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Factors Affecting Tolerance to Low Night Temperature Differ by Fruit Types in Tomato

Eun-Young Yang [1,†], Sherzod Nigmatullayevich Rajametov [1,†], Myeong-Cheoul Cho [1], Hyo-Bong Jeong [1] and Won-Byoung Chae [2,*]

[1] Vegetable Research Division, Department of Horticultural Crop Research, National Institute of Horticultural & Herbal Science, Rural Development Administration, Wanju 55365, Korea; yangyang2@korea.kr (E.-Y.Y.); sherzod_2004@list.ru (S.N.R.); chomc@korea.kr (M.-C.C.); bong9846@korea.kr (H.-B.J.)

[2] Department of Environmental Horticulture, Dankook University, Cheonan 31116, Korea

* Correspondence: wbchae75@dankook.ac.kr; Tel.: +82-41-550-3642

† Equal contribution.

Abstract: Tolerance to low night temperature (LNT) can be a practical and economical target in tomato breeding programs for energy saving in greenhouses. This study was conducted to investigate the physiological and biochemical responses to LNT using four tomato accessions with cherry or large fruit types having LNT tolerance or sensitivity. The accessions were grown in two polyethylene film greenhouses with night temperature set-points of 10 and 15 °C for heating. LNT significantly reduced the plant height, and photosynthetic parameters were also lower in 10 than 15 °C among all accessions. Photosynthetic rate in 10 °C during the early growth period was reduced more in LNT-tolerant than -sensitive accessions. The numbers of flowers in 10 °C were significantly reduced in cherry but not in large fruit types. Fruit set in 10 °C significantly decreased in LNT-sensitive accessions of both fruit types, which was due to abnormal flower morphology. Proline accumulation patterns between 10 and 15 °C significantly differed between cherry and large fruit types as well as between LNT-tolerant and -sensitive accessions. Chlorophyll content at later growth stages in 10 °C was significantly higher in LNT-tolerant than -sensitive accessions in both fruit types. These results suggest that different tomato fruit types may have different mechanisms for LNT tolerance, possibly due to different proline accumulation patterns between cherry and large fruit types.

Keywords: tomato; low night temperature; flower; fruit; chlorophyll content; electrolyte conductivity; proline; photosynthesis

1. Introduction

Abiotic stress significantly affects the vegetative and reproductive growth of plants and, eventually, their survival. Abiotic stresses such as low or high temperature, drought and salinity due to unexpected environmental changes can cause almost 50% losses in the yield of major crops [1]. Especially, low temperature is one of the critical factors affecting crop yield, by influencing various growth and development stages. Low temperature is also the main factor that limits the geographical distribution of crops, particularly those which originated from the tropical zone and are widely cultivated in the temperate zone.

In tomato, low temperature significantly reduces growth rate [2–5], days to flowers [6–8], the number of flowers [6,8–10] and fruit set [8,10–12], all of which affect fruit yield. Tomato plants suffer from chilling injury when they are exposed to temperatures ranging from 0 to 15 °C in all growth stages [13–17]. Biochemical and physiological responses such as electrolyte leakage [4,18–20], proline content [21–23], chlorophyll contents [4,5,8,24,25] and photosynthetic rate [3,8,19,25,26] are known to be related to low-temperature tolerance in tomato. Low temperature also affects fruit quality by lowering vitamin C, soluble solid content and lycopene [25]. Although several hypotheses have been proposed to explain

tolerance or sensitivity to low temperature, the physiological mechanisms responsible for low-temperature tolerance remain unclear [27].

Tomato plants tolerant to low night temperature (LNT) can be a practical and economical breeding target for energy saving because heating demand in greenhouses is significantly higher during the night of winter. Additionally, the increase in temperature during the day can compensate for the retarded growth of tomato plants during the night [28]. Energy costs can be reduced by 16% if the temperature set-point in greenhouses decreases by 2 °C [29] and lowering greenhouse temperatures by about 5 °C can greatly save on heating costs in winter tomato cultivation. Chilling injury threshold is about 15 °C in tomato [13] and, therefore, a practical breeding target for LNT tolerance can be tomato cultivars that tolerate a night temperature around 10 °C.

Various tomato types differing in fruit size exist and have different cultivation physiology. Tomato accessions with different fruit sizes showed different physiological responses to high temperature, and traits associated with tolerance significantly differed by fruit size [30]. Therefore, it is also possible that the responses to low temperature may also differ among tomato accessions with different fruit sizes; however, no previous study on low-temperature tolerance has been conducted based on fruit type.

This study was conducted to investigate the effect of LNT on physiological traits such as plant height, the number of flowers, fruit-set and photosynthetic parameters, and biochemical traits such as electrolyte leakage and proline and chlorophyll contents. Tomato accessions with cherry or large fruit types, tolerant or sensitive to LNT, were grown in greenhouses maintained at 10 and 15 °C.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Four accessions with indeterminate growth type were selected based on fruit size and LNT tolerance from our previous research [8]. Accessions 'AVTO1020' (20 g) and 'Power guard' (32 g) having relatively small fruit sizes (cherry type) were sensitive and tolerant to LNT, respectively, and thus designated as T7SS (small sensitive) and T14ST (small tolerant), respectively. Similarly, '12AVT-14 × Dafnis' (72 g) and 'AVTO1314' (82 g) with relatively large fruit sizes were sensitive and tolerant to LNT, respectively, and, therefore, designated as T24LS (large sensitive) and T27LT (large tolerant), respectively.

The seeds of four tomato accessions were sown in plug trays (52 cm × 26 cm in size, 6 cm × 6 cm for each cell) containing a 1:1 ratio of sand and commercial bed soil (Bio Sangto, Korea). The commercial bed soil consisted of coco peat (47.2%), peat moss (35%), zeolite (7%), vermiculite (10.0%), dolomite (0.6%), humectant (0.006%) and fertilizers (0.194%). A liter of water was applied every day to plants in a tray and the trays were placed in a glasshouse (28/18 °C in day/night with relative humidity within 65–70%) in the National Institute of Horticultural and Herbal Science, South Korea (35°83′ N, 127°03′ E).

Seedlings with 10–12 true leaves and the first truss were transplanted on 21 November 2019 into two double-layer polyethylene film greenhouses (light transmittance of about 70%) with exactly the same covering materials to exclude the effect of light intensity. The ridge and furrow system (1.2 and 0.7 m in width, respectively) with double rows were applied and spacing between and within rows was 40 × 40 cm. The ridges were mulched with black plastic films. All plants (four biological replicates per accession) in both greenhouses were grown in the same condition, except for the temperature. Temperature set-point for heating in the first two weeks was maintained at 15 °C in both greenhouses to ensure seedlings' adaptation to a new environment. Temperature set-point for LNT treatment was changed to 10 °C from 14 days after transplanting (DAT). The soil in the two greenhouses was equally prepared according to the recommendations of the Korea Soil Information System (https://soil.rda.go.kr (accessed on 1 November 2019)) with pre-plant broadcast manure at a dose of 1 kg m^{-2} and basal fertilizer containing 16 g m^{-2} N, 8 g m^{-2} K_2O and 16 g m^{-2} P_2O_5. Plants were regularly watered with drip irrigation system and fertigated weekly with solution A (N 5.5%, K 4.5%, Ca 4.5%, B 0.00014%, Fe 0.05%, Zn

0.0001% and Mo 0.0002%) and B (N 6%, P 2%, K 4%, Mg 1%, B 0.05%, Mn 0.01%, Zn 0.005% and Cu 0.0015%) (Mulpure, Daeyu Co. Ltd., Seoul, Korea).

Data on the ambient average and lowest night temperatures during the entire growth period were collected every day using the data logger (WatchDog 1450, Spectrum Technologies Inc., Aurora, IL, USA) in both 10 and 15 °C greenhouses from December 10 to March 9 (Supplementary Figure S1). The ambient average temperatures were 10.2–16.8 and 14.8–18.3 °C, and the lowest temperatures were 8.3–11.0 and 13.0–16.5 °C for 10 and 15 °C greenhouses, respectively, during the entire growth period (Supplementary Figure S1).

2.2. The Effect of Low Night Temperature on the Growth and Development of Tomato Accessions

All investigation was conducted on the same day in both greenhouses. The plants' heights were measured from 20 to 100 DAT with 20 day intervals. The photosynthetic rate (μmol CO_2 m^{-2}s^{-1}), stomatal conductance (mol H_2O m^{-2}s^{-1}) intercellular CO_2 concentration (μmol CO_2 mol^{-1}) and transpiration rate (mmol H_2O m^{-2}s^{-1}) were measured using a portable photosynthesis measurement system (LI-6400, LI-COR Bioscience, Lincoln, NE, USA). Data were recorded in three biological replicates from the mid part of leaves in 30, 60, 90 and 120 DAT between 10:00 and 12:00 a.m. Light response curves (PAR) were set to 600 μmol m^{-2}s^{-1}, the temperature of the leaf chamber was set to 25 °C and the intercellular CO_2 concentration was maintained at 400 μmol (CO_2) mol^{-1}. The photosynthetic rate was automatically measured after 3–4 min of light exposure [26].

The number of flowers and fruit set per truss were counted from the second to fifth trusses at the same day in both greenhouses. Fruit set was determined as follows:

$$\text{Fruit set } (\%) = \frac{\text{The number of fruits}}{\text{The number of flowers}} \times 100$$

2.3. Electrolyte Conductivity, Total Chlorophyll and Proline Content in Leaves

Leaf samples were collected in 30, 60, 90 and 120 DAT, near the 3rd, 4th, 5th and 6th trusses for large-fruit-type accessions and the 4th, 5th, 6th and 7th trusses for cherry-type accessions, respectively, with four technical replicates. The leakage of electrolyte from tomato leaves was measured in 30, 60, 90 and 120 DAT according to Camejo et al. [31] with minor modifications. Briefly, leaf discs were perforated with a radius of 5.5 mm. Each disc was placed in a 15 mL tube containing 10 mL of deionized water and then incubated on a shaker at 25 °C for 30 min. At this time, the electrolyte conductivity 1 (EC1) of water was measured using a STARA-HB conductivity meter (Thermo Orion, Waltham, MA, USA). The tube was heated in a boiling water bath for 30 min and cooled at room temperature for 20 min, and then EC2 was measured. Final EC content was expressed as the percentage of EC1/EC2.

Total chlorophyll content was estimated from the mid leaves of tomato accessions using a SPAD meter (Konica Minolta, Tokyo, Japan) on 30, 60, 90 and 120 DAT.

Free total proline content in tomato leaves was measured on 30, 60, 90 and 120 DAT using colorimetric assay [21]. Leaf samples were prepared as mentioned above in the determination of EC. All leaves were lyophilized (−72 °C) in a Freezer dryer (IlShin BioBase, Gyeonggi, Korea) for three days. The leaf sample of 100 mg (dry weight) was homogenized with 2 mL of 3% (*w/v*) aqueous sulfosalicylic acid solution. The homogenate was centrifuged at 14,000 rpm for 7 min and then 1 mL of supernatant was transferred to 5 mL microtubes containing 1 mL each of glacial acetic acid and acid ninhydrin. The ninhydrin reaction was prepared by adding ninhydrin (2.5 g/100 mL) to a solution containing glacial acetic acid, distilled water and 85% of 6M ortho-phosphoric in a ratio of 6:3:1, respectively. The reaction mixtures were kept in a boiling water bath (95 °C) for 1 h and the reaction was stopped at 4 °C for 20 min. The reading was taken at a wavelength of 546 nm by spectrophotometer (EON, BioTek Instruments, Winooski, VT, USA).
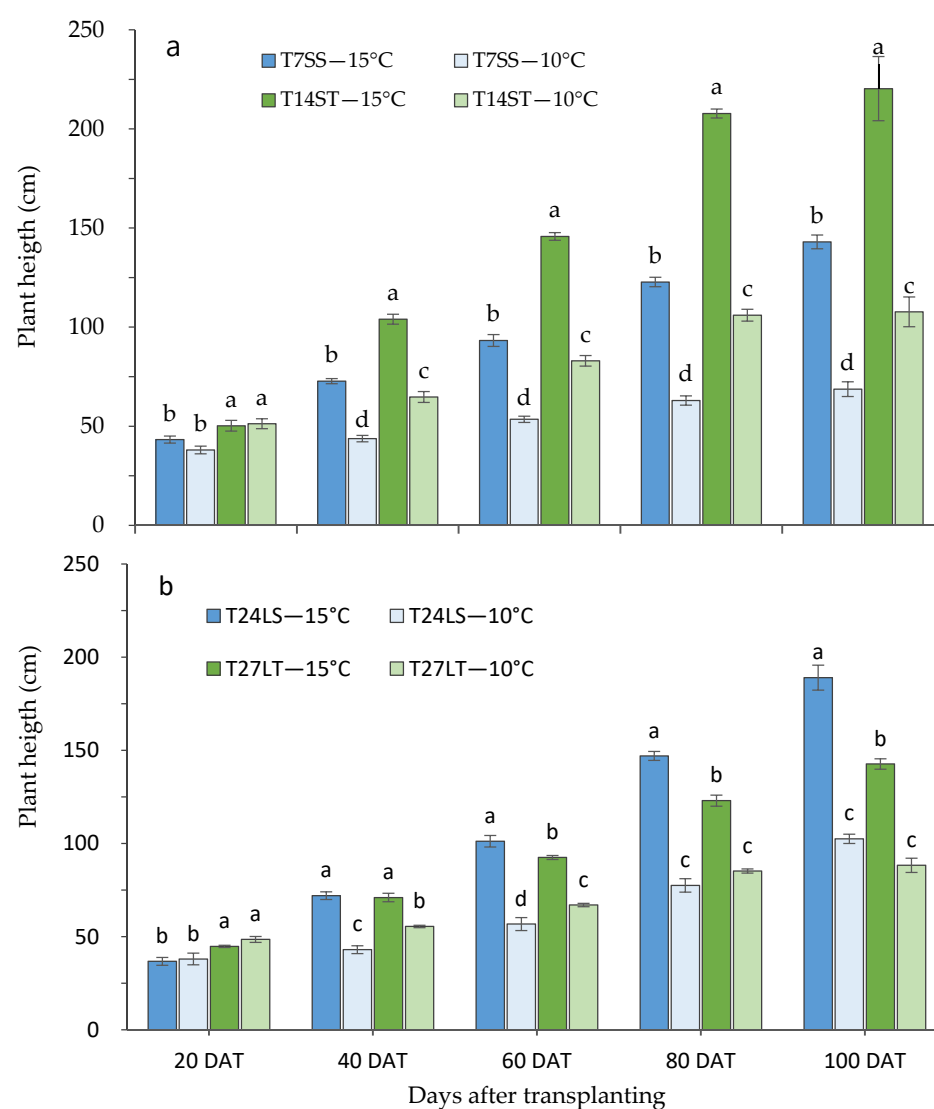
2.4. Statistical Analyses

All statistical analyses were performed using the SAS Enterprise Guide 7.1 (SAS Institute Inc., NC, USA). Mean values of plant height among accessions were compared with a significance level of 5% using Duncan's multiple range test. The Student's t-test for the number of flowers, fruit set, EC, proline and chlorophyll contents and photosynthetic parameters were conducted between tolerant and sensitive accessions in each fruit type at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ levels.

3. Results

3.1. Effect of Low Night Temperature on the Growth and Development of Tomato Accessions

LNT significantly affected plant height in all growth stages, except for 20 DAT, regardless of fruit type and LNT tolerance of tomato accessions (Figure 1). Plant heights of T7SS and T14ST accessions, which are cherry types, were significantly reduced in 10 °C after 40 DAT (Figure 1a). Likewise, plant heights of large fruit types, T24LS and T27LT, showed a significant reduction in 10 °C from 40 DAT (Figure 1b).

Figure 1. Changes in the average plant height of tomato accessions during entire growth period in 10 and 15 °C for cherry (**a**) and large fruit (**b**) type accessions. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. The vertical bars indicate the means ± SE (n = 4). Different letters above bars indicate a significant difference based on Duncan's multiple range test ($p \leq 0.05$) among accessions in 10 and 15 °C within each number of days after transplanting.

Photosynthetic rate, stomatal conductance, transpiration rate and intercellular CO_2 concentration were generally lower in 10 than 15 °C at early growth stages in all accessions (Figures 2 and 3). There was no clear pattern of difference between LNT-sensitive and -tolerant accessions except for photosynthetic rate, which was significantly reduced in LNT-tolerant accessions during the early growth period in both fruit types (Figures 2 and 3). In cherry types, photosynthetic rate was significantly lower in 10 than 15 °C at 30 and 60 DAT in T14ST (Figure 2b). Stomatal conductivity was significantly lower in 10 °C at 30 to 60 DAT in both accessions (Figure 2c,d) and additionally at 120 DAT in T7SS (Figure 2c). Exactly the same pattern as stomatal conductivity was observed in transpiration rate (Figure 2e,f). There was no significant difference in intercellular CO_2 concentration between 10 and 15 °C in both T7SS (Figure 2g) and T14ST (Figure 2h), except for 60 DAT in T7SS (Figure 2g).

In large fruit types, photosynthetic rate was also significantly lower in 10 than 15 °C at 30 and 60 DAT in T27LT (Figure 3b). Exactly the same patterns as cherry types (Figure 2c–f) were observed in the stomatal conductance and transpiration rate of large fruit types (Figure 3c–f). Intercellular CO_2 concentration was not significantly different between 10 and 15 °C in the whole growth period of T24LS (Figure 3g), but was significantly different at 30 and 60 DAT in T27LT (Figure 3h).

LNT significantly affected the number of flowers in cherry types but not in large fruit types (Figure 4a). The number of flowers was significantly reduced in 10 °C in both cherry fruit types, T7SS and T14ST (Figure 4a). However, in T24LS and T27LT with large fruit types, no significant differences between 10 and 15 °C were observed in the number of flowers (Figure 4a).

Fruit set was significantly affected by LNT in sensitive accessions but not in tolerant ones (Figure 4b). In T7SS and T24LS, the LNT-sensitive accessions with cherry and large fruit types, respectively, fruit sets were significantly reduced in 10 °C; however, no difference was observed in T14ST and T17LT, LNT-tolerant accessions (Figure 4b).

LNT significantly affected the floral morphology of LNT sensitive accessions regardless of fruit types (Figure 5a–d), showing abnormal structure of floral organs such as petals, pistils (stigma, style and ovary) and stamens (anther and filament) (Figure 5a,c). Many flowers of cherry types in 10 °C did not set fruits in a sensitive (Figure 5e) but in a tolerant accession (Figure 5f). In large fruit types, flowers in 10 °C barely set fruits in LNT sensitive accession (Figure 5g) but set many fruits in a tolerant accession (Figure 5h). However, fruits from LNT tolerant accessions in 10 °C were seedless in both fruit types (Supplementary Figure S2).
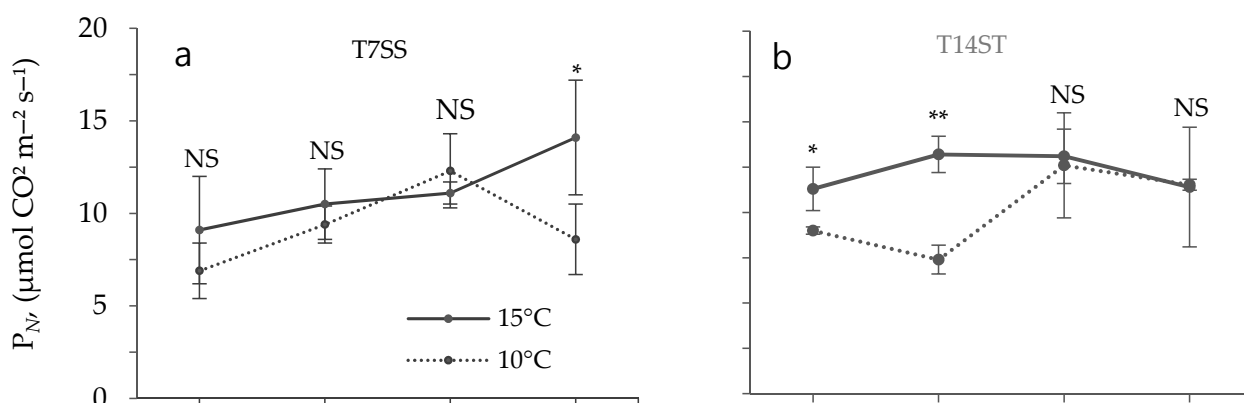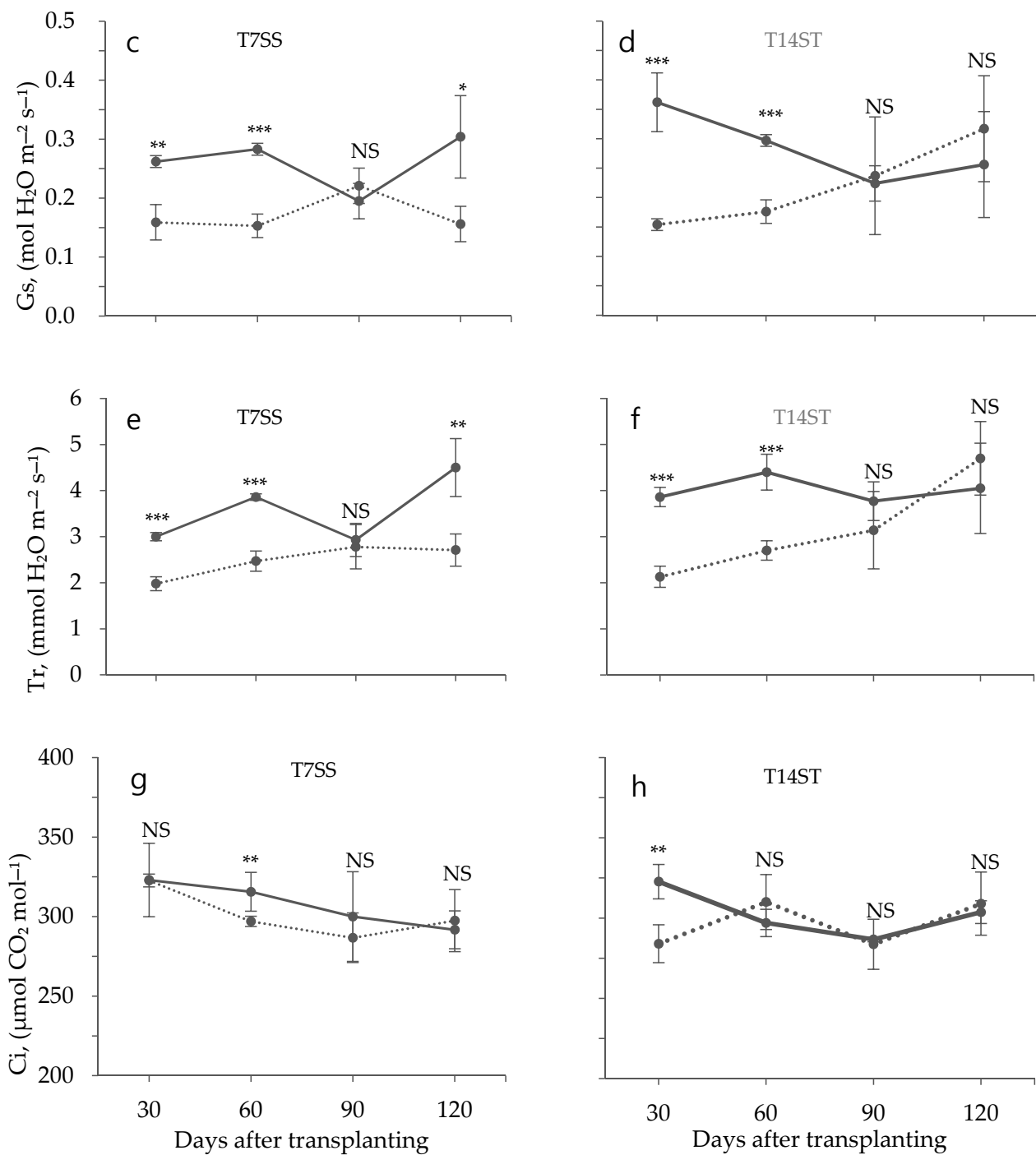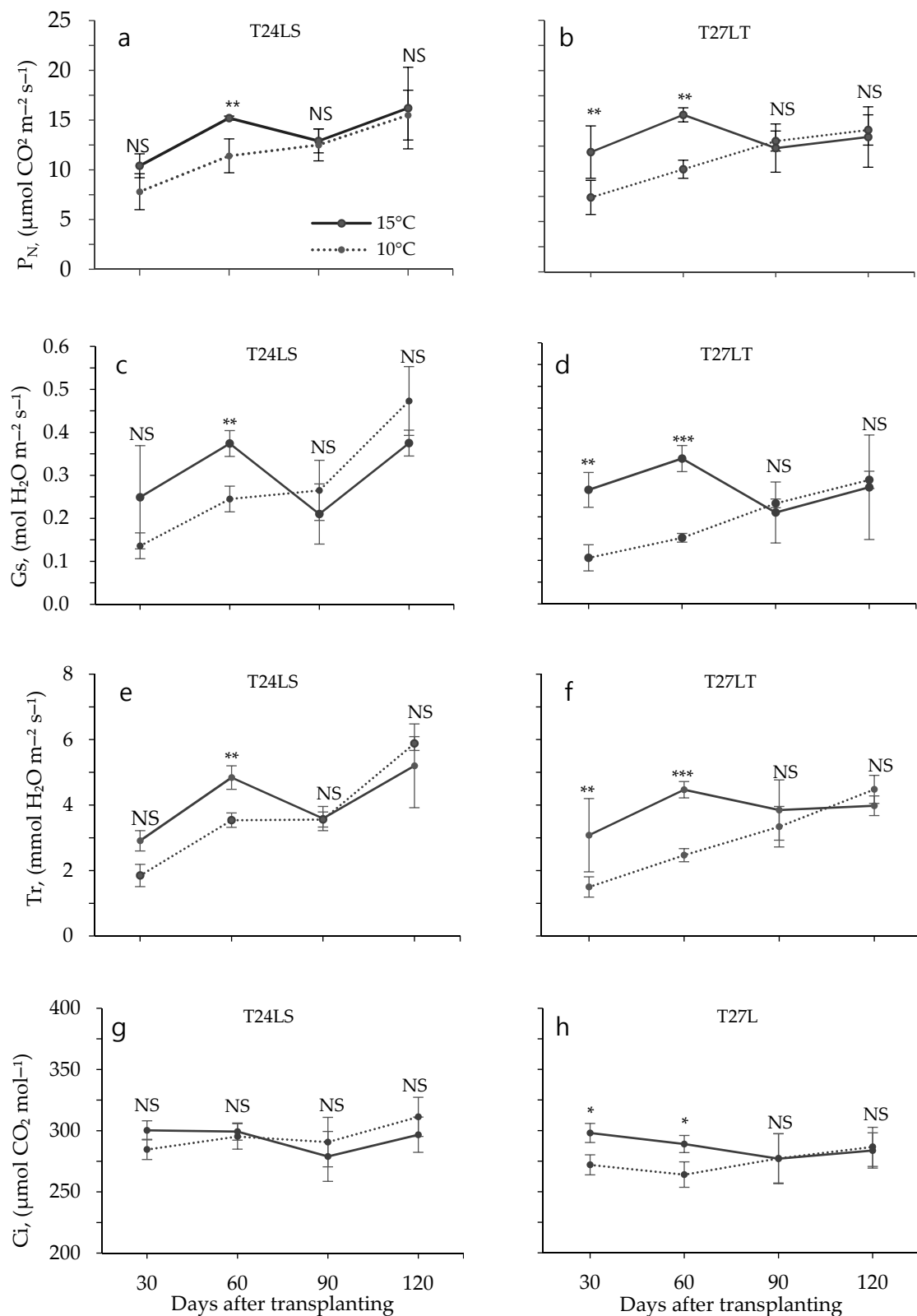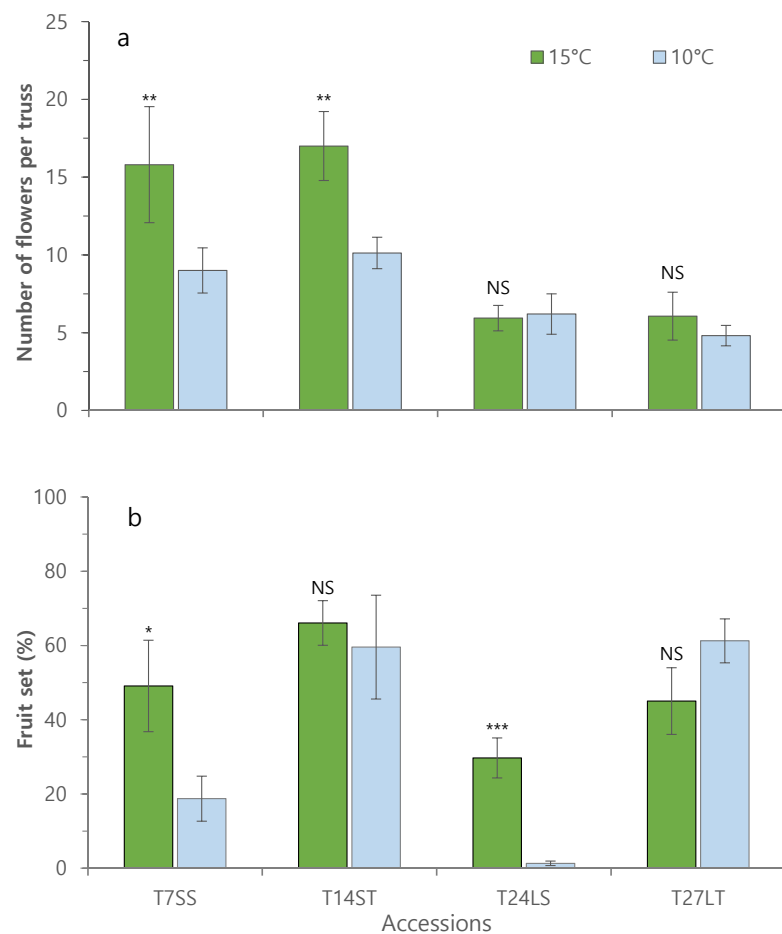

Figure 2. *Cont.*

Figure 2. Changes in photosynthetic parameters of cherry-fruit-type accessions sensitive or tolerant to low night temperature grown in 10 and 15 °C. P_N—photosynthesis rate (**a**,**b**) Gs—stomatal conductance (**c**,**d**), Tr—transpiration rate (**e**,**f**) and Ci—intercellular CO_2 concentration (**g**,**h**) were presented for LNT-sensitive and -tolerant accessions, respectively. SS: small sensitive, ST: small tolerant. Values are means ± SD (n = 3). NS, *, ** and *** indicate not significant and significant at the $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ levels in *t*-test, respectively.

Figure 3. Changes in photosynthetic parameters of large-fruit-type accessions sensitive or tolerant to low night temperature grown in 10 and 15 °C. P_N—photosynthesis rate (**a**,**b**), Gs—stomatal conductance (**c**,**d**), Tr—transpiration rate (**e**,**f**) and Ci—intercellular CO_2 concentration (**g**,**h**) were presented for sensitive and tolerant accessions, respectively. LS: large sensitive and LT: large tolerant. Values are means ± SD (n = 3). NS, *, ** and *** indicate not significant and significant at the $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ levels in *t*-test, respectively.

Figure 4. Effects of low night temperature on the number of flowers (**a**) and fruit set ratio (**b**) among tomato accessions. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Vertical bars represent means $\pm$ SD (n = 4). NS, *, ** and *** indicate not significant and significant at the $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ levels in *t*-test, respectively.
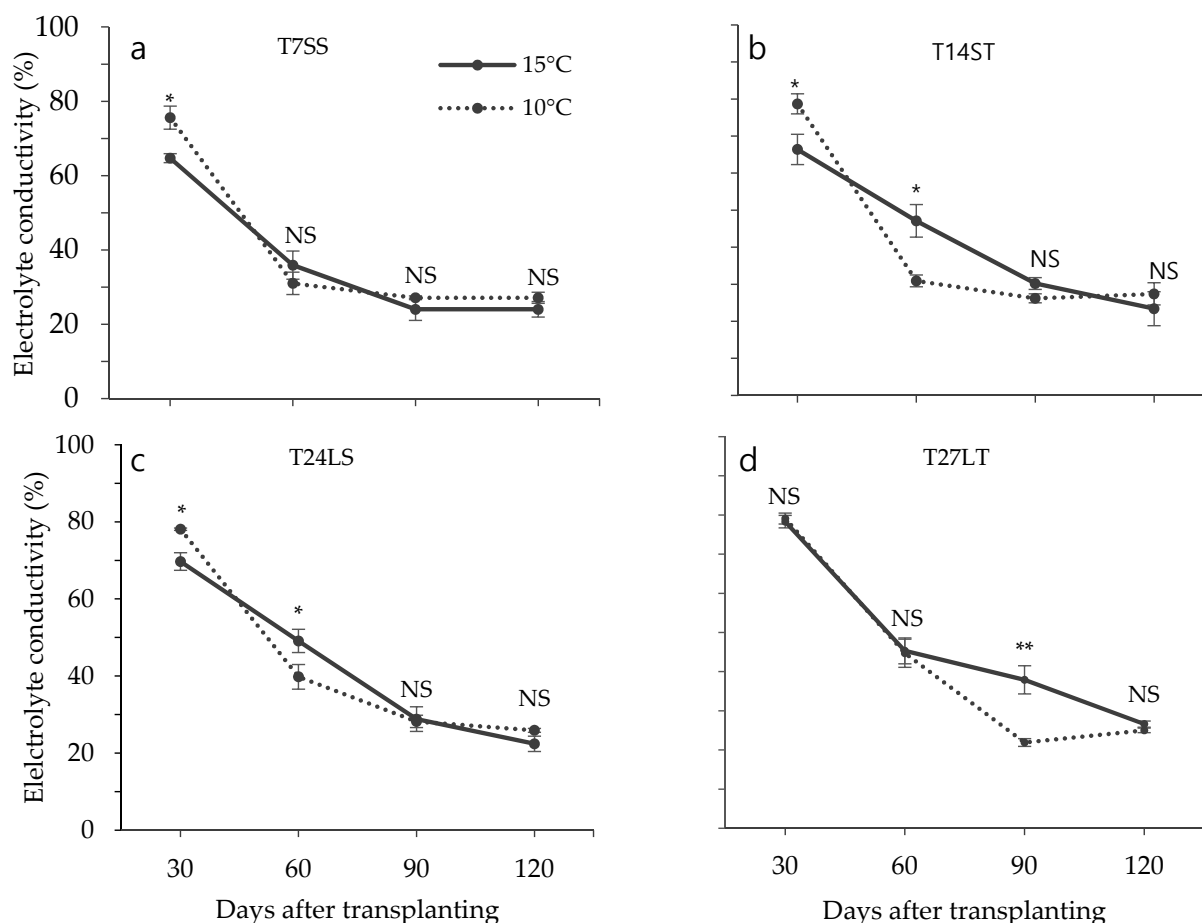

Figure 5. Different responses to low night temperature between tolerant and sensitive accessions in the development of tomato flowers and fruits. Abnormal (**a**) and normal flowers (**b**) of T7SS and T14ST, respectively; abnormal (**c**) and normal (**d**) flowers of T24LS andT27LT, respectively; no fruit set (**e**) and fruits (**f**) of T7SS and T14ST, respectively; small fruit set (**g**) and fruits (**h**) of T24LS and T27LT, respectively. All plants were grown in the night temperature of 10 °C.
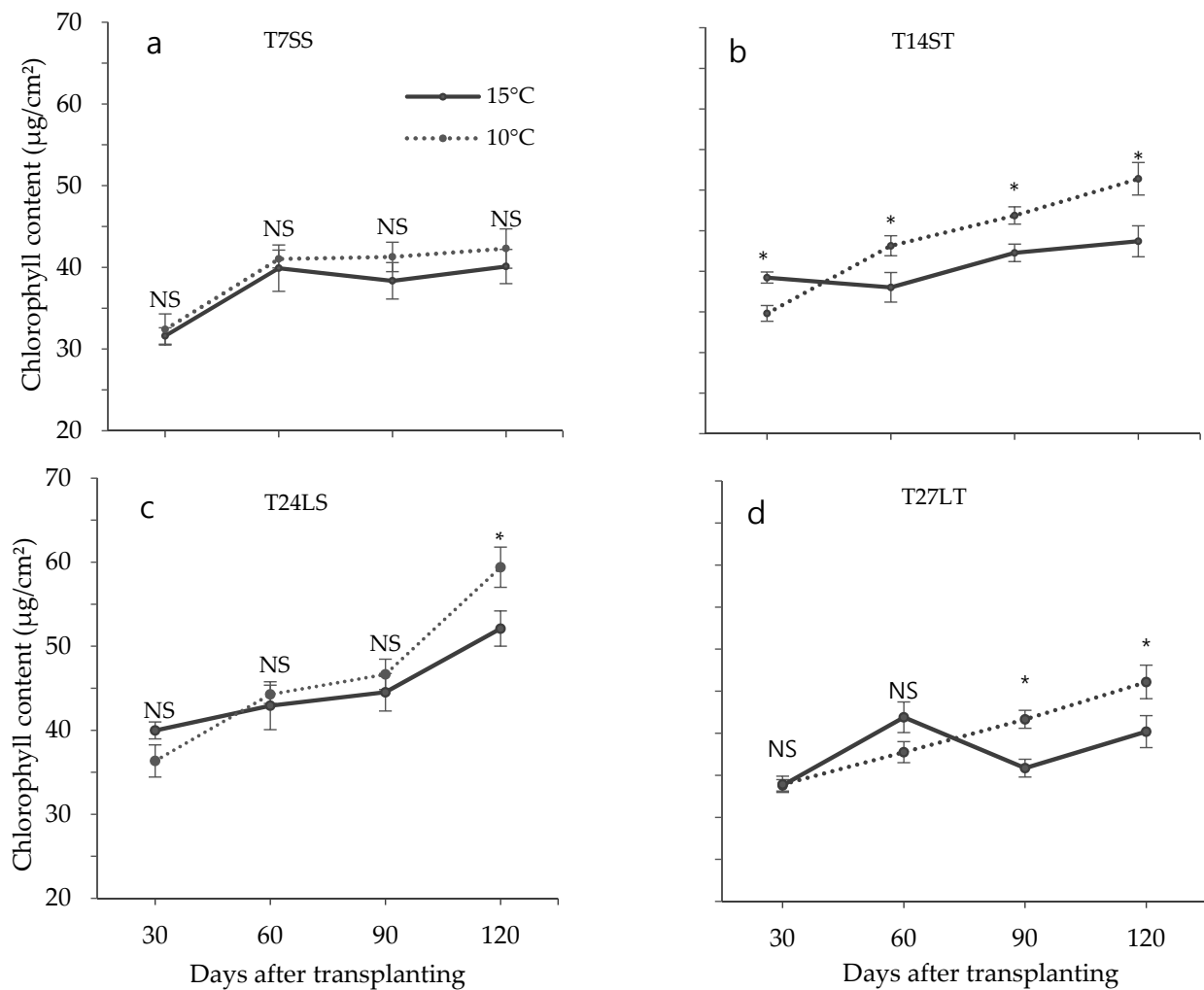
3.2. Effect of Low Temperature on Biochemical Characteristics

EC gradually decreased as tomato plants grew in all accessions regardless of temperature conditions (Figure 6). In cherry types, T7SS showed no significant difference in EC between 10 and 15 °C greenhouses except for 30 DAT (Figure 6a). In T14ST, EC was initially higher in 10 °C and then lower at 60DAT, and there were no significant difference thereafter (Figure 6b). A similar pattern was observed in T24LS (Figure 6c), a large-fruit-type accession. In T27LT, there were no significant differences in EC in all growing periods, except for 90 DAT (Figure 6d).
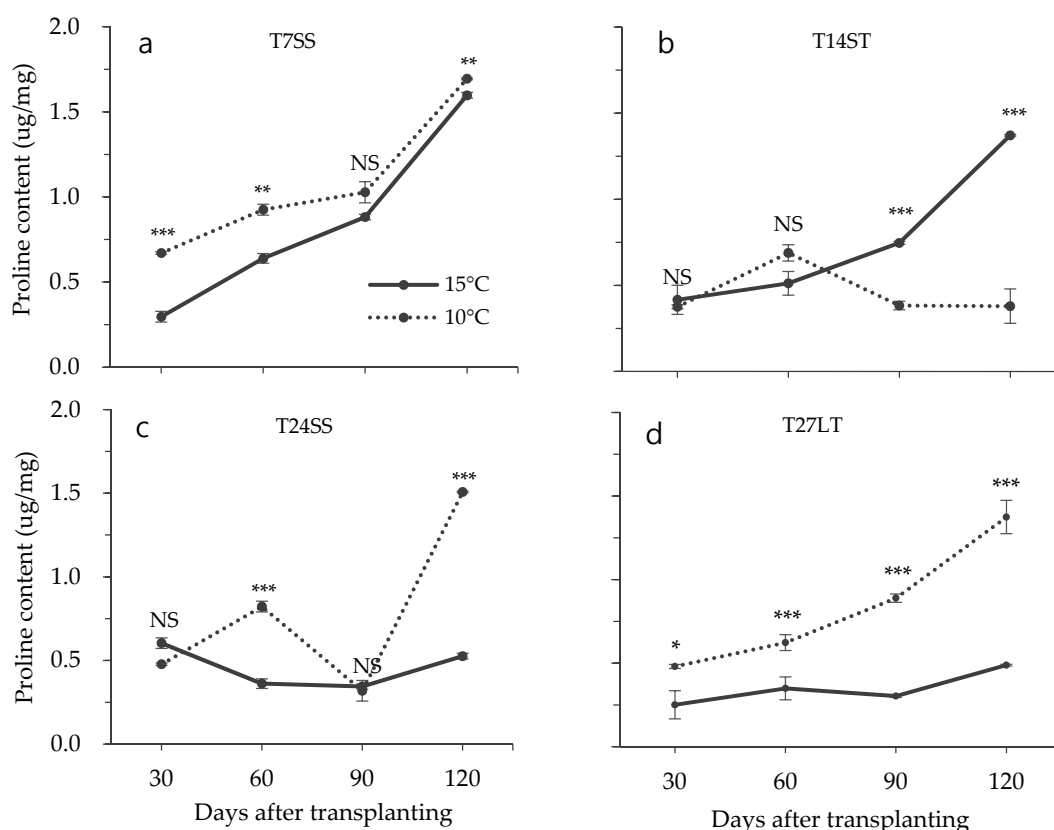

Figure 6. Changes in electrolyte conductivity in the leaves of cherry-type accessions T7SS (**a**) and T14ST (**b**), and of large-fruit-type accessions T24LS (**c**) and T27LT (**d**) grown in 10 and 15 °C. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Values are means ± SD (n = 3). NS, * and ** indicate not significant and significant at the $p \leq 0.05$ and $p \leq 0.01$ levels in *t*-test, respectively.

Chlorophyll content was significantly higher at the later growth stages of LNT-tolerant accessions grown in 10 °C, but not of sensitive ones (Figure 7). In cherry types, no clear difference in chlorophyll content between 10 and 15 °C was observed in T7SS (Figure 7a). However, chlorophyll content in T14ST was significantly higher in 10 than 15 °C from 60 DAT (Figure 7b). In large fruit types, chlorophyll content of T24LS in 10 °C was also significantly higher only in 120 DAT (Figure 7c), but that of T27LT was significantly higher from 90 DAT (Figure 7d).

Figure 7. Changes in chlorophyll contents in the leaves of cherry-type accessions T7SS (**a**) and T14ST (**b**), and of large-fruit-type accessions T24LS (**c**) and T27LT (**d**) grown in 10 and 15 °C. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Values are means ± SD (n = 3). NS and * indicate not significant and significant at the $p \leq 0.05$ level in *t*-test, respectively.

Accumulation patterns of free total proline of tomato plants in 10 and 15 °C were clearly different between cherry- and large-fruit-type accessions and between LNT-tolerant and -sensitive accessions (Figure 8). In 15 °C, proline content continuously increased in all cherry types, T7SS (Figure 8a) and T14ST (Figure 8b), but did not show much change in all large fruit types, T24SS (Figure 8c) and T27LT (Figure 8d). In cherry types, the proline content of T7SS showed a continuous increase in 10 °C, significantly higher than 15 °C (Figure 5a); however, that of T14ST showed little change during the entire growing period and, therefore, became significantly lower in 10 than 15 °C from 90 DAT (Figure 5b). In large fruit types, proline content in 10 °C was significantly higher in T27LT (Figure 5d) but fluctuated in T24SS (Figure 5c).

Figure 8. Changes in proline contents in the leaves of cherry-type accessions T7SS (**a**) and T14ST (**b**), and of large-fruit-type accessions T24SS (**c**) and T27LT (**d**) grown in 10 and 15 °C. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Values are means ± SD (n = 3). NS, *, ** and *** indicate not significant and significant at the $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$ levels in *t*-test, respectively.

4. Discussion

Tomato accessions with different fruit types have different genetic backgrounds and cultivation physiology. Therefore, mechanisms to deal with low temperatures may differ by tomato fruit type. Although several mechanisms for the survival of tomato plants under artificially induced low-temperature conditions were suggested [4,5,25,26,32,33], these studies were conducted during a relatively short period and without the consideration of fruit types. Additionally, most of these studies did not consider that night temperature can be a practical breeding target for reducing heating costs in winter tomato cultivation. In the present study, tomato accessions with various genetic backgrounds and differences in fruit type and LNT tolerance were selected and grown for a sufficiently long period in the night temperatures of 10 and 15 °C.

Fruit set in 10 °C was significantly reduced in LNT-sensitive but not in tolerant accessions in both cherry and large fruit types (Figure 4b), implying that fruit set can be the key factor to confer LNT tolerance upon tomato plants regardless of fruit type. The high fruit set ratio in LNT-tolerant accessions might be due to better fertility of pollens or viability of ovule and stigma, which are generally not good below 10 °C [11,34]. Similar results were observed in the present study. Floral morphology of LNT-tolerant accessions was phenotypically normal in 10 °C, whereas that of LNT-sensitive accessions was abnormal (Figure 5). In addition, the number of flowers was significantly affected by LNT in cherry fruit types but not in large fruit types, regardless of LNT tolerance levels (Figure 4a), showing genotype-specific responses.

Tomato plants subjected to low temperatures frequently suffer membrane damage, which can be evaluated by the relative electrolyte leakage [4,19,23]. EC in the early growth stage was highest and gradually decreased in subsequent stages of 'fruit developing' and

'maturing' (Figure 6). However, the effect of EC on tomato LNT tolerance remains in question since there was no clear pattern of difference in EC between sensitive and tolerant accessions (Figure 6). This may be due to the relatively high temperature set point for the low temperature, 10 °C, in this experiment, compared to previous studies.

Previous studies demonstrated the pivotal role of proline under abiotic stress in tomato plants [21–23,33]. Our results show the different accumulation pattern between cherry and large fruit types in both 10 and 15 °C (Figure 8). The sharp increase in proline content of cherry (Figure 8a,b) but not of large fruit types (Figure 8c,d) in 15 °C implies the innate sensitivity to LNT in cherry-type accessions. The different proline accumulation patterns between LNT-tolerant cherry and large fruit types also imply that there may be different LNT tolerance mechanisms depending on tomato fruit type. The lower proline content in later growth stages may be related to active proline degradation by proline dehydrogenase, which may give cherry-type accessions resistance to the low-temperature stress [22]. However, our results are based on only four genotypes and cannot rule out the possibility that other genotypes within a fruit type show different proline accumulation patterns. Further studies with a large set of accessions are needed to investigate the different mechanisms depending on tomato fruit types.

The chlorophyll contents in all tomato accessions steadily increased during the entire growth period regardless of temperature conditions (Figure 7). Previous studies reported the reduction in the chlorophyll content after cold treatment in the short term [4,19,25,33], which was observed in the present study in some cases (Figure 7b,c). In the long term, however, plants in the 10 °C condition showed higher chlorophyll contents than those in 15 °C (Figure 7), and this trend was more prominent in LNT-tolerant accessions (Figure 7b,d).

The plant growth of all four accessions was significantly delayed in LNT condition (Figure 1), similar to the previous studies [8,25,32,35]. This is because of the decreased photosynthetic activity in all tomato accessions during the early growth stages (Figures 2 and 3). However, the difference in plant height between 10 and 15 °C was scarcely narrowed, although the photosynthetic activity of all accessions in LNT was restored in the subsequent fruit-maturing stage (Figures 2 and 3). The restoration of photosynthetic activity was partly due to that of stomatal conductance and transpiration rate (Figures 2 and 3). Our results are in accordance with a previous study reporting that plant height correlated with photosynthetic rate [25]. Considering the increased photosynthetic rate in the later growth stages, it would be interesting if the correlation between photosynthetic rate and fruit weight in the early and late growth stages, respectively, were investigated in order to study the relationship between early photosynthesis and fruit harvest.

5. Conclusions

The present study provides evidence that tomato genotypes with different fruit type and LNT tolerance show clearly different patterns in photosynthesis, the number of fruits, fruit set and chlorophyll and proline contents. These results suggest tomato fruit types have different physiological and biochemical responses to LNT and, therefore, may have different mechanisms for LNT tolerance, which are a practical target for reducing heating costs in winter. It may be related to proline accumulation patterns that differ by fruit type, as well as LNT tolerance. However, we cannot rule out the possibility of different genotypic effects within a fruit type because of the limited number of accessions used in the experiment. More detailed experimental designs and a larger set of tomato accessions are necessary for dissecting the mechanisms underlying LNT tolerance among different tomato fruit types.

Abbreviations

LNT—low night temperature, DAT—days after transplanting, EC—electrolyte conductivity, P_N—photosynthetic rate, Gs—stomatal conductance to H_2O, Tr—transpiration rate, Ci—intercellular CO_2 concentration, SS—small sensitive, ST—small tolerant, LS—large sensitive, LT—large tolerant.

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