Chapter 20
Light Quality Effects on Intumescence (Oedema) on Plant Leaves

Kimberly A. Williams, Chad T. Miller, and Joshua K. Craver

Abstract Intumescence is a physiological disorder that is characterized by abnormal outgrowths of epidermal and/or palisade parenchyma cells on the leaf, petiole or stem surfaces of affected plants. Intumescences are a different disorder than oedema based on anatomy of affected cells and causal agents. This disorder is most often observed on crops produced in controlled environments and has been reported on a wide range of plant species, including ornamental sweet potato (*Ipomoea batatas*), cuphea (*Cuphea* spp.) and solanaceous crops of tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*). When susceptible crops are grown under ultraviolet-deficient environments, such as light-emitting diode (LED) sole-source lighting that supplies only red wavelengths, intumescences are most severe. However, the incidence of the disorder can be diminished or prevented if crops are grown in environments providing ample blue or ultraviolet wavelengths of light. End-of-day far-red lighting has also shown some promise in mitigating the disorder.

Keywords Blue light • Oedema • Far-red light • LED • Tomato • Ultraviolet light

20.1 Introduction

Intumescence is a physiological disorder that is characterized by abnormal outgrowths of cells on leaf, petiole and stem surfaces (Morrow and Tibbits 1988; Wetzstein and Frett 1984). The disorder has long been observed on many crops produced in controlled environments and, more recently, on those grown under LEDs lacking wavelengths in the blue spectrum. The first description of the disorder in the literature was by Sorauer in 1899, who reported that intumescences developed on many different plant species, including mono- and dicotyledonous

K.A. Williams (✉) • C.T. Miller
Kansas State University, Manhattan, KS, USA
e-mail: kwilliam@ksu.edu

J.K. Craver
Department of Horticulture and Landscape Agriculture, Purdue University, 625 Agriculture Mall Drive, West Lafayette, IN 47907-2010, USA

T. Kozai et al. (eds.), *LED Lighting for Urban Agriculture*,
DOI 10.1007/978-981-10-1848-0_20

angiosperms, gymnosperms and ferns (La Rue 1932). While there are many disorders with similar symptoms to intumescence, the terms used to name them are often used interchangeably and include intumescence, edema or oedema, excrescence, neoplasm, gall, genetic tumour, leaf lesion and enation (Pinkard et al. 2006). The body of literature with reports of these disorders includes a wide variety of plant species, but development on solanaceous crops such as tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*) is the most commonly documented.

In addition to the long lists of terminology and plant species subject to these disorders, the list of environmental factors that have been reported to contribute to their development is also extensive. Plant water status; temperature; hormones, including ethylene; plant genetics; pest damage, including injury by insects and fungal infection; mechanical and chemical injury; nutrient status; and, of course, light quality and availability have all been reported as agents that contribute to foliar intumescence in various plant species (Pinkard et al. 2006). Thus, the literature is muddled by lack of clarity regarding the nomenclature and proper identification of these disorders, as it is unlikely that they are all the same.

In particular, the terms intumescence and oedema are frequently used interchangeably to describe such disorders on several plant species produced in controlled environments. However, Lang and Tibbits (1983) suggested that these terms should instead refer to completely different disorders. They defined oedema as 'a 'watery swelling of plant organs or parts,' resulting from water congestion in plant tissue'. On the other hand, they indicated that the disorder observed in their research with tomatoes should be called intumescence because plants showed symptoms when the relative humidity 'was low and there was no water congestion in the tissue'. Morrow and Tibbitts (1988) added to this differentiation by stating that 'oedema' typically forms under conditions where excess water and high relative humidity prevent sufficient transpiration by the plant, whereas their research showed that UV radiation aided in preventing intumescence on solanaceous species. Further, in research of Rangarajan and Tibbitts (1994) where far-red light failed to inhibit oedema injury on ivy geranium, they suggested that the causative factors and physiological systems that regulate oedema on *Pelargonium* spp. and intumescence on *Solanum* spp. were different. Williams et al. (2015) used light and scanning electron microscopy to study lesions as they developed on five plant species and concluded that the anatomy of intumescence in tomato (*Solanum lycopersicum* 'Maxifort'), ornamental sweet potato (*Ipomoea batatas* 'Blackie'), and cuphea (*Cuphea llavea* 'Tiny Mice') appeared different than oedema in interspecific (*Pelargonium* x 'Caliente Coral') and ivy geraniums (*Pelargonium peltatum* 'Amethyst 96'). Therefore, because environmental causes and anatomy of intumescence and oedema have been found to be different, the two terms do not seem to refer to the same physiological disorder. Interactions may exist between absence of ultraviolet light and other environmental factors, such as plant water status, but this remains to be studied with future research. The focus of this chapter is narrowed to light quality effects on the occurrence of what we believe to be intumescence, though the disorder may have been reported as other abiotic leaf damage.

20.2 Description and Impact of Intumescences

20.2.1 Anatomy and Morphology

Intumescence begins with a group of epidermal cells or palisade parenchyma cells just below the epidermal layer, enlarging and undergoing hypertrophy. As the disorder progresses, the cells become increasingly elongated and translucent (Figs. 20.1 and 20.2), often coalescing into lesions comprised of groups of cells. Depending on plant species, lesions may begin on the adaxial or abaxial leaf surface or both. The affected area expands as lesions develop, though under some conditions, a single intumescence will senesce and abscise from the leaf surface with no further expansion. Typically, though, as lesions senesce, the apex blackens (ornamental sweet potato, Fig. 20.2), turns brown and collapses (tomato) and/or coalesces into larger, necrotic spots (e.g. cuphea, Fig. 20.3; Craver et al. 2014a).

20.2.2 Genetics

The formation of intumescences has been shown to be under genetic control for the variety of plant species on which the disorder has been studied, including potato, *Solanum tuberosum* (Petitte and Ormrod 1986; Seabrook and Douglass 1998); tomato, *Solanum lycopersicum* (e.g. Sagi and Rylski 1978); cuphea, *Cuphea* sp. (Jaworski et al. 1988); and ornamental sweet potato, *Ipomoea batatas* (Craver et al. 2014b). For example, in Petitte and Ormrod's (1986) work with potato, they found that two early to midseason cultivars ('Norchip' and 'Superior') were resistant to the disorder, while two late-maturing cultivars ('Kennebec' and 'Russet Burbank') were susceptible. In Sagi and Rylski's work with tomato, the variety 'Hosen Eilon' developed the disorder, while 'Viresto' did not. In Jaworski's work on *Cuphea* sp., it was noted that intumescences could be avoided in *C. wrightii* by selecting accession numbers of plants that were not susceptible to the disorder (Jaworski et al. 1988). In a large screening trial of ornamental sweet potato varieties, only 8 out of 36 varieties were considered highly symptomatic with 20 % or more leaves affected by intumescence (Craver et al. 2014c). Rud (2009) and Craver et al. (2014c) suggested that perhaps one of the best options for control of intumescence was the selection and production of resistant cultivars.

20.2.3 Photosynthesis and Yield

One of the most detrimental impacts of severe intumescence development is the impairment of photosynthesis (Lang et al. 1983; Pinkard et al. 2006). The negative impacts of intumescence on plant tissue can include chlorosis, senescence

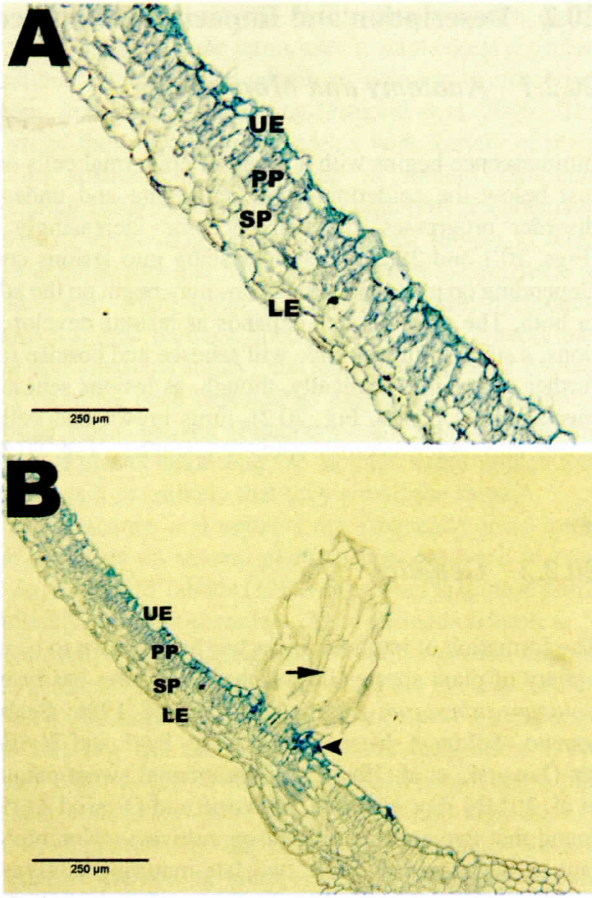

Fig. 20.1 Light microscopy cross sections of asymptomatic ornamental sweet potato leaf (**a**) and symptomatic intumescent leaf (**b**) stained with Toluidine Blue O. Upper epidermis (*UE*); palisade parenchyma (*PP*), spongy parenchyma (*SP*) and lower epidermis (*LE*). Hypertrophic PP cells are shown (*arrow*) protruding above the UE, pushing aside UE cells (point). (Images by Craver)

(Wetzstein and Frett 1984), leaf abscission (Rud 2009) and the downward curling of leaves (Figs. 20.2, 20.3 and 20.4). Lang et al. (1983) reported that hypertrophied palisade and chlorenchyma cells of tomato (*S. lycopersicum*) had few or no chloroplasts. Pinkard et al. (2006) furthered the idea of impaired photosynthesis by stating that intumescences may reduce the amount of leaf surface area available for light absorption (Fig. 20.5). Eventual plant death can occur if the disorder is left unchecked (Rud 2009).

Craver et al. (2014b) found that ultraviolet light prevented intumescence development on the susceptible cultivar of ornamental sweet potato, 'Ace of Spades'. In this study, plant growth as measured by fresh and dry weights and width at harvest was similar across treatments with and without ultraviolet light. These results indicate that if intumescence development is not severe, growth is not measurably affected.

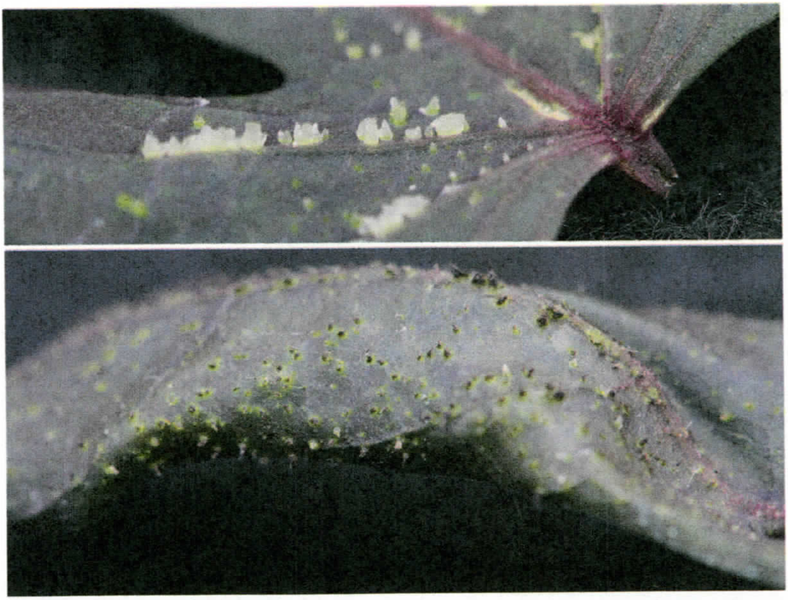

Fig. 20.2 Ornamental sweet potato (*Ipomoea batatas*) showing early to mid-stage intumescence development on the adaxial leaf surface (*top*) and late stages of intumescence development with necrotic lesions (*bottom*). Note the downward curling of the leaf blade (*bottom*). (Images by Craver)

20.2.4 Aesthetic and Economic Impact

Some of the most intumescent or symptomatic species grown for commercial use (e.g. cuphea, ornamental sweet potato) are produced solely for ornamental purposes. Intumescences not only impair the physiological processes of the plant but also negatively affect the overall aesthetic quality and, ultimately, marketability of the crop. Severely intumescent plants may appear to be diseased which decreases salability and product value (Figs. 20.2, 20.3 and 20.4).

20.3 Light Quality Affects Intumescence

Light quality has long been viewed a strong candidate for a causative factor or potential preventative measure for intumescence development because of observations that the disorder occurs predominantly in controlled environments.

Fig. 20.3 *Cuphea llavea* 'Tiny Mice' leaves showing early to mid-stages (*top*) and late stages with necrotic regions (*bottom*) of intumescence development on leaves. Note the downward curling of the leaf blade (*bottom*). (Images by Craver)

20.3.1 Ultraviolet Light

Ultraviolet (UV) radiation includes UVA (315–400 nm), UVB (280–315 nm) and UVC (100–280 nm). This range of light quality is thought to be related to intumescence development because many greenhouse glazing materials block UV wavelengths, and intumescences have frequently been observed on crops grown under cover, but not on the same crops growing outside of the protected environment. Greenhouse plastic, or polyethylene, for example, includes a UV-block additive to slow degradation under solar radiation and extend its useful life.

Recent research has linked specific benefits of UV light to plants, including regulation of plant metabolism and morphology (Jansen and Bornman 2012; Jenkins 2009). Bridgen (2015) and Franz et al. (2012) have suggested that UV light could be used to manage plant growth during crop production. Reductions in leaf growth have commonly been observed in response to UV radiation. Wargent et al. (2009a) studied leaf response across a range of organizational scales to evaluate underlying mechanisms of effect.

Fig. 20.4 An ornamental sweet potato (*Ipomoea batatas* 'Ace of Spades') leaf showing severe intumescence development, primarily along the major leaf veins, and *downward* leaf curling. (Image by Craver)

Fig. 20.5 Tomato (*Solanum lycopersicum* 'Maxifort') leaves showing severe intumescence damage, with large, necrotic areas that result in reduced photosynthetic area for the plant. (Image by Craver)

20.3.1.1 Prevention of Intumescence

The benefit of UV light related to intumescence is the consistent findings that UVB radiation effectively prevents the development of this disorder on susceptible plant species. At low enough doses, intumescence is prevented by UVB light and negative impacts on growth from these wavelengths do not occur. While discussing the many physiological disorders that occur during crop production for life support systems in space, Wheeler (2010) indicated that near UV light (300–400 nm) can effectively prevent intumescence from occurring.

Lang and Tibbitts (1983) placed tomato plants in exposure boxes constructed of Plexiglas G (blocked wavelengths below 330 nm) and Plexiglas G II-UVT (transmitted wavelengths above 230 nm). They found that the tomato plants grown in the Plexiglas G-II-UVT boxes were free from injury, while those plants grown in the Plexiglas G boxes displayed severe intumescence. Continuing with this line of research, Morrow and Tibbitts (1987) looked at intumescence development on tomato leaf disks. Leaf disks were induced with intumescences by blocking the UV radiation emitted from cool-white fluorescent lamps with UV-absorbing Plexiglas.

Rud (2009) found similar results in that UVB light greatly reduced the occurrence of intumescences on tomato (*Solanum lycopersicum* 'Maxifort'). She hypothesized that there may be a threshold mechanism involved with this response. That is, 'if a plant susceptible to the development of intumescences receives a certain amount or intensity of UV light, intumescence development may be prevented'.

In greenhouse experiments, Craver et al. (2014b) established a similar relationship between lack of UVB and intumescence development on ornamental sweet potato 'Ace of Spades', a susceptible variety. The addition of UVB radiation significantly reduced the number of leaves affected with intumescences when compared to plants grown under other light treatments lacking these wavelengths.

20.3.1.2 Molecular Mechanisms

UV RESISTANCE LOCUS8 (UVR8) has been shown to regulate UV-protective gene expression responses and is involved in controlling aspects of leaf growth and morphogenesis, though inhibition of epidermal cell division in response to UVB is largely independent of UVR8 (Wargent et al. 2009b). Interestingly, while recent studies have shown that UV radiation reduces epidermal cell expansion (e.g. Jacques et al. 2011; Wargent et al. 2009a), other studies provide evidence that intumescences—which occur in the absence of UVB—are hypertrophied epidermal and/or palisade parenchyma cells (e.g. Craver et al. 2014a).

There is no research that has evaluated gene regulation or the genetic mechanism of intumescence occurrence. One study subjected leaf tissue with and without intumescences from a susceptible tomato variety, *Solanum lycopersicum* 'Maxifort', to microarray analysis for comparison of gene expression profiles

(Williams et al. 2011). A number of genes that could be induced by UVB treatment but that were suppressed in the leaves with intumescences were identified. Among them, 3-beta-hydroxysteroid dehydrogenase (*3β-HSD*) was identified as potentially playing a key role in UVB inhibiting intumescence development.

As Robson et al. (2015) indicate, future research will need to disentangle the complex interactions that occur at the threshold UV dose where metabolic regulation and stress-induced morphogenesis overlap.

20.3.2 Blue and Green Light

Blue and green light have been found to have an inhibitory effect on intumescence development. In very early work, Dale (1901) observed that intumescence would not develop on hibiscus (*Hibiscus vitifolius*) under blue, yellow or green 'glasses'. Similarly, Morrow and Tibbitts (1988) found that intumescences were not induced when tomato leaf disks were exposed to blue wavelengths of light providing a photosynthetic photon flux density (*PPFD*) of 25 μmol m^{-2} s^{-1}, and only 3 % of leaf disk area had intumescences when exposed to green wavelengths at the same *PPFD*.

Seabrook and Douglass (1998) reported the only exception to this result with blue-green light. They observed that intumescences were reduced in potato (*Solanum tuberosum* 'AC Brador' and 'Shepody') plantlets grown in vitro under a yellow filter that eliminated the blue-green (380–525 nm) portion of the spectrum. This result suggested that blue-green light is putatively involved in the occurrence of intumescence.

In early research with LED lamps, Massa et al. (2008) reported that when the percentage of blue light (440 nm peak) was maintained at less than 10–15 % of total photosynthetic photons, resulting in a red light-dominant (660 nm peak) environment, cowpea (*Vigna unguiculata*) developed intumescences on older leaves. 'Triton' pepper (*Capsicum annuum*) plants grown with either intracanopy or overhead red (R) + blue (B) LED lighting also developed severe intumescences, though for this species, symptoms were not mitigated by using higher percentages of blue light as occurred for cowpea.

In recent work with LED lamps, Wollaeger and Runkle (2013) observed intumescence on tomato 'Early Girl' in all treatments grown under only 10 % each of B and green (G) LEDs with the remaining light from orange (O; peak = 596 nm) to R (peak = 634 nm) to hyper-red (HR; peak = 664 nm) wavelengths; a *PPFD* of 160 μmol m^{-2} s^{-1} was provided. In a follow-up study, Wollaeger and Runkle (2014) grew tomato 'Early Girl' under combinations of B, green (G) and R LEDs or under fluorescent lamps, again providing a *PPFD* of 160 μmol m^{-2} s^{-1}. The resulting LED treatment percentages were B_{25}+G_{25}+R_{50}, B_{50}+G_{50}, B_{50}+R_{50}, G_{50}+R_{50}, R_{100} and B_{100}. Tomato plants developed the most leaflets with intumescence when grown under solely red light, while the disorder was absent or nearly so when grown under at least 50 % blue light or fluorescent light. Additionally, the blue light (31 μmol m^{-2} s^{-1}) and small quantity of UVA (<5 μmol m^{-2} s^{-1}) light emitted from the fluorescent lamp were almost sufficient to prevent intumescence development.

Next, Wollaeger and Runkle (2015) found that tomato 'Early Girl' grown under B_{50}+G_{50} or fluorescent lighting resulted in plants with no or nearly no intumescences (Wollaeger and Runkle 2015). Intumescences developed on 40 % fewer leaflets for tomatoes grown under $G_{50} + R_{50}$ compared to R_{100}, but $G_{50} + R_{50}$ treated plants had about 70 % more leaflets with intumescences than those grown under B_{25}+G_{25}+R_{50}. This work supports the mitigation of the disorder with increasing blue wavelengths.

As more research with LED lights occurs and the greenhouse industry adopts their use, observations that are consistent with the above trends are being reported for other crops. For example, Yelton et al. (2014) observed that the occurrence of 'oedema' on basil was reduced under higher levels of blue light; treatments were 0, 8, 16, 24 and 32 % B with a *PPFD* of 250 μmol m^{-2} s^{-1} under a 14 h day^{-1} photoperiod.

20.3.3 Red and Far Red

UV and blue light have not been the sole focus of studies involving the relationship of light and intumescence development. Research by Morrow and Tibbitts (1988) looked at the potential involvement of phytochrome in intumescence development on leaf disks of a wild tomato, *Solanum lycopersicum* var. *hirsutum*. Various photon spectra were created by using different lamps and filters. They found that solely red light resulted in intumescence on 63 % of the sample leaf area of the disks and that increased photon flux density of red light resulted in greater occurrence of the disorder. However, when leaf disks were also subjected to far-red light, the effects of the red light on intumescence development seemed to diminish, such that if ample amounts of far-red light were made available, intumescence injury was effectively inhibited. The authors speculated that this inhibitory action by far-red wavelengths suggested the involvement of phytochrome in this disorder. They expanded this hypothesis by proposing that there were two photosynthetic photon density responses involved—a prolonged red response and a reversible red/far-red response. In this case, the prolonged red response would control induction of this disorder on the plant, while the red/far-red response would directly control expression (Morrow and Tibbitts 1988).

Wollaeger and Runkle (2014) have routinely observed the greatest incidence of intumescence on tomato when produced under only red wavelengths of light. As discussed above, plants grown under the $G_{50} + R_{50}$ treatment developed 40 % fewer leaflets with intumescences than those under R_{100}.

In recent research, Eguchi et al. (2015) reported on using end-of-day far-red lighting from LEDs as a cost-effective alternative to UV to inhibit intumescences in tomato seedlings. Tomato rootstock 'Beaufort' were grown under LED light ratios of $B_{10} + R_{90}$ or $B_{75} + R_{25}$ providing a *PPFD* of 100 μmol m^{-2} s^{-1} under an 18 h day^{-1} photoperiod. Varied doses (1, 2, 4, 9 or 74 mmol m^{-2} d^{-1}) of end-of-day far-red lighting were applied to the seedlings, and intumescence development was compared to a control that did not receive any additional far-red light. Evaluation for intumescence occurred 16 days after seeding. For the seedlings grown under the $B_{10} + R_{90}$ treatment, the 1 mmol m^{-2} d^{-1} end-of-day far-red treatment (5.2 μmol m^{-2} s^{-1} for 3.3 min) reduced the incidence of stem intumescence from 63 % to none and the incidence of leaf intumescence from 62 % to 42 % compared to control plants. However, the efficacy of the end-of-day far-red lighting was the same regardless of dose. The authors concluded that, in combination with production under blue wavelengths, the subjection of tomato seedlings to end-of-day far-red lighting was useful in mitigating the occurrence of intumescences.

20.3.4 Concluding Summary

Intumescence appears to be a physiological disorder that occurs at the threshold between beneficial and harmful UV dose. Research is rapidly enhancing our understanding of the role of light quality in various aspects of plant metabolism. At the same time, LEDs are increasingly popular for many reasons, including their ability to expose crops to specific wavelengths of light. With the development of a mechanistic understanding of the underlying causes of intumescence, LED spectra can be modified in commercial applications to optimize plant growth and development while minimizing physiological disorders such as intumescence.

References

Bridgen M (2015) Using ultraviolet-C light as a plant growth regulator. Acta Hortic 1085:167–169

Craver JC, Miller CT, Williams KA et al (2014a) Characterization and comparison of lesions on ornamental sweetpotato 'Blackie', tomato 'Maxifort', interspecific geranium 'Caliente Coral', and bat-faced cuphea 'Tiny Mice'. J Am Soc HortScience 139(5):603–615

Craver JC, Miller CT, Williams KA et al (2014b) Ultraviolet radiation affects intumescence development in ornamental sweetpotato (*Ipomoea batatas*). HortScience 49(10):1277–1283

Craver JC, Miller MG, Cruz et al (2014c) Intumescences: further investigations into an elusive physiological disorder. Greenhouse Product News (GPN) 9:32–40

Dale E (1901) Investigations on the abnormal outgrowths or intumescences on *Hibiscus vitifolius* Linn.—a study in experimental plant pathology. Phil Trans R Soc Lond B 194:163–182

Eguchi T, Hernandez R, Kubota C (2015) End-of-day far-red lighting to mitigate intumescences on tomato seedlings grown under LEDs. HortScience 50(9):S219–S220, Abstr

Frantz J, Heckathorn SA, Rud N et al (2012) Short-term UV light exposure can lead to long-term plant growth regulation. HortScience 47(9):210–211, Abstr

Jacques E, Hectors K, Guisez Y et al (2011) UV radiation reduces epidermal cell expansion in *Arabidopsis thaliana* leaves without altering cellular microtubule organization. Plant Signal Behav 6(1):83–85

Jansen M, Bornman J (2012) UV-B radiation: from generic stressor to specific regulator. Physiol Plant 145(4):501–504

Jaworski C, Bass MH, Phatak SC et al (1988) Differences in leaf intumescences between Cuphea species. HortScience 23:908–909

Jenkins G (2009) Signal transduction in responses to UV-B radiation. Ann Rev Plant Biol 60:407–431

La Rue C (1932) Intumescences on poplar leaves. I. Structure and development. Am J Bot 20 (1):1–17

Lang S, Tibbitts T (1983) Factors controlling intumescence development on tomato plants. J Am Soc HortScience 108(1):93–98

Lang S, Struckmeyer BE, Tibbitts TW (1983) Morphology and anatomy of intumescence development on tomato plants. J Am Soc HortScience 108(2):266–271

Massa G, Kim H, Wheeler RM et al (2008) Plant productivity in response to LED lighting. HortScience 43(7):1951–1956

Morrow R, Tibbitts T (1987) Induction of intumescence injury on leaf disks. J Am Soc HortScience 112(2):304–306

Morrow R, Tibbitts T (1988) Evidence for involvement of phytochrome in tumor development on plants. Plant Physiol 88:1110–1114

Petitte J, Ormrod D (1986) Factors affecting intumescence development on potato leaves. HortScience 21(3):493–495

Pinkard E, Gill W, Mohammed C (2006) Physiology and anatomy of lenticel-like structures on leaves of *Eucalyptus nitens* and *Eucalyptus globulus* seedlings. Tree Physiol 26:989–999

Rangarajan A, Tibbitts T (1994) Exposure with far-red radiation for control of oedema injury on 'Yale' ivy geranium. HortScience 29(1):38–40

Robson TM, Klem K, Urban O et al (2015) Re-interpreting plant morphological responses to UV-B radiation. Plant Cell Environ 38(5):856–866

Rud, N (2009) Environmental factors influencing the physiological disorders of edema on ivy geranium (*Pelargonium peltatum*) and intumescences on tomato (*Solanum lycopersicum*). Master's thesis. Kansas State University, Manhattan, KS

Sagi A, Rylski I (1978) Differences in susceptibility to oedema in two tomato cultivars growing under various light intensities. Phytoparasitica 6(3):151–153

Seabrook J, Douglass L (1998) Prevention of stem growth inhibition and alleviation of intumescence formation in potato plantlets in vitro by yellow filters. Am J Potato Res 75:219–224

Wargent JJ, Moore JP, Ennos AR et al (2009a) Ultraviolet radiation as a limiting factor in leaf expansion and development. Photochem Photobiol 85:279–286

Wargent JJ, Gegas VC, Jenkins GI et al (2009b) UVR8 in *Arabidopsis thaliana* regulates multiple aspects of cellular differentiation during leaf development in response to ultraviolet B radiation. New Phytol 183:315–326

Wetzstein H, Frett J (1984) Light and scanning electron microscopy of intumescences on tissue-cultured, sweet potato leaves. J Am Soc HortScience 109:280–283

Wheeler R (2010) Physiological disorders in closed environment-grown crops for space life support. 38th COSPAR scientific assembly

Williams KA, Wu Q, Park S et al (2011) Understanding the mechanisms regulating the development of intumescences in tomato through genomic analyses. HortScience 46(9):S267–S268, Abstr

Williams KA, Craver JK, Miller CT et al (2015) Differences between the physiological disorders of intumescences and edemata. Acta Hortic XXIX International Horticultural Congress on Horticulture: sustaining lives, livelihoods and landscapes (IHC2014): 1104, pp 401–406

Wollaeger H, Runkle E (2013) Growth responses of ornamental annual seedlings under different wavelengths of red light provided by light-emitting diodes. HortScience 48(12):1478–1483

Wollaeger H, Runkle E (2014) Growth of impatiens, petunia, salvia, and tomato seedlings under blue, green, and red light-emitting diodes. HortScience 49(6):734–340

Wollaeger H, Runkle E (2015) Growth and acclimation of impatiens, salvia, petunia, and tomato seedlings to blue and red light. HortScience 50(4):522–529

Yelton M, Byrtus J, Chan G (2014) Better tasting basil grown with LED lighting technology. LumiGrow, Inc., Research Brief. http://www.lumigrow.com/download-the-basil-steering-study/