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Effects of High Root-Zone Temperature on the Physiology and Growth of Pear (*Pyrus communis* L., cv. Bartlett) and Quince (*Cydonia oblonga* Mill., cv. BA29) Plants

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Abstract

Global warming, with rising average temperatures and increasingly frequent extreme heat events, poses a major threat to fruit production systems and food security. Understanding how fruit trees respond to soil thermal stress is therefore critical for developing climate-resilient orchards. In this study, we investigated the physiological and growth responses of potted pear (*Pyrus communis*) and quince (*Cydonia oblonga*) plants to root-zone heating. Plants were exposed to different substrate heating regimes, and gas exchange, water status, chlorophyll content, shoot growth, and biomass allocation were assessed. Short-term extreme heating (50 °C for 36 h) caused immediate reductions in gas exchange, severe root and shoot damage, and rapid plant mortality in both species. By contrast, prolonged heating at 40/35 °C induced significant declines in gas exchange, shoot growth, and root biomass, with species-specific differences. Pear exhibited greater sensitivity than quince, showing lower shoot growth, root dry weight, and gas exchange. These findings highlight the vulnerability of pear trees to high root-zone temperatures and the limited contrast between the tested rootstocks. Accordingly, there is a clear need for targeted soil management practices that promote root growth and soil exploration to enhance orchard resilience under future climate scenarios.

Keywords: heat stress; pear; quince; soil; root growth; physiology

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1. Introduction

Currently, climate change and the increasing global population and food demand are among the main challenges for sustainable crop production. The frequency and intensity of extreme weather events are rising, posing a growing threat to agriculture and food security [1]. Among abiotic drivers of climate change, high temperature is one of the most critical constraints, with negative impacts on fruit tree growth, development, and productivity, and in some cases, threatening fruit yield and quality [2,3]. High temperatures often coincide with other stressors, such as prolonged drought, which can further amplify the detrimental effects of heat stress. With increasingly extreme summer conditions, the areas suitable for cultivating fruit trees are expected to diminish in the future [4].

Heat stress in fruit trees affects biological processes from the cellular to the whole-plant level [5]. Reported physiological injuries include leaf scorching, premature senescence and abscission, inhibition of shoot and root growth, and reductions in photosynthetic efficiency, which ultimately decrease tree productivity [6–9]. In addition, elevated temperatures

increase evapotranspiration, thus raising the irrigation demand of fruit orchards [10]. Even brief episodes of heat stress can significantly impair photosynthesis by damaging PSII reaction centers, inhibiting Rubisco activity, and lowering overall photosynthetic performance [11,12].

Soil temperature is a key component of the plant–soil-atmosphere system, influencing both soil processes and plant physiology. Recent studies report that soil temperatures are rising in Northern European countries, and predictions suggest that this increase can be pronounced in Southern Europe [13]. Seasonal soil warming is further worsened by low soil moisture levels in the top layers, which affect their thermal buffering capacity. In addition, soil temperature can be affected by several factors, including soil characteristics (texture, color, and organic matter content), management practices (tillage, irrigation, and mulching) [14], and orchard characteristics (density, canopy size, and row orientation) [15]. Extreme soil temperatures approaching or exceeding 50 °C can occur under field conditions and in container-grown nursery plants, especially when the upper soil layers are directly exposed to intense solar radiation [15,16].

Although most studies about heat stress in tree crops focus on air temperatures and canopy responses, studies on soil temperatures and the impact of heat stress on plant ecophysiology and root biology are very limited and have focused primarily on annual crops and grassland species [17].

In general, elevated soil temperatures impair photosynthetic performance by reducing carboxylation efficiency and disrupting carbon assimilation [18]. These changes are often accompanied by a decline in stomatal conductance and leaf relative water content, together with an accumulation of intercellular CO_2.

Moderate soil temperatures generally increase root growth up to a species-specific threshold at which the growth declines [19]. High soil temperatures can directly inhibit root elongation and proliferation, alter root architecture by reducing branching and fine root development, and accelerate root senescence and turnover [20,21]. Root growth and function can be impaired by both short and long-term root-zone heating, leading to decreased water and nutrient uptake, and ultimately resulting in a reduction in overall plant growth [22,23].

The challenges posed by high temperatures are further aggravated in modern intensive fruit orchard systems. In modern high-density pear orchards, dwarfing rootstocks are commonly used to promote early fruit production and control canopy size in order to promote simplified management and the mechanization of some cultivation practices [24]. These orchards are often characterized by frequent replanting conditions, which may extend soil sickness, as reported for apple [25,26]. Dwarf rootstocks are characterized by shallow root systems, which may increase pear tree susceptibility to soil temperature fluctuations and water stress [27]. The vulnerability to sudden climatic extreme conditions could accelerate senescence and shorten orchard lifespan, especially in Southern European countries in the Mediterranean basin [23,28]. In this region, characterized by a warm transitional climate with xeric soil moisture regimes, precipitation is concentrated in winter while summers are dry [15].

Quince (*Cydonia oblonga*) dwarfing rootstocks are known to have a strong size-control effect and a good compatibility with many pear cultivars [29]. However, its sensitivity to abiotic stress, particularly heat and drought, has raised concerns about its resilience under climate change [30]. In vitro-propagated pear, on the other hand, is emerging as a potential alternative rootstock [29], but its response to high soil temperature remains poorly understood.

Despite the growing importance of root-zone stress under climate change, little is known about how pear and quince root systems respond to elevated soil temperatures. To

the best of our knowledge, no study has investigated the response of pear and quince to high soil temperature. Therefore, the objective of this study was to evaluate the physiological responses and the canopy and root growth of pear and quince potted plants subjected to root-zone heating and grown in a glasshouse. Understanding these responses is essential to provide insights into the potential role of rootstocks in mitigating the effects of soil warming in intensive pear orchards.

2. Materials and Methods

2.1. Plant Material and Growth Conditions

One-year-old micropropagated pear plants (*Pyrus communis* L., cv. Williams) and bare root quince plants (*Cydonia oblonga* Mill., cv. BA29) were used in this study. On 30 April 2024, dormant plants (before bud break) were transplanted into 7 L polyethylene pots filled with substrate composed of 90% lapilli and pumice mix and 10% of zeolite enriched with Leonardite. Before potting, the roots were pruned and the main stem was cut to uniform the total height of the plants at 40 cm. Also, all the lateral shoots were removed. Plants were grown inside the experimental glasshouse of the Department of Agriculture, Food and Environmental Sciences at the Polytechnic University of Marche, Ancona, where environmental parameters were not artificially controlled but maintained at ambient conditions (Figure 1). Roof vents opened and closed automatically to moderate temperature, and from June onward, a shading net was deployed to limit excess irradiance. During the experiment, the plants were irrigated two to three times daily with 100 mL per irrigation. All plants were fertilized equally with 10 g per plant using a slow-release NPK fertilizer (NPK Original Gold, COMPO EXPERT., Münster, Germany), and a standard pest control protocol was applied throughout the experiment.

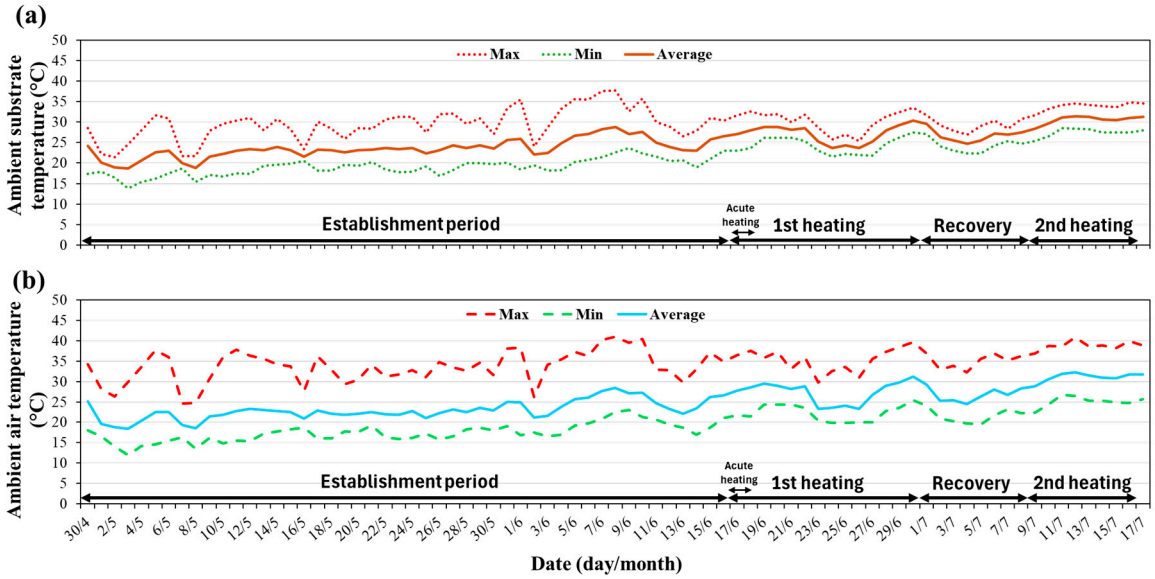

Figure 1. Ambient substrate (**a**) and air (**b**) temperatures inside the greenhouse during the experiment. Values are shown as daily maximum (Max), minimum (Min), and average temperatures.

2.2. Experimental Design and Treatments

After the establishment period (from planting date to 16 June 2024), a total of 60 plants were arranged in a completely randomized design. Root-zone heating treatment was applied by wrapping heating cables around each pot and regulating substrate temperature with programmable thermostats equipped with probes. To limit heat dissipation, all pots (including controls) were then surrounded by an insulating film, and the substrate surface was covered with a 20 mm thick polystyrene sheet.

Treatments consisted of applying two day/night root-zone temperature regimes: 35/30 °C and 40/35 °C. The higher temperature was applied from 8 am to 6 pm, and the lower from 6 pm to 8 am. Control plants were maintained at ambient substrate temperature (Figure 1). All treatments began on 17 June 2024 and lasted for 14 days, followed by an 8-day recovery at ambient substrate temperature, after which a second 8-day root-zone heating identical to the first one was imposed. In addition, an acute root-zone heating treatment was applied simultaneously with the above-mentioned treatments at the start of the experiment (17 June 2024). Substrate temperature in this treatment was raised to an average of 50 °C for a duration of 36 h to simulate an extreme, short-term soil heatwave. Plants were visually inspected, heating was terminated at 36 h, and plants were returned to ambient substrate temperature when initial foliar symptoms were observed. This acute root-zone heating was applied to investigate the effects of extreme short-term heating compared to moderate and prolonged substrate temperatures, and to determine the threshold of root-zone temperature at which irreversible damage occurs in the root and shoot of pear and quince plants. Temperature data loggers (Elitech RC-5+; ±0.5 °C accuracy, Elitech Ltd., London, UK) equipped with probes were inserted at 8 cm depth in one pot of each treatment, and temperature was registered at 10 min intervals. Air temperature and relative humidity inside the greenhouse were monitored and registered using a temperature data logger.

2.3. Measurements

Plants were monitored daily during the heating treatment. External symptoms were visually assessed to record the onset and progression of leaf discoloring, burning, and wilting. At the end of the experiment, plants were harvested. Shoot length and main stem diameter were recorded. Root and shoot were separated and oven dried at 60 °C to constant weight, to determine the dry biomass. In addition, plant growth was assessed during the experiment period by measuring the elongation of newly emerging lateral shoots using a ruler. Total shoot length was recorded at four time points: the beginning of the treatment, the end of the first heating phase, the end of the recovery period, and the end of the second heating phase. Growth increments (ΔG) were calculated for each phase as follows:

$$\Delta G = \text{final shoot length} - \text{initial shoot length} \quad (1)$$

Net photosynthetic rate (P_n, μmol CO_2 $m^{-2}s^{-1}$), transpiration rate (E, mmol H_2O $m^{-2}s^{-1}$), and stomatal conductance (g_s, mmol H_2O $m^{-2}s^{-1}$) were measured on one fully expanded leaf per plant using an ADC-LCA3 portable infrared gas analyzer (ADC Bioscientific Ltd., Hoddesdon, UK). Measurements were taken with at least five replicates per treatment. Water use efficiency (WUE) was then calculated as the ratio of P_n to E. Gas exchange measurements were planned at the beginning of the experiment, then at the end of each treatment phase (first heating, recovery, and second heating) to assess the physiological state of each phase (Figure 2). However, due to cloudy conditions resulting in low photosynthetically active radiation (PAR) during the first days after the beginning of the trial, the first reliable measurements were taken on Day 4 of the treatment. The CO_2 concentration was set at 380 ppm. The first two measurements were performed under natural greenhouse irradiance. The other subsequent measurements were conducted using the instrument's artificial light source set to deliver 800 μmol m^{-2} s^{-1} at the leaf surface (Q_{leaf}). Leaf chlorophyll content index (CCI) was assessed with a chlorophyll content meter (Apogee Instruments, North Logan, USA) on all plants, using two fully expanded leaves per plant. One reading per leaf was taken and averaged for each plant.

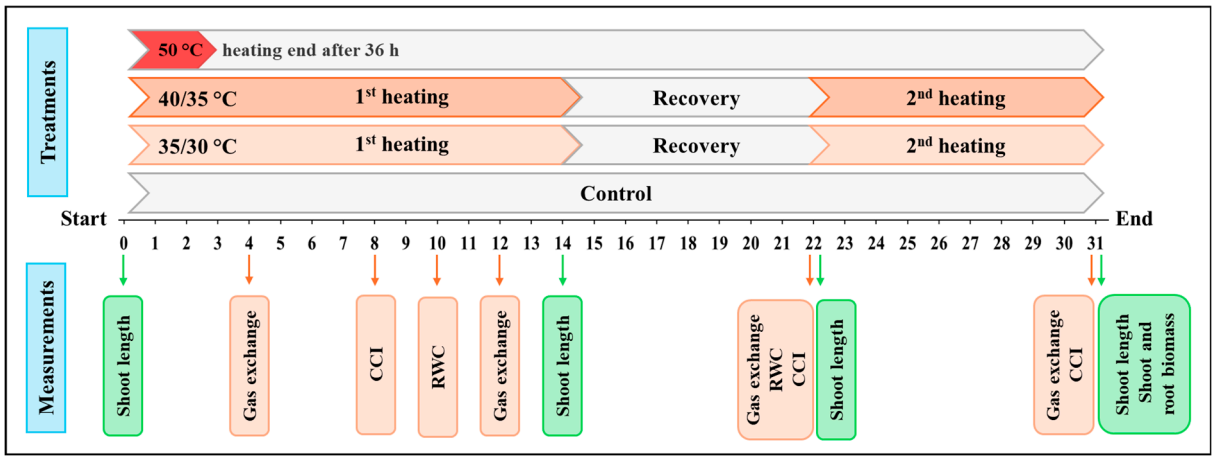

Figure 2. Experimental timeline showing root-zone heating treatments and measurements schedule. Control plants (gray) were kept at ambient substrate temperature (average of 27 ± 3 °C). During the recovery period, plants were kept at ambient substrate temperature. Physiological measurements, including gas exchange, chlorophyll content (CCI), and relative water content (RWC), are represented in orange. Growth measurements, including shoot length and final shoot and root biomass, are represented in green.

The leaf relative water content was determined on Day 10 (first heating) and at the end of the recovery period. Leaves were sampled and immediately weighed to obtain fresh weight (FW), then were immersed in distilled water and kept in the dark at 4 °C for 24 h, then weighed to determine the turgid weight (TW). Finally, leaves were oven-dried at 60 °C to constant weight, and dry weight (DW) was recorded. Leaf relative water content (RWC) was calculated as follows:

$$\text{RWC (\%)} = (\text{FW} - \text{DW})/(\text{TW} - \text{DW}) \times 100 \quad (2)$$

2.4. Statistical Analysis

For all response variables, data were analyzed using a two-way factorial Analysis of Variance (ANOVA) with species (pear, quince) and treatment (Control, 35/30 °C, 40/35 °C, Acute 50 °C) as fixed factors. The experiment was conducted with 10 biological replicates per species × treatment combination, except for the 35/30 °C and 50 °C treatments, which included only 5 replicates due to space limitations. Analyses were conducted using a linear model with Type III sums of squares. When significant effects were detected, main effects were interpreted, and post hoc comparisons were conducted using Tukey's Honest Significant Difference (HSD) test. In addition, treatment means were compared within each species using Tukey-adjusted pairwise comparisons. Differences were considered significant at $p < 0.05$, and results are presented as means ± standard error. All statistical analyses were performed using RStudio integrated development environment (version 2024.12.1+563).

3. Results

3.1. Morphological Responses

On pear and quince plants subjected to acute root-zone heating (substrate temperature of 50 ± 5 °C maintained for 36 h), visible foliar damage was first observed within 36 h of treatment start (Figure 3). Early symptoms consisted of marginal leaf burn, which appeared as necrosis starting at the leaf edges. By Day 7, basal leaves progressively turned dark brown and began to wilt, while the apical foliage remained green and apparently viable. However, by Day 12, foliar damage had progressed throughout the canopy, resulting in

complete desiccation and irreversible wilting. All plants exposed to the acute treatment ultimately died, while no visible symptoms were observed in any of the other treatments during the experiment.

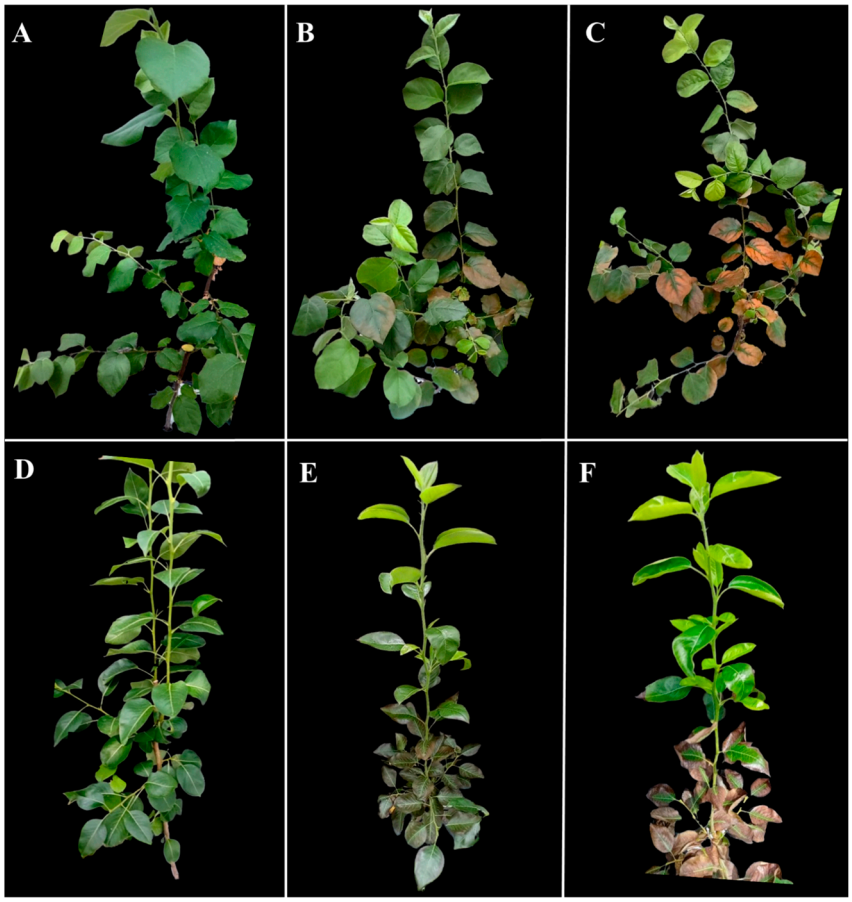

Figure 3. Visual symptoms of quince (**top**) and pear (**bottom**) plants subjected to 36 h of acute root-zone heating at 50 °C, photographed immediately after treatment (**B**,**E**) and on Day 7 (**C**,**F**). Control plants maintained at ambient root-zone temperature are shown in panels (**A**,**D**).

At the end of the experiment, the root system was separated from the shoot and washed. The visual assessment revealed marked differences in root morphology among treatments (Figure 4). Plants subjected to acute 50 °C root-zone heating showed small, dark brown root systems, damaged and clearly less developed than in other treatments. In plants exposed to 40/35 °C temperature, roots were visibly less developed than control and 35/30 °C plants and showed dark brown discoloration indicative of heat-induced damage. By contrast, control and 35/30 °C plants developed vigorous root systems, characterized by a light brown coloration with abundant new fine root formation. Although the overall pattern of response to heating was similar in both species, quince plants consistently developed a larger and more extensive root system than pear.

3.2. Growth Responses

Shoot elongation was monitored throughout the experiment at four key time points: the start of heating, the end of the first heating period, the end of the recovery phase, and the end of the second heating period.

During the first heating period, in both species, plants exposed to acute root-zone heating (50 °C for 36 h) ceased shoot elongation immediately after treatment started, and no further growth was observed. In contrast, plants in the other treatments continued to grow, although shoot elongation tended to decline with increasing root-zone temperature.

The highest increments in shoot length were recorded in the non-heated control plants, while growth was reduced at 35/30 °C and was the lowest at 40/35 °C. However, these differences were not statistically significant during the first heating phases (Figure 5).

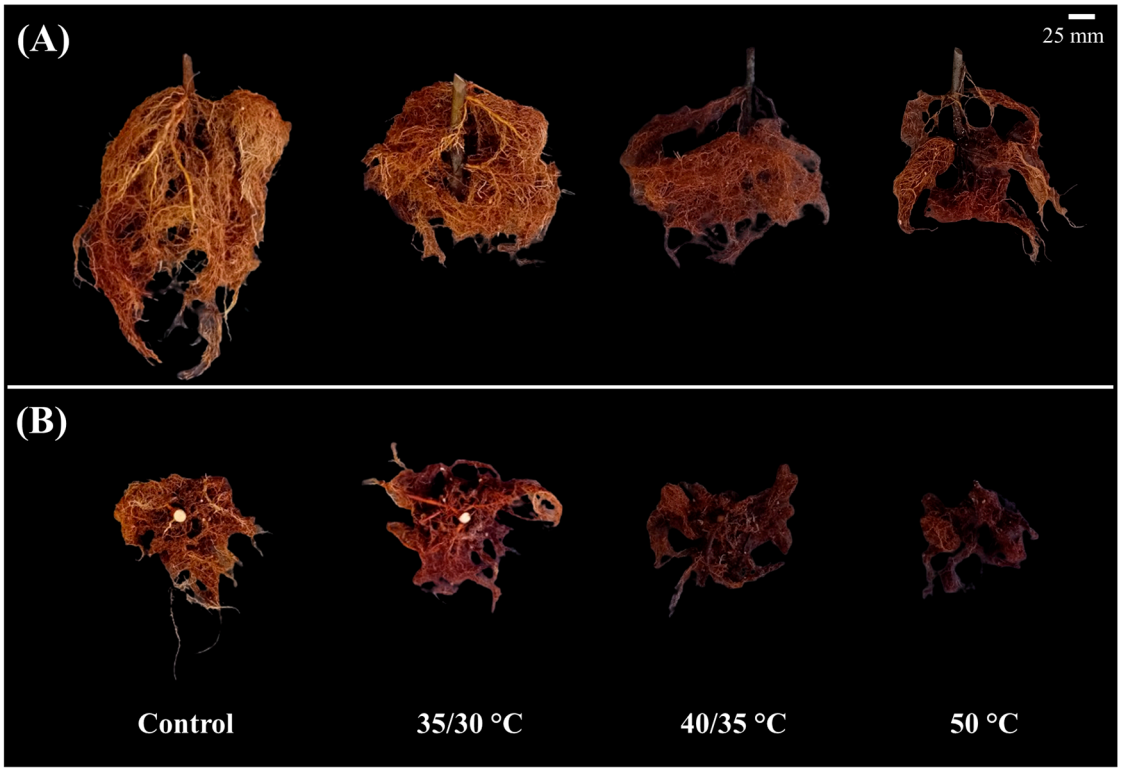

Figure 4. Root systems of quince (**A**) and pear (**B**) plants at the end of the experiment. For each species, representative root systems are shown for control (ambient substrate temperature), 35/30 °C, 40/35 °C, and Acute 50 °C treatments. Images were taken from a side view for quince and from a front view for pear plants to better display root architecture and development. Scale bar = 25 mm.

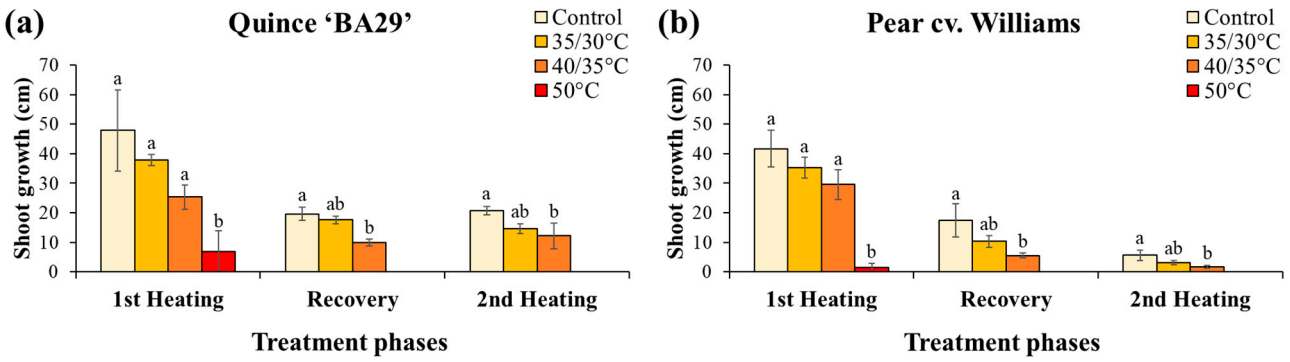

Figure 5. Shoot length increase in quince (**a**) and pear (**b**) subjected to different substrate temperatures during the first heating period (14 days), the recovery period (8 days), and the second heating period (8 days). Data are means ± standard error (n = 10 for control and 40/35 °C treatments; n = 5 for 35/30 °C and 50 °C treatments). Different letters indicate significant differences between treatments within each species and treatment phase ($p < 0.05$).

At the end of the recovery period, quince and pear plants exposed previously to 40/35 °C showed limited growth, with significantly shorter cumulative shoot length compared to control plants. At the end of the second heating period, differences among treatments persisted in both species. The applied 40/35 °C root-zone temperature significantly reduced shoot elongation compared to control plants. During the recovery and

second heating periods, quince plants exhibited significantly greater shoot length increment than pear plants, regardless of treatment (Table A1).

Since the acute root-zone high temperature resulted in growth suppression at the end of the experiment, the assessment of the effect of the treatment on growth parameters was performed without considering plants subjected to acute heating (50 °C).

Main stem diameter was not significantly affected by root heating in either species (Figure 6A,B). Similarly, shoot dry weight of both quince and pear plants remained unaffected by different treatments (Figure 6C,D). In quince, the root dry weight did not differ significantly among treatments, although plants exposed to 40/35 °C tended to have lower root biomass than non-heated and 35/30 °C plants (Figure 6E). By contrast, pear plants were more sensitive to high root-zone temperature, where plants exposed to 40/35 °C exhibited a significant reduction in root dry weight by 39% compared to controls, while the 35/30 °C treatment had no significant effect (Figure 6F). Consistently, the root-to-shoot ratio of pear plants was significantly reduced under 40/35 °C compared to the control (Figure 6H). In quince, no significant differences in root-to-shoot ratio were detected among treatments.

3.3. Physiological Responses

On Day 4, both quince and pear plants subjected to acute root-zone heating (50 °C) showed a drastic reduction in gas exchange compared to all other treatments (Figure 7). In quince, stomatal conductance (g_s) dropped from 80 ± 12.4 mmol m^{-2} s^{-1} in control to 3.33 ± 3.33 mmol m^{-2} s^{-1} in 50 °C plants, while transpiration (E) decreased from 2.43 ± 0.26 to 0.42 ± 0.06 mmol $m^{-2}s^{-1}$. Pear plants exhibited a similar response, with g_s decreased from 136.66 ± 13.58 in control to 20 ± 0.0 mmol m^{-2} s^{-1} under acute 50 °C heating, and E declined from 3.38 ± 0.19 to 0.8 ± 0.07 mmol m^{-2} s^{-1}. However, no significant differences in stomatal conductance and transpiration were observed at 35/30 °C and 40/35 °C compared to the control in both species. In addition, net photosynthesis was not significantly affected by different root-zone treatments on Day 4 in either species.

Since the wilting of plants subjected to acute heating (50 °C) rapidly expanded after this first gas exchange measurement, they were excluded from further assessments.

By Day 12, the effects of root-zone heating were apparent and species-specific. Pear plants subjected to a 40/35 °C regime exhibited significant reductions in stomatal conductance and transpiration rate by 57% and 43%, respectively, compared to control pear plants, and by 65% and 47%, respectively, compared to pear plants at 35/30 °C (Figure 7B,D). On Day 12, net photosynthesis declined with increasing substrate temperature in both species, but the decrease was statistically significant only in quince, where P_n of plants at 40/35 °C dropped by 73% compared to the control (Figure 7E).

Following the recovery period of 8 days, quince plants subjected to 40/35 °C showed a significant reduction in stomatal conductance by 40% compared to control plants. Similarly, pear plants showed a significant reduction in stomatal conductance and net photosynthesis by 37% and 34% compared to control plants, respectively. At the end of the second heating, neither species showed a significant difference among treatments in the measured gas exchange parameters.

Factorial ANOVA revealed that species significantly influenced stomatal conductance (g_s) and transpiration (E) during the first heating period, where pear plants showed significantly higher values than quince plants regardless of treatment (Table A3). However, no species effect was detected during recovery or the second heating phase. By contrast, the treatment factor had a significant effect on g_s, E, and net photosynthesis (P_n) during the first heating and recovery periods, but not at the end of the second heating phase. No significant interactions between species and treatment were detected for any parameter.

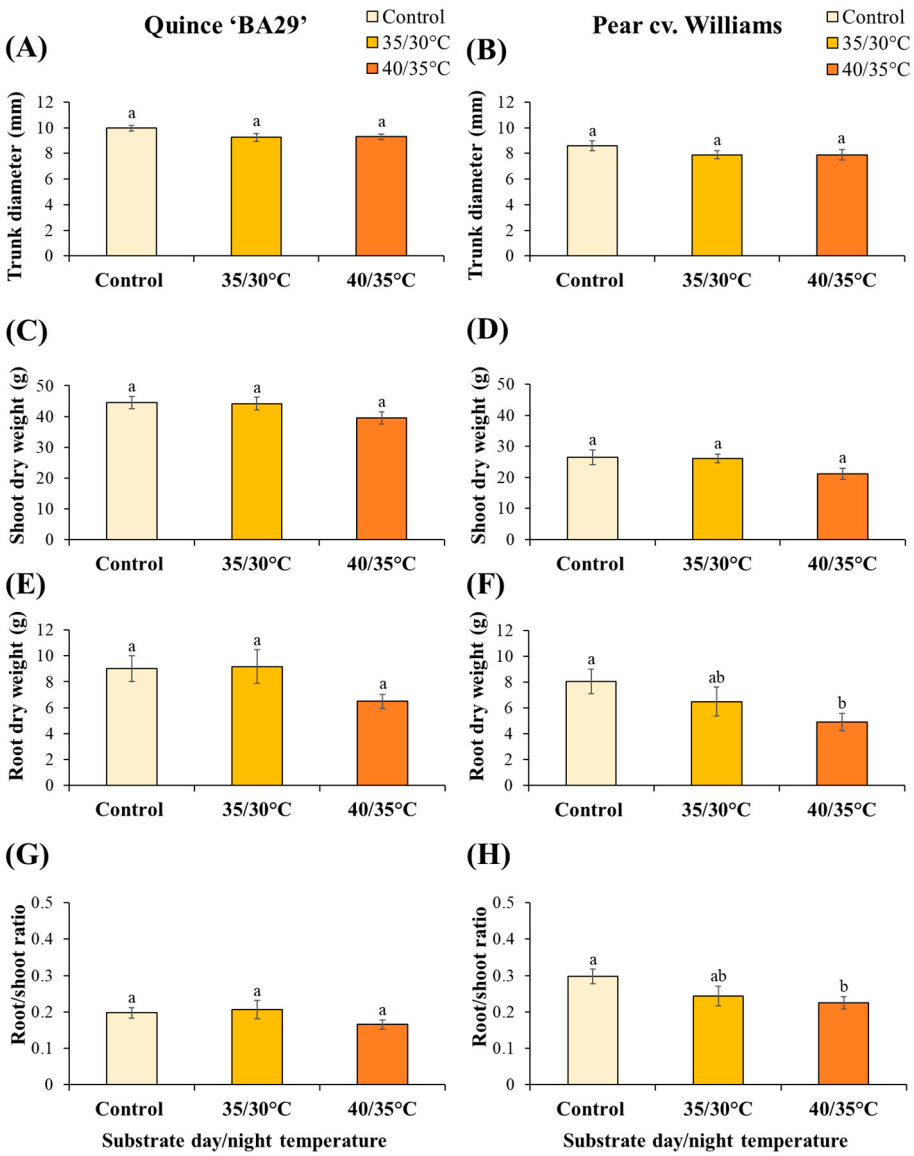

Figure 6. Final stem diameter (**A**,**B**), shoot biomass (**C**,**D**), root biomass (**E**,**F**), and root/shoot ratio (**G**,**H**) of quince and pear plants subjected to different substrate temperatures. Data are means ± standard error (n = 10 for control and 40/35 °C treatments; n = 5 for 35/30 °C and 50 °C treatments). Different letters indicate significant differences between treatments within each species ($p < 0.05$).

Leaf relative water content (RWC) measured on Day 10 revealed that the acute 50 °C root-zone heating markedly impaired plant water status in both species. In quince, plants subjected to 50 °C treatment had significantly lower RWC than control plants, while the 35/30 °C and 40/35 °C treatments caused only slight, non-significant reductions (Figure 8). In pear, RWC in the 50 °C treatment was significantly reduced compared to all other treatments. In addition, pear plants showed significantly higher RWC than quince plants across treatments (Table A4). After the recovery period, the RWC did not differ among the compared treatments in both species. As shown in Figure 9, the chlorophyll content index (CCI) in both quince and pear leaves was generally unaffected by root-zone heating during the experiment. No significant differences were detected among treatments during the first heating or recovery phases. However, by the end of the second heating period, quince plants subjected to 35/30 °C showed significantly lower CCI values compared to those exposed to 40/35 °C. In addition, no significant differences in CCI were observed between quince and pear, regardless of treatment (Table A5).

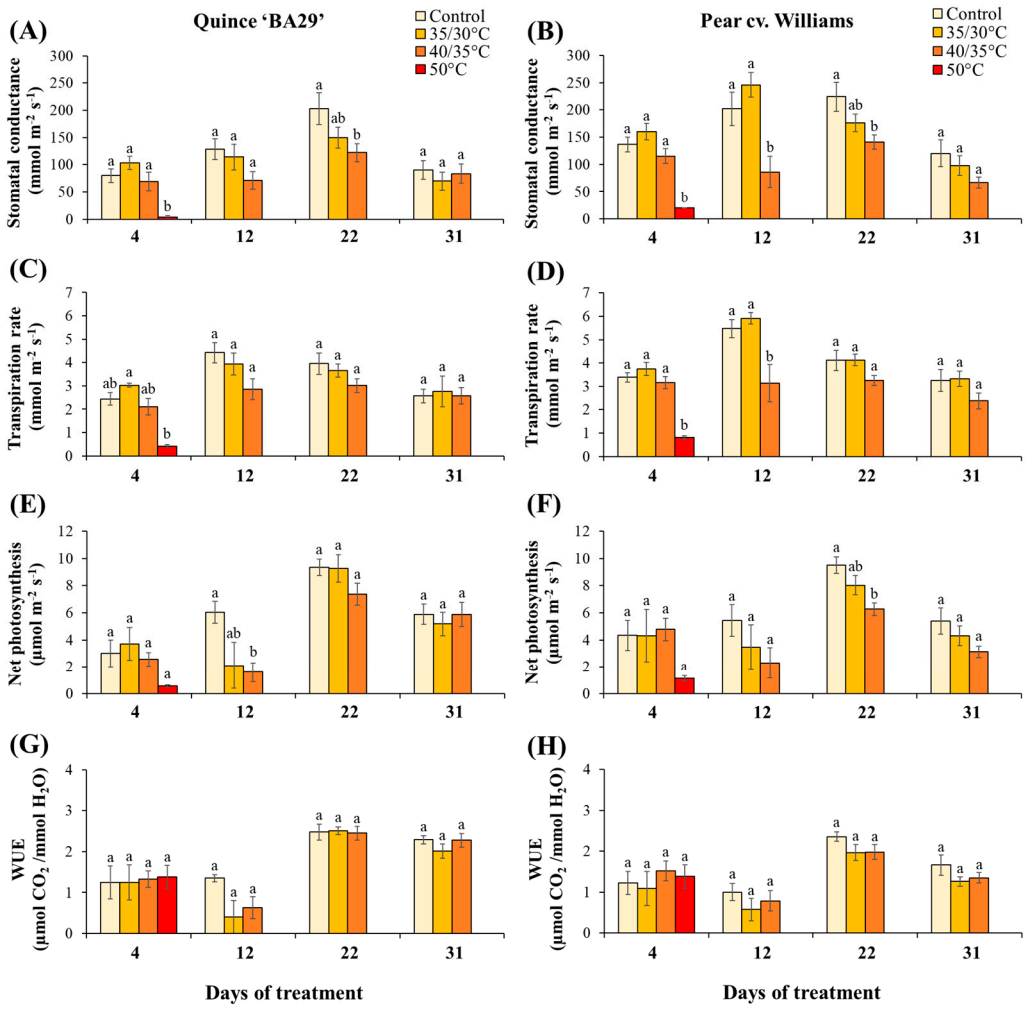

Figure 7. Effect of different treatments on stomatal conductance (**A**,**B**), transpiration rate (**C**,**D**), net photosynthesis (**E**,**F**), and water use efficiency (**G**,**H**) of quince and pear plants, respectively, during the experiment. Data are means ± standard error (n ≥ 5 for each treatment). Different letters indicate significant differences between treatments within each day ($p < 0.05$).

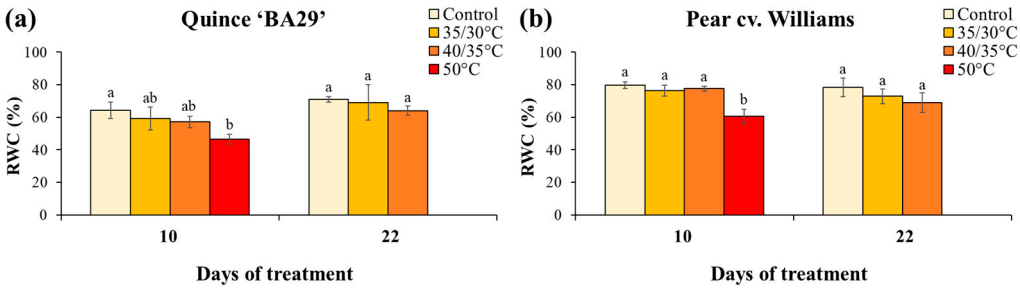

Figure 8. Leaf relative water content (RWC) of quince (**a**) and pear (**b**) plants subjected to different substrate temperatures on Day 10 of the first heating treatment and at the end of the recovery period (Day 22). Data are means ± standard error (n = 5 for each treatment). Different letters indicate significant differences between treatments within each species and sampling date ($p < 0.05$).

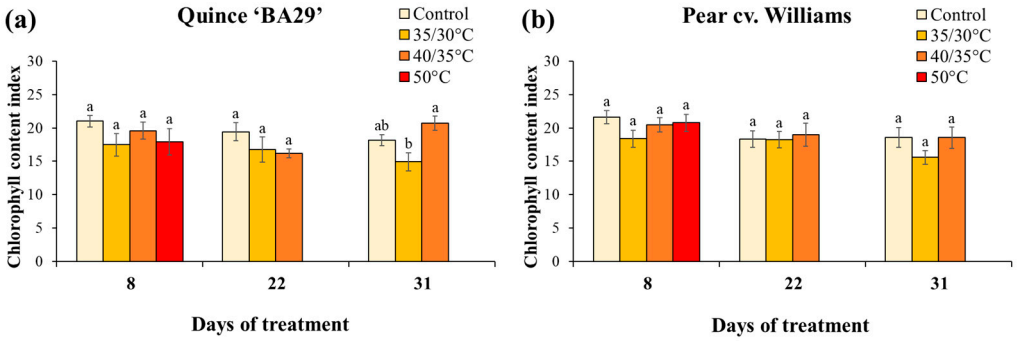

Figure 9. Chlorophyll content index (cci) of quince (**a**) and pear (**b**) plants subjected to different root-zone heating treatments on day 8 of the first heating period, at the end of the recovery period (day 22), and at the last day of the second heating phase (day 31). data are means ± standard error (n = 10 for control and 40/35 °c treatments; n = 5 for 35/30 °c and 50 °c treatments). different letters indicate significant differences between treatments within each species and measurement date ($p < 0.05$).

4. Discussion

Heat stress is one of the most significant environmental factors limiting crop growth and productivity globally [19]. Supra-optimal temperatures have been reported to cause leaf burn, wilting, and abscission in plants [6]. In our study, pear and quince plants subjected to extremely elevated root-zone temperatures exhibited rapid leaf necrosis that progressed over time, leading to irreversible wilting and plant death. These results suggest that shoot tissues are sensitive to extreme heat events, particularly when the stress originates in the root zone and disrupts water balance. Similar observations have been reported in other fruit tree species [16,31]. For instance, kiwifruit seedlings exposed to 45 °C for 8 h exhibited pronounced leaf desiccation and water loss [32], while young apple trees subjected to 48 °C for 24 h showed 40% mortality even after a 48 h recovery period at moderate temperature [8]. Elevated root-zone temperatures beyond the plant species-specific thresholds can inhibit root elongation and fine root development and even cause severe damage [5,16,20]. In our study, exposure to an acute temperature of 50 °C caused visible root damage and complete growth inhibition. Previous studies have shown that root systems of plants exposed to supra-optimal root-zone temperatures generally exhibit reduced biomass, darker coloration, apical tip necrosis, and decreased succulence compared with plants grown under optimal conditions. Similarly, in our study, pear and quince plants subjected to prolonged root-zone heating at 40/35 °C showed a clear reduction in overall root system volume and fine root density, as observed during visual examination. Our results highlighted that even short-term exposure to extreme temperatures can lead to irreversible damage in young pear and quince plants. These results emphasize that roots are susceptible to heat stress and that high root-zone temperatures impaired their growth. Such sensitivity is in line with previous studies where high soil temperature caused cell injury and irreversible membrane damage, and a reduction in root vitality [16,33].

The acute 50 °C heating caused an immediate stop of shoot elongation, which is consistent with the severe root injury and consequent root water uptake collapse (Figures 4 and 8). By contrast, the chronic 40/35 °C regime resulted in slower, cumulative reductions in shoot growth that became significant only after recovery and following the second heating period. However, the root-zone temperature of 35/30 °C was found not to affect shoot elongation. Similar findings have been reported in previous studies on grapevine and apple trees, where elevated root-zone temperatures significantly reduced fine-root activity, inhibited mineral nutrient absorption, and ultimately suppressed shoot growth [34,35]. Generally, heat stress causes changes in biomass allocation and metabolite redistribution within plants.

It is well established that supra-optimal root-zone temperatures, even when below the threshold causing direct tissue injury, can alter biomass partitioning between roots and shoots [16]. The biomass results revealed clear species-specific differences in responses to elevated root-zone temperatures (Table A2). Our results showed that while stem diameter and shoot dry weight remained unaffected in both quince and pear, root biomass showed contrasting patterns. In quince, root dry weight was not significantly influenced by substrate temperature, while pear showed a significant reduction in shoot dry weight and root to shoot ratio under 40/35 °C heating treatment. This reduction in belowground biomass may reflect root injury induced by root-zone heating, leading to membrane damage, loss of fine roots, and a reduced absorptive surface. These findings suggest that pear roots were far more sensitive to high root-zone temperatures, while quince maintained a more balanced biomass partitioning under the same conditions. Our observations are consistent with previous studies reporting the vulnerability of woody plant roots to supra-optimal temperatures of 40 °C, where increases in shoot-to-root ratios were observed [16]. Similarly, previous works demonstrated that root-zone heating at 35 °C of M9 apple rootstock led to a 57% reduction in root fresh weight compared to 25 °C. Comparable responses have been documented in other fruit species, where growth of peach roots was almost completely inhibited at 35 °C, and pecan roots showed near growth cessation with shoot tip dieback at 38 °C [35]. Taken together, these results reinforce the notion that, although both shoots and roots are affected by heat stress, roots are generally more sensitive to elevated root-zone temperatures [22,36,37].

Elevated temperatures are known to alter several key physiological processes in plants [19]. Among these, gas exchange is particularly sensitive to temperature fluctuations. In our study, acute root-zone heating at 50 °C caused a rapid and drastic collapse of stomatal conductance and transpiration within a few days, leading to progressive canopy desiccation and plant mortality. These responses indicate an impairment of water supply to the shoot due to heat-induced injury of roots. Similar responses have been reported in tree species and crops, where extreme soil or aerial temperatures rapidly reduced water uptake and stomatal conductance [8,32]. Reductions in photosynthesis rate at extreme soil temperature have been suggested to be caused by injury to the photosynthetic process due to leaf desiccation [16]. By contrast, in our study, the prolonged heating at 40/35 °C produced slower, species-specific declines. The results showed that pear plants exhibited pronounced g_s and E reductions, contrary to quince. Furthermore, we observed that quince exhibited a large decrease in photosynthesis rate during the first heating, while this reduction was observed after the recovery period in pear plants. This pattern is consistent with a recent study showing that long-term high root-zone temperatures markedly decreased the photosynthetic capacity in grapevine [34]. A similar study reported that one-year-old apple rootstock trees subjected to prolonged supra-optimal root-zone temperature showed a decrease in photosynthesis and transpiration rates [35]. Such reductions can be caused by heat-induced water stress leading to stomatal closure [16]. Our results are in line with other studies reporting severe photosynthetic decline and an increase in intercellular CO_2 under high-temperature exposure in young apple trees [8] and reduced leaf carbon assimilation and stomatal conductance following elevated root-zone temperatures [38,39]. Moreover, the absence of treatment differences observed after the second heating may reflect that this period coincided with a rise in ambient temperature (daily maximum temperature peaked at 40.9 and 39.9 °C on Day 26 and 30, respectively; Figure 1). This may have caused additional heat stress and is likely the reason for the reduction in stomatal conductance across root-zone treatments. Elevated soil temperature is generally reported to increase water use or induce plant water stress [16]. In our study, acute root-zone heating at 50 °C caused a significant reduction in leaf relative water content in both species, indicating a severe

disruption of water uptake likely resulting from direct root injury. This impairment led to irreversible desiccation and plant death. Critical root-zone temperatures are species-specific but generally range between 30 and 40 °C [16]. However, our results showed that 35/30 and 40/35 °C root-zone heating treatments did not significantly affect the relative water content in either species. This contrasts with previous findings in apple, where a supra-optimal root-zone temperature of 36 °C led to a decrease in leaf water content [35]. Previous studies reported that high root-zone temperatures can cause a decrease in chlorophyll content, which in turn contributes to reduced photosynthetic activity [34,35]. In contrast, our results showed that root-zone heating did not significantly affect the leaf chlorophyll content index in either species.

In our study, the impairment of water uptake induced by root damage in pear plants subjected to 40/35 °C root-zone heating likely contributed to the significant decrease in stomatal conductance during the first heating, which persisted even after the recovery period. This response can be interpreted as a stomatal closure mechanism aimed at preventing excessive water loss and leaf desiccation.

5. Conclusions

In intensive orchard systems, the soil under the trees is often kept bare through tillage or herbicide use, making the upper soil layers more susceptible to high temperatures caused by intense solar radiation. The results observed in our study show that short, extreme increases in root-zone temperature can cause rapid root injury and collapse of water uptake, leading to canopy loss and plant death, regardless of rootstock genotype. Sustained root-zone heating at 40 °C produced more gradual but persistent effects, including reductions in gas exchange and significant losses in root biomass. The shallow root system of dwarfing rootstocks (e.g., quince) may therefore exacerbate susceptibility to soil surface heat waves and limit the tree's capacity to buffer transient soil temperature extremes [28]. Our results could provide a physiological and growth baseline for future studies on pear and quince rootstock responses to soil warming. However, determination of rootstock resilience under future climate change requires further, broader screening and in-depth molecular, biochemical, and genetic assays across a wider range of genotypes, soil types, and management regimes.

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Appendix A

Table A1. Results of two-way ANOVA testing the effect of species (S), treatment (T) and their interaction (S × T) on shoot length increment at different experiment phases.

Factor	*p*-Value		
	1st Heating	**Recovery**	**2nd Heating**
S	0.828 ns	<0.001 ***	0.001 **
T	<0.001 ***	<0.001 ***	<0.001 ***
S × T	0.832 ns	0.949 ns	0.958 ns

ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table A2. Results of two-way ANOVA testing the effect of species (S), treatment (T), and their interaction (S × T) on shoot and root growth parameters.

Response	Factor		
	S	**T**	**S × T**
Trunk diameter	<0.001 ***	0.051 ns	0.997 ns
Shoot dry weight	<0.001 ***	0.018 *	0.994 ns
Root dry weight	0.027 *	0.003 **	0.688 ns
Root/shoot ratio	<0.001 ***	0.012 *	0.414 ns

ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table A3. Results of two-way ANOVA testing the effect of species (S), treatment (T), and their interaction (S × T) on gas exchange parameters.

Parameter	Factor	*p*-Value			
		Day 4	**Day 12**	**Day 22**	**Day 31**
g_s	S	<0.001 ***	<0.001 ***	0.210 ns	0.379 ns
	T	<0.001 ***	<0.001 ***	<0.001 ***	0.234 ns
	S × T	0.693 ns	0.057 ns	0.985 ns	0.329 ns
E	S	0.002 **	0.01 *	0.305 ns	0.310 ns
	T	<0.001 ***	< 0.001 ***	0.014 *	0.342 ns
	S × T	0.758 ns	0.241 ns	0.915 ns	0.480 ns
P_n	S	0.126 ns	0.617 ns	0.251 ns	0.054 ns
	T	0.043 *	0.008 **	0.001 **	0.342 ns
	S × T	0.806 ns	0.705 ns	0.615 ns	0.329 ns
WUE	S	0.981 ns	0.751 ns	0.010 *	<0.001 ***
	T	0.837 ns	0.042 *	0.582 ns	0.167 ns
	S × T	0.953 ns	0.526 ns	0.619 ns	0.625 ns

ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table A4. Results of two-way ANOVA testing the effect of species (S), treatment (T), and their interaction (S × T) on leaf relative water content (RWC).

Factor	*p*-Value	
	Day 10	**Day 22**
S	<0.001 ***	0.115 ns
T	<0.001 ***	0.101 ns
S × T	0.851 ns	0.895 ns

ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table A5. Results of two-way ANOVA testing the effect of species (S), treatment (T), and their interaction (S × T) on leaf chlorophyll content index (CCI).

Factor	*p*-Value		
	Day 8	**Day 22**	**Day 31**
S	0.180 ns	0.357 ns	0.733 ns
T	0.093 ns	0.521 ns	0.017 *
S × T	0.872 ns	0.310 ns	0.479 ns

ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

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