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Intumescence Response by Tomato Plants Grown in a Greenhouse or Indoors Using Two Types of Soilless Culture Systems

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Abstract. **The main objective of this study was to characterize intumescence injury of three susceptible tomato cultivars grown in a greenhouse or indoors using two types of soilless culture systems. Plants of cultivars Maxifort, Camaro, and Patio were grown in either an indoor environment with broadband white and red light-emitting diode (LED) fixtures providing a daily light integral (DLI) of 12.7 mol·m^{-2}·day^{-1} [photosynthetic photon flux density (PPFD) of 220 ± 3 μmol·m^{-2}·s^{-1} for 16 h·d^{-1}] or in a glass-glazed greenhouse with supplemental lighting provided by high-pressure sodium lamps that delivered a PPFD of ~150 μmol·m^{-2}·s^{-1}. Plants were grown using deep-water culture hydroponic systems or containers with a peat-based substrate. The growing environment had a larger effect on intumescence incidence and severity than the growing system, likely due to differences in ultraviolet radiation (100 to 400 nm), but other factors such as day/night temperature and relative humidity (RH), could have affected the response. Across cultivars, the probability of developing intumescence was higher indoors (≥91%) than in the greenhouse. Indoor-grown plants also developed symptoms of the disorder from 2 to 6 days earlier than those in the greenhouse. Similarly, intumescence incidence was higher in plants from all cultivars grown indoors than in the greenhouse, but differences between the two environments were generally greater for Patio and Camaro than for Maxifort, which was the most susceptible cultivar. Greenhouse conditions were more conducive to active plant growth. For example, plants in the greenhouse were more than 2 times taller and had at least 12 times greater leaf area than those indoors, which resulted in large differences in shoot dry mass. However, environmental effects on intumescence response also contributed to differences in growth, as plants that were most affected by the disorder experienced severe leaf abscission and/or senescence. Our overall findings show that intumescence is greatly affected by the production environment, but injuries are likely to change based on genetic susceptibility.**

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Intumescence is an abiotic-induced physiological disorder that causes hypertrophy of epidermal and palisade parenchyma cells of susceptible plants, commonly observed on leaves but sometimes present on petioles or stems (Williams et al. 2016). Although intumescence has been widely studied in tomato (*Solanum lycopersicum*) plants (Eguchi et al. 2016a; Massa et al. 2008; Williams et al. 2016), it can affect other vegetable crops, such as pepper (*Capsicum annuum*) and eggplant (*Solanum melongena*) (Cruz et al. 2023; Eisa and Dobrenz 1971; Massa et al. 2008; Savvas et al. 2008). Various studies have shown that intumescence develops in controlled environments lacking ultraviolet radiation (Craver et al. 2014a; Lang and Tibbitts 1983; Hikosaka et al. 2021), and low doses of ultraviolet-B (280 to 320 nm) or far-red (700 to 800 nm) light can suppress the disorder, but exact control mechanisms are unknown (Eguchi et al. 2016b; Kubota et al. 2017; Retana-Cordero et al. 2022). In extreme cases, intumescence injury leads to leaf senescence and abscission, which can affect plant productivity through reductions in whole-plant photosynthesis or cause pathogen infections that enter through the abscission zone (Cruz and Gómez 2022).

The terms "intumescence" and "oedema" (also known as "edema") are often used interchangeably. However, Rangarajan and Tibbitts (1994) and Craver et al. (2014b) suggested they are different physiological disorders based on the anatomy of affected cells and their causal agents. Intumescence is thought to be primarily affected by light quality (Williams et al. 2016), although RH (Douglas 1907; Eisa and Dobrenz 1971; Lang and Tibbitts 1983; Suzuki et al. 2020), temperature (Eisa and Dobrenz 1971; Lang and Tibbitts 1983), light intensity (Cruz and Gómez 2022), and plant nutrient status (Perez-Lugones et al. 2022) seem to affect the disorder. In contrast, oedema is a form of cell swelling in response to conditions that hinder transpiration such as high RH or hypoxia (Morrow and Tibbitts 1988; Morrow and Wheeler 1997), which cause water congestion in mesophyll cells and can form blister-like lesions that ultimately tear tissue layers and collapse (Craver et al. 2014b).

The ultraviolet transmission in a greenhouse varies with the type of glazing material. Most glazing plastics have additives that block ultraviolet wavebands in effort to increase longevity, with transmission values ranging from ~20% to 50% (Both 2002). However, as these additives degrade over time, the ultraviolet transmission in a plastic greenhouse tends to change. In contrast, glass-glazed greenhouses have a more stable ultraviolet transmission of ~70% (Both 2002; Runkle 2020). Intumescence has been shown to occur in greenhouses with low ultraviolet transmission values (Craver et al. 2014a; Pinkard et al. 2006; Rud 2009; Wu et al. 2017). However, the disorder is more commonly reported on plants grown indoors that rely on sole-source lighting, which is increasingly being provided by light-emitting diode (LED) fixtures that often lack ultraviolet radiation (Williams et al. 2016). There are numerous environmental differences between greenhouse and indoor plant-production systems, including daily and seasonal fluctuations in light quality and intensity, RH, and temperature inside greenhouses, which are often difficult to replicate indoors. Thus, plant growth and development comparisons between greenhouse and indoor environments with sole-source lighting cannot be attributed to a single factor. However, the level of susceptibility to intumescence between plants grown in these two environments is unclear and warrants further investigation.

Although some studies on intumescence have used hydroponic systems (Hikosaka et al. 2021; Kitayama et al. 2019), a comparison of liquid or substrate-based soilless culture has

not been reported. To understand the effect of substrate water status on intumescence, Rud (2009) found that tomato plants grown in containers watered daily were more affected by intumescence than those that received longer intervals between irrigation events. In another study, Miyama and Yasui (2021) concluded that intumescence is more likely to affect plants exposed to dry-down cycles than those grown under continuous sub-irrigation. Results from both studies suggest that intumescence response is affected by substrate water status, which regulates water potential of plants and likely differs between hydroponic and container-grown plants (Bugbee and Salisbury 1989). The main objective of this study was to characterize intumescence injury of three susceptible tomato cultivars grown in a greenhouse or indoors using hydroponic systems or containers with substrate. A secondary objective was to compare growth and physiological responses under these conditions.

Materials and Methods

Plant material and growing conditions. Two experimental runs were conducted in this study. For the first and second runs, seeds of tomato cultivars Maxifort (De Ruiter Seeds, St. Louis, MO, USA), Patio (Seminis, St. Louis, MO, USA), and Camaro (Sakata Seed Co., Yokohama, Japan) were sown on 13 Oct 2022 and 11 Nov 2022, respectively, using industry-standard 72-cell propagation trays (41 mL, individual cell volume; T.O. Plastics, Inc., Clearwater, MN, USA) filled with horticultural grade substrate (Berger BM2 Seed Germination; Berger, Saint-Modeste, QC, Canada). All cultivars are susceptible to intumescence based on previous studies (Retana-Cordero et al. 2022). 'Maxifort' is a rootstock commonly used for grafting, whereas both 'Patio' and 'Camaro' are determinate tomato plants with compact to medium growth habit.

Seedlings were grown for 12 d in a glass-glazed greenhouse in West Lafayette, IN, USA, and were irrigated as needed with acidified tap water with a pH of 6.0 and an electrical conductivity (EC) of 0.8 dS·m^{-1}. The greenhouse had retractable shade curtains, pad-and-fan evaporative cooling, and radiant hot-water-pipe heating regulated by an environmental control system (Maximizer Precision 10; Priva Computers, Vineland Station, ON, Canada). Supplemental lighting was delivered by 1000-W high-pressure sodium lamps (P.L. Light Systems Inc.; Beamsville, ON, Canada) used for 16 h·d^{-1} (0500 to 1900 HR) providing a photosynthetic photon flux density (PPFD) of ~150 µmol·m^{-2}·s^{-1}. Temperature and RH were measured with a datalogger (HOBO UX100-023, Onset Computer Corporation; Bourne, MA, USA), and DLI was measured using two quantum sensors (SQ-500-SS; Apogee Instruments Inc., Logan, UT, USA) interfaced to a datalogger (CR1000; Campbell Scientific Logan, UT, USA). Sensors were placed above-canopy height in the center of the experimental bench (7.3-m long × 1.8-m wide). Measurements were recorded at 60-min intervals. At 8 d after sowing, seedlings were fertilized with a complete fertilizer solution (20N–1.3P–15.7K; ICL Specialty Fertilizers, Dublin, OH, USA) at a concentration of 150 mg·L^{-1} nitrogen. The DLI, average daily temperature (ADT), and RH (± *SD*) recorded during propagation were 15.5 ± 2 mol·m^{-2}·d^{-1}, 23.8 ± 1 °C, 43 ± 6%, and 15.9 ± 2 mol·m^{-2}·d^{-1}, 23.3 ± 1 °C, and 43 ± 6% in the first and second experimental runs, respectively. Ultraviolet radiation in the greenhouse was approximately 4% of total photon flux density, as measured with a spectroradiometer (BLACK-Comet ultraviolet-VIS model C; StellarNet Inc., Tampa, FL, USA).

Transplanting occurred on 25 Oct 2022 and 23 Nov 2022 in the first and second experimental runs, respectively. Sixteen uniform seedlings of each cultivar were individually transplanted into 19-cm-diameter plastic containers (2.8 L) filled with horticultural grade substrate (Berger BM8 Water Saving Mix; Berger) and top-dressed with 14 g of controlled-release fertilizer (14N–6.1P–11.62K; Osmocote® 3 to 4 months; The Scotts Co., Marysville, OH, USA). Plants in containers were irrigated with tap water when their weight dropped below 40% from container capacity, which was adjusted weekly as plants grew based on data collected in a preliminary experiment. Another group of 16 'Maxifort' and 'Patio' seedlings were individually placed in 5.1-cm-diameter net cups after the substrate had been carefully washed off the roots. 'Camaro' seedlings were not grown hydroponically due to lack of uniform plant material. Net cups were covered with a foam collar and individually placed in the center of 7.6-L cylindrical deep-water culture hydroponic systems. A black plastic tube with a 0.6-cm diameter was attached

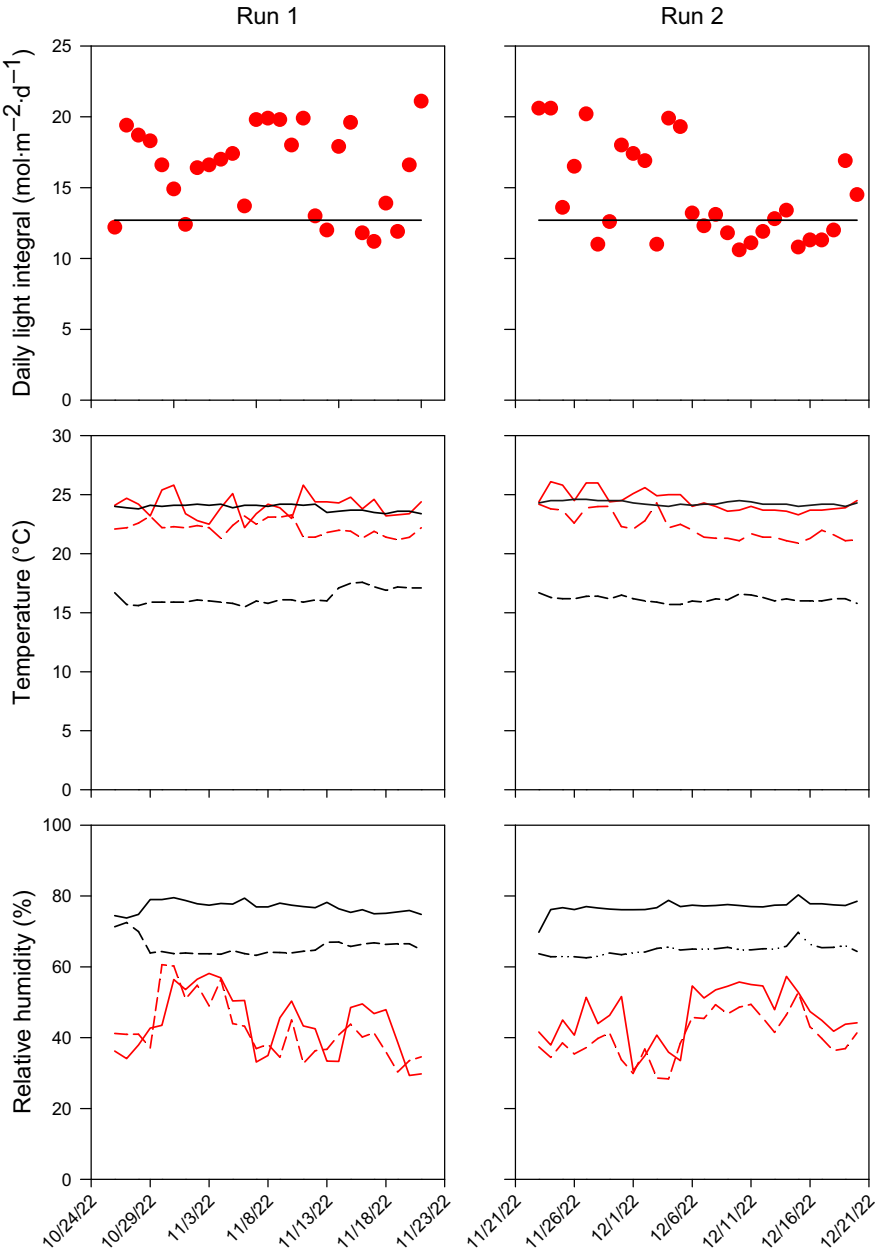

Fig. 1. Environmental conditions in greenhouse (red) and indoor (black) environments used in two experimental runs evaluating intumescence response in three tomato cultivars. Solid and dashed lines in the two bottom graphs indicate data collected during the day and night, respectively.

to an air pump [320 gal/h (Dual Diaphragm Air Pump; General Hydroponics; Santa Rosa, CA, USA)] and placed inside each reservoir to provide continuous aeration to the nutrient solution, which was comprised of a water-soluble fertilizer (MaxiGro™ 10N–2.1P–11.6K; General Hydroponics) dissolved in tap water at a concentration of 150 mg·L^{-1} N, resulting in an EC of 1.5 ± 0.5 dS·m^{-1}. Reservoirs were refilled with 1/4 strength nutrient solution every time they reached 80% of their volume capacity. Solution pH was measured weekly using a handheld meter (HI9813–6; Hanna Instruments, Inc., Woonsocket, RI, USA); pH was adjusted weekly to 6.0 ± 0.5 using an acid or a base (pH Down or pH Up, General Hydroponics), which added either phosphoric acid and citric acid, or potassium carbonate and potassium silicate, respectively.

Growing environments. After transplanting, eight plants of each cultivar and from each growing system were moved to one of two environments and grown for 28 and 29 d during the first and second experimental runs, respectively. Each replicate plant was considered an experimental unit (n = 8). In the greenhouse, the experiment was arranged as a completely randomized design. Plants were placed on a metallic bench (7.3 m long × 1.8 m wide) located in the same greenhouse compartment used for propagation and spaced 25 cm apart. Temperature and RH setpoints in the greenhouse were kept at 24/22 °C (day/night) and 65%, respectively. These setpoints were selected because the same greenhouse compartment was being used for other experiments. However, RH was difficult to maintain within the desired setpoint due to the use of winter heating. No carbon dioxide (CO_2) supplementation was provided in the greenhouse, but concentrations were maintained at ambient levels by providing active ventilation, as measured periodically with a portable CO_2 sensor (GM70D; Vaisala Corporation, Helsinki, Finland). The same sensors previously described were used to record environmental data in the greenhouse. The DLI, ADT, and RH recorded during the first and second experimental runs were 16.3 ± 3 mol·m^{-2}·d^{-1}, 23.1 ± 1 °C, and 43 ± 9%, and 14.4 ± 2 mol·m^{-2}·d^{-1}, 23.4 ± 2 °C, and 43 ± 8%, respectively. The DLI, and day/night temperature and RH for both experimental runs in the greenhouse are shown in Fig. 1.

The experiment indoors was conducted in a walk-in growth chamber (C6 Control System with ECoSysTM Software; Environmental Growth Chambers, Chagrin Falls, OH, USA). The chamber had two opposite shelving units (180 cm long × 188 cm tall × 80 cm wide), each with an upper and a lower compartment (180 cm long × 80 cm wide) lined with insulation foam at the bottom. A black fabric curtain (240 cm long × 205 cm tall) was hanged from the center of the chamber to block radiation leakage between opposite shelving units (<3 μmol·m^{-2}·s^{-1}). The experiment was arranged as a randomized complete block design where each compartment was regarded as a block containing two replicate plants per cultivar per growing system, all spaced 30 cm apart.

Two broadband white LED fixtures (Ray 66 Indoor; Fluence Bioengineering, Austin, TX, USA; 167-cm length) with peak wavelengths of 446, 599, and 664 nm, and a single red LED fixture (RAY66 AnthoSpec^{TM}; Fluence Bioengineering) with peak wavelength of 664 nm, were placed in each compartment to provide a DLI of 12.7 mol·m^{-2}·d^{-1} (PPFD of 220 ± 3 μmol·m^{-2}·s^{-1} for 16 h·d^{-1} from 0500 to 1900 HR). Fixtures were dimmed to achieve the target PPFD at midcanopy height based on 8-point radiation maps recorded in each treatment compartment using a spectroradiometer (LI-180; LI-COR Biosciences, Lincoln, NE, USA). The spectral composition in each compartment consisted of 9% blue, 19% green, 69% red, and 3% far-red light.

Setpoints for temperature, RH, and CO_2 concentration in the chamber were 24/16 °C (day/night), 65%, and 500 μmol·mol^{-1}, respectively. The temperature setpoints were selected to reflect what is typically used for tomato production. Temperature and RH were measured with dataloggers (HOBO UX100-023, Onset Computer Corporation) placed above-canopy height in the center of each compartment. Measurements were recorded at 60-min intervals. Average CO_2 concentration was logged every 15 min using a built-in datalogger (DL1 Datalogger; Environmental Growth Chambers). During the first and second experimental runs, ADT, RH, and CO_2 concentration were 20.1 ± 4 °C, 71% ± 6%, 539 ± 150 μmol·mol^{-1}, and 20.3 ± 4 °C, 70% ± 9%, 541 ± 150 μmol·mol^{-1}, respectively. The DLI, and day/night temperature and RH for both experimental runs indoors are shown in Fig. 1.

Data collection. As intumescence progressed throughout each experimental run, leaves that were severely affected either senesced or abscised off the plants, affecting some parameters as described subsequently. Intumescence incidence was calculated at 7, 14, 21, and 28 d after transplanting (DAT) by counting the number of leaves with intumescence (including nodes from leaves that had senesced or abscised) and dividing that number by the total number of leaves >1 cm (including nodes from senesced or abscised leaves). Intumescence severity was visually assessed daily once the fifth leaf of each plant showed signs of the disorder, and the date of this event was recorded to quantify the disorder progression. The fifth leaf was selected for sampling to ensure it had fully developed in the different environments and growing systems. A subjective severity scale ranging from 0 to 6 was used based on Cruz and Gómez (2022), with modifications, where 0 = no intumescence; 1 = 1% to 10% of the leaf affected and minimal isolated intumescence on terminal leaflets; 2 = 11% to 25% of the leaf affected and first signs of epinasty; 3 = 26% to 50% of the leaf affected and pronounced epinasty; 4 = 51% to 75% of the leaf affected and first signs of leaf necrosis; 5 = 76% to 100% of the leaf affected and severe necrosis; and 6 = whole leaf senescence or abscission.

The first and second experimental runs ended on 22 Nov 2022 and 22 Dec 2022, respectively. Before termination, stomatal conductance (g_s) and transpiration (E) were measured on three points of the third newest leaf >1 cm using a porometer (LI-600; LI-COR Biosciences). Chlorophyll concentration was immediately measured on that same leaf using a chlorophyll meter (MC-100; Apogee Instruments), and data were averaged based on three measurements per leaf. Before each destructive harvest, stem height was measured with a ruler. Shoots were then cut at the base of the substrate surface, and leaves (>1 cm) that were still left on each plant were measured with a leaf area meter (LI-3100C; LI-COR Biosciences). Shoots and

Table 1. Probability of developing intumescence on any leaf within the whole plant and on the fifth leaf of three tomato cultivars grown in a greenhouse or indoors using hydroponic systems or containers with substrate.

	Whole plant			Fifth leaf		
Treatment	Probability of injury (%)	Affected plants (n)	*P* value	Probability of injury (%)	Affected plants (n)	*P* value
'Maxifort'						
Environment						
Greenhouse	100	32	—	97	32	0.2417
Indoors	100	31		100	31	
Growing system						
Hydroponics	100	31	—	100	31	0.2417
Container	100	32		97	32	
'Patio'						
Environment						
Greenhouse	25	32	<0.0001	0	32	<0.0001
Indoors	100	32		91	32	
Growing system						
Hydroponics	56	32	0.3008	50	32	0.4509
Container	69	32		41	32	
'Camaro'						
Environment						
Greenhouse	100	32	—	50	32	0.0002
Indoors	100	32		100	32	
Growing system						
Hydroponics	—	—	—	—	—	—
Container	100	16		75	16	

Table 2. Intumescence incidence in three tomato cultivars grown in a greenhouse or indoors using hydroponic systems or containers with substrate.

Treatment	Incidence per affected plant (%) on different sampling days (D)			
	D7	D14	D21	D28
'Maxifort'				
Environment				
Greenhouse	51.1 b	73.1 b	97.1 b	100.0 b
Indoors	89.2 a	91.7 a	99.1 a	99.3 a
Growing system				
Hydroponics	72.5 a	76.5 ab	97.0 ab	99.3 a
Container	67.8 a	88.3 a	99.3 a	100.0 a
'Patio'				
Environment				
Greenhouse	40.6 b	23.3 b	18.1 b	14.5 b
Indoors	65.3 a	72.0 a	73.6 a	88.2 a
Growing system				
Hydroponics	56.7 a	46.2 a	46.1 a	46.4 a
Container	49.2 a	50.8 a	54.0 a	56.3 a
'Camaro'				
Environment				
Greenhouse	30.0 b	33.3 b	40.2 b	42.2 b
Indoors	94.0 a	96.3 a	99.1 a	100.0 a
Growing system				
Hydroponics	—	—	—	—
Container	63.1	63.7	69.6	71.1

For each cultivar, environment, and growing system, means within columns followed by the same letter are not different based on Student's t test at $P \leq 0.05$ (n = 32 except for 'Camaro' in containers, where n = 16).

leaves were subsequently placed in a paper bag for drying. Samples were dried in a forced-air oven (SMO28G-2; Shel Laboratory, Sheldon Manufacturing Inc. Cornelius, OR, USA) for 72 h at 60 °C, and subsequently measured as shoot dry mass using an electronic balance.

Histological and microscopy samples were collected on plants from the first experimental run following procedures of Caldwell and Iyer-Pascuzzi (2019), with modifications. One 5-mm leaf sample was collected from the sixth leaf of four replicate plants per cultivar, environment, and growing system. Leaves were sampled when they showed the first visible sign of intumescence, characterized as a small protrusion. On the basis of differences in the presence of calcium oxalate (CaOx) crystals observed in images between plants in the two environments, samples were processed to quantify the number of CaOx.

Data analyses. Data were pooled for plants in both experimental runs, as the variances between experiments were not different, and the statistical interactions between cultivar and experimental run were not significant ($P \leq 0.05$). Data were analyzed by cultivar to document unique cultivar trends. The influence of the different categorical independent variables (i.e., environment and growing system) and their possible interaction on each of the continuous dependent variables were analyzed with JMP Pro (Version 16; SAS Institute Inc., Cary, NC, USA) using a two-way analysis of variance. Due to the general lack of environment × growing system interaction ($P \leq 0.05$), data were pooled for main effect treatment means (n = 32) and compared using Student's t test at ($P \leq 0.05$), except for data from 'Camaro', which only included plants grown in containers (n = 16). Similarly, 'Patio' data for some intumescence parameters were only included for indoor-grown plants because of the lack of susceptibility observed on the fifth leaf in greenhouse-grown plants (n = 16).

To assess the probability of intumescence development, a contingency analysis was used, where any presence of symptoms was denoted as "Injury" and the absence of symptoms was denoted as "No Injury." A chi-square test ($P \leq 0.05$) was used to assess the disparity between the distribution of affected plants across the two environments and growing systems. In addition, to assess the advancement of intumescence severity on the fifth leaf, a Kaplan–Meier survival function estimation with the log-rank test ($P \leq 0.05$) was used, which modeled the probability of leaves reaching severity 2, 4, or 6. Data were analyzed using R version 4.2.1 (R Core Team 2022).

Table 3. Physiological, anatomical, and growth parameters measured in three tomato cultivars grown in a greenhouse or indoors using hydroponic systems or containers with substrate.

Treatment	First sign of intumescence (DAT)[i]	Calcium oxalate crystals (No.)	Stem ht (cm)	Leaf area (cm^2)	Shoot dry mass (g)	Stomatal conductance ($mol \cdot m^{-2} \cdot s^{-1}$)	Transpiration ($mol \cdot m^{-2} \cdot s^{-1}$)	Chlorophyll concn ($\mu mol \cdot m^{-2}$)
'Maxifort'								
Environment								
Greenhouse	12 a[ii]	8.9 b	43.9 a	1600.3 a	9.5 a	0.274 b	4.9 a	12.2 a
Indoors	10 b	11.0 a	25.4 b	77.4 b	0.8 b	0.443 a	4.1 b	10.7 a
Growing system								
Hydroponics	12 a	9.8 a	36.1 a	982.6 a	5.8 a	0.399 a	4.6 a	11.5 a
Container	10 b	10.2 a	33.3 a	695.1 b	4.4 b	0.324 a	4.5 a	10.3 a
E × GS significance[iii]	*	NS	NS	NS	NS	NS	NS	NS
'Patio'								
Environment								
Greenhouse	—	3.9 a	22.4 a	1717.2 a	12.2 a	0.569 a	7.3 a	32.8 a
Indoors	18	4.6 a	14.1 b	141.6 b	1.2 b	0.501 a	4.5 b	18.4 b
Growing system								
Hydroponics	21 a	4.5 a	17.2 b	1065.8 a	7.0 a	0.649 a	6.8 a	26.3 a
Container	14 b	4.0 a	19.3 a	793.1 b	6.4 a	0.421 b	5.0 b	24.9 a
E × GS significance	—	NS	NS	NS	NS	NS	NS	***
'Camaro'								
Environment								
Greenhouse	23 a	2.5 b	49.1 a	1820.9 a	14.4 a	0.403 a	4.9 a	39.4 a
Indoors	17 b	6.2 a	21.3 b	19.6 b	0.5 b	0.323 a	3.6 a	8.2 b
Growing system								
Hydroponics	—	—	—	—	—	—	—	—
Container	20	4.3	32.5	920.2	7.4	0.363	4.3	23.8

[i] Measured on the fifth leaf; DAT = days after transplanting.

[ii] For each cultivar, environment, and growing system, means within columns followed by the same letter are not different based on Student's t test at $P \leq 0.05$ (n = 32 except for 'Camaro' in containers and calcium oxalate crystals, where n = 16 and 8, respectively).

[iii] NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Results

Intumescence response. The probability for 'Maxifort' and 'Camaro' plants to develop intumescence on any leaf was high (100%), regardless of production environment and growing system, whereas 'Patio' had a higher probability to develop the disorder in at least some leaves when grown indoors (100%) than in the greenhouse (25%) (Table 1). However, no differences were measured in the probability for 'Patio' plants to develop intumescence in the two growing systems. 'Maxifort' plants also showed a high probability (>97%) to develop the disorder on the fifth leaf in both environments and growing systems. In contrast, the probability of developing intumescence on the fifth leaf of 'Patio' and 'Camaro' plants was much higher indoors (91% and 100%, respectively) than in the greenhouse (0% and 50%, respectively). 'Camaro' plants also showed a 75% probability to develop intumescence on the fifth leaf when grown in containers.

Across cultivars, intumescence incidence measured on different days was higher in plants grown indoors than in the greenhouse (Table 2), but differences between the two environments were generally greater for 'Patio' and 'Camaro' than for 'Maxifort' (Table 2). For example, at 21 DAT, incidence per plant was only 2% higher in 'Maxifort' grown indoors than in the greenhouse, whereas on that same sampling day, incidence in 'Patio' and 'Camaro' were 307% and 145% higher indoors than in the greenhouse, respectively. Furthermore, no differences in intumescence incidence were measured between susceptible 'Maxifort' and 'Patio' plants in the two growing systems. Incidence in susceptible 'Maxifort' and 'Camaro' plants generally increased during the different sampling days. In contrast, intumescence incidence in 'Patio' plants either decreased or remained relatively constant across sampling days when plants were grown in the greenhouse or in hydroponics, respectively.

The first sign of intumescence on the fifth leaf was recorded 2 and 6 d earlier in 'Maxifort' and 'Camaro' plants grown indoors than in the greenhouse, respectively, and at 18 DAT in 'Patio' plants grown indoors (Table 3). Although 'Patio' plants in the greenhouse showed symptoms of intumescence during the first week of the experiment (Table 2), they never developed intumescence on the fifth leaf. The first sign of intumescence on the fifth leaf of 'Maxifort' and 'Patio' was recorded 2 and 7 d earlier, respectively, when plants were grown in containers than in hydroponics, and at 20 DAT in 'Camaro' plants in containers. Furthermore, leaves from both 'Maxifort' and 'Camaro' plants had 24% and 148% more CaOx crystals when grown indoors than in the greenhouse, but no other differences were measured for the number of CaOx crystals.

Across cultivars, the severity of intumescence displayed temporal patterns (Figs. 2–4). For example, at 2, 4, and 7 d after the first sign of intumescence, the fifth leaf of 'Maxifort' plants started to develop symptoms characteristic of severity levels 2, 4, and 6, respectively, and leaves from all plants had reached severity level 6 by day 13. Kaplan–Meier estimates were only generated for 'Patio' plants grown indoors, as the fifth leaf of plants in the greenhouse was unaffected by intumescence. From those, all leaves had reached severity 2 at 4 d after the first sign of intumescence. Although the fifth leaf from all 'Patio' plants in containers reached severity levels 4 and 6 at 8 and 12 d after the first sign of intumescence,

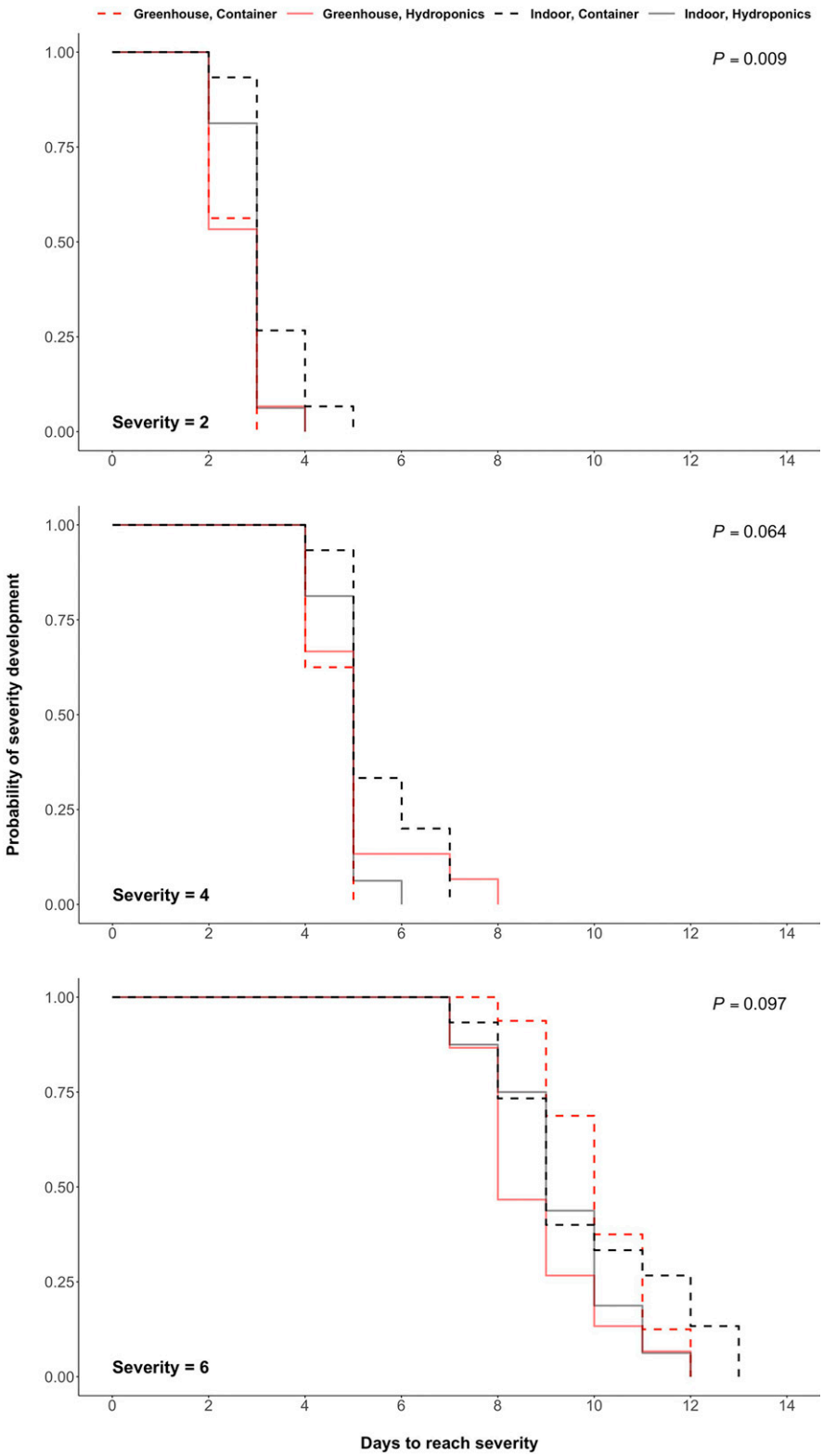

Fig. 2. Kaplan–Meier estimates of time to reach different intumescence severity levels for 'Maxifort' plants grown under two environments and using two growing systems (n = 16), where 2 = 11% to 25% of the leaf affected and first signs of epinasty; 4 = 51% to 75% of the leaf affected and first signs of leaf necrosis; and 6 = whole leaf senescence or abscission.

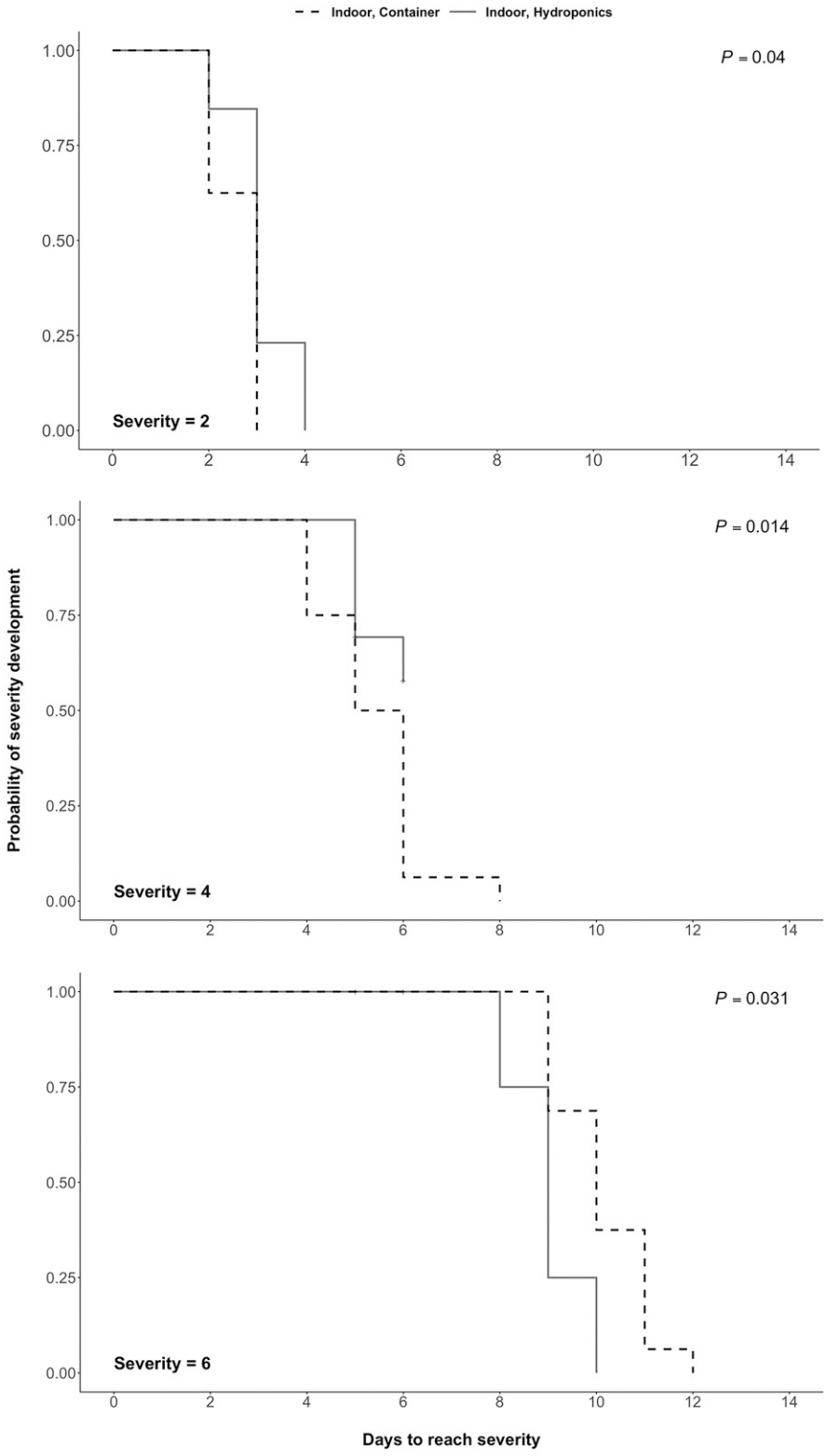

Fig. 3. Kaplan–Meier estimates of time to reach different intumescence severity levels for 'Patio' plants grown indoors using two growing systems (n = 16), where 2 = 11% to 25% of the leaf affected and first signs of epinasty; 4 = 51% to 75% of the leaf affected and first signs of leaf necrosis; and 6 = whole leaf senescence or abscission.

respectively, only 38% of those in hydroponics reached severity 4, and from those, all leaves had reached severity 6 at 10 d after the first sign of intumescence. For 'Camaro', the fifth leaf from all plants grown indoors or in the greenhouse reached severity 2 at 3 or 5 d after the first sign of intumescence, respectively. However, the fifth leaf of 'Camaro' plants in the greenhouse never showed symptoms of severity levels 4 and 6. In contrast, the fifth leaf from most 'Camaro' plants grown indoors (94%) reached severity 4 at 7 d after the first sign of intumescence, but only 20% of those reached severity 6 by day 12.

Growth and physiological responses. Plants in the greenhouse were more than two times taller than those indoors, with stem height in the greenhouse ranging from 22.4 cm for 'Patio' to 49.1 cm for 'Camaro' (Table 3). Similarly, leaf areas of 'Maxifort', 'Patio', and 'Camaro' were over 20, 12, and 95 times greater when plants were grown in the greenhouse compared indoors, which contributed to the large differences in shoot dry mass measured between plants in the two environments. Although not statistically compared, 'Camaro' had the highest shoot dry mass in the greenhouse (14.4 g), followed by 'Patio' (12.2 g) and 'Maxifort' (9.5 g). In contrast, shoot dry mass of indoor-grown plants was highest in 'Patio' (1.2 g), followed by 'Maxifort' (0.8 g) and 'Camaro' (0.5 g). The only growth differences between plants in the two systems were measured in leaf area and shoot dry mass, whereby leaves of 'Maxifort' and 'Patio' were 29% and 92% smaller in containers than in hydroponics, respectively, and shoot dry mass was 24% lower in 'Maxifort' plants grown in containers.

Stomatal conductance was 62% higher in 'Maxifort' plants grown indoors than in the greenhouse, but no differences in g_s were measured between 'Patio' and 'Camaro' plants in the two environments (Table 3). In contrast, E was 20% and 62% higher in 'Maxifort' and 'Patio' plants grown in the greenhouse than indoors, respectively, but similar in 'Camaro' plants grown in the two environments. The only differences in g_s and E between plants in the two growing systems were measured for 'Patio', both of which were higher when plants were grown in hydroponics than containers. Chlorophyll content was similar between 'Maxifort' plants in the two environments, but 78% and 380% higher in 'Patio' and 'Camaro' plants, respectively, grown in the greenhouse than indoors. Although chlorophyll content of both 'Maxifort' and 'Patio' plants was similar between the two growing systems, 'Maxifort' had less than half the chlorophyll content of the two other cultivars, regardless of system.

Discussion

Environmental effects on intumescence. The growing environment had a much larger effect on intumescence incidence and severity than the growing system (Tables 1–3, Figs. 2–4). Although definitive conclusions cannot be made about the exact cause for these responses due to the many differing factors that plants in our study were exposed to (e.g., different day and night temperatures, fluctuating light quality and intensity, and variations in RH) (Fig. 1), the lack of ultraviolet radiation indoors was likely a key determinant in the development of the disorder. In contrast, ultraviolet in the greenhouse (~4% of total photon flux density) helped mitigate intumescence, particularly for 'Patio' and 'Camaro' plants, which were less susceptible to the disorder

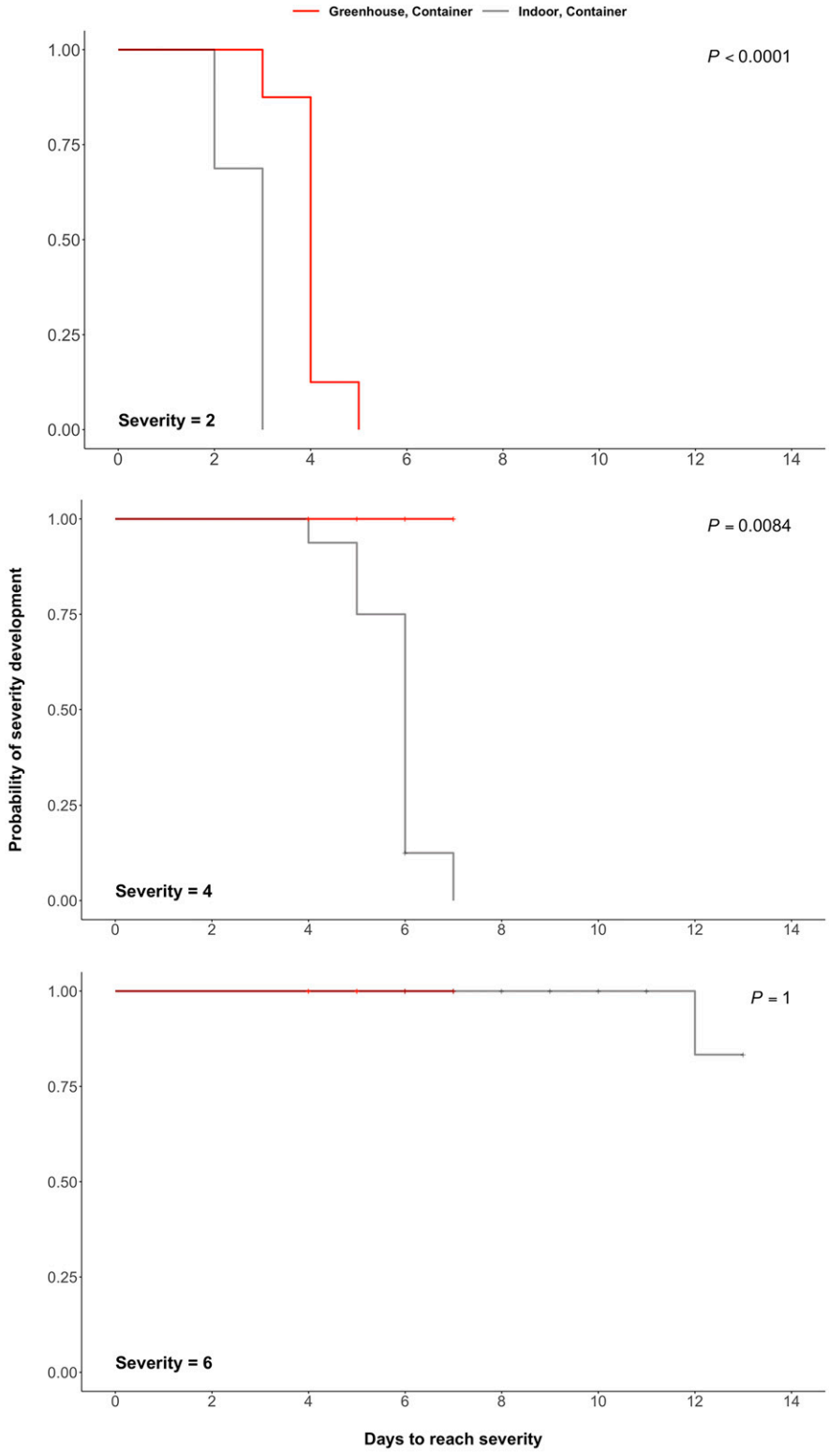

Fig. 4. Kaplan–Meier estimates of time to reach different intumescence severity levels for 'Camaro' plants grown in containers under two environments (n = 16), where 2 = 11% to 25% of the leaf affected and first signs of epinasty; 4 = 51% to 75% of the leaf affected and first signs of leaf necrosis; and 6 = whole leaf senescence or abscission.

than 'Maxifort'. Wu et al. (2017) found that ultraviolet radiation regulates the expression of a series of genes that may prevent the development of intumescence in tomato plants, including some that affect photosynthesis, flavonoid synthesis, and ethylene-signaling processes. Accordingly, Kubota et al. (2017) and Myung et al. (2023) showed that providing low dosages of ultraviolet-B radiation can suppress intumescence injury in tomato seedlings grown indoors.

Although others have reported intumescence in greenhouse-grown plants (Craver et al. 2014a, 2014b; Dale 1901; Rud 2009; Zhao et al. 2008), most published studies on tomato have evaluated the disorder indoors under sole-source lighting (Williams et al. 2016). Therefore, limited information exists describing plant responses to intumescence in greenhouse environments, which typically enable some ultraviolet transmission from sunlight. In an evaluation with 20 compact tomato cultivars suitable for container gardening in small spaces, Cruz et al. (2022) found that four cultivars developed the disorder indoors under broadband white LED fixtures, but no plants developed intumescence when grown in polycarbonate greenhouses. Similar findings were reported by the authors in another cultivar evaluation with 14 compact pepper plants, where seven cultivars showed symptoms of intumescence indoors but none in the greenhouse (Cruz et al. 2023). In both cases, the authors attributed differences in intumescence response to the ultraviolet transmission in the greenhouse (~26% to 34% of outdoor levels), which was likely sufficient to suppress the disorder (Cruz et al. 2022, 2023). Considering that glazing materials vary in their amount of ultraviolet transmission, with glass-glazing often providing higher transmission than plastic (Both 2002), the ability to mitigate intumescence injury in greenhouse environments will primarily depend on the type of glazing material but can likely change based on genetic susceptibility. Furthermore, the presence of other factors that may be conducive to intumescence can also affect susceptibility to this disorder. For example, Perez-Lugones et al. (2022) reported an increase in intumescence incidence in response to increasing N rates when growing compact pepper plants in a polycarbonate greenhouse.

Two other factors that could explain the differences in intumescence response between plants in the two environments are temperature and RH. The ADT in our study ranged from ~20 to 23 °C (Fig. 1), which are similar to the setpoints evaluated by Lang and Tibbitts (1983), who reported higher intumescence ratings in tomato grown under 20 and 25 °C than under 30 °C. In contrast, Eisa and Dobrenz (1971) found that warmer temperatures were more conducive to intumescence development on eggplants grown in a plastic greenhouse. Intumescence response to temperature is unclear, but it is plausible that the different day/night temperatures in the two environments used in our study affected development of the disorder. In addition, the drastic differences in RH between the two environments could have affected intumescence response, as others have reported higher severity levels as RH increases (Lang and Tibbitts 1983; Suzuki et al. 2020). In our study, RH was consistently higher indoors than in the greenhouse. High RH affects the development of the cuticular layer, which is thought to make tissues more susceptible to the disorder (Lang and Tibbitts 1983). However, high RH is not known to cause intumescence, but instead is considered a factor that can exacerbate development of the disorder under otherwise conducive conditions. In an experiment evaluating four susceptible tomato cultivars, including both Maxifort and Camaro, Retana-Cordero et al. (2022) found minimal

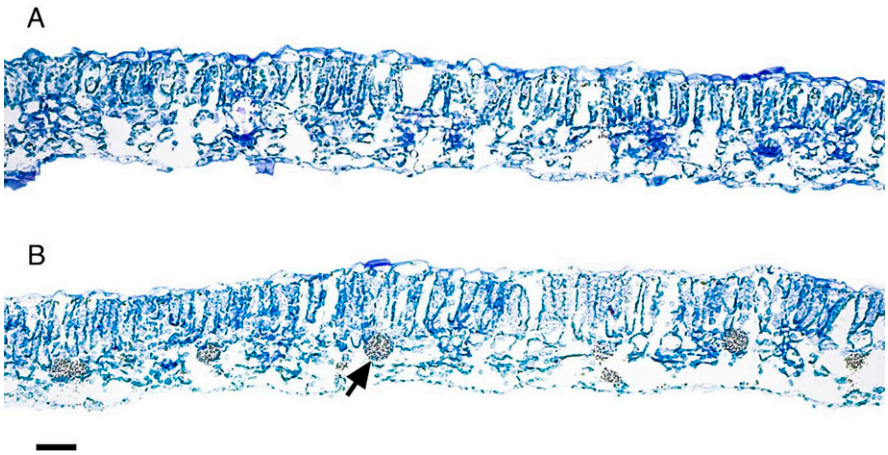

Fig. 5. Light microscopy of a 'Maxifort' tomato leaf cross-section (**A**) without and (**B**) with calcium oxalate crystals. Bar = 100 µm.

effects of RH on intumescence but reported significant effects by various light-quality treatments. Although differences in both temperature and RH between the two environments in our study possibly affected intumescence response, changes in light quality, particularly in the amount of ultraviolet radiation, were likely the primary factor affecting development of the disorder.

The higher number of CaOx crystals measured in 'Maxifort' and 'Camaro' plants grown indoors compared with the greenhouse may correspond with the incidence of intumescence (Table 3, Fig. 5). Dale (1901) also showed an accumulation of CaOx crystals on the leaves of susceptible hibiscus (*Hibiscus vitifolius*) plants grown in a glass-glazed greenhouse. Khan et al. (2023) recently stated that CaOx crystals may accumulate under stress-inducing conditions, possibly due to a biochemical process referred to as "alarm photosynthesis." The exact function of CaOx crystals in plants is unclear, and their relationship with intumescence response should be further investigated. Some postulate their presence reflects an accumulation of calcium in plants that is unavailable for various physiological processes (Khan et al. 2023). Considering that calcium is a key element for cell-wall structure, it is plausible that an accumulation of CaOx crystals limits the availability of calcium for proper tissue development, thereby increasing susceptibility to intumescence injury. Accordingly, Schabow and Palta (2019) found that 'Russet Burbank' potato (*Solanum tuberosum*) plants supplemented with 10 mM calcium in a fertilizer solution had a lower percentage of intumescence injury (5%) than those with 1 mM (65%). Similar results were recently reported by Sita et al. (2023), who showed that calcium sprays helped reduce intumescence injury in tomato seedlings. Findings from both studies suggest that intumescence can be alleviated by exogenous calcium applications.

Cultivar responses to intumescence. The decrease in intumescence incidence measured over time in 'Patio' plants, coupled with the fact that the fifth leaf of plants in the greenhouse never developed intumescence, suggest that this cultivar is less susceptible to the disorder than Maxifort and Camaro (Tables 1–3, Figs. 2–4). Furthermore, 'Maxifort' seems to be more susceptible to intumescence than 'Camaro', as indicated by its higher probability of injury development. Similar findings were reported by Retana-Cordero et al. (2022), who evaluated seven susceptible tomato cultivars (including all three used in our study) when comparing the effect of radiation quality and RH on intumescence injury. Kovach (2020) also found a higher degree of intumescence susceptibility in Maxifort seedlings compared with four other tomato cultivars. Interestingly, differences in intumescence incidence over time between plants in the two environments were generally smaller in 'Maxifort' than in the other two cultivars, which also corresponds with the findings of Kovach (2020), who showed that over a 10-d period, 'Maxifort' seedlings had the lowest increase in intumescence injury. These results are likely explained by the fact that as a highly susceptible cultivar, Maxifort develops symptoms of intumescence more rapidly than less susceptible cultivars, and thus treatment differences over time become less apparent (Table 3).

Intumescence incidence generally increased over time (Tables 1 and 2). This corresponds with the findings of Retana-Cordero et al. (2022), who suggested that a developmental factor is associated with the disorder. In contrast, Cruz et al. (2022) noted that intumescence incidence and severity in susceptible tomato cultivars decreased with plant age (Tables 1 and 2, Figs. 2–4). Similar observations were reported by Cruz and Gómez (2022) in a study evaluating different DLIs for indoor gardening of compact tomato plants. The authors postulated that changes in whole-plant gas exchange tied to plant growth over time affect development of the disorder (Cruz and Gómez 2022). Perez-Lugones et al. (2022) found that although intumescence severity in compact pepper plants decreased over time, incidence across different fertilizer treatments was higher at the end of a 25-week experiment compared with that measured at 11 weeks. Our findings suggest that for highly susceptible cultivars such as Maxifort, and to a lesser extent, Camaro, intumescence can develop throughout the entire growing cycle. However, it is plausible that the disorder progression decreases over time in cultivars with lower levels of susceptibility such as Patio, which corresponds with the findings of Cruz et al. (2022) and Cruz and Gómez (2022).

According to Zhao et al. (2008), the high susceptibility of 'Maxifort' to this disorder relates to its genetic inheritance from the wild tomato species *Lycopersicon hirsutum*. Bayer (1982) postulated that the causing factor of tumor-like lesions in susceptible plants could be traced to the inheritance of a dominant gene. Wu et al. (2017) found more than 1600 differentially expressed genes in 'Maxifort' leaves with and without intumescence. More recently, Prinzenberg et al. (2022) suggested that a quantitative trait locus on top of chromosome 01 could be a target for breeders to develop plants with lower susceptibility to the disorder. Considering the increasing interest in growing fruiting vegetables such as tomato in controlled environments that rely on sole-source lighting (Kwon 2023), identifying methods to breed cultivars that are not susceptible to the disorder is important because, depending on severity, intumescence can potentially reduce fruit yield by affecting photosynthetic leaf tissues.

Growth and physiological responses. Across cultivars, plants grown in the greenhouse were larger than those indoors, which is the combined result of differences in plant height, leaf area, and shoot dry mass (Table 3). Although plants indoors were exposed to larger differences between day and night temperatures, which are known to increase stem height in tomato (Inthichack et al. 2013), greenhouse conditions were more conducive to active plant growth (Fig. 1). For example, optimal DLI, ADT, and RH setpoints for commercial tomato production range from 25 to >30 $mol \cdot m^{-2} \cdot d^{-1}$, 18 to 32 °C, and 50% to 70%, respectively (Dorais et al. 2017; Palmitessa et al. 2021; Shamshiri et al. 2018). Therefore, the higher DLI and ADT in the greenhouse, coupled with the lower RH, likely explain the differences in growth between plants in the two environments. In addition, environmental effects on intumescence injury greatly affected leaf area and consequently, shoot dry mass, particularly for 'Maxifort' and 'Camaro', which experienced severe leaf abscission and/or senescence indoors. Interestingly, leaf area was smaller in 'Maxifort' and 'Patio' plants grown in containers than in hydroponics (Table 3), which may be explained by differences in water availability for cell expansion in the two growing systems. In addition, the different fertilizers used in the two growing systems could have contributed to variations in leaf area between plants of these two cultivars.

The higher g_s measured in 'Maxifort' plants grown indoors compared with the greenhouse may be explained by its severe response to intumescence because leaf injuries likely affected stomatal function (Table 3). Although not significant, a similar trend was reported by

Pinkard et al. (2006) in a study evaluating intumescence response on eucalyptus (*Eucalyptus globulus*) leaves. In contrast, the higher *E* and chlorophyll concentration generally measured in greenhouse-grown plants could be explained by environmental differences, which, as previously mentioned, were more conducive to active plant growth than those indoors, plausibly increasing transpirational demands and enabling a more efficient production of chlorophyll pigments (Fig. 1).

In conclusion, although overall plant growth was higher in the greenhouse, the three susceptible tomato cultivars evaluated in this study had a higher probability of developing intumescence indoors. In contrast, the growing system had small effects on intumescence response and minor effects on plant growth. Plants grown indoors developed symptoms of intumescence earlier than those in the greenhouse, but progression of the disorder varied by cultivar. 'Maxifort' plants had the highest susceptibility to intumescence, followed by 'Camaro' and 'Patio'. Our findings confirm that intumescence is greatly affected by the production environment, but incidence and severity will likely differ based on genetic susceptibility.

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