doi:10.20944/preprints202106.0390.v1

Article

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

Eun Young Yang[1†], Sherzod Nigmatullaevich 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, Republic of Korea; yangyang2@korea.kr (E.Y.); sherzod_2004@list.ru (S.N.R.); chomc@korea.kr (M.C.); bong9846@korea.kr (H.J.)
[2]Department of Environmental Horticulture, Dankook University, Cheonan 31116, Republic of Korea
[†]Equal contribution
*Correspondence: wbchae75@dankook.ac.kr; Tel: +82-41-550-3642

Abstract: Low night temperature (LNT) can be a practical and economical target in tomato breeding programs in terms of energy saving in greenhouses. This study was conducted to investigate the physiological responses to LNT using four tomato accessions of cherry and large fruit types with LNT tolerance and sensitivity grown in two greenhouses with night temperature set-points of 10 and 15°C for heating. LNT significantly reduced plant height regardless of fruit types and LNT tolerance. The number of flowers were significantly reduced in 10°C in cherry but not in large fruit types. Fruit set in 10°C was significantly lower in LNT sensitive accessions than tolerant ones regardless of fruit types, which was due to abnormal flower morphology in 10°C. Proline accumulation patterns between 10 and 15°C significantly differed between fruit types as well as between LNT tolerant and sensitive accessions. Chlorophyll content in 10 °C was significantly higher at later growth stages in LNT tolerant accessions than sensitive ones in both fruit types. No clear difference in photosynthetic parameters was observed between fruit types or tolerance and sensitive accessions except for photosynthetic rate, which was significantly lower in tolerant than sensitive accessions during early growing period. These results suggest that different tomato fruit types may have different mechanisms for LNT tolerance.

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

1. Introduction

Abiotic stress significantly affect 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 critical for determining the crop yield, by influencing various growth and development stages. Low temperature is also a main factor that limits geographical distribution of crops sensitive to low temperature, particularly those originated from the tropical zone but widely cultivated in the temperate zone, including tomato.

In tomato, low temperature significantly reduces growth rate [2-5], days to flowers [6-8], the number of flowers [6,8-10] as well as fruit set [8,10-12], all of which affects fruit yield. Tomato plants suffer from chilling injury when exposed to temperatures in the range between 0 and15°C in all growth stages [13-17]. Physiological responses such as electrolyte leakage [4,18-20] and proline content [21-23], as well as chlorophyll contents [4,5,8,24,25] and photosynthetic rate [3,8,19,25-27] are known to be related with low temperature tolerance in tomato. Although several hypotheses have been proposed to explain tolerance or sensitive to low temperature, the physiological mechanisms responsible for low temperature tolerance are remain unclear [28].

Tomato plants tolerant to low night temperature (LNT) can be a practical and economical breeding target in terms of energy saving because heating demand in greenhouses is significantly higher during the night. Besides, temperature rise during the day can compensate for the retarded growth of tomato plants during the night [29]. Energy cost can be reduced by 16% if temperature set-point in greenhouses decreases by 2 °C [30] and lowering greenhouse temperature about 5 °C can greatly save the cost for winter tomato cultivation. Chilling injury threshold for tomato is about 15°C [13] and, therefore, practical breeding target for tomato cultivars in winter can be LNT tolerance around 10 °C. However, previous studies did not consider LNT in tomato.

Various tomato types with different fruit sizes are existed and they may have different cultivation physiology. Tomato accessions with different fruit sizes showed different physiological responses to high temperatures and traits associated with high temperature tolerance are significantly different by fruit sizes [31]. It is possible that fruit sizes can also affect the low temperature but no previous study on low temperature tolerance was conducted based on fruit sizes.

This study was conducted to investigate the effect of LNT on the physiological traits such as plant height, the number of flowers, fruit-set, electrolyte leakage, proline content, chlorophyll contents and photosynthetic parameters, using tomato accessions with cherry and large fruit types with tolerant and sensitive to LNT for both types.

2. Materials and Methods

2.1 Plant materials and growth conditions

Four accessions were selected based on fruit sizes and LNT tolerance from our previous research [8]. Accessions ‘AVTO1020’ (20g) and ‘Power guard’ (32g) had relatively small- cherry fruit sizes and sensitive and tolerant to low temperature, respectively, and thus designated as T7SS (Small-Sensitive) and T14ST (Small-Tolerant) accessions, respectively. Similarly, ‘12AVT-14 x Dafnis’ (72g) and ‘AVTO1314’ (82g) had relatively large fruit sizes and sensitive and tolerant to low temperature, respectively, and therefore, designated as T24LS (Large-Sensitive) and T27LT (Large-Tolerant) accessions, respectively.

The seeds of four tomato accessions were sown in plug trays (52 x 26 cm in size, 6 x 6 cm for each cell) containing 1:1 ratio of sand and commercial bed soil (Bio Sangto, South Korea) consisting of coco peat (47.2%), peat moss (35%), zeolite (7%), vermiculite (10.0%), dolomite (0.6%), humectant (0.006%), and fertilizers (0.194%). The trays were watered 1 liter daily, and placed in a glasshouse (28/18°C in day/night with relative humidity within 65-70%) in 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 with the spacing of 40 × 40 cm on 21 November 2019 into two polyethylene greenhouses. All plants (4 biological replicates per accession) in both greenhouses were grown in the same condition, except for temperature. Temperature set-point for heating in the first two weeks were maintained at 15 °C in both greenhouses in night time to ensure seedlings to adapt new environment. Night temperature set-points were changed to 10 °C for LNT from 14 days after transplanting (DAT). The soil in two greenhouses were prepared according to the recommendations of the Korea Soil Information System [https://soil.rda.go.kr] equally 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, 16 g m^{-2} P_2O_5 and regularly watered to avoid drought and fertilized weekly (Mulpure, Daeyu Co. Ltd., Gyeongsan, South Korea).

Data on ambient temperature during the entire growing period were collected using data logger (WatchDog 1450, Spectrum Technologies Inc., Aurora, USA) in both 10 °C and 15 °C greenhouses (Supplementary figure 1), from December 10 to March 9, with interval one weeks. The ambient average temperatures were ranged 10.2-16.8 °C and 14.8-18.3 °C for 10 °C and 15 °C greenhouses, respectively, during the winter.

2.2. Vegetative and reproductive growth

All investigation was conducted at the same day in both greenhouses. The plant height were measured from 20 to 100 days after transplanting (DAT) with 20 day intervals. The number of flowers and fruit set per truss were counted from the second to fifth trusses. 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

The leakage of electrolyte from tomato leaves was measured were measured from 30, 60, 90 and 120 DAT according to Camejo et al. [32] with minor modifications. Leaves from mid part of plants (used four technical replications) were perforated into discs 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 minutes, and then EC2 was measured. Final EC content was expressed as the percentage of EC1/EC2.

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

Free total proline content in tomato leaves was measured from 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, South 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 minute. Then 1 mL of supernatant was transferred to 5 mL microtubes containing 1mL of each glacial acetic acid and acid ninhydrin. The ninhydrin reaction was prepared by adding ninhydrin (2.5 g/100ml) to a solution containing glacial acetic acid, distilled water, 85% of 6M ortho-phosphoric as a ratio of 6:3:1 receptively. The reaction mixtures were kept in a boiling water bath (95 °C) for 1 hour and the reaction was stopped at 4 °C for 20 minutes. The reading were taken at a wavelength of 546 nm by spectrophotometer (EON, BioTek Instruments, Winooski, Vermont, USA).

2.4. Measurement of photosynthetic rate in tomato accessions

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 plants from mid part of leaves with interval 30, 60, 90 and 120 DAT between 10:00-12:00 am. Light response curves (PAR) were set to 600 μmol $m^{-2}s^{-1}$, the temperature of leaf chamber was set to 25 °C, and the intercellular CO_2 concentration was maintained at 400 μmol (CO2) mol^{-1}. The photosynthetic rate was automatically measured after 3-4 min light exposure [26].

2.5. Statistical analyses

Statistical analysis (ANOVA) was performed using the SAS Enterprise Guide 7.1 (SAS Institute Inc., NC, USA), and 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 ≤ 0.05, p ≤ 0.01, and p ≤ 0.001 levels.

3. Results

3.1. Effect of low night temperature on the growth and development of tomato accessions

The ambient average temperature in both greenhouses were shown in (Supplementary figure 1). LTN significantly affected plant height in all growth stages, except for 20 DAT, regardless of fruit types and tolerance of tomato accessions (Figure 1). Plant heights of T7SS and T14ST accessions, which are cherry types, significantly reduced in 10 °C after 40 DAT (Figure 1a). Likewise, plant heights of T24LS and T27LT showed significant differences from 40 DAT (Figure 1b).

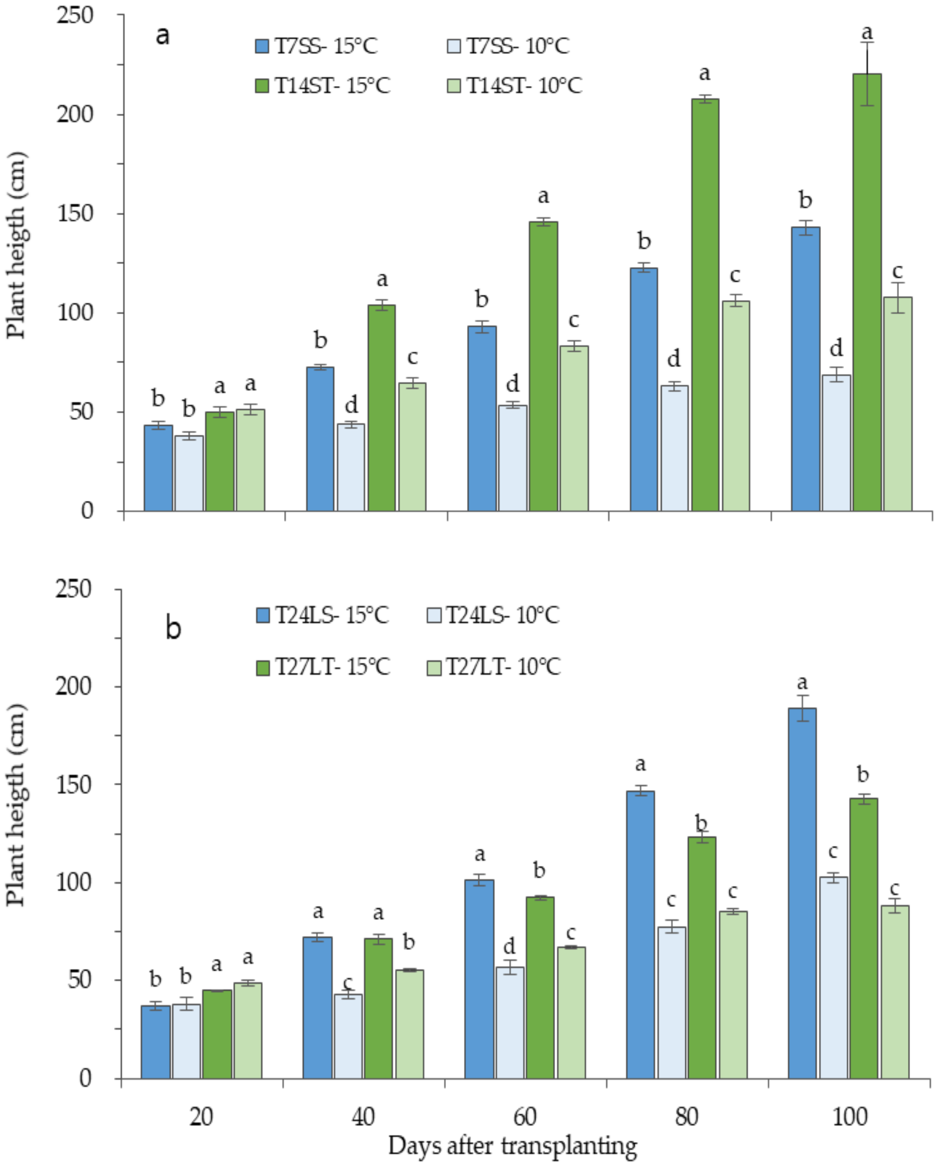


Figure 1. Changes in the average plant height of tomato accessions during entire growing period in 10 and 15 °C. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. The vertical bars indicate the means ± SE (n = 4). Different letters above bars indicate significant difference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

LNT significantly affect the number of flowers in cherry type tomato accessions but not in large fruit types (Figure 2a). The number of flowers was significantly reduced in accessions with cherry type fruits in both T7SS and T14ST accessions (Figure 2a). However, in the accessions with large fruit sizes, no significant differences between 10 and 15 °C were observed in the number of flowers for both T24LS and T27LT accessions (Figure 2a).

Fruit set was significantly affected by LNT in sensitive accessions but not in tolerant ones (Figure 2b). In T7SS and T24LS, 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 2b).

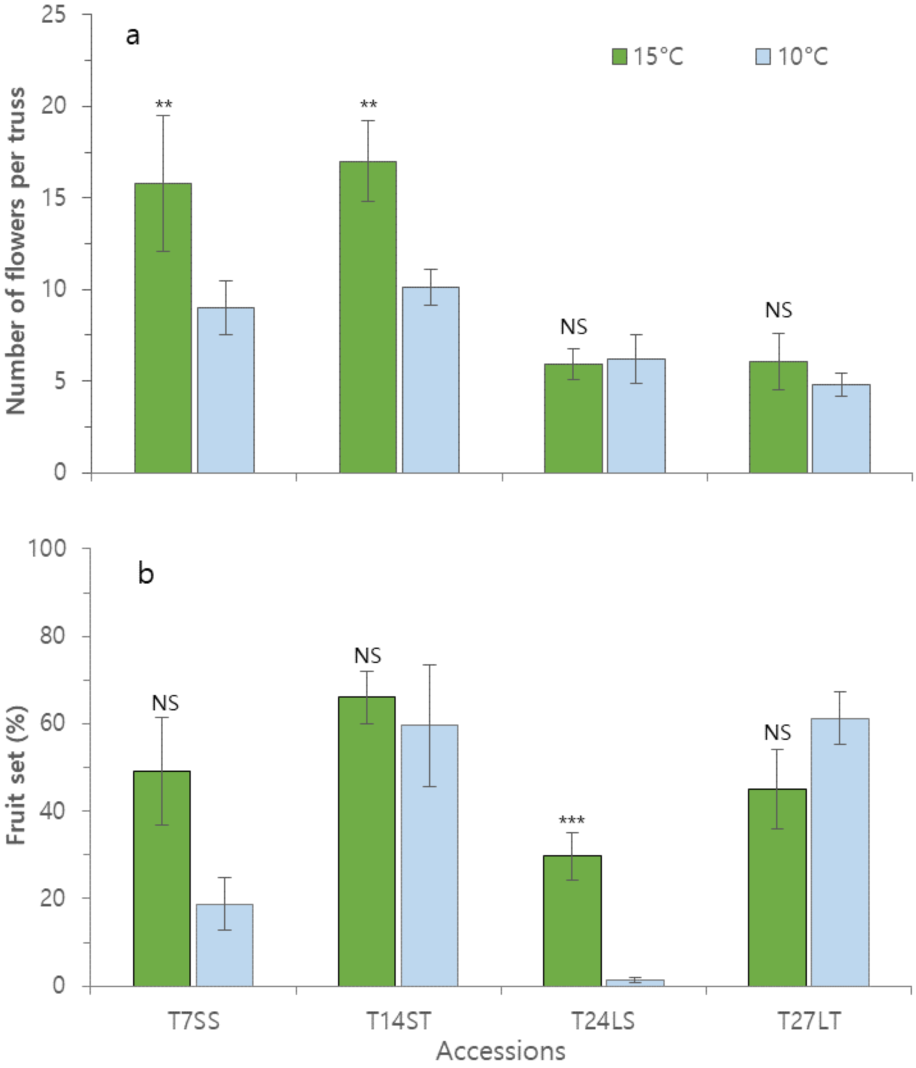


Figure 2. Effect of low night temperature on the number of flowers (a) and fruit set ratio (b) among tomato accessions. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Vertical bars represent means ± SE (n = 4). NS, ** and *** indicate not significant and significant at the $p \leq 0.01$ and $p \leq 0.001$ levels in t-test, respectively.

LNT significantly affected the floral morphology in both cherry (Figures. 3a and b) and large fruit types (Figures 3c and d), showing abnormal structure of floral organs such as staminal cone, petals, pistil style (stigma, style and ovary) and stamen (anther and filament) (Figures 3a and c). Most flowers of cherry types in 10 °C did not produce fruits in a sensitive (Figure 3e) but in a tolerant accession (Figure 3f). In large fruit types, flowers in 10 °C barly produced fruits from in a LNT sensitive accession (Figure 3g) but many fruits in a tolerant accession (Figure 3h).

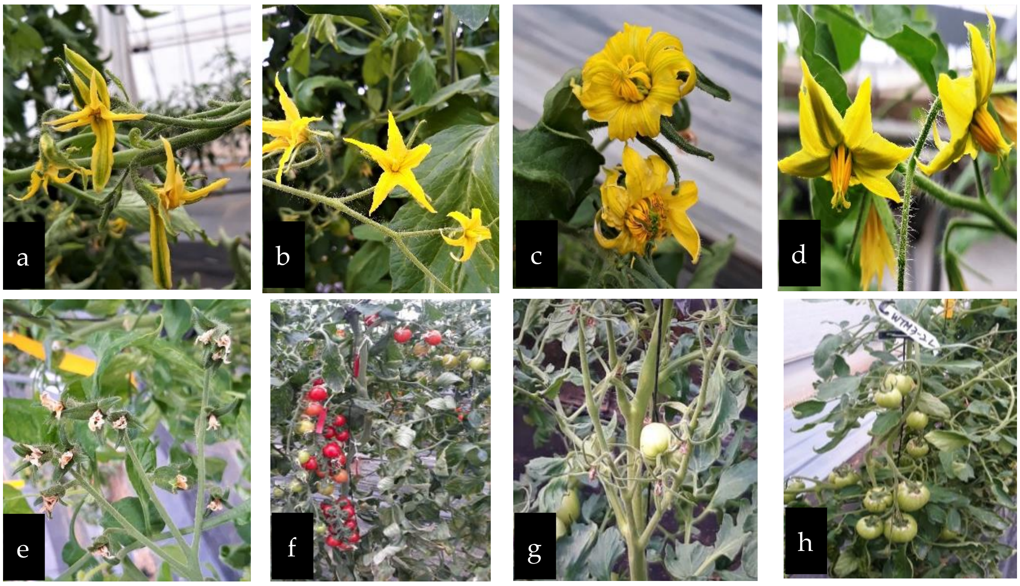
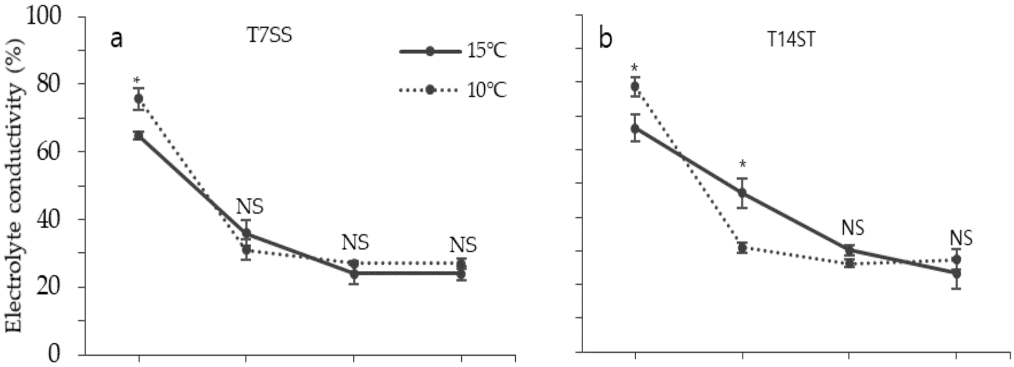


Figure 3. Effect of night temperature on the development of tomato flowers and fruits. Abnormal flower formation (a) and normal (b) in cherry fruit type accessions; abnormal flower formation (c) and normal (d) in large fruit type accessions; no fruit set (e) or produced only seedless fruits (f) in cherry fruit type accessions; no fruit set (g) or produced only seedless fruits (h) in large fruit type accessions.

3.2. Effect of low temperature on physiological characteristics

EC gradually decreased as tomato plants grew regardless of accessions and temperatures, and no clear pattern of difference between 10 °C than 15 °C was observed (Figure 4). In cherry types, T7SS showed no significant difference in EC between 10°C than 15°C greenhouses except for 30 DAT (Figure 4a). In T14ST, EC was initially higher in 10 °C and then lower in 10 °C in 60DAT, and there were no difference later (Figure 4b) and similar pattern was observed in T24LS (Figure 4c), a large fruit type accession. In T27LT, there were no differences in EC in all growing period except for 90 DAT (Figure 4d).



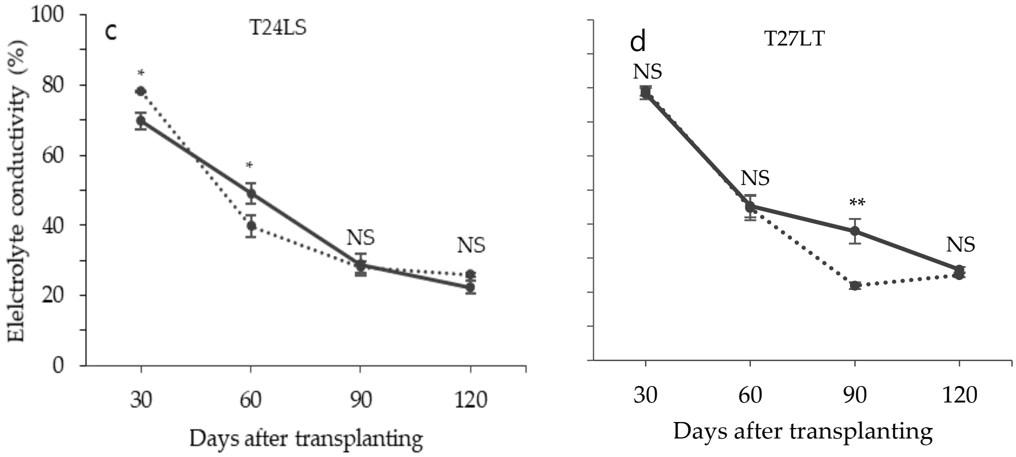
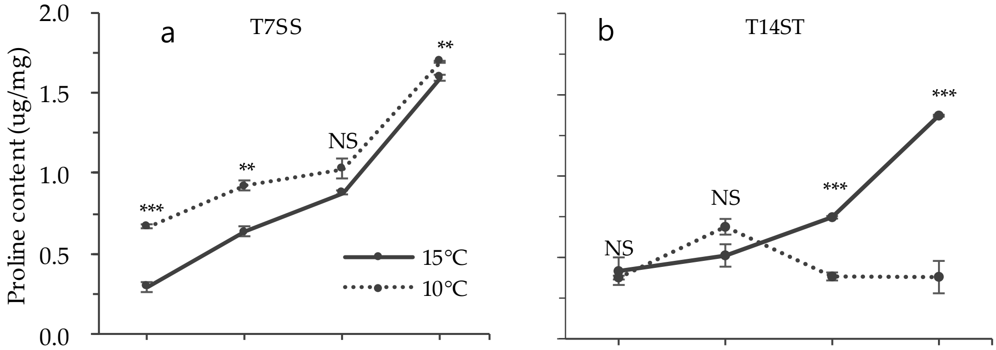


Figure 4. Changes in electrolyte conductivity in the leaves of cherry type accessions sensitive (a) and tolerant (b), and of large fruit type accessions sensitive (c) and tolerant to low night temperature (d) grown in 10 and 15 °C, respectively. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Values are means ± SE (n = 3). NS, * and ** indicate not significant and significant at the P≤0.05 and P≤0.01 levels in T-test, respectively.

Accumulation pattern of free total proline was clearly different between cherry and large fruit type accessions in both 10 °C than 15 °C night temperature conditions (Figure 5). In 15 °C, proline content continuously increased in cherry types, T7SS (Figure 5a) and T14ST (Figure 5b) but did not show much change in large fruit types, T24SS (Figure 5c) and T27LT (Figure 5d). However, the proline content of LNT sensitive accession showed continuous increase in 10 °C, significantly higher than 15 °C (Figure 5a), but that of LNT tolerant one showed little changes, significantly lower than 15 °C from 90 DAT (Figure 5b). In large fruit types, proline content in 10 °C significantly was higher in a tolerant accession (Figure 5d) but fluctuated in a sensitive accession (Figure 5c).



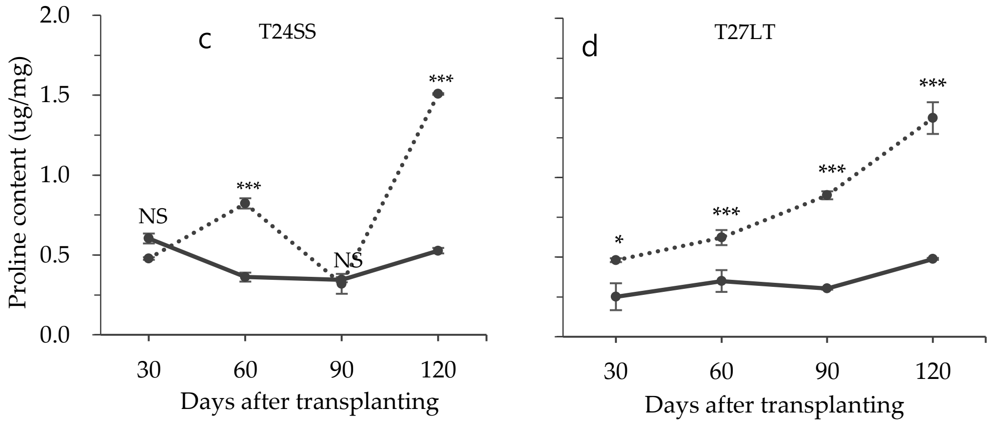
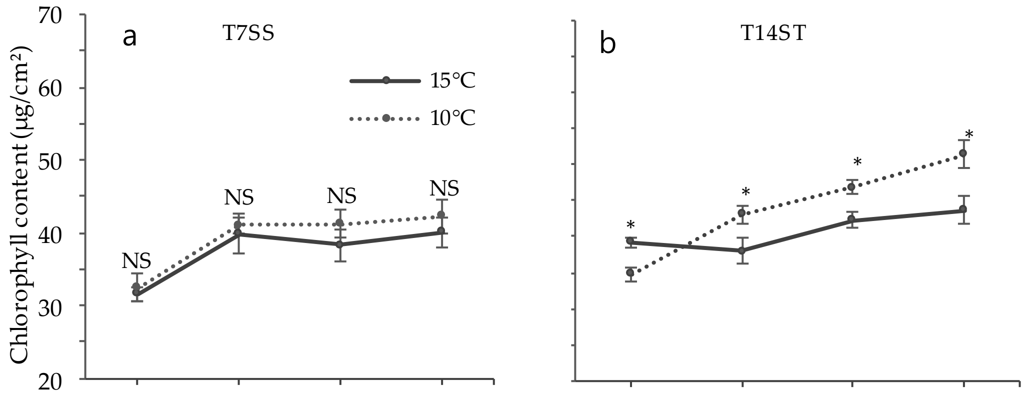


Figure 5. Changes in proline contents in the leaves of cherry type accessions sensitive (a) and tolerant (b), and of large fruit type accessions sensitive (c) and tolerant to low night temperature (d) grown in 10 and 15 °C, respectively. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Values are means ± SE (n = 3). NS, *, ** and *** indicate not significant and significant at the P ≤ 0.05, P ≤ 0.01 and P ≤ 0.001 levels in T-test, respectively.

Chlorophyll content was significantly higher in later growth stages in LNT tolerant accessions grown in 10 °C but not in sensitive ones (Figure 6). In cherry type, no clear difference in chlorophyll content between 10 and 15 °C was observed in T7SS but it was significantly higher in T14ST grown in 10 °C than that in 15 °C from 60 DAT. Similarly in large fruit types, Chlorophyll content of T24LS in 10 °C was significantly higher only in 120 DAT (Figure 6c) but that of T27LT was significantly higher from 90 DAT (Figure 6d).



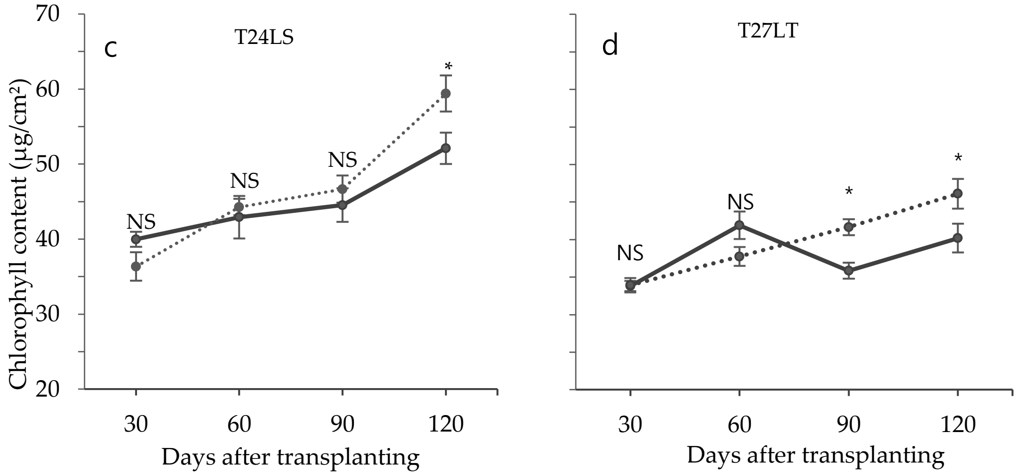
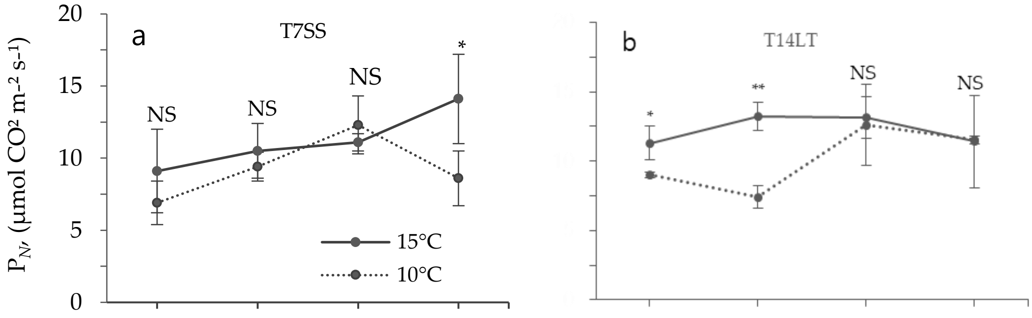


Figure 6. Changes in chlorophyll contents in the leaves of cherry type accessions sensitive (a) and tolerant (b), and of large fruit type accessions sensitive (c) and tolerant to low night temperature (d) grown in 10 and 15 °C, respectively. SS: small sensitive, ST: small tolerant, LS: large sensitive and LT: large tolerant. Values are means ± SE (n = 3). NS, *, ** and *** indicate not significant and significant at the P ≤ 0.05, P ≤ 0.01 and P ≤ 0.001 levels in T-test, respectively.

3.3. Photosynthetic activity

Photosynthetic rate, stomatal conductance, transpiration rate and intercellular CO_2 concentration was generally lower at the early growth stages in all accessions and no clear pattern of difference between LNT sensitive and tolerant accessions except for photosynthetic rate, which was significantly lower in LNT tolerant accessions during early growing period (Figures 7 & 8). In cherry type, photosynthesis was significantly lower in 10 °C only at 120 DAT in T7SS (Figure 7a) but from 30 to 60 DAT in T14LT (Figure 7b). Stomatal conductivity was significantly lower in in 10 °C at 30 to 60 DAT and then no difference was observed in 90 DAT in both accessions (Figures 7c & d); however, it was significantly lower again in T7SS at 120 DAT (Figure 7c). Exactly same pattern was observed in transpiration rate (Figures 7e and f). There was no significant difference in intercellular CO_2 concentration between 10 and 15 °C in both T7SS (Figure 7g) and T14ST (Figure 7h), except for 60 DAT in T7SS (Figure 7g).



doi:10.20944/preprints202106.0390.v1

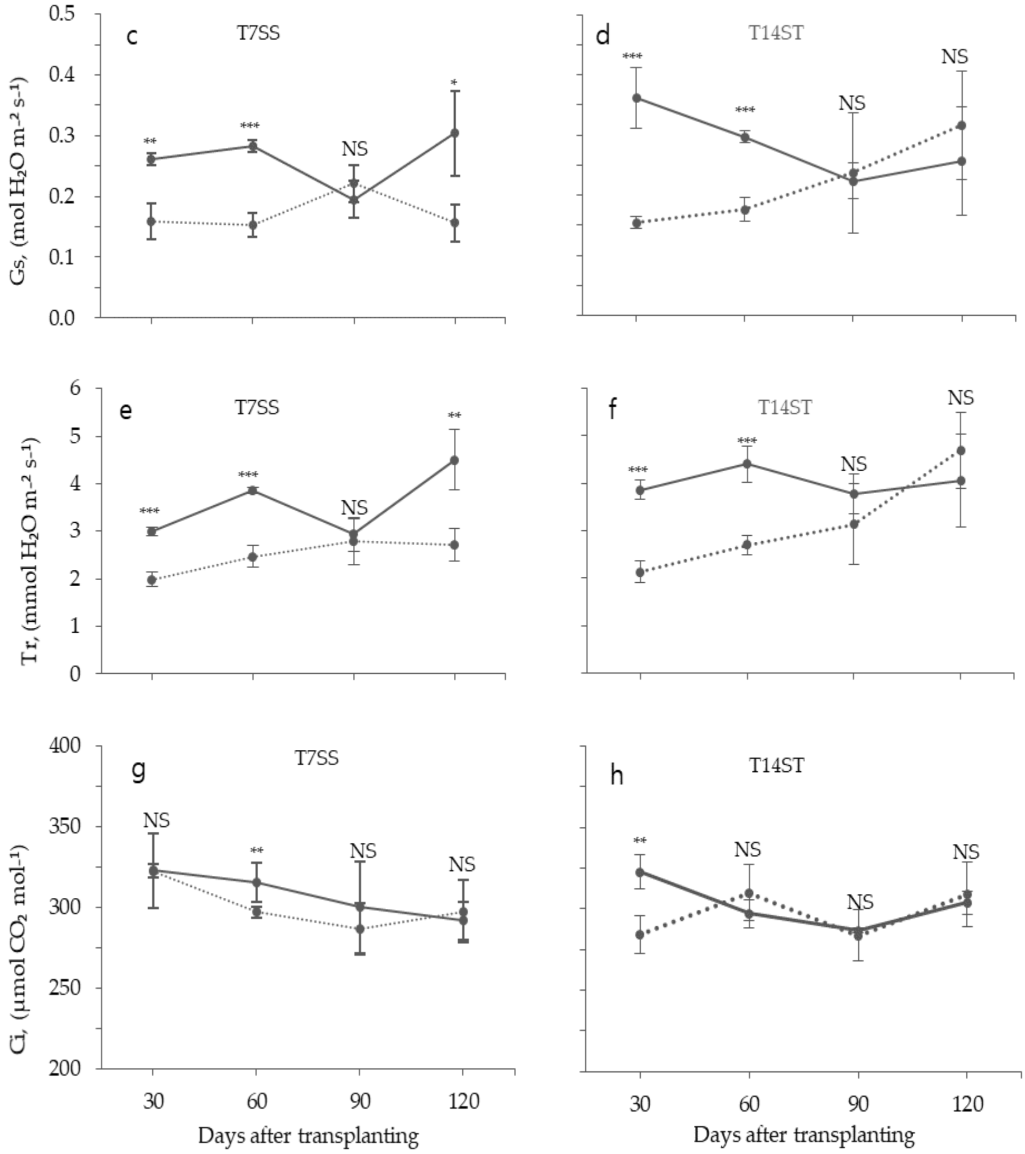


Figure 7. Changes in photosynthetic parameters of cherry fruit type accessions with sensitive and tolerant to low night temperature grown in 10 and 15 °C. P_N- Photosynthesis rate (a, b) Gs- stomatal conductance (c, d), Tr- transpiration rate (e, f) and Ci- intercellular CO_2 concentration (g, h) were presented for sensitive and tolerant accessions, respectively. 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.

In large fruit types, photosynthesis was significantly lower in 10 °C only at 60 DAT in T24LS (Figure 8a) but from 30 to 60 DAT in T27LT (Figure 8b). Exactly same patterns as cherry types ((Figures 7c, d, e & f) were observed in stomatal conductance and transpiration rate of large fruit types (Figures 8c, d, e & f). There was no clear difference between 10 and 15°C in intercellular CO_2 concentration of T24LS (Figure 8g) in all growing period but significantly differ in 30 and 60 DAT in T27LT (Figure 8h).

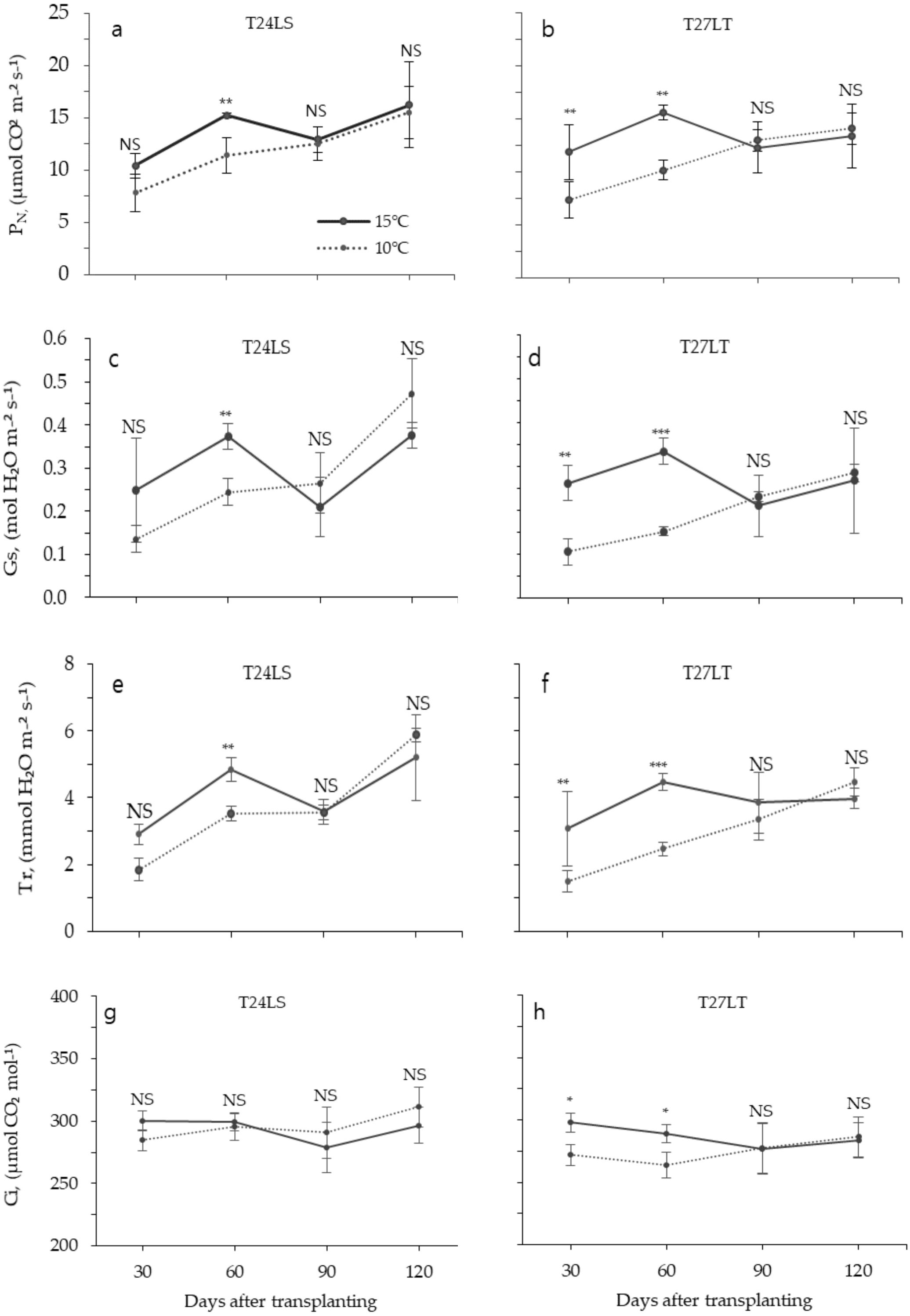


Figure 8. Changes in photosynthetic parameters of large fruit type accessions with sensitive and tolerant to low temperature grown in 10 and 15 °C. P_N- Photosynthesis rate (a, b) Gs- stomatal conductance (c, d), Tr- transpiration rate (e, f) and Ci- intercellular CO_2 concentration (g, h) were presented for sensitive and tolerant accessions, respectively. 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 cultivation physiology and, therefore, may have different mechanisms to deal with low temperatures. Although

doi:10.20944/preprints202106.0390.v1

several mechanisms for the survival of tomato plants were suggested under artificially induced low temperature conditions [4,5,25,26,33,34], these researches have been conducted during relatively short period and without the consideration of fruit types. Besides, most studies have did not consider night temperature that can be practical breeding target for reducing heating cost in winter tomato cultivation. In the present study, different fruit types tolerant or sensitive to LNT were grown for sufficiently long period in 10 and 15°C.

The number of flowers was significantly affected by LNT in cherry fruit types, but not in large fruit types regardless of LNT tolerant and sensitive accessions (Figure 2a), showing fruit type specific responses. For fruit set, however, sensitive accessions in both cherry and large fruit types showed significant reduction (Figure 2b). These results imply that the effect of LNT on the number of flowers is genotype specific. Also, high fruit set ratio gives to tomato plants LNT tolerance in both fruit types. 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 [11,35]. In the present study, floral morphology of LNT tolerant accessions was phenotypically normal whereas that of LNT sensitive accessions was not (Figure 3).

Tomato plants subjected to low temperatures frequently suffer membrane damage, which can be evaluated by the relative electrolyte leakage [4,19,23]. However, the effect of EC on tomato LNT tolerance remains in question since there was no clear pattern in EC between sensitive and tolerant accessions (Figure 4). This may be due to the difference in relatively high temperature set point for low temperature, 10 °C, in this experiment compared to previous studies. Besides, EC within 30 DAT, in the early growth stage, was highest and gradually decreased in subsequent stages ‘fruit developing’ and ‘maturing’ regardless of LNT tolerance or sensitivity.

Previous studies have demonstrated a pivotal role of proline under abiotic stress in tomato plants [21-23,34]. Our results showed the different accumulation pattern between cherry and large fruit types in both 10 and 15 °C (Figure 5). The sharp increase in proline content of cherry (Figures 5a & b) but not of large fruit types (Figures 5c & d) in 15 °C implies the innate sensitivity to LNT in cherry type tomato. The different proline accumulation patterns between LNT tolerant cherry and large fruit types also imply there may be different LNT tolerance mechanisms depending on tomato fruit types. The lower proline content in later growth stages may be related to active proline degradation by proline dehydrogenase which may give a cherry type tomato plant resistance to stress [22]. Further study is 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 6). Previous studies reported the reduction in the chlorophyll content after cold treatment in tomato plant leaves in the short term [4,19,25,34], which was observed in the present study in some cases (Figures 6b & c). In the long term, however, plants in 10 °C condition showed higher chlorophyll contents (Figure 6) than those in 15 °C [8] and it was more prominent in LNT tolerant accessions (Figures 6b & d).

The plant growth of all four accessions was significantly delayed in LNT condition (Figure 1), similar to the previous researches on low temperature [8,25,33,36]. This is because decreased photosynthetic activity in all tomato accessions in the early growth stages (Figures 7 & 8). However, the difference in plant height between 10 and 15 °C was scarcely narrowed although photosynthetic activity in LNT was restored in subsequent fruit maturing stage regardless of accessions (Figures 7 & 8). The restoration of photosynthetic activity was partly due to that of stomatal conductance and transpiration rate (Figures 7 & 8). Our results in accordance with a previous study reporting that plant height correlated with photosynthetic rate [25]. Considering increased photosynthetic rate in the later growth stages, further study is need to investigate the correlation between photosynthetic rate and fruit weight in the early and late growth stage in order to study the relationship between photosynthesis and fruit harvest.

doi:10.20944/preprints202106.0390.v1

5. Conclusions

The present study suggests tomato fruit types have different physiological responses to LNT and, therefore, may have different mechanisms for LNT tolerance, which are practical target for reducing heating cost. It may be related to proline accumulation patterns that differ by fruit types. More detailed experimental designs and large set of tomato accessions are necessary for dissecting mechanisms underlying LNT tolerance among different tomato fruit types in the future.

Supplementary Materials: Figure S1: The ambient average air temperature in 10 and 15 °C greenhouses during the period of tomato growth and development.

Author Contributions: Conceptualization, M.C. and E.Y.; methodology, E.Y., M.C., and S.N.R.; investigation, S.N.R., and H.J.; data curation, S.N.R. and W.C.; writing—original draft preparation, S.N.R. and W.C.; writing—review and editing, W.C.; visualization, W.C., and S.N.R.; supervision, E.Y., and H.J. All authors have read and agreed to the published version of the manuscript.

Funding: This study was supported by a grant (Project No: PJ01266202 “Breeding and selection of tomato lines with tolerance to abnormal temperatures”) from the National Institute of Horticultural and Herbal Science, Rural Development Administration, South Korea.

Data Availability Statement: The datasets presented in this study are available to request from the corresponding author.

Conflicts of Interest: The authors declare no conflict of interest.

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.

References

1. Mahajan, S.; & Tuteja, N. Cold, salinity and drought stresses: An overview. Arch. Biochem. Biophys. **2005**, 444, 139–158.
2. Hoek, H.I.S.; Hanisch Ten Cate, C.H.; Keijzer, C.J.; Schel, J.H.; Dons, H.J.M. Development of the fifth leaf is indicative for whole plant performance at low temperature in tomato. Ann. Bot. **1993,** 72, 367–374.
3. Venema, J.H.; Posthumus, F.; de Vries, M.; van Hasselt, P.R. Differential response of domestic and wild Lycopersicon species to chilling under low light: growth, carbohydrate content, photosynthesis and the xanthophyll cycle. J. Physiologia Plantarum **1999**, 105, 81–88.
4. Liu, H.; Ouyang, B.; Zhang, J.; Wang, T.; Li, H.; et al. Differential Modulation of Photosynthesis, Signaling, and Transcriptional Regulation between Tolerant and Sensitive Tomato Genotypes under Cold Stress. PLoS ONE **2012**, 7(11), e50785. http://doi:10.1371/journal.pone.0050785
5. Chen, H.; et al. A comparison of the low temperature transcriptomes of two tomato genotypes that differ in freezing tolerance: Solanum lycopersicum and Solanum habrochaites. BMC Plant Biology **2015,** 15, 132. http://doi:10.1186/s12870-015-0521-6
6. Wittwer, S.H.; Tuebner, F.G. Cold exposure of tomato seedlings and flower formation. J. Am. Soc. Hortic. Sci. **1957**, 67, 369–376.
7. Hurd, R.G.; Graves, C.J. Some effects of air and root temperatures on the yield and quality of glasshouse tomatoes. J. Hortic. Sci. **1985,** 60, 359–371.
8. Rajametov, Sh.; Yang, E.Y.; Cho, M.C.; Chae, S.Y.; Kim, J.H.; Nam, C.W.; & Chae, W.B. Traits Affecting Low Temperature Tolerance in Tomato and its Application to Breeding Program. J. Plant Breed. Biotech. **2019**, 7 (4), 350-359.
9. Calvert, A. Effect of the early environment on development of flowering in the tomato. I. Temperature. J. Hortic. Sci. **1957**, 32, 9–17.

doi:10.20944/preprints202106.0390.v1

10. Rylski, I. Fruit set and development of seeded and seedless tomato fruits under diverse regimes of temperature and pollination. J. Am. Soc. Hortic. Sci. **1979**, 104, 835–838.
11. Picken, A.J.F. A review of pollination and fruit set in the tomato (Lycopersicon esculentum Mill.) J. Hortic. Sci. **1984**, 59, 1-13.
12. Ercan, N.; and Vural, H. The effects of low temperatures on fruit set of tomatoes. Acta Horticulturae, **1994**, 36, 65-72.
13. Graham, D.; and Patterson, B.R. Responses of plants to low, nonfreezing temperatures: proteins, metabolism, and acclimation. Ann. Rev. Plant Physiol. **1982**, 33, 347-372.
14. Foolad, M.; Lin, G. Relationship between cold tolerance during seed germination and vegetative growth in tomato: germplasm evaluation. J. Am. Soc. Hortic. Sci**. 2000,** 125, 679–683.
15. Zhang, X.; Fowler, S.G.; Cheng, H.; Lou, Y.; Rhee, S.Y.; et al. Freezing-sensitive tomato has a functional CBF cold response pathway, but a CBF regulon that differs from that of freezing-tolerant Arabidopsis. Plant J. **2004**, 39, 905–919.
16. Yu, C.; Wang, H.S.; Yang, S.; Tang, X.F.; Duan, M.; Meng, Q.W. Overexpression of endoplasmic reticulum omega-3 fatty acid desaturase gene improves chilling tolerance in tomato. Plant Physiol Biochem **2009**, 47, 1102–1112
17. Miura, K.; Shiba, H.; Masaru, O.M.; Kang, S.W.; Sato, A.; Yuasa, T.; Iwaya-Inoue, M.; Kamada, H.; Ezura, H. SlICE1 encoding a MYC-type transcription factor controls cold tolerance in tomato, Solanum lycopersicum. J. Plant Biotech. **2012**, 29, 253–260. DOI: 10.5511/plantbiotechnology.12.0303a
18. Campos, P.S.; Quartin, V.; Ramalho, J.C.; Nunes, M.A. Electrolyte leakage and lipid degradation account for cold sensitivity in leaves of Coffea sp. plants. J. Plant Physiol. **2003**, 60, 283–292.
19. Munir, S.; Liu, H.; Xing, Y.; Hussain, S.; Ouyang, B.; Zhang, Y.; Li, H.; & Ye, Zh. Overexpression of calmodulinlike (ShCML44) stress-responsive gene from Solanum habrochaites enhances tolerance to multiple abiotic stresses. Sci. Rep. **2016**, 6, 31772; doi:10.1038/srep31772.
20. Hu, T.; Wang, Y.; Wang, Q.; Dang, N.; Wang, L.; Liu, Ch.; Zhu, J.; & Zhan, X. The tomato 2-oxoglutarate-dependent dioxygenase gene SlF3HL is critical for chilling stress tolerance. J. Hortic. Res. **2019**, 6, 45. https://doi.org/10.1038/s41438-019-0127-5
21. Claussen, W. Proline as a measure of stress in tomato plants. J. Plant Science **2005,** 168, 241-248.
22. Rosales, M.A.; Ríos, J.J.; Castellano, R.; López-Carrión, A.I.; Romero, L.; & Ruiz, J.M. Proline metabolism in cherry tomato exocarp in relation to temperature and solar radiation. J. Hortic. Sci. & Biotech. **2007**, 82(5), 739-744. DOI:10.1080/14620316.2007.11512299
23. Ding, F.; Liu, B.; Zhang, Sh. Exogenous melatonin ameliorates cold-induced damage in tomato plants. J. Scientia Horticulturae **2017**, 219, 264–271.
24. Janssen, L.H.J.; Van Oeveren, J.C.; Van Hasselt, P.R.; and Kuiper, P.J.C. Genotypic variation in chlorophyll fluorescence parameters, photosynthesis and growth of tomato grown at low temperature and low irradiance. Photosynthetica **1995,** 31, 301-314.
25. Xiaoa, F.; Yang, Z.; Zhua, L. Low Temperature and Weak Light Affect Greenhouse Tomato Growth and Fruit Quality. J. Plant Sci. **2018**, 6(1), 16-24. http://doi:10.11648/j.jps.20180601.14
26. Hu, W.H.; Zhou, Y.H.; and Du, Y.S. Differential response of photosynthesis in greenhouse-and field-ecotypes of tomato to long-term chilling under low light. Journal of Plant Physiology **2006**, 163, 1238-1246.
27. Fang, X.; Zaiqiang, Y.; Liyun, Z. Low temperature and weak light affect greenhouse tomato growth and fruit quality. J. Plant Sci. **2018**, 6, 16-24.
28. Goodstal, F.J.; Kohler, G.R.; Randall, L.B.; Bloom, A.J.; St Clair, D.A. A major QTL introgressed from wild Lycopersicon hirsutum confers chilling tolerance to cultivated tomato (*Lycopersicon esculentum*). J. Theor. Appl. Genet. **2005**, 111, 898–905.

---

29. De Koning, A.N.M. The effect of different day/night temperature regimes on growth, development and yield of glasshouse tomatoes. J. Hortic. Sci. **1988**, 63, 465–471.
30. Elings, A.; Kempkes, F.L.K.; Kaarsemaker, R.C.; Ruijs, M.N.A.; Van De Braak, N.J.; Dueck, T.A. The energy balance and energy-saving measures in greenhouse tomato cultivation. Acta Hortic. **2005**, 691, 67–74.
31. Rajametov, S.; Yang, E.Y.; Cho, M.C.; Chae, S.Y.; Chae, W.B. Physiological traits associated with high temperature tolerance differ by fruit types and sizes in tomato (*Solanum lycopersicum* L.). *Hortic. Environ. Biotechnol*. **2020**, *61*, 837–847.
32. Camejo, D.; Rodrı´guez, P.; Angeles Morales, M.; et al. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. Plant Physiol. **2005**, 162, 281–2896.
33. Choudhury, F.K.; Rivero, R.M.; Blumwald, E.; & Mittler R. Reactive oxygen species, abiotic stress and stress combination. J. Plant **2017**, 90, 856–867.
34. Ghorbanpour, A.; Salimi, A.; et al. The effect of Trichoderma harzianum in mitigating low temperature stress in tomato (*Solanum lycopersicum* L.) plants. J. Scientia Hortic. **2018**, 230, 134–141.
35. Fernandez-Munoz, R.; and Cuartero, J. Effects of temperature and irradiance on stigma exertion, ovule viability and embryo development in tomato. J. Hortic. Sci. **1991**, 66, 395-401.
36. Crafts-Brandner, S.J.; and Salvucci, M.E. Sensitivity of photosynthesis in a C4 plant, maize, to heat stress. J. Plant Physiol. **2002**, 129, 1773-1780.