

Effect of Silicon Application on Peach Tree Responses to Water Stress

MARTOS-GARCÍA, INMACULADA¹, BENLLOCH-GONZÁLEZ, MARÍA^{1*}, FERNÁNDEZ-ESCOBAR, RICARDO¹, JUAN CARLOS MELGAR²

Additional index words: Drought, foliar Si application, nutrient uptake

Abstract

Water deficits during the first years after planting fruit trees can impact future productivity by reducing vegetative growth and canopy development. Previous studies have shown that silicon (Si) application enhances plant tolerance to abiotic stresses such as drought, specifically improving growth, nutrient uptake, and physiological mechanisms related to water status and leaf anatomy. Therefore, this study aimed to evaluate the effect of Si on water status, sap flow, gas exchange, and potassium (K) and nitrogen (N) uptake in young peach trees under water stress. The experiment was conducted with young peach trees under greenhouse conditions using a completely randomized block design with four treatments: two water regimens (well-watered at 100% and water-stressed at 50% of evapotranspiration requirements) combined with two Si concentrations (0 or 20 mg L⁻¹) foliar sprayed. Si application enhanced water status in water-stressed trees, although this improvement was not associated with changes in sap flow, gas exchange, or stomatal density. Vegetative growth increased only in well-watered plants receiving Si. Additionally, Si applications increased K concentration in leaves and spring shoots of water-stressed trees, with no effect observed in well-watered trees. Leaf N concentration increased under both Si application and water deficit, but no interaction between these factors was detected. These findings suggest that Si foliar application may be a promising strategy to maintain trees water status under water deficit.

Introduction

Water availability is critical for plant growth and productivity, as it affects a wide range of processes such as photosynthesis, nutrient uptake, and cellular expansion (Seleiman et al. 2021). In areas of the southeastern United States, young peach trees are often not irrigated until the third year, when fruit production begins (Casamali et al. 2021), as the region generally receives substantial precipitation to cover evapotranspirative needs. However, drought conditions can develop and intensify quickly (flash droughts; Minton et al. 2025) and water deficit in juvenile trees can impact future tree productivity through a reduction in vegetative growth and canopy development.

One of the earliest responses to water deficit is

stomatal closure driven by reduced leaf turgor pressure (McAdam and Brodribb 2015). In parallel, reduced cellular water content and turgor pressure inhibit cell expansion, further suppressing vegetative growth (Zia et al. 2021). Also, drought conditions reduce soil water availability, which is essential for nutrient solubilization, root uptake, and translocation (Bárzana and Carvajal 2020; Bista et al. 2018). Among essential nutrients, potassium (K) plays a key role in plant water relations. Its involvement in osmotic regulation is critical for maintaining cell turgor pressure which supports cell expansion and stomatal function thereby influencing plant growth and transpiration efficiency (Ashokan et al. 2024; Benlloch-González et al. 2008). Therefore, maintaining sufficient K uptake is a key adaptive

¹Departamento de Agronomía, Escuela Técnica Superior de Ingeniería Agronómica y de Montes, Universidad de Córdoba, Campus de Excelencia Internacional Agroalimentario, ceiA3, Ctra. Madrid-Cádiz, Km. 396, 14071 Córdoba, Spain.

²Department of Plant and Environment Sciences, Clemson University, 105 Collings Street BRC 204, Clemson, SC 29634, USA.

*Corresponding author email: g72begom@uco.es.

Acknowledgements: This study was supported by the University of Cordoba through their student travel scholarship “Ayudas de Movilidad Internacional 2022/2023” program. The authors also thank Dr. Sruthi Narayanan for providing space at her greenhouse, and Neil Mayberry from Yara for providing the product for the experiment.

This is an open access article distributed under the CC BY-NC license (<https://creativecommons.org/licenses/by-nc/4.0/>).

mechanism for enhancing plant drought tolerance (Benlloch-González et al. 2015). Nitrogen (N) metabolism and uptake in plants is also impaired by drought, as reduced soil moisture restricts the transport of mineral N to the root via mass flow (González-Dugo et al. 2010), which could lead to reduced N accumulation in plant tissues.

Silicon (Si) has recently emerged as a beneficial element that enhances plant tolerance to abiotic stresses, including drought. Although not essential, Si contributes to stress mitigation by modulating physiological responses, improving water relations, and enhancing nutrient uptake (Pavlovic et al. 2021). It is the second most abundant element in the Earth's crust and primarily absorbed by plants as monosilicic acid (Epstein 1999). It can be taken up through root and foliar pathways, including cuticular diffusion, stomatal penetration, and trichome-mediated uptake (Puppe and Sommer 2018). Foliar uptake is particularly relevant in rainfed orchards, where limited soil moisture restricts root uptake and foliar spraying becomes the primary method for agrochemical delivery (Fernández-Escobar 2019). Thus, foliar applications can be ideal for young trees that do not receive irrigation until they begin bearing fruit (Nascimento-Silva et al. 2023). Si can reach up to 10% dry weight (DW) in plant tissues of Si-accumulator plants (Ma and Yamaji 2015) but remains below 0.5% DW in most fruit trees (Gao et al. 2022). Nevertheless, its beneficial effects in plants under abiotic stress are not proportional to its accumulation in plants (Wang et al. 2021a).

Si plays a key role in maintaining plant water balance by regulating water uptake, transport and losses (Wang et al. 2021a). Its deposition beneath the cuticle forms a double silica layer that reduces leaf transpiration (Ma 2004). Si can also increase stomatal density and size (Martos-García et al. 2024), and promote faster stomatal closure by increasing guard cell K efflux (Vandegheer et al. 2021), which together with improvement in CO₂ assimilation can increase plant water use efficiency (Gao et al. 2022). Furthermore, Si has been found to improve plant nutrients acquisition, especially under nutrient-scarce conditions (Pavlovic et al. 2021); for instance, Si has been observed to

increase leaf N, P and K concentrations in mango trees (Helaly et al. 2017). However, Si did not influence N or K uptake in apple trees (Karagiannis et al. 2021). These differences highlight the need for better understanding the influence of Si on nutrient dynamics under drought stress, especially for non-accumulator species such as most fruit trees. Therefore, the aim of this study was to evaluate the feasibility of Si foliar-applied as a sustainable strategy to improve water status and mineral nutrition, specifically K and N, in young peach trees subjected to water deficit.

Materials and Methods

Tree growth conditions. In fall 2023, 24 two-year-old peach trees [*Prunus persica* L. 'Julyprince'] were planted in 19-L plastic containers containing a mixture of 2:1 of potting soil Fafard 3B (Sun Gro, Agawam, MA, USA): sand, 3.5 g·L⁻¹ of lime and 3.5 g·L⁻¹ Osmocote® 14-14-14 fertilizer (Scotts, Marysville, OH, USA). Trees were brought into a greenhouse at Clemson University, SC, in mid-January 2024, after having accumulated enough chill during winter. They bloomed and leafed out in early February 2024. Then, trees were watered to field capacity for a month, estimating the required amount of water gravimetrically, as in Romero-Conde et al. (2014). Briefly, each tree was irrigated to saturation and weighed one hour after water stopped draining. Three days later, trees were reweighed. The difference over the three-day interval was used to estimate the daily water loss, which averaged 0.4 L·day⁻¹. Based on this estimate, each tree received 1.2 L of tap water every three days throughout the month before the treatments started. The greenhouse had temperatures between 18 °C and 24 °C and a photoperiod of 12 h of light throughout the experiment.

Treatments. The experiment was arranged in a completely randomized design, with six replicates and four treatments resulting from the combinations of two irrigation regimens (well-watered or water-stressed) and two levels of foliar Si application (0 or 20 mg·L⁻¹). The experiment was conducted over a 10-week period, from early March to early May 2024, and was divided into two phases.

In phase I, 24 trees were grouped into two sets of 12, each subjected to one of the following irrigation treatments: 1) Well-watered (100% ET): trees received 100% of their evapotranspirative (ET) requirements. Whole-plant ET requirements were determined weekly using a gravimetric method, as described above. ET demands were recalculated weekly to account for increasing canopy development and associated water use. 2) Water-stressed (50% ET): trees received 50% of the irrigation volume applied to the well-watered group.

Irrigation was applied every three days using tap water (electrical conductivity, EC: $72.3 \pm 0.3 \mu\text{S}\cdot\text{cm}^{-1}$). This approach ensured that the total water applied did not exceed the water-holding capacity of the substrate, thereby preventing drainage and maintaining consistent soil moisture levels. This phase lasted two weeks. Upon observing treatment differences on tree water status (midday stem water potential; see measurements, below), phase II commenced.

In phase II (8 weeks), foliar Si treatments were introduced. Trees from each irrigation group (100 and 50% ET) were further divided into two subgroups receiving either 0 (No Si) or $20 \text{ mg}\cdot\text{L}^{-1}$ (Si) of foliar silicon (YaraVita ACTISIL®; BioMinerals N.V., Belgium) which contains 0.5% (w/v) Si in the form of choline-stabilized orthosilicic acid. The selection of Si dose and source was based on findings by Nascimento-Silva et al. (2023), who evaluated the efficiency of different Si doses (0, 10, 20 and $40 \text{ mg}\cdot\text{L}^{-1}$) and sources (YaraVita ACTISIL® and Sigma Aldrich) on peach trees. In that study it was reported that $20 \text{ mg}\cdot\text{L}^{-1}$ significantly improved water status in stressed peach trees, with no significant differences between the evaluated Si sources.

To prepare the Si solution, 4 mL of ACTISIL® was diluted in 1 L of distilled water to achieve a concentration of 0.4% (v/v), equivalent to $20 \text{ mg}\cdot\text{L}^{-1}$ of Si. Trees receiving Si were sprayed weekly (7 weeks) with 0.40 L of the solution per tree (equivalent to 8 mg of Si), using battery-powered backpack sprayers, until dripping point. Control trees (No Si) were sprayed with distilled water following the same protocol.

Measurements. Sap flow rate was monitored using sap flow sensors (Model SGEX25 and Flow32-1K, Dynamax, Houston, TX, USA) from the beginning of the experiment. Sap flow sensors were installed in three trees per treatment approximately 20 cm above the graft union and covered with reflective wrap to prevent extraneous heat flow and reduce the effect of external radiation. Sap flow sensors were connected to a data logger (CR1000, Campbell Scientific, Logan, UT, USA), which monitored and recorded data every two minutes from March to May.

Midday stem water potential (Ψ_{stem}) was measured weekly from the beginning of the experiment, using six leaves per each treatment and a Scholander pressure chamber (PMS Instrument Company, Albany, OR). Before measurements, leaves were introduced in foil-laminated zip-lock type bag for at least 1 h to minimize transpiration and allow for an equilibrium between leaf and stem water potential (McCutchan and Shackel 1992).

Upon the initiation of Si treatments, leaf gas exchange was measured weekly in each plant. The net photosynthetic rate (P_n [$\mu\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$]), leaf transpiration rate (E_{leaf} [$\text{mmol H}_2\text{O m}^{-2}\cdot\text{s}^{-1}$]) and stomatal conductance (g_s [$\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$]) of fully developed leaves (4–5th node) from six trees per treatment were measured using a portable photosynthesis system (LICOR 6400-XTR, Li-COR, Lincoln, NE, USA). All measurements were taken from 09:00 to 11:00 am, under PAR of $1000 \mu\text{mol m}^{-2}\cdot\text{s}^{-1}$, leaf temperatures of $26 \pm 2^\circ\text{C}$, and VPD of $2.4 \pm 0.4 \text{ kPa}$.

During the last week of the experiment, the number of shoots, total shoot length (shoot growth during experiment), and mean shoot length (total shoot length/number of shoots) as well as stomatal density and size were determined. Twelve fully developed leaves per treatment were used for stomatal size and density determination, and three different areas per leaf were selected. Transparent acrylic nail varnish was applied to the underside of leaves. A few minutes later, when the varnish was dried, a piece of transparent packing tape was used to peel off the nail polish. Each tape was placed onto a microscope slide, and observed at 40x magnification (Olympus BX41, Olympus,

Center Valley, PA, USA). Two areas of 6.87 mm² per each slide were randomly selected and images were captured with a digital camera (Canon EOS Rebel T3i, Canon, Melville, NY, USA). Stomata were counted and their size was determined using ImageJ (v1.48, National Institutes of Health, Bethesda, MD, USA).

At the end of the experiment, hydraulic conductance was measured for each tree. Each shoot was cut 10 ± 2 cm above the graft union and measurements were taken with a high-pressure flow meter (HPFM Gen 3, Dynamax, Houston, TX, USA) connected to a compressed nitrogen gas tank. Deionized water was perfused into the stem opposite to the normal direction of flow during transpiration; then water flow was plotted versus the pressure of the root system and hydraulic conductance was determined as the resulting slope. Measurements were taken every two seconds at 22 ± 1 °C until pressure reached 550 kPa under quasi-steady-state conditions (Tyree et al. 1995). Then, each tree was separated into leaves, spring stems, one-year-old stems, trunk, and roots. Each organ was individually rinsed with deionized water, dried in an oven at 60 °C and their DW was measured. Samples of each organ were collect-

ed, ground to powder, and stored in an oven at 70 °C until analysis. Ground samples were ashed at 600 °C overnight, and nutrients were extracted using 10 ml of 0.1 N HCl and then filtered. K concentration was determined by atomic absorption spectrophotometry (PinAAcle 500, Perkin Elmer, Waltham, MA, USA) in all plant organs and in fully developed leaves collected at different moments along the experiment: at the end of phase I and at weeks 2, 5 and 7 of phase II. N concentration was analysed through a modified Dumas method (Harry and Jones 1991) in fully developed leaves collected at the end of phase II.

Statistical Analysis. A two-way factorial analysis was conducted to evaluate the main effects of *Water regimens* and *Levels of foliar Si application*, as well as their interaction. When the ANOVA indicated a significant F-value, treatment means were separated using Tukey's test. All percentage values were transformed using the arcsine of the square root before analysis. In all the analyses, residual plots were generated to identify outliers and to confirm that the variance was common and normally distributed.

Results

Peach trees watered with 50% ET became stressed

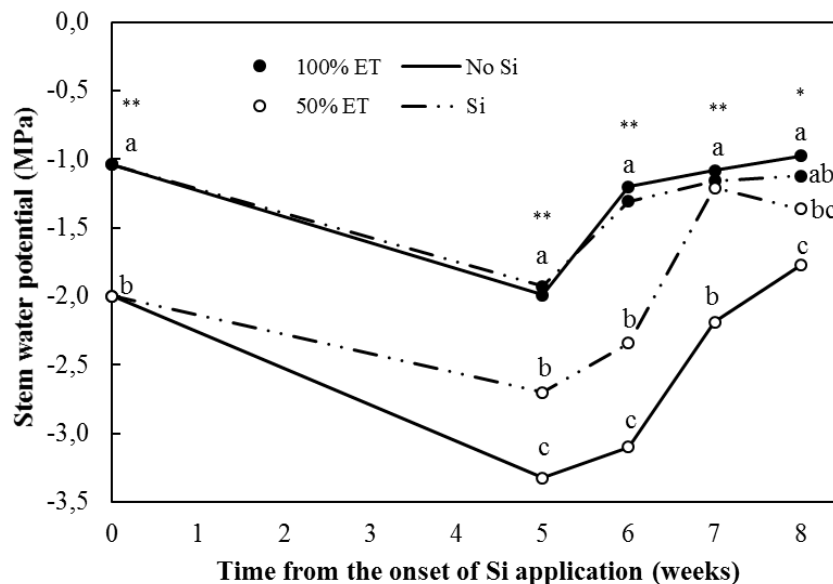


Figure 1. Effect of Si application and water regimens on stem water potential of young peach trees. Trees were grown in containers inside a greenhouse and irrigated at 100 or 50% of their evapotranspirative needs (ET) for two weeks (Phase I). Subsequently, foliar Si treatments (0 or 20 mg·L⁻¹; No Si and Si, respectively) were applied weekly for eight weeks (Phase II). Irrigation levels were maintained throughout the experiment and applied every three days. Different letters indicate significant differences. NS, Non-significant or *, **, significant at $P \leq 0.05$ or $P \leq 0.01$, respectively.

Table 1. Effect of Si application (No Si and Si, at 0 and 20 mg·L⁻¹, respectively) and water regimens (100 and 50% ET; evapo-transpirative needs) on shoot growth parameters (n=6). Growth conditions are described in Fig. 1.

Treatments	Number of shoots	Total shoot length (cm)	Mean shoot length (cm/n° shoot)
100% ET × No Si	11.1 b	44.7 ab	3.8
100% ET × Si	16.8 ab	67.9 a	3.9
50% ET × No Si	19.6 a	51.1 ab	3.1
50% ET × Si	11.7 b	35.6 b	3.0
Significance ¹	***	*	NS
CV (%) ²	22.8	35.5	22.3

Different letters indicate significant differences.

¹NS, *, **, *** Non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ or $P \leq 0.001$, respectively.

²Coefficient of variation of full experiment.

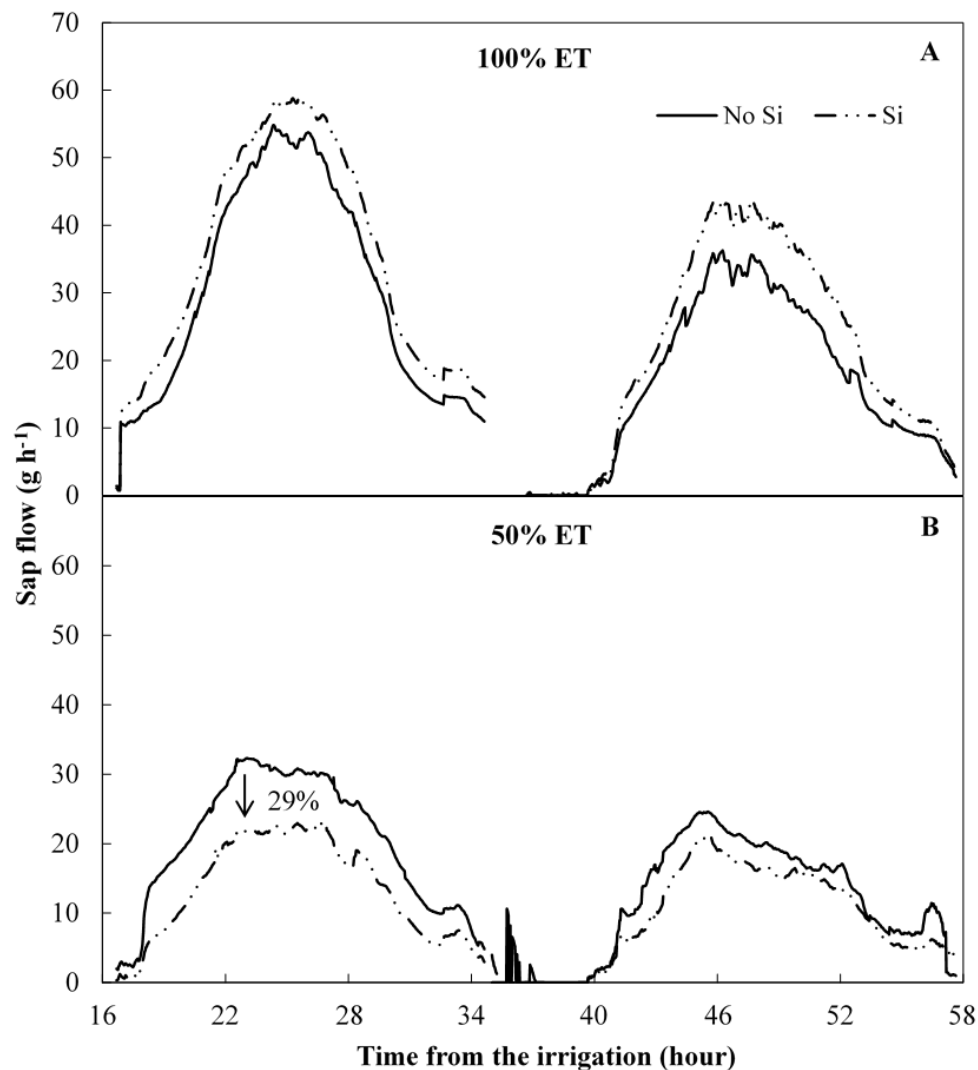


Figure 2. Average sap flow profile of well-watered (100% ET; A) and drought-stressed (50% ET; B) peach trees receiving different Si foliar applications. Data was collected from 16 to 58 hours after each irrigation event. Plants were irrigated every three days. Continuous line represents trees that did not received Si (No Si: 0 mg·L⁻¹); dashed line represents trees that received Si (20 mg Si·L⁻¹). Each value represents the mean of 9 irrigation cycles. Growth conditions are described in Fig. 1.

during phase I (without Si), reaching Ψ_{stem} values of -2.0 MPa after two weeks of water stress (Fig. 1). Typically, vegetative growth starts to decrease at values around -1.4 MPa (Rahmati et al. 2018), and greatly reduced growth at values between -1.5 and -2.0 MPa (Mirás-Avalos et al. 2013). From the onset of Si treatments, Ψ_{stem} of control trees (100% ET) was always at or above -1.0 MPa, except for measurement on week 5. Ψ_{stem} was affected by the interaction between water regimens and Si application; Si improved water status in water-stressed trees, reaching similar levels to well-watered trees by weeks 7 and 8, but did not affect Ψ_{stem} in well-wa-

tered trees (Fig. 1).

Well-watered trees (100% ET) treated with Si showed increased sap flow during the three days following an irrigation event, with the most pronounced effect occurring between 45 and 50 h after irrigation (Fig. 2A). In contrast, foliar Si applications decreased sap flow in water-stressed trees, with the greatest reduction (29%) around 24 h after irrigation (Fig. 2B). However, when water stress was more marked (i.e., between 2-3 days after the irrigation event; Fig. 2B), Si applications did not have any effect.

P_n significantly decreased when trees were sub-

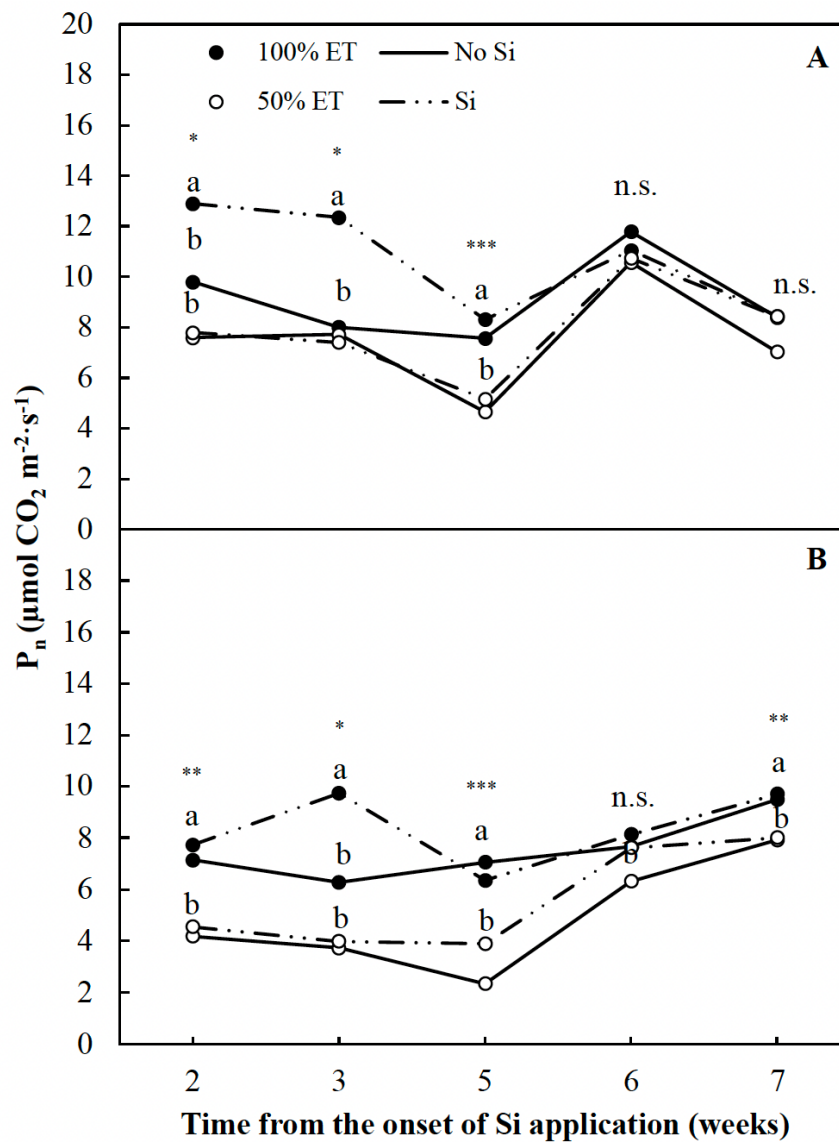


Figure 3. Net photosynthesis rate (P_n) of young peach trees receiving different Si foliar applications (No Si and Si, at 0 and 20 $\text{mg} \cdot \text{L}^{-1}$, respectively) under two water regimens (100 and 50% ET; evapotranspirative needs). Data was collected once a week, 24 and 48 hours after an irrigation event (A and B, respectively), on fully developed leaves. Each value represents the mean of 6 replicates. Different letters indicate significant differences. NS, *, **, *** Non-significant or significant at $P \leq 0.05$, $P \leq 0.01$ or $P \leq 0.001$, respectively. Growth conditions are described in Fig. 1.

Table 2. Effect of Si application (No Si and Si, at 0 and 20 mg·L⁻¹, respectively) and water regimens (100 and 50% ET; evapotranspirative needs) on potassium concentration (%) of different plant organs (n=6). Growth conditions are described in Fig. 1.

Treatments	Leaf	Shoot T ₀ ⁴	Shoot T ₁ ⁵	Shoot T ₂ ⁶	Root
100% ET × No Si	3.27 a	1.34 a	0.52	0.32	0.41
100% ET × Si	2.92 ab	1.17 ab	0.47	0.25	0.39
50% ET × No Si	2.43 b	0.92 b	0.49	0.32	0.49
50% ET × Si	3.08 a	1.28 a	0.48	0.34	0.48
Significance ¹	*3	*3	NS	NS	NS
CV (%) ²	16.1	29.0	11.6	29.6	19.6

Different letters indicate significant differences.

¹NS, *, Not significant or significant at $P \leq 0.05$, respectively.

²Coefficient of variation of full experiment.

³LSD test.

⁴Shoot growth during the experiment (spring shoot).

⁵One-year-old shoot.

⁶Two-year-old shoot.

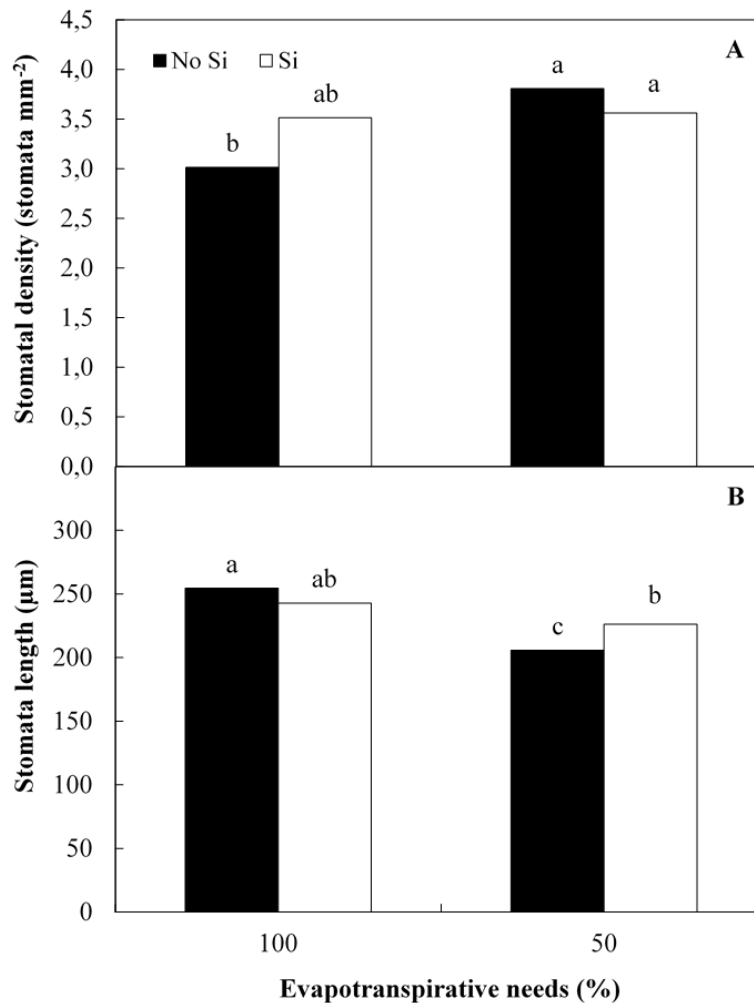


Figure 4. Effect of Si application (No Si and Si, at 0 and 20 mg·L⁻¹, respectively) and water regimens (100 and 50% ET; evapotranspirative needs) on stomatal parameters: density (A) and length (B). Measurements were performed on fully developed leaves collected during the last week of the experiment. Each value represents the mean of 6 replicates. Different letters indicate significant differences at $P \leq 0.05$.

jected to water stress (50% ET; Fig. 3). At the beginning of phase II (Si application), Si increased P_n in well-watered trees 24 h after irrigation, but these differences gradually disappeared by week 5 (Fig. 3A). However, Si did not improve P_n in water-stressed trees within the 24 h period after the applications, nor did it affect P_n in well-watered or drought-stressed trees 48 h after irrigation (Fig. 3B). Similar results were observed in g_s and leaf transpiration E_{leaf} (data not shown). Si applications did not affect hydraulic conductance under any irrigation regimen (data not shown).

In general, trees watered with 50% ET showed higher stomatal density (Fig. 4A) and smaller stomata (Fig. 4B) than trees that received 100% ET. However, Si applications did not significantly affect stomatal density regardless of irrigation treatments (Fig. 4A). Si application did not affect stomata length in well-watered trees, but it alleviated the decrease of stomata length caused by water stress (Fig. 4B).

Si application reduced the number of shoots of trees under water stress conditions, while it increased total shoot length under optimal irrigation (Table 1). Water-stressed trees also showed a significant decrease in leaf DW compared to control trees (26.3 g in 50% ET trees vs. 36.6 g in 100% ET trees) and spring shoot (1.0 g in 50% ET trees vs. 1.7 g in 100% ET trees), but there was no significant interaction between irrigation and Si applications on the DW of other organs.

During the experiment, water stress led to a reduction in leaf K concentration, but Si applications kept leaf K concentrations in water-stressed trees similar to those of well-watered trees, which remained unaffected by Si application (Fig. 5). Similar results were observed at the end of the experiment: Si increased K concentration of leaf and shoots grown during the experiment in 50% ET trees but did not influence leaf K concentrations in well-watered trees or the other organs (Table 2). Regarding N, both water stress and Si applications increased leaf N concentrations (Fig. 6), but there was no interaction between both factors.

Discussion

Silicon is not considered an essential element, but

many studies have highlighted its beneficial effects on plants, particularly under abiotic stresses such as drought (Frew et al. 2018; Wang et al. 2021b). Nevertheless, there is a need for exploring and understanding the mechanisms underlying Si-mediated drought tolerance on fruit trees, which are considered Si non-accumulator plants (Fernández-Escobar 2019).

In our experiment, Si improved the water status of water-stressed trees, which showed less negative Ψ_{stem} than trees without Si. Habibi and Hajiboland (2013) attributed the improvement of water status in drought-stressed pistachio seedlings receiving Si applications to the alleviation of gas exchange parameters (2013). However, in our experiment, gas exchange parameters (P_n , g_s , E_{leaf}) in water-stressed trees were unaffected by Si. Furthermore, the changes in stomatal length observed were not sufficient to induce changes in gas exchange parameters. Water stress has been reported to increase stomatal density and reduce stomatal length in trees (Drake et al. 2013) and annual species (Driesen et al. 2023). Leaf structural adaptations such as an increased number of small stomata can induce a faster open and close stomatal control, enhancing maximum conductance under adequate environmental conditions while reducing stomatal water loss under adverse conditions, such as drought. Si applications increased the number and size of stomata of annual crops under salt stress conditions (Abbas et al. 2015), and acid rain (Ju et al. 2017). Si applications also increased stomata size, not stomatal density, in non-stressed olive trees (Martos-García et al. 2024), and peach seedlings (Gao et al. 2022). However, in our experiment, water-stressed trees had a higher stomatal density and smaller stomata (the opposite, i.e. a combination of reduced density and larger stomata, is linked to reduced transpiration; Doheny-Adams et al. 2012), and Si alleviated the decrease of stomata length caused by water stress but did not affect the stomatal density. Therefore, it was assumed that the improved water status in Si-treated stressed trees was due to reduced cuticular transpiration, as reported by Nascimento-Silva et al. (2023).

In our experiment, Si increased sap flow

in well-watered trees but decreased it in water-stressed trees. Applications of Si to the soil solution in different crops have increased root water uptake and enhanced sap flow (Wang et al. 2021b) but the effect of foliar applications has not been previously documented. The only reference to foliar Si being effective at enhancing root water uptake is an increased sap exudation observed in decapitated soybean plants (Hussain et al. 2021) and in sunflower plants under stress conditions (Mulligan and Benlloch-González, personal communication). On the other hand, water-stressed trees had a significant sap flow reduction compared to well-watered trees, and Si applications did not increase sap flow but reduced it in water-stressed trees, especially during the first 24 h after an irrigation event.

These results match with vegetative growth data by the end of the experiment: Si increased total shoot length in well-watered trees but reduced number of shoots and total shoot length in water-stressed trees. In nature, taller species (i.e., large vegetative growth) with high water availability typically have wider xylem vessels and higher hydraulic conductivity (Liu et al. 2019). However, water stress normally causes a reduction of leaf water potential and sap flow that leads to a decreased of their hydraulic conductivity (Bhusal et al. 2019). Carneiro-Carvalho et al. (2020) suggested that the higher Ψ_{stem} in water-stressed chestnut trees with soil and foliar Si applications was related to changes in the structure of xylem vessels, specifically a reduction of diameter and increased number of xylem vessels, which play a significant role in stem sap flow (Bhusal et al. 2018). Si may also improve resistance to water stress by increasing root hydraulic conductance (Shi et al. 2016). We did not perform xylem histological analyses, but Si did not have any impact on stem hydraulic conductivity. We cannot rule out homeostatic mechanisms involving adjustments in hydraulic properties (e.g., stem water storage and use patterns or altered daily dynamics of discharge and recharge of stored water) and this area still deserves more research (Martín-Gómez et al. 2023), especially in trees and when Si is applied foliarly; nevertheless, the effect of Si on increasing both

sap flow and vegetative growth in well-watered trees but decreasing them in water-stressed trees seems to indicate that changes in sap flow were linked to changes in growth. These results, together with those on improved tree water status, suggest that Si might influence stress mitigation by improving water retention in trees under moderate water stress.

Regarding nutrient uptake, Si has a positive effect on K and N uptake, and their leaf concentration under drought stress (Bakır et al. 2022) and nutritional deficiencies (Costa et al. 2023) when Si applied to the soil solution. The effect on K concentration has previously been attributed to an improved H^+ -ATPase activity (Liang 1999), and enhanced remobilization and K transporter regulation (Beier et al. 2022). However, there is scarce literature on the effect of foliar Si on leaf nutrient concentration. In olive plants, it was observed that K uptake was influenced by Si foliar concentrations (Martos-García et al. 2024). This effect was also observed in N uptake of young olive plants growing in pots (Martos-García et al. 2025).

In our study, Si application alleviated the reduction of K concentration in leaves and new shoots of water-stressed trees, reaching levels similar to those of well-watered trees. The mechanism behind this effect is yet to be identified, although it does not seem to be linked to root K uptake and translocation as changes in K concentration were not observed in roots, trunk, or one-year-old shoots. Our results also showed that Si increased leaf N concentration, although there was no interaction between Si applications and water stress. Leaf K and NO_3^- contents may also contribute to a protective effect against water stress through osmotic adjustment by the accumulations of osmolytes (Zahoor et al. 2017). The osmotic adjustment implies a passive accumulation of solutes that cannot be used for growth; Munns and Weir (1981) suggested that solute accumulation in wheat may occur at the expense of growth in order to maintain turgor.

Conclusion

In conclusion, foliar application of Si offers a sustainable strategy to mitigate drought stress in

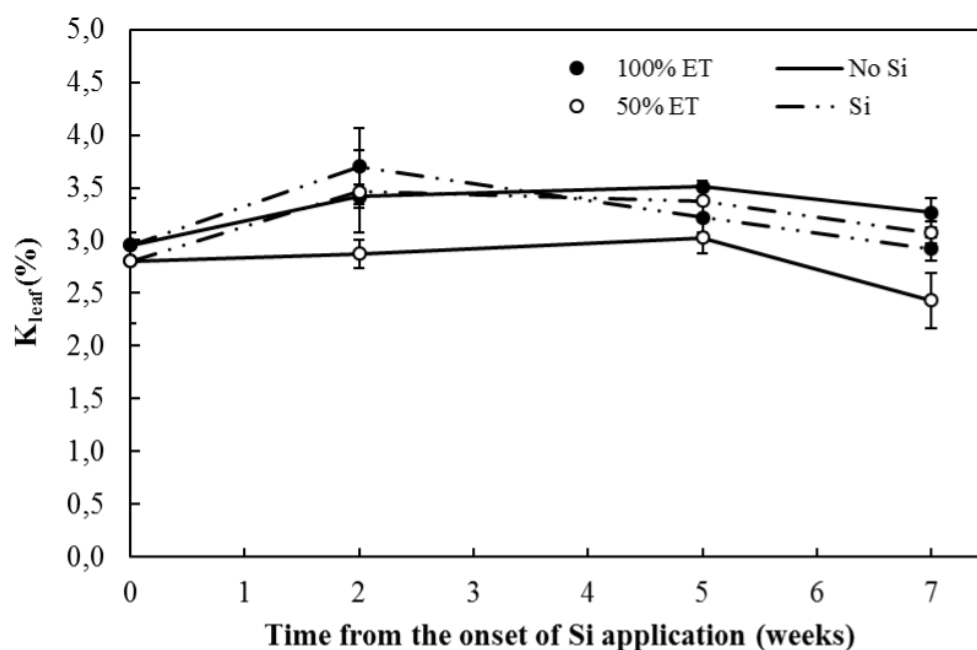


Figure 5. Effect of Si application (No Si and Si, at 0 and 20 mg·L⁻¹, respectively) and water regimens (100 and 50% ET; evapotranspirative needs) on the temporal evolution of leaf potassium concentration (%) in fully developed leaves collected throughout the experiment. Error bars indicate the means of three replicates $\pm$ standard error.

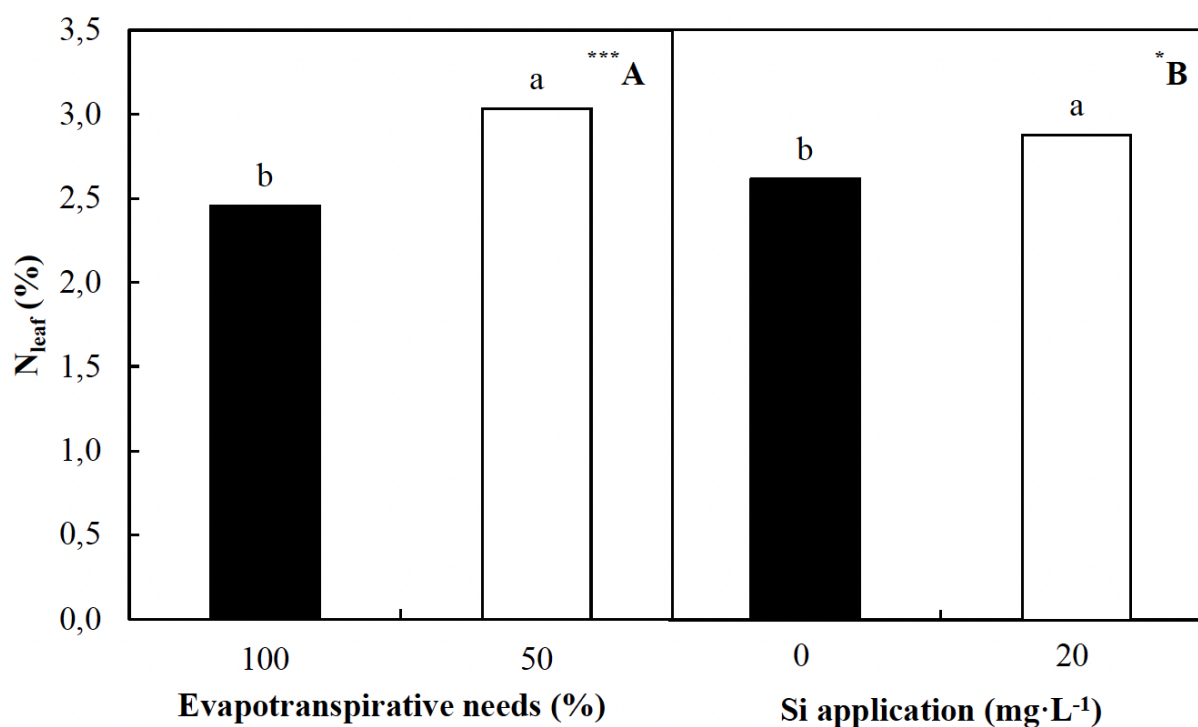


Figure 6. Leaf nitrogen concentration (%) in response to different water regimens (100 and 50% ET; evapotranspirative needs) (A) and Si foliar application (0 and 20 mg Si·L⁻¹) (B) in fully developed leaves collected at the end of the experiment. Different letters indicate significant differences. *, *** significant at $P \leq 0.05$ or $P \leq 0.001$.

peach trees, particularly under conditions where low soil moisture limits nutrient uptake and the effectiveness of irrigation-based nutrient delivery. In this study, Si application improved the water status of water-stressed trees, likely through its influence on sap flow and by increasing foliar concentrations of K and N. Si appears to play a role in enhancing water retention under moderate drought conditions, potentially contributing to improved stress tolerance. However, the observed improvements in water status could not be fully explained by changes in gas exchange parameters or leaf anatomical traits such as stomatal density and size, suggesting additional physiological or biochemical mechanisms are involved. Further research is needed to elucidate the underlying pathways through which Si confers drought resilience in deciduous fruit trees.

Data availability statements

The data underlying this article will be shared on reasonable request to the corresponding author.

References

- Abbas T, Balal RM, Shahid MA, Pervez MA, Ayyub CM, Aqueel MA, Javaid MM. 2015. Silicon-induced alleviation of NaCl toxicity in okra (*Abelmoschus esculentus*) is associated with enhanced photosynthesis, osmoprotectants and antioxidant metabolism. *Acta Physiol Plant*. 37:1-15. <https://doi.org/10.1007/s11738-014-1768-5>.
- Ashokan A, Mini V, Rani B, Anand S. 2024. Mitigation of abiotic stresses in plants through nutrient management. *Int J Environ Clim Change*. 14(7):254-267. <https://doi.org/10.9734/ijec/2024/v14i74267>.
- Bakır AG, Bolat I, Korkmaz K, Hasan MM, Kaya O. 2022. Exogenous nitric oxide and silicon applications alleviate water stress in apricots. *Life*. 12(9):1454. <https://doi.org/10.3390/life12091454>.
- Bárcana G, Carvajal M. 2020. Genetic regulation of water and nutrient transport in water stress tolerance in roots. *J Biotechnol*. 324:134–142. <https://doi.org/10.1016/j.jbiotec.2020.10.003>.
- Beier S, Marella NC, Yvin JC, Hosseini SA, von Wirén N. 2022. Silicon mitigates potassium deficiency by enhanced remobilization and modulated potassium transporter regulation. *Environ Exp Bot*. 198:104849. <https://doi.org/10.1016/j.envexpbot.2022.104849>.
- Benlloch-González M, Arquero O, Fournier JM, Barranco D, Benlloch M. 2008. K⁺ starvation inhibits water-stress-induced stomatal closure. *J Plant Physiol*. 165(6):623–630. <https://doi.org/10.1016/j.jplph.2007.05.010>.
- Benlloch-González M, Quintero JM, García-Mateo MJ, Fournier JM, Benlloch M. 2015. Effect of water stress and subsequent re-watering on K⁺ and water flows in sunflower roots. A possible mechanism to tolerate water stress. *Environ Exp Bot*. 118:78-84.
- Bhusal N, Bhusal SJ, Yoon TM. 2018. Comparisons of physiological and anatomical characteristics between two cultivars in bi-leader apple trees (*Malus × domestica* Borkh.). *Sci Hortic*. 231:73–81. <https://doi.org/10.1016/j.scienta.2017.12.006>.
- Bhusal N, Han S-G, Yoon TM. 2019. Impact of drought stress on photosynthetic response, leaf water potential, and stem sap flow in two cultivars of bi-leader apple trees (*Malus × domestica* Borkh.). *Sci Hortic*. 246:535–543. <https://doi.org/10.1016/j.scienta.2018.11.021>.
- Bista DR, Heckathorn SA, Jayawardena DM, Mishra S, Boldt JK. 2018. Effects of drought on nutrient uptake and the levels of nutrient-uptake proteins in roots of drought-sensitive and tolerant grasses. *Plants*. 7(2). <https://doi.org/10.3390/plants7020028>.
- Carneiro-Carvalho A, Anjos R, Lousada J, Marques T, Pinto T, Gomes-Laranjo J. 2020. Ecophysiological study of SiK impact on *Castanea sativa* Mill. tolerance to drought stress. *Photosynthetica*. 58(5):1078–1089. <https://doi.org/10.32615/ps.2020.030>.
- Casamali B, van Iersel MW, Chavez DJ. 2021. Plant growth and physiological responses to improved irrigation and fertilization management for young peach trees in the southeastern United States. *HortScience*. 56(3):336–346.

- <https://doi.org/10.21273/HORTSCI15505-20>.
- Costa MG, de Mello Prado R, dos Santos Sarah MM, de Souza AES, de Souza Júnior JP. 2023. Silicon mitigates K deficiency in maize by modifying C, N, and P stoichiometry and nutritional efficiency. *Sci Rep.* 13(1):16929. <https://doi.org/10.1038/s41598-023-44301-5>.
- Doheny-Adams T, Hunt L, Franks PJ, Beerling DJ, Gray JE. 2012. Genetic manipulation of stomatal density influences stomatal size, plant growth and tolerance to restricted water supply across a growth carbon dioxide gradient. *Philosophical Transactions of the Royal Society B: Biol Sci.* 367(1588):547–555. <https://doi.org/10.1098/rstb.2011.0272>.
- Drake PL, Froend RH, Franks PJ. 2013. Smaller, faster stomata: scaling of stomatal size, rate of response, and stomatal conductance. *J Exp Bot.* 64(2):495–505. <https://doi.org/10.1093/jxb/ers347>.
- Driesen E, De Proft M, Saeys W. 2023. Drought stress triggers alterations of adaxial and abaxial stomatal development in basil leaves increasing water-use efficiency. *Hortic Res.* 10(6). <https://doi.org/10.1093/hr/uhad075>.
- Epstein E. 1999. Silicon. *Annu Rev Plant Biol.* 50(1):641–664. <https://doi.org/10.1146/annurev.arplant.50.1.641>.
- Fernández-Escobar R. 2019. Olive nutritional status and tolerance to biotic and abiotic stresses. *Front Plant Sci.* 10:1151. <https://doi.org/10.3389/fpls.2019.01151>.
- Frew A, Weston LA, Reynolds OL, Gurr GM. 2018. The role of silicon in plant biology: A paradigm shift in research approach. *Ann Bot.* 121(7):1265–1273. <https://doi.org/10.1093/aob/mcy009>.
- Gao H, Yu W, Yang X, Liang J, Sun X, Sun M, Xiao Y, Peng F. 2022. Silicon enhances the drought resistance of peach seedlings by regulating hormone, amino acid, and sugar metabolism. *BMC Plant Biol.* 22(1):1–17. <https://doi.org/10.1186/s12870-022-03785-5>.
- Gonzalez-Dugo V, Durand JL, Gastal F. 2010. Water deficit and nitrogen nutrition of crops. A review. *Agron Sustain Dev.* 30(3):529–544. <https://doi.org/10.1051/agro/2009059>.
- Habibi G, Hajiboland R. 2013. Alleviation of drought stress by silicon supplementation in pistachio (*Pistacia vera* L.) plants. *Folia Hortic.* 25(1):21–29. <https://doi.org/10.2478/fhort-2013-0003>.
- Harry AM, Jones JB. 1991. N Determination, in Jones Jr., JB, Wolf B, Mills HA (eds): *Plant Analysis Handbook. A practical sampling, preparation, analysis, and interpretation guide.* Micro-Macro Publishing, Athens, GA. USA.
- Helaly MN, El-Hoseiny H, El-Sheery NI, Rastogi A, Kalaji HM. 2017. Regulation and physiological role of silicon in alleviating drought stress of mango. *Plant Physiol Biochem.* 118:31–44. <https://doi.org/10.1016/j.plaphy.2017.05.021>.
- Hussain S, Shuxian L, Mumtaz M, Shafiq I, Iqbal N, Brestic M, Shoaib M, Sisi Q, Li W, Mei X, Bing C, Zivcak M, Rastogi A, Skalicky M, Hejnak, V, Weiguo L, Wenyu Y. 2020. Foliar application of silicon improves stem strength under low light stress by regulating lignin biosynthesis genes in soybean (*Glycine max* (L.) Merr.). *J Hazardous Materials.* 401:123256. <https://doi.org/10.1016/j.jhazmat.2020.123256>.
- Ju S, Wang L, Zhang C, Yin T, Shao S. 2017. Alleviatory effects of silicon on the foliar micromorphology and anatomy of rice (*Oryza sativa* L.) seedlings under simulated acid rain. *PLoS ONE.* 12(10):1–18. <https://doi.org/10.1371/journal.pone.0187021>.
- Karagiannis E, Michailidis M, Skodra C, Molasiotis A, Tanou G. 2021. Silicon influenced ripening metabolism and improved fruit quality traits in apples. *Plant Physiol Biochem.* 166:270–77. <https://doi.org/10.1016/j.plaphy.2021.05.037>.
- Liang Y. 1999. Effects of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. *Plant Soil.* 209(2):217–224. <https://doi.org/10.1023/A:1004526604913>.
- Liu H, Gleason SM, Hao G, Hua L, He P, Goldstein G, Ye Q. 2019. Hydraulic traits are coordinated with maximum plant height at the global scale. *Sci Adv.* 5(2). <https://doi.org/10.1126/sciadv.aav1332>.
- Ma JF. 2004. Role of silicon in enhancing the re-

- sistance of plants to biotic and abiotic stresses. *Soil Sci Plant Nutr.* 50(1):11–18. <https://doi.org/10.1080/00380768.2004.10408447>.
- Ma JF, Yamaji N. 2015. A cooperative system of silicon transport in plants. *Trends Plant Sci.* 20(7):435–442. <https://doi.org/10.1016/j.tplants.2015.04.007>.
- Martín-Gómez P, Rodríguez-Robles U, Oge J, Wingate L, Sancho-Knapik D, Peguero-Pina J, Dos Santos Silva JV, Gil-Pelegrín E, Pemán J, Ferrio JP. 2023. Contrasting stem water uptake and storage dynamics of water-saver and water-spender species during drought and recovery. *Tree Physiol.* 43(8):1290–1306. <https://doi.org/10.1093/treephys/tpad032>.
- Martos-García I, Fernández-Escobar R, Benloch-González M. 2024. Silicon is a non-essential element but promotes growth in olive plants. *Sci Hortic.* 323. <https://doi.org/10.1016/j.scienta.2023.112541>.
- Martos-García I, Fernandez-Escobar, R, Benloch-González M. 2025. Silicon affects growth and nitrogen uptake of young olive plants. *HortScience.* 60(1):1-4. <https://doi.org/10.21273/HORTSCI18259-24>.
- McAdam SA, Brodribb TJ. 2015. The evolution of mechanisms driving the stomatal response to vapor pressure deficit. *Plant Physiol.* 167(3):833–843.
- McCutchan H, Shackel KA. 1992. Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French). *J Am Soc Hortic Sci* jashs. 117(4):607–611. <https://doi.org/10.21273/JASHS.117.4.607>.
- Minton B, Ellenburg WL, Junod R, Wickham ED, Muth M. 2025. Facing future droughts: lessons from the Southeast's 2023 fall flash drought. U.S. Department of Commerce. NOAA Tech Rep OAR-NIDIS-005. <https://doi.org/10.25923/4pvv-6f69>.
- Mirás-Avalos JM, Alcobendas R, Alarcón JJ, Pedrero F, Valsesia P, Lescourret F, Nicolás E. 2013. Combined effects of water stress and fruit thinning on fruit and vegetative growth of a very early-maturing peach cultivar: assessment by means of a fruit tree model, QualiTree. *Irrig Sci.* 31:1039–1051. <https://doi.org/10.1007/s00271-012-0385-6>.
- Munns R, Weir R. 1981. Contribution of sugars to osmotic adjustment in elongating and expanded zones of wheat leaves during moderate water deficits at two light levels. *Funct Plant Biol.* 8(1):93. <https://doi.org/10.1071/pp9810093>.
- Nascimento-Silva K, Coulombe L, Melgar JC. 2023. Influence of silicon on tolerance to water deficit of peach trees. *HortScience.* 58(4):449–452. <https://doi.org/10.21273/HORTSCI16881-22>.
- Pavlovic J, Kostic L, Bosnic P, Kirkby EA, Nikolic M. 2021. Interactions of silicon with essential and beneficial elements in plants. *Front Plant Sci.* 12. <https://doi.org/10.3389/fpls.2021.697592>.
- Puppe D, Sommer M. 2018. Experiments, uptake mechanisms, and functioning of silicon foliar fertilization—A review focusing on maize, rice, and wheat. *Adv Agron.* 152:1–49. <https://doi.org/10.1016/bs.agron.2018.07.003>.
- Rahmati M, Mirás-Avalos JM, Valsesia P, Lescourret F, Génard M, Davarynejad GH, Bannayan M, Azizi M, Vercambre G. 2018. Disentangling the effects of water stress on carbon acquisition, vegetative growth, and fruit quality of peach trees by means of the QualiTree model. *Front Plant Sci.* 9(3). <https://doi.org/10.3389/fpls.2018.00003>.
- Romero-Conde A, Kusakabe A, Melgar JC. 2014. Physiological responses of citrus to partial rootzone drying irrigation. *Sci Hortic.* 169:234–238. <https://doi.org/10.1016/j.scienta.2014.02.022>.
- Seleiman MF, Al-Suhaibani N, Ali N, Akmal M, Alotaibi M, Refay Y, Dindaroglu T, Abdul-Wajid HH, Battaglia ML. 2021. Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants.* 10(2):1–25. <https://doi.org/10.3390/plants10020259>.
- Shi Y, Zhang Y, Han W, Feng R, Hu Y, Guo J, Gong H. 2016. Silicon enhances water stress tolerance by improving root hydraulic conductance in *Solanum lycopersicum* L. *Front Plant Sci.* 7:196. <https://doi.org/10.3389/fpls.2016.00196>.
- Tyree MT, Patiño S, Bennink J, Alexander J. 1995.

- Dynamic measurements of roots hydraulic conductance using a high-pressure flowmeter in the laboratory and field. *J Exp Bot.* 46(1):83-94. <https://doi.org/10.1093/jxb/46.1.83>.
- Vandegheer RK, Zhao C, Cibils-Stewart X, Wuhler R, Hall CR, Hartley SE, Tissue DT, Johnson SN. 2021. Silicon deposition on guard cells increases stomatal sensitivity as mediated by K^+ efflux and consequently reduces stomatal conductance. *Physiol Plant.* 171(3):358–370. <https://doi.org/10.1111/ppl.13202>.
- Wang D, Hou L, Zhang L, Liu P. 2021a. The mechanisms of silicon on maintaining water balance under water deficit stress. *Physiol Plant.* 173(3):1253–1262. <https://doi.org/10.1111/ppl.13520>.
- Wang M, Wang R, Mur LAJ, Ruan J, Shen Q, Guo S. 2021b. Functions of silicon in plant drought stress responses. *Hortic Res.* 8(1):1–13. <https://doi.org/10.1038/s41438-021-00681-1>.
- Zahoor R, Zhao W, Abid M, Dong H, Zhou Z. 2017. Potassium application regulates nitrogen metabolism and osmotic adjustment in cotton (*Gossypium hirsutum* L.) functional leaf under drought stress. *J Plant Physiol.* 215:30–38. <https://doi.org/10.1016/j.jplph.2017.05.001>.
- Zia R, Nawaz MS, Siddique MJ, Hakim S, Imran A. 2021. Plant survival under drought stress: Implications, adaptive responses, and integrated rhizosphere management strategy for stress mitigation. *Microbiol Res.* 242:126626. <https://doi.org/10.1016/j.micres.2020.126626>.