Effect of heat treatment on physiological and recovery growth status of two tomato cultivars with different heat susceptibility

Sh. N. Rajametov[1*], E. Y. Yang[1†], H. B. Jeong[1†], M. Ch. Cho[1†], S. Y. Chae[1] and N. Paudel[1,2]

[1] National Institute of Horticultural & Herbal Science, Rural Development Administration, Wanju, 55365, Republic of Korea.

[2] Department of Applied Plant Science, Kangwon National University, Chuncheon 24341, Republic of Korea.

[*] Correspondence: sherzod_2004@list.ru Phone: 82-63-238-6691 Fax: 82-63-238-66050

[†] Equal contribution

Abstract: High temperature seriously effects on plant vegetative and reproductive development and reduces productivity of plants, while to increase crop yield is the main target in most crop heat stress tolerance improvement breeding programs, not just survival, under high temperature. Our aim was to compare temperature stress tolerance in two commercial tomato cultivars "Dafnis" (big fruit size) and "Minichal" (cherry fruit size) to develop early screening methods and find out survival rate and physiological responses of tomato cultivars on high temperature (40°C and within 70% RH, day/night) in 4-5 true leaf seedling stage- (4LS) and identifies the linkage of heat tolerance with fruit set and leaf heat damage rates (LHD) in seedling stage with subsequent vegetative traits at recovery. Results showed that heat stress significantly affected on physiological-chemical and vegetative parameters of seedlings regardless of tomato cultivars. Survival and the threshold level of high temperature tolerance in the seedlings of cv. "Dafnis" and "Minichal" were identified on days 7 and 9, respectively. Our findings revealed that photosynthesis (P_N, Gs, Ci, Tr) parameters were increased and CHL content persisted steady value in cv. "Minichal" during heat stress period, however EC and RPL rates were lower than cv. "Dafnis". Heat stress reduced the SFW in both cultivars in seedling stage, but PH and RFW were significantly decreased in the heat tolerant cv. "Minichal", whereas this parameters were not significantly ranged in the heat susceptible cv. "Dafnis". Additionally, there no found linkage between vegetative parameters with decreasing of P_N and CHL rates during HT of seedlings. In plants of cv. "Minichal" with LHD-25, 50 and 75% were no found significant differences in PH, whereas in cv. "Dafnis" significant differences were determined in plants with LHD-75%, and the significant differences in rates of SFW and RFW were observed in plants of cv. "Dafnis" having LHD-75% for 28 days of recovery at NT condition. Taken together, we concluded that heat stress affected on physiological parameters regardless of tolerance level, and to identify heat tolerant genotype in tomato breeding program, screening and selection genotypes have to be evaluated at the vegetative and reproductive stages with consideration fruit size types. Since we could not find linkage between heat tolerances in seedling stage with fruit set at the reproductive stage and fruit set cannot be used as a general predictor of heat tolerance.

Keywords: tomato; temperature; damage; seedling; plant; root; weight; photosynthesis; proline; electrical conductivity

1. Introduction

Temperature stress has become and will continue to be a great concern in agriculture cultivation due to climate change. Agricultural crops, including tomato (*Solanum lycopersicum* L.) cultivars have a narrow range of optimal growing temperatures, with tomato's optimum temperature ranging from 25 to 30°C during the daytime and 20°C at the night

[1-3] and are affected by both high [3-5] and low temperature stress [6-8]. Due to intensive breeding of a few desired traits during domestication, the genetic diversity of commercial cultivars of tomato declined [9] while wild species maintained larger number of valuable genes [10,11].

High temperature prevents to increase the cultivation area of stress susceptible tomato cultivars, where negative impact on plant growth and development higher temperatures than optimal range [4,12-18].

The cultivation area of tomato has been increasing annually around the world and reaching more than 5 million hectares (http://www.fao.org/faostat/). However, while reproductive tolerance during heat stress is an important value for the evaluation of tomato cultivars yield [12,19-22], tomato, in vegetative and reproductive stages, are sensitive to high temperature and have varying sensitivity to stress [23,24].

Furthermore, many research work were conducted to evaluate heat tolerance and understand of mechanism and physiological responses to high temperature of tomato genotypes to identify tolerant one [3,18,24,25]. As a result, many methods to screen for heat tolerance and validate tomato genotypes under heat stress at different growth stages were developed [3-5,16,19,21,24,26].

Therefore, the main strategy of this study is to identify early screening methods for heat tolerant genotypes; find out survival rate and physiological responses of tomato cultivars on high temperature at seedling growth stage; and identify the linkage of heat damage rates to subsequent vegetative traits at recovery.

2. Results

2.1. Screening for heat tolerant in tomato seedlings

Heat damage symptoms were determined on day 2 and were found to not significantly differ among tomato seedlings. Survival ability and leaf heat damage rates after 3 days of exposure to heat stress showed significant differences among tomato seedlings (Fig. 1). On day 7, differences in heat tolerance and survival among tomato cultivars significantly ranged, where in seedlings of cv. "Dafnis" were identified as critical (over 60%) LHD and screened as heat susceptible, while cv. "Minichal" remained stable heat tolerant (Fig. 2).
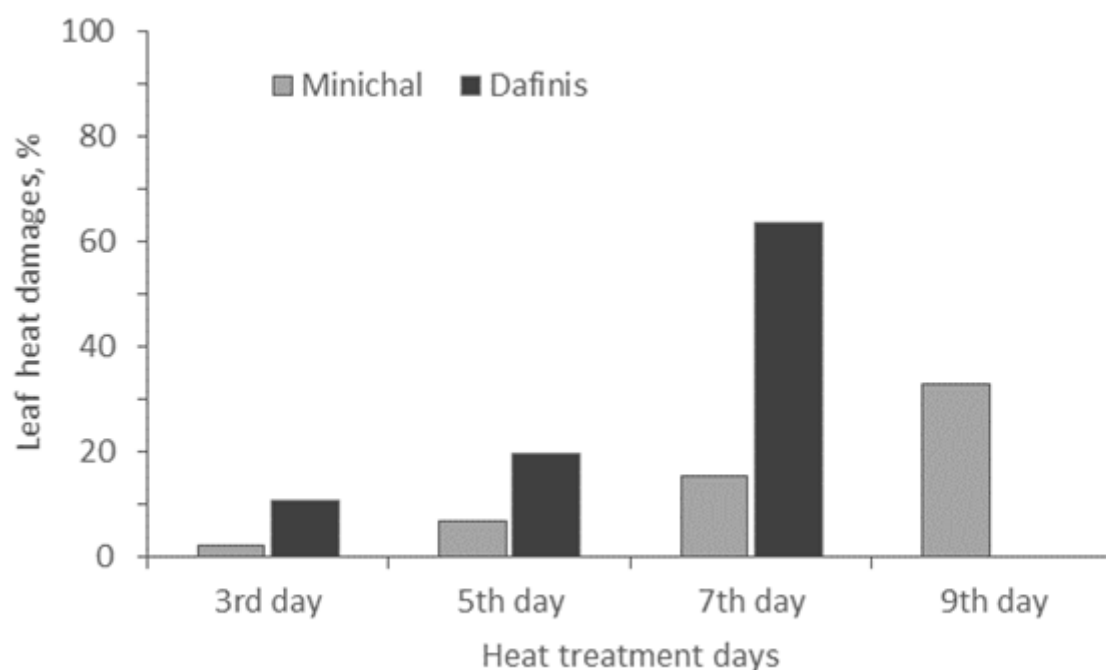
Figure 1. Changing of heat tolerance among seedlings of tomato cultivars.

Figure 2. Differences in heat tolerance after 7 days of stress among seedlings of tomato cultivars "Minichal" (left) and "Dafnis" (right).

2.2. Chlorophyll content and photosynthesis in seedlings at heat treatment

The total chlorophyll content of leaves subjected to heat treatment showed significant differences among tomato cultivars. After 3 days of exposure to the heat stress, degradation of the CHL in seedlings of heat susceptible tomato cv. "Dafnis" (Fig. 3) was found. Significant lower value than those in heat tolerant cv. "Minichal", while maintaining a steady CHL during HT, showed on day 7.
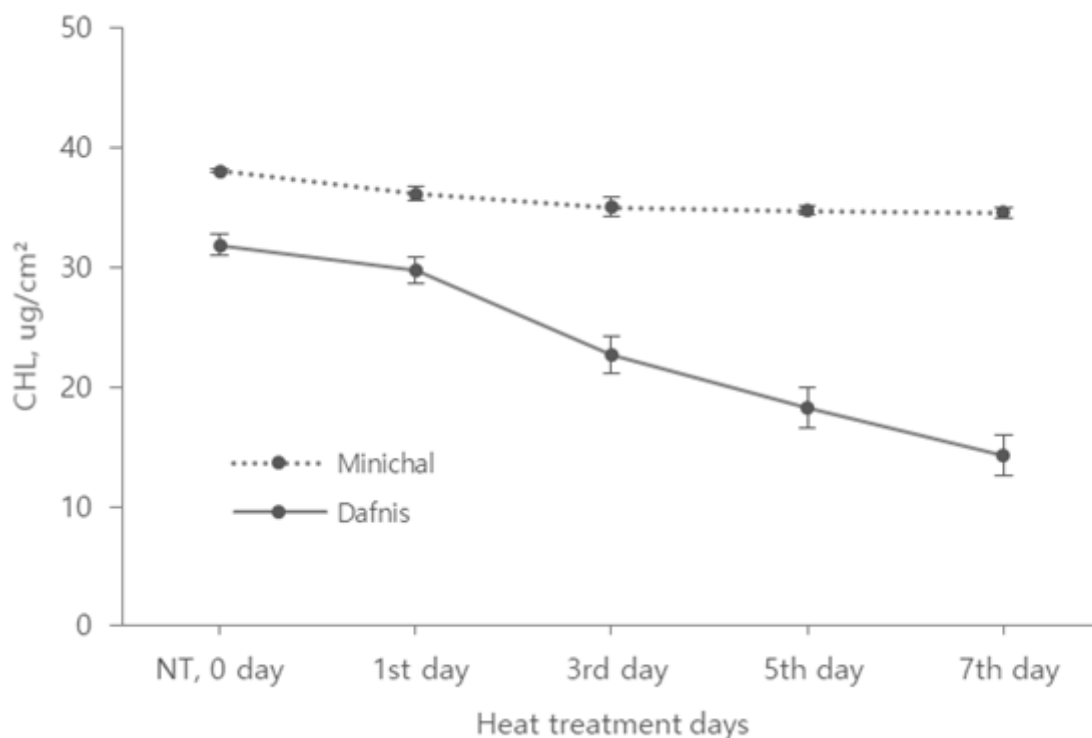
Figure 3. Changing of total chlorophyll content in leaves (4LS) at heat treatment period. Vertical bars represent standard error (n = 3).

Photosynthetic characteristics like P_N, G_s, C_i and Tr significantly varied by the treatment period of high temperature stress in comparison with the initial rates in NT plants (Fig. 4A-D). Two tomato cultivars belonging to the heat-susceptible and tolerant maintained not similar P_N at NT and HT conditions (Fig. 4A), where susceptible tomato cv. "Dafnis" showed significantly lower P_N in NT ($p<0.05$) than tolerant cv. "Minichal". The P_N rates decreased after 1 day of exposure to heat stress among seedlings, but it was ranged in both tomato cultivars, where the seedlings of cv. "Dafnis" showed significantly

lower index of P_N than those in the cv. "Minichal". The same pattern persisted on stress day 3, where cv. "Dafnis" had significant reduction of P_N than heat tolerant cv. "Minichal". The Gs was higher in cv. "Minichal" than in seedlings of cv. "Dafnis" at NT condition (Fig. 4B).

On day 1, heat stress had significantly elevated the value of Gs in the heat tolerant cv. "Minichal", but in contrast, heat stress significantly decreased the index of Gs in the heat susceptible cv. "Dafnis". After 3 days of exposure to heat stress, seedlings showed significant decrease of Gs among both cultivars but heat tolerant cv. "Minichal" had higher value of Gs than those in susceptible cv. "Dafnis".

The Ci was unaffected in both commercial cultivars under heat stress compared with the values in NT and at HT conditions (Fig. 4C), where no identified significant variation in the value of the Ci, and in this case the Ci was higher in the heat tolerant cv. "Minichal" during the HT. Evaluation of the Tr value in both cultivars showed that it was similar in tomato seedlings of the cv. "Minichal" and "Dafnis" at NT condition (Fig. 4D). However, on day 1, heat stress led to a significant increase in the value of Tr in cv. "Minichal" and this trend persisted until day 3 of HT. The Tr index in cv. "Dafnis" was affected in NT and HT conditions but was lower than in cv. "Minichal" during the HT.
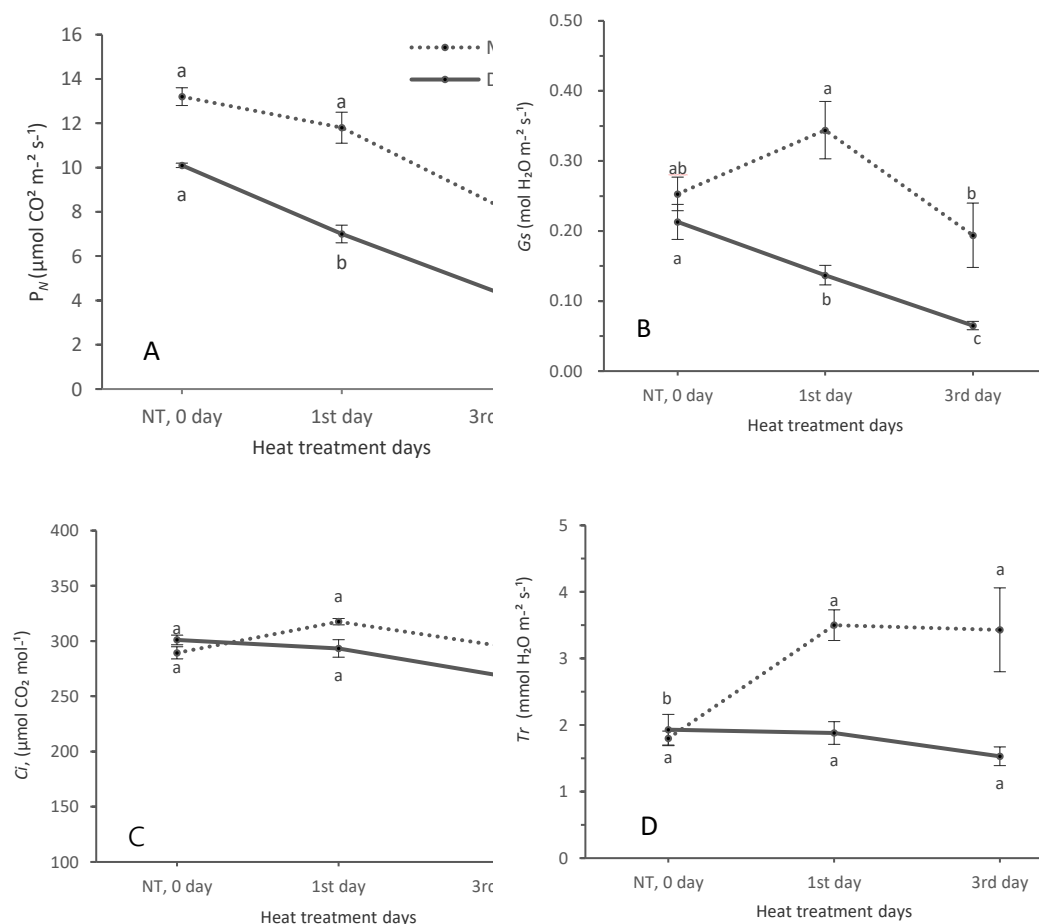
Figure 4. Effect of heat treatment on physiological activity in seedling stage of tomato. Photosynthesis (A), Stomatal conductivity (B), Intercellular CO_2 concentration (C), Transpiration rate (D). The mean data indicate the means ± SE (n = 3). Different letters above bars indicate significant differences at $p<0.05$.

2.3. Electrolyte leakage and proline accumulation

Data on the easurement of the EC among tomato seedlings showed did not it not significantly vary at NT and HT conditions, but significant differences among cultivars

were identified (Fig. 5A). The highest rate of EC was determined in heat susceptible cv. "Dafnis", while the lowest value remained in cv. "Minichal".

The PRL significantly increased in the heat susceptible seedlings of cv. "Dafnis" during the 3 days of HT compared with the NT. Tolerant one cv. "Minichal" was found to have no significant difference in index of PRL and persisted steady value at NT and HT conditions (Fig. 5B). However, in contrast, evaluation of the effect of LHD on PRL content in tomato plants at recovery on day 5, in evaluation of effect the LHD on PRL content in tomato plants on day showed an, opposite pattern, where PRL increased significantly in all plants of heat tolerant cv. "Minichal" regardless of LHD than plants in NT and decreased in heat susceptible "Dafnis".
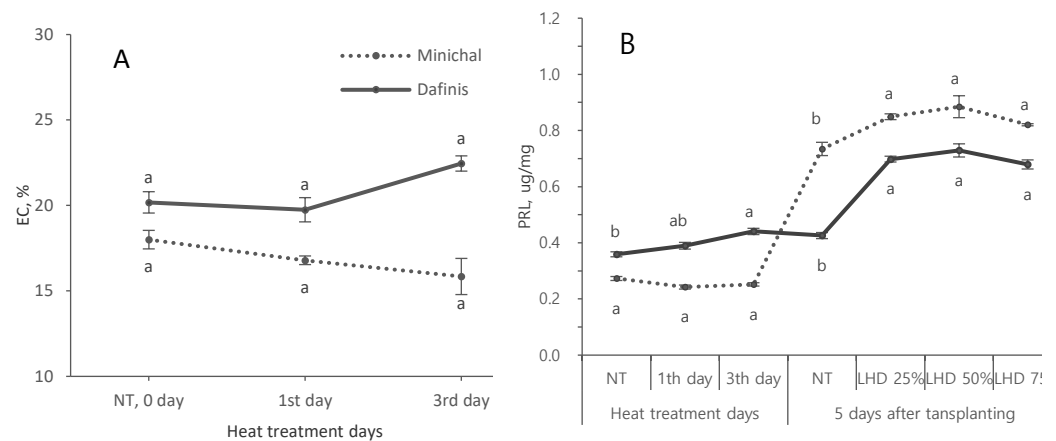
Figure 5. Changes of electrical conductive (A) and total proline content (B) in tomato seedlings at heat treatment and recovery periods. Vertical bars represent ± SE (n = 3). Means with different letters indicate significant differences at p<0.05.

2.4. Effects of heat treatment on biomass and vegetative parameters

Heat stress significantly decreased the PH, SFW and RFW of heat tolerant seedlings cv. "Minichal" than in NT condition (Fig. 6A-C). Seedlings of the heat susceptible cv. "Dafnis" showed no significant difference in values of PH and RFW during treatment under high temperature.
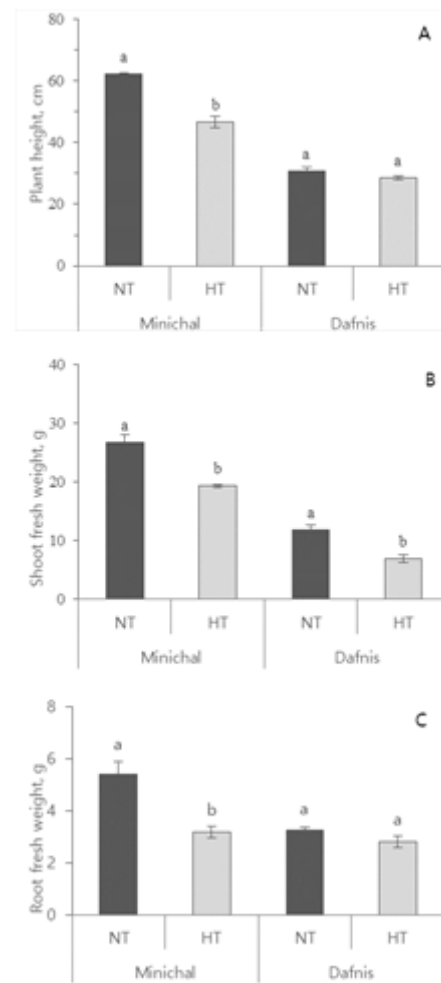
Figure 6. Effect of heat treatment on tomato seedlings vegetative parameters. Values are means ± SE (n = 3). Within each parameter, histograms with the same letter indicate that values are similar (p<0.05).

Evaluation of the PH growth activity of the two tomato cultivars subjected to heat stress and having different LHD rates and recovered in glass greenhouse NT condition for 28 days showed that no significant differences compared with NT plants (Fig. 7A-C).However, as compared with NT, the plants with LHD 75% significantly decreased the growth rate activity in the heat susceptible cv. "Dafnis" (Fig. 7A). By comparison of both cultivars, the index of the PH growth activity in all LHD and NT plants were higher in the heat tolerant cv. "Minichal" than heat susceptible cv. "Dafnis" (Fig. 8).
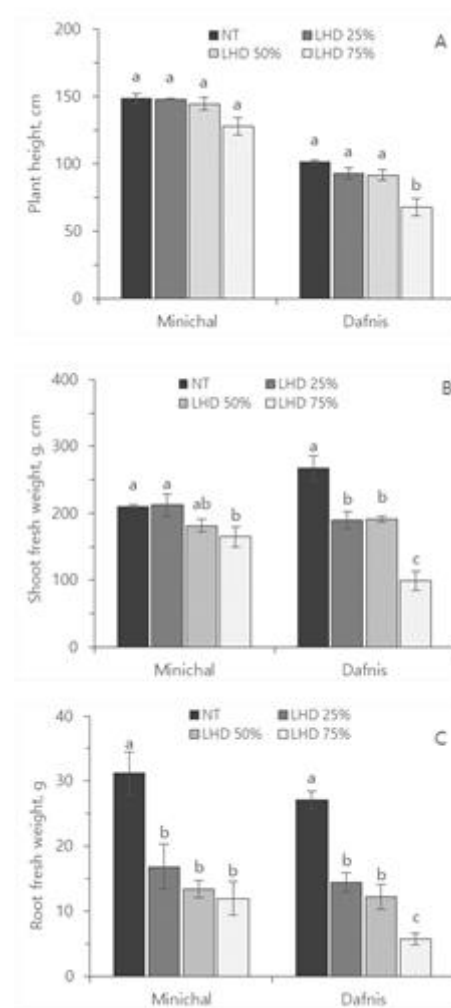
Figure 7. Recovery ability of tomato seedlings with different LHD at normal condition (A- "Mini-chal" and B- "Dafnis"). Vertical bars represent ± SE (n = 3). Values with different letters indicate significant differences at p<0.05.

In comparison to NT plants, the SFW of cv. "Dafnis" in all LHD plants significantly decreased (*p*<0.05), but did not significantly decrease in plants of cv. "Minichal" with LHD-25 and 50%. It decreased significantly only in plants with LHD-75% (Fig. 7B). The RFW in both tomato cultivars significantly decreased in all LHD plants than NT (Fig. 7C), and the significant difference were identified in plants of heat susceptible cv. "Dafnis" with LHD-75% (Fig. 8).
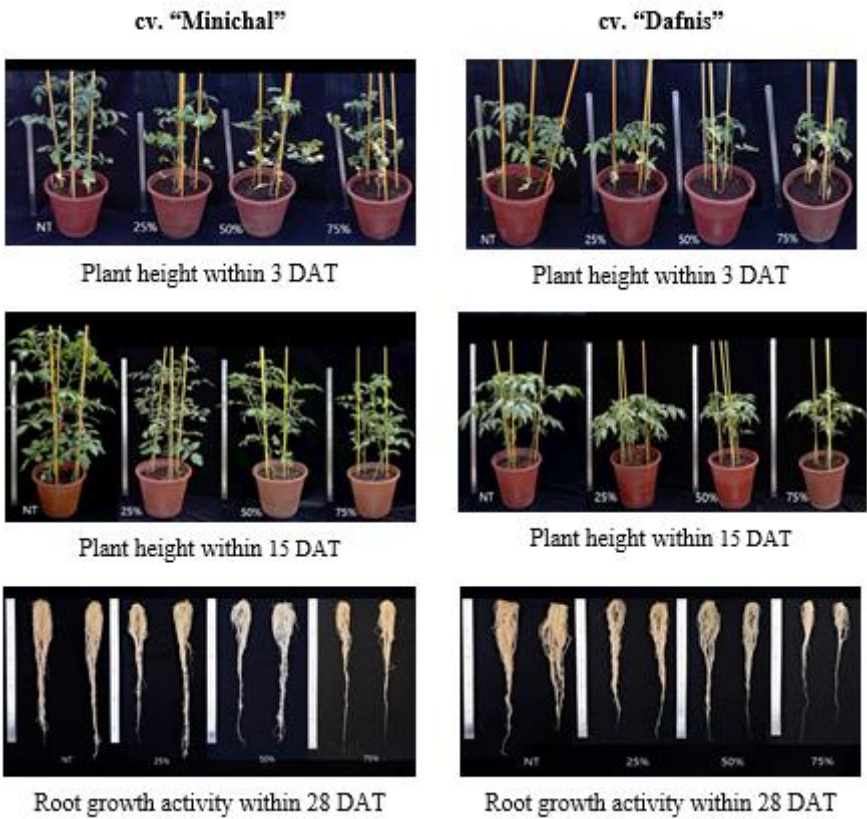
Figure 8. Effect of different leaf heat damage rates on tomato plants growth and roots development. From left cv. "Minichal" and from right cv. "Dafnis".

3. Discussion

Abiotic stress, such as the heat tolerance in tomato plants, is quite complex and demands multiple evaluations of genotypes to understand how the physiological parameter [5,18,27] and tolerance are altered at different growth stages [12,21,22,28,29].

In the present experiment, evaluation of the tomato heat tolerance did not show significant heat injury symptoms as recorded on stress day 2 in tomato seedlings regardless of tolerance. On day 3 of exposure to stress, the differences among cultivars significantly appeared, where in cv. "Dafnis" symptoms increased, while in cv. "Minichal" persisted, specifically on the green part of leaves. Survival and the threshold level of high temperature tolerance in the seedlings cv. "Dafnis" were identified on day 7, where the LHD was over 60% and was screened as heat susceptible, while cv. "Minichal" maintained its stable heat tolerance. As the environmental temperature of over 30°C is the overhead threshold temperature and harmful for the growth of tomatoes [4,30,31], identifying a tomato genotype with high steady overhead threshold temperature and a study on the genotype behavior in seedling stages may be used as extremely favorable methods to estimate heat tolerance.

Comparison of the heat tolerance of tomato cultivars in seedling stage with fruit set in HT condition showed that heat tolerance level in seedling stage cannot be related always with fruit set, and we assume that fruit set cannot be used as a general predictor of heat tolerance.

Screening the tomato seedlings under high temperature showed that the CHL content was reduced than initial index in NT condition, demonstrating that heat stress affects CHL [3, 5,16,18,26,32].

However, there were found differences among tomato cultivars, where the significant reduction of CHL in leaves had been identified in susceptible cv. "Dafnis". This can be due to the decrease in chlorophyll a and b and carotenoid content, premature chlorosis and withered leaves of tomato at heat stress condition [3,26]. While in the heat tolerant cv. "Minichal" seedling leaves were stay-green and magnitude of the change of CHL was smaller than in non-tolerant in accordance with previous reports [16,32-34]. Also, in a previous study were reported, that the reduced P_N value could be partially explained by the decreased leaf CHL content under heat stress as pigment content and composition are closely related to photosynthesis [35].

Stay-green of leaves in the heat tolerant plants may contribute to the maintenance of yield at high temperatures [16,36,37], while the decrease in PN may be linked to the reduction in CHL as a result of reduced antenna pigments, the alteration of chloroplast structure [15,38,39], carbohydrate synthesis [5,24] and lowering the light yield during heat stress [35,40].

The present results showed that heat stress contributes to reduction in P_N in tomato seedlings [24,26], but significant differences between tolerant and susceptible cultivars during treatment period persist [3,24,41]. It has been shown that high rates of CHL, P_N, Gs and Tr in the heat tolerant tomato cv. "Minichal" compared with the susceptible cv. "Dafnis" at high temperature may allow better leaf cooling, while in the susceptible had lower values and high leaf temperature [5,16,24,42].

However, Zhou et al. [24] reported that heat stress negatively affect photosynthesis, carbohydrate synthesis and reproductive parameters in the heat susceptible tomato cultivar, where heat stress mainly reduces the P_N, carbohydrate and CHL contents in the leaves of heat susceptible cultivar accompanied by abnormal bud and flower abscission. We did not find significant differences in the rate of Ci in both cultivars at HT [5], whereas depends on genotypes and treatment conditions it can be varied [3]. However, it was higher in tolerant cv. "Minichal" than that of susceptible, and it may result to non-stomatal factors showing no difference in Ci [43] or the stomatal conductance limited the function of P_N [3,4,17,27].

Electrical conductivity is a reflects stability of the cell membrane to the abiotic stress of a variety of crops, where sub-optimal temperatures can alter the membrane structure

of a plant cell, leading to increased membrane permeability and certain small molecules within the cell flow out, causing an increase in electrical conductivity [23]. Therefore, it is a universally granted technique in measuring cell integrity regarding cell membrane thermo stability under stress condition [27,35,44-47].

A significant difference in values of EC under HT and NT conditions was not found in both cultivars, but an increase electrical leakage was determined in stressed cv. "Dafnis" plants than cv. "Minichal". Numerous similar reports have been published that high rate of EC in susceptible tomato plants indicating alterations in the permeability of the membranes and a reduction in their ability to retain solutes and water due to high temperature [4,48]. Moreover, in the tolerant tomato genotype did not modify the permeability of the membrane by heat-shock treatment, thus indicating the maintenance of its functioning.

Proline plays positive roles in enhancing plant tolerance to abiotic stress [49-51] and stabilizes and protects the structure of enzymes and proteins, maintains membrane integrity and scavenges reactive oxygen species [52]. On one hand, accumulation of PRL is considered a strong indicator of abiotic stress [53,54], but high accumulation of PRL in plants during HT is detrimental for plant growth at recovery, which is not always a compatible solute during environmental stresses and high doses will impart toxic effects [51,55,56].

We found that the PRL content in the heat susceptible cv. "Dafnis" was higher than tolerant cv. "Minichal" [57] and was positively linked to the EC rate during HT of seedlings, however this trend did not persist in the recovery period, and instead showed opposite tendency. According to our results, PRL level has not always been associated with values in heat treatment and post treatment (recovery) conditions, it can vary depending on genotypes and growth stages [58], and it cannot be used as an main indicator to measure of level of tolerance [53,58].

Measurement of the effect HT on vegetative parameters of seedlings showed that regardless of cultivar, the SFW of seedlings decreased than NT seedlings at heat stress period [18]. PH and RFW rates significantly decreased in the heat tolerant cv. "Minichal", whereas this parameters did not significantly vary in the heat susceptible cv. "Dafnis". We could not find links between vegetative parameters with decreases in P_N and CHL rate during HT, where photosynthesis and CHL deficit may disrupt the metabolic pathways and reduce the growth rate and biomass, whereas the tolerant genotypes accumulated more biomass, with lower heat injury index and higher fruit yield [5,16,18].

According to results of evaluation of the effect of different LHD on recovery parameters of tomato plants were identified that response of plants is different, but we can assume that heat tolerant genotype can well recovery than susceptible one. So, at present study were no observed significant differences in values PH of cv. "Minichal" with LHD-25, 50 and 75% for 28 days at recovery condition, whereas in cv. "Dafnis" significant differences were determined in plants with LHD-75%. The shoot fresh weight significantly reduced in all LHD plants of "Dafnis" compared to the heat tolerant cv. "Minichal". Also, the significant differences in rates of SFW and RFW were observed in plants of cv. "Dafnis" having LHD-75%. High rates of PH and SFW in the heat tolerant cv. "Minichal" plants with different LHD in comparison with NT plants may be associated with high concentration of CHL, photosynthesis activities and PRL content after post treatment at recovery.

Moreover, as we reported in our previous study the selection criteria for high temperature tolerance in breeding programs should be considered depending on fruit types of the target cultivars [22], which is also confirmed in present study, where revealed significant differences in heat tolerance of seedlings cherry and big size type tomato cultivars with high fruit set under high temperature condition, since the mechanisms controlling heat stress response in plants are complex and response of genotypes and their physiological parameters on HT is different and in growth stages may vary [12,21,24,30,44,49,53].

Therefore, more studies are required to precisely identify mechanisms of heat tolerance during vegetative and reproductive development interactions.

4. Materials and Methods

4.1. Plant materials and growing condition

Two commercial cultivars of tomato, "Dafnis" (big size) and "Minichal" (cherry size) were selected to understand the interrelation of the heat tolerance in seedling stage with physiological traits. Both cultivars were selected as tolerant to high temperature among tomato genotypes during evaluation in summer growth periods of 2019-2020 in a vinyl house with day temperature 40°C and where average fruit set in cv. "Dafnis" and "Mini-chal" were 33.8 and 44.8%, respectively. The seeds for experiment were sown in 15th May of 2020 in plastic trays containing 1:1 sand: peat by volume and grown in a glass green-house with day and night temperatures 28/18°C (D/N) in National Institute of Horticul-tural and Herbal Science. Tomato seedlings with 4LS after sowing of seeds on 30 days were transferred into growth chamber on 16th June of 2020, where D/N temperatures were maintained at 40°C, light intensity 800μmol m^{-2}s^{-1} (16/8h) and relative humidity was within 70%. Heat tolerance treatment (HT) was continued for 7 and 9 days for cv. "Dafnis" and "Minichal", respectively. All seedlings of tomato cultivars, after high temperature treatment, were transferred into normal condition (NT) and recovered after 3 days. In or-der to avoid drought in the substrate in both conditions, all seedlings were watered daily. A total of thirty-two (32) seedlings were treated for each cultivar. The seedlings with leaf heat damage rates (LHD) over 60% were used as a critical level during heat treatment and the seedlings were transferred into NT for recovery.

4.2. Measurement of heat tolerance among tomato seedlings

The plants of tomato were grouped in five categories based on heat stress symptoms according to Zhou et al. [5] and Chen et al. [34] with some modifications. The leaf heat damage symptoms in tomato seedlings were calculated in % and divided on 5 grades: grade 1, normal growth- no damage; grade 2, fewer than 1/10 damage of the leaves (-<10%) become lightly yellowed-whited or desiccated; grade 3, damages of the leaves from 11-25%, become lightly yellowed-whited or desiccated-dried; grade 4, damages 25-50% of the leaves, become lightly yellowed-whited or desiccated-dried; grade 5, damages 50-75 of the leaves become yellowed-whited or desiccated-dried; grade 6, damages >75% of the leaves become severely yellowed-whited or the whole plant dies.

4.3. Measurement of chlorophyll content and photosynthesis in seedlings at heat treatment

Total chlorophyll content (CHL) was measured using SPAD meter (Konica Minolta, Japan) in tomato leaves on 0 (NT), 1, 3, 5 and 7 days of HT.

The photosynthetic rate- P_N (μmol CO_2 m^{-2}s^{-1}), stomatal conductance - Gs (mol H_2O m^{-2}s^{-1}) intercellular CO_2 concentration - Ci, (μmol CO_2 mol^{-1}), and transpiration rate - Tr (mmol H_2O m^{-2}s^{-1}) were measured from 3rd-4th leaves of seedlings at NT (0 day) and on heat stress day 1 and day 3 between 10:00-12:00 am. Data were recorded in three plants per accessions using a portable photosynthesis measurement system (LI-6400, LI-COR Bi-oscience, Lincoln, NE, USA). Light response curves (PAR) was set to 800 μmol m^{-2}s^{-1}, the leaf chamber temperature was set to 25°C, and the intercellular CO_2 concentration was maintained at 400 μmol (CO_2) mol^{-1}. The photosynthetic rate was measured automatically at each irradiation level after 3-4 min light exposure.

4.4. Determination of electrolyte leakage potential in leaves

The leakage of electrolyte from tomato leaves was measured according to Hong et al. [59] with minor modifications. In detail, leaves were perforated into discs with a radius of 5.5 mm, and each disc was placed in a 15-mL tube containing 10 mL of deionized water and incubated on a shaking table at 25°C for 30 min. At this time, the conductivity (EC_1) of water was measured using a Thermo Orion STARA-HB conductivity meter (Thermo Orion., Waltham, MA, USA). The tube was heated in a boiling water bath for 30 minutes, then cooled at room temperature for 20 minutes, and the conductivity (EC_2) was measured again. Final EC content was expressed as the percentage of EC_1/EC_2.

4.5. Extraction of free total proline content in leaves

Free total proline content (PRL) in tomato leaves was measured using colorimetric assay [60]. Leaf samples from heat treated plants and control were lyophilized (-72°C) in Freezer dryer (IlShin BioBase, South Korea) for 3 days. Each leaf samples, weighing 100 mg (dry weight) was homogenized with 2 ml of 3% (w/v) aqueous sulfosalicylic acid solution. The homogenate was centrifuge at 14,000 rpm for 7 minutes. Then 1 ml of supernatant was transferred to 5 ml micro tubes, 1ml of glacial acetic acid, and 1 ml of acid ninhydrin. Acid ninhydrin was prepared by adding ninhydrin (2.5 g/100ml) to solution containing glacial acetic acid, distilled water, and 6M ortho-phosphoric acid 85% at ratio of 6:3:1 receptively. Immediately the reaction mixtures were kept in boiling water bath (95°C) for one hour. The reaction was stopped (boiled micro tubes were kept) at 4°C for 20 minutes and reading were taken at wavelength of 546 nm by spectrophotometer (EON, BioTek Instruments, USA).

4.6. Sampling of leaves for assaying EC and PRL.

The leaves for EC and PRL measurements were selected from 3rd and 4th leaves of 4LS seedlings at NT (0 day) and from HT with interval 1 and 3 days. The leaves for PRL test collected from mid part of tomato plants on the 5th DAT at recovery.

4.7. Evaluation of the effect the LHD rates on tomato plants recovery

To evaluate the effect of heat treatment on post physiological traits the seedlings of tomato with LHD from grades 3, 4, and 5 were selected. All heat treated seedlings from grades 3, 4, and 5 and from control (no treated) were transplanted into pots after 3 days of recovery on 26th June of 2020 and then recovered in glass greenhouse NT condition (D/N 30-32/22-24°C) for 28 days. The soil in pots were prepared uniformly using pre-plant broadcast manure at a dose of 10,000 kg ha^{-1} and basal fertilizer containing 160 kg ha^{-1} N, 80 kg ha^{-1} K$_2$O, 160 kg ha^{-1} P$_2$O$_5$ and regularly watered to avoid drought and fertilized on a weekly basis (Daeyu, Mulpure).

4.8. Measurement of the plant height and biomass of tomato plants at heat treatment and recovery periods

The plant height (PH) and biomass such as shoot (SFW) and roots fresh weight (RFW) were measured using ruler and electron Micro Weighing Scale MW-II (CAS), respectively.

4.9. Statistical analysis

The experimental design of this study was completely randomized. Statistical analysis (ANOVA) performed using the SAS Enterprise Guide 7.1 (SAS Institute Inc., NC, USA) for three replicates to measure the parameters of interest (n = 3), and mean values were compared with a significance level of 5% using Duncan's multiple range test.

5. Conclusions

The present worked showed that heat stress not only damages the appearance of tomato plants but also significantly affects the physiological-chemical and vegetative parameters. For the identification of heat tolerant genotype in tomato breeding program, screening and selection genotypes have to be done at the vegetative and reproductive stages with consideration on fruit types. However, linkage between heat tolerances in seedling stage with fruit set at the reproductive stage was not found, therefore we presume that fruit set cannot be used as a general predictor of heat tolerance. In order to find out real tolerance, mechanism expression analysis of various gene products from tolerant genotypes selected according to screening at the vegetative and reproductive stages is needed

Author Contributions: Cho supervision; Cho, Yang, Rajametov and Jeong designed experiments; Rajametov performed experiments; Cho and Yang data curation, Rajametov, Jeong and Chae formal

analysis; Rajametov writing – original draft preparation; Rajametov, Yang, Cho, Niroj Paudel, Chae and Jeong writing- review and editing

Data Availability Statement: The datasets generated during and/or analyzed during the current study are available from the corresponding author on responsible request.

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Conflicts of Interest: This article does not contain any studies involving animals or human References

Abbreviations: HT- heat treatment, DNT- normal treatment, /N- day/night; LS- true leaf stage, LHD- leaf heat damage, PH – plant height; DAT- days after transplanting; SFW- shoots fresh weight, RFW- roots fresh weight, P_N- the photosynthetic rate, Gs- stomatal conductance, Ci- intercellular CO_2 concentration, Tr- transpiration rate

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