

Article

Physiological Traits of Thirty-Five Tomato Accessions (*Solanum lycopersicum* L.) in Response to Low Temperature

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Abstract: Tomato is exposure to diverse abiotic stresses. Cold stress is one of harsh environmental stresses and abnormal low temperature affects tomato growth and development including physiological disorders, flower drops, and abnormal fruit morphology, causing the decrease of tomato yield and a fruit quality. It is important to identify low temperature-(LT) tolerant tomato (*Solanum lycopersicum* L.) cultivars relying on different fruit types. This study focused on analyzing physiological traits of 35 tomato accessions with three different fruit types (cherry, medium, and large sizes) under night temperature set-points of 15°C for normal temperature (NT) and 10°C for LT, respectively. Plant heights (PH) of most tomato accessions in LT were remarkably decreased compared to those in NT. The growth of leaf length (LL) and leaf width (LW) was reduced depending on the genotypes under LT. In addition, the number of fruits (NFR), fruit set (FS), fruit yield (FY), and marketable yield (MY) were negatively affected in LT. The variation was further investigated by the correlation analysis, the principal component (PCA), and the cluster analysis. Interestingly, positive correlations between different vegetative and reproductive traits were uncovered. Multivariate analysis including the PCA and hierarchical clustering classified LT-treated 35 tomato accessions into four major groups. The identified accessions were associated with vegetative and reproductive parameters on positive directions and might be utilized for breeding programs on selecting LT-tolerant cultivars.

Keywords: Tomatoes; Night low temperature; Fruit types; Physiological traits; Tomato breeding; Principal component analysis; Cluster analysis

1. Introduction

Tomato plant (*Solanum lycopersicum* L.) is one of sessile organisms, which experiences multiple abiotic stresses including cold stress, heat stress, high salinity stress, and drought stress during the periods of vegetative and reproductive growth [1-4]. The importance of tomato crops has been gradually increasing and the cultivation area of tomatoes is widely expanded among agricultural crops. According to Food and Agriculture Organization (FAO, <http://www.fao.org/faostat/>) in 2019 and Korean Statistical Information Service (KOSIS, <https://kosis.kr/eng/>) in 2021, the cultivation area and tomato production reached approximately 4.8 million hectares and 182 million metric tons in the world and around six thousand hectares and four hundred four hundred twenty thousand metric tons in South Korea, respectively. However, owing to global warming and climate changes, the unpredictable agriculture weather such as low and high temperatures have critically limited the yields and the area of agricultural cultivation in tomato plants [5-8].

Low temperature (LT) is a critical factor for maintaining and improving the crop yield of tomato plants (*Solanum lycopersicum* L.) during the periods of growth and development stages [5,7]. LT (0-20°C) above the freezing temperature (below 0°C), which referred to sub-optimal temperature [5,9], plays an important role in the leaf morphology

[10], the truss appearance and growth [10-13], and the fruit development [14-17] during vegetative and reproductive stages. Recent diverse studies have demonstrated that LT significantly influenced plant height (PH), plant diameter (PD), leaf length (LL), and leaf width (LW) in vegetative parameters [10,12,18,19] and flowering time (FT) [18,20], the number of flowers (NFL) and fruits (NFR) [18,20,21], fruit set (FS) [21], and fruit yield (FY) [18,21,22] in reproductive parameters. Moreover, the relationships of the same traits during either vegetative or reproductive stages have been investigated under high temperature (HT) conditions [23,24] but the correlation of vegetative traits with reproductive traits remain unexplored under LT condition.

The temperature control is one of the essential factors for the tomato cultivation in greenhouse condition and approximately 15°C in winter is maintained for the optimal temperature set-points, which provide tomatoes to grow healthy without severe cold stress [10,25,26]. The studies on optimal temperature set-point have reported that the reduction of temperature by around 2°C in greenhouse was able to decline around 16% of winter heating cost in tomato cultivation [18,27], implying that the temperature lowering from 15°C to 10°C in winter greenhouse would lead to the significant decrease in the heating cost of tomato cultivation in agriculture. As well as, heating demand is increased at night time in winter greenhouse compared to the daytime [28,29]. However, a few studies have been dissected in the relationship of physiological traits and night low temperature (NLT) [18,28,29]. Thus, it is reasonable that practical breeding programs for low temperature (LT)-tolerant tomato cultivars economically considers keeping low temperature (10°C) during the night.

It is essential to utilize the large number of genotypes with various fruit types to provide proper indices to breeders for selecting LT-tolerant tomatoes. Although a few of studies were performed with more than twenty genotypes [5,18], most studies have been determined in the impact of the LT with limited genotypes, ranging from one to fifteen genotypes [18,19]. A few of studies have been reported in the selection criteria for LT-tolerant cultivars depending on different fruit types and it is still required to prove that the physiological characterizations and mechanisms in response to LT with the large-scale accessions and different fruit types of tomatoes.

In this work, we investigated the physiological traits of 35 tomato genotypes with different fruit types, which were grown in two different greenhouse conditions with night temperature set-points at 10°C for low temperature (LT) and 15°C for normal treatment (NT), respectively, and analyzed the vegetative parameters of PH, SD LL, and LW and the reproductive parameters of NFL, NFR, FS, FY, and MY with different fruit types through the correlation coefficient, PCA, and cluster analysis.

2. Materials and Methods

2.1. Plant material and growth conditions

The plant material and growth conditions were followed as previously described in Rajametov et al. [2019]. Total 35 of tomato breeding lines from National Institute of Horticultural and Herbal Science (NIHHS) (Wanju, South Korea) were used in this research (Table 1). All accessions were classified into two wild (<10 g), twenty cherry (10-30 g), eleven medium (31-80 g), and two large (>81 g) depending on fruit sizes [18]. The seeds of 35 accessions were sown on 31 August, 2020 in plastic trays (52 x 26 cm in size, 6 x 6 cm cells with pot volume 5 liter) containing 1:1 sand and commercial bed soil (Bio Sangto, Seoul, Korea) containing 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 provided to each tray daily, and the trays were placed in a glasshouse (26/18 °C in day/night with relative humidity within 65-70%). Seedlings with 20-25 cm height and first truss were transplanted on 28 October, 2020. The seedlings were transferred into two plastic film greenhouses, where night temperature set-point was maintained at 15°C for 14 days in both greenhouses, adapting the seedlings to new environment conditions. Subse-

quently, night temperature set-point of each greenhouse was controlled for low temperature (LT) at 10 °C and normal treatment (NT) at 15°C, respectively. Tomato seedlings of five plants per accession were planted with a plant distance of 140 cm by 40 cm between plants in both LT and NT greenhouses. All tomato accessions were randomly selected and planted with keeping the same arrangement of the accessions between LT and NT greenhouses.

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 K₂O, and 16 g m⁻² P₂O₅ and regularly watered to avoid drought and fertilized weekly with solution A (N 5.5%, K 4.5%, Ca 4.5%, B 0.00014%, Fe 0.05%, Zn 0.0001%, Mo 0.0002%) and B (N 6%, P 2%, K 4%, Mg 1%, B 0.05%, Mn 0.01%, Zn 0.005%, Cu 0.0015%) mixed in 1200 liter of water (Mulpure, Daeyu Co. Ltd., Gyeongsan, South Korea).

The temperature was monitored in both LT and NT greenhouses during the periods of whole growth and development using data logger (Figure S1) (WatchDog 1450, Spectrum Technologies Inc., Aurora, USA). Night time temperature was maintained by heating machine (Model TKP-800, Tae Kwang Machine Co. LTD., Daegu, South Korea) when the temperature went down below 10 °C and 15 °C and overall the relative humidity (RH) was approximately within 40% to 60% in both greenhouses, respectively.

2.2. Data collection on vegetative and reproductive growth

The vegetative parameters of plant height (PH), leaf length (LL), leaf width (LW), and stem diameter (SD) were measured using 70-d-old plants after transplanting (DAT) from five plants per accession in both greenhouses. The reproductive parameters of the number of flowers (NFL), the number of fruits (NFR), fruit set (FS), fruit yield (FY), marketable yield (MY), and output of marketable yield (OMY) were evaluated by calculating from the third to six trusses of each plant. Differences in FS and FY parameters between plants grown in 10°C and 15°C greenhouses were calculated by subtracting index of FS and FY of NT from LT, respectively [18]. Fruit set (FS, %) with diameter ≥ 0.5 cm was calculated as follows [6]: Fruit set (%) = (The number of fruits / The number of flowers) × 100. In addition, fruit yield (FY) was determined by the sum of fresh weight (FW) in kg of all fruits harvested from the third to sixth trusses from five individual plants.

2.3. Data analysis

The significance of difference in vegetative parameters of PH, SD, LL, and LW, and reproductive parameters of NFL, NFR, FS, TY, MY, and OMY under LT and NT was assessed as described in the figure legends with student's *t*-test and the analysis of correlation coefficients was performed among total population (n = 35) for correlation coefficient with EXCEL 2016 (Microsoft, WA, USA). Principal components analysis (PCA) was implemented using SPSS (IBM SPSS v27.0., Chicago, USA) to study the sample patterns and cluster analysis. The adequacy of the samples was tested by The Kaiser-Meyer-Olkin (KMO) and the Bartlett's test of Sphericity (BTS) was conducted to estimate the relationship between variables.

3. Results

3.1. The analysis of the vegetative traits with different fruit type

To study the vegetative traits including plant height (PH), stem diameter (SD), leaf length (LL), and leaf width (LW) in tomato plants under LT condition, we analyzed 35 tomato accessions with different fruit types classified into wild, cherry, medium, and large fruit size (Table S1). The PH of most tomato accessions in LT were remarkably reduced at 70 days after transplanting (DAT) compared to those in NT except for T32 accession in medium size (Figure 1A), while SD in LT were not significantly different from those in

NT except for T21 accession in cherry size (Figure 1B). Next, the LL and LW were investigated at 70 DAT and 25 tomato accessions were decreased in LT, whereas 10 tomato accessions including T04, T07, T09, T12, T13, T19, and T22 in cherry size, T28 and T31 in medium size, and T35 in large size were not significantly influenced by LT (Figure 2A and 2B).

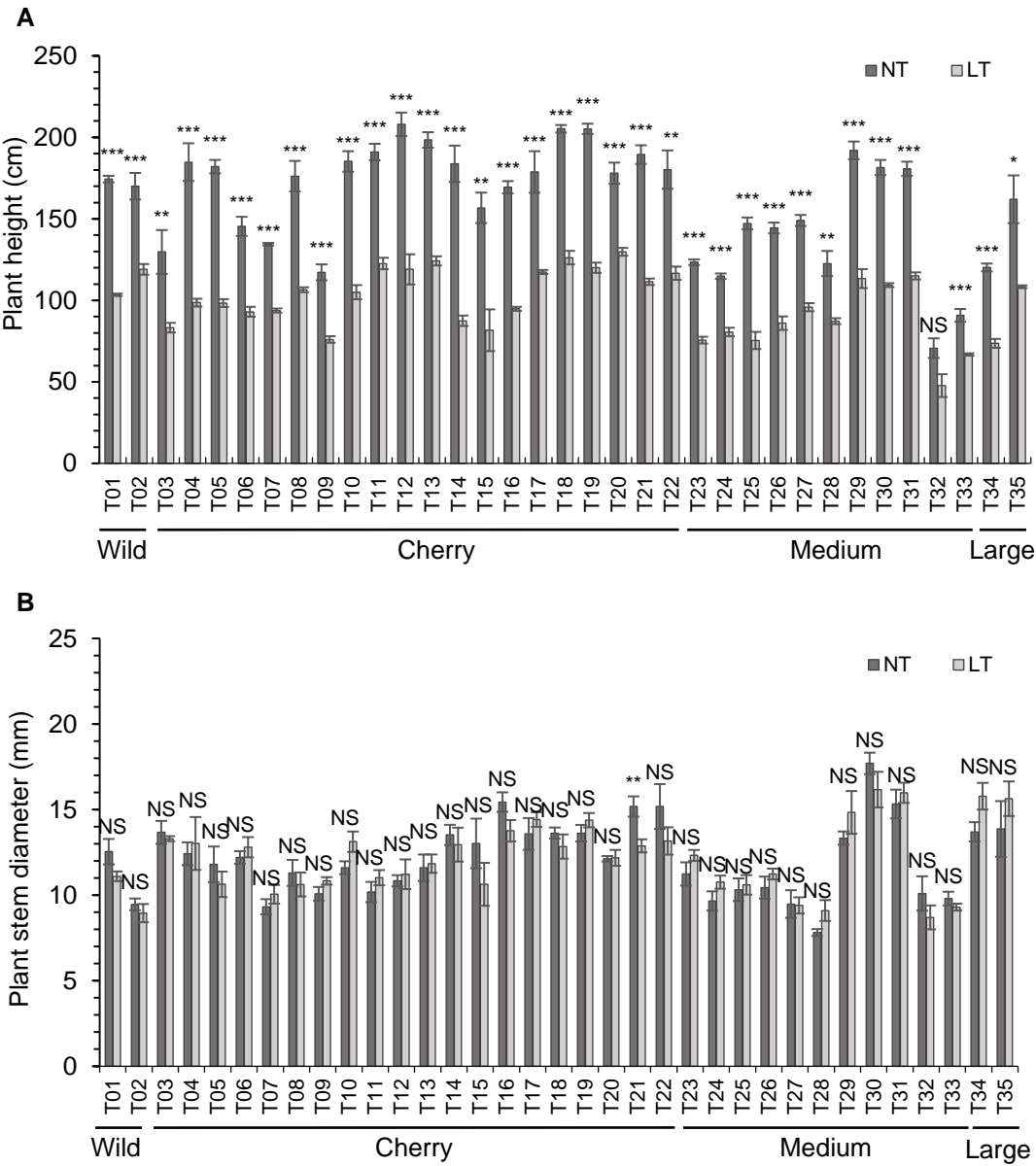


Figure 1. The analysis of vegetative traits on (A) plant height and (B) plant stem diameter among 35 tomato accessions with different fruit types under NT and LT greenhouses. Plant height and stem diameter were measured at 70 days after transplanting. Significant differences were evaluated with student's *t*-test ($p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$) and denoted by *, **, and ***, respectively. NS indicates not significant and bars indicate \pm standard deviation ($n = 5$).

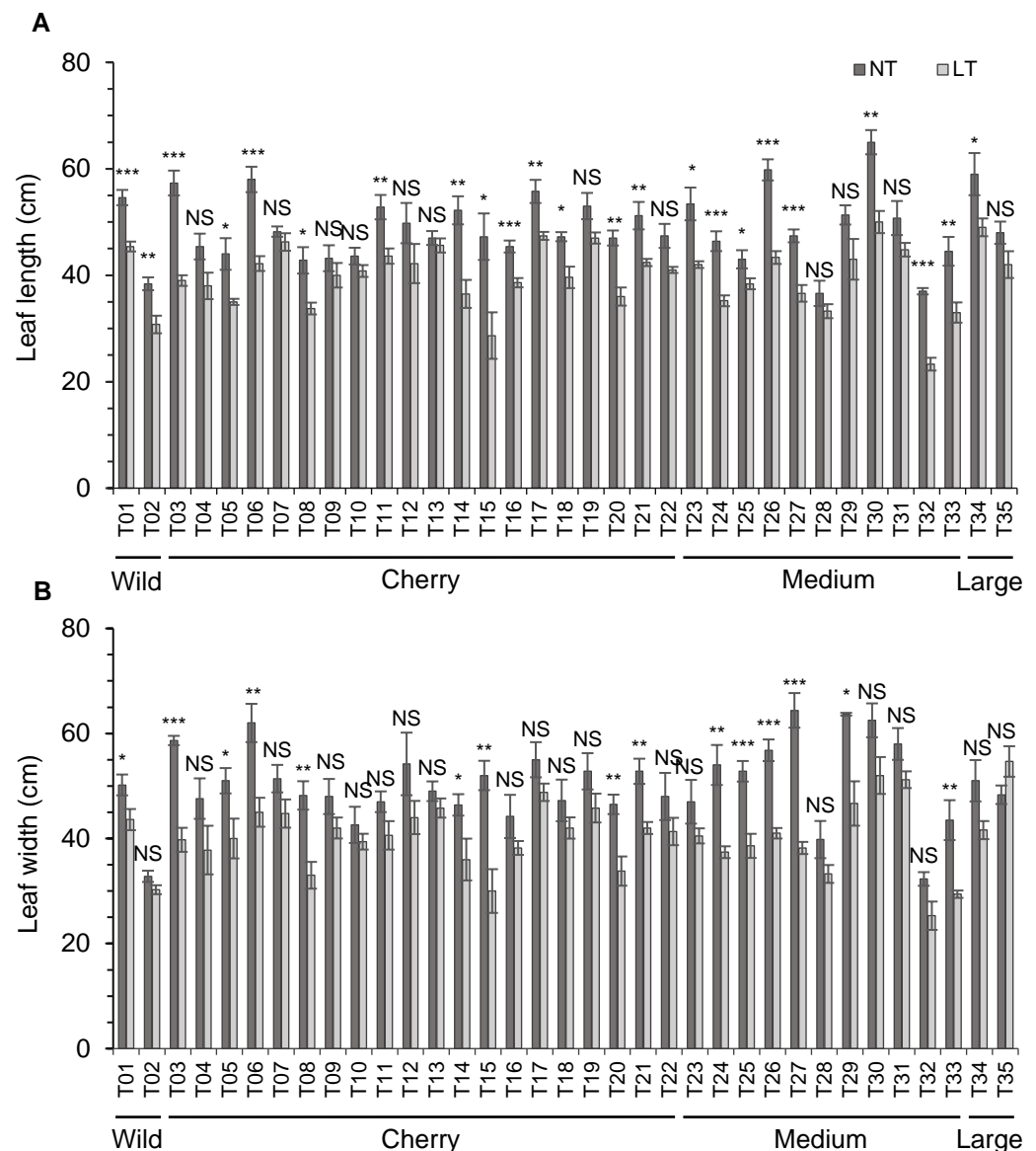


Figure 2. The analysis of vegetative traits on (A) leaf length and (B) leaf width among 35 tomato accessions with different fruit types under NT and LT greenhouses. Leaf length and width were measured at 70 days. Significant differences were evaluated with student's t-test ($p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$) and denoted by *, **, and ***, respectively. NS indicates not significant and bars indicate \pm standard deviation ($n = 5$).

3.2. The analysis of the reproductive traits with different fruit type

The reproductive traits including the number of flowers (NFL), the number of fruits (NFR), fruit set (FS), fruit yield (FY), and marketable yield (MY) were evaluated among 35 tomato accessions under LT and NT condition. The NFL of T04 and T20 accessions in LT positively increased, whereas the NFL of T15, T29, and T31 accessions in LT was negatively decreased compared to that in NT condition (Figure 3A). The NFR was also assessed among 35 tomato populations. Only T11 accession in cherry type was increased in LT more than that in NT, whereas 2 genotypes (T01 and T02) in wild, 13 genotypes (T04, T08, T09, T10, T14, T15, T16, T17, T18, T19, T20, T21, and T22) in cherry size, 4 genotypes (T27, T30, T31, and T33) in medium size, and 1 (T35) in large size under LT were remarkably reduced compared to that of NT (Figure 3B). On the other hand, 7 genotypes (T03, T05, T06, T07, T12, and T13) in cherry type, 7 genotypes (T23, T24, T25, T26, T28, T29, and

T32) in medium, and 1 genotype (T34) in large type were identified in no significant difference between LT and NT conditions (Figure 3B). In addition, the fruit set (FS) ratio was calculated with all tomato accession. Interestingly, the FS of only T11 accession in cherry type was significantly higher in LT than that in NT (Figure 3C). In contrast to this, 2 genotypes (T01 and T02) in wild, 15 genotypes (T04, T07, T08, T09, T10, T12, T14, T15, T16, T17, T18, T19, T20, and T21, T22) in cherry type, 3 genotypes (T27, T30, and T31) in medium type, and 2 genotypes (T34 and T35) in large type under LT were dramatically decreased compared to those in NT (Figure 3C). 4 genotypes (T03, T05, T06, and T13) in cherry type, 7 genotypes (T23, T24, T25, T26, T28, T29, and T32) in medium type were observed with no significant difference in both NT and LT conditions.

In order to estimate the fruit marketability, the reproductive traits including fruit yield (FY), marketable yield (MY), and output marketable fruit (OMF) were determined among 35 tomato populations. The FY and MY were drastically reduced in 8 genotypes (T04, T05, T08, T09, T15, T16, T18, and T21) in cherry type, 5 genotypes (T23, T25, T27, T31, and T33) in medium type, and 2 genotypes (T34 and T35) in large type under LT compared to NT, whereas FY was noticeably increased in T24 in medium type in LT (Figure 4A and 4B). It was remarkable that the OMF over 60% between LT and NT was observed 4 genotypes (T05, T17, T19 and T20) in cherry type, 4 genotypes (T23, T25, T28, and T32) in medium type, and 1 genotype (T34) in large type, whereas 6 genotypes (T06, T07, T11, T14, T20 and T22) in cherry type and 4 genotypes (T28, T29, T30 and T32) in medium type were observed in no significant difference (Figure 4C). Next, we compared the difference in FS ratio between NT and LT. The difference of FS exhibited that T06, T11, T13, T23, T24, and T29 were positively influenced under LT condition. The most positive difference over 20% were observed in T13 (21.0%) and T11 (52.1%), and the most negative difference below 50% were found in T09 (-51.5%), T20 (-60.5%) and T04 (-64.0%) (Figure S2A). The difference in FY in LT showed that the most positive difference over 0 kg was observed in T24 (0.15 kg), T02 (0.08 kg), and T11 (0.05 kg), while the most negative difference below 1.0 kg was assessed in T31 (-1.48 kg), T15 (-1.37 kg), T35 (-1.26 kg), T30 (-1.22 kg) and T34 (-1.09 kg) (Figure S2B).

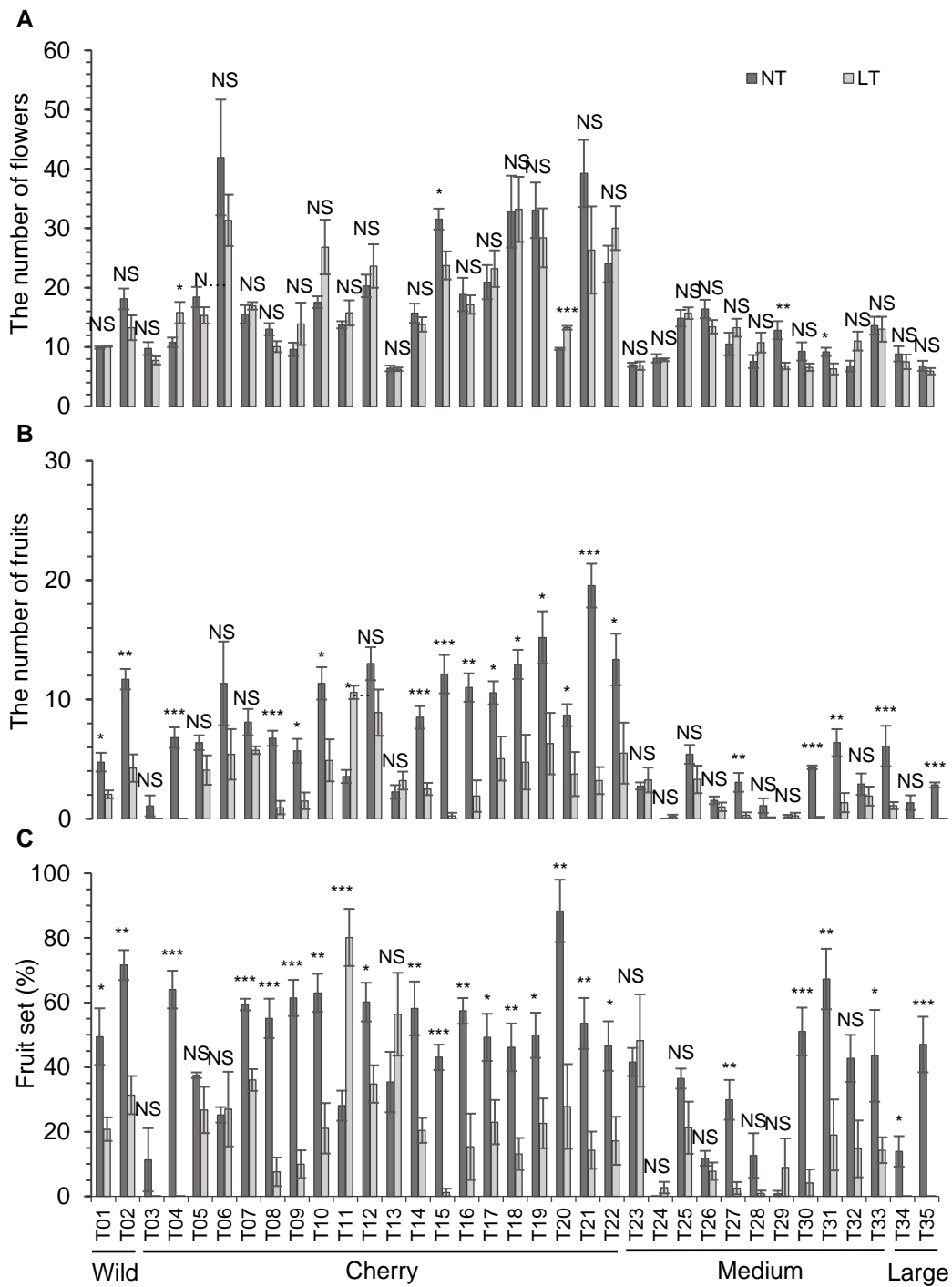


Figure 3. The analysis of reproductive traits on (A) the number of flowers, (B) the number of fruits, and (C) fruit set among 35 tomato accessions with different fruit types under NT and LT green-houses. Significant differences were evaluated with student's *t*-test ($p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$) and denoted by *, **, and ***, respectively. NS indicates not significant and bars indicate \pm standard deviations (n = 5).

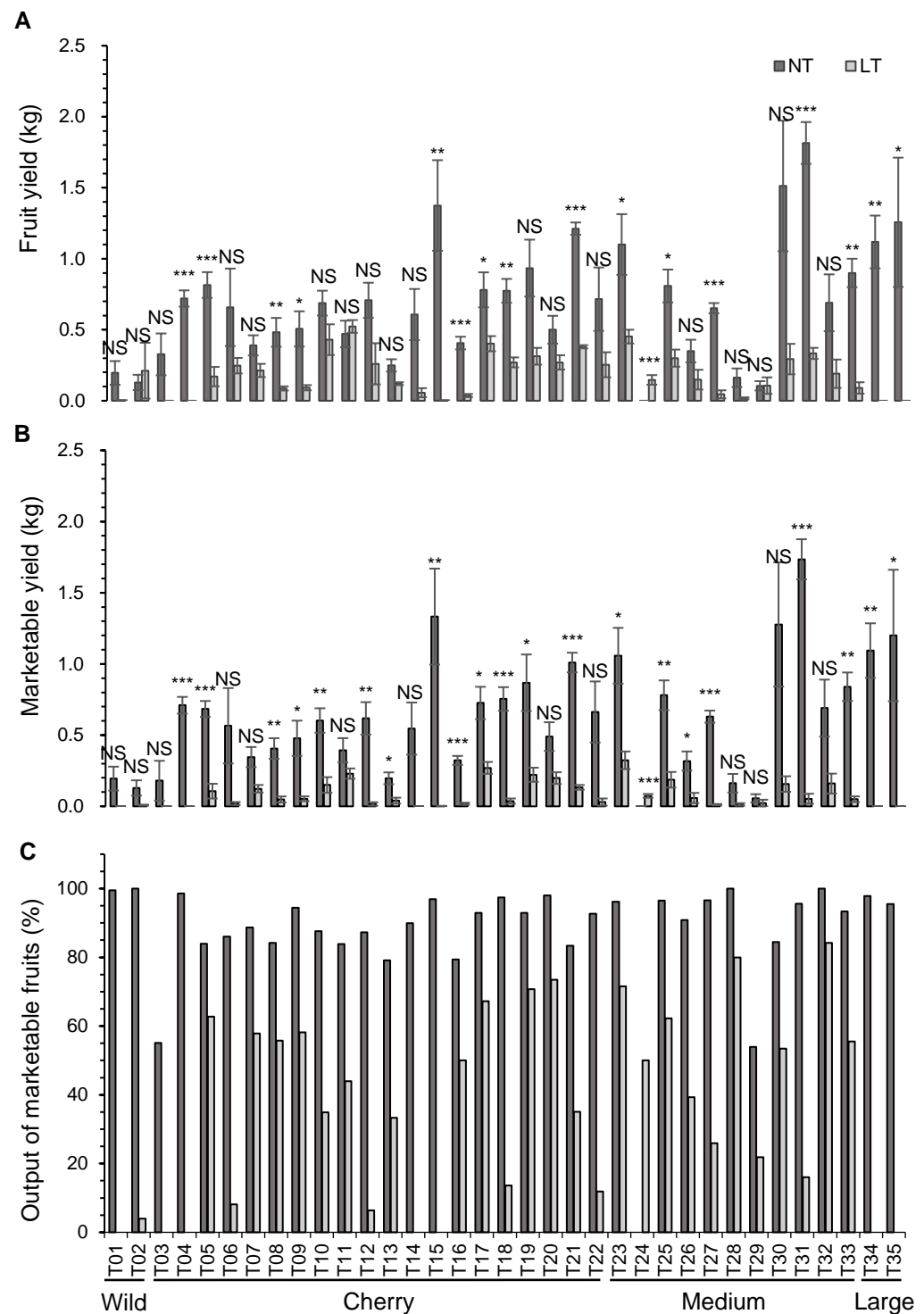


Figure 4. The analysis of reproductive traits on (A) fruit yield, (B) marketable yield, and (C) output of marketable fruit among 35 tomato accessions with different fruit types in NT and LT greenhouses. Significant differences were evaluated with student's *t*-test ($p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$) and denoted by *, **, and ***, respectively. NS indicates not significant and bars indicate \pm standard deviation ($n = 5$).

3.3. The principal component analysis (PCA) of physiological traits

In order to approach the multivariate analysis, the principal component analysis (PCA) was performed together with the correlation matrix of 9 variables measured under LT conditions (Figure S3). The Kaisere-Meyere-Olkin (KMO) for sampling adequacy on

vegetative and reproductive score data was 0.643 in LT. Bartlett's Test of Sphericity (BTS) was significantly lower than 0.001. The first three principal components showed the eigenvalues were greater than 1 (Table S2). Total variance of the data was explained with the 67.65% which composed of 41.02% from component factor 1 (PC1) and 26.63% from component 2 (PC2), respectively, and the traits (scores > 0.30) were loaded onto PC1 and PC2 (Table S2). PC1 and PC2 were clearly separate from vegetative and reproductive parameters with positive trend (Figure 5). PC1 was combined primarily vegetative parameters (LL, LW, and SD) and PC2 was associated with reproductive parameters (FS, NFR, and FY).

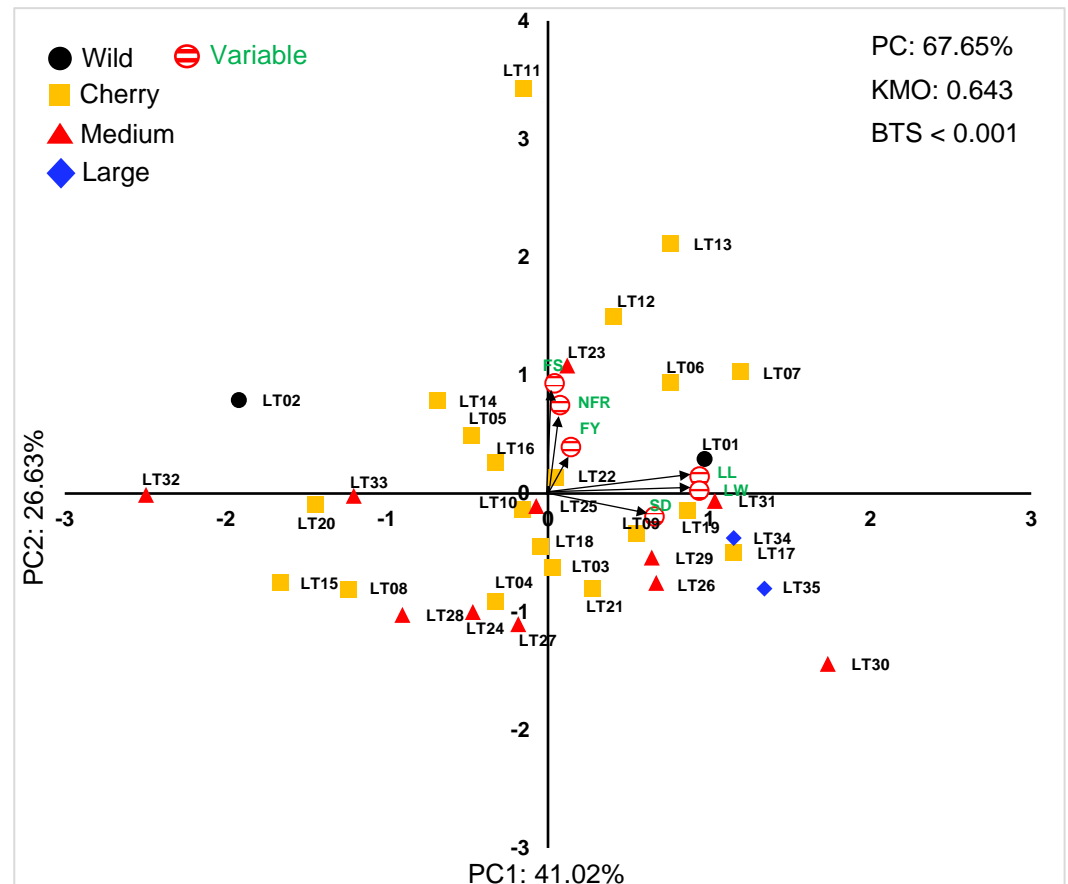


Figure 5. Biplot for first two principal components was analyzed using the principal component analysis (PCA) for 9 physiological traits among 35 tomato accessions depending on fruit types under LT condition. Leaf width (LW), leaf length (LL), stem diameter (SD), plant height (PH), number of flowers (NFL), number of fruits (NFR), fruit setting (FS), fruit yield (FY), and marketable yield (MY).

3.4. Clustering analysis

A score plot was illustrated using the component factor 1 and factor 2 in LT, displaying 35 tomato accessions with different fruit types (Figure 5). The factors were further subjected to hierarchical cluster analysis using the Euclidean distance matrix via Ward's method of agglomeration (Figure 6). Based on the dendrogram result, four major groups were observed in LT. The cluster 2 consisted of vegetative parameters related to SD, LL, and LW and the cluster 3 was associated with reproductive parameters related to NFR, FS, and FY.

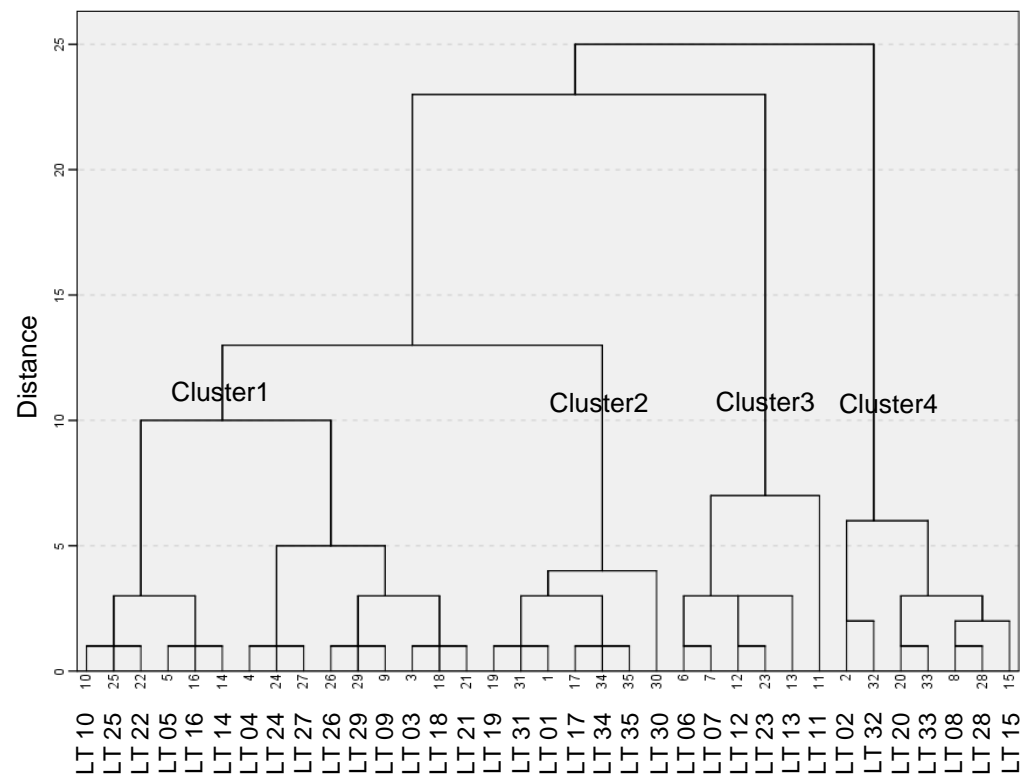


Figure 6. Dendrogram was exhibited by the cluster analysis of 35 tomato accessions based on the Euclidean distance using components factors 1 and factors 2 under LT condition.

4. Discussion

Tomato plants have been evolved against adverse environment factors and current tomato plants harbor the several mechanisms to overcome cold stress [30-35]. Previous studies have mainly focused on the response to low temperature stress with several limited genotypes as well as a short period of the treatment during the growth stage under cold conditions [19,32,36-39]. In this study, we observed 35 tomato accessions with vegetative and reproductive traits during entire growth stages in LT and NT under winter greenhouse. As such, LT noticeably influenced vegetative traits including PH, LL, and LW in tomato plants at 70 DAT compared to NT. In particular, the PH in LT condition was remarkably decreased in most accessions except for one accession, T32, which was not significant different between LT and NT (Figure 1A). The result was identical with previous researches that proved the retarded growth of tomato plants in night low temperature (LTN) condition [5,26,28,29]. However, SD of most accessions in LT was similar to NT, except for T21 accession which showed more inhibited growth of SD in LT (Figure 1B). Intriguingly, LL and LW in LT was inhibited 100% of accession (2 out of 2) and 50% of accession (1 out of 2) in wild, 60% of accession (12 out of 20) and 40% of accession (6 out of 11) in cherry types, and 50% of accession (1 out of 2) and 0% of accession (0 out of 2) in large types, respectively, compared to those in NT (Figure 2). Our results may suggest that the effect of LL and LW in LT may be varied in all accessions regardless of fruit types.

We analyzed the reproductive parameters including NFL, NFR, and FS in LT and NT. However, LT did not affect NFL in most accessions (Figure 3A) and only NFL of 2 accessions (T04 and T21) was increased in LT more than NT, whereas NFL of 3 accessions (T15, T28, and T31) were decreased in LT (Figure 3A). Furthermore, the effect of LT on NFR uncovered that 70.0% of accessions (14 out of 20) in cherry type and only 36.36% of accessions (4 out of 11) in medium type was affected compared to those in NT (Figure 3B). The result suggests that the differences of NFL in the accessions may be involved in the effect of genotype, not in fruit types [5].

Previous studies have demonstrated that FS plays a key role in determining LT tolerant-tomato cultivars [18,20-22]. Based on the parameter of FS, a wide range of tomato accessions were chosen and recent report has proven that NFR could be used as an index for FS in HT, which was positively correlated with FS in HT [23]. We also studied the effect of LT on FS (Figure 3C) and the effect of NFR in LT was closely related to the FS which showed 80% (16 out of 20) in cherry type and 36.36% (4 out of 11) in medium type was declined (Figure 3C). FS of most accessions in LT was drastically decreased, except for T11 accession which exhibited the remarkable increase of FS under LT. Considering that the NFL were not affected in most accession regardless of fruit types, the poor quality of flower pollens among the accessions in LT condition might influence the decrease in FS of the accessions [14,20,22]. However, the development of ovule and stigma could not be related to FS [40-42] although it needs to be further confirmed with experiments such as pollen germination and pollen grain staining to measure pollen activity [6,20,22]. In addition to this, the FY and MY were significantly decreased in 40% of cherry type, 45% of medium type, and 100% of large type under LT compared to NT (Figure 4), indicating that FY and MY were not associated with fruit types of tomatoes used for the experiment.

The correlation matrix were applied to PCA analysis to identify the critical physiological traits between multiple variables under LT condition. The first two PCA explained 41.02% and 26.63% of total physiological variables among 9 traits. 6 traits (with score > 0.30) were loaded onto PC1 and PC2 (Table S2). These were utilized to find out the distinct difference among 35 tomato accessions. The angle between the vectors of traits including LL, LW, SD in PC1 and NFR, FY, and FS in PC2 was lower than 90°, suggesting that they were positively correlated. The biplot analysis was drawn to figure out the multivariate relationship among 35 tomato accessions. The biplot exhibited that 35 tomato genotypes were not grouped with fruit types (Figure 5). Rather, the accessions were sporadically located in a plot regardless of fruit types. This might result from the tomato accessions that possess the genetic diversity within the same fruit type [43]. Moreover, the cluster analysis exhibited four major clusters (Figure 6) and the cluster 1 and 4 might be negatively involved in vegetative and reproductive traits and/or might be less associated with them on positive trends. The cluster 2 and 3 consisted of vegetative (SD, LL, and LW) and reproductive parameters (NFR, FS, and FY) with positive directions, respectively. Interestingly, 5 out of 6 were cherry type in cluster 3, but different fruit types were grouped in cluster 2, implying that cherry types in cluster 3, with the consideration of reproductive parameters, might be more tolerant to LT than other accessions. The selected genotypes in cluster 2 and 3 could be further used for the breeding program to select LT-tolerant tomatoes with the parameters.

5. Conclusions

The current study has been determined in the physiological traits of thirty-five tomato accessions in the response to night low temperature, which is economically important for the tomato cultivation of winter greenhouse. Based on correlation coefficient, PCA, and cluster analysis, some accessions were closely involved in vegetative and reproductive parameters depending on genotypes. Future researches will be required to evaluate more accessions of large fruit type in LT and the selected accessions will be focused on the determination of the physiological and the molecular functions, combined with DNA- and RNA-seq.

Supplementary Materials: Figure S1: Air temperature was measured in LT and NT greenhouse during the period of tomato growth and development, respectively. Figure S2: The analysis of difference in FS and FY among 35 tomato accessions in LT and NT. Figure S3: The correlations coefficients between vegetative and reproductive traits in total population of tomatoes in LT, Table S1: Tomato accessions for the evaluation of physiological traits against low temperature in winter 2020-2021. Table S2: Loading matrix associated with the principal components analysis (PCA) for 9 physiological traits.

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