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

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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 m3m-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 these 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 0.256 to 0.058 m3m-3 soil 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 m3m-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 (Villarel 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 a 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

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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 μmol·m⁻²·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, 1963) and 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 numbers of each plant at each harvest was counted. Adventitious root samples from each plant at each harvest were prepared for anatomical observations through free-hand sectioning and staining with Safranine 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 cambium 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 (X₀) were estimated using sigmoidal functions with given storage root numbers (Y) and DAT (X).

\[ Y = \frac{\text{MSRN}}{1 + \exp\left(-X - X_0/b\right)} \]  

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 (R²) 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
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 PROCNLM 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 m³·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 m³·m⁻³ (78% FC) for ‘Evangeline’ and 20.8 d for ‘Beauregard’ at 0.167 m³·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 m³·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 m³·m⁻³ (100% FC) compared with 0.216 m³·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 m³·m⁻³ soil (65.6% and 78.1% FC), respectively, based on the fitted equations. These results indicate that the two

![Image](90x131 to 353x571)

**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, \( Y = \text{MSRN} / \left[1+\exp(-x-x_0/b)\right] \), where \( Y \) is the number of storage roots developed over each harvesting time, \( b \) is the shape and steepness of the curve, \( x_0 \) 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.
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 on root traits in response to varying soil moisture conditions. In this study, we observed a few storage roots formed at 14 d after planting with 0.164 m·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 and the activation of primary cambium of the adventitious roots along with the growth and development of root ends (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 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 m·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

![Graph](image-url)
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.

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