

Does Tomato Breeding for Improved Performance Under LED Supplemental Lighting Make Sense?

Aina E. Prinzenberg

Wageningen Universiteit en Researchcentrum Plant Research International BV: Wageningen University and Research Wageningen Plant Research

Hanneke van der Schoot

Wageningen Universiteit en Researchcentrum Plant Research International BV: Wageningen University and Research Wageningen Plant Research

Olivier van Deth

Wageningen University and Research Wageningen Plant Research

Theoharis Ouzounis

Wageningen Universiteit en Researchcentrum Plant Research International BV: Wageningen University and Research Wageningen Plant Research

Suzan Gabriëls

Wageningen Universiteit en Researchcentrum Plant Research International BV: Wageningen University and Research Wageningen Plant Research

Fien Meijer-Dekens

Wageningen University and Research Wageningen Plant Research

Leo F.M. Marcelis

Wageningen University and Research Wageningen Plant Research

Richard G. F. Visser

Wageningen University and Research Wageningen Plant Research

Ep Heuvelink

Wageningen University and Research Wageningen Plant Research

Henk J Schouten (✉ henk.schouten@wur.nl)

Wageningen UR: Wageningen University & Research <https://orcid.org/0000-0003-4495-1951>

Research Article

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Abstract

Differences in growth have been reported for tomato under LED compared to HPS light, however, it is not clear if breeding specific for LED supplemental light is worthwhile. Therefore, we derived four recombinant inbred line (RIL) tomato populations from parents with contrasting growth responses to different light spectra. These RIL populations were grown for four weeks under supplemental HPS or 95% red and 5% blue LED light in the greenhouse. For one population we also studied fruit production. Plant height and size of the side shoots of the young plants were strongly reduced under LED supplemental lighting compared to HPS in all populations. The adult plants showed shorter internode lengths, less trusses, less fruits, and lower yield of ripe fruits per plant under LED. However, when the unripe fruits at the last harvest day were included, the difference in yield between HPS and LED disappeared, indicating that the plants under LED light were compacter and slower in development, but in the end produced similar yield. We found numerous QTL, but hardly any of these QTL appeared to be significantly LED-specific. Also, we found very significant genetic effects of maternally inherited plastids and mitochondria, showing the importance of using a parental genotype as mother or as father. However, these effects were very similar between the two light conditions. We conclude that our study does not justify tomato breeding programs that are specifically targeted at 95% red and 5% blue LED supplemental lighting.

Introduction

Year-round tomato production in temperate climates with long winter periods of low light and low temperature requires greenhouses with supplemental lighting. Those are not only costly for the grower but also leave a large ecologic footprint due to the energy usage. The supplemental light is often provided by High Pressure Sodium (HPS) lamps that emit a warm, relatively broad light spectrum that proved favourable for many plant species. However, HPS lamps consume considerable amounts of energy. Narrow band Light-Emitting Diodes (LED) -lamps could be an alternative as these consume far less energy for the same light output (Gómez and Mitchell 2015; Kaiser et al. 2019). By providing the plants with a narrow spectrum of supplemental lighting, the lighting energy can be focussed on a more efficiently used light spectrum (Paradiso et al. 2011). Tomato plants grown in climate rooms under red and blue (RB) LED lighting had a higher CO₂ assimilation rate than under white light from fluorescent tubes (Arena et al. 2016). However, the plants in the study of Arena et al. (2016) had, despite the higher CO₂ assimilation rate, in RB-light a lower biomass compared to the white light control.

Light composition not only influences photosynthesis and biomass accumulation, but influences plant performance in many other ways: The concentration of soluble sugars is influenced by the quality of the light regime (Lanoue et al. 2017) which in turn is involved in oxidative stress signalling (Couée et al. 2006) and metabolic regulation (Smeekens et al. 2010). Photoreceptors, like phytochromes, influence flowering time (Strasser et al. 2010; Cao et al. 2015), and root and leaf growth (Rao et al. 2011; Costigan et al. 2011). The light regime under which plants grow also affects secondary metabolites (Carvalho and Folta 2014) and thereby could indirectly influence quality traits and disease resistance.

The genotype by environment interaction is important in the selection of the optimal spectral composition for a crop. Next to species specific responses (Bantis et al. 2018), natural variation for light responses was also identified between different tomato accessions (Ouzounis et al. 2016). In tomato, quantitative trait loci (QTL) for plant architecture that could influence light absorption in the canopy were identified (Nakano et al. 2016; Fulop et al. 2016) and also QTL for photosynthetic traits (Oyanedel et al. 2000; de Oliveira Silva et al. 2018) but light spectrum differences were not taken into account. Velez-Ramirez et al. (2014) identified a QTL for continuous light tolerance in tomato and developed from this a genotype that showed up to 20% higher yield when grown under continuous light. This study from Velez-Ramirez et al. is thus an example for the possibilities of genetic adjustments for light use efficiency in tomato. Nonetheless, there are, as far as we know, no QTL studies in tomato looking at light spectrum effects. Therefore, we aimed at identification of QTL that are LED or HPS specific.

Chloroplasts are critical in light perception and photosynthesis, and mitochondria are important for energy use. Chloroplasts and mitochondria are inherited from the mother, and contain their own genomes, and can thereby contribute to the genetic variation (Gray 1993). Therefore, we did not focus on genetic effects located in nuclei only (the QTL), but in addition we studied the effects of maternally inherited plastids and mitochondria. For this purpose, we made reciprocal crosses when developing F1 hybrids. Per combination of parents, half of the RILs were derived from F1 plants from Parent A x Parent B, whereas the other half of the RILs was derived from an F1 from the reciprocal cross Parent B x Parent A. As a result, the first half of the RILs from this population harboured the plastids and mitochondria from Parent A, and the other half of the RILs contained the plastids from Parent B. We did this for all four RIL populations, leading to eight sub-populations.

We hypothesised that there is natural variation relevant for breeding that is specific to LED light cultivation using tomato as a representative species that is often grown in protected conditions. The effect of red, blue and white LED light on biomass and physiological traits was determined for 40 genotypes in climate rooms. According to contrasting light reactions of those plants, crosses were made between selected genotypes and four different RIL populations were developed. Reciprocal crosses allowed the study of effects from plastids and mitochondria for each RIL population. We grew those populations in greenhouse conditions with supplemental HPS and LED light to identify physiological and morphological trait differences in the two light environments and investigated the underlying genetics by means of QTL mapping. We analysed four RIL populations in three replications in young plant stages and one RIL population of full-grown fruit yielding plants under HPS versus LED supplemental lighting, and genetically mapped plant growth and yield.

Materials And Methods

The initial 40 tomato accessions

In an initial experiment 40 tomato genotypes, including cultivars and wild accessions (Table S1), were tested for their biomass under different lighting conditions (Ouzounis et al. 2016; Ji et al. 2020). These 40

accessions were grown in climate rooms (Ji et al. 2020) with artificial lighting. The plants were pre-grown in potting soil under fluorescent light for seven to nine days after sowing and then transferred to sterile river sand and grown in one of the following LED conditions: white light with additional UVB (ca. 0.16 W m⁻²) and FR (ca 26 μmol m⁻² s⁻¹) or R/B LEDs at a 16h photoperiod (light intensities ca. 130 μmol m⁻² s⁻¹). The white light was created with white/red LEDs (GreenPower LED-TL-DR/W-MB-VISN, Philips, The Netherlands), and the additional UVB and FR was provided by Philips GreenPower LED production modules far-red (GreenPower LED -PM-FR-150), cool fluorescent tubes (38W, Philips) and Philips Broadband TL 20W/12 RS Ultraviolet-B lamps. The R/B LEDs had 88% red light and 12% blue light (GreenPower LED-PM-DR/B-MB-150, Philips). The temperature and humidity of the climate room were approximately 22°C and 70%, respectively. Destructive measures for total dry biomass (roots, shoots and leaves) were done three weeks after transplanting.

Development of four RIL populations

From the 40 accessions, genotypes were selected that showed contrasting responses to the different light environments. The following four combinations of contrasting genotypes were selected for development of RIL populations: Ailsa Craig (LA2838A) and Kentucky Beefsteak (TR00021) hereafter abbreviated with “A ~ K”; LA1578 (EA00674; *S. pimpinellifolium*) and Rutgers (EA00465; *S. lycopersicum*) “L ~ R”; Moneymaker (CGN14330; *S. lycopersicum*) and Momotaro (Tough Boy; TR0003; *S. lycopersicum*) “Mm ~ Mo”; and Kentucky Beefsteak (TR00021; *S. lycopersicum*) and NunhemsFM001 (*S. lycopersicum*) “K ~ N”. For each of these cross-combinations a reciprocal cross was performed, swapping the two parents, and therefore each RIL population consisted of two subgroups differing in maternally inherited plastids and mitochondria. All individuals of the populations were grown via single seed descent at least to the F5 generation (the Mm ~ Mo RIL population was an F6). The F1 hybrids were made at Wageningen University and Research (WUR), whereas the RIL populations were developed in greenhouses in the Netherlands by Nunhems Netherlands B.V. (BASF Vegetable Seeds), Rijk Zwaan Nederland B.V., and Bejo Zaden B.V. For each subpopulation ca. 75 individual RILs were grown, leading to ca. 150 RILs per QTL analysis.

Growth conditions for the four RIL populations analysed in young stage

For the screening of the RIL populations, the plants were grown in glasshouses at Unifarm, Wageningen University and Research. In each experiment the same set of RILs was grown in parallel in two different compartments, one with HPS supplemental lighting and one with LED supplemental lighting.

Plants for both supplemental light treatments were germinated under HPS-supplemental lighting. Of each genotype ca. 12 seeds were sown. The seeds were placed on stone-wool plugs (Gro Plug, Grodan Rockwool B.V., Roermond, The Netherlands), covered with Agra-Vermiculite (PULL Rhenen, Rhenen, The

Netherlands) and a transparent foil for additional humidity for approximately the first five days. The plugs were soaked with nutrient solution: NH_4 1.2 mM, K 7.2 mM, Ca 4 mM, Mg 1.82 mM, NO_3 12.4 mM, SO_4 3.32 mM, P 1 mM, Fe 35 μM (as mixture of Fe-DTPA/ Fe-EDDHA), Mn 8 μM , Zn 5 μM , B 20 μM , Cu 0.5 μM and Mo 0.5 μM . The macronutrients were provided as a mixture of fertilizers from Yara Benelux BV (Rotterdam–Vlaardingen, The Netherlands) and the micronutrients were from the Agrispoor product line of Horticoop BV (Bleiswijk, The Netherlands). The pH was between 5.5 and 5.8 (adjusted with KOH) and the EC was approximately 2.0 dS m^{-1} .

Seedlings with fully expanded cotyledons were selected for transfer after one week. The plants were transferred to 10 cm x 10 cm x 6 cm stone-wool blocks (Grodan Delta, Grodan Rockwool B.V., Roermond, The Netherlands). Upon transfer the plants were divided among the two compartments, one with supplemental HPS-lighting (Master green power, cgt 400W, Philips) and one with supplemental DR/LB LED-lighting (Green Power LED top lighting module DR/B LB, 190W, Philips).

The light spectra of the lamps were measured (Figure S1) with a Field Spectroradiometer (SS-110, Apogee Instruments, Logan, UT, USA) and PSS values calculated according to the method of Sager et al. (1988). For the analysis, blue light over the wavelength range 400-500nm, green over 500-600nm, red over 600-700nm and FR over 700-800nm were considered (individual intensity measures per wavelength were used for the average if above 0.05 $\mu\text{mol s}^{-1} \text{m}^{-2}$). Percentages of those wavelengths in the spectrum were compared to the overall intensity in the PAR range from 400 to 800 nm and rounded to 5% intervals. To shield the experiment from light of adjacent compartments, the walls of the compartments were covered with white horticultural foil. The supplemental light intensity was about 200 $\mu\text{mol s}^{-1} \text{m}^{-2}$ (in a wavelength range from 400 to 700 nm) during 16 h, starting 16 h before sunset each day. The compartments were heated and set to an air temperature of 22°C during the supplemental lighting period and of 19°C outside the supplemental lighting time. Climate data inside the greenhouse were measured by a climate box (PT500 Temp./ RH sensor, Hoogendoorn Automatisering) every 20 s and averaged over 5 min intervals. The incoming solar light and other environmental factors were recorded and averaged over time (Table S2). The solar light was measured on top of the greenhouse. Eight light measurements (light meter LI-250A from LI-COR) inside the empty greenhouse were taken at the approximate plant height on one day. With this data a coefficient between incoming light and the light measured on top of the glasshouse was calculated to estimate the incoming solar light for all experiments. In case the solar radiation (in the third and fourth experiment) outside the greenhouse was above 200 W m^{-2} , an energy screen (Harmony 4215 O FR) was closed above the lamps in the greenhouse (leading to 42% less light at 100% screen-closure, the light-coefficient was adapted accordingly). For the mature plants the intensity of the solar light received by the plants was estimated using the measured solar radiation outside the greenhouse and a transmissivity factor of 0.62 (based on previous measurements). In addition, the measured solar radiation was reduced to 47%, as this is the approximate amount of photosynthetically active photon flux density in the solar radiation; and then assuming that 1 W m^{-2} solar light equals 4.57 $\mu\text{mol m}^{-2} \text{s}^{-1}$ the conversion into $\mu\text{mol m}^{-2} \text{s}^{-1}$ was done (McCree 1972; Britton and Dodd 1976).

The RILs of the populations L ~ R, A ~ K and Mm ~ Mo were grown together in three, repeated experiments between October 2018 and March 2019 with one replicate per RIL and experiment, giving three replicates in time. The population A ~ N was grown in one experiment in March/ April 2019 with three replicates per RIL simultaneously. The seven parents of those RIL populations were grown in each experiment with four replicates. The first experiment was harvested 5 weeks after sowing and the consecutive three experiments were harvested in week 4 after sowing. The individual plants of each experiment were divided into four batches and sown on four consecutive days each on one ebb-and-flood table. Destructive measurements were performed during four consecutive days as well, so that the growth-period was the same for all plants. All plants were distributed in a randomized design over the four tables. For the first three experiments the tables were divided into four areas (front, back and two middle parts of the rectangular tables) for the randomization pattern with similar numbers of plants from each RIL-population and reciprocal cross per area. From the parents one replicate was grown per table. The parents used for one population were situated close to each other on each table.

Plants were watered by flushing the stone-wool blocks for 5 minutes with nutrient solution (see above) on the ebb- and flood-tables. The watering schedule over the course of the experiment was irregular, it aimed at keeping the blocks always moist but not wet.

Phenotyping during the growth of the young plants

The operating quantum yield of electron transport of photosystem II (Φ_{PSII} ; "Phi PSII") was estimated, using the closed FluorCam 800MF (Photon Systems Instruments, Brno, Czech Republic) and a self-written program to determine Ft under actinic light (ca. $200 \mu\text{mol s}^{-1} \text{m}^{-2}$) and Fm (after max. light pulse) with the software FluorCam7 (version 1.2.4.4 Photon Systems Instruments, Brno, Czech Republic). The measurement was done four or five weeks after sowing on the second or third leaflet of a fully expanded leaf that was as much as possible perpendicular to the light. Measurements were done between 09.00 and 14.00 o'clock, alternating between the HPS supplemental light and LED supplemental light greenhouses approximately every 30 minutes (measuring batches of the same 22 genotypes in both HPS and LED supplemental lighting). Flavonol, anthocyanin and chlorophyll indices were obtained for all plants three weeks after sowing with the Force-A Dualex Scientific+™ sensor (Dynamax Inc., Houston, USA).

Destructive measurements of biomass related traits of the young plants

At the end of the growth period, four or five weeks after sowing (depending on the experiment), the plant stems were cut at the height of the stone-wool blocks and leaves were separated from the stem. In the axil of the true leaves, side shoots developed in most genotypes. The numbers of true leaves (TL) and side shoots were counted separately from the second experiment onwards. The leaf/ shoot-structures

were counted in case they were longer than ca. 5mm and the total respective fresh weights per plant determined. Final leaf area (of true leaves and side-shoots) was determined with an area meter (Li-cor, LI-3100C Area Meter, Li-cor Inc., Lincoln, Nebraska, USA). True leaves, side shoots and stems were put into separate paper bags and placed into a ventilated oven at 70°C for 24 hours followed by 105°C for 24 hours, after which the dry weight was measured (in the first experiment the side shoot and true leaf dry weight was determined together, in all the following experiments separately). The specific leaf area (SLA) was determined as the ratio between leaf area and leaf dry weight.

Growth conditions of the fruiting RIL population

For the phenotyping of fruits of the RIL population “K ~ N” (‘Kentucky Beefsteak’ ~ NunhemsFM001) the plants were grown in glasshouses of Unifarm (Wageningen University and Research). The plants were sown in September 2020. The RIL population was chosen for the similar sizes and weights of their fruits of its parental lines, as well as the resistance to tomato mosaic virus (TMV) of the NunhemsFM001 parent. The plants were pre-grown for four and a half weeks on ebb and flood tables in a greenhouse. If within a 16h light period the outside global radiation was below 250W m^{-2} , the natural light was supplemented with approximately $100\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ HPS light. Subsequently, the plants were divided among two compartments of 12 m by 12 m each at a plant density of approximately 2.2 plants per m^2 . For avoidance of border effects, at each side of the greenhouse a border row of plants was grown. In both compartments about $220\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ supplemental lighting was applied of either HPS in one compartment (Master green power, cgt 400W, Philips) or 95% red and 5% blue LEDs (Green Power LED top lighting module DR/B LB, 190W, Philips) in the other compartment. The light was measured ca 2.5 m over ground which was the height of the canopy top. The plants were kept at a height of approximately 2.5 m in order to keep 1 m of distance to the lamps above, and obtain equal light distribution. The duration of supplemental light was gradually increased, starting at five hours one month after sowing and reaching a maximum of 15 hours of supplemental HPS/LED light per day from four months after sowing onwards.

Stone-wool (Rockwool Grodan B.V., Roermond, The Netherlands) was used as planting medium, and the plants were drip-irrigated using the same nutrient solution as for the young plants. The EC of the nutrient solution in the stone wool slab was on average $3.8\ \text{ds m}^{-1}$ under HPS versus $3.2\ \text{ds m}^{-1}$ under LED. The compartments were heated if the temperature dropped below ca. 22°C (in a later stage of the experiment 24°C) during the supplemental lighting period or 19°C outside the supplemental lighting time. In compartment with LED supplemental lighting, heating pipes below the plants and above the lamps were used, to compensate for the heat irradiance from the HPS lamps. The HPS compartment was only heated by pipes below the plants. For pollination we used bumblebees (Koppert, biological systems). Harvesting and measurements started in week 17 after sowing and continued up until week 28. In each compartment the same set of 136 RILs was grown with one replicate each, as well as 11 replicates of each parent of the RIL population.

Growth abnormalities in the young RIL populations

The RIL populations were grown under two different supplemental lighting conditions in the greenhouse, under standard HPS lighting and R/B supplemental LED lighting. In some plants the formation of callus like structures starting at the veins on the abaxial side of leaves, called intumescence, was observed in both supplemental lighting conditions (Figure S2). Although all populations had individual plants with light intumescence symptoms (Williams et al. 2016), in some populations the occurrence was more severe. Intumescence was scored from 0 (no intumescence) to 3 (most of the leaves affected) and because this invasive physiological trait could affect other measured traits, genotypes that had a score of 2 and above were excluded from further analysis (0.1 to 19.2% of all individual plants, depending on the population).

Measuring fruit traits

The number of fruit trusses was counted on week 17 and week 25 after sowing. The fruit trusses were labelled in order of development, starting at truss number 1. The number of fruits were counted on week 17 and week 25 after sowing as well. Internode length was measured once during the trial on week 17 after sowing. This length was measured in centimetres from the third truss to the fifth truss. Fruit fresh weight was measured throughout the trial with intervals of three to four days between measurements, with the measurements starting in week 17 and ending in week 28 after sowing. The fresh fruits were measured from the breaker stage and onwards. This breaker stage is defined as the phase at which the fruit starts developing orange/red colour on its surface skin. During the last harvest during week 28 after sowing, all fruits were collected, including the non-ripe ones. By adding the weight of all unripe fruits per plant to the yield of ripe fruits of that plant, a total fruit yield (both ripe and unripe) was calculated per plant. By taking the number of fruits per plant into account, the average fruit weight per plant was obtained. Dry weight was measured for fruits from the 3rd and the 5th truss. This was done by cutting the fruits and subsequent drying the cut pieces in a ventilated oven for the first 12 hours at 70 °C and followed for at least 84 hours at 105 °C. Subsequently the weight of the dried fruit was determined.

Genotyping of the RIL populations

The four RIL populations were genotyped by Bejo Zaden B.V., Rijk Zwaan B.V, and Nunhems Nederlands B.V. The genotyping was done with 185, 219, 183 and 177 KASP markers for the populations A ~ K, L ~ R, Mm ~ Mo, and N ~ K, respectively, with approximately 2.9%, 12.5%, 5.2%, and 6.7 % of the marker calls scored as heterozygous.

Statistical Analysis

A Wilcoxon rank sum test was used to determine the significance of the light condition or reciprocal cross effect on the individual populations, using R (version 3.5.0; www.r-project.org). Descriptive statistics were done with the R package psych (version 1.8.4; Revelle 2018). All graphics were made with the R package ggplot2 (version 3.0.0; Wickham 2016). For the relative trait value in HPS and LED light, the trimmed mean under LED light, excluding the phenotypically upper 10% and lower 10% of individuals of each population (for A ~ K, L ~ R and Mm ~ Mo over three experiments), was expressed as percentage of the trimmed mean in HPS light ($\text{Mean}_{\text{LED}} * 100 / \text{Mean}_{\text{HPS}}$). For the relative trait range per population, the trimmed average (again with a fraction of 0.1 of extremes trimmed at each end) trait value of the top 10% and bottom 10% plants within each population was calculated, and the difference between those values in percent as $((\text{top} - \text{bottom}) / \text{top}) * 100$ was calculated. Equally the relative difference between the subgroups of the RIL population that were derived from the reciprocal crosses were calculated, by comparing the trimmed means per subgroup as $((\text{High}_{\text{GroupMean}} - \text{Low}_{\text{GroupMean}}) / \text{High}_{\text{GroupMean}}) * 100$. A Shapiro-Wilk normality test per condition, population and experiment showed that nearly 2/3 of the trait values were not normally distributed. Broad sense heritability was estimated by using the mean sum of squares values (Mean Sq) from a two-factor ANOVA (type III SS) on the rank-transformed data, that uses the RIL-genotypes and the experiment as main factors or in case of the population "K ~ N" from a single ANOVA with genotype as factor. The ANOVA was done with the R package car (version 3.0-0; Fox and Weisberg 2019). For the estimation of the heritability, we used the equation $H^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_e^2)$. The Mean Sq of the residuals was used as environmental variance (σ_e^2) and $((\text{Mean Sq}_{\text{RIL-genotype}} - \text{Mean Sq}_{\text{residuals}}) / \text{replicate number})$ gave the genotypic variation (σ_g^2). To test for an interaction of the light treatments and the subgroups derived from the reciprocal crosses, a two-factor ANOVA on the rank transformed data was done as described above per population, using the subgroups and light-environment as interacting factors.

The QTL analysis was performed using the R package R/qtl (Broman et al. 2003; Broman and Sen 2009). The genetic map was based on the position information from the companies and re-calculated for each RIL population. A single QTL analysis was performed with the non-parametric mapping function for both the young and mature RIL populations, using individual values per experiment as input. However, in case of the young population N ~ K for which all replicates were grown within the same experiment an average value per genotype was used for the QTL analysis. In addition, a single QTL analysis with the non-parametric mapping function was performed for differences in response under LED and HPS, using as parameter $(x_{\text{LED}} - x_{\text{HPS}}) / x_{\text{HPS}}$. For the populations A ~ K, L ~ R and Mm ~ Mo we used the BLUE function from the R package polyqtlR (Bourke et al. 2021) in the following way: BLUE(data=data, model = pheno~geno, random = ~1|experiment, genotype.ID = "geno"). In case of the population N~K the block in which the replicates were grown was used as random effect.

Also, a multiple QTL analysis was performed for the young populations with the multiple imputation method of Sen and Churchill (Sen and Churchill 2001) using rank transformed data as input, and in case of the first young three populations the experiment number was used as covariate. All permutation tests for LOD-thresholds/ penalties were done with 1000 permutations. In the single QTL analysis, the LOD

threshold was determined specifically per population, trait and condition. For the multiple QTL analysis, the automated stepwise procedure was used (assuming a maximum of 7 possible QTL) with a penalized LOD score criterion balancing heavy and light interaction penalties. For computational reasons the penalties were calculated based on one trait with a median level heritability under HPS light conditions in the population N ~ K. LED-specific QTL were selected based on the multiple QTL analysis for the young population. For the mature population, these were selected based on the single QTL analysis. For the young population, QTL on the same chromosome were considered different if their approximate 99% Bayes credible intervals did not overlap. The significance of the QTL that were only identified under LED light was verified with an ANOVA for the effect of the allele distribution at the peak-marker on the phenotype under LED light. Also, the allele by light-condition interaction of those LED-specific QTL was assessed with an ANOVA (using the peak marker and the light condition as interacting factors explaining the trait). For both ANOVAs the rank transformed data from the individual plants was used and for the young populations A ~ K, L ~ R and Mm ~ Mo, the experiment number was used as a block factor. The phenotypic mean difference of the two QTL with significant allele by light interaction was tested with a Tukey HSD-test with the package Agricolae (De Mendiburu 2020).

Results

Selection of contrasting parental genotypes for the four RIL populations

In an initial study 40 cultivars and wild accessions (Table S1) were compared on the basis of their total dry biomass in different light conditions. Contrasts between genotypes in different light conditions were used to select parents for crosses to construct RIL populations. In the two light conditions, i.e. R/B LED light and white LED light with UVB and FR, Moneymaker, Momotaro, Ailsa Craig and Kentucky Beefsteak were among the genotypes with the largest difference in biomass comparing plants growing in white light with plants growing in R/B light. Moneymaker and Kentucky Beefsteak had a higher biomass in R/B while Momotaro and Ailsa Craig had a higher biomass under the white light (Figure S3). In R/B light, Rutgers was among the genotypes with the highest biomass and LA1578 was among the genotypes with the lowest biomass. The genotype NunhemsFM001 had an approximately median biomass under both conditions and one of the smallest differences in biomass between the light treatments. It was in contrast to Kentucky Beefsteak which had one of the largest biomass in R/B light and the largest difference in biomass when compared between the two light environments. Those contrasting genotypes were used to create four RIL populations: Ailsa Craig (LA2838A) and Kentucky Beefsteak (TR00021), abbreviated as "A ~ K"; LA1578 (*S. pimpinellifolium*) and Rutgers "L ~ R"; Moneymaker and Momotaro "Mm ~ Mo"; and Kentucky Beefsteak and NunhemsFM001 "K ~ N". In view of possible effects from chloroplasts and mitochondria on the light use efficiency under LED and HPS, and considering that the plastids and mitochondria are maternally inherited, for each RIL population two subgroups were made, by swapping the parents when making the F1 hybrids.

Young plants were compacter, and had smaller side shoots under LED

For each RIL population a relative trait value was calculated to compare LED to HPS, where the trimmed average trait value of the plants grown under HPS light represents 100% of the trait value (Figure 1, Figure S4). Despite few traits that were most likely more affected by the seasonal changes than by the population, the overall trend between the populations' average light responses was similar. In all four populations, the plants grown under LED supplemental lighting had on average less biomass, were more compact, darker pigmented and had smaller side shoots with less biomass compared to plants grown under the standard HPS supplemental lighting. Among the different traits, the side shoot size and the height of the plants were lowest in LED light compared to HPS light. The leaf area of the side shoots under LED supplemental lighting was between 65% and 79% of that of plants under HPS lighting, depending on the RIL population. Likewise, the dry weight (DW) of the side shoots under LEDs was considerably lower, being 63% to 85% compared to those under HPS lighting. Moreover, the area and DW of the true leaves was lower under LED (between 84% to 90% of HPS). However, the reduction of the side shoots size and biomass was on average greater than that of the true leaves (TL), as the ratio of side shoots to true leaves was significantly smaller for plants grown under LED light compared to those under HPS (ratio side shoots/ TL area, Ratio side shoots/ TL DW; Figure 1). Also the total number of leaves and side shoots was slightly but significantly lower for LED than HPS grown plants. The anthocyanin and flavonol content indices were in all populations between 12% and 50% higher in LED compared to HPS grown plants. Chlorophyll content was in most populations also slightly increased in LED grown plants but overall similar between the conditions (Figure 1). For all mentioned observations, we see a similar pattern for the parental genotypes (Figure S5). The efficiency of operating electron transport of photosystem II (Φ_{PSII}) was 2% to 3% lower in LED light compared to HPS in the first three experiments.

Side shoot size and plant height showed high heritability

We showed significant differences in overall trait values between HPS and LED supplemental light grown young plants. The ranges of the trait values within a RIL population were calculated by taking the relative difference between the highest and the lowest trait value, after removing the 10% highest and 10% lowest values (Figure 2). Traits related to side shoots (area, SLA, DW) and anthocyanin content index, had the highest relative trait range compared to all other traits. These trends were independent of the light spectrum.

The range of the traits within a population shows the variability of the trait but not how much of the trait is genetically or environmentally driven. This genetic component can be estimated by the heritability of the trait. Across all populations, the heritability estimate for side shoot size and plant height was the highest (up to 0.68 for side shoot area, 0.72 for the area ratio between side shoot and true leaves or 0.66 for plant height; Figure 2). The lowest heritability was identified in all populations for Φ_{PSII} and SLA (side

shoots as well as true leaves). In the case of Φ_{PSII} it is possible that the light fluctuations in the greenhouse caused fluctuations in Φ_{PSII} measurement that were confounding the analysis.

From these data we conclude that the largest variation and highest heritability were found for the size of the side shoots. This holds both for the absolute size and weight of the side shoots, and the relative size and relative weight compared to the main shoot. The height of the seedlings four weeks after sowing showed a reasonable variation, but a very high heritability. These conclusions hold for both light environments.

Genetic differences between maternally inherited plastids showed considerable impact on side shoots and plant size under both light conditions

Each RIL population consisted of two sub populations from reciprocal crosses, which means that half of a RIL population was derived from a cross between parent A and parent B (A x B), using A as mother and B as father, whereas the other half of the population was derived from B x A, in which parent B was used as mother and A as father. The rationale behind this was that photosynthesis and energy related processes occur for a large part in chloroplasts and mitochondria. These plant cell organelles are maternally inherited. Figure 3 shows that there was a clear impact of the reciprocal cross group on the evaluated traits, especially on plant size and architecture. The population in which the most traits were different between the sub populations, meaning strong effects of maternally inherited plastids, was L ~ R. The ratio of side shoots to true leaves was most affected in this population under LED-supplemental lighting. When the *S. pimpinellifolium* LA1578 was used as mother the side shoots were 35% larger compared to using Rutgers (EA00465; *S. lycopersicum*) as mother. Apparently, the formation of side shoots is significantly under control of maternally inherited plastids in the L ~ R population. For the K ~ N RIL population the height of four-week-old seedlings was very significantly influenced by the maternally inherited organelles too: When N (*S. lycopersicum* NunhemsFM001) was the mother, the seedlings were ~ 5 % longer compared to K (*S. lycopersicum* Kentucky Beefsteak) as maternal parent. The plants were not only 5 % longer, the dry weight and area of the true leaves were also 5% higher when the Nunhems accession was used as mother rather than as father. Apparently, the plant size was significantly influenced by the origin of the plastids in this population.

Remarkably, the maternal effects were very similar between the two light conditions. An ANOVA did not show any significant interactions between the light treatments and the subgroups (except for Φ_{PSII} in the population L ~ R with a significant interaction at a p-value of 0.03).

Numerous reproducible QTL for young plant traits under both LED and HPS, but hardly any differential light impact

Comparing the QTL detected in a single QTL analysis for all traits and populations, under HPS and LED light, showed that the distribution of QTL largely differed per population (Figure 4). Detailed information about trait values, raw marker data, and the LOD-scores per trait are provided in the Suppl. Files 1 and 2. Related traits like the area and dry weight of the true leaves or side shoots, or the DW and height of the stem were often co-localizing for each population (Figure 4). The QTL for true leaves and side shoots are at different locations. Although the location of most QTL differed between populations, the QTL for DW and area of the side shoots (and the related ratios of the side shoots to the true leaves) are co-locating in the populations that share Kentucky Beefsteak as a parent, i.e. A ~K and K ~ N. In both cases the presence of the Kentucky Beefsteak-allele at the QTL gave a lower trait value.

The QTL patterns within one population were overall similar for the two light conditions (Figure 4). However, some QTL were only detected in one of the light conditions. The QTL that emerged only in LED light treatment with a multiple QTL analysis, and not at HPS supplemental light, are graphically represented per chromosome, population and trait in Figure 5. More detailed information about the positions and LOD-scores can be found in the Suppl. File 2. Figure 5 shows in total 44 putative LED-specific QTL, with LOD scores between 1.4 and 11.3 and an explained variance between 1.8 and 17.2% (Figure S6). We used an ANOVA to evaluate if the allelic effect at the QTL was significantly different for the two light conditions (interaction term in the ANOVA) beyond the overall difference in phenotype caused by the different lights. If the interaction would be significant, the allelic variation at the QTL can be useful for breeding for LED specific conditions. For only two out of those 44 QTL a significant ($p < 0.05$) allele by light interaction was determined i.e., for leaf distance (= internode length) in the population Mm ~ Mo, and for anthocyanin content index in the population A ~K, although the differential impact was not very strong for these two QTL (Table 1).

As an alternative approach, the relative difference in trait value per genotype for the two light environments was calculated, using the expression $(x_{LED} - x_{HPS}) / x_{HPS}$. Subsequently, we used this relative difference in light response in a QTL analysis. No QTL were identified for this response value for the populations A ~K, N ~ K and L~R for the selected traits. For population Mm~Mo the QTL for leaf distance on ch06 was identified again, with a peak LOD score of only 2.78 just above the threshold, confirming the weak LED specific QTL for this trait (Figure S7).

We conclude that we found many QTL in the four populations for the evaluated traits. Usually, these QTL appeared in both light environments, but 44 QTL could be LED specific when looking at the QTL graphs. However, a more robust statistical evaluation of these 44 QTL showed that the allelic effects were not significantly different for the two light conditions, apart from two exceptions. This means that only two small effect QTL were really LED-specific for the young plants.

LED reduced internode length, plant development, and number of fruits per plant, but eventually no yield reduction

For one out of the four RIL populations we also analysed fruit traits, namely for the K ~ N population (Kentucky Beefsteak ~ NunhemsFM001). The reason for selecting this population was that one parent (NunhemsFM001) is a recent variety and its performance represents better modern varieties than old varieties like Moneymaker do. In addition, the parents had similar fruit sizes, i.e. NunhemsFM001 245.48 ± 7.25 g/ fruit and Kentucky Beefsteak 281.95 ± 15.18 g/ fruit under HPS light, which should prevent a very pronounced segregation of fruit size in the RIL population. This is relevant for analysing fruit yield.

We evaluated this fruiting RIL population under LED and HPS supplemental lighting. The population showed significantly ($p = 0.02$) shorter internode lengths under LED compared to HPS supplemental lighting in mature plants, 8% and 18% less trusses respectively in week 17 ($p = 0.002$) and week 25 ($p = 1.0e-10$), 8% and 17% less fruits during these weeks ($p = 0.018$ and $1.2e-05$, respectively), and 15% lower yield of ripe fruits per plant ($p = 5.2e-07$, Figure S8, Suppl. File 3). However, when the unripe fruits at the last harvest day were included, the difference in yield between HPS and LED disappeared, indicating that the plants under LED light were a bit compacter, slower in development, but in the end produced similar yield.

Interestingly, the fraction of dry matter partitioned to the fruits was similar for HPS and LED. Furthermore, the average weight per fruit was 8% higher for LED, which was a significant difference ($p = 0.035$). Apparently, the lower number of fruits per plant under LED was compensated by a somewhat larger fruit size, giving a similar yield eventually.

High correlations between fruit traits

As expected, the number of trusses per plant in week 17 was highly correlated with the number of trusses in week 25, and highly correlated with the number of fruits per plant during these weeks (Figure 6). The weight per fruit was very clearly negatively correlated with number of fruits per plant (Figure 6). There was a weaker positive correlation between the number of fruits and number of trusses at the one hand, and the total fruit yield (in kg per plant) at the other hand. The table also shows that the number of fruits per plant showed a higher correlation with yield than weight per fruit did. Both, number of trusses and weight per fruit, contribute to yield, but apparently, the number of trusses was a more important driver for yield.

Several major QTL for fruit traits under LED and HPS, but no convincing LED specific ones

To identify possible LED-specific QTL for the measured traits, a QTL analysis was performed on data from both lighting systems individually. Significant QTL were found on ch01 and ch11 for the following traits: number of trusses in week 17 and 25, number of fruits in these two weeks, and fresh weight per fruit (Figure 7; Suppl. File 2). These five traits are physiologically closely related, showed therefore a high

correlation (Figure 7), and apparently are under control of the same QTL on ch01 and ch11. These two QTL emerged under both lighting conditions.

For the fruit yield (kg per plant) we found weak QTL on ch11 for HPS, and on ch01 and ch10 for LED (Figure 7, Suppl. File 2). The presence of QTL under LED light, and absence of these QTL under HPS light, may indicate LED-specific QTL. To study this in more detail, we mapped the relative differences for these traits between the two lighting conditions, using the expression $(x_{LED} - x_{HPS}) / x_{HPS}$. However, no light specific QTL were found, neither on ch01, nor on ch11 (Figure 7C). For none of the five traits, LED-specific QTL emerged, showing the absence of a LED-specific QTL for number of trusses, number of fruits, and fresh weight per fruit in the K ~ N population.

Also, for internode length and the dry matter fraction of the fruits we detected QTL with low LOD scores that seemed to be different between the lighting conditions (Figure 7A, B). However, again no QTL for the differential light effect was found (Figure 7C).

We conclude that we were able to detect QTL for the different fruit traits and internode length, but none of these QTL appeared to be significantly specific to one light condition.

Discussion

We showed that there was a large phenotypic range for the evaluated traits of young plants and of fruiting plants, with varying degrees of genetic influences. Especially the architectural traits height and side shoot size showed high levels of heritability. Also other studies in tomato found a high heritability for architectural traits, especially height but also to varying degree for number of primary branches (Mohamed et al. 2012; Shankar et al. 2013; Taiana et al. 2015). For height, side shoot area, and weight of the young plants, QTL were identified in each population though there is a discrepancy between the explained variance by the QTL and the heritability estimate. This so called missing heritability can be explained by e.g. smaller effect QTL or interactions that are not detected by the analysis (Eichler et al. 2010; Yi 2010).

For one RIL population we also studied fruit traits. The number of fruit trusses per plant, number of fruits per plant, and average weight per fruit per plant showed a strong genetic impact with clear QTL on ch01 and ch11. These traits could be linked to the *fruit weight 11.3 (fw11.3)* or *fasciated (fas)* loci, which have been shown to be located at the bottom of ch11 in different tomato cultivars (Huang and van der Knaap 2011). The presence of the loci increase fresh fruit weight, either by increasing mesocarp size (*fw11.3*) and by increasing the locule number of the fruit (*fas*; Lippman and Tanksley 2001; Cong et al. 2008; Mu et al. 2017). The QTL on ch01 might be linked to a locus similar to *fw11.3* or *fas*, possibly the *fruit weight 1.1 (fw1.1)* locus (Lippman and Tanksley 2001; Hernández-Bautista et al. 2015), as the QTL on ch01 has a similar pattern as the QTL on ch11 (Figure 7).

Between the young populations the identified QTL were mainly different, reflecting the diverse genetic background used in this experiment. The parents of the RIL populations were selected according to their

diverse light responses and the QTL identified were therefore largely specific to the respective genotypes. Only the populations with one common parent, Kentucky Beefsteak, showed co-locating QTL (for side shoot area and DW). Overall, this suggests a complex regulation of light responses and a large diversity among the evaluated accessions. The reliability of the series of QTL described in this study was generally high, as for three of the four populations, the effect of three experimental replications was taken into account for the analysis. In addition, the similarity in QTL pattern (Figure 4) between the two light conditions for young plants shows not only the similar genetic control in both light setups but further also the reproducibility of the data, obtained from parallel experiments.

The overall trait ranges and heritabilities were considerably consistent across populations and light conditions. There were a few differences, especially between the populations tested in the first three experiments compared to the population K ~ N that was tested in the fourth experiment. These differences may have resulted from the increased solar light period and higher light intensity during the fourth experiment. Though there was a strong impact of the light spectrum on the overall plant performance, the QTL patterns for most traits were similar between the conditions within one population. Only two QTL out of the 44 LED-specific QTL were found to have a significant interaction with the light environment, which points to a general shift in phenotype in the different light conditions, but all tested genotypes responded in a similar way. Also Wolyn et al. (2004) studied an *A. thaliana* RIL population in five different light qualities for hypocotyl length and out of eight QTL only one QTL, specific for red light, was found to have a significant genotype by environment interaction. So, although the parental accessions of our RIL population were selected based on differences to light responses, the data on the RIL populations gave no strong indication for a differential interaction between the tested tomato genotypes and the two light conditions. The more fluctuating environmental conditions and additional solar light in the greenhouse compared to the climate chamber experiment under which the parents of the RIL population were characterized may account for the difference in environmental response.

Next to the nuclear genome, the organelle genomes in the mitochondria and plastids carry genetic information (Gray 1993) which is passed on via the maternal line to the offspring. The organelle genomes contribute to plant performance and environmental responses, e.g. plastome gene expression can be light regulated (Yen et al. 1997; Lupaşcu et al. 2015; Facella et al. 2016). Although a number of spontaneous chloroplast mutations were described (Massouh et al. 2016), there may be little variation in plastomes of modern tomato cultivars (Kahlau et al. 2006; Raime and Remm 2018). Similar intraspecific studies for the mitochondrial genome of tomato are missing but the mitogenome is less conserved than the plastome and intraspecific variation for different species was shown (Sloan et al. 2012; Kim and Lee 2018). The effects from the reciprocal crosses varied between the populations, and the sizes of these effects were lower compared to the overall genetic trait range. Plastid and mitochondrial specific metabolic processes were found to influence axillary bud break by providing energy as well as metabolites that act in the light induced phytohormonal signalling (Mason et al. 2014; Signorelli et al. 2018). This important role of the organelles in bud outgrowth could explain the differences we observed in side shoot formation between the two sub-groups from reciprocal crosses. Chloroplasts are critical in light perception and photosynthesis, and therefore genetic differences in chloroplasts might lead to

differences in responses to HPS and LED supplemental light. However, we did not observe this in our experiments, as clear interactions between supplemental lighting and reciprocal crosses were not found.

Across all RIL populations, the plants were more compact and had less biomass under LED compared to the standard HPS supplemental lighting in the greenhouse. Specifically, they had shorter internodes, the biomass and leaf area were reduced, while the specific stem height was identical to growth under HPS. Also, the fruiting population showed significant shorter internodes under LED compared to HPS supplemental lighting. HPS lamps emit more far red (FR) light than the LEDs, with a phytochrome stationary state values of 0.852 for HPS vs 0.883 for LED. Low ratios of R/FR light and corresponding lower phytochrome stationary state (PSS) values can lead to plant elongation. Previous studies showed that R/B LED supplemental lighting led to compacter growth compared to HPS and R/B lighting with FR (Hogewoning et al. 2012). Decreasing PSS values from 0.88 to 0.80 increased stem height, leaf area, and total dry weight (Kalaitzoglou et al. 2019). Our data confirm that this is a common trend amongst a wider range of tomato genotypes. The lower PSS values may explain the taller stems and thinner leaves with a larger leaf area under HPS-supplemental lighting in our study.

Higher levels of green light or lower blue to green ratios were implicated in e.g. shade avoidance (Zhang et al. 2011; Fraser et al. 2016) that also lead to hypocotyl and maybe (early) stem elongation (Folta 2004; Sellaro et al. 2010). Therefore, the green light in the HPS lamps (ca. 50%) may also play a role in the morphological differences compared to LED light. Another factor that could affect the plant growth was that the HPS emit radiative heat, the broad range HPS radiation has more infrared light and may lead to a higher meristem temperature at the top of the plants. This could favour leaf initiation and outgrowth. We have seen a slightly higher leaf number under HPS light, which could be a meristem temperature effect (Savvides et al. 2016).

Most striking for the young plants were the sizes of the side shoots compared to the true leaves, both regarding high heritability and difference between the light conditions. When looking at side shoot formation we should subdivide into axillary bud outgrowth that breaks its quiescence, and consecutive side shoot development. The first could be indicated in our study by the number of side shoots and the second by the overall size and dry weight of these side shoots. The number of axillary buds was less affected than the size of the side shoots by the different supplemental lighting conditions.

Tucker (1976) proposed that far red triggers abscisic acid formation near the auxiliary bud and thereby inhibits its outgrowth. He showed that a pulse of far red light stunts side shoot formation in young tomato plants. Generally, a low R/ FR ratio can favour apical growth instead of side shoot growth (Girault et al. 2008; Evers et al. 2011; Dierck et al. 2017). The R/ FR ratio is higher in the LED-compartment, so we would expect more side shoots there than under HPS supplemental lighting. These assumptions conflict with our experimental outcome of less and smaller side shoots in LED light. Blue light was also found to impact axillary bud outgrowth but the effect seems to vary between species and genotypes (Leduc et al. 2014; Huché-Thélier et al. 2016). However, the percentage of supplemental blue light is similar between our two conditions (ca. 5% in both). Therefore, also other light quality differences seem to impact side

shoot outgrowth. In our experiments, this could be a lower blue/red ratio (0.03 in compared to 0.12) or the lack of green light in LED supplemental lighting.

The significantly elevated levels of anthocyanin content in the plants grown under LED light compared to HPS light could indicate stress (Chalker-Scott 1999; Kovic et al. 2015). It is not easy to determine if a plant is in an optimal growing condition or stressed state. The reduction of Δ_{PSII} is a possible stress indicator. In three of the four populations Δ_{PSII} was indeed lower in LED than HPS grown plants, however the difference was minor and the Δ_{PSII} was with an average of 0.7 (over all populations and experiments) still at a healthy level. In addition, the plants grew otherwise visually normally. Studies in *Arabidopsis* showed phytochrome induced upregulation of anthocyanin inducing genes with increasing red light (Shin et al. 2007; Liu et al. 2015). Red light was overrepresented in LED compared to HPS supplemental lighting, activating more phytochrome which in turn could activate transcription factors, like PIF3 and HY5 (Shin et al. 2007), that upregulate anthocyanin biosynthesis genes.

The adult plants showed on average less fruit trusses, less fruits, and lower yield of ripe fruits per plant under LED compared to HPS (Suppl. File 3). However, when the unripe fruits at the last harvest day were included, there was no significant yield difference between HPS and LED. The average weight per fruit was a bit higher under LED, probably compensating the lower number of fruits per plant. We conclude that the plants under LED light were compacter, slower in development, but in the end produced similar yield compared to plants under HPS supplemental lighting.

Conclusions

The primary aim of this study was discovery of LED-specific QTL for growth related traits and fruit yield. That could help plant breeders when developing modern cultivars that are optimal for greenhouses with supplemental LED-lighting, and developing other cultivars that are optimal for HPS supplemental light. Therefore, we developed four RIL populations, that were derived from parents that showed contrasting phenotypes under different light environments. We observed numerous QTL, both at HPS and LED supplemental lighting, at the seedling stage and at the fruiting stage. However, we detected hardly any light environment-specific QTL. Therefore, our study indicates that breeding for optimal tomato cultivars for greenhouses with supplemental HPS simultaneously leads to optimal cultivars for supplemental LED lighting. And the other way around, cultivars that perform well under LED, very likely also perform well under HPS.

Moreover, we made reciprocal crosses for the four RIL populations, in view of possible effects of the maternally inherited plastids, such as chloroplasts, and the mitochondria, which are critical for photosynthesis and energy regulation. Again, we found very clear and significant effects from the maternally inherited plastids and mitochondria, showing the importance of using a parent either as mother or as a father. However, these differences did not interact significantly with the light environment. So, similarly as for the genetic factors from the nuclei (the QTL), the genetic factors from the maternally inherited plastids and mitochondria, are of paramount importance for plant architecture and fruit traits,

but these genetic factors did not show a specific interaction with either supplemental HPS or supplemental LED light.

Therefore, our data do not support tomato breeding for specific light environments in greenhouses, as far as supplemental 95% red and 5% blue LED light is concerned.

Declarations

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Conflicts of interest

The authors declare that there is no conflict of interest.

Availability of data and material

The allelic marker scores and raw data are provided in the supplemental material.

Code availability

The R scripts are added to the supplemental material

Authors' contributions

A. E. P. planned the RIL experiments, and conducted and analysed the young plant experiments; H. v. d. S. helped with the planning of all the RIL experiments and the measurements; O. D. and S. G. conducted and analysed the experiment with adult plants; T. O. planned, conducted and analysed the initial experiment on the parents of the RILs; F. M.-D. made the F1 hybrids for the RILs; L. F. M. M. , R. G. F. V., E. H. and H. J. S. initiated the project and contributed with discussions. All authors contributed to varying degrees in the writing of the manuscript.

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References

1. Arena C, Tsonev T, Doneva D, et al (2016) The effect of light quality on growth, photosynthesis, leaf anatomy and volatile isoprenoids of a monoterpene-emitting herbaceous species (*Solanum lycopersicum* L.) and an isoprene-emitting tree (*Platanus orientalis* L.). *Environ Exp Bot* 130:122–132. <https://doi.org/10.1016/j.envexpbot.2016.05.014>
2. Bantis F, Smirnakou S, Ouzounis T, et al (2018) Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs). *Sci Hortic* 235:437–451. <https://doi.org/10.1016/j.scienta.2018.02.058>
3. Bourke P, Hackett C, Maliepaard C, et al (2021) polyqtlR: QTL Analysis in Autopolyploid Bi-Parental F1 Populations. Version 0.0.6 URL <https://CRAN.R-project.org/package=polyqtlR>
4. Britton CM, Dodd JD (1976) Relationships of photosynthetically active radiation and shortwave irradiance. *Agric Meteorol* 17:1–7. [https://doi.org/10.1016/0002-1571\(76\)90080-7](https://doi.org/10.1016/0002-1571(76)90080-7)
5. Broman K, Sen S (2009) *A Guide to QTL Mapping with R/qtl*. Springer-Verlag, New York
6. Broman KW, Wu H, Sen S, Churchill GA (2003) R/qtl: QTL mapping in experimental crosses. *Bioinformatics* 19:889–890. <https://doi.org/10.1093/bioinformatics/btg112>
7. Cao K, Cui L, Zhou X, et al (2015) Four Tomato FLOWERING LOCUS T-Like Proteins Act Antagonistically to Regulate Floral Initiation. *Front Plant Sci* 6:1213. <https://doi.org/10.3389/fpls.2015.01213>
8. Carvalho SD, Folta KM (2014) Sequential light programs shape kale (*Brassica napus*) sprout appearance and alter metabolic and nutrient content. *Hortic Res* 1:8. <https://doi.org/10.1038/hortres.2014.8>
9. Chalker-Scott L (1999) Environmental significance of anthocyanins in plant stress responses. *Photochem Photobiol* 70:1–9
10. Cong B, Barrero LS, Tanksley SD (2008) Regulatory change in YABBY-like transcription factor led to evolution of extreme fruit size during tomato domestication. *Nat Genet* 40:800–804.

<https://doi.org/10.1038/ng.144>

11. Costigan SE, Warnasooriya SN, Humphries BA, Montgomery BL (2011) Root-Localized Phytochrome Chromophore Synthesis Is Required for Photoregulation of Root Elongation and Impacts Root Sensitivity to Jasmonic Acid in *Arabidopsis*1[W][OA]. *Plant Physiol* 157:1138–1150. <https://doi.org/10.1104/pp.111.184689>
12. Couée I, Sulmon C, Gouesbet G, El Amrani A (2006) Involvement of soluble sugars in reactive oxygen species balance and responses to oxidative stress in plants. *J Exp Bot* 57:449–459. <https://doi.org/10.1093/jxb/erj027>
13. De Mendiburu F (2020) Statistical Procedures for Agricultural Research. Version R package version 1.3-3. URL <https://CRAN.R-project.org/package=agricolae>
14. de Oliveira Silva FM, Lichtenstein G, Alseekh S, et al (2018) The genetic architecture of photosynthesis and plant growth-related traits in tomato. *Plant Cell Environ* 41:327–341. <https://doi.org/10.1111/pce.13084>
15. Dierck R, Dhooche E, Van Huylenbroeck J, et al (2017) Light quality regulates plant architecture in different genotypes of *Chrysanthemum morifolium* Ramat. *Sci Hortic* 218:177–186. <https://doi.org/10.1016/j.scienta.2017.02.016>
16. Eichler EE, Flint J, Gibson G, et al (2010) Missing heritability and strategies for finding the underlying causes of complex disease. *Nat Rev Genet* 11:446–450. <https://doi.org/10.1038/nrg2809>
17. Evers JB, Krol AR van der, Vos J, Struik PC (2011) Understanding shoot branching by modelling form and function. *Trends Plant Sci* 16:464–467. <https://doi.org/10.1016/j.tplants.2011.05.004>
18. Facella P, Carbone F, Placido A, Perrotta G (2016) Cryptochrome 2 extensively regulates transcription of the chloroplast genome in tomato. *FEBS Open Bio* 7:456–471. <https://doi.org/10.1002/2211-5463.12082>
19. Folta KM (2004) Green light stimulates early stem elongation, antagonizing light-mediated growth inhibition. *Plant Physiol* 135:1407–1416. <https://doi.org/10.1104/pp.104.038893>
20. Fox J, Weisberg S (2019) An R companion to applied regression, third edition. SAGE Publications, Inc, Thousand Oaks, USA (CA)
21. Fraser DP, Hayes S, Franklin KA (2016) Photoreceptor crosstalk in shade avoidance. *Curr Opin Plant Biol* 33:1–7. <https://doi.org/10.1016/j.pbi.2016.03.008>
22. Fulop D, Ranjan A, Ofner I, et al (2016) A New Advanced Backcross Tomato Population Enables High Resolution Leaf QTL Mapping and Gene Identification. *G3 Genes Genomes Genet* 6:3169–3184. <https://doi.org/10.1534/g3.116.030536>
23. Girault T, Bergougnoux V, Combes D, et al (2008) Light controls shoot meristem organogenic activity and leaf primordia growth during bud burst in *Rosa* sp. *Plant Cell Environ* 31:1534–1544. <https://doi.org/10.1111/j.1365-3040.2008.01856.x>
24. Gómez C, Mitchell CA (2015) Growth Responses of Tomato Seedlings to Different Spectra of Supplemental Lighting. *HortScience* 50:112–118. <https://doi.org/10.21273/HORTSCI.50.1.112>

25. Gray MW (1993) Origin and evolution of organelle genomes. *Curr Opin Genet Dev* 3:884–890. [https://doi.org/10.1016/0959-437X\(93\)90009-E](https://doi.org/10.1016/0959-437X(93)90009-E)
26. Hernández-Bautista A, Lobato-Ortiz R, Cruz-Izquierdo S, et al (2015) Fruit size QTLs affect in a major proportion the yield in tomato. *Chil J Agric Res* 75:402–409. <https://doi.org/10.4067/S0718-58392015000500004>
27. Hogewoning SW, Trouwborst G, Meinen E, van Ieperen W (2012) Finding the optimal growth-light spectrum for greenhouse crops. *Acta Hort* 956:357–363. <https://doi.org/10.17660/ActaHortic.2012.956.41>
28. Huang Z, van der Knaap E (2011) Tomato fruit weight 11.3 maps close to fasciated on the bottom of chromosome 11. *TAG Theor Appl Genet Theor Angew Genet* 123:465–474. <https://doi.org/10.1007/s00122-011-1599-3>
29. Huché-Théliet L, Crespel L, Gourrierc JL, et al (2016) Light signaling and plant responses to blue and UV radiations—Perspectives for applications in horticulture. *Environ Exp Bot* 121:22–38. <https://doi.org/10.1016/j.envexpbot.2015.06.009>
30. Ji Y, Ouzounis T, Schouten HJ, et al (2020) Dissecting the Genotypic Variation of Growth Responses to Far-Red Radiation in Tomato. *Front Plant Sci* 11:614714. <https://doi.org/10.3389/fpls.2020.614714>
31. Kahlau S, Aspinall S, Gray JC, Bock R (2006) Sequence of the Tomato Chloroplast DNA and Evolutionary Comparison of Solanaceous Plastid Genomes. *J Mol Evol* 63:194–207. <https://doi.org/10.1007/s00239-005-0254-5>
32. Kaiser E, Ouzounis T, Giday H, et al (2019) Adding Blue to Red Supplemental Light Increases Biomass and Yield of Greenhouse-Grown Tomatoes, but Only to an Optimum. *Front Plant Sci* 9:2002. <https://doi.org/10.3389/fpls.2018.02002>
33. Kalaitzoglou P, van Ieperen W, Harbinson J, et al (2019) Effects of Continuous or End-of-Day Far-Red Light on Tomato Plant Growth, Morphology, Light Absorption, and Fruit Production. *Front Plant Sci* 10:322. <https://doi.org/10.3389/fpls.2019.00322>
34. Kim HT, Lee JM (2018) Organellar genome analysis reveals endosymbiotic gene transfers in tomato. *PLOS ONE* 13:e0202279. <https://doi.org/10.1371/journal.pone.0202279>
35. Kovinich N, Kayanja G, Chanoca A, et al (2015) Abiotic stresses induce different localizations of anthocyanins in *Arabidopsis*. *Plant Signal Behav* 10:e1027850(1-4). <https://doi.org/10.1080/15592324.2015.1027850>
36. Lanoue J, Leonardos ED, Ma X, Grodzinski B (2017) The Effect of Spectral Quality on Daily Patterns of Gas Exchange, Biomass Gain, and Water-Use-Efficiency in Tomatoes and *Lisianthus*: An Assessment of Whole Plant Measurements. *Front Plant Sci* 8:1076. <https://doi.org/10.3389/fpls.2017.01076>
37. Leduc N, Roman H, Barbier F, et al (2014) Light Signaling in Bud Outgrowth and Branching in Plants. *Plants* 3:223–250. <https://doi.org/10.3390/plants3020223>

38. Lippman Z, Tanksley SD (2001) Dissecting the genetic pathway to extreme fruit size in tomato using a cross between the small-fruited wild species *Lycopersicon pimpinellifolium* and *L. esculentum* var. Giant Heirloom. *Genetics* 158:413–422
39. Liu Z, Zhang Y, Wang J, et al (2015) Phytochrome-interacting factors PIF4 and PIF5 negatively regulate anthocyanin biosynthesis under red light in *Arabidopsis* seedlings. *Plant Sci* 238:64–72. <https://doi.org/10.1016/j.plantsci.2015.06.001>
40. Lupașcu G, Grigorcea S, Mihnea N (2015) The influence of the maternal factor on the effects of gene involved in the control of quantitative characters in tomato. *Olten Stud Si Comun Stiintele Nat* 25:43–46
41. Mason MG, Ross JJ, Babst BA, et al (2014) Sugar demand, not auxin, is the initial regulator of apical dominance. *Proc Natl Acad Sci U S A* 111:6092–6097. <https://doi.org/10.1073/pnas.1322045111>
42. Massouh A, Schubert J, Yaneva-Roder L, et al (2016) Spontaneous Chloroplast Mutants Mostly Occur by Replication Slippage and Show a Biased Pattern in the Plastome of *Oenothera*. *Plant Cell* 28:911–929. <https://doi.org/10.1105/tpc.15.00879>
43. McCree KJ (1972) The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. *Agric Meteorol* 9:191–216. [https://doi.org/10.1016/0002-1571\(71\)90022-7](https://doi.org/10.1016/0002-1571(71)90022-7)
44. Mohamed SM, Ali EE, Mohamed TY (2012) Study Of Heritability And Genetic Variability Among Different Plant And Fruit Characters Of Tomato (*Solanum Lycopersicum* L.). *Int J Sci Technol Res* 1:55–58
45. Mu Q, Huang Z, Chakrabarti M, et al (2017) Fruit weight is controlled by Cell Size Regulator encoding a novel protein that is expressed in maturing tomato fruits. *PLOS Genet* 13:e1006930. <https://doi.org/10.1371/journal.pgen.1006930>
46. Nakano H, Sasaki K, Mine Y, et al (2016) Quantitative trait loci (QTL) controlling plant architecture traits in a *Solanum lycopersicum* × *S. pimpinellifolium* cross. *Euphytica Dordr* 211:353–367. <http://dx.doi.org/10.1007/s10681-016-1744-9>
47. Ouzounis T, Heuvelink E, Ji Y, et al (2016) Blue and red LED lighting effects on plant biomass, stomatal conductance, and metabolite content in nine tomato genotypes. *Acta Hort* 251–258. <https://doi.org/10.17660/ActaHortic.2016.1134.34>
48. Oyanedel E, Wolfe DW, Owens TG, et al (2000) Quantitative trait loci analysis of photoinhibition under chilling stress in tomato. *Acta Hort* 521:227–232. <https://doi.org/10.17660/ActaHortic.2000.521.25>
49. Paradiso R, Meinen E, Snel JFH, et al (2011) Spectral dependence of photosynthesis and light absorptance in single leaves and canopy in rose. *Sci Hort* 127:548–554. <https://doi.org/10.1016/j.scienta.2010.11.017>
50. Raime K, Remm M (2018) Method for the Identification of Taxon-Specific k-mers from Chloroplast Genome: A Case Study on Tomato Plant (*Solanum lycopersicum*). *Front Plant Sci* 9:6. <https://doi.org/10.3389/fpls.2018.00006>

51. Rao AQ, Bakhsh A, Nasir IA, et al (2011) Phytochrome B mRNA expression enhances biomass yield and physiology of cotton plants. *Afr J Biotechnol* 10:1818–1826
52. Revelle W (2018) psych: Procedures for Personality and Psychological Research, Northwestern University, Evanston, Illinois, USA. <https://CRAN.R-project.org/package=psych>
53. Sager JC, Smith WO, Edwards JL, Cyr KL (1988) Photosynthetic Efficiency and Phytochrome Photoequilibria Determination Using Spectral Data. *Trans ASAE* 31:1882–1889. <https://doi.org/10.13031/2013.30952>
54. Savvides A, Dieleman JA, Ieperen W van, Marcelis LFM (2016) A unique approach to demonstrating that apical bud temperature specifically determines leaf initiation rate in the dicot *Cucumis sativus*. *Planta* 243:1071. <https://doi.org/10.1007/s00425-015-2464-4>
55. Sellaro R, Crepy M, Trupkin SA, et al (2010) Cryptochrome as a sensor of the blue/green ratio of natural radiation in *Arabidopsis*. *Plant Physiol* 154:401–409. <https://doi.org/10.1104/pp.110.160820>
56. Sen S, Churchill GA (2001) A statistical framework for quantitative trait mapping. *Genetics* 159:371–387
57. Shankar A, Reddy RVSK, Sujatha M, Pratap M (2013) Genetic Variability Studies in F1 Generation of Tomato (*Solanum lycopersicon* L.). *IOSR J Agric Vet Sci* 4:31–34. <https://doi.org/10.9790/2380-0453134>
58. Shin J, Park E, Choi G (2007) PIF3 regulates anthocyanin biosynthesis in an HY5-dependent manner with both factors directly binding anthocyanin biosynthetic gene promoters in *Arabidopsis*. *Plant J Cell Mol Biol* 49:981–994. <https://doi.org/10.1111/j.1365-313X.2006.03021.x>
59. Signorelli S, Agudelo-Romero P, Meitha K, et al (2018) Roles for Light, Energy, and Oxygen in the Fate of Quiescent Axillary Buds. *Plant Physiol* 176:1171–1181. <https://doi.org/10.1104/pp.17.01479>
60. Sloan DB, Müller K, McCauley DE, et al (2012) Intraspecific variation in mitochondrial genome sequence, structure, and gene content in *Silene vulgaris*, an angiosperm with pervasive cytoplasmic male sterility. *New Phytol* 196:1228–1239. <https://doi.org/10.1111/j.1469-8137.2012.04340.x>
61. Smeekens S, Ma J, Hanson J, Rolland F (2010) Sugar signals and molecular networks controlling plant growth. *Curr Opin Plant Biol* 13:274–279. <https://doi.org/10.1016/j.pbi.2009.12.002>
62. Strasser B, Sánchez-Lamas M, Yanovsky MJ, et al (2010) *Arabidopsis thaliana* life without phytochromes. *Proc Natl Acad Sci* 107:4776–4781. <https://doi.org/10.1073/pnas.0910446107>
63. Taiana T, Rashid M, Parveen S, et al (2015) Selection strategies to choose better parents in tomato using genetic parameters. *Plant Knowl J* 4:33–39
64. Tucker DJ (1976) Effects of Far-red Light on the Hormonal Control of Side Shoot Growth in the Tomato. *Ann Bot* 40:1033–1042. <https://doi.org/10.1093/oxfordjournals.aob.a085211>
65. Velez-Ramirez AI, van Ieperen W, Vreugdenhil D, et al (2014) A single locus confers tolerance to continuous light and allows substantial yield increase in tomato. *Nat Commun* 5:4549. <https://doi.org/10.1038/ncomms5549>

66. Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer Publishing, New York
67. Williams KA, Miller CT, Craver JK (2016) Light quality effects on intumescence (oedema) on plant leaves. In: Kozai T, Fujiwara K, Runkle ES (eds) LED Lighting for Urban Agriculture. Springer, Singapore, pp 275–286
68. Wolyn DJ, Borevitz JO, Loudet O, et al (2004) Light-Response Quantitative Trait Loci Identified with Composite Interval and eXtreme Array Mapping in *Arabidopsis thaliana*. *Genetics* 167:907–917. <https://doi.org/10.1534/genetics.103.024810>
69. Yen HC, Shelton BA, Howard L, et al (1997) The tomato high-pigment (hp) locus maps to chromosome 2 and influences plastome copy number and fruit quality. *Theor Appl Genet* 95:1069–1079. <https://doi.org/10.1007/s001220050664>
70. Yi N (2010) Statistical analysis of genetic interactions. *Genet Res* 92:443–459. <https://doi.org/10.1017/S0016672310000595>
71. Zhang T, Maruhnich SA, Folta KM (2011) Green light induces shade avoidance symptoms. *Plant Physiol* 157:1528–1536. <https://doi.org/10.1104/pp.111.180661>

Tables

Table 1. Allelic effect size and position of the two LED specific QTL with significant interaction between allelic variation and light condition. Two LED-specific QTL were identified for the growth of young plants of which the allelic variation at the QTL peak marker had a significant interaction with the light environment in an ANOVA model. Those two QTL were for anthocyanin content index and leaf distance (which is internode length). The effect per allele call, Ailsa Craig (A), Kentucky Beefsteak (K), Moneymaker (Mm) or Momotaro (Mo) is shown as mean phenotypic value with letters indicating significant different groups at an alpha of 0.05 honest significant difference test. For each QTL the flanking marker (approximate 99% Bayes credible interval) and physical interval is given.

Population	A ~ K	Mm ~ Mo
Trait	Anthocyanin content index	Leaf distance (cm)
Chromosome	9	6
Flanking marker	mT03241773 - mT03245229	SL06_09 - SL06_08
Physical interval (SL2.5; Mbp)	Ch09: 66.037-70.953	Ch06: 0.753 - 33.012
P-value of interaction term allele x light	0.04	0.02
Mean phenotype in HPS of allele: A or Mm	0.020 c	2.59 ab
Mean phenotype in HPS of allele: K or Mo	0.023 c	2.72 a
Mean phenotype in LED of allele: A or Mm	0.027 b	2.08 c
Mean phenotype in LED of allele: K or Mo	0.035 a	2.38 b

Figures

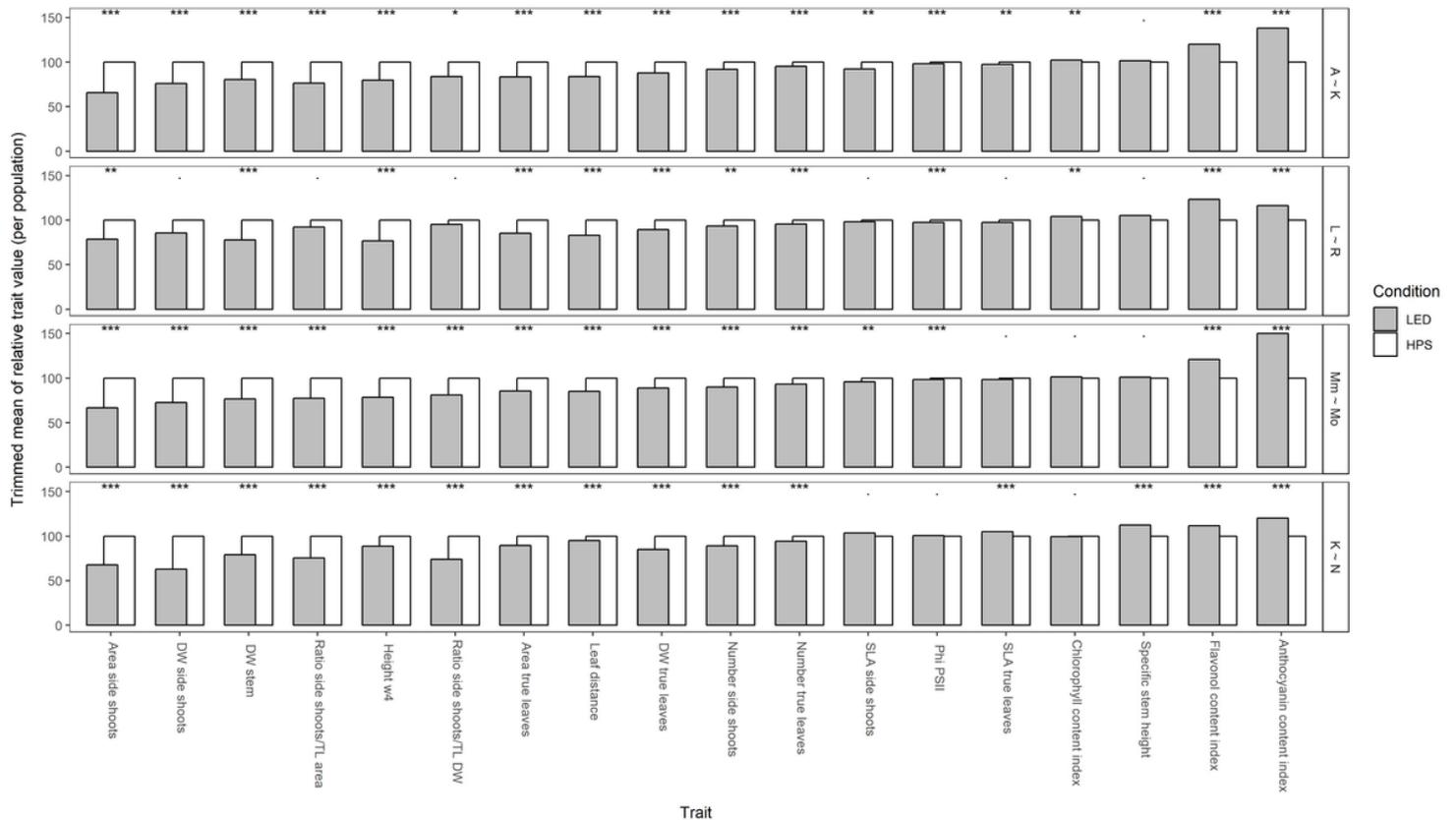


Figure 1

Relative trait values for seedlings of the four RIL populations under LED compared to HPS supplemental light. The four RIL populations were derived from the following crosses: Ailsa Craig and Kentucky Beefsteak abbreviated as “A ~ K”; LA1578 (*S. pimpinellifolium*) and Rutgers “L ~ R”; Moneymaker and Momotaro “Mm ~ Mo”; and Kentucky Beefsteak and NunhemsFM001 “K ~ N”. Each RIL was phenotyped in three replicates under LED and HPS. The values of all experiments were taken together and per population a trimmed mean was determined. The relative trait values express the trimmed mean under LED light compared to HPS-supplemental lighting with the latter representing 100% of trait value. A Wilcoxon rank sum test on the untransformed, individual plant-data was used to determine if there was a significant effect of the light treatments (* p-value<0.05; ** p-value<0.01; *** p-value<0.001). The area and dry weight (DW) of true leaves and side shoots are presented as well as the ratio of those traits between side shoots and true leaves (TL). The leaf distance approximates the internode length and was calculated as stem length divided by the number of true leaves. The specific leaf area (SLA) is the ratio of leaf area to dry weight of the leaves, and the specific stem height is the ratio of the stem length to stem dry weight. “Phi PSII” is the operational quantum yield of electron transport by photosystem II (ΦPSII). The destructive measures for weight, area and leaf number were determined five weeks after sowing in experiment one and four weeks after sowing in experiment two and three; as the resulting trait values are not comparable across the experiments, only the data from the second and third experiment was used for the averages of

the populations A ~ K, L ~ R and Mm ~ Mo. The stem length of the plants was determined in all experiments four weeks after transplanting (Height w4).

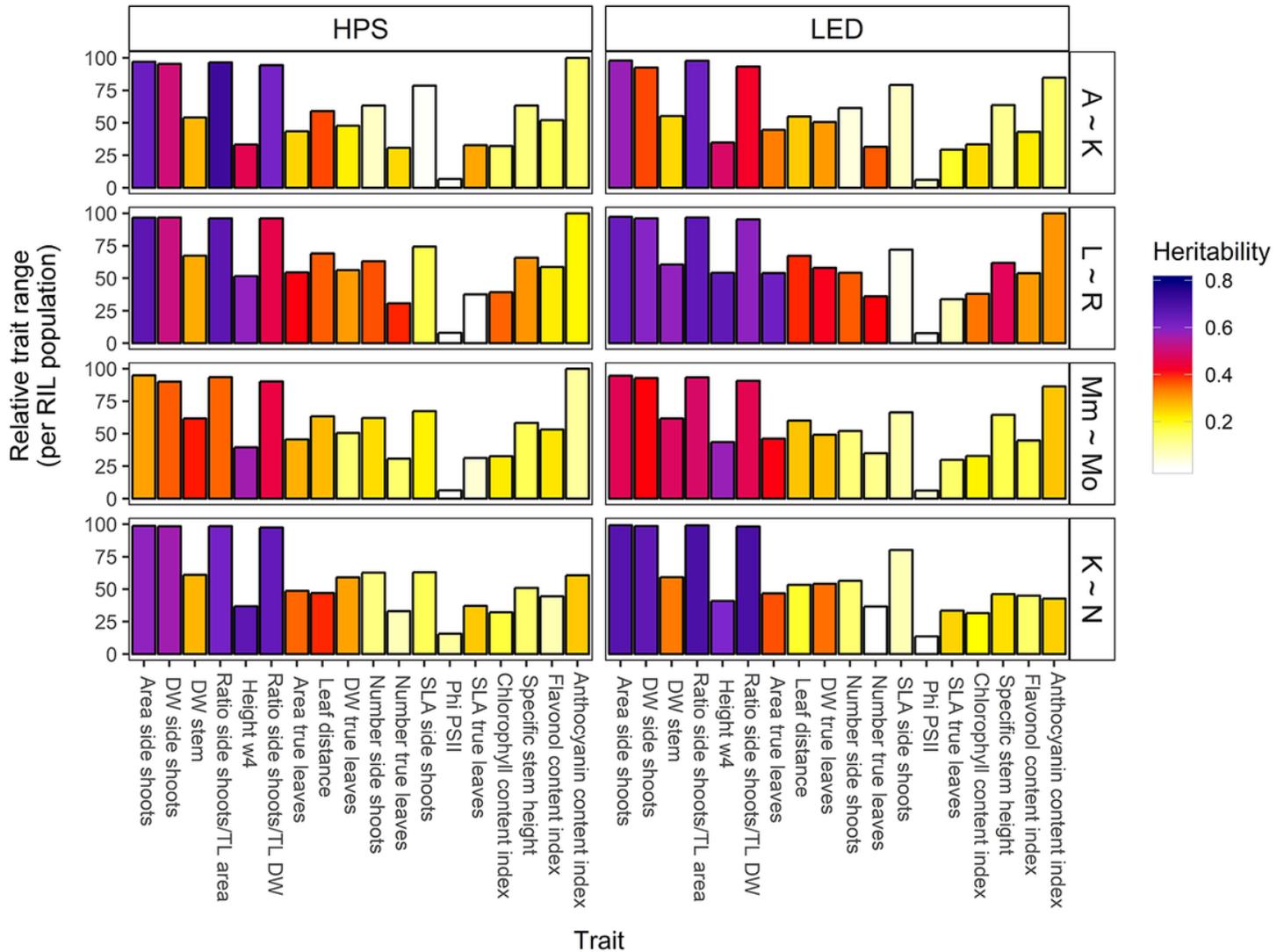


Figure 2

Relative trait range and heritability of different tomato populations. The coloured bars indicate the relative trait range between all genotypes within a population, calculated from the trimmed top and bottom 10% of all the plants in the population, indicating the percental difference between the lowest trait values compared to the highest. An estimate of broad sense heritability is shown as a colour gradient for each trait, population and light condition. The traits are sorted by their responsiveness to supplemental lighting quality.

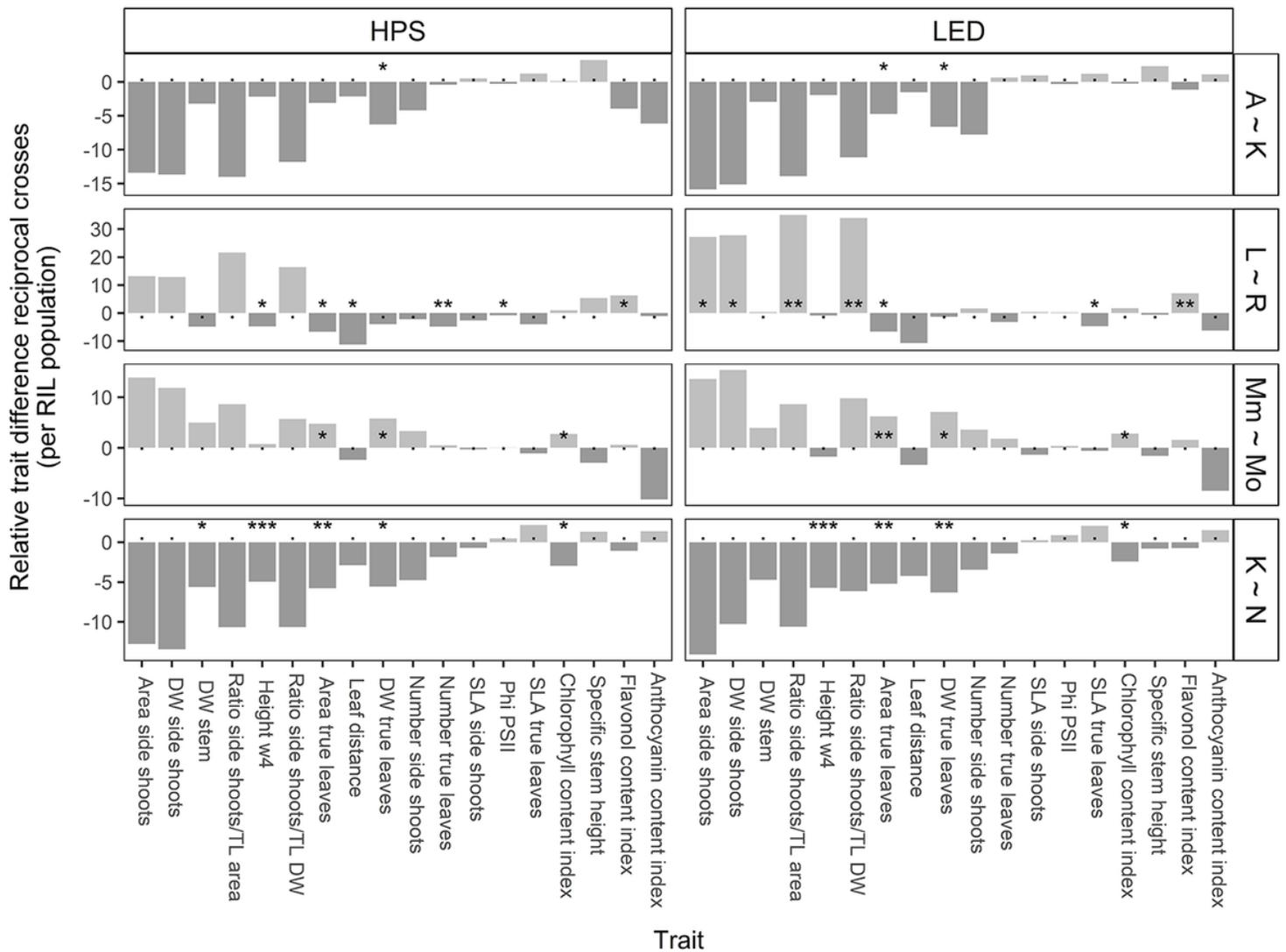


Figure 3

Effects of maternally inherited plastids and mitochondria in the different tomato populations. For each combination of parents, two sub populations were derived, swapping the father and mother of the crossing. We refer to this as reciprocal crosses. The bars represent the trimmed mean difference between these subgroups of each RIL population. In the case that the bars are displayed as positive effect (light grey color), the sub-populations A x K, L x R, Mm (Moneymaker) x Mo (Momotaro) and K x N had the higher trait value (the parent that is named first in the crosses is the maternal line). Bars with negative effect value (dark grey) represent that the other maternally inherited plastids (sub-populations K x A, R x L, Mo x Mm and N x K) gave the higher trait value. Significances of differences between the subgroups are indicated as follows: "." means no significant difference; * means p-value < 0.05, ** p-value < 0.01, and *** p-value < 0.001). The traits are sorted by their responsiveness to supplemental lighting quality, and are divided by the supplemental lighting conditions, HPS or R/ B LED light.

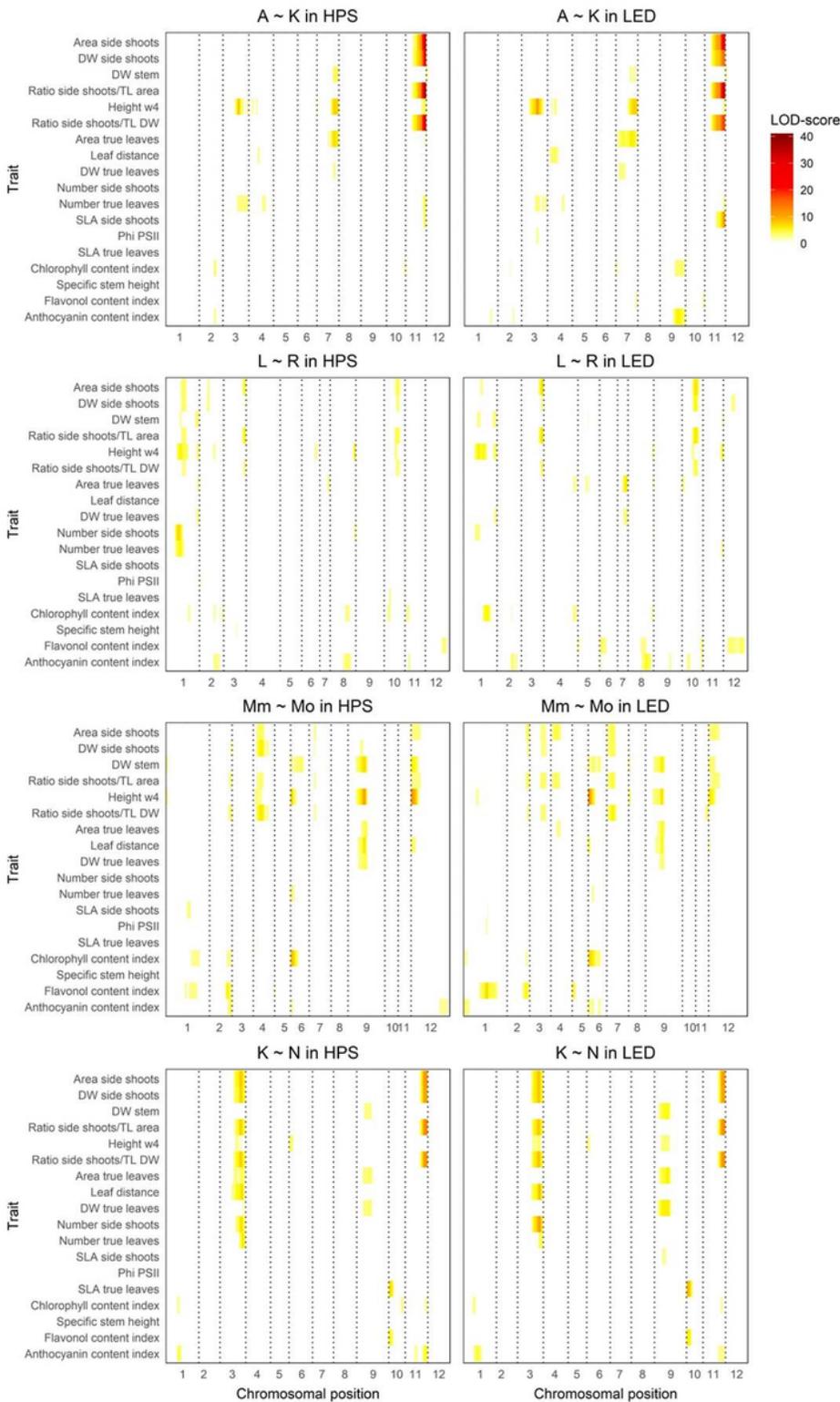


Figure 4

QTL pattern for the four different tomato RIL populations. The heatmaps show per population (from top to bottom) and condition, HPS (left) and LED (right), the LOD of QTL from a single QTL analysis. Only LOD scores above the trait specific LOD threshold are depicted. The x-axis of each heatmap shows the genetic maps of the respective RIL population and the chromosomes (1 to 12, written from left to right)

are separated by vertical, dotted lines. The traits are on the y-axis in the same order as the previous graphs. Detailed LOD values and intervals are provided in Suppl. File 2.

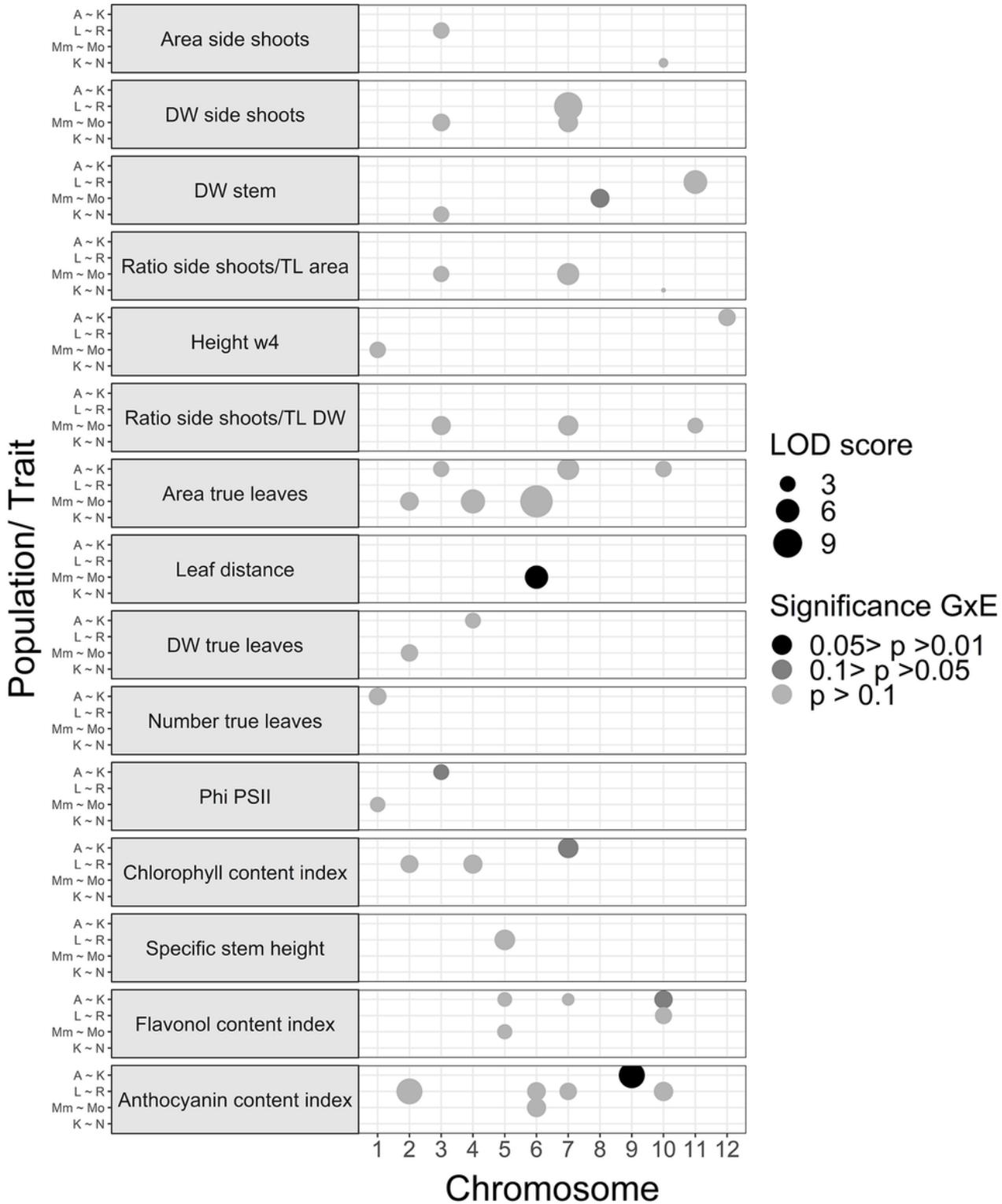


Figure 5

QTL that were only identified under LED light The QTL that were only identified under LED conditions are presented as circles. The sizes represent the LOD scores. The colour of the circles indicates the significance of the allele by light-condition interaction of the peak marker of those QTL between HPS and

LED light, determined by an ANOVA analysis. Detailed LOD values and intervals are provided in Suppl. File 2.

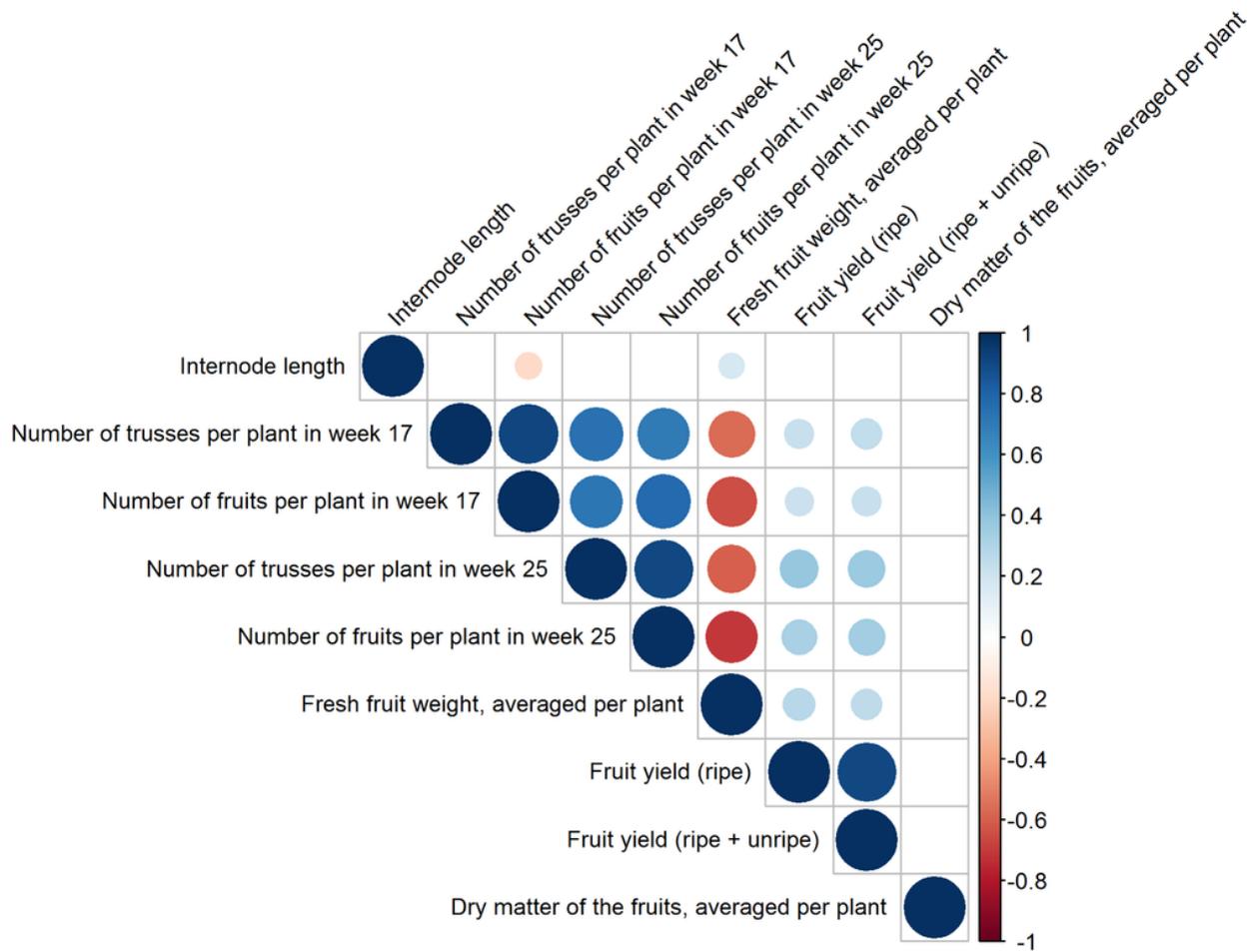


Figure 6

Correlations of traits of adult plants of the N ~ K RIL population.

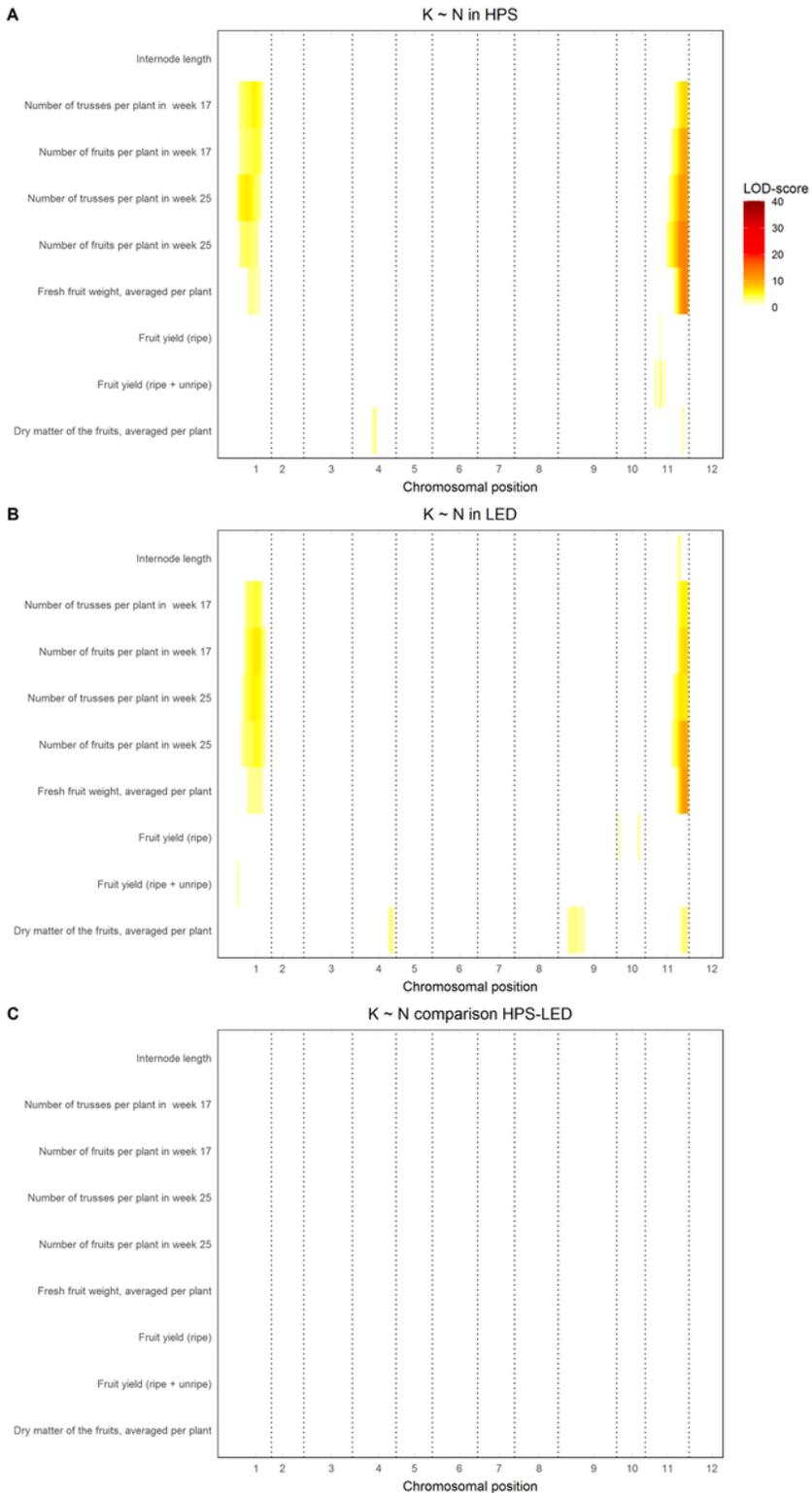


Figure 7

QTL analysis of adult plants of the N ~ K population in a greenhouse with A) HPS supplemental lighting; B) LED supplemental lighting. Only significant LOD scores are shown. At the horizontal axis, positions of the 177 markers on tomato chromosomes 1 to 12 are shown. C) QTL analyses of the relative differences in trait values under LED compared to HPS. No significant QTL appeared here.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementalmaterial.docx](#)
- [SupplFile1Rawdataallpopulations.xlsx](#)
- [SupplFile2LODscores.xlsx](#)
- [SupplFile3Fruittraits.xlsx](#)