

Transient heat stress during tuber development alters post-harvest carbohydrate composition and decreases processing quality of chipping potatoes

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Abstract

BACKGROUND: Adverse air and soil temperatures are abiotic stresses that occur frequently and vary widely in duration and magnitude. Heat stress limits productivity of cool-weather crops such as potato (*Solanum tuberosum*) and may degrade crop quality. Stem-end chip defect is a localized discoloration of potato chips that adversely affects finished chip quality. The causes of stem-end chip defects are poorly understood.

RESULTS: Chipping potatoes were grown under controlled environmental conditions to test the hypothesis that stem-end chip defect is caused by transient heat stress during the growing season. Heat stress periods with 35 °C days and 29 °C nights were imposed approximately 3 months after planting and lasted for 3, 7 or 14 days. At harvest and after 1, 2 and 3 months of storage at 13 °C, potato tubers were evaluated for glucose, fructose, sucrose and dry matter contents at the basal and apical ends. Chips were fried and rated for defects at the same sampling times. Differences in responses to heat stress were observed among four varieties of chipping potatoes. Heat stress periods of 7 and 14 days increased reducing sugar content in the tuber basal and apical ends, decreased dry matter content, and increased the severity of stem-end chip defects.

CONCLUSION: Transient heat stress during the growing season decreased post-harvest chipping potato quality. Tuber reducing sugars and stem-end chip defects increased while dry matter content decreased. Planting varieties with tolerance to transient heat stress may be an effective way to mitigate these detrimental effects on chipping potato quality.

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Keywords: high temperature stress; post-harvest storage quality; potato sugars; potato crisp color; tuber specific gravity; reducing sugars; sucrose

INTRODUCTION

Potato (*Solanum tuberosum* L.) is the world's third most important food crop for human nutrition after wheat and rice.¹ Potato grows best under cool conditions,^{2–5} and yield of harvested tubers is frequently greatest when diurnal temperatures vary within the range of 16 to 27 °C.^{3,6–8} Sustained^{8–11} or transient^{12,13} warm temperatures decrease potato yield by decreasing net CO₂ assimilation rate,¹⁴ increasing respiration rate¹⁵ and shifting carbon allocation toward vine growth at the expense of tuber growth.^{8,9,11,16,17} Elevated soil^{16–20} and air temperatures⁷ reduce potato yields. Tuber dry matter content, which consists primarily of starch, also decreases when potato is grown at greater than optimal temperatures.^{8,9,12,17,21} Models for climate change suggest that transient and persistent warm temperature periods may become more frequent in the coming decades. Concerns have been raised that potato productivity may be negatively impacted through direct temperature-dependent effects on yield and indirect effects resulting from increased disease and pest pressure.^{3,22} Less attention has been given to the effects that transient warm temperatures might have on potato processing

quality defects. Warm temperatures are associated with increased frequency of internal necrosis²³ and are thought to exacerbate the effect of water deficits on development of sugar end defects in fry processing potatoes.^{24,25}

Since the 1950s, chipping potatoes have been selected for high dry matter content and for their ability to produce light-colored chips.²⁶ High tuber dry matter content is beneficial because it reduces oil absorption during frying and increases recovery of chips from raw product.²⁷ The color of fried chips is dependent primarily on tuber concentrations of the reducing sugars glucose and fructose.^{28,29} Glucose and fructose accumulate after harvest

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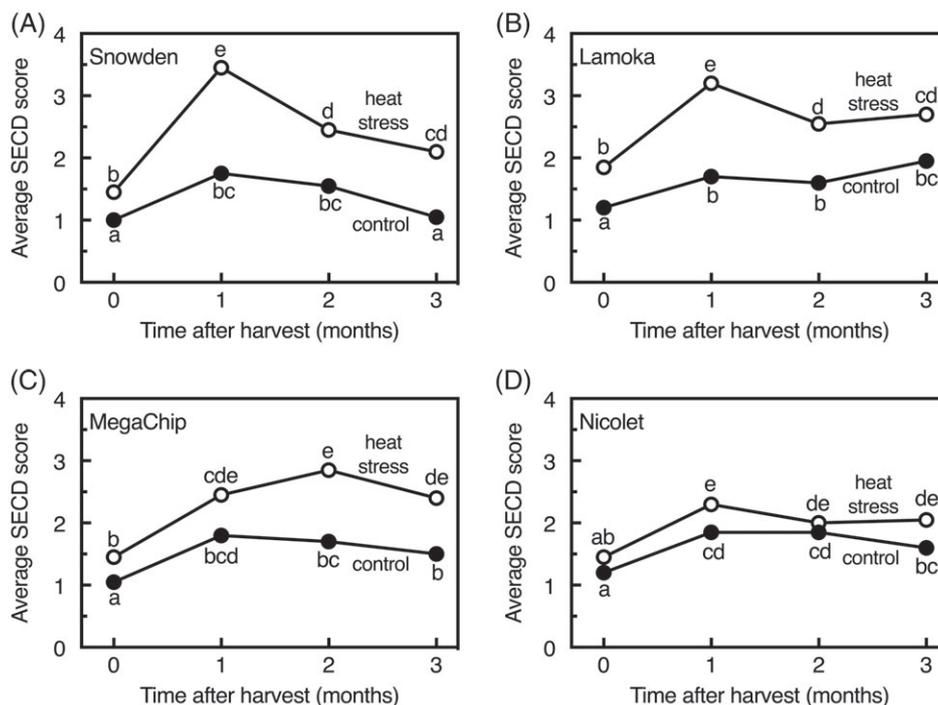


Figure 1. Transient in-season heat stress increased average stem-end chip defect (SECD) scores for potato varieties (A) ‘Snowden’, (B) ‘Lamoka’, (C) ‘MegaChip’ and (D) ‘Nicolet’ at harvest and after 1, 2 and 3 months of storage at 13 °C. Data points with different letter designations within each panel of the figure have significantly different SECD scores at the level of $P < 0.05$.

as a result of sucrose hydrolysis by vacuolar acid invertase.^{30–32} Reducing sugars react with amino groups in a non-enzymatic Maillard reaction to produce dark-colored pigments during chip frying.³³ Potatoes that do not produce high-quality chips can be rejected at processing plants, and this possibility introduces a significant financial risk for producers and may lead to supply problems for processors.

Stem-end chip defect (SECD) is an important tuber quality concern for the potato chip industry. SECD is a post-fry, dark coloration of the vascular tissue and associated ground tissue at a position corresponding to the basal, or stem, end of the tuber. The dark-colored region expands to include the cortical tissue adjacent to the vascular tissue in more severe cases of SECD.³⁴ Potatoes that produce chips in which dark color is limited to the vasculature at the tuber basal end are acceptable to chip processors. More extensive dark areas extending away from the vasculature and toward the center of the chip can result in rejection of raw product at processing plants.³⁵

SECD appears erratically across years and locations.^{36,37} Bussan *et al.*³⁵ suggested heat stress was possibly involved in SECD symptom development. Wang *et al.*³⁴ found that moderate water or heat stress did not consistently influence the incidence or severity of SECD. Wang *et al.*³⁴ proposed that day temperatures higher than 30 °C or night temperatures greater than 18 °C might be necessary for consistent SECD development. Data from a multi-year field survey suggested that greater SECD severity was associated with elevated night temperatures during bulking in July and August.³⁶ SECD development was greater in North American field trials conducted in 2012, when summer temperatures were above historical averages, than in 2013, which had an atypically cool growing season.³⁷

Tubers with severe SECD had both elevated glucose concentrations at the tuber basal end and elevated acid invertase

activity.^{34,38} Glucose concentration at the tuber basal end was, in some cases, weakly correlated with SECD development.^{34,38} The glucose content at the tuber apical end has been consistently reported to be less than 0.1 mg g⁻¹ fresh weight, and a correlation between apical-end glucose content and SECD severity has not been observed.³⁶

The present study was undertaken to determine whether heat stress during tuber bulking is sufficient to cause SECD. Given the role that glucose and fructose play in the Maillard reaction and chip color darkening, we investigated carbohydrate profiles in tubers from harvest through 3 months of storage. Finally, we examined the effects that heat stress duration had on SECD development and tuber dry matter contents.

MATERIALS AND METHODS

Plant growth

In the first experiment, certified B-sized (3.8–5.7 cm diameter) seed tubers of chipping potatoes ‘Lamoka’, ‘Nicolet’, ‘MegaChip’ and ‘Snowden’ were planted in 20-L pots filled one-third full of Metromix 366P soil (Sun Gro Horticulture, Bellevue, WA, USA). Soil was added to pots as plants grew until the pots were full. All trials were conducted in temperature-controlled, air-conditioned glasshouses at the University of Wisconsin-Madison Biotron. The air temperature was 22 °C during the day and 18 °C at night in control treatment glasshouses. A minimum day length of 16 h was provided by natural illumination supplemented by sodium vapor lights as needed to keep photosynthetically active radiation above 500 μmol L⁻¹ m⁻² s⁻¹. Plants were watered daily as needed using drip irrigation lines fed by time-activated pumps. Irrigation solution was one-quarter-strength Hoagland’s solution with micronutrients³⁹ with the following modifications: boron increased to 0.25 ppm, sodium added to 6 ppm and chlorine

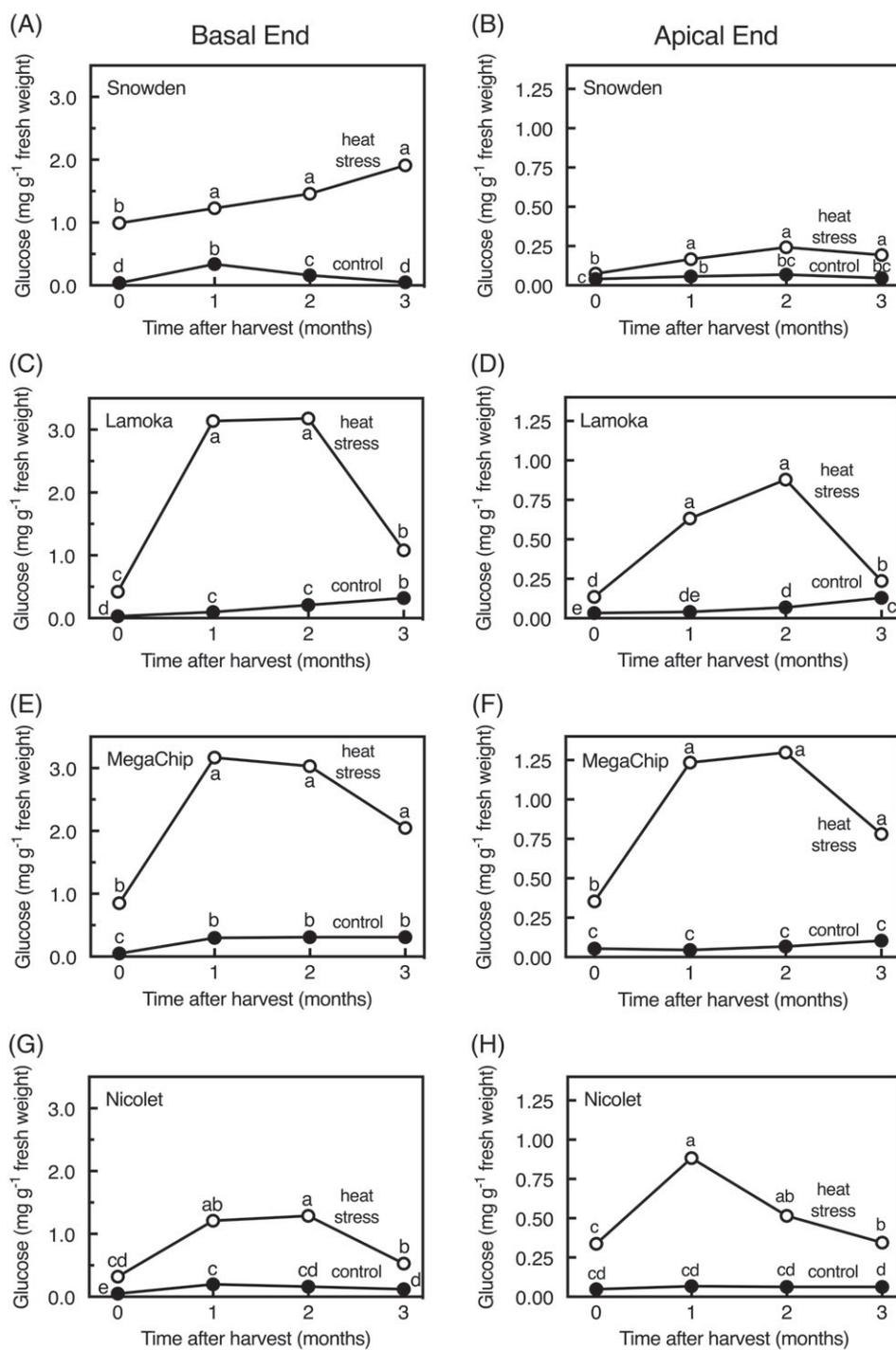


Figure 2. Transient in-season heat stress increased glucose content at the basal (A, C, E, G) and apical (B, D, F, H) ends of tubers from varieties 'Snowden', 'Lamoka', 'MegaChip' and 'Nicolet'. The post-harvest storage temperature was 13 °C. Data points with different letter designations within each panel of the figure have significantly different glucose contents at the level of $P < 0.05$.

added to 8 ppm. For all treatments, soil moisture content was kept high by irrigating to field capacity each day. Pots were out-fitted with 1.22 m tall wire mesh cages that constrained plants as they grew upward and prevented tangling of vines. Aphids and thrips were controlled as needed with foliar sprays of Avid®, active ingredient abamectin at 0.63 mL L⁻¹ (Syngenta Crop Protection AG, Basel, Switzerland), Pylon®, active ingredient chlorfenapyr at 1.0 mL L⁻¹ (BASF Corp., Research Triangle Park, NC, USA),

and insecticidal soap. A soil drench of *Bacillus thuringiensis* was applied as needed for fungus gnat (*Sciaroidea* spp.) control.

Stress treatments

In the first experiment, 15 plants of each variety were subjected to the heat stress treatment for 14 days, starting 99 days after planting, a time when field-grown plants might experience heat stress conditions. The stress treatment consisted

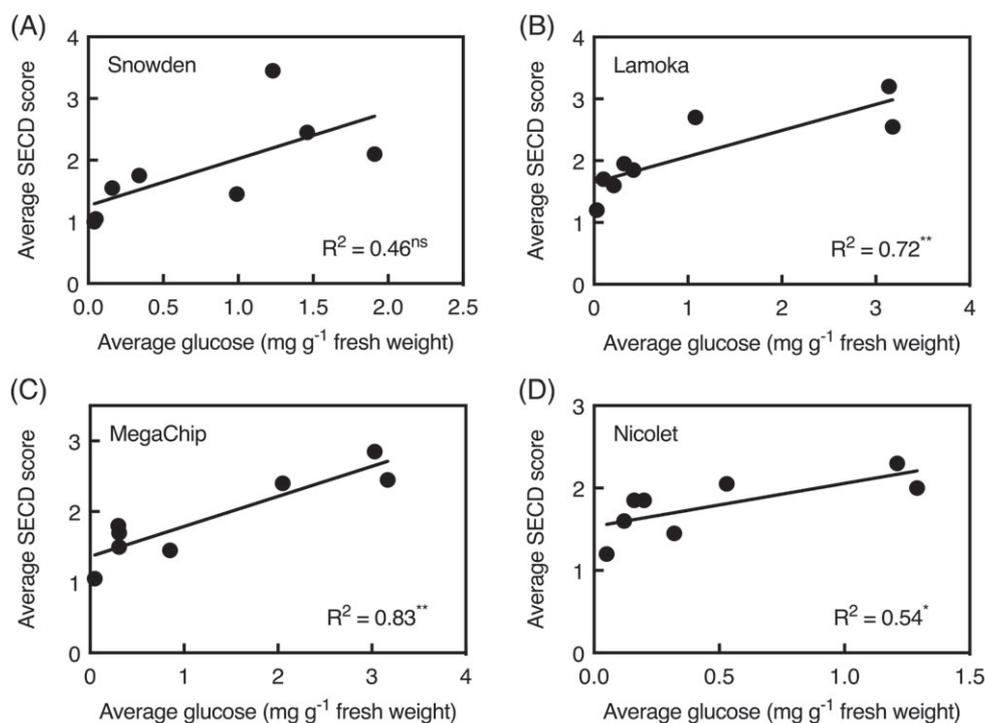


Figure 3. Stem-end chip defect (SECD) severity was correlated with glucose content at the tuber basal end for potato varieties (A) ‘Snowden’, (B) ‘Lamoka’, (C) ‘MegaChip’ and (D) ‘Nicolet’.

of 35 °C day and 29 °C night temperatures. Day length and lighting were the same as for the control plants. Plants were watered with quarter-strength Hoagland’s solution, and watering frequency was adjusted to keep soil water content near field capacity. All plants were returned to control conditions at the end of the heat stress period.

Post-stress period plant growth and harvest

Immediately after the heat stress period, irrigation water for both treatments was changed from quarter-strength Hoagland’s solution to reverse osmosis water to encourage senescence of vines and maturation of tubers. Plants were harvested after leaves and stems had senesced naturally. ‘Lamoka’ and ‘Nicolet’ tubers were harvested 172 days after planting. ‘MegaChip’ and ‘Snowden’ tubers were harvested 186 days after planting. For a given potato variety and treatment, tubers from all plants were combined, and random samples of 20 tubers were used for chip and biochemical analysis 1 day after harvest and after 1, 2 and 3 months in storage at 13 °C. Moderately warm temperature storage was utilized to exclude the possibility of chip darkening caused by cold-induced sweetening.⁴⁰

Length of heat stress period

In the second experiment, the duration of the heat stress period was varied, but all other procedures were as described earlier. For this experiment, the cultivar ‘Snowden’ was used because it was found to be moderately susceptible to SECD development. Heat stress periods of 3, 7 and 14 days were imposed 98, 91 and 91 days after planting, respectively. The 3-day treatment began later than the other two treatments to avoid crowding in the heat stress glasshouse and to have all plants at a similar age during the heat stress period. Each of the four treatment groups contained 18

plants. All tubers were harvested after vine senescence, 155 days after planting. Vines senesced more rapidly in the second experiment than in the first experiment, perhaps because of differences in nutrient solution uptake. Tubers were sampled at harvest and after 1, 2 and 3 months of storage at 13 °C. Four additional experiments with the 0- and 7-days heat stress treatments only and 20, 10, 10, and 10 plants per treatment were conducted with ‘Snowden’ in 2014, 2015, 2016 and 2017, respectively. SECD ratings were collected each year and dry matter content at tuber apical and basal ends was evaluated in 2014, 2016 and 2017.

Chip processing and SECD rating

Potatoes were cut from apical to basal end. A 1-mm thick slice through the stolon attachment point was removed from one half-tuber using a custom-built mandolin and fried in vegetable oil at 185 °C for 2 min 10 s or until bubbling ceased. Fried chips were scored for SECD relative to background chip color using a modification of the method described by Wang *et al.*³⁴ Briefly, chips scored 0 when no color development was observed. Dark color only in the basal-end vascular tissue or extending ≤ 1.5 mm into the chip was scored 1. Dark-colored cortical tissue adjacent to the vascular tissue and extending ≤ 3 mm into the chip was scored 2. Dark color that extended 3–9.5 mm into the basal end of the chip was scored 3. Dark color extending 9.5–12.5 mm into the basal end of the chip was scored 4. Dark color extending more than 12.5 mm into the basal end of the chip was scored 5. Chips scoring 3 to 5 may be rated as defects by chip processors.

Quantification of sugars

Tissue samples weighing approximately 0.75 g were collected approximately 1 cm from the basal and apical ends of each tuber, weighed for fresh weight, frozen at –80 °C, lyophilized, weighed for dry weight, ground to a fine powder with glass beads in a

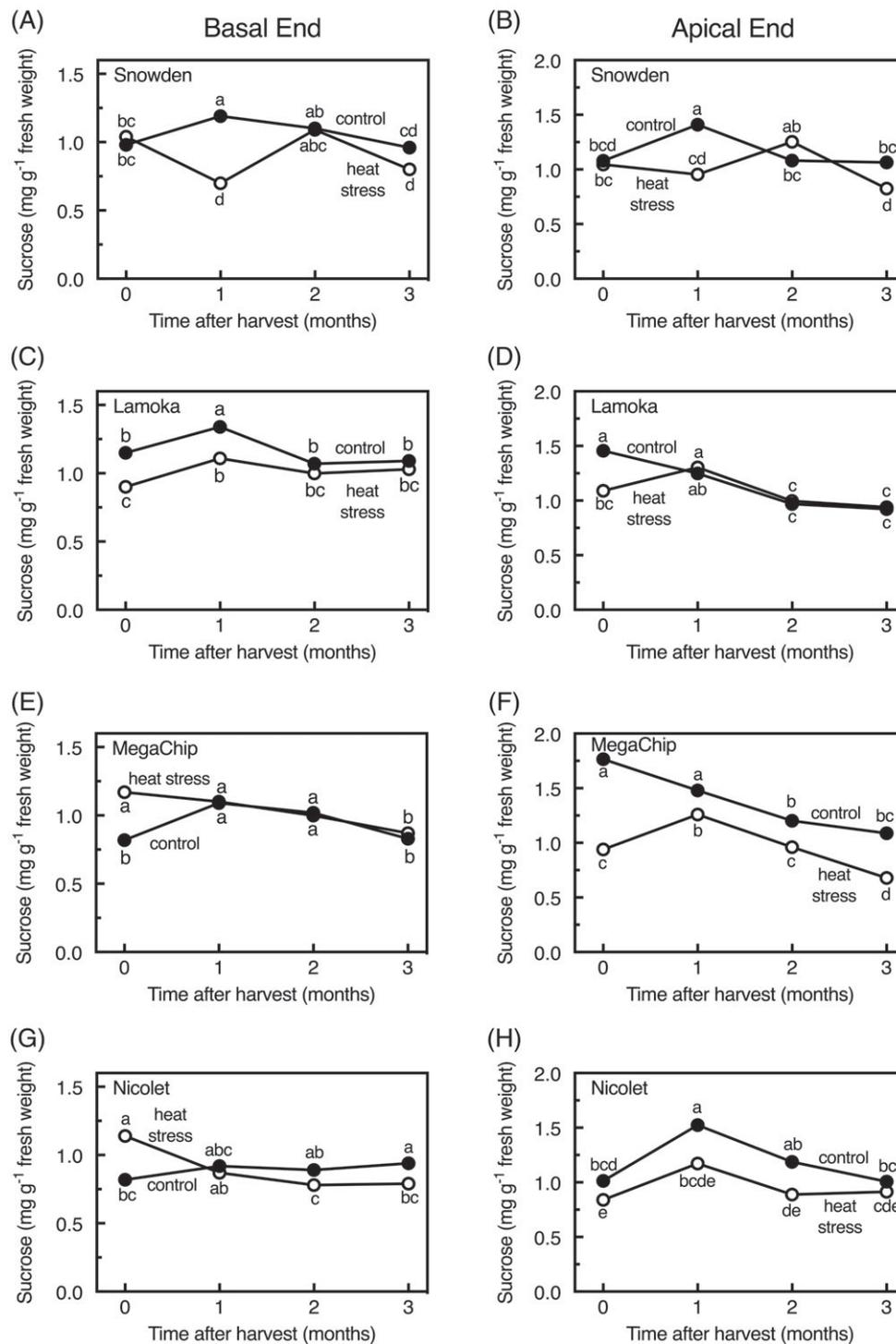


Figure 4. Effect of transient in-season heat stress on sucrose content at the basal (A, C, E, G) and apical (B, D, F, H) ends of tubers from potato varieties 'Snowden', 'Lamoka', 'MegaChip' and 'Nicolet', at harvest and after 1, 2 and 3 months of storage at 13 °C. Data points with different letter designations within each panel of the figure have significantly different sucrose contents at the level of $P < 0.05$.

modified paint shaker, and extracted twice for 24 h with 4 mL of 80% ethanol in a shaking water bath at 60 °C. Combined extracts were brought to a final volume of 10 mL with 80% ethanol. Samples of 1.5 mL were dried to completion, suspended in 1 mL ultrapure water, filtered through 0.2 µm syringe filters, and 10 µL used for quantification of tuber sucrose, glucose and fructose with high pressure liquid chromatography equipment.⁴¹

Statistics

Data from the first experiment were analyzed using SAS version 9.3 (SAS Institute Inc., Cary, NC, USA). The experiment was designed and analyzed as a two-way analysis of variance with interaction. The non-parametric rank score of the data was analyzed using the SAS MIXED procedure with a model including the main effects

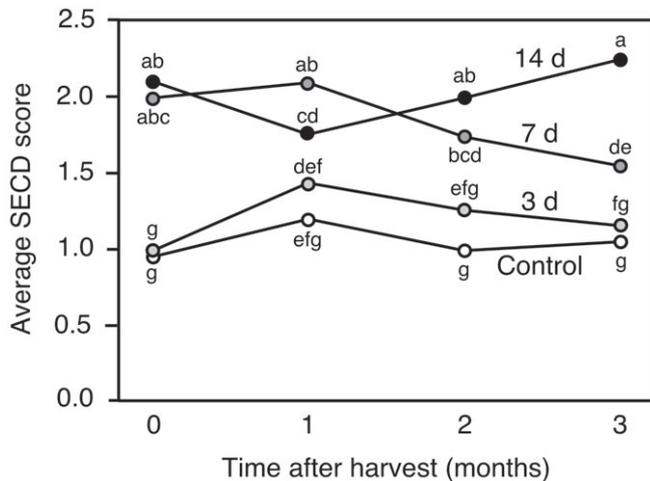


Figure 5. Transient in-season heat stress for 7 and 14 days increased the severity of stem-end chip defects (SECDs) in potato variety ‘Snowden’. The post-harvest storage temperature was 13 °C. Data points with different letter designations have significantly different values ($P < 0.05$) for stem-end defect score.

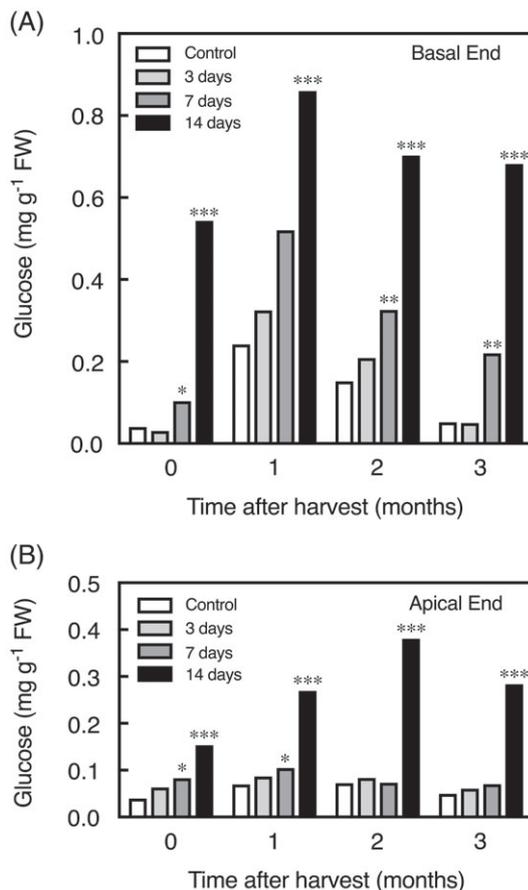


Figure 6. Post-harvest glucose content at the ‘Snowden’ tuber basal (A) and apical (B) ends increased with duration of in-season heat-stress treatment. The post-harvest storage temperature was 13 °C. Differences in glucose content at the basal end of tubers between control and heat stress treatments at each sampling time are indicated by asterisks as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

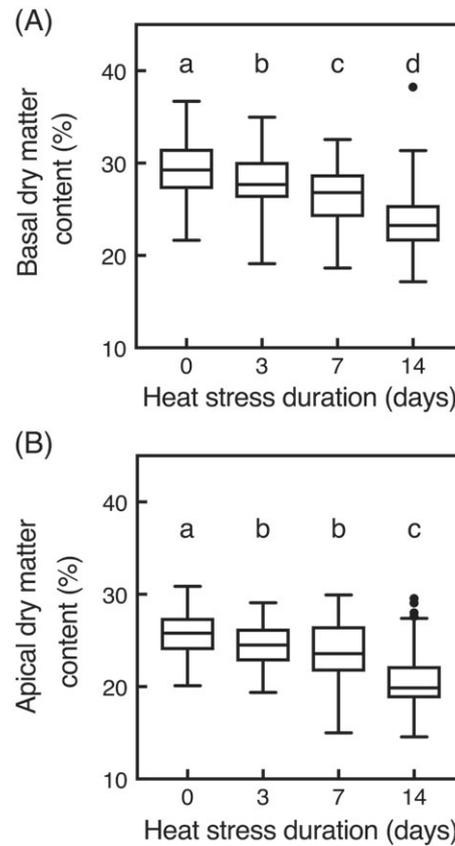


Figure 7. Transient in-season heat stress decreased ‘Snowden’ tuber dry matter content at the basal (A) and apical (B) ends. Dry matter content data are pooled from measurements made at harvest and after 1, 2 and 3 months of storage at 13 °C. Stress period durations with different letter designations differ in dry matter content at the level of $P < 0.05$.

of storage time, heat stress and their interaction for each cultivar. Mean separation was performed using the PDMIX800 macro.

Differences in tuber glucose and dry matter contents between heat stress treatments of varying durations were computed using analysis of variance with Tukey’s HSD (honestly significant difference) as a post-test in R version 3.4.3.⁴² To remove skewness from the glucose data, calculations were performed following a glucose^{-0.5} transformation. Differences between control and 7-days heat stress treatments in the development of SECD were analyzed using the non-parametric rank of SECD score since SECD scores were not normally distributed. Analysis of variance and Tukey’s HSD were computed in R to assess the contributions of heat stress, sampling time and year to SECD scores. Whisker lengths in boxplots were drawn as suggested by Tukey.⁴³

RESULTS

Stem-end chip defects (SECDs)

The impact that in-season heat stress had on SECD severity from harvest through 3 months of storage is illustrated in Fig. 1. Chips from control plants consistently exhibited fewer and less severe SECD than chips from heat-stressed plants for each of the four varieties evaluated (Fig. 1). Average SECD scores for heat-stressed ‘Snowden’, for example, were greater than those for chips from control ‘Snowden’ from harvest through 3 months of storage (Fig. 1(A)). A similar pattern was observed for chips from ‘Lamoka’

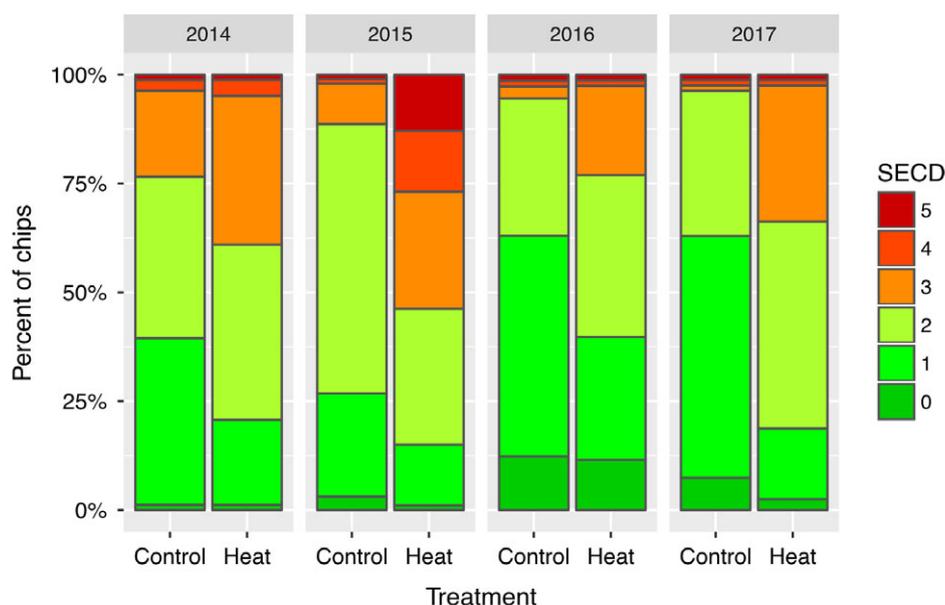


Figure 8. Transient in-season heat stress for 7 days increased the proportion of chips with severe stem-end chip defect (SECD) scores for potato variety 'Snowden'. Data are from independent experiments conducted in years 2014–2017 and represent pooled SECD scores from chips prepared at harvest and after 1, 2, and 3 months of storage at 13 °C.

and 'MegaChip' (Fig. 1(B),(C)). Although differences between heat stress and control treatments in average SECD score were smallest for 'Nicolet', chips from plants exposed to the stress treatment had higher SECD scores than controls at 1 and 3 months after harvest.

Tuber sugar contents

Tubers from heat-treated plants had higher amounts of glucose at the basal end than those from control plants for each of the varieties evaluated (Fig. 2). For example, the glucose concentration of tubers from heat-treated 'Snowden' increased from harvest through 3 months of storage, when it was 1.91 mg g⁻¹ fresh weight (Fig. 2(A)). In contrast, tubers from control 'Snowden' had basal-end glucose contents less than 0.1 mg g⁻¹ fresh weight 3 months after harvest (Fig. 2(A)). Mean basal-end glucose concentrations of tubers from heat-treated 'Lamoka' (Fig. 2(C)) and 'MegaChip' (Fig. 2(E)) increased rapidly after harvest and exceeded 3.0 mg g⁻¹ fresh weight at the 1- and 2-month sampling times. Mean basal-end glucose content in 'Nicolet' tubers peaked at 1.29 mg g⁻¹ fresh weight 2 months after harvest before declining to 0.53 mg g⁻¹ fresh weight at 3 months (Fig. 2(G)). The glucose concentration at the basal end of tubers from heat-stressed plants was higher than that of tubers from control plants at harvest and 1 and 2 months after harvest in all four varieties (Fig. 2). Mean tuber basal-end glucose concentration across treatment and sampling periods was moderately well correlated with mean SECD score (Fig. 3). Correlation coefficients were 0.55, 0.73, 0.81, and 0.63 for 'Snowden', 'Lamoka', 'MegaChip', and 'Nicolet', respectively. Tuber fructose concentrations closely matched glucose concentrations (Supporting Information Fig. S1). Increases in glucose (Fig. 2) and fructose (Fig. S1) contents caused by the heat-stress treatment were two to four times less at the tuber apical end than at the basal end but followed similar patterns (Fig. 2, Fig. S1).

Sucrose concentrations at the tuber basal end were approximately 1.0 mg g⁻¹ fresh weight regardless of variety, sampling

time or treatment (Fig. 4). Differences in basal-end sucrose content between tubers from heat-stressed and control plants were observed, but the timing and extent of those differences were not consistent between varieties. For example, sucrose content at the tuber apical end was greater in control relative to heat-stress tubers of 'MegaChip' and 'Nicolet' (Fig. 4). Sucrose contents at the apical end were comparable, however, between treatments for 'Snowden' and 'Lamoka' (Fig. 4).

Duration of stress period on SECD development and tuber carbohydrates

'Snowden' plants were exposed to heat stress periods of 0, 3, 7 and 14 days duration. A 7-day or 14-day heat-stress event resulted in significantly elevated SECD scores relative to controls at each of the four sampling times (Fig. 5). In contrast, a 3-day long heat stress event did not increase SECD scores at harvest or through 3 months of storage (Fig. 5). Glucose contents at the tuber basal and apical ends were greater in tubers from the 14-day heat stress treatment than in tubers from controls at all sampling times. Basal-end glucose was elevated in response to a 7-day heat stress at all sampling times except for 1 month (Fig. 6(A)). Apical-end glucose was elevated in the 7-day heat stress treatment at harvest and after 1 month of storage (Fig. 6(B)). No differences in tuber basal- and apical-end glucose content were observed between control and 3-day heat stress treatments (Fig. 6). Dry matter content at the tuber basal and apical ends decreased as heat stress duration increased (Fig. 7). Mean dry matter content at the basal end of tubers from plants that received a 14-day heat stress was 19% less than that in tubers from control plants (Fig. 7(A)).

'Snowden' plants were exposed to a 7-days heat stress period in four subsequent experiments (2014–2017) to test the hypothesis that a 7-days heat stress period was sufficient to induce SECD. A visual summary of the SECD score data is presented in Fig. 8, which illustrates the distribution of SECD scores for each experiment. The 7-days heat stress period increased the SECD score ($P < 0.001$) and

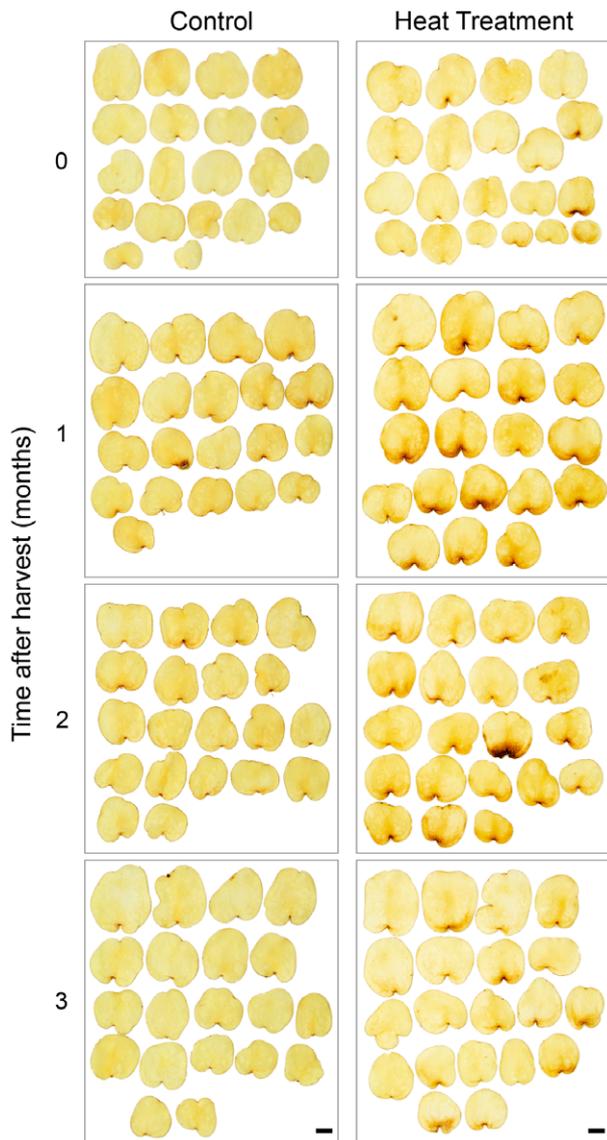


Figure 9. Heat stress of ‘Snowden’ potato plants results in a degradation of post-harvest chip quality. Photographs show potato chips prepared at harvest and after 1, 2 and 3 months of storage at 13 °C. Each chip was prepared from a different tuber and chips are oriented with the basal end down. Control plants were grown with 22 °C days and 18 °C nights. Plants from the heat-stress treatment (Heat treatment) were exposed to 35 °C days and 29 °C nights for 7 days approximately 6 weeks before harvest. Scale bar equals 2 cm.

the percentage of chips having more severe SECD scores of 3 to 5 in each experiment (Fig. 8). Data from the 0, 1, 2 and 3-month sampling periods were combined in Fig. 8 to illustrate more clearly the trends in the data. Analysis of the full four-year data set showed that heat stress treatment ($P < 0.001$), sampling time ($P < 0.001$) and year ($P < 0.001$) were all significant contributors to the observed SECD scores. SECD scores were not different between the 1-month and 2-month sampling times, but SECD scores at 1 and 2 months were greater than those at harvest and at 3 months ($P < 0.001$). Representative chips from the control and 7-day heat stress treatments are shown in Fig. 9.

The 7-day heat stress treatment decreased dry matter content at the tuber basal end in each year the data were collected (Fig. 10(A)–(C)). Dry matter content at the

tuber apical end, however, was unchanged in two of three years (Fig. 10(D)–(F)).

DISCUSSION

The data presented here demonstrate that a 7- 14 day heat stress period was sufficient to cause an increase in reducing sugars in chipping potatoes (Figs 2 and 6, Fig. S1). This increase was observed at harvest and increased in magnitude during the first 2 months of post-harvest storage. The increase in reducing sugars was much larger at the basal than the apical end of the tuber. Dark-colored SECDs appeared at positions corresponding to high concentrations of reducing sugars at the tuber basal end but did not appear at the tuber apical end, where tuber reducing sugar contents were lower.

The transient high temperature growth conditions used for this experiment are expected to reduce carbon assimilation by leaves significantly and severely restrict carbon allocation to tubers. Dry matter content of tubers was reduced by heat stress (Figs 7 and 10), and the extent of the reduction was roughly proportional to the duration of the heat stress period (Fig. 7). This finding indicates that the relationship between tuber growth and starch accumulation had been altered by the heat stress treatment such that tuber enlargement exceeded the rate of starch deposition. Whether this occurred during or after the heat stress period remains an unanswered question.

In these experiments, a transient heat stress was imposed during late tuber development. Although modest effects of the stress were observed at harvest, the highest concentrations of tuber reducing sugars and the most severe chip defects were observed one or more months after harvest. It is worth noting, however, that tubers from control plants, which were grown in near optimal conditions often had modest increases in basal-end reducing sugars and chip defects during the same post-harvest period (Figs 1, 2 and 6; Fig. S1). It may be that heat stress, acting through an unknown regulatory mechanism, exacerbates post-harvest changes in sugar profiles that are inherent to many chipping potatoes.

Pots in all treatments were watered to field capacity one or more times per day in order to minimize the contribution of water stress to the observed responses. Despite this, the heat stress treatment also exposed plants to a large increase in vapor pressure deficit. This is likely to have contributed to temperature-dependent reductions in net photosynthesis since potato is relatively sensitive to low water potential.¹⁴ One can only speculate about other ways in which a sudden increase in evaporative demand might affect post-harvest characteristics of potato tubers.

CONCLUSIONS

Potatoes with high dry matter content that produce defect-free chips are commercially desirable. The data presented here indicate that transient warm weather during the tuber-bulking portion of the growing season can permanently degrade post-harvest chipping potato quality. Thus, maintaining chip quality in locations that experience transient high temperatures will be challenging. The data presented in Figs 1 and 2 and previous studies,^{36,37} suggest that chipping potato varieties differ in their susceptibility to reducing sugar accumulation and SECD formation in response to transient high temperature conditions. Breeding chipping potatoes for reduced sensitivity to heat stress and planting resistant

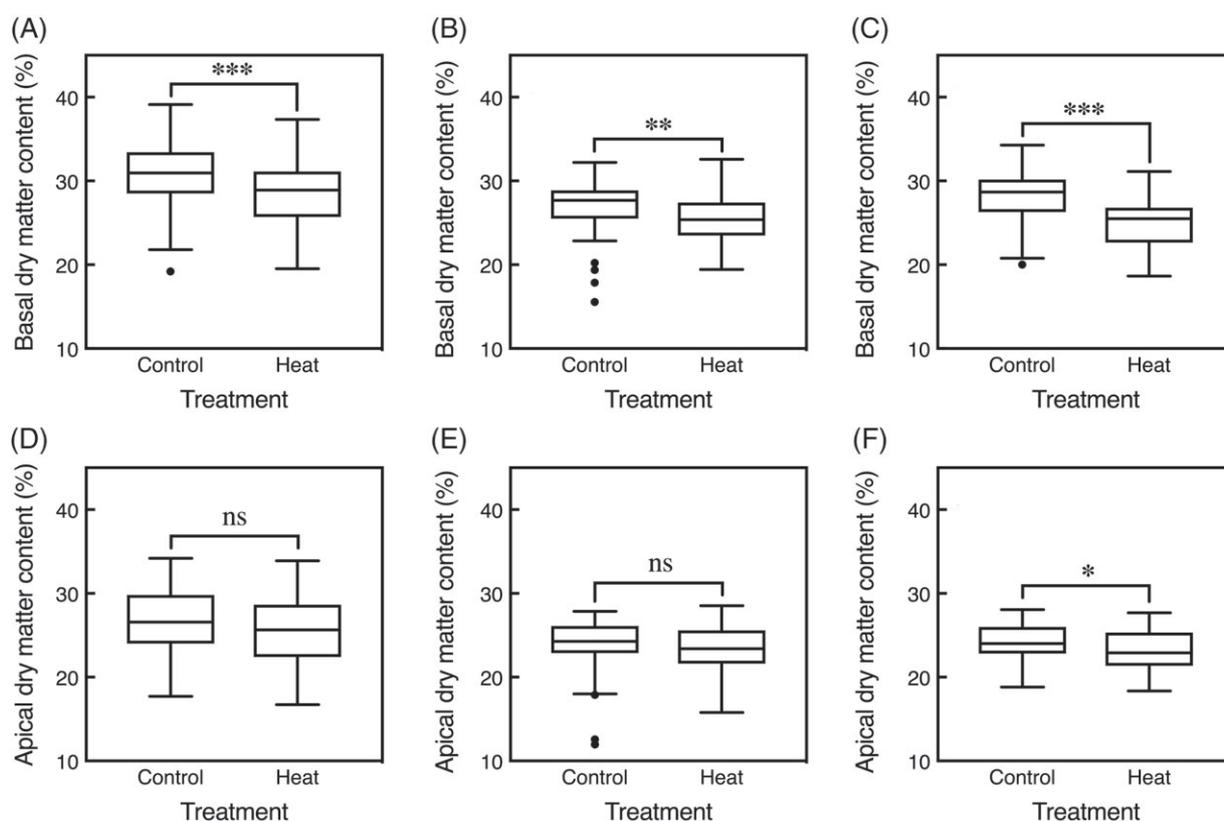


Figure 10. Transient in-season heat stress for 7 days affected tuber dry matter content at the basal and apical ends. Tissue samples were removed from basal (A–C) and apical (D–F) positions of potato tubers at harvest and after 1, 2, and 3 months of storage at 13 °C in 2014 (A, D), 2016 (B, E) and 2017 (C, F).

varieties in areas prone to heat stress will be required for consistent production of a high-quality crop.

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AUTHOR CONTRIBUTIONS

James Busse assisted with experimental design, collected and analyzed data and participated in writing the manuscript. Amy Wiberley-Bradford assisted with data collection and manuscript preparation. Paul Bethke assisted with experimental design, analyzed data and participated in writing the manuscript.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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