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Both major QTL and plastid-based inheritance of intumescence in diverse tomato (*Solanum lycopersicum*) RIL populations under different light conditions

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Abstract

Intumescence is a physiological disorder in tomato and other plant species that encompasses callus formation on leaves and stems. Next to a genetic predisposition, it has also been shown to be influenced by environmental factors like light spectrum. We grew tomato plants of four different recombinant inbred line (RIL) populations under high-pressure sodium (HPS) and red/blue LED supplemental lighting in a greenhouse and determined the severity of intumescence on 4-week-old plants, in three subsequent replicates. The intumescence severity was scored on a scale from 0 to 3. The severity of intumescence was highly genotype dependent in three out of the four tested tomato populations, with the heritability ranging from 54% to 83%. In those three populations, two to eight QTL for intumescence were identified. One major effect quantitative trait locus (QTL) on the top of chromosome 1 was at a similar position in two genetically different RIL populations. The amount of genetic variation explained for these QTL ranged from 30% to 70% depending on the population. Next to chromosomal influences, we also identified differences in effects from maternal plastids on intumescence, by using reciprocal crosses. The cultivation of the tomato plants under HPS lamps or under red/blue LED supplemental lighting had no significant influence on intumescence score. All major QTLs appeared to be reproducible among the three replicates and among the two light conditions. Significant, though, low negative correlations were identified between the intumescence score and the area of leaves, chlorophyll content index, photosynthesis efficiency and fresh weight to dry weight ratio, which can reflect possible effects of the disorder on multiple aspects of plant performance.

KEYWORDS
intumescence, LED, light spectrum, natural variation, QTL, *Solanum lycopersicum*, *Solanum pimpinellifolium*, tomato

1 | INTRODUCTION

Intumescence is a physiological, non-pathogenic disorder that leads to blister or callus-like outgrowth (Figure 1) on leaves and stems that has been observed in different plant species (Morrow & Tibbitts, 1988; Williams et al., 2016). Usually, it starts with the enlargement of epidermal cells or palisade parenchyma cells (Williams et al., 2016). Following cross-sections of those blister-like structures in several plant species, different developments were observed; in tomato, epidermal cells enlarge (hypertrophy) followed by the collapse of cells in the centre of the enlarged tissue. The lesion then progresses to the surrounding tissue (Craver, Miller, Williams, & Boyle, 2014; Williams et al., 2015). Ultimately, the lesions can become necrotic, the leaves curl downwards and leaf abscission may occur (Williams et al., 2016). In addition, there are fewer chloroplasts, and leaf photosynthesis can be negatively affected in intumescent leaves (Lang et al., 1983; Pinkard et al., 2006).

Different environmental factors were linked to this specific disorder: water status, temperature (Lang et al., 1983), injury (Wolf, 1918), nutrient status (Schabow & Palta, 2019) and light quality (Kubota et al., 2017; Massa et al., 2008). Pinkard et al. (2006) induced intumescence in eucalyptus by transferring it to a greenhouse with 80% humidity. An environment with (combined) elevated temperature and humidity could cause a higher water absorption by plant tissues compared with the water loss by transpiration, which could be a factor inducing intumescence. Several studies focussed on light effects on intumescence. It was found that UV-B light reduces or inhibits the visual formation of intumescence in tomato (Kubota et al., 2017; Wu et al., 2017). Plants grown in growth cabinets or greenhouses would usually be exposed to little or no UV-B light and therefore be more prone to intumescence. However, also other light treatments were studied for their effects on intumescence. End-of-day far red light was found by Eguchi et al. (2016) to reduce intumescence in tomato seedlings, while Rangarajan and Tibbitts (1994) found this effect of far red light to be dependent on the photosynthetic photon flux in geranium. With the upcoming of LED lighting, monochromatic lights were associated with intumescence. High ratios of red to blue light seem to induce intumescence: Cowpeas grown under red light with less than 15% blue light seem to be more susceptible to intumescence (Massa et al., 2008). Also in tomato, plants grown under higher percentages of blue light (25% or 50%) had significantly less or no intumescent leaves compared with plants under 100% red light (Wollaeger & Runkle, 2014). Another study in tomato (Hernández et al., 2016) also reported decreasing intumescence at an increasing percentage of blue light.

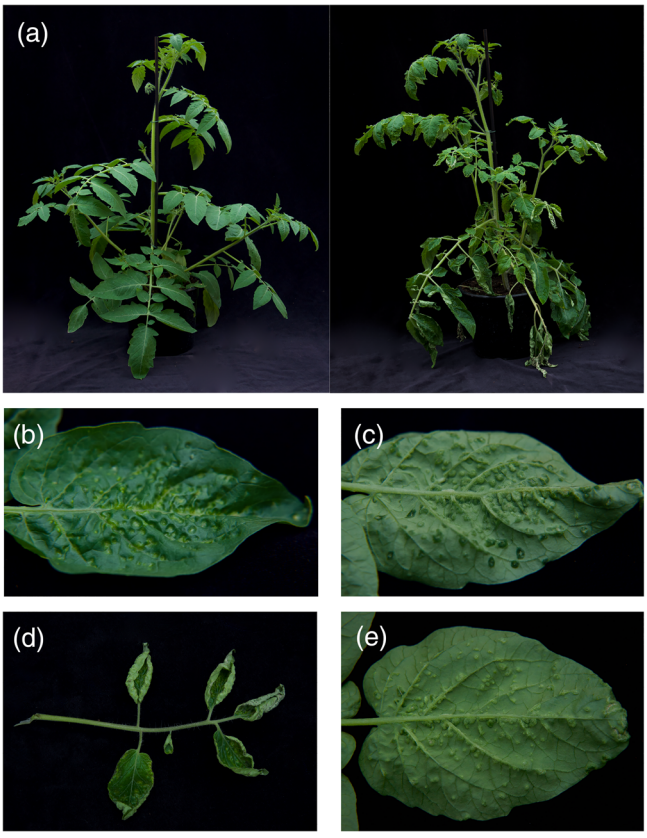

FIGURE 1 Photos of intumescence on young tomato plants. Intumescence was identified as gall like structure, mainly positioned along the veins on the lower side of the leaves. The severity of intumescence was determined by a visual score from 0 to 3, where 0 indicated plants without symptoms and 3 indicated plants with symptoms on nearly all leaves. Comparing a healthy (a) with a severe intumescent plant (b), the latter can show loss of leaflets and wilting. The gal structure is often only visual on the lower side of the leaves but can also impact on the adaxial leaf side (c). The intumescence gals can vary in size (d, e) and can be accompanied by leaf curling (f)

Differences within species have been described; for example, in sweet potato, in a screen of 36 genotypes, 19 were found to have no intumescence, whereas the other genotypes had varying percentages of leaves affected (Craver, Miller, Cruz, & Williams, 2014). Craver, Miller, Williams, and Bello (2014) also showed that the intumescence-inhibiting effect of UV-B light on intumescence is genotype dependent in sweet potato. With lower light intensities, the tomato variety 'Hosen Eilon' showed increasing degrees of intumescence, while the variety 'Viresto' did not develop intumescence at all (Sagi & Rylski, 1978). Hernández et al. (2016) tested two tomato cultivars under different light qualities in a growth chamber of which only one of the cultivars developed intumescence. Despite the natural variation that was already identified, to our understanding, the only quantitative genetic analysis for intumescence was done in eucalyptus, identifying multiple loci to be involved (Ammitzboll et al., 2018).

Different expression patterns were identified for 1604 genes between samples from leaves with and without intumescence in tomato (Wu et al., 2017). The intumescence was suppressed by extra UV-B light. Differentially expressed genes were involved in metabolic and hormonal pathways, DNA and cell wall synthesis and repair. They found that genes in primary and secondary metabolism as well as those involved in photosynthesis or DNA repair were mainly downregulated. Genes involved in biotic and abiotic stress response were upregulated as well as ethylene synthesis and signalling genes. Previous studies already suggested a link between (prolonged) higher levels of ethylene production in leaves and intumescence (Kargiolaki et al., 1991; Wallace, 1928).

The main aim of this study was identification of genetic loci associated with intumescence and to establish whether maternal effects via inheritance of plastids play a role as well. Furthermore, we

investigated whether the spectral difference between high-pressure sodium (HPS) and LED supplemental lighting in the greenhouse had an effect on intumescence. In view of these aims, we scored the intumescence development in four experimental recombinant inbred line (RIL) populations of tomato under two different horticultural supplemental lighting conditions, with HPS lamps or red (95%)/blue (5%) LED lights. A quantitative genetic study was performed per RIL population and light conditions, taking the maternal effects into account.

2 | MATERIALS AND METHODS

2.1 | Plant materials

Four RIL populations were made by crossing the parents: LA1578 ("L"; EA00674; *Solanum pimpinellifolium*) and Rutgers ("R"; EA00465; *S. lycopersicum*) hereafter abbreviated with "L ~ R"; Moneymaker ("Mm"; CGN14330;*S. lycopersicum*) and Momotaro ("Mo"; Tough Boy; TR0003; *S. lycopersicum*) "Mm ~ Mo"; Ailsa Craig ("A"; LA2838A; *S. lycopersicum*) and Kentucky Beefsteak ("K"; TR00021; *S. lycopersicum*) "A ~ K"; and Kentucky Beefsteak and the modern inbred line Nunhems-FM001 ("N") designated "K ~ N". The RILs of each population were developed via single seed decent to the F_5 generation or in case of the population Mm ~ Mo an F_6, at the greenhouse sites of Bejo Zaden B.V., Nunhems Netherlands B.V. and Rijk Zwaan B.V. in the Netherlands. For each of these four combinations of parental plants, a reciprocal cross was performed. Therefore, each RIL population consists of two subgroups from those reciprocal crosses. For each RIL population, approximately 150 individual RILs were grown, with approximately half of the individuals from each reciprocal cross.

2.2 | Growth conditions

The plants were grown in glasshouses of Unifarm (Wageningen University & Research). The same set of RILs was grown in parallel in two different compartments, one with HPS supplemental lighting and one with LED supplemental lighting. The supplemental light was given in addition to the incoming solar light. The RIL populations L ~ R, A ~ K and Mm ~ Mo were grown together. The tests were repeated during three consecutive experiments between October 2018 and March 2019 with one replicate per RIL per experiment, adding to three replicates in time. The first experiment was ended with a destructive sampling five weeks after sowing, and the consecutive other two experiments ended in week four after sowing. The population N ~ K was grown in the fourth consecutive experiment (in March/April 2019) with three replicates per RIL, and the destructive harvest took place in week four after sowing. The plants were grown on stonewool (Grodan Rockwool B.V., Roermond, The Netherlands), drenched with nutrient solution: NH_4 1.2 mM, K 7.2 mM, Ca 4.0 mM, Mg 1.8 mM, NO_3 12.4 mM, SO_4 3.3 mM, P 1.0 mM, Fe 35 μM (as mixture of Fe-DTPA/Fe-EDDHSA), Mn 8 μM, Zn 5 μM, B 20 μM, Cu 0.5 μM and Mo 0.5 μM. The macronutrients came from a mixture of fertilizers from Yara Benelux BV (Rotterdam–Vlaardingen, The Netherlands). The micronutrients were added by the Agrispoor product line of Horticoop BV (Bleiswijk, The Netherlands). The final nutrient solution had a pH between 5.5 and 5.8 (adjusted with KOH) and an EC of 2.0 dS/m. All seeds were germinated under the HPS supplemental lighting and after one week transferred to the two light regimes. Seedlings with fully expanded cotyledons were transferred to the two compartments, one with supplemental HPS-lighting (Master green power CG T 400 W, Philips) and one with supplemental red/blue LED lighting (Green Power LED top lighting module 95% DR/5% LB, 190 W, Philips). The light spectra of the lamps were determined (curtesy of Tijmen Kerstens) with the field spectroradiometer SS-110 (Apogee Instruments, Logan, UT, USA) on one isolated lamp, respectively (two replicate measurements in case of the HPS lamp); percentages per wavelength-interval were calculated compared with the total wavelength range measured (400–800 nm) and rounded to 5% accuracy. On average, approximately 200 μmol s^{-1} m^{-2} of supplemental light was given for 16 h daily, starting 16 h before sunset of each day. The air temperature was regulated to be approximately 22°C during the supplemental lighting period and 19°C outside the supplemental lighting time. If the solar radiation that was measured on top of the greenhouse was above 200 W m^{-2}, an energy screen (Harmony 4215 O FR) was reducing the incoming light, leading to 42% less natural light at 100% screen-closure. An estimate of the average incoming sunlight in the greenhouse per day ranged between 16 and 61 μmol*m^{-2}*s^{-1} for each experiment. This estimate was calculated based on a ratio of a light average measured inside the greenhouse compared with the light measurement on top of the greenhouse that was determined on one day without plants inside the greenhouse. The relative humidity was set to 70%. No supplemental CO_2 was provided.

2.3 | Scoring intumescence

Intumescence severity was quantified by a visual score from zero to three on young plants at week four after sowing. The score "0" meant no visible symptoms; "1" meant that less than half of all leaves showed symptoms. The severity of the symptoms per leaf was of no relevance for the score, purely the number of affected leaves, though in most cases the amount of intumescence galls per leaf was higher in plants with more affected leaves. A score of "2" meant that more than half the leaves showed symptoms; however, not the entire plant was impacted, and "3" meant nearly all or all the leaves showed symptoms (which in extreme cases meant abscission of a majority of leaves). Intumescence was scored on true leaves (see below), not on side shoots. Raw data are in supporting information Table S1.

2.4 | Measuring growth-related and physiological traits

Growth-related traits, as stem height, number and area of leaves and fresh and dry weight of the individual plant organs, were determined four or five weeks after sowing. From the second experiment onwards, the leaves were distinguished in "true leaves" and side

shoots (axillary leaf structures that started growing in the axils of the true leaves), and separate measures were taken (the presented leaf data therefore has only two replicates for the populations A ~ K, L ~ R and Mm ~ Mo from the second and third experiments). The area of the leaves was determined with an area metre (Li-cor, LI-3100C Area Meter, Li-cor Inc., Lincoln, Nebraska, USA). To dry the plant material for dry matter measurements, all material was placed in ventilated ovens (24 h at 70°C followed by 24 h at 105°C).

To obtain a value for photosynthesis efficiency, the quantum yield of electron transport of photosystem 2 in the light was determined by chlorophyll fluorescence imaging. This measurement was done on a freshly cut, fully expanded first or second leaflet (of a leaf that was preferably perpendicular to the light) of each plant at the time of destructive sampling, using the closed FluorCam 800MF and related software (Photon Systems Instruments, Brno, Czech Republic).

The pigmentation content index was determined on one leaflet per plant (with the same criteria as for photosynthesis measurement; see above) with Force-A Dualex Scientific+™ sensor (Dynamax Inc., Houston, USA) 3 weeks after sowing.

2.5 | Genotyping of the RIL populations

Three RIL populations, L ~ R, N ~ K, and Mm ~ Mo, were used for a genetic analysis, as the fourth RIL population (A ~ K) did not show sufficient individuals with intumescence for a QTL analysis. The previous generation (F4, F4 and F5, respectively) of the used RIL populations were genotyped by Bejo Zaden B.V., Nunhems Netherlands B.V. and Rijk Zwaan B.V. The genotyping was done with 219, 183 and 148 KASP markers, respectively. Approximately 12.5%, 7.2% and 5.2% of the marker calls were scored as heterozygous in the populations L ~ R, N ~ K, and Mm ~ Mo, respectively. This is likely due to the limited number of inbreeding cycles for the populations at the time of genotyping.

2.6 | Statistical analysis

The significances of the light condition and reciprocal cross effect were determined with a Wilcoxon rank sum test in R (version 3.5.0; www.r-project.org). Chi-square test, Kruskal–Wallis rank sum test and Kendall correlations were also performed in R. All graphics were made in R, mainly with the package ggplot2 (version 3.0.0; Wickham, 2016). The broad sense heritability was determined from the environmental variance (σ_e^2) and genotypic variance (σ_g^2) using the equation $H^2 = \sigma_g^2/(\sigma_g^2 + \sigma_e^2)$. The variances were estimated from the mean sum of squares (Mean Sq) of an ANOVA (type III SS) model. The ANOVA was done with the R package car (version 3.0-0; Fox & Weisberg, 2019). The Mean Sq of the residuals was used as environmental variance (σ_e^2) and ([Mean $Sq_{RIL\text{-}genotype}$-Mean $Sq_{residuals}$]/sample number) gave the genotypic variation (σ_g^2). The data for both light conditions were used together for the heritability estimate, and each experiment was included as block effect in the analysis of variance (ANOVA) model for the populations A ~ K, L ~ R and Mm ~ Mo. Since the ANOVA requirement of normal distribution cannot be met with this dataset due to the discrete intumescence classes, the heritability estimate should only be seen as a guideline.

For the genetic maps per RIL population and for the downstream QTL analysis, we used the package R/qtl (Broman et al., 2003). The genetic maps were recalculated per population starting with the marker order provided by the companies. Averages of all intumescence scores over the three replicates of each genotype were formed and those values rank transformed the reciprocal cross group as cofactor in the QTL analysis. This transformed intumescence score was used for a parametric, single QTL analysis with the in R/qtl implemented multiple imputation method (Sen & Churchill, 2001). The analysis was done following Broman and Sen (2009). A multiple QTL analysis was done with the automated "stepwise" function of the R/qtl package (using main effect and heavy interaction penalty only; for computational reasons, the penalties calculated for the population N ~ K under HPS light were also used for the LED condition). The logarithm of odds (LOD) score threshold was calculated based on 1000 permutations, and 100 imputations (300 in case of the multiple QTL analysis) were used for the estimation of the genotype probabilities. To test for the intumescence QTL per experiment, the untransformed intumescence scores from a single experiment were analysed by a non-parametric mapping; the individual values of all RILs were used as input, and a LOD score threshold based on 1000 permutations was calculated.

For the genes harboured by the QTL on the top of chromosome 1 (chr 01), a candidate list with functional annotations was obtained via the webtool J Browse (version 1.12.1; Buels et al., 2016) from the Solanaceae Genomics Network (https://solgenomics.net/; SL ITAG4.0 gene models). To compare the genes identified in the expression analysis of Wu et al. (2017) with our candidate gene list, sequences for all differentially transcribed genes of Wu et al. (2017) were obtained from NCBI (https://www.ncbi.nlm.nih.gov/) and aligned to the genes in the database "Tomato Genome CDS (ITAG release 4.0)" of the Solanaceae Genomics Network. For the graphical mapping, the average of the intumescence score for both light conditions was calculated (as there was no significant impact from the light environment on the QTL). The individual RILs were sorted by their intumescence score, and recombinations between allelic values in the genotype scores in the QTL region were visualized.

3 | RESULTS

3.1 | Three out of four populations show a clear broad sense heritability for intumescence

The parents Ailsa Craig and Kentucky Beefsteak showed hardly any sign of intumescence (only 1 or 2 plants with a score of "1"). In agreement with this, the population with the least intumescence (32 out of 886 plants) was also A ~ K which was derived from these two parental genotypes. The other three RIL populations, L ~ R, Mm ~ Mo and K ~ N, had considerable numbers (between 40% and 57%) of affected

plants (Figure 2). An estimate of the broad sense heritability for intumescence score was 54% for the population Mm ~ Mo, 75% for the population L ~ R and 83% for the population K ~ N. As expected, the population A ~ K with hardly any intumescence had a heritability estimate of 0%. Apparently, there is a clear genetic component in the intumescence.

3.2 | The genetic basis of intumescence is partly based on maternally inherited plastids

Each of the RIL populations consisted of two subgroups that were derived from reciprocal crosses. Differences between those subgroups would point to maternally inherited genetic differences. Two of the three populations with intumescence indeed showed a significant difference between the reciprocal cross derived subgroups: L ~ R ($p = .044$) and K ~ N ($p = .0001$). The *S. pimpinellifolium* accession LA1578 (L) and even more Nunhems-FM001 (N) conferred a higher rate of intumescence when used as a mother in the cross, compared with when used as father.

A chi-square for independence between each pair of the reciprocal cross groups revealed significant differences between the groups of the populations L ~ R, Mm ~ Mo and K ~ N (Table 1). The Pearson residuals for those chi-square tests (supporting information Figure S2) indicated that the dependency between those groups mainly came from a higher number of unaffected plants from the cross K × N compared with a higher number of plants with an intumescence score of "1" from the reciprocal cross N × K. In the population L ~ R, the main difference between the reciprocal cross groups seemed to be a higher proportion of highly affected plants (score above 2) in the group L × R compared with R × L. In the population Mm ~ Mo, there was a slight tendency for more plants with an intumescence score of "2" if Mo was the mother of the cross.

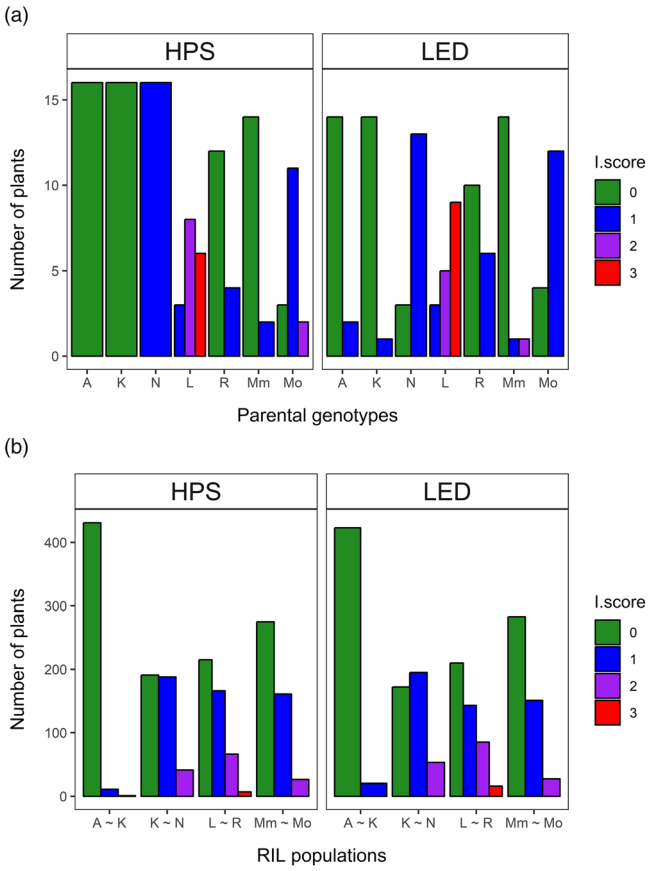

FIGURE 2 Distribution of intumescence scores for four tomato RIL populations and their parents. The bar charts indicate, per genotype and condition, the number of occurrences of plants with intumescence. The degree of intumescence was scored with numbers from 0 to 3. Panel a shows the occurrence of intumescence for the parental genotypes ($n = 16$) of the RIL populations and panel b for the RILs (n = approximately 440 of the four different RIL populations. The names of the genotypes were abbreviated as follows: LA1578 ("L") and Rutgers ("R"); the resulting RIL population that consists of both reciprocal crosses was abbreviated with "L ~ R"; Moneymaker ("Mm") and Momotaro ("Mo") and the RIL population "Mm ~ Mo"; Ailsa Craig ("A") and Kentucky beefsteak ("K") with the RIL population "A ~ K"; and Kentucky beefsteak and the modern inbred line Nunhems-FM001 ("N") with the RIL population designated "K ~ N"

3.3 | Several major, reproducible QTLs emerged, especially on chr 01

A QTL analysis on the three populations that showed large numbers of genotypes with intumescence revealed several significant QTLs. In the population L ~ R major QTLs with LOD scores between 3 and 8.8 were identified under both light conditions on approximately the middle of chromosomes 05 and 07 (Table 2). In addition, there is one smaller HPS light-specific QTL on top of chromosome 5 that was only detected in the HPS condition (LOD score of 3.8; Figure 3a). In contrast, in the population Mm ~ Mo, one major QTL (LOD score of about 11) on the top of chr 01 was identified and another QTL on top of chr 06 (LOD score of about 6; Figure 3b). Both QTL were at similar positions and had similar LOD scores in both light conditions. In the population N ~ K, a large QTL (score above 35) was again identified on top of chr 01. The QTL positions were identical for the two light treatments and also the heights of the LOD scores were similar (Figure 3c). The major QTLs identified in this study were also detected when only the data of single experiments were used, with the exception of one experimental replication in the population Mm ~ Mo (supporting information Figures S3 and S4), confirming the reproducibility of these major QTLs. In addition, the near identical QTLs for the two light conditions provided further proof of the QTL locations.

The peak marker of the QTL on chr 01 that was identified in two populations was in population Mm ~ Mo at approximately 1.1 Mb (or at 0.9 Mb in case the analysis was done for both light conditions together; SL3.0) and in population N ~ K at approximately 0.9 Mb. In the population Mm ~ Mo 33% of the intumescence score variation is explained by the QTL on chr 01 under HPS as well as LED light. In the population N ~ K, 74% and 72% of the of the genetic effect were explained be the QTL on chr 01 in HPS and LED light, respectively. The peak of the QTL on chr 06 in the population Mm ~ Mo was,

TABLE 1 Differences in intumescence between reciprocal crosses

Population	A ∼ K		L ∼ R		K ∼ N		Mm ∼ Mo	
Reciprocal cross group	A × K	K × A	L × R	R × L	K × N	N × K	Mm × Mo	Mo × Mm
Intumescence: 0	0.97	0.96	0.45	0.48	0.5	0.36	0.63	0.58
Intumescence: 1	0.03	0.04	0.31	0.36	0.39	0.52	0.34	0.34
Intumescence: 2	0	0	0.19	0.15	0.1	0.12	0.04	0.08
Intumescence: 3	0	0	0.05	0.01	0	0	0	0
p-value of Wilcoxon rank sum test	0.66		0.04		0.0001		0.07	
p-value of Chi^2-test	0.5		0.0008		0.0001		0.02	

Note: The frequency distributions of intumescence scores for the different RIL populations, separated for using either one or the other parent as mother. The significances of the differences between there reciprocal crosses were evaluated, using the Wilcoxon rank sum test and a Chi^2 test. The Wilcoxon rank sum test indicates the likelihood of the influence of the reciprocal cross group on the intumescence score. The Chi^2 test determines the likelihood of independence of the two cross groups for the number of occurrences in the different intumescence score classes (0 to 3), indicating not only if overall but also if relative severity is different between the populations.

TABLE 2 Overview of all QTL identified for intumescence

Population	Condition	Chromosome	Start QTL	End QTL	Peak LOD score	Average value allele A	Average value allele B
L ∼ R	HPS	5	0.345	6.711	3.80	R: 0.92 ± 0.05	L: 0.51 ± 0.05
L ∼ R	HPS	5	62.863	65.634	3.01	R: 0.55 ± 0.05	L: 0.88 ± 0.05
L ∼ R	HPS	7	3.748	59.84	7.32	R: 0.42 ± 0.05	L: 0.97 ± 0.05
L ∼ R	LED	5	63.385	65.634	4.32	R: 0.61 ± 0.06	L: 1.00 ± 0.06
L ∼ R	LED	7	3.748	59.84	8.81	R: 0.5 ± 0.06	L: 1.04 ± 0.05
Mm ∼ Mo	HPS	1	0.676	2.376	10.6	Mm: 0.28 ± 0.04	Mo: 0.71 ± 0.04
Mm ∼ Mo	HPS	6	0.753	36.959	4.9	Mm: 0.31 ± 0.04	Mo: 0.61 ± 0.04
Mm ∼ Mo	LED	1	0.878	2.3765	10.94	Mm: 0.28 ± 0.04	Mo: 0.67 ± 0.04
Mm ∼ Mo	LED	6	0.753	36.959	5.97	Mm: 0.29 ± 0.04	Mo: 0.6 ± 0.04
N ∼ K	HPS	1	0.906	1.507	42.77	K: 0.08 ± 0.03	N: 1.08 ± 0.03
N ∼ K	LED	1	0.906	1.507	35.60	K: 0.16 ± 0.04	N: 1.15 ± 0.03

Note: The QTL that were identified in all populations and light conditions based on the single QTL analysis (with reciprocal cross group as cofactor in the populations L ∼ R and N ∼ K) are listed with their peak LOD score and allelic effect at the marker with the highest LOD score peak of each QTL (letters indicate the parental allele). The start and end of the QTL were determined by the markers flanking of a 1.8-LOD support interval and their positions given in Mb (rounded to the first decimal, version SL3.0).

depending on the light condition, between 1.2 and 2.2 Mb (in case the QTL analysis was done for both light conditions together than the peak of this QTL is at 1.2 Mb) and the QTL explained 10% or 12% of the variation, in HPS and LED light, respectively.

A QTL with a high LOD score as in the population N ∼ K can mask smaller QTLs. A multiple QTL mapping approach revealed additionally one low effect QTL (2% explained variance) on chromosome 9 (supporting information Figure S6) in the HPS light condition, still keeping the largest part of the explained variance (71%) at the QTL on chr 01. The Momotaro and Nunhems-FM001 allele, respectively, conferred a higher intumescence score at this locus. Those were also the parental lines of those RIL populations that had more severe intumescence than the crossing partner (Moneymaker or Kentuckey Beefsteak). Also on chr 06, the Momotaro allele gave the higher intumescence score at this locus. In case both loci carry Momotaro alleles, the intumescence score was the highest ($p = .003$ compared with the genotype group that had Mo on chr 01 and Mm on chr 06); if both loci carried the Moneymaker allele, the intumescence severity was considerably lower (Figure 4a). Of those genotypes that carried Moneymaker alleles at both QTL, only 9% has intumescence symptoms in contrast to 68% of the plants that carried Momotaro alleles at both positions. The average intumescence score was lowest when the allele at the QTL on chr 01 was from Kentucky Beefsteak (Figure 4b); only 10% of all genotypes with this allele on chr 01 showed signs of intumescence (only with a score of 1 not higher), while 72% of those with a Nunhems-FM001 allele did.

Using average values for the intumescence score of N ∼ K from both conditions showed a binominal distribution pointing to a monogenic trait (supporting information Figure S7 and Table S2). This is the QTL on chr 01. Markers flanking a 95% Bayes credible interval of the QTL on chr 01 were determined. Those markers included in both populations the first marker on the chromosome, so the candidate gene region started from the top of chr 01. In this case, the candidate gene region spans 2.38 Mb in the population Mm ∼ Mo and 1.51 Mb

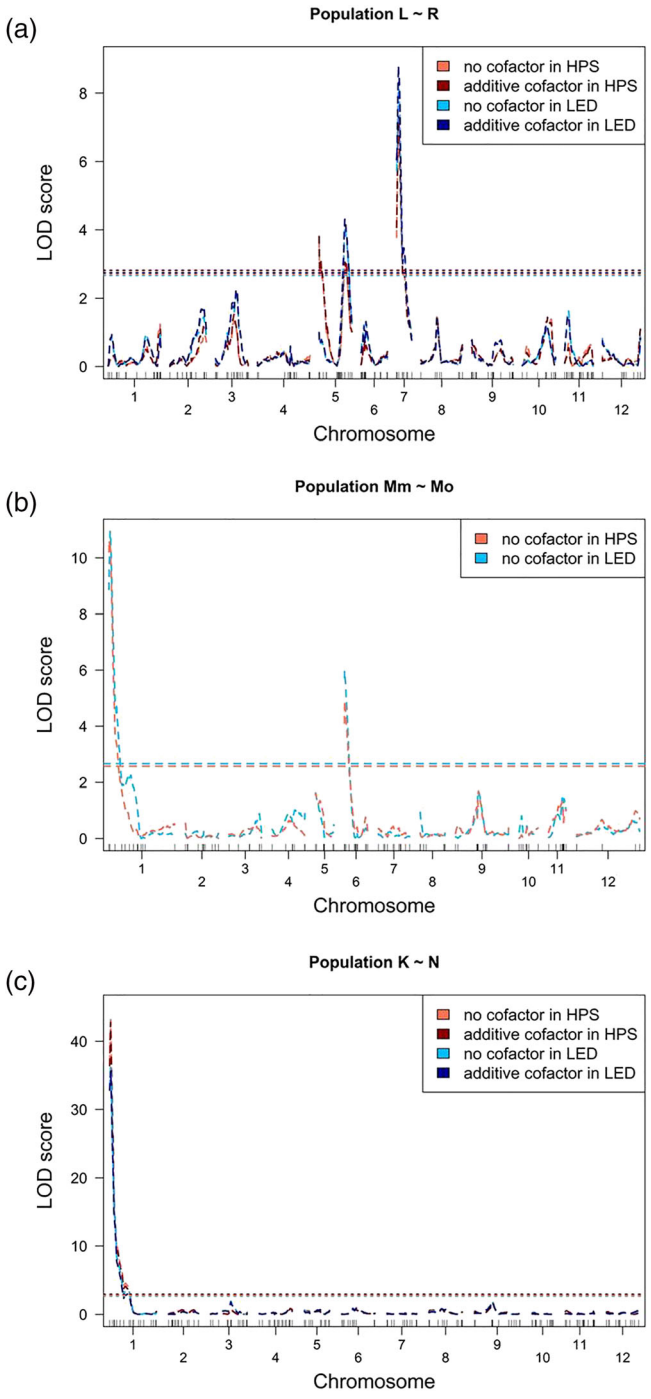

FIGURE 3 LOD scores for intumescence in three different RIL populations. A QTL analysis was performed for the three RIL populations L ~ R (a), Mm ~ Mo (B) and K ~ N (C) for each condition (high-pressure sodium [HPS] or LED supplemental lighting) separately. The threshold is determined per condition (HPS or LED lighting) by a permutation test ($n = 1000$), and the higher threshold of the two is displayed in the graphics

in the population N ~ K. A graphical mapping for the population N ~ K was performed that has the major effect QTL on chr 01 with little further interference from the genetic background. Sorting all RILs by their average intumescence score revealed that on top of chr 01, the region between a marker at 0.9 Mb and at 1.5 Mb (SL4.0) was co-segregating with the binominal trait groups. In this 600-kb region are, according to the reference genome sequence of *S. lycopersicum* (100 Tomato Genome Sequencing Consortium et al., 2014; Consortium, 2012), 60 predicted genes. This list contains genes that are annotated to be involved in signalling pathways, fatty acid synthesis and ethylene associated factors. Comparing those genes with the genes that were identified by Wu et al. (2017) to be differentially regulated in tomato in intumescent and non-intumescent leaves, seven genes were identical (supporting information Table S3). Those are extensin-like proteins, enzymes that could be involved in fatty acid synthesis or potential signalling components (receptor like protein, calcium dependent kinase). More dedicated fine mapping studies have to be conducted in order to zoom in on the causal gene for this trait.

3.4 | Maternal effects from the plastids were independent of the QTLs from the nucleus

The QTLs in the populations with a significant overall maternal effect, K ~ N and L ~ R, were tested for the influence of maternal effects by adding the reciprocal cross group as cofactor in the QTL analysis. For the population L ~ R, there was no effect of an additive or interactive cofactor that incorporated the maternal effect on the QTL analysis. For the population K ~ N, an interaction of low significance between a locus on ch10 under HPS light and the maternal effect was detected (genome scan adjusted *p*-value of .036; supporting information Figure S5). However, there is no QTL for intumescence on ch10, so the significant interaction is likely due to chance variation. We conclude that the maternal effects did not show a significant interaction with the QTLs.

3.5 | Correlations show that intumescent plants are taller with less leaf area

Taking the data from all populations together, there was a positive correlation (Kendall's τ of approximately 0.1, $p < .001$) between intumescence score and stem height or stem weight measures of 4-week-old plants. The area and the weight of side shoots were also positively correlated (Kendall's τ of approximately 0.1, $p < .001$) with the intumescence score, while the area of the true leaves was negatively correlated (Kendall's τ of $-.03$, $p = .03$). Equally, the fresh weight to dry weight (FW/DW) ratio of the stems and true leaves was negatively correlated with intumescence, while it was positively correlated with the FW/DW ratio of the side shoots; this ratio was negatively correlated for the true leaves. The side shoots developed later than the true leaves, and their development varied largely per genotype; this could confound the correlation data of side shoots. Photosynthesis efficiency (Φ_{PSII}), estimated by chlorophyll fluorescence imaging of leaves, was for all plants together negatively correlated with the intumescence score (Kendall's τ of $-.17$, $p < .001$), equally was the chlorophyll content index (Kendall's τ of $-.05$, $p < .001$). The anthocyanin

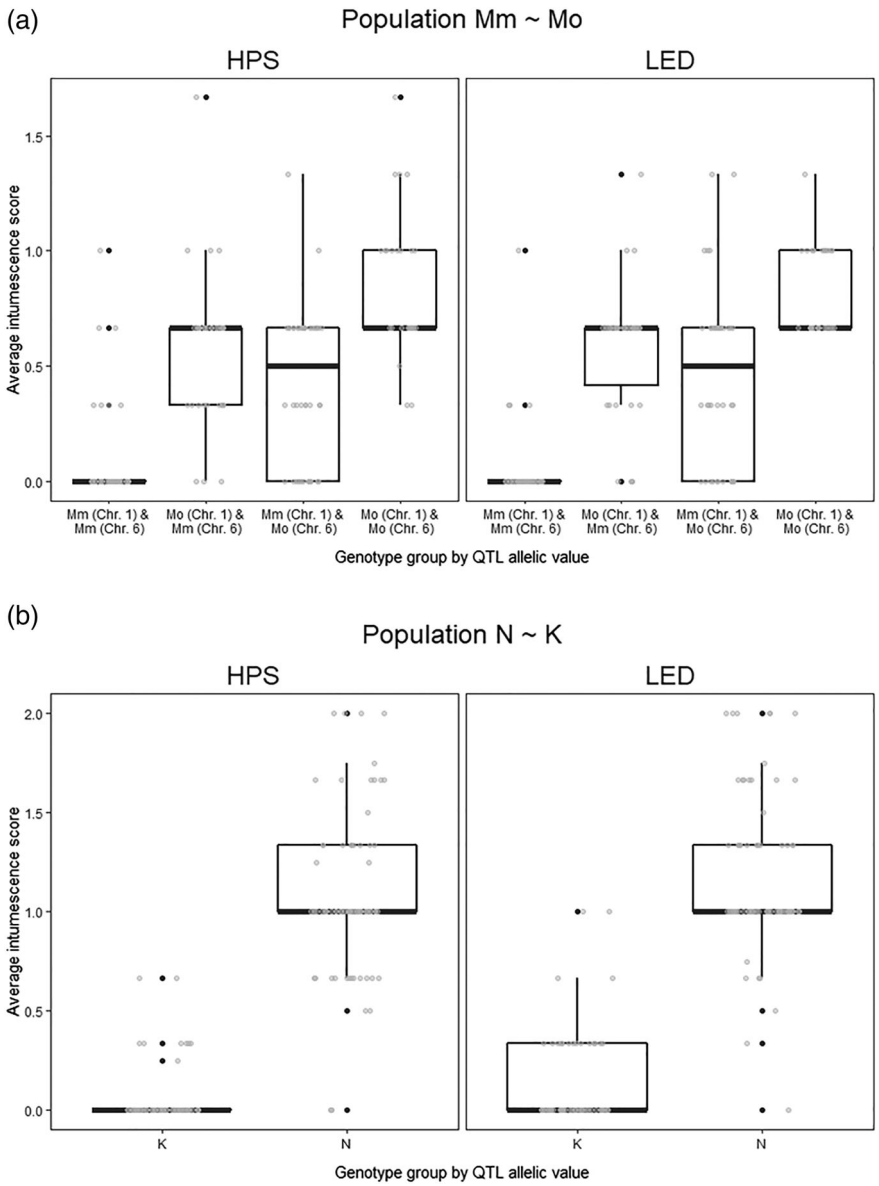

FIGURE 4 Allelic effect at the QTL position on the intumescence score. The RILs of the populations Mm ~ Mo (a) and the population N ~ K (b) were sorted according to the homozygote allelic variation at the detected two or three QTL positions, respectively. The mean and standard error of the intumescence score are plotted for each genotype group as well as the individual data (overlapping, open circles)

and flavonol content indexes were positively correlated with the intumescence score (Kendall's τ of .1, $p < .001$). Supporting information Table S4 shows all significances, per reciprocal cross.

4 | DISCUSSION

4.1 | Genetic analysis reveals a common genetic factor between populations on chromosome 1

The RIL populations derived from parents that showed less intumescence symptoms had also less intumescence themselves. This was a first indication for a genetic contribution to intumescence in the studied tomato genotypes. It was validated by the significant genotype effect and high heritability of intumescence score for the three populations with intumescence. The intumescence characterization by visual scoring enabled us to screen many plants in replicate experiments, which showed reproducibly. Although the visual score was not very detailed, it turned out to be sufficiently accurate to determine very significant QTLs and other significant effects.

In two out of the four RIL populations, there was also an effect of what were non-chromosomal but presumably maternally inherited chloroplasts and/or mitochondria effects, with Nunhems-FM001 or the *S. pimpinellifolium* "LA1578" as mother showing more intumescent progeny. These factors appeared to be a large contributing factor to the genetics of intumescence. Maternally inherited or cytoplasmic effects were identified for several growth- and fruit-related traits, as well as for leaf developmental changes associated with variegation in tomato (Bonnema et al., 1995; Saleem et al., 2013; Singh & Pathania, 2009). However, to our knowledge, this has not been studied for intumescence before. In our study, we could not identify that there is an interaction between the maternally inherited organellar genome and the chromosomally inherited genetic component of intumescence. This indicates that the organelle-coded factors work

independently of the genetic factors from the nucleus in promoting intumescence.

Due to the near identical position of the major effect QTL on chr 01 in the populations Mm ~ Mo and K ~ N, it is likely that the same genetic factor is responsible in both populations. However, intumescence can be influenced by other genetic loci too, as appeared from our study, and as was reported before (Ammitzboll et al., 2018; Wu et al., 2017). It is also possible that several (interacting) genetic factors are at the location of the QTL on chr 01. Nevertheless, even if several genetic factors would underlie the QTL on chr 01, they would be relatively close together (in an approximately 0.6-Mb region). That would mean that with a high likelihood, they would be inherited together as linked genes and could be treated in a breeding programme as one factor. Overall, the presence of one major effect QTL at a similar location in two out of three populations points to an ideal breeding target that could be present in a variety of genetic material. Wu et al. (2017) showed that intumescence negatively affected gene expression involved in metabolic functions and cell wall biosynthesis, while ethylene signalling pathway components were a prevalently upregulated. Therefore, the genes in those functional classes could be potential candidates for the QTL on chr 01. From our candidate short list, especially, the extensin-like proteins are likely candidates. Extensins are a family of glycoproteins involved in primary cell wall formation, stability and wound responses (Borassi et al., 2016; Lamport et al., 2011). They could favour cell outgrowth and wall expansion in the intumescence galls or be a secondary response to the tissue wounding in the progression of intumescence development.

4.2 | No apparent effect of the lighting condition

No significant difference in intumescence score was observed between the two light conditions, that is, supplemental HPS or red/blue LED light. Nevertheless, in the population L ~ R, one smaller effect size QTL was identified that may be specific to one of the light conditions. This is also the population with the largest variation in intumescence score, which could be statistically relevant for the detection of a light-specific QTL. In contrast to studies that grew plants solely under combinations of monochromatic light, we did not see significant differences in intumescence occurrence between the HPS light with approximately 40% red light (intensity wavelength region 600–700 nm compared with the overall PAR spectrum) and approximately 5% blue (wavelength region 400–500 nm) and the high red (95%)/blue (5%) ratio LED light. As our lighting setup was supplemental, both light-condition groups received solar radiation. Although the average solar light intensity perceived by the plants was lower than the supplemental lighting, it seems to have been sufficient to suppress the intumescence fostering effect of the high red to blue ratio of the LED light condition (Massa et al., 2008; Wollaeger & Runkle, 2014). Equally far red (wavelength region 700–800 nm) was present with a lower percentage (approximately 5%) in HPS lamps but barely present in the LEDs, and also, this difference had no effect on the intumescence in our study.

4.3 | Interdependency with other morphological or physiological traits

The negative correlation that we found between intumescence and photosynthesis or chlorophyll content index is in line with previous findings that the intumescence injury has a negative effect on photosynthesis and chlorophyll content and causes leaf yellowing (Pinkard et al., 2006; Wu et al., 2017). The smaller leaf area of intumescent plants could be a consequence of the injury that hampered the build-up of biomass, tissue expansion and/or due to the lower photosynthetic activity. We also identified a positive correlation between anthocyanin content index and intumescence score. A higher accumulation of anthocyanins in intumescent plants could be a reaction of a perceived stress or the mechanical injury (Gould et al., 2002). Wu et al. (2017) showed that biotic and abiotic stress genes were upregulated in intumescent leaves; accumulation of anthocyanins was often observed together with stress responses (Chalker-Scott, 1999; Kovinich et al., 2015). Hernández et al. (2016) identified a negative correlation between higher blue/red grow light ratios and accumulation of anthocyanin, and in conditions with more blue light, they identified less intumescence. The strongest correlated trait with the intumescent score in our study was the FW/DW ratio of the leaves. Plants with a higher intumescence score had a trend towards a higher FW/DW ratio, and this would link to the hypothesis that one causal factor of intumescence formation is the water status of the plants (Pinkard et al., 2006).

We summarize that the severity of intumescence impacted plant growth and physiology in an early stage of development. Growing the plants under two different horticultural supplemental lighting systems, HPS and R/B LED top lighting had no significant influence on the severity of intumescence. Intumescence was determined strongly by genetics including the maternal background. In two out of three different RIL populations, a major QTL was identified at a similar position on chr 01, making this locus a breeding target for plants with lower susceptibility to intumescence. The major QTLs are reproducible among the three replicates in time. Moreover, they appear under both light conditions, again showing the reproducibility of these QTLs. The maternal effect did not interact with the identified QTL, which could make breeding for intumescence resistance easier. An optimal maternal genotype could be selected independently and crossed with a genotype carrying an allele that confers low intumescence susceptibility. Independent selection of maternal background and a resistant locus on chr 01 could drastically lower intumescence occurrence and symptoms. Extensin-like proteins, located at this position, could be candidate genes underlying the intumescence QTL.

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CONFLICT OF INTEREST

There are no conflicts of interest.

AUTHOR CONTRIBUTIONS

A. E. Prinzenberg planned, conducted and analysed the RIL experiments; H. Van der Schoot helped with the planning of the RIL experiments and the measurements; L.F.M. Marcelis, E. Heuvelink, R. G. F. Visser and H. J. Schouten initiated the project and contributed with discussions. All authors contributed in varying degrees to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

The raw data are added in a supplementary file.

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