

Ultraviolet Radiation Affects Intumescence Development in Ornamental Sweetpotato (*Ipomoea batatas*)

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Abstract. Intumescences are a physiological disorder characterized by hypertrophy and possibly hyperplasia of plant tissue cells. Ultimately, this disorder results in the death of the affected cells. Previous observations and research suggest that the quality and quantity of light to which plants are exposed may be a factor in development of the disorder. The purpose of this study was to assess the preventive effect of ultraviolet-B (UVB) radiation on intumescence development in ornamental sweetpotato (*Ipomoea batatas*). Two sweetpotato cultivars, Sidekick Black and Ace of Spades, were grown under light treatments consisting of 1) normal greenhouse production conditions; 2) supplemental UVB lighting; 3) supplemental UVB lighting with Mylar[®] sleeves over the lamps to block UVB radiation; and 4) control lighting with full spectrum lamps. Treatments were administered for 2 weeks, and the experiment was repeated twice. ‘Ace of Spades’ was highly susceptible to intumescence development, whereas ‘Sidekick Black’ was much less susceptible to the disorder. For ‘Ace of Spades’, the addition of UVB radiation significantly reduced the number of leaves affected with intumescences when compared with plants grown under the other light treatments; this UVB effect was not apparent for ‘Sidekick Black’. Furthermore, there was no evidence for reduced plant growth under UVB light in either cultivar, but side effects from the radiation included leaf discoloration and deformities. This study indicates a cultivar-specific effect of UVB light in preventing intumescence development on ornamental sweetpotato, therefore suggesting a potential genetic component in intumescence susceptibility. These results provide further insight in better understanding intumescence development and how to prevent the disorder.

Intumescences are a physiological disorder that develops sporadically on the leaf tissue of many plant species, including some varieties of tomato (*Solanum lycopersicum*

‘Maxifort’; Rud, 2009), sweetpotato (Wetzstein and Frett, 1984), and cuphea (*Cuphea* sp.; Jaworski et al., 1988). This disorder is often described as abnormal, translucent outgrowths on the leaf surface with a gall or wart-like appearance (J.K. Craver, C.T. Miller, K.A. Williams, and D.L. Boyle, in press; Morrow and Tibbitts, 1988; Wetzstein and Frett, 1984). This disorder was first observed and named as intumescence by Sorauer (1899) and was found at that time to develop on numerous plant species (La Rue, 1932). Although the term intumescence is commonly used to describe this disorder, other common and interchangeably used nomenclature in the published literature includes excrescences, neoplasms, galls, genetic tumors, leaf lesions, enations, and oedemata (Pinkard et al., 2006).

Intumescences can have a substantial impact on both the economic and aesthetic value of affected plants (Balge et al., 1969; Rangarajan and Tibbitts, 1994). Many of the species most susceptible to this disorder are

grown solely for ornamental purposes, and intumescences can greatly impair the overall aesthetics of the crop. Additionally, severe cases of intumescence development can result in impaired photosynthesis (Pinkard et al., 2006; Roloff and Scherm, 2004). Thus, this physiological disorder presents a substantial problem for growers attempting to produce crops that may be prone to its development.

The causative factors related to intumescence development remain somewhat elusive. One key finding has been that this disorder predominantly occurs on plants being produced in controlled environments (Jaworski et al., 1988; Lang and Tibbitts, 1983; Petite and Ormrod, 1986; Wetzstein and Frett, 1984). For the most part, no pathogen has been found to be involved in intumescence development, which leads most to agree that this is a physiological disorder (Rangarajan and Tibbitts, 1994). Some of the most commonly proposed causative factors include air contamination (Kirkham and Keeney, 1974; Lang and Tibbitts, 1983), hormones and hormone concentrations (Kirkham and Keeney, 1974; Lang and Tibbitts, 1983; Morrow and Tibbitts, 1988; Petite and Ormrod, 1986; White, 1951), humidity (Douglas, 1907; Eisa and Dobrenz, 1971), temperature (Balge et al., 1969; Eisa and Dobrenz, 1971), and light (Lang and Tibbitts, 1983; Morrow and Tibbitts, 1987; Rud, 2009; Wheeler, 2010). Excess water has also been cited as a potential causative factor and is commonly found when referring to the development of oedema on geranium (*Pelargonium* sp.; Balge et al., 1969; Metwally et al., 1970, 1971).

Light quality is one of the strongest candidates as a causative factor or, conversely, as a potential preventive measure for intumescence development. Ultraviolet (UV) light, in particular, is thought to be connected to the disorder because many greenhouse-glazing materials block ultraviolet light wavelengths (100 to 400 nm) and intumescences occur in protected culture. Lang and Tibbitts (1983) found that ultraviolet light, specifically UVB, effectively prevented intumescence development on tomato (var. *hirsutum* and var. *esculentum* ‘Oxheart’). Similar results have been observed by Rud (2009) on tomato ‘Maxifort’ and by Morrow and Tibbitts (1987) on tomato var. *hirsutum*. However, the exact mechanism by which ultraviolet light effectively inhibits intumescence development remains uncertain.

Ornamental sweetpotato is an annual ornamental crop commonly produced in greenhouses during the spring season; it is a popular species because of its trailing habit and striking foliage colors with several new cultivar introductions in recent years. However, the species is prone to intumescence development when produced in greenhouses, as indicated in a recent patent application for a new variety (Yencho et al., 2012).

Intumescences on sweetpotato have not been extensively studied, and very few published research articles discuss the development of this disorder on the crop. One paper, “Intumeszenze fogliari di ‘Ipomoea batatas,’”

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was published by A. Trotter in 1904. This research was cited by Wetzstein and Frett (1984) as they evaluated intumescence anatomy on sweetpotato leaves based on light and electron microscopy. However, very little is known about specific causative factors that may contribute to the occurrence of this disorder on ornamental sweetpotato. Therefore, the goal of this study was to assess the effect of UVB radiation in the prevention of intumescence development on two cultivars of ornamental sweetpotato.

Materials and Methods

Rooted cuttings of two ornamental sweetpotato cultivars, Ace of Spades and Sidekick Black, were obtained from a commercial supplier. The cuttings were potted on 1 Mar. 2013 in 11.43-cm diameter (465 mL volume) pots using a peat-based media (Fafard #2; Conrad Fafard Inc., Agawam, MA) and were grown in a glass greenhouse of Kansas State University's Throckmorton Plant Sciences Center (Manhattan, KS). The greenhouse temperature was set at 22 °C day and 20 °C night. Data loggers (Onset Computer Corporation, Bourne, MA) were placed within each treatment to monitor for any differences in temperature or relative humidity between treatments. Plants were fertigated with a 200 mg·L⁻¹ nitrogen constant liquid feed using 20N-4.4P-16.6K (Peters Professional Peat-Lite Special; Everris NA Inc., Dublin, OH) when greater than half of the plants reached ≈45% container capacity as a result of water loss.

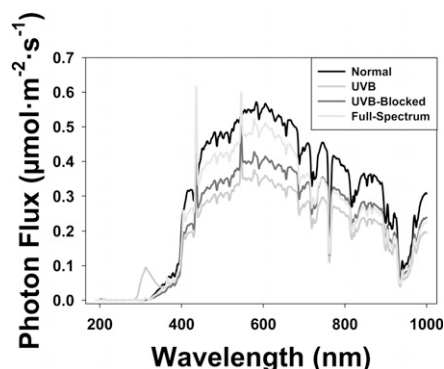


Fig. 1. Average photon flux ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) on 2 May 2013 across the full spectrum for each of the four light treatments ($N=3$). Measurements were collected using a portable ultraviolet-VIS spectroradiometer (BLACK-Comet; StellarNet, Tampa, FL).

Supplemental lighting, using full spectrum lamps (Verilux, Inc., Waitsfield, VT) providing a spectrum similar to that provided by solar radiation, was provided to achieve a 13-h photoperiod before treatment initiation. These lamps provided control lighting that simulated the light quality to which plants would be exposed in outdoor production where intumescences are not observed (as adapted from Morrow and Tibbitts, 1988). A greenhouse experiment using both sweetpotato cultivars was conducted using a two-way factorial treatment structure in a replicated row-orthogonal experimental design with subsampling. Treatment factors consisted of light treatments (described later) and cultivars (i.e., 'Ace of Spades' and 'Sidekick Black'). Within the greenhouse where the experiment was conducted, benches (total of three, each measuring 1.2×6.4 m) constituted complete blocks and defined the rows of the design. On each bench, four 1.2×1.5 -m separate sections were designated so that all light treatments could be represented. Distance from the fans (total of four) constituted balanced incomplete blocks and defined the columns of the design. A total of three individual plants from each cultivar were randomly assigned to a light treatment on each bench. Because each combination of cultivar and light treatment occurred on each bench (row), the treatments were orthogonal to the rows. Within each light treatment on a bench, individual plants of each cultivar represented the observational units and, thus, the level of subsampling. The experiment was repeated, thus defining two experimental runs.

The first experimental run was conducted 4.5 weeks after potting, whereas the second run followed at 7.5 weeks after potting; thus, plant age was different for each run. In each experimental run, plants were subjected to light treatments for 2 weeks, during which data and observations were recorded.

Light treatments. The four light treatments evaluated included 1) normal: typical glass-glazed greenhouse growing conditions (no supplemental lighting); 2) UVB: supplemental UVB lighting (280 to 315 nm) provided with UVB-313 lamps (Q-Laboratory Corporation, Westlake, OH); 3) UVB-blocked: the same as treatment UVB with the addition of Mylar® sleeves (North Solar Screen, Andover, MA) placed over the lamps to block UVB light; and 4) full-spectrum: control lighting using full spectrum lamps, as previously described. Supplemental lighting for treatments UVB, UVB-blocked, and full-spectrum was provided using a single 121-cm long light ballast

(American Fluorescent, Waukegan, IL) suspended 72 cm from the surface of the bench within each treatment. The light periods were timed to mimic the natural daylength with a 13-h photoperiod. For treatments UVB and UVB-blocked, economy-grade polystyrene lighting panels (Plaskolite Inc., Columbus, OH) were suspended 7.5 cm from the base of the ballast to diffuse the emitted light in an attempt to prevent extensive plant damage from the high levels of UVB. As a result of degradation of the diffusion panels, the panels used in treatment UVB were replaced every 2 d to maintain consistent levels of UVB light. To prevent cross-contamination between light treatments across adjacent bench sections, ultraviolet-blocking plastic film (DuraGreen Marketing USA, Mount Dora, FL) was used to isolate treatment sections on each bench. The total amount of UVB radiation ($\text{W}\cdot\text{m}^{-2}$) within each of the treatments was measured in each bench section every 3 d using a portable ultraviolet-VIS spectroradiometer (BLACK-Comet; StellarNet, Tampa, FL). Measurements of UVB radiation were later used to validate light treatments. As an additional reference, the average photon flux ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) on 2 May 2013 across the full spectrum for each of the four light treatments is included in Figure 1.

Data collection. During each experimental run, plants were observed every 3 d for intumescence development. At each observation, leaves displaying any sign of intumescence development were individually tagged. After 2 weeks, the total number of leaves displaying intumescence development was recorded. Total leaf count per plant was also obtained at the end of each run. To quantify potential plant growth differences that may have occurred under different light treatments, plant widths were measured at initiation and completion of each experimental run. Plant width was obtained by averaging the linear measurement of the plant at the greatest width and a second linear measurement perpendicular to the first. In addition, fresh and dry weights were recorded for the group of three plants of each cultivar under the same light treatment at the end of each experimental run. Also, at the end of each run, one representative plant of each cultivar was selected from each bench section and rated qualitatively on a 1 to 5 scale (Table 1) to evaluate salability. The salability ratings considered two criteria: 1) the severity of intumescence development; and 2) the severity of UVB side effects (e.g., leaf curling and discoloration) resulting from UVB light.

Table 1. Plant salability rating scale used to quantify damage on plants as a result of intumescence development and ultraviolet B damage.

Rating scale	Intumescence	Ultraviolet B
1	None; smooth leaves	None; normally developed leaves
2	Few (1 to 2) leaves with solitary growths	Few leaves with minor bronze discoloration
3	Multiple (3 to 4) leaves with mass groupings appearing along the veins of the plant	Multiple leaves with severe bronze discoloration and deformity (such as leaf curling)
4	Many (5 to 6) leaves with mass groupings forming sporadically across the leaf surface	Many leaves displaying severe bronze discoloration and deformity
5	Majority of leaves senescing resulting from severe development	Majority of leaves with severe bronze discoloration and deformity resulting in leaf senescence

Statistical analysis. Response variables of interest subjected to statistical analyses included fresh and dry weight, plant width, affected leaves per plant, plant ratings, daily temperature, relative humidity, and UVB measurements. General or generalized linear mixed models were fitted to each of these response variables, depending on whether the responses were continuous or categorical in nature, respectively. In general, the linear predictor for these statistical models included the fixed effects of experimental run (i.e., two runs), light treatment (four levels: normal, UVB, UVB-blocked, and full-spectrum), and cultivar (two levels: ‘Ace of Spades’ or ‘Sidekick Black’) as well as all two- and

three-way interactions. More specifically, the statistical model for plant width also included time (i.e., start vs. end of the experimental run) and all interactions with remaining fixed effects. For daily temperature and relative humidity, the model included the fixed effects of run, light, temperature, and time as well as all interactions. For the response on number of affected leaves per plant, separate analyses were conducted for each cultivar resulting from problems with quasi-complete separation of data points under conditions of higher-order interactions. The logit and cumulative logit link functions were used to connect the binomial probability of intumescence-affected leaf and the ordered categorical probability of plant rating with their respective linear predictors.

For all variables, the random effects of bench nested within run and also its cross-products with light treatment were considered in the linear predictor to recognize the appropriate experimental unit for each of the fixed effect factors. For this same reason, random effects for the model on plant width also included cross-products with treatment-cultivar combinations and with plant nested within treatment-cultivar combinations.

Whenever necessary, as dictated by the model fit Bayesian Information Criteria, heterogeneous residual variances were fitted to ensure that model assumptions were properly met. All variance components were estimates using residual (pseudo)likelihood. Degrees of freedom were estimated using Kenward-Roger’s procedure and then fine-tuned, as needed, to accommodate zero estimates for some of the variance components, whenever necessary. For general linear mixed models, model assumptions were evaluated using externally Studentized residuals and were considered to be appropriately met. For generalized linear mixed models, overdispersion was evaluated using the maximum likelihood-based fit statistic Pearson χ^2 over df. No evidence for overdispersion was apparent in any case.

All statistical models were fitted using the GLIMMIX procedure of SAS (Version 9.2; SAS Institute, Cary, NC) implemented using

Newton-Raphson with ridging as the optimization technique. Relevant pairwise comparisons were conducted using either the Tukey-Kramer or Bonferroni adjustment, as appropriate in each case, to avoid inflation of a Type I error rate resulting from multiple comparisons.

Results and Discussion

UVB validation. Light treatments were validated using UVB measurements collected with a spectroradiometer. Throughout both experimental runs, treatment UVB had significantly higher ($P < 0.0001$) levels of UVB radiation than any of the other three treatments (Fig. 2). As a point of reference, outdoor UVB radiation in Manhattan, KS, during clear conditions on 19 Apr. 2014 was measured at $1.31 \text{ W}\cdot\text{m}^{-2}$.

Cultivar differences. Across both experimental runs of the study, cultivars were found to be significantly different ($P < 0.0001$) in their incidence of intumescent leaves regardless of treatment. More specifically, ‘Sidekick Black’ showed almost no intumescence development (estimated probability of intumescence-affected leaf $\pm \text{SE} = 0.06\% \pm 0.02\%$), whereas ‘Ace of Spades’ was significantly more likely to develop intumescences (estimated probability of intumescence-affected leaf $\pm \text{SE} = 11.82\% \pm 0.85\%$). Differences in cultivar susceptibility to this disorder have been noted for other species, including potato (*Solanum tuberosum*; Petite and Ormrod, 1986; Seabrook and Douglass, 1998), eggplant (*Solanum melongena*; Eisa and Dobrenz, 1971), cuphea (Jaworski et al., 1988), and tomato (Metwally et al., 1970). Based on these cultivar differences, Eisa and Dobrenz (1971) suggested that genetic composition may play a partial role in the development of intumescences, although it is still uncertain as to what specific attributes or genetic factors may be affecting this resistance and susceptibility response.

Intumescent leaves. As a result of the observed low susceptibility of ‘Sidekick Black’ to intumescence development, it was not possible to evaluate the light treatment effects on this cultivar. Thus, treatment effects on ‘Sidekick Black’ are not discussed further. For ‘Ace of Spades’, treatment UVB significantly decreased the probability of intumescence development compared with the other three light treatments ($P < 0.0001$; Fig. 3). More specifically, the estimated probabilities of affected leaves for treatments normal and UVB-blocked exceeded that of treatment UVB by more than 10 times and were not significantly different from each other ($P = 0.1872$). For treatment full-spectrum, the probability of intumescence development was roughly half that of treatments normal and UVB-blocked ($P = 0.0016$) but was still greater than that of treatment UVB ($P < 0.0001$).

Our results are consistent with the findings of Lang and Tibbitts (1983), Morrow and Tibbitts (1987), and Rud (2009), by which UVB light effectively prevented

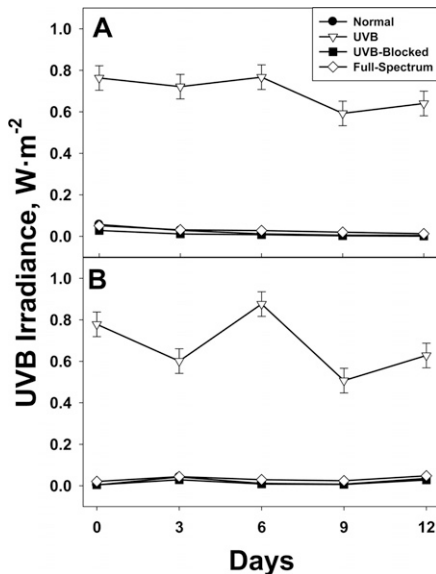


Fig. 2. Estimated least squares mean ultraviolet B (UVB) intensity ($\text{W}\cdot\text{m}^{-2}$) ($\pm \text{SE}$) for each of the four light treatments in experimental Runs 1 (A) and 2 (B) as determined using a portable ultraviolet-VIS spectroradiometer (BLACK-Comet; StellarNet, Tampa, FL). Measurements were taken every 3 d with a total of five measurements during the 2-week observation period of each experimental run. Measurements were collected on a spectrum ranging from 280 to 315 nm.

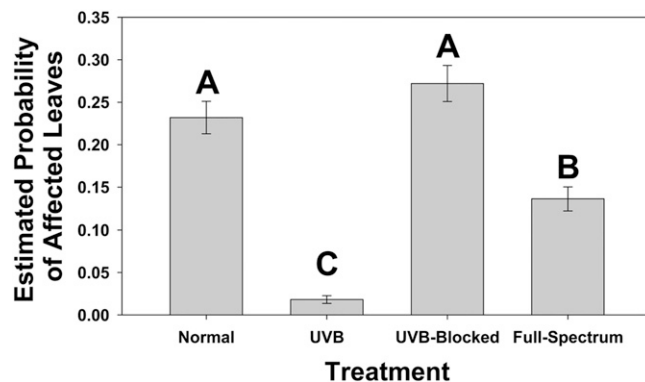


Fig. 3. Least square mean estimated probability of intumescence-affected leaves ($\pm \text{SE}$) on ‘Ace of Spades’ for each of the four light treatments. Different letters indicate significant differences between treatments ($P < 0.05$).

intumescence development on tomato plants. Our results further indicate that UVB radiation can be used as a means to effectively minimize the disorder on ornamental sweetpotato.

The reduced occurrence of intumescences on plants in treatment full-spectrum (Fig. 3) was initially believed to be related to expected higher levels of UVB radiation in this treatment compared with treatments normal and UVB-blocked. However, levels of UVB radiation emitted under treatment full-spectrum were not consistently greater than treatment normal. In particular, UVB radiation under treatment full-spectrum was significantly greater than under treatment normal only on Days 6 and 9 for experimental Run 1 and Days 0, 6, and 9 for experimental Run 2. Moreover, estimated differences in levels of UVB radiation emitted between these treatments never exceed $0.017 \text{ W}\cdot\text{m}^{-2}$. Thus, it seems unlikely that the low levels of UVB radiation emitted from treatment full-spectrum had a major role in preventing intumescence development. However, it is possible that the presence of other wavelengths of light in treatment full-spectrum such as red and far-red radiation may have played a contributing role in the moderate prevention of intumescence development observed. This idea is supported by the findings of Morrow and Tibbitts (1988) who reported that red light induced intumescence development on tomato, whereas far-red light seemed to diminish these effects. These authors further implicated the involvement of phytochrome in this disorder.

The plants in treatment UVB were not completely void of intumescence development. Occasional intumescences formed on the leaves under treatment UVB, but the severity of the lesions and number of leaves affected was significantly less than for the other treatments. However, with intumescences not typically observed in the natural environment, one would expect that the UVB light supplied to the plants under treatment UVB to be sufficient for the prevention of the disorder. A similar observation was made by Kirkham and Keeney (1974), who came to

the conclusion that ultraviolet light may act to alleviate enation development but will not completely prevent it. Rud (2009) also discussed this phenomenon concerning intumescences forming on tomato leaves regardless of UVB exposure. In that study, Rud suggested that the occurrence of intumescences under these conditions may be the result of either shading from the upper canopy leaves reducing UVB exposure or to naturally cloudy days, which could have reduced the overall ultraviolet levels in the treatments.

Although the differences in UVB exposure resulting from natural light conditions in the greenhouse seem marginal for our study, leaves developing intumescences in treatment UVB were often shaded by the upper canopy. We suspected the upper canopy likely reduced the levels of UVB light reaching the lower canopy leaves, thus contributing to their development of intumescences. To further assess this possibility, we collected pilot data to conduct a preliminary evaluation of a potential shading effect by the upper canopy leaves on UVB radiation. We measured UVB radiation by placing the spectroradiometer probe directly above and below the upper leaf canopy on six 'Ace of Spades' plants under UVB lighting. These measurements were collected after completion of the study presented here and are only intended to support future work evaluating the proposed shading mechanism. These pilot data were analyzed using a general linear mixed model that fit a randomized complete block design with heterogeneous residual variances, following procedures described in the "Statistical Analysis" section. As expected, levels of UVB radiation were significantly lower ($P < 0.0001$) under the upper leaf canopy ($0.014 \pm 0.003 \text{ W}\cdot\text{m}^{-2}$) compared with above it ($0.945 \pm 0.013 \text{ W}\cdot\text{m}^{-2}$). These pilot data support the shading mechanism suggested by Rud (2009) and display that the upper canopy may cause a substantial decrease in the UVB radiation reaching the lower canopy leaves. This reduction in UVB may lead to potential intumescence development within the lower

canopy. Future research should further investigate this phenomenon.

To further support the possible involvement of shading, Rud (2009) hypothesized that a threshold mechanism may be involved, specifically that intumescence development on susceptible plants may be prevented if plants are exposed to a specific duration and/or intensity of ultraviolet light. This idea should be further evaluated by subjecting plants to UVB of various time intervals or intensities.

The specific mechanism by which UVB radiation prevents intumescence development is still uncertain. One theory states that the plant hormone auxin may act in the development of these intumescence growths. Morrow and Tibbitts (1988) cited that auxin may be involved in intumescence development as a result of its role in cell expansion. They suggested that the inhibitory action of ultraviolet light on intumescence development may be the result of the ability of these wavelengths to degrade auxins. This theory of auxin inactivation or degradation by ultraviolet light is further supported in a review published by Springer (1978). However, why auxin levels would become more prevalent within a controlled environment in the first place is still uncertain. One could hypothesize that the lack of UVB radiation may be causing the increase in auxin levels, but the inability of treatment UVB to completely eradicate these levels, as a result of the occurrence of few intumescences, leaves one questioning this theory. One possible explanation is the shading effect by upper canopy leaves discussed previously. Under these conditions, auxin in the lower canopy leaves may not be effectively degraded as a result of the observable reduction in UVB radiation. Additional plant hormones such as cytokinin (Morrow and Tibbitts, 1988) and ethylene (Kirkham and Keeney, 1974; Wallace, 1928) have also been theorized to play a role in intumescence development.

Plant growth. No evidence for treatment differences on fresh and dry weight nor start and harvest width were apparent throughout the experiment ($P > 0.05$; Table 2). Thus, we concluded that no significant reduction in

Table 2. Least square mean estimates (\pm SE) for start and harvest plant width and for fresh and dry weight of 'Ace of Spades' and 'Sidekick Black' grown under light treatments.^z

Cultivar	Run	Treatment	Fresh wt (g)	Dry wt (g)	Start width (cm)	Harvest width (cm)
Ace of Spades	1	Normal	49.7 \pm 2.8	5.1 \pm 0.3	33.3 \pm 1.2	43.0 \pm 1.2
		UVB	43.1 \pm 2.8	4.5 \pm 0.3	34.0 \pm 1.2	42.3 \pm 1.2
		UVB-blocked	46.0 \pm 2.8	4.6 \pm 0.3	31.9 \pm 1.2	41.3 \pm 1.2
		Full-spectrum	49.6 \pm 2.8	5.0 \pm 0.3	33.4 \pm 1.2	44.7 \pm 1.2
	2	Normal	93.9 \pm 8.1	10.0 \pm 0.9	43.4 \pm 1.2	56.3 \pm 1.2
		UVB	101.2 \pm 8.1	10.2 \pm 0.9	42.2 \pm 1.2	57.4 \pm 1.2
		UVB-blocked	95.6 \pm 8.1	9.9 \pm 0.9	43.8 \pm 1.2	56.4 \pm 1.2
		Full-spectrum	101.6 \pm 8.1	10.5 \pm 0.9	44.0 \pm 1.2	58.8 \pm 1.2
Sidekick Black	1	Normal	50.2 \pm 2.8	5.4 \pm 0.3	30.5 \pm 1.2	40.9 \pm 1.2
		UVB	40.7 \pm 2.8	4.2 \pm 0.3	30.3 \pm 1.2	36.0 \pm 1.2
		UVB-blocked	45.3 \pm 2.8	4.6 \pm 0.3	29.3 \pm 1.2	40.2 \pm 1.2
		Full-spectrum	48.8 \pm 2.8	5.2 \pm 0.3	28.9 \pm 1.2	39.4 \pm 1.2
	2	Normal	121.1 \pm 2.8	12.7 \pm 0.3	39.5 \pm 1.2	49.2 \pm 1.2
		UVB	113.9 \pm 2.8	11.0 \pm 0.3	38.7 \pm 1.2	49.9 \pm 1.2
		UVB-blocked	126.4 \pm 2.8	13.0 \pm 0.3	41.4 \pm 1.2	52.1 \pm 1.2
		Full-spectrum	128.5 \pm 2.8	13.2 \pm 0.3	39.9 \pm 1.2	50.9 \pm 1.2

^zRegardless of cultivar, there were no significant differences among any of the response variables ($P > 0.05$).

UVB = ultraviolet B.

plant growth occurred from ultraviolet light. These findings differ from those of Frantz et al. (2012), whereby ultraviolet light was found to be a potential means of regulating plant growth in plugs. This contrast could be the result of differences in plant age, because plugs may be more vulnerable to growth inhibition from ultraviolet light than the plants in our study or that dose differences between studies impacted the results (Frantz et al., 2012).

However, plant growth differences were found between cultivars regardless of treatment (Table 2). In particular, during experimental Run 2, plants from ‘Sidekick Black’ had significantly greater fresh ($P = 0.0003$) and dry ($P = 0.0008$) weights compared with ‘Ace of Spades’. Additionally, ‘Ace of Spades’ plants were wider than ‘Sidekick Black’ plants at both the beginning and end of each experimental run ($P < 0.0001$). ‘Sidekick Black’ exhibited more compact and dense plants, whereas ‘Ace of Spades’ showed a more trailing habit.

Plant ratings. Although plant growth was not significantly affected by the UVB radiation in this study, negative effects to plant aesthetics were observed in treatment UVB. Both leaf deformities and discoloration were observed during plant salability ratings of our study, similar to those reported by Frantz et al. (2012). Nevertheless, no significant treatment effects were apparent in the overall plant salability ratings ($P = 0.2058$). We speculate that by accounting for both damage resulting from intumescence development and that caused by UVB radiation, the rating scale yielded no significant differences between treatments (Fig. 4). Thus, although the UVB effectively reduced intumescence development, the negative effects on plant aesthetics seemed to nullify this benefit. It may be possible to minimize these side effects with a better understanding of the critical minimum levels of UVB intensity and dosage necessary to prevent intumescence development.

Plant rating differences were apparent between the two cultivars regardless of treatment ($P < 0.0001$; Fig. 5). In particular, ‘Sidekick Black’ received an overall lower cumulative probability of high (undesirable) ratings compared with ‘Ace of Spades’. This was to be expected following from our observations that ‘Sidekick Black’ plants were more resistant to intumescence development than those of ‘Ace of Spades’.

Temperature associated with light treatments. Average daily temperature fluctuated over the duration of each experimental run (Fig. 6). Additionally, temperatures were often greater than the original set points of 22 °C day and 20 °C night. These escalated temperatures were likely the result of the ultraviolet-blocking plastic film that was used to isolate treatment sections on each bench. This plastic film potentially reduced the efficiency of the fan and pad evaporative cooling system used within this greenhouse. Regardless, during experimental Run 1 and most of experimental Run 2, no differences

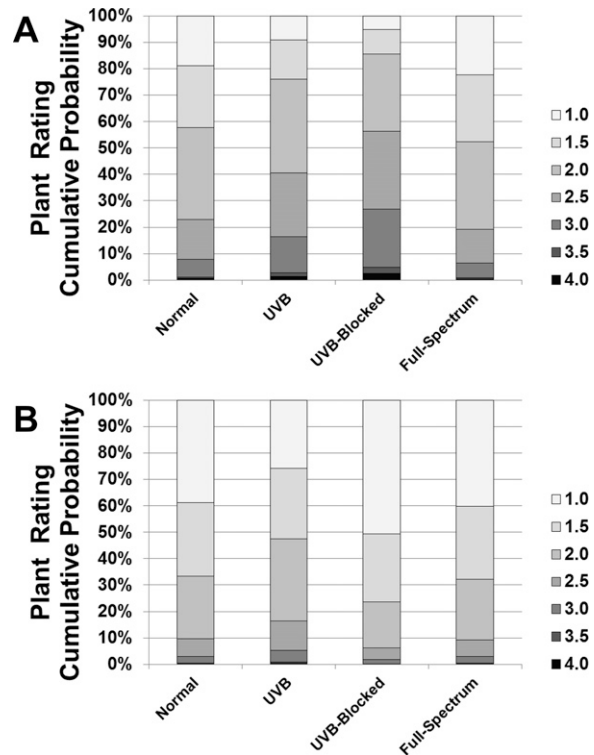


Fig. 4. Estimated cumulative probability of a plant displaying damage equivalent to or greater than the rating administered to plants of ‘Ace of Spades’ (A) and ‘Sidekick Black’ (B) under light treatments. The rating system was based on a 1 to 5 scale considering the number of leaves displaying intumescence and ultraviolet B (UVB) damage as well as the severity of damage, where 1 = none; 2 = few (one to two); 3 = multiple (three to four); 4 = many (five to six); 5 = majority. A rating of 5 is not included in this table as a result of damage severity in this study never exceeding a rating of 4. No evidence for main treatment effects or interactions involving treatment was apparent based on $\alpha = 0.05$.

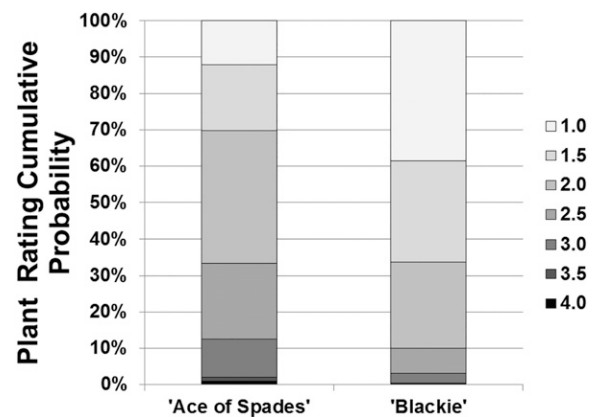


Fig. 5. Estimated cumulative probability of a plant displaying damage equivalent to or greater than the rating administered to plants of ‘Ace of Spades’ and ‘Sidekick Black’, adjusted for treatments. The rating system was based on a 1 to 5 scale considering the number of leaves displaying intumescence and ultraviolet B (UVB) damage as well as the severity of damage, where 1 = none; 2 = few (one to two); 3 = multiple (three to four); 4 = many (five to six); 5 = majority. A rating of 5 is not included in this histogram as a result of damage severity in this study never exceeding a rating of 4.

were apparent between treatments in average daily temperature ($P > 0.05$). However, during Days 1, 3, 4, 5, 9, 12, 13, and 15 of experimental Run 2, average daily temperature under treatment UVB was significantly increased relative to treatment UVB-blocked ($P < 0.05$). Additionally, on Day 5 of experimental Run 2, treatment UVB had a greater average daily temperature than treatment

full-spectrum ($P = 0.0107$). The estimated differences in average daily temperature never exceeded 3 °C (Fig. 6). No evidence for differences in average daily temperature was apparent between other treatments ($P > 0.05$).

Even with the slightly higher temperatures recorded in treatment UVB during experimental Run 2, intumescence development was still

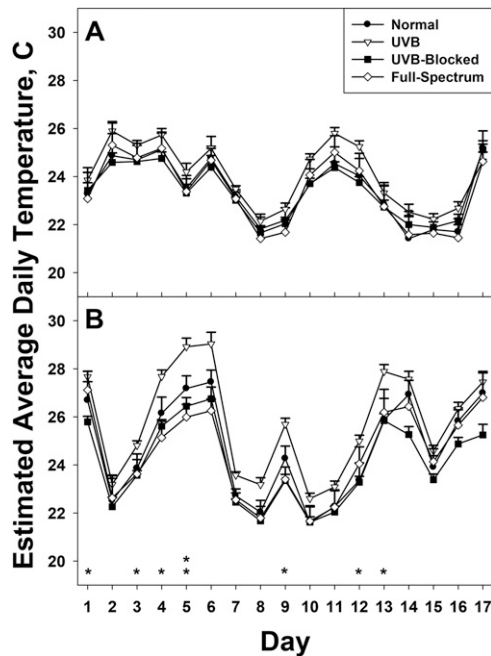


Fig. 6. Least square mean estimates of average daily temperatures ($^{\circ}\text{C} \pm \text{SE}$) under light treatments during experimental Runs 1 (A) and 2 (B). During Days 1, 3, 4, 5, 9, 12, 13, and 14 of experimental Run 2, average daily temperatures under treatment ultraviolet B (UVB) were significantly higher than under treatment UVB-blocked ($P < 0.05$). Also on Day 5 of experimental Run 2, the average daily temperature of treatment UVB was significantly higher than treatment full-spectrum ($P < 0.05$). Days displaying significant differences are noted on the graph with a “*” above the corresponding day.

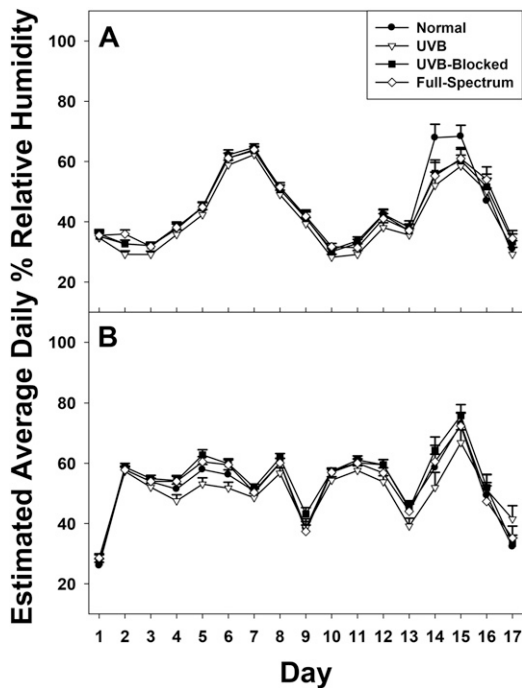


Fig. 7. Least square mean estimates of average daily relative humidity ($\% \pm \text{SE}$) under light treatments during experimental Runs 1 (A) and 2 (B). Treatment ultraviolet B (UVB) had a significantly lower relative humidity than treatments normal ($P = 0.0049$), UVB-blocked ($P = 0.0009$), and full-spectrum ($P = 0.0084$) regardless of run or bench based on multiple comparisons at $\alpha = 0.05$.

suppressed. In regard to temperature, Balge et al. (1969) and Eisa and Dobrenz (1971) found that high temperatures were necessary for oedema and intumescence development on zonal geranium and eggplant respectively. However, Lang and Tibbitts (1983) found that intumescence

development on tomatoes was more severe at cooler temperatures. Although it is possible that temperature may act synergistically with other factors to increase severity or occurrence of intumescence development, it appears that the quality of light the plants are subjected to may

override those conditions to prevent intumescence development on ornamental sweetpotato.

Relative humidity associated with light treatments. For all light treatments, levels of relative humidity fluctuated greatly over the course of the study (Fig. 7). However, relative humidity was lowest under the conditions of treatment UVB compared with any of the other treatments regardless of the experimental run ($P < 0.001$; Fig. 7). On average, this significant difference in relative humidity did not exceed 3.4%. Eisa and Dobrenz (1971) reported relative humidity as being a potential causative factor for intumescence development on eggplant; in contrast, Lang and Tibbitts (1983) stated that this factor did not contribute to intumescence development on tomato. Given the results of this study, we speculate that a mechanism similar to that proposed for temperature may be at work. Namely, although relative humidity may act synergistically with other factors to increase the occurrence or severity of intumescence development, it appears that light quality may override these conditions and act to prevent their development on ornamental sweetpotato.

Conclusions

The results from this study show that UVB light plays a significant role in the prevention of intumescence development on ornamental sweetpotato. The striking cultivar differences in susceptibility to intumescence development observed are also of interest, because it suggests the role of a genetic component. At this point, the best recommendation for intumescence control would seem to be cultivar or variety selection (Jaworski et al., 1988). Future research on genetic control of susceptibility to intumescence development in ornamental sweetpotato is warranted. Additionally, the fact that treatment UVB still had the occasional leaf develop intumescences suggests that a more complex interaction, likely involving other factors such as temperature, humidity, hormones, etc., may be at work. This insight will assist in an enhanced understanding of intumescence development and the mechanism by which this disorder develops.

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