Preharvest Foliar Applications of Ethephon Increase Skin Lignin/Suberin Content and Resistance to Skinning in Sweetpotato Storage Roots

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Abstract. Skinning or surface abrasion in sweetpotato [*Ipomoea batatas* (L.) Lam.] roots during harvest causes a substantial loss of marketable products in storage as a result of rots, loss of moisture, and simply unattractive marketable appearance. In 2008, 2010, and 2011, changes in skinning incidence/severity and skin lignin/suberin content in response to preharvest foliar applications of ethephon or defoliation/devining were investigated. Field-grown ‘Beauregard’ (B-14) sweetpotato plots were treated with ethephon at 0.84, 1.68, and 2.52 kg·ha⁻¹ (based on the recommendations for tobacco) applied at 1, 3, and 7 days before harvest (DBH). Defoliated/devined treatments were applied at 0, 1, 3, and 7 DBH. Skinning incidence and severity were reduced with ethephon when applied 3 and 7 DBH in 2 of 3 years compared with 1 DBH. The force required to skin the storage root was measured at harvest in 2011 and it increased with defoliation/devining and ethephon applications at 3 and 7 DBH. Skin lignin/suberin was higher in roots from ethephon-treated plants but was weakly correlated ($r = 0.51$) with the force required to peel the skin. Ethephon applications also increased cortex phenolic content and either decreased or maintained skin phenolic content in storage roots compared with defoliated/devined treatments. These results suggest that skin set and/or skinning resistance in sweetpotato appears to be influenced by other factors in addition to skin lignification/suberization.

Sweetpotato [*Ipomoea batatas* (L.) Lam.] is an important crop in developing countries and has many uses, ranging from consumption of fresh roots or leaves to processing into animal feed, starch, flour, candy, and alcohol. In the United States, it is an important vegetable crop with more than 59,000 ha planted in 2012 (U.S. Department of Agriculture–National Agricultural Statistics Service, 2013). ‘Beauregard’ is the most popular sweetpotato variety grown for the fresh market in Mississippi and the Gulf South (Boudreaux,

2012; Meyers et al., 2013) but is prone to skinning (surface abrasion) during harvest and postharvest handling. Skinned areas become susceptible to pathogen infections and moisture loss, which results in an unattractive appearance for the fresh market (Clark et al., 2013). Therefore, skinning is associated with losses resulting from decay as well as unmarketable produce.

The periderm in sweetpotato is the first line of defense and is critical to reduce or avoid skinning and wounding at harvest (Clark et al., 2013). It is composed of three layers: phellem, phellogen, and phelloderm. The phellogen (meristematic cell layer) generates the phelloderm toward the inside of the root and the phellem (skin) toward the outside. Skinning occurs when an abrasion forces the periderm to fracture across the phellem (tensile fracture) and along the phellogen (shear fracture) resulting in the separation of the phellem from the phelloderm (Hammerle, 1970; Lulai, 2002; Sabba and Lulai, 2002; Webster et al., 1973). The wound healing process is characterized by suberization/lignification of the exposed cells and developing of the new periderm beneath (Lulai and Suttle, 2004;

St. Amand and Randle, 1989). In addition, ethylene has been reported to have a role in wound healing (St. Amand and Randle, 1989).

Lignin and suberin contribute to both cell wall strength and resistance to water loss during plant growth and development (Bernards and Lewis, 1998; Boudet, 2000). Although lignin is composed of phenolic (aromatic) polymers, suberin contains both a polyaliphatic domain and polyphenolics domain, which are often linked to lignin. Biosynthesis of lignin/suberin shares common intermediates (hydroxycinnamoyl-CoA derivatives) from which the lignification pathway diverges from the suberization pathway. Lignification/suberization has been extensively studied in other plants during wound healing (Bernards and Lewis, 1998; Boudet, 2000); however, very little information is available about the relationship between lignification/suberization of the native periderm in sweetpotato and skinning resistance. A trend, although non-significant, between skin adhesion and lignin content was suggested in sweetpotato exposed to different temperatures (Villavicencio et al., 2007). Furthermore, setting the skin to reduce skinning in sweetpotato at harvest has been achieved to some degree by preharvest foliar application of ethephon or devining (LaBonte and Wright, 1993; Schultheis et al., 2000), but skin lignin/suberin content was not determined. Therefore, we hypothesize that foliar application of ethephon enhances skin lignification and/or suberization in storage roots promoting skinning resistance. The objectives of this study are 1) to compare the effectiveness of preharvest foliar applications of ethephon and defoliation/devining in reducing skinning incidence and severity at harvest; 2) to determine the changes in skin lignification/suberization produced by these preharvest practices; and 3) to associate skin lignification/suberization with skinning resistance in sweetpotato storage roots.

Materials and Methods

Skinning incidence and severity. The role of preharvest treatments (ethephon or defoliation/devining) on skinning incidence and severity was investigated at the Pontotoc Ridge-Flatwoods Branch Experiment Station (lat. 42°1' N, long. 93°38' W), Mississippi State University, MS, in 2008, 2010, and 2011. ‘Beauregard’ (B-14) sweetpotato was grown in an Adaton soil type following standard production practices (Thompson et al., 2002). The experimental design for each year was a split plot with ethephon rates as the main effect (plots) and DBH when treatment was applied as a secondary effect (subplots) with three replications (blocks). Each experimental unit (subplot) consisted of four rows (6 m long) and the two middle rows were harvested for evaluation. Plant spacing was 1 m between rows and 30 cm within row. Preharvest foliar applications of ethephon at rates of 0.84, 1.68, and 2.52 kg·ha⁻¹ (based on the rate range recommended for cotton and tobacco) were applied at 1, 3, and 7 DBH with a four-row

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boom sprayer calibrated to 200 L·ha⁻¹. Defoliation/devined treatments (ethephon at 0 L·ha⁻¹) were applied at 0, 1, 3, and 7 DBH with a two-row UFT flail mower/deviner Model FB-080 (United Farm Tools Inc., South Charleston, WV). Ethephon treatments were defoliated/devined the harvest day. Time of treatment before harvest was based on the time of preharvest defoliation/devining practiced by sweetpotato growers in Mississippi. Trials were harvested on 30 Sept. 2008, 7 Oct. 2010, and 18 Oct. 2011 with a one-row riding mechanical harvester (Easley Mfg. Inc., Houston, MS). The harvester consists of a digger that undercut the roots, which are picked up by a moving chain that separates the dirt and brings them up through the platform where personnel hand pick the roots and put them in boxes. Harvested storage roots were not cured and stored at 15 °C and ambient relative humidity (50% to 70%) to augment the sunken symptom of the wound scar. After 2 months, 10 uniform U.S. no.1 storage roots were randomly selected from each subplot and the skinning scars were counted visually. Skinning incidence and skinning severity were determined by the percent of storage roots with at least one scar and the number of scars per root, respectively.

Skin chemical analysis. Changes in skin total phenolics and lignin/suberin content were evaluated in relation to preharvest foliar applications of ethephon in 2010 and 2011. Treatments selected from the experiment were ethephon at 1.68 and 2.52 kg·ha⁻¹ in 2010 and 0.84 and 1.68 kg·ha⁻¹ in 2011 applied at 1, 3, and 7 DBH and the defoliated/devined control (ethephon at 0 L·ha⁻¹) at 0, 1, 3, and 7 DBH. At harvest, three storage roots (one per replications) per treatment at each DBH were collected for analysis.

Total phenolic content was determined by a modification of the Folin-Denis method (Padda and Picha, 2007; Swain and Hillis, 1959). Skin and cortex samples were freeze-dried (FreeZone 2.5 L; Labconco Co., Kansas City, MO) before analysis. Cortex tissue (3 to 5 mm deep) was cut out after skin removal. Dry tissue samples (0.5 g) were ground in 10 mL methanol with a homogenizer (Power Gen 500; Fisher Scientific, Pittsburgh, PA). Samples were incubated in a water bath at 80 °C for 15 min. After vigorously shaking, samples were cooled and centrifuged at 4000 g for 20 min. The supernatant was collected and brought to a final volume of 10 mL with methanol. An aliquot of 100 µL

was added into a clean test tube followed by the addition of 2 mL of distilled water and 100 µL of Folin-Denis reagent. After 3 min, 200 µL of 1 N Na₂CO₃ was added and mixed gently, and the solution was allowed to stand for 1 h at room temperature (22 °C). Absorbance of the resulting blue complex was measured at 750 nm using a spectrophotometer (Genesys 10S Vis; Fisher Scientific). Chlorogenic acid was used as the standard. Total phenolic content was expressed as chlorogenic acid equivalents.

Lignin/suberin (aromatic domain) content was determined spectrophotometrically by the thioglycolysis method (Bruce and West, 1989; García-Pineda et al., 2010). The methanol insoluble residue after total phenolic extraction was dried and used to extract and determine the aromatic groups. Samples (50 mg) were mixed with 5 mL of 2 N HCl and 0.5 mL of thioglycolic acid and incubated in a water bath at 100 °C for 4 h. After cooling to room temperature, samples were centrifuged at 4000 g for 45 min. The supernatant was discarded and the pellet was resuspended in 5 mL of 0.5 N NaOH and gently rotated at 25 °C for 18 h to extract the lignin/suberin thioglycolate. The sample was centrifuged at

Fig. 1. Skinning incidence (left panel) and severity (right panel) in sweetpotato storage roots at harvest in response to preharvest foliar applications of ethephon or defoliation/devining in 2008, 2010, and 2011. Skinning incidence is defined as the proportion of roots with at least one wound. Skinning severity is defined as the number of wounds per root. Ethephon rates were 0.84, 1.68, and 2.52 kg·ha⁻¹ and applied at 1, 3, and 7 d before harvest (DBH). Control treatments were defoliated/devined at 0, 1, 3, and 7 DBH. Ten roots were evaluated per experimental unit and each point is the mean of four replications. Bars represent the SEM.

4000 g for 10 min at room temperature and the supernatant saved for analysis. A sample (0.6 mL) of supernatant was placed in a 2-mL tube and 0.6 mL of concentrated HCl (37%) was slowly added, and then the lignin/suberin–thioglycolate complex was allowed to precipitate at 4 °C for 4 h. The tube was centrifuged at 10,000 g for 10 min, and the brown pellet was dissolved in 1 mL of 0.5 N NaOH. The absorbance at 280 nm was measured using 0.5 N NaOH as a blank. Lignin alkali (Sigma Chemical Co., St. Louis, MO) dissolved in 0.5 N NaOH was used as the standard.

Skinning force. In 2011, a digital force gauge (DS2-11; Imada Inc., Northbrook, IL) was acquired to determine the force required to break and scrape off the skin at harvest. The same storage roots used for skin chemical analysis described previously were used. Treatments were ethephon at 0.84 and 1.68 kg·ha⁻¹ and defoliation/devining at 0, 1, 3, and 7 DBH. Storage roots were carefully washed immediately after harvest to remove the dirt from the surface and blot-dried immediately. The combined force required to cut across the skin or phellem (resistance to tensile fracture) and the force required to separate the phellem along the phellogen (resistance to shear fracture) were measured with the digital force gauge equipped with a slanted bar 4 mm wide (Hammerle, 1970; Webster et al., 1973). The edge of the slanted bar was used to cut and scrape off the skin with a short tangential upward movement and the peak combined force was recorded. The skinning force was measured five times per root and the mean was used for analysis.

All statistical analyses were conducted with SAS Version 9.2 for Windows statistical software package (SAS Institute Inc., Cary, NC). Incidence data are presented in actual percentages but were transformed [arcsin (square root)] for statistical analysis to equalize the variances and comply with the analysis of variance assumptions. Analysis of variance was performed by Proc Mixed and differences among means were adjusted by Tukey's multiple range test ($P \leq 0.05$).

Results

Changes in skinning incidence (percent skinned roots) and severity (wounds per root) in storage roots from plants treated with foliar applications of ethephon were inconsistent throughout the years (Fig. 1). In 2008, skinning incidence in storage roots from ethephon-treated plants 1 DBH was ≈95% and similar to the defoliated/devined control at 0 and 1 DBH. At application time 3 and 7 DBH, ethephon treatments, but not defoliation/devining, reduced the skinning incidence compared with 1 DBH. In contrast, the apparent reduction in skinning incidence with increasing ethephon rate was not significant and similar to the defoliated/devined treatment at 3 and 7 DBH ($P > 0.157$ and 0.094 , respectively). Similarly, skinning severity decreased with DBH as the main factor from five

to six wounds per root (1 DBH) to less than two wounds per root (3 and 7 DBH), but ethephon rates had no effect at each application time and were similar to defoliating/devining. The apparent slight reduction in skinning incidence and severity by defoliating/devining plants with increasing DBH was not significant. In 2010, skinning incidence and severity were not significantly reduced by increasing ethephon rate and were the same as defoliation/devining at each application time. However, both incidence and severity were reduced with application time as the main factor from 1 DBH to 3 and 7 DBH. In 2011, ethephon applications had no effect on skinning incidence, which stayed between 90% and 100% for all treatments

and application times. Skinning severity, however, increased with 0.84 kg·ha⁻¹ ethephon compared with all other treatments at 3 DBH and compared with 2.52 kg·ha⁻¹ at 7 DBH. In contrast, ethephon at 2.52 kg·ha⁻¹ reduced skinning severity compared with defoliation/devining at 7 DBH. In addition, skinning incidence and severity in 2011 were unaffected by time of harvest after treatment.

Total phenolic content changed in the skin and cortex of sweetpotato storage roots from plants subjected to preharvest foliar applications of ethephon (Fig. 2). There were no major differences among time of harvest after treatments each year, so data were combined over DBH, except defoliation/devining at 0 DBH. Skin phenolics in storage roots

Fig. 2. Changes in total phenolics [as chlorogenic acid equivalents (CAE)] in the skin (A) and cortex (B) and lignin content (C) in sweetpotato storage roots at harvest in response to preharvest treatments in 2010 and 2011. Treatments were defoliation/devining and foliar applications of ethephon at 1.68 and 2.52 kg·ha⁻¹ in 2010 and at 0.84 and 1.68 kg·ha⁻¹ in 2011. Time of treatments was 1, 3, and 7 d before harvest. Each point is the mean of three application times and three replications. Bars represent the SEM.

stayed the same in 2010 or decreased in 2011 as ethephon rate increased compared with roots from defoliated/devined plants (Fig. 2A). Overall in 2011, phenolic content in the skin was reduced by 13.2% (from 30.3 to 26.3 mg·g⁻¹) and 22.4% (from 30.3 to 23.5 mg·g⁻¹) at ethephon rates of 0.84 kg·ha⁻¹ and 1.68 kg·ha⁻¹, respectively, compared with roots from defoliated/devined plants. In contrast, phenolic content in the cortex increased after ethephon treatments compared with roots from defoliated/devined plants in both years (Fig. 2B). Phenolics in the cortex were increased by 35% (from 4.6 to 6.2 mg·g⁻¹) and 50% (from 4.6 to 6.9 mg·g⁻¹) at ethephon rates of 1.68 kg·ha⁻¹ and 2.52 kg·ha⁻¹, respectively, in 2010 and by 28% (from 4.3 to 5.5 mg·g⁻¹) and 128% (from 4.6 to 9.8 mg·g⁻¹) at 0.84 kg·ha⁻¹ and 1.68 kg·ha⁻¹, respectively, in 2011. In contrast to skin phenolic content, skin lignin/suberin content (aromatic domain) increased in sweetpotato storage roots from plants treated with ethephon before harvest compared with roots from defoliated/devined plants (Fig. 2C). The lignin/suberin content in the skin increased by 77% (from 19 to 33.6 mg·g⁻¹) and 129% (from 19 to 43.5 mg·g⁻¹) with ethephon rates of 1.68 and 2.52 kg·ha⁻¹, respectively, in 2010 and by 23% (from 24.3 to 30 mg·g⁻¹) and 34% (from 24.3 to 32.5 mg·g⁻¹) with ethephon rates of 0.84 and 1.68 kg·ha⁻¹, respectively, in 2011. Although to a lesser extent, defoliation/devining also increased skin lignin/suberin content in 2011 from 21 mg·g⁻¹ at 0 DBH to 24.8, 24.5, and 26.8 mg·g⁻¹ at 1, 3, and 7 DBH, respectively.

The combined shear and tensile forces required to fracture the skin and peel the storage roots from plants that were defoliated/devined or treated with ethephon increased with harvest time after treatment in 2011 (Fig. 3). Skinning force ranged between 1.5 and 1.6 N at 0 and 1 DBH and between 1.7 and 1.9 N at 3 and 7 DBH. There were no differences in peeling force among ethephon rates and defoliated/devined treatments at each harvest time. Because storage roots from defoliated/devined plants had less lignin/suberin content, the combined peeling force was weakly correlated ($r = 0.51$) with skin lignin content (data not shown).

Discussion

Although inconsistently, preharvest foliar application of ethephon reduced skinning in sweetpotato storage roots at harvest. A previous study in North Carolina also found a reduction in skinning incidence with foliar applications of ethephon 1 to 2 weeks before harvest (Schultheis et al., 2000). Ethephon applied 3 and 7 DBH reduced skinning incidence and severity 2 of 3 years when compared with 1 DBH (Fig. 1), which suggests that other factors may be involved in skin set (toughening and adhesion). High temperature and soil moisture have been reported to increase and reduce, respectively, skinning resistance in sweetpotato determined by the mechanical force required to peel the skin or by the pressure of a water jet necessary to wound the root (Villavicencio et al., 2007; Webster et al., 1973). In fact, the harvest in 2011 was later in the season than previous years and cooler temperatures may have affected the response to the treatments and/or affected skin set and, therefore, skinning incidence and severity were not reduced (Fig. 1). Although the reduction in skinning incidence and severity by defoliation/devining was not clearly established in this study, there are other reports with reductions in skinning incidence resulting from defoliation (LaBonte and Wright, 1993; Schultheis et al., 2000). Furthermore, considering the similar skinning incidence and severity between defoliation/devining and ethephon treatments, and the association of ethephon applications with postharvest physiological disorders (Arancibia et al., 2013; Dittmar et al., 2010), defoliating/devining is still the best viable practice to reduce skinning at harvest in sweetpotato.

Preharvest foliar application of ethephon increased skin lignin/suberin (aromatic domain) content, reduced or maintained skin phenolic content, and increased cortex phenolic content in storage roots when compared with roots from defoliated/devined plants in 2010 and 2011 (Fig. 2). Similarly, defoliation/devining increased skin lignin/suberin content, but to a lesser extent. The reduction in skin phenolics may be related to the increase in skin lignin/suberin because certain phenolics are the precursors of lignin

and suberin (Lapierre et al., 1996; Walter and Shadel, 1983). This response suggests that ethephon applied to the foliage influences the methylpropanoid pathway and the synthesis of lignin/suberin in the root epidermis; however, the mechanism is still unknown. Nonetheless, these results support the hypothesis that defoliation/devining and preharvest foliar applications of ethephon increase skin lignification/suberization in storage roots. To our knowledge, this is the first report that associates and increases lignin/suberin content in the skin of sweetpotato storage roots from defoliated/devined plants and from plants treated with preharvest foliar applications of ethephon.

The combined tensile and shear forces required to cut and scrape the skin were increased by ethephon applications as well as by defoliation/devining at 3 and 7 DBH in 2011 (Fig. 3). However, the peeling force was weakly correlated with skin lignin/suberin content because it was higher in roots from ethephon-treated plants than from defoliated/devined plants, but the peeling force was the same. Our results are in agreement with a previous analytical study that suggested a trend, although not significant, between skin adhesion and lignin content in sweetpotato storage roots grown at increasing temperatures (Villavicencio et al., 2007). The number of cell layers, the thickness of the phellem, and the strength of the cell walls have been suggested to influence skinning resistance in sweetpotato (Hammerle, 1970; Villavicencio et al., 2007; Webster et al., 1973); however, recent studies in potato have reported that skinning resistance depends mostly on the shear fracture component and the tensile fracture resistance is minimal (Lulai, 2002; Lulai and Freeman, 2001; Sabba and Lulai, 2002). Based on anatomical studies, they concluded that the source of development of resistance to shear fracture (skin adhesion) and skinning is the strength of the radial walls of the phellogen and that their liability and proneness to fracture depends on the level of phellogen meristematic activity. Therefore, lignification/suberization in response to preharvest ethephon applications may have strengthened mainly cell walls in the phellem and strengthening of the phellogen radial cell walls may have been minimal. This evidence suggests that other factors, including temperature and soil moisture, may be influencing phellogen meristematic activity and radial cell wall strengthening and consequently skin adhesion. Methods that can differentiate resistance to shear fracture from tensile fracture are necessary to investigate in detail the factors influencing skin adhesion and resistant to skinning.

In summary, preharvest foliar applications of ethephon and defoliation/devining can reduce skinning in sweetpotato, but environmental factors may influence this response. Ethephon, however, has been shown to increase the incidence of tip rot and internal necrosis in sweetpotato storage roots (Arancibia et al., 2013; Dittmar et al., 2010). Thus, defoliation/devining is still the best viable practice to

Fig. 3. Force required to cut and scrape off the skin (combined tensile and shear fracture) of sweetpotato storage root at harvest in response to preharvest defoliation/devining or ethephon foliar applications in 2011. Ethephon rates were 0.84 and 1.68 kg·ha⁻¹ and applied at 1, 3, and 7 d before harvest (DBH). Defoliation/devining was at 0, 1, 3, and 7 DBH. Each point is the mean of three replications. Bars represent the SEM.

reduce skinning at harvest. Skin lignification and/or suberization was weakly correlated with skinning resistance suggesting that other factors, in addition to lignifications/suberization, are involved in strengthening skin adhesion.

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