, 2007; Ku et al., 2008). Production of sweetpotato is an important agricultural business (U.S. Department of Agriculture, Agricultural Research Service, 2002) in the southern states of the United States and contributed more than \$500

million to the country's economy in 2012 (U.S. Department of Agriculture, 2013). Many sweetpotato cultivars have shown wide adaptability to various environmental conditions (Martin, 1988); however, production is constrained by various abiotic stresses. Both Togari (1950) and Villordon et al. (2012) emphasized that the growing environment during the early season (first 20 d) has a direct and significant impact on storage root initiation and thus final yield. Sweetpotato is grown as a rain-fed crop in Mississippi and subjected to fluctuating soil moisture conditions in the field. Sweetpotato is also grown under furrow or drip-irrigated conditions in California (Stoddard et al., 2013). Soil moisture stress is one of the crucial abiotic stress factors that limits growth and development of sweetpotato, affecting storage root production and yield (Indira and Kabeerathumma, 1988; Pardales and Esquibel, 1997).

Drought is a dry weather condition for an extended period of time characterized by a shortage of water supply to plants and causes extensive losses to agricultural production worldwide (Acquaah, 2007; Chaves et al.,

2002). Agricultural drought relates to the soil moisture deficits in the root zone. Soil moisture deficit is defined as the induction of turgor pressure below the maximal potential pressure and the magnitude of such stress is determined by the extent and duration of the deprivation (Pugnaire et al., 1999). Sweetpotatoes are often cultivated on non-irrigated lands and have been considered drought-tolerant (Constantin et al., 1974), although the response to moisture stress varies with cultivar (Villareal et al., 1979). According to Nair (2000), sweetpotato possesses moderate drought tolerance, but storage root yield decreases if drought conditions prevail during the storage root initiation period, estimated to be between 10 and 30 d after treatment. Edmond and Ammerman (1971) also reported reduced root yields if drought occurred within the first 6 weeks after transplanting.

Sweetpotato storage root formation is a complex developmental process associated with the expression of several genes, which are influenced by several environmental factors (Ravi et al., 2009). Transplanted slips produce adventitious roots, some of which develop into economically important storage roots through proliferation of cambial cells that form starch-accumulating parenchyma cells (Belehu et al., 2004; Ravi et al., 2009; Villordon et al., 2009a). This developmental process starts ≈13 d after transplanting of slips in the field (Villordon et al., 2010). Thus, any moisture deficit before and during this stage will detrimentally impact final storage root numbers and yield. In the early stage of root development, sweetpotato forms colorless adventitious roots. As root development proceeds, some of these adventitious roots become pigmented and begin to swell and finally develop into storage roots. Many efforts have been directed toward early identification of sweetpotato storage roots based on anatomical features. Accordingly, the development of anomalous cambia was identified as an important factor to determine the formation of storage roots and its appearance marks the initiation phase of storage root formation (Kokubu, 1973; Wilson and Lowe, 1973). A similar approach was used by Villordon et al. (2009a) in early identification of the storage roots. They investigated many related anatomical features associated with storage root development and finally selected the appearance of regular vascular cambium and anomalous cambia to identify the storage roots. Therefore, appearance of cambia can be used to reliably identify and measure storage root initiation in sweetpotato.

'Beauregard' and 'Evangeline' are among various popular cultivars grown by producers in the Mississippi Delta and mid-South United States. Compared with 'Beauregard', 'Evangeline' is more resistant to root-knot nematode infestation and has higher sucrose content in storage roots (La Bonte et al., 2008). However, few studies have been conducted to compare the responses of the cultivars to abiotic variables such as soil moisture stress. We hypothesized that storage root initiation and subsequent growth of sweetpotatoes

Received for publication 13 June 2013. Accepted for publication 17 Oct. 2013.

This work was in part funded by the USDA-NIFA Specialty Crop Research Initiative grant number 2009-51181-06071, the Mississippi Sweetpotato Council, and the USDA-UVB Monitoring and Research Program, USDA-NIFA-2011-34263-30654, G-1405-2.

Approved for publication as journal article no. 12329 of the Mississippi Agricultural and Forestry Experiment Station, Mississippi State University.

¹Graduate Research Assistant.

²Professor.

³Assistant Professor.

⁴To whom reprint requests should be addressed; e-mail kreddy@pss.msstate.edu.

would be reduced under deficit soil moisture conditions. This study aimed to quantify the effects of different degrees of soil moisture availability on storage root initiation and early-season growth in two different sweetpotato cultivars and to develop functional algorithms for storage root development under a wide range of soil moisture conditions.

Materials and Methods

Sweetpotato cultivars Beauregard (Rolston et al., 1987) and Evangeline (La Bonte et al., 2008) were evaluated at five levels of soil moisture under greenhouse conditions at the R.R. Foil Plant Science Research Center, Mississippi State University, Mississippi State (lat. 33°28' N, long. 88°47' W), Mississippi. The temperatures in the greenhouse were maintained between 24 and 33 °C during the experimental period, May to June 2012. The photosynthetically active radiation measured with a line quantum sensor (LI-191 Line quantum sensor; LI-COR, Inc., Lincoln, NE) on clear days at 1200 HR was over 1200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Thirty-two 2-L plastic pots (17 cm diameter and 16 cm height) were used for each moisture treatment per cultivar to accomplish eight harvests. The experiment was arranged as a completely randomized design with four replicates. Pots were filled with a growth substrate (1:3 soil:river sand mixture) tested at the Mississippi State University Extension Service Soil Testing Laboratory and having sandy clay loam textural class (72% sand, 23% clay, and 5% silt). Pots were arranged in rows oriented east to west on benches in the greenhouse. Pots were fully saturated using full-strength Hoagland nutrient solution (Hewitt, 1952) initially and five levels of soil moisture treatments, 0.256, 0.216, 0.164, 0.107, and 0.058 $\text{m}^3\cdot\text{m}^{-3}$ soil, representing 100%, 84%, 64%, 42%, and 23% of field capacity (FC), respectively, were imposed 2 weeks before transplanting of sweetpotato slips (Fig. 1). Soil moisture treatment levels were monitored and maintained based on the volumetric water content determined by moisture sensors (Model EC-5; Decagon Devices, Inc.,

Pullman WA) inserted at a depth of 10 cm in every five random pots of each soil moisture treatment. All sensors were connected to data loggers that were configured to record data every 15 min (Model EM50R; Decagon Devices, Inc.). Based on the treatment and measured soil moisture content (SMC), the required amount of water with nutrient solution to be applied was calculated twice a day. Using the known discharge rate of drip emitters (50 $\text{mL}\cdot\text{min}^{-1}$), the time to be irrigated (min) to meet the desired soil moisture level was calculated using Eq. [1].

Irrigation time (min.)

$$= \frac{(\text{treatment SMC} - \text{measured SMC})}{\text{emitter discharge rate}} \quad [1]$$

Irrigation was supplied using drippers and plastic tubing connected to a water pump and required levels of soil moisture were maintained in each treatment accordingly. Once the desired soil moisture levels for all treatments were achieved, sweetpotato slips were transplanted by placing two nodes in the soil and two nodes above the soil surface. Full-strength Hoagland nutrient solution, which provided a balanced mixture of nutrients was used to fertigate the plants.

Root number and identification of storage roots were determined based on anatomical features and visual observation. Four random pots were removed on 5-d intervals starting at 14 d after transplanting from each soil moisture treatment until 50 DAT. Roots were washed with water and shoots and roots were separated and the plant growth measurements were recorded. Total adventitious root number from each plant at each harvest was counted. Adventitious root samples from each plant at each harvest were taken and cross-sections were prepared for anatomical observations through free-hand sectioning and staining with Safranin and Toluidine blue as described by Eguchi and Yoshida (2008). Root cross-section samples were taken from a 3-cm section located 7 to 10 cm from the proximal end. After staining, the development of anomalous cambia around primary

and secondary xylem tissues was identified as described by Villordon et al. (2009a, 2009b). Accordingly, the identification of storage roots was performed based on the appearance of anomalous cambia in the stellar region, which stained very lightly, and non-storage roots based on a lignified stele section, which stained dark in color. After ≈ 20 DAT, storage roots were already visible by bulking of the adventitious roots and identification was carried out visually. Anomalous primary cambia developed around the central metaxylem cells and protoxylem elements and anomalous secondary cambia developed around secondary xylem elements (Wilson and Lowe, 1973) were collectively referred to anomalous cambium in our study and also by Villordon et al. (2009a). The number of storage and non-storage roots per plant was recorded at every harvest based on these criteria.

Curve-fitting procedure for storage root development time. The numbers of storage roots developed (Y) over each harvesting time (X), measured by DAT (d) during the experimental period, were fitted to a three-parameter sigmoidal function [Eq. (2)] using SigmaPlot 11.0 (Systat Software, Inc., San Jose, CA) as described by Gajanayake et al. (2011), Garcia-Huidobro et al. (1982), and Shafii and Price (2001). Maximum storage root numbers (MSRN) at a given time (X), the shape and steepness of the curve (b), and the time to develop 50% of MSRN (X_0) were estimated using sigmoidal functions with given storage root numbers (Y) and DAT (X).

$$Y = \text{MSRN} / \{1 + \exp[(-X - X_0)/b]\} \quad [2]$$

The MSRNs and the reciprocal of time to develop 50% of maximum storage root numbers [storage root development rate (SRDR)] were used to determine their responses to soil moisture treatments.

Determination of maximum storage root numbers and storage root developmental rates. Both linear and non-linear models were used to analyze MSRN and SRDR responses to soil moisture content. The best models were determined based on the overall highest coefficient of determination (R^2) and the least root mean square error values. Linear and quadratic equation estimates for each replicate of the treatment and cultivar were estimated by the non-linear regression procedure, PROC NLIN (SAS Institute Inc., Cary, NC) using a modified Newton Gauss iterative method.

Based on these criteria, the linear model best described the MSRN response to soil moisture content, whereas quadratic functions best described both SRDR and time to 50% storage root development. The estimated MSRNs for each soil moisture treatment using sigmoidal function [Eq. (2)] were used to generate the responses of MSRN against different soil moisture treatments. Also, Eq. [2] was used to estimate the time to 50% storage root initiation for each soil moisture treatment. The soil moisture treatment level, which minimized the time to form storage roots, was determined using the time function. The

Fig. 1. Volumetric soil moisture content across treatments before and during the experimental period were maintained using sensor-based monitoring and irrigation system. The arrow indicates the day sweetpotato slips were planted and the time when all the soil moisture levels reached the desired treatment levels.

storage root initiation rate was calculated as the reciprocal of estimated time to 50% storage root initiation for each soil moisture treatment. Similar to the time function, the soil moisture treatment level, which maximized the rate to form storage roots (soil moisture optima), was determined. SigmaPlot 11 was used to plot the relationships and the non-linear regression procedure PROCNLIN in SAS was used to estimate the parameters in sigmoidal curves. Replicated values for other measured parameters were analyzed using the one-way analysis of variance (ANOVA) procedure (PROC GLM) in SAS. Means were separated using Fisher's protected least

significant difference test ($P < 0.05$). Storage root number and time to 50% storage root initiation were treated as dependent variables and the soil moisture levels as independent variables.

Results and Discussion

Using soil moisture sensor-based monitoring and irrigation to set up and maintain several precise soil moisture regimes worked well to quantify storage root initiation as affected by the treatments in this study (Figs. 1 and 2). To our knowledge, this is the first report to identify the functional relationships

of storage root initiation and storage root number of sweetpotato in response to a wide range of soil moisture regimes that could be useful for management decisions in the field. Furthermore, soil moisture status is one of the crucial and readily manageable variables to produce a profitable crop (Taylor et al., 1983).

Storage root production time course and rate of storage root initiation

Soil moisture regimes markedly influenced storage root initiation and development of both sweetpotato cultivars (Fig. 2). A three-parameter sigmoidal function best described the storage root production time course across different soil moisture regimes in both cultivars. The ANOVA results indicate significant differences between the two cultivars and among the soil moisture levels ($P < 0.001$) within each cultivar, except at the two highest soil moisture levels for cultivar Evangeline. The maximum storage root number, time to 50% storage root initiation, and storage root initiation rate, estimated from the fitted sigmoidal curves, were all affected by moisture levels (Fig. 3).

Maximum storage root number increased linearly with increasing soil moisture levels in both cultivars ($P < 0.0001$; slope = 23.23; Fig. 3A). Time to 50% storage root initiation, on the other hand, showed a significant and quadratic decline with increasing soil moisture levels in both cultivars until soil moisture levels reached 0.167 and 0.199 $\text{m}^3\cdot\text{m}^{-3}$ soil in the cultivars Beauregard ($R^2 = 0.83$) and Evangeline ($R^2 = 0.98$), respectively (Fig. 3B). The minimum time required to 50% storage root initiation was 21.3 d at a soil moisture level of 0.199 $\text{m}^3\cdot\text{m}^{-3}$ (78% FC) for 'Evangeline' and 20.8 d for 'Beauregard' at 0.167 $\text{m}^3\cdot\text{m}^{-3}$ soil (65% FC). With increasing soil moisture, time to reach 50% storage root initiation was markedly higher for soil maintained at 0.167 and 0.199 $\text{m}^3\cdot\text{m}^{-3}$ for cultivars Beauregard and Evangeline, respectively (Fig. 3B). We observed significantly ($P < 0.05$) less storage root number at soil moisture content of 0.256 $\text{m}^3\cdot\text{m}^{-3}$ (100% FC) compared with 0.216 $\text{m}^3\cdot\text{m}^{-3}$ soil (84% FC) from 19 to 50 DAT for the cultivar Beauregard. Watanabe (1979) reported that sweetpotato showed a luxurious vegetative growth and little "tuber" development when soil moisture content was high or the soil was compacted. However, Van Heerden and Laurie (2008) found no significant differences in sweetpotato storage root yields between 100% and 80% FC treatments harvested at 91 DAT. Our results at the two highest soil moisture treatments corroborate these findings.

The rate of storage root initiation, which is an inverse relationship of time to 50% storage root initiation, showed a significant and quadratic increment with increasing soil moisture levels in both cultivars (Fig. 3C). Estimated optimum soil moisture levels for maximum storage root initiation with the cultivars Beauregard and Evangeline were 0.167 and 0.199 $\text{m}^3\cdot\text{m}^{-3}$ soil (65.6% and 78.1% FC), respectively, based on the fitted equations. These results indicate that the two

Fig. 2. Time-series analysis of storage root development in two sweetpotato cultivars, Beauregard and Evangeline, across five soil moisture regimes. Symbols are observed cumulative storage root data and solid lines are fitted storage root initiation using a three-parameter sigmoidal function, $Y = \text{MSRN} / \{1 + \exp[-(x - x_0)/b]\}$, where Y is the number of storage roots developed over each harvesting time, b is the shape and steepness of the curve, and x_0 is the time to develop 50% of MSRN and x is the days after transplanting. Each data point is a mean cumulative storage root number of four individual plants and SEMs are shown when larger than the symbols. The three-parameter sigmoidal functions fitted to various soil moisture treatments were significant ($P < 0.0001$) in both the cultivars. MSRN = maximum storage root numbers.

Fig. 3. Influence of soil moisture content on (A) maximum storage roots numbers per plant, (B) time to 50% storage root formation, and (C) storage root initiation rate in two sweetpotato cultivars, Beauregard and Evangeline. Symbols are derived data on time to 50% storage root initiation and rate of storage root initiation and solid lines are predicted values of the respective fitted equations. Error bars indicate the SEMs ($n = 4$). RMSE = root mean square error.

cultivars responded differently to soil moisture levels during early-season storage root development. Pardales and Yamauchi (2003) also reported pronounced varietal differences on root traits in response to varying soil moisture regimes similar to our observations in this study. Results from our study confirm that sweetpotato storage root production can be improved by managing production practices such as irrigation during the early season.

Total and storage number and storage root production efficiency

Total and storage root number. Adventitious roots are typically produced at the nodal positions and at the cut end of the slips when transplanted. The majority of the adventitious roots produced during early stages of sweetpotato crop growth have similar anatomical structures and thus have the potential to develop into storage roots under favorable environmental conditions (Villordon et al., 2009b, 2012). Therefore, considerable efforts have been devoted to estimate adventitious and storage roots during the early season because of a close correlation between total

roots (adventitious roots and storage roots) produced during early stages of crop growth and number of harvestable storage roots at the end of the season (Villordon et al., 2009a). The total number of adventitious roots produced and their response to soil moisture regimes were significantly different between the cultivars ($P < 0.05$). The storage root number production response to soil moisture conditions was quadratic in both cultivars ($R^2 = 0.91$ and 0.98 for 'Beauregard' and 'Evangeline', respectively; Fig. 4A). However, cultivar Evangeline showed a steeper increase in total root numbers compared with the cultivar Beauregard as soil moisture increased. Pardales and Esquibel (1997) found that a low irrigation frequency, once every 4 d, had a significant reduction on number and length of adventitious roots compared with higher irrigation frequencies that coincide with soil moisture conditions and root responses observed in this study. These results further indicate that adequate soil moisture is crucial to maximize root establishment at early stages of crop growth. Under favorable soil moisture conditions, initiation of

adventitious roots can begin as early as 1 DAT slips in the field (Pardales, 1993; Pardales and Yamauchi, 2003) and maintaining optimum soil moisture levels is crucial for root development during the early stages of crop growth. Villordon et al. (2009b) found that sweetpotato storage roots form ≈ 13 DAT under favorable soil moisture and other environmental conditions. In our study, we observed a few storage roots formed at 14 d after planting with $0.164 \text{ m}^3 \cdot \text{m}^{-3}$ soil moisture levels (64% FC) in both cultivars (Fig. 2).

Storage root production efficiency. To fully comprehend how sweetpotato storage roots are formed, studies on morphogenesis have been carried out over a considerable period of time. Lowe and Wilson (1974) revealed that storage roots originate from the activation of primary cambium of the adventitious roots along with the anomalous and vascular cambia during the secondary growth. Belehu et al. (2004) also observed that slips produce adventitious roots and some of those roots develop into storage roots. To date, there are no studies on conversion efficiency of storage roots from the total roots produced under different environmental conditions. In this study, we calculated storage root production efficiency, defined as the percentage of storage roots to total roots produced, under five soil moisture levels in two commonly cultivated sweetpotato cultivars in the U.S. Delta and mid-South regions. Storage root production efficiencies between cultivars and soil moisture levels were significantly different (Fig. 4B). The response to soil moisture content was linear with the cultivar Beauregard ($R^2 = 0.87$, $P = 0.02$) and stable in the 'Evangeline' (Fig. 4B). These results highlight that storage root production efficiency is higher with the cultivar Evangeline than the cultivar Beauregard at lower soil moisture levels. Furthermore, 'Evangeline' is more stable under a wide range of soil moisture levels during the early stages of root growth. However, 'Beauregard' showed improved storage root production efficiency at and above the soil moisture regimes of $0.107 \text{ m}^3 \cdot \text{m}^{-3}$ soil (42% FC). Similar cultivar differences have been observed by others. Villordon et al. (2009a) reported a considerable variation in adventitious root number during early stages of growth (5 to 21 DAT) between two cultivars, Beauregard and Georgia Jet. Significant variation in root counts of thick and "tuberous" roots among three cultivars ('Koganesengan' and 'Beniako' with three basal nodes and *Ipomoea trifida* with two basal nodes) was reported at the fourth week after transplanting (Nakatani and Komeichi, 1991). However, conversion efficiency using adventitious and storage root numbers was not reported in these studies.

Conclusion

The present study investigated sweetpotato storage root growth and initiation in response to soil moisture regimes in two major sweetpotato cultivars. Results suggest that the rate of storage root initiation of

Fig. 4. Total root numbers (A) and storage root production efficiency (B), calculated as a percentage of storage roots to total roots produced across five levels of soil moisture of two sweetpotato cultivars, Beauregard and Evangeline. Symbols are derived data on total root numbers and calculated storage root production efficiency and solid lines are predicted values of the respective fitted equations. Error bars indicate the SEMs (n = 4). RMSE = root mean square error; NS = non-significant at $P \leq 0.05$.

sweetpotato is delayed by deficit soil moisture levels in both cultivars. The rate of storage root development showed a quadratic relationship with soil moisture level and the optimum rates were achieved at the soil moisture contents of 0.168 (64% FC) and 0.199 m³·m⁻³ soil (75% FC) in 'Beauregard' and 'Evangeline', respectively. These results suggest that managing soil moisture is crucial for storage root production during the early stages of sweetpotato crop growth. In addition, the functional soil moisture and storage root growth and developmental algorithms could be used to develop simulation models for sweetpotato under varying soil moisture conditions in predicting yield while taking into consideration of other abiotic and edaphic factors. However, temperature-dependent functional algorithms will be needed to improve the models that could be used to optimize planting dates and soil moisture levels by scheduling irrigation at appropriate times in the field.

Literature Cited

Acquaah, G. 2007. Principles of plant genetics and breeding. Blackwell, Malden, MA.
Belehu, T., P.S. Hammes, and P.R. Robertse. 2004. The origin and structure of adventitious roots in sweetpotato (*Ipomoea batatas*). Aust. J. Bot. 52:551–558.
Bovell-Benjamin, A. 2007. Sweetpotato: A review of its past, present, and future role in human nutrition. Adv. Food Nutr. Res. 52:1–59.
Chaves, M.M., J.S. Pereira, J. Maroco, M. Rodrigues, C.P.P. Ricardo, M.L. Osório, I. Carvalho, T. Faria, and C. Pinheiro. 2002. How plants cope with water stress in the field? Photosynthesis and growth. Ann. Bot. (Lond.) 89:907–916.

Constantin, R.J., T.P. Hernandez, and L.G. Jones. 1974. Effect of irrigation and nitrogen fertilization on quality of sweetpotatoes. J. Amer. Soc. Hort. Sci. 99:308–310.
Edmond, J.B. and G.R. Ammerman. 1971. Sweetpotatoes: Production, processing, and marketing. Avi Pub. Co., Inc., Westport, CT.
Eguchi, T. and S. Yoshida. 2008. Effects of application of sucrose and cytokinin to roots on the formation of tuberous roots in sweetpotato [*Ipomoea batatas* (L.) Lam.]. Plant Root 2:7–13.
Gajanayake, B., B.W. Trader, K.R. Reddy, and R.L. Harkess. 2011. Screening ornamental pepper cultivars for temperature tolerance using pollen and physiological parameters. HortScience 46:878–884.
Garcia-Huidobro, J., J. Monteith, and G. Squire. 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.): 1. Constant temperature. J. Expt. Bot. 33:288–296.
Hewitt, E.J. 1952. Sand and water culture methods used in the study of plant nutrition. Tech. Comm. Commonwealth Bureau of Horticulture and Plantation Crops Commonwealth Agr. No. 22. Commonwealth Agr. Bur., Farnham Royal, England, UK.
Indira, P. and S. Kabeerathumma. 1988. Physiological response of sweetpotato under water stress. 1. Effect of water stress during the different phases of tuberization. J. Root Crops 14:37–40.
Kokubu, T. 1973. Thremmatological studies on the relationship between the structure of tuberous root and its starch accumulating function in sweetpotato varieties. Bul. Fac. Agr. Kagoshima Univ. 23:1–126.
Ku, A.T., Y. Huang, Y. Wang, D. Ma, and K. Yeh. 2008. *IbMADS1* (*Ipomoea batatas* *MADS-box I* gene) is involved in tuberous root initiation in sweetpotato (*Ipomoea batatas*). Ann. Bot. (Lond.) 102:57–67.

La Bonte, D.R., P.W. Wilson, A.Q. Villordon, and C.A. Clark. 2008. Evangeline sweetpotato. HortScience. 43:258–259.
Lowe, S.B. and L.A. Wilson. 1974. Comparative analysis of tuber development in six sweetpotato [*Ipomoea batatas* (L.) Lam.] cultivars. 1. Tuber initiation, tuber growth and partition of assimilate. Ann. Bot. (Lond.) 38:307–317.
Martin, F.W. 1988. Genetic and physiological basis for breeding and improving the sweetpotato, p. 749–762. In: Degras, L. (ed.). Proc. of the VIIth Symposium of the International Society for Tropical Root Crops, Guadeloupe, French West India, INRA editions, Paris, France.
Nair, G.M. 2000. Cultural and manurial requirements of sweetpotato production technology of tuber crops. p. 44–72. In: Mohankumar, C.R., G.M. Nair, C. George, S. Ravindran, and V. Ravi (eds.). Production technology of tuber crops. Kerala, CTCRI, India.
Nakatani, M. and M. Komeichi. 1991. Changes in the endogenous level of zeatin riboside, abscisic acid and indole acetic acid during formation and thickening of tuberous roots in sweet potato. Jpn. J. Crop. Sci. 60:91–100.
Pardales, J.R., Jr. 1993. Inhibitory influences of sweetpotato used soil on the root growth of sweetpotato plants. Philipp. J. Crop Sci 18: 181–185.
Pardales, J.R., Jr. and C.B. Esquibel. 1997. Root development in sweetpotato stem cuttings as influenced by pre-planting, planting, and post-planting practices. Ann. Trop. Res 19:56–65.
Pardales, J.R., Jr. and A. Yamauchi. 2003. Regulation of root development in sweetpotato and cassava by soil moisture during their establishment period. Plant Soil 255:201–208.
Pugnaire, F.I., L. Serrano, and J. Pardos. 1999. Constraints by water stress on plant growth, p. 271–284. In: Pessaraki, M. (ed.). Handbook of plant and crop stress. Marcel Dekker Inc., New York, NY.
Ravi, V., S.K. Naskar, T. Makesh Kumar, B. Babu, and B.S.P. Krishnan. 2009. Molecular physiology of storage root formation and development in sweet potato [*Ipomoea batatas* (L.) Lam.]. J. Root Crops 35:1–27.
Rolston, L.H., C.A. Clark, J.M. Cannon, W.M. Randle, E.G. Riley, P.W. Wilson, and M.L. Robbins. 1987. 'Beauregard' sweetpotato. HortScience 22:1338–1339.
Shafii, B. and W. Price. 2001. Estimation of cardinal temperatures in germination data analysis. J. Agr. Biol. Environ. Stat. 6:356–366.
Stoddard, C.S., R.M. Davis, and M. Cantwell. 2013. Sweetpotato production in California. Univ. California Vegetable Research and Information Center, Division of Agriculture and Natural Resources, University of California, Vegetable production series, Publication 7237, Richmond, CA.
Taylor, H.M., W.R. Jordan, and T.R. Sinclair. 1983. Limitation to efficient water use in crop production. ASA-CSSA-SSSA, Madison, WI.
Togari, Y. 1950. A study of tuberous root initiation in sweetpotato. Bull. Natl. Agr. Exp. Stn. Tokyo 68:1–96.
U.S. Department of Agriculture. 2013. Crop values 2012 summary. 7 Aug. 2013. <<http://usda01.library.cornell.edu/usda/current/CropValuSu/CropValuSu-02-15-2013.pdf>>.
U.S. Department of Agriculture, Agricultural Research Service. 2002. Sweetpotatoes: Getting to the Root of Demand, Commodity Spotlight, Agricultural Outlook/13–17 November. 22 Nov. 2012. <<http://webarchives.edlib.org/swlhm53n4b/http://www.ers.usda.gov/publications/agoutlook/Nov2002/ao296e.pdf>>.

- Van Heerden, P.D. and R. Laurie. 2008. Effects of prolonged restriction in water supply on photosynthesis, shoot development and storage root yield in sweetpotato. *Physiol. Plant.* 134: 99–109.
- Villareal, R.L., S.L. Lin, and S.H. Lai. 1979. Variations in yielding ability of sweetpotato under drought stress and minimum input conditions. *HortScience* 14:31–32.
- Villordon, A., D.R. La Bonte, N. Firon, Y. Kfir, Y. Pressman, and A. Schwartz. 2009a. Characterization of adventitious root development in sweetpotato. *HortScience* 44:651–655.
- Villordon, A., D.R. La Bonte, and N. Firon. 2009b. Development of a simple thermal time method for describing the onset of morpho-anatomical features related to sweetpotato storage root initiation. *Sci. Hort.* 121:374–377.
- Villordon, A., D.R. LaBonte, J. Solis, and N. Firon. 2012. Characterization of lateral root development at the onset of storage root initiation in Beauregard sweetpotato adventitious roots. *HortScience* 47:961–968.
- Villordon, A., J. Solis, D.R. LaBonte, and C. Clark. 2010. Development of a prototype Bayesian network model representing the relationship between some agroclimatic variables and fresh market yield in ‘Beauregard’ sweetpotato grown in Louisiana. *HortScience* 45:1167–1177.
- Watanabe, K. 1979. Agronomic studies on the mechanism of excessive vegetation growth in sweetpotato (*Ipomoea batatas*). *J. Cent. Agr. Exp. Stn.* 29:1–94.
- Wilson, L.A. and S.B. Lowe. 1973. The anatomy of the root system in West Indian sweetpotato [*Ipomoea batatas* (L.) Lam.] cultivars. *Ann. Bot. (Lond.)* 37:633–643.