Comparative Evaluation of the Effects of Gibberellic Acid Concentrations on Dormancy Break in Tubers of Solanum chacoense

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Additional index words. potato, sprout number, tuber size

SUMMARY. Solanum chacoense is a wild relative of potato (Solanum tuberosum) that is native to South America. It has been evaluated for several traits of interest for future incorporation in commercially produced potato, such as greater root biomass linked to higher nitrogen uptake efficiency (Errebbi et al., 1999, 1998), late blight resistance (Colon and Budding, 1988), resistance to verticillium wilt [Verticillium dahlia (Lynch et al., 1997; Uribe et al., 2014)], resistance to potato virus Y (PYY) [Potyvirus (Sato et al., 2006)], and potato leafroll virus (PLRV) [Poleovirus (Brown and Thomas, 1993)]. This species also accumulates a number of glycoalkaloid compounds that work as natural deterrents of Colorado potato beetle [Leptinotarsa decemlineata (Barbinger et al., 1996; Mwectwa et al., 2011; Sinden et al., 1980)]. S. chacoense naturally produces unreduced gametes (Cape et al., 2002; Leue and Peloquin, 1980), which allows for the transmission of these valuable genes from diploid S. chacoense to tetraploid S. tuberosum via 4x-2x crosses. However, newly harvested material of S. chacoense across populations, also referred to as accessions, has shown uneven dormancy and plant emergence. Below the surface of the soil, a potato plant produces both roots and stem organs called stolons. Flowering in potato plants generally coincides with the swelling of stolon tips in which a majority of the tuber is formed by randomly oriented cell division and expansion (Jackson, 1999). Deposited in these cells are storage carbohydrates and proteins, including starch and patatin, respectively (Shewry, 2003), making tubers strong storage sink organs (Fernie and Willnitzer, 2001). Coinciding with tuber formation is the onset of dormancy. Dormancy can be described as the halting of all meristematic activity in the stolon apex and nodes (Sonnewald, 2001; Xu et al., 1998), and it serves physiological adaptation by allowing survival during periods of unfavorable conditions (Sonnewald, 2001). According to Suttle (2011), there are three stages of dormancy in potato tubers. The first stage of dormancy is referred to as endodormancy, during which endogenous factors restrict the formation of sprouts even under ideal conditions. The second stage of dormancy is referred to as paradormancy, during which sprouting is restricted by external physiological factors. The third stage of dormancy is referred to as ecodormancy, during which meristematic activity is halted by external environmental factors. Immediately after harvest, tubers enter endodormancy and will not produce sprouts when stored at temperatures of 3 °C or below (Suttle, 2011). Aside from the effects of temperature during the development and storage of tubers (Davidson, 1958), time to sprouting in potato tubers can vary among varieties between years (Kim et al., 1999; Van Ittersum, 1992), by tuber size (Claassen and Vreugdenhil, 2000, Krijthoe, 1962; Van Ittersum, 1992), and between species (Hermundstad and Peloquin, 1985; Thompson et al., 1980). Among wild species of tuber-bearing

<table>
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<th>Units</th>
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<th>U.S. unit</th>
<th>SI unit</th>
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<td>cm</td>
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<td>°F</td>
<td>°C</td>
<td></td>
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</tbody>
</table>

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Solana num species, the tuber dormancy length can range from a short period such as 20 d (Thompson et al., 1980) to up to 8 years (Ramberg, 2010).

At the time of sprouting, the tuber becomes repurposed from a storage organ to a source organ for newly developing sprouts (Sonnewald, 2001). Premature potato tuber sprouting during storage can lead to decreased crop values and loss of quality due to remobilization of starch and proteins (Börnke et al., 2007), whereas delayed sprouting after planting can lead to reduced yields (Gandarillas and Nylund, 1949). To simultaneously evaluate populations of tuber-bearing Solana num species for rooting or tuber traits, uniform breaking of tuber dormancy is required. Literature discussing breaking physiological dormancy in tubers suggested using gibberellic acid (GA3) (Brian et al., 1955; Galun, 2010; Jansky and Hamernik, 2014; Rappaport, 1956; Rappaport et al., 1957; Sasani et al., 2009) or a combination of ethylene gases (ethylene chlorohydrin, 1,2-dichloroethane, and carbon tetrachloride at the 7:3:1 proportion), often referred to as rindite (Bryan, 1989; Kim et al., 1999; McDonald and Coleman, 1988). The major issue with rindite is the toxicity of the three components. When they are mixed together, rindite creates high toxicity risks for the workers handling the chemicals and the environment (Hansen et al., 2002). Limited information regarding breaking dormancy exists for Solan um chacoense. The objective of this study was to determine an appropriate GA3 concentration and soak time treatment to encourage sprout development across four accessions of Solan um chacoense.

Materials and methods

Plant material and growth conditions. Eleven S. chacoense clones across four accessions were selected for a seed nursery at the U.S. Department of Agriculture (USDA) Agricultural Research Station in Beltsville, MD. The accessions were previously obtained from the USDA Potato Genebank in Sturgeon Bay, WI. Accessions A (PI 275136; clones A-3, A-5, and A-6) and B (PI 320288; clones B-3, B-5, and B-10) originated from Argentina. Accessions C (PI 537025; clones C-6 and C-8) and D (PI 566738; clones D-6, D-7, and D-8) originated from Bolivia and Paraguay, respectively. These clones were selected based on tuber availability and the ability to tuberize in pots. Tubers were cultivated from tuberlings in 6-inch-diameter containers using peat moss potting mixture (ProMix Flex; Premier Tech Horticul- ture, Delson, QC, Canada) under a 12-h photoperiod and fertilized using 24N–3.5P–13.3K water-soluble fertilizer (MiracleGro All-Purpose Fer- tilizer; Scotts, Marysville, OH). Tubers were harvested on 1 Oct. 2013 at the USDA facility in Beltsville, MD, and shipped overnight to the University of Florida in paper bags.

Experimental treatments. Immediately after arrival, tubers were maintained in complete darkness at 25 °C for 5 d after harvest before treatment. A total of 72 tubers of each of the 11 clones were divided evenly into three tuber size classes (small, medium, and large) and exposed to four GA3 concentrations for each of the three desired soak times (12 treatments total). The average fresh weights (±SD) were 1.4 ± 0.03, 2.6 ± 0.06, and 5.6 ± 0.14 g for small, medium, and large classes, respectively. The factors were four GA3 concentrations (0, 50, 100, and 150 µg·mL−1), three soak periods (5, 45, and 90 min), tuber size class (small, medium, and large), and accession (A, B, C, and D). The concentrated GA3 (Fisher Scientific, Toronto, ON, Canada) was dissolved in distilled deionized (DDI) water at 20 °C and homogenized for 2 h. Treatments were applied at a rate of 24 tubers in 200 mL of GA3 solution. Treated tubers were then removed and allowed to air-dry for 3 h before placement inside two calibrated incubators (MIR-153; Sanyo Electric Co., Moriguchi, Japan) on 6 Oct. 2013, and maintained at 23 °C. Tubers were periodically removed from the incubators into a lighted room to collect data. To ensure that all tubers were exposed to light for the same length of time, a 12-h photoperiod was supplied by a fluorescent lamp (15 W, 6500 °K, 198 µmol·m−2·s−1).

Data collection. The experiment was conducted for 46 d after treatments (DAT). The number and length of sprouts were determined every 2 d and summed on a per-tuber basis at the end of the experiment. The number of sprouts per tuber was determined by counting viable sprouts, which was determined as a sprout at least 2 mm long that showed no signs of desiccation. Time to sprouting was determined as DAT required for the average sprout number (with a minimum length of 2 mm) in a single replicate to equal or exceed one. The percentage of sprouted tubers was calculated as the number of tubers sprouted divided by the total number of tubers in that treatment 46 DAT. After 46 DAT, nonsprouted tubers started to shrivel and become desiccated.

Statistical analysis. The experiment was a factorial arrangement of treatments in a completely randomized design with three replicates. An analysis of variance (ANOVA) for each measured variable was conducted using the PROC GLM procedure. Treatments were compared using Tukey-Kramer of the SAS statistical package (version 9.4 for Windows; SAS Institute, Cary, NC).

Results and discussion

Number of sprouted tubers. The ANOVA showed that the GA3 concentration, accession, and tuber size class significantly affected the percentage of sprouted tubers of Solan um chacoense. Application of GA3 significantly increased the number of sprouted tubers. Treatments including 50, 100, and 150 µg·mL−1 GA3 resulted in 48%, 40%, and 43% of sprouted tubers, respectively, whereas the non-GA3 treatment resulted in only 29% of sprouted tubers at 46 DAT (Fig. 1A). Application of GA3 accelerated sprout formation compared with non-GA3 treatment. The 50 µg·mL−1 GA3 resulted in the earliest formation of sprouts at 9 DAT (Fig. 2A). The 100 and 150 µg·mL−1 GA3 treatments and 50 µg·mL−1 GA3 treatment resulted in similar percentage of tubers sprouted at 19 and 46 DAT. The effect of exogenous GA3 application on sprouting promotion has been previously reported for potato (Alexopoulus et al., 2008), but it has not yet been reported for Solan um chacoense tubers.

There was a significant variation in the percentage of sprouted tubers across the four accessions. The overall percentages of sprouted tubers were 60%, 63%, 34%, and 3% for accessions A, B, C, and D, respectively (Fig. 1B). Accession A was the most effective for producing sprouts, with 69% of tu-bers sprouted in the absence of GA3, followed by accession B with 38%
Only 2% of tubers from accession C and 6% of tubers from accession D produced sprouts in the absence of GA₃, indicating a relatively high level of endodormancy. Accessions A and B were more effective for producing sprouts earlier in the study, resulting in a greater percentage of tubers sprouted at 19 DAT and for the remainder of the study (Fig. 2B). Accession C was less effective for producing sprouts, followed by accession D, which produced minimal sprouts 46 DAT (Fig. 2B).

The interaction of GA₃ concentration × accession on the percentage of sprouted tubers at 46 DAT was significant (Table 1). The percentage of sprouted tubers was significantly higher with the application of GA₃, regardless of concentration, for accessions B and C.

Application of 50, 100, and 150 μg·mL⁻¹ of GA₃ significantly increased tuber sprouting in 61% to 77% and 43% to 50% in accessions B and C, respectively, compared with non-GA₃ treatment. There were no significant differences among the 50, 100, and 150 μg·mL⁻¹ GA₃ treatments on sprouted tubers within accessions, indicating that 50 μg·mL⁻¹ of GA₃ was a sufficient concentration to break dormancy of three of the four tested accessions of S. chacoense. The use of GA₃, regardless of concentration, had no effect on the percentage of sprouted tubers for accessions A and D due to opposite reasons. Accession D showed a stronger endodormancy mechanism (Table 1) and no sensitivity to GA₃ treatments, whereas accession A showed very weak dormancy, producing a similar percentage of sprouted tubers when they were treated or not treated with GA₃. The variability of dormancy among potato species and varieties is expected (Bisognin et al., 2018; Brandt et al., 2003; Kim et al., 1999) and, in most of the cases, some variation in the dormancy of tubers can be attributed to the genetic makeup of individuals. Acceleration of breaking dormancy with GA₃ has been extensively studied in several potato varieties (Alexopoulos et al., 2008; Hartmann et al., 2011; Van Ittersum, 1992). The present study represents a small proportion of the genetic variability of S. chacoense because only four of the 174 available accessions of S. chacoense from the USDA Potato Genebank were evaluated. The accessions of the present study were selected based on their ability to tuberize in pots and the availability of tubers at harvest. Therefore, much greater variations in
Table 1. Interaction between gibberellic acid (GA3) concentration treatments and accession of *Solanum chacoense* on the percentage of sprouted tubers and time to sprouting at 46 d after treatments.

<table>
<thead>
<tr>
<th>GA3 (μg·mL⁻¹)</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprouted tubers [mean ± SE (%)]</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>0</td>
<td>69.4 ± 5.1 a' A¹</td>
<td>38.3 ± 5.4 b B</td>
<td>1.9 ± 1.0 b C</td>
<td>5.6 ± 2.8 a C</td>
</tr>
<tr>
<td>50</td>
<td>58.3 ± 5.1 a A²</td>
<td>76.5 ± 4.8 a A</td>
<td>50.0 ± 6.9 a B</td>
<td>5.6 ± 3.9 a C</td>
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<tr>
<td>100</td>
<td>56.9 ± 5.9 a A</td>
<td>61.2 ± 5.4 a A</td>
<td>42.6 ± 6.8 a A</td>
<td>0.0 ± 0.0 a B</td>
</tr>
<tr>
<td>150</td>
<td>54.2 ± 5.9 a B</td>
<td>76.5 ± 4.7 a A</td>
<td>42.6 ± 6.8 a A</td>
<td>0.0 ± 0.0 a C</td>
</tr>
<tr>
<td>Time to sprouting [mean ± SE (d)]</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>32 ± 1.3 a B</td>
<td>41 ± 0.9 a A</td>
<td>&gt;46 ± 0.4 a A</td>
<td>&gt;46 ± 0.2 a A</td>
</tr>
<tr>
<td>50</td>
<td>31 ± 1.3 a B</td>
<td>29 ± 1.2 b B</td>
<td>39 ± 1.5 b A</td>
<td>&gt;46 ± 1.9 a A</td>
</tr>
<tr>
<td>100</td>
<td>31 ± 1.6 a B</td>
<td>31 ± 1.4 b B</td>
<td>40 ± 1.2 b A</td>
<td>&gt;46 ± 0.0 a A</td>
</tr>
<tr>
<td>150</td>
<td>32 ± 1.6 a B</td>
<td>30 ± 1.3 b B</td>
<td>39 ± 1.3 b A</td>
<td>&gt;46 ± 0.0 a A</td>
</tr>
</tbody>
</table>

¹1 μg·mL⁻¹ = 1 ppm.
²Values within columns followed by the same lowercase letter indicate that means are not significantly different at P < 0.05 according to the Tukey-Kramer test between GA3 concentrations within each *S. chacoense* accession.

Table 2. Interaction between tuber size class and accession of *Solanum chacoense* on sprout length and time to sprouting 46 d after treatment. Tuber size classes were classified according to the average tuber weight in small (1.5 g), medium (2.4 g), and large (5.8 g).

<table>
<thead>
<tr>
<th>Tuber size class</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
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<tbody>
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<td>Sprout length [mean ± SE (mm)]</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>7.4 ± 0.9 a A²</td>
<td>3.3 ± 0.5 b B</td>
<td>3.6 ± 0.5 a B</td>
<td>0.0 ± 0.0 b C</td>
</tr>
<tr>
<td>Medium</td>
<td>7.1 ± 0.7 a A</td>
<td>3.7 ± 0.3 ab B</td>
<td>3.5 ± 0.5 b A</td>
<td>0.0 ± 0.0 b C</td>
</tr>
<tr>
<td>Large</td>
<td>6.4 ± 0.5 a A</td>
<td>5.6 ± 0.4 a A</td>
<td>3.5 ± 0.7 a B</td>
<td>3.0 ± 0.4 a C</td>
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<tr>
<td>Time to sprouting [mean ± SE (d)]</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>36 ± 0.9 a B</td>
<td>35 ± 0.9 a B</td>
<td>42 ± 1.1 a A</td>
<td>&gt;46 ± 1.3 a A</td>
</tr>
<tr>
<td>Medium</td>
<td>30 ± 1.1 b B</td>
<td>32 ± 1.0 ab B</td>
<td>42 ± 1.3 a A</td>
<td>&gt;46 ± 1.6 a A</td>
</tr>
<tr>
<td>Large</td>
<td>27 ± 0.9 b D</td>
<td>31 ± 0.9 b C</td>
<td>39 ± 1.1 a B</td>
<td>&gt;46 ± 1.3 a A</td>
</tr>
</tbody>
</table>

¹1 g = 0.0353 oz; 1 mm = 0.0394 inch.
²Values within columns followed by the same lowercase letter indicate that means are not significantly different at P < 0.05 according to the Tukey-Kramer test between tuber size class within each *S. chacoense* accession.

The initial separation of tubers into size classes (small, medium, large) significantly affected the percentage of sprouted tubers of *S. chacoense* (Fig. 1C). In the smaller class, 29% of the tubers had sprouted at 46 DAT; however, in the medium and large tuber classes, 40% and 50% of the tubers had sprouted at 46 DAT. Large tubers produced sprouts much earlier than the medium and small classes. Approximately 39% of the large tubers sprouted at 25 DAT; however, at the same DAT, the percentages of sprouted tubers were 31% and 24% for medium and small tuber classes, respectively. The difference in sprouting among tuber size classes was maintained until the end of the study (Fig. 2C). These results corroborate previous research evaluating potato (Claassens and Vreugdenhil, 2000; Van Ittersum, 1992) that indicated that larger tubers exhibited a higher percentage of sprouted tubers earlier in the study.

Soak time had no significant effect on the percentage sprouted tubers of *S. chacoense*. Soak time has been shown to have no effect on the rate or nature of sprouting on potato tubers (Rappaport et al., 1958).

**Time to Sprouting.** GA3 concentration, accession, and tuber size class had effects on time to sprouting of *S. chacoense*. Again, the minutes of soak time had no effect on time to sprouting. Overall, treatments with GA3 shortened dormancy by 4 d (Fig. 1D). Under 0 μg·mL⁻¹ GA3 treatment, accession A had the shortest dormancy, only 32 d to sprout, but there were no significant differences among accessions B, C, and D, which required more than 41 d to sprout (Table 1).

There were interactions between GA3 and accession and between accession and tuber size for days required to sprout. GA3 significantly reduced time to sprouting, regardless of concentration, by an average of 10 d for accession B and 7 d for accession C, but not for accessions A and D. Under the conditions of this study, accession A did not require the application of exogenous GA3 to accelerate or increase the emergence of sprouts. For accessions B and C, the 50 μg·mL⁻¹ concentration of GA3 was sufficient to increase sprouting by 33% and 41%, respectively. However, for accession D, none of the GA3 concentrations was effective for shortening tuber dormancy. Acceleration of dormancy breaking with the use of GA3 has been reported with doses lower than 50 μg·mL⁻¹ for several potato varieties (Alexopoulos et al., 2008; Hartmann et al., 2011; Van Ittersum, 1992). A practical application of breaking dormancy of potato tubers was demonstrated by Mustefa et al. (2017), who indicated that applications of 10 and 20 μg·mL⁻¹ of GA3 on tubers of *Budu* significantly reduced the dormancy period from 102 d for non-treated seed to 83 and 70 d, respectively.

Larger tubers tended to require a shorter time to sprout than smaller tubers (Fig. 1F). In accession A, tuber dormancy was significantly shorter in medium and large tubers than in small tubers (Table 2). In accession B, tuber dormancy was significantly shorter in large than in small tubers. In accessions C and D, tuber size had no effect on tuber dormancy (Table 2).

The effect of tuber size on dormancy has also been observed for potato: smaller tubers required longer periods to produce sprouts and larger tubers exhibited shorter dormancy (Lommen, 1994; Nipa et al., 2013; Van Ittersum, 1992). However, as observed for accessions C and D, there is not always a significant
and negative correlation between tuber size and the time required to remove dormancy. The absence of a relationship between time to sprouting and tuber size has been reported for some potato varieties (Van Itersum, 1992).

**Sprout number and length.** The GA3 concentration and soak time had no significant effects on sprout number. The sprout number was significantly affected by accession and tuber size only. Accession A had the highest number (+SD) of sprouts per tuber (1.9 ± 0.1); followed by accession B (1.6 ± 0.1), accession C (1.6 ± 0.1), and accession D (1.0 ± 0.0). The large tuber class produced the highest number of sprouts per tuber (1.8 ± 0.1), with no significant differences between medium (1.6 ± 0.1) and small (1.6 ± 0.1) tuber classes.

The GA3 concentrations and accession had significant effects on the sprout length of *S. chacoense* (Table 2). The soak time of GA3 showed no significant effect on sprout length. Without any GA3 treatment, the average sprout length was 3.4 ± 0.3 mm. The GA3 concentration of 50 μg.mL−1 resulted in the longest sprouts (5.9 ± 0.4 mm), which was significantly greater than the sprout length when treated with 100 μg.mL−1 (4.9 ± 0.4 mm) and 150 μg.mL−1 (5.3 ± 0.4 mm) of GA3.

Across accessions, accession A produced the longest sprouts (6.9 ± 0.4 mm), followed by accession B (4.4 ± 0.3 mm), accession C (3.5 ± 0.3 mm), and accession D (2.0 ± 1.0 mm). There was a significant interaction between accession and tuber size on sprout length (Table 2). Accessions A and C showed no significant effect of tuber size class on the sprout length of *S. chacoense* (Table 2). In accession B, sprout length increased with increasing tuber size. The large tuber class was the only class to produce sprouts in accession D.

These results corroborated previous research that indicated that the application of exogenous GA3 was used to break dormancy and elongate sprouts in several potato varieties (Galun, 2010; Sasani et al., 2009). It is noteworthy that previous research has shown that warm white fluorescent lights inhibit the elongation of potato sprouts even in the presence of exogenous GA3 (Morris, 1967). Therefore, sprout lengths may have been negatively affected by the presence of artificial lights during the exposure time for the evaluations in this study.

**Conclusions**

The effectiveness of GA3 treatments on dormancy breaking of *S. chacoense* was mostly dependent on the accession and tuber size. The accessions used in this study represented a small number of the total number of accessions of *S. chacoense* available in the USDA Potato Genebank, and they exhibited different levels of endodormancy and response to the dormancy breaking treatments. Accessions A and B exhibited weaker dormancy mechanisms overall, whereas accessions C and D exhibited moderate and strong dormancy mechanisms, respectively.

The GA3 concentration of 50 μg.mL−1 successfully broke tuber dormancy in accessions B and C; however, for accessions A and D, there was no difference in time to sprouting due to GA3 treatment. GA3 concentrations more than 50 μg.mL−1 showed no increase in the sprouting rate or total percentage of tuber sprouted up to 46 DAT. Future studies should investigate GA3 rates lower than 50 μg.mL−1. The soaking time showed no significant effect on breaking dormancy of *S. chacoense*, with 5 min of soaking time being sufficient for breaking dormancy. The tuber size significantly impacted the percentage of sprouting, time to sprouting, and number of sprouts on *S. chacoense*. For those accessions with strong dormancy, alternative methods to break dormancy may be required.

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