Preference of Silicon Accumulation on the Shaded Foliage of Tree Crowns and its Implications for Juniperus chinensis L

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Abstract

The passive accumulation of silicon (Si) generally depends on the regulation of plant transpiration rates. It is challenging to comprehend how plants use Si to adapt to shaded habitats where they have low transpiration rates. Therefore, we hypothesized that Si accumulation is partly due to physiological demand rather than being entirely dependent on transpiration regulation. To test this hypothesis, the concentrations of Si and total minerals at various positions of shaded foliage and branches within the crowns of *Juniperus chinensis* L. trees were examined to determine whether shaded foliage and branch had a physiological demand allocation to resist shade. The concentrations of total minerals and Si in the foliage were consistently higher in shaded areas than in sunny areas within the same crown, regardless of the position within the crown or foliar age. However, foliar Si accumulation displayed more dependent on available light, which is linked to crown orientation. Additionally, branch Si accumulation displayed a weak dependence on the available light. These results suggested that Si, an energy-saving element that supplements cell walls, could also supplement carbon-based components in photosynthetic organs to balance energy limitations in shaded habitats. Thus, the high Si accumulation in shaded foliage, not in shaded branches, was explained by the physiological demand to make up for the decreased energy supply caused by shade.

Introduction

Silicon (Si) is the second most abundant element in the earth's crust and is ubiquitous as a beneficial element in most plants (Wedepohl 1995). It is also considered to be an essential element in diatoms and horsetail plants. Additionally, it has no negative consequences, even when taken in and stored in abundance in plant tissues (Ma et al. 2001). Due to its numerous positive effects on plants and ecologically friendly nutrition, Si has recently been attracting growing amounts of attention in agriculture and plant physiology (Deshmukh and Ma 2017; Minden and Schaller 2021). Si fertilizers are thought of as a plant nutrition supplement that is environmentally sustainable (Johnson et al. 2022). However, there is a lack of understanding around the regulatory mechanisms of Si allocation and accumulation in plants after uptake (Schaller et al. 2018).

The accumulation of Si in plants is generally associated with physiological functions (Yamaji and Ma 2014). For instance, diatoms and horsetail plants with Si as an essential element are more abundant than ferns, gymnosperms, and angiosperms with Si as a non-essential element (Hodson et al. 2005). Moreover, the physiological function of Si usually depends on a large amount of extracellular accumulation. Amorphous Si is transported through the xylem and mainly loaded into apoplast or intercellular spaces in shoots of vascular plants, where it is then normally polymerized and hydrated into silica mainly in cell walls, the intercellular region, or silica cells of the tissues (Harrison 1996; Currie and Perry 2009). Consequently, high silica enhances the rigidity and stability of the tissue (He et al. 2015). Silica acting as a physical barrier in the tissues can partly explain its positive physiological functions against abiotic or biotic stresses, although this does not fully explain why supplemental Si is more suitable for defending against exogenous stresses in plants (Luyckx et al. 2017). Some hormonal signals associated with Si

(Ghareeb et al. 2011; Kim et al. 2014) have been suggested to prompt metabolism by enhancing response effectiveness to exterior stimuli (Luyckx et al. 2017). However, due to a lack of evidence about its direct physiological actions, our understanding of the mechanism(s) by which Si participates in protecting plants against biotic and abiotic stresses is limited. A cooperative perception of the response of Si distribution to environmental changes may also be an important aspect in explaining the protection mechanisms of Si in plants.

Si is taken up by roots and then transported toward transpiration termini through the tracheid or vessel, which comprises a cell wall of dead cells. It is generally believed that Si accumulation and distribution are attributed to the transpiration rate in conifers (Cornelis et al. 2010). Similarly, Si deposition was also found high at the end of transpiration flow (in the extreme tips of needles) and increased with foliar age in white pine (Hodson and Sangster 2002). However, Lsi1 (influx transporter gene) and Lsi2 (efflux transporter gene) were found to transport Si in rice (Ma et al. 2006, 2007). Namely, the active absorption and excretion of Si in live cells occur independently of the control of transpiration flows. Additionally, nodes serve as connections between leaves and branches and act as hubs for the dispersion of mineral elements in monocots (Yamaji and Ma 2014). It's significant to note that sunny and shaded foliage usually have different transpiration rates, while both differences in Si concentration vary among species in tropical forests (Schaller et al. 2018). Therefore, in vivo Si distribution cannot be fully explained by transpiration dependence. We concluded that its distribution must be linked to the requirements of specific organs in environmental changes. However, it is still difficult to understand how Si nutrients are delivered preferentially to these organs in low transpiration areas, especially for *Juniperus* plants absorbing less Si (Hodson et al. 2005).

In most cases, the allocation of plant nutrition in vivo helps plants to better adapt to their surroundings (Zhang et al. 2021). Since Si accumulation consumes significantly less energy than lignin accumulation in cell walls (Raven 1983), Si is viewed as an energy-saving substitute for compression-resistant lignin (Neu et al. 2017). It has also been proposed that Si could partly substitute carbon-based defenses due to its low metabolic energy consumption (Neu et al. 2017; Cooke et al. 2012; Tombeur et al. 2021). Thus, Si allocation aids in the optimal utilization of resources when carbon supplies are constrained or limited. Considering the low energy consumption of Si metabolism and the role of foliar photosynthetic carbon source, this resource optimization is more likely to occur in foliage rather than in branches, which contributes to the metabolic energy balance in the shadow environment. As a result, greater Si allocation probably contributes to increased resistance to shade due to its energy-saving role in foliage.

We hypothesized that more Si would accumulate in shaded foliage, which would be conducive to offsetting the limited carbon supplies in shaded conditions. *Juniperus chinensis* L. is widely used in landscaping, reforestation, and medicine (Kim et al. 2016). To verify this hypothesis, we chose to examine the differences in Si and total mineral concentrations between the sunny areas and shaded areas within the same canopies of *Juniperus chinensis* L. trees and compared their differences between branches and foliage. This study could provide evidence of the regulation of Si distribution under various available light

conditions and its potential physiological role in energy conservation. The Si distribution rules and their regulatory mechanisms should be taken into account in further studies on the functions of Si.

Materials And Methods

Field Sampling

The sample field was located on Zhoushan Mountain, Luoyang, Central China (E 112°22'31.22", N 34°38'22.77"). The climate in the field region is warm, temperate, and continental monsoonal. The annual average temperature is 14.6 ℃, the average relative humidity is 59.6%, and the annual precipitation is 590mm, according to local meteorological records (E112°15'36", N34°29'24") from the previous ten years (2010–2019).

The cylindrical crowns of *Juniperus chinensis* L. trees have rather uniform branching architectures from bottom to top and between the sunny and shaded areas. In this study, the foliar samples were taken in late April 2019. The five trees that were randomly selected exhibited clear gaps around the edges of their stands and were a consistent height (about 6.5 m). The distance between the trees on Zhoushan Mountain is at least 500 m. To study the responses of foliage of different ages to available light (which was linked to crown orientation) at a height of 1 m above the ground, we cut 4–5 branches at random from the outermost crown of each sample tree on the sunny and shaded sides of the crown (i.e., the south facing and north facing sides of the crowns). More current-year foliage and litter foliage are produced and easily distinguished in April, and current-year foliage, annual foliage, and litter foliage were also gathered from each side. To further study the differences between the sunny and shaded sides of the crowns, 9–10 branches from inside and outside the crowns were also cut at a height of 1 m to gather annual foliar, the xylem (namely sapwood of stem xylem) and the phloem (including stem cambium and phloem) of 6–7 mm diameter branches from the sunny and shaded sides of the crowns. To study the influence of transport distance on Si and total mineral accumulation, annual foliar samples were taken from the outermost 4–5 branches on the sunny and shaded sides at heights of 1 m, 2 m, 3 m, 4 m, and 5 m. The samples were cleaned with deionized water to eliminate dust, absorbed water with blotting paper, baked at 105°C for 15 min, and then dried at 70°C to a constant weight. The dried samples were ball-milled into powder.

Measurement Of Ash Content

Previously weighed nickel crucibles were added to 5.000 g of the subsamples, which were then placed in a muffle furnace. The organic material was then vaporized using a step-by-step heating procedure (1 h at 200 ℃, 30 min at 300 ℃, 1 h at 400 ℃, and 5 h at 600 ℃). The crucibles containing the mineral residue were weighed after cooling in silica gel desiccators and the total mineral content (or ash) was determined from the mass difference. The total mineral content was expressed as a percentage of the dry mass.

Measurement Of Total Si And Soluble Si Contents

Si concentration was measured using a modified Van der Vorm method (1987). Briefly, dry-ashed plant material was added to polyethene bottles containing 0.5 M H_2SO_4 and 2.3 M HF (1:2) and distilled water at pH 2 (with 0.08 M sulfuric acid) to measure the total Si and soluble Si concentrations, respectively. Over-night, the solutions were shaken in the closed bottles. After centrifugation at 10,000 ×g for 10 min, 50 µl of the supernatant was retained and added to 3.2% boric acid, dye reagent (0.08 M H_2SO_4 and 5.4% ammonium heptamolybdate), 10% tartaric acid, and 0.4% ascorbic acid. The Si concentrations in the solutions were measured photometrically at 811 nm.

Statistical Analyses

Differences in the physiological parameters were evaluated using one-way analysis of variance (ANOVA), with crown orientation (sun vs. shade), crown position (inside vs. outside), and crown height (from 1 m to 5 m) as independent factors. Differences with $p < 0.05$ were considered statistically significant. OriginPro 2022 software (Learning Edition) was used to calculate and draw box plot diagrams.

Results

Differences in foliar total mineral and Si concentrations between the sunny and shaded sides of tree crowns

To examine the responses of total mineral and Si concentrations to changes in available light caused by crown orientation, we compared the changes in the foliage of different ages from the sunny and shaded sides of the trees. The total mineral and Si concentrations in the current-year foliage, annual foliage, and litter foliage from the shaded sides of the crowns were all higher than those from the sunny sides. However, the differences in the total Si and soluble Si concentrations were statistically significant ($p < 0.05$), but the differences in total mineral content were not ($p > 0.05$) (Fig. 1). This showed that Si accumulation was easily affected by available light due to crown orientation and that foliage of different ages had consistent responses to available light.

Total Mineral And Si Concentrations In Inner And Outer Crown Foliage

To further analyze the responses of total mineral and Si concentrations to changes in available light caused by crown orientation, we evaluated the changes in foliage from inside and outside tree crowns in conjunction with the shaded and sunny sides. The total and soluble Si concentrations were statistically higher in the shaded areas of the inner or outer crowns than in the sunny areas ($p < 0.05$), while the total mineral concentrations were not statistically different ($p > 0.05$)(Fig. 2). In contrast to the total mineral concentrations, the total Si concentrations were higher on the outside of the crowns than on the inside

(Fig. 2). As a result, the Si and total mineral concentrations showed distinct responses to transport distances along the transpiration flows in the crowns in the radial direction.

Foliar Total Mineral And Si Concentrations At Different Crown Heights

To clarify the influence of transport distance on Si and total mineral accumulation, both concentrations were analyzed at different crown heights because crown height is linked to transport distance in the xylem. As shown in Fig. 3, the influence of crown height was different in the two concentrations. With an increase in crown height, the total mineral concentrations decreased significantly ($p < 0.001$), while the total Si concentrations showed fluctuating increased trends ($p > 0.05$). Thus, the total mineral concentrations were more dependent on the transport distance than the Si concentrations, although both concentrations had different responses to the transport distance in the xylem.

Total Si Concentrations In Xylem And Phloem Of Inside And Outside Branches Of The Crown

To examine the effect of available light on Si accumulation in non-foliar organs, branches growing on the sunny and shaded sides of the crown were used to examine the total Si content of the phloem and xylem. The xylem and phloem of branches have no statistically significant difference on the sunny and shaded sides of the crown for the total Si content ($p > 0.05$). However, the phloem Si had a significant difference between the inside and outside of the crown ($p < 0.05$), whereas the xylem Si did not ($p > 0.05$) (Fig. 4). Phloem Si variation in the different position branches should be attributed to transport distance rather than available light. Thus, the effect of available light on Si accumulation does not occur in the transport tissue of non-photosynthetic organs.

Discussion

We examined the differences in foliar Si accumulation between the sunny and shaded sides of the crowns of *Juniperus chinensis* L. trees and tested whether shaded foliage has a higher Si distribution, where they have low transpiration rates. As mentioned above, the foliage from the shaded sides of the crowns tended to have higher Si accumulation than that from the sunny sides. Importantly, this trend remained stable with changes in foliar age (i.e., the current-year, annual, and litter foliage) (Fig. 1) and position within the crowns (i.e., inside and outside) (Fig. 2). However, this trend was not found in branches, a non-photosynthetic organ (Fig. 4), and also inconsistent with previous conclusions that passive Si accumulation depends on water uptake or transpiration flows because sunward foliage usually has a stronger transpiration rate (Peters et al. 2008) and intraspecific differences between sun and shade foliage also were observed in tropical forests (Schaller et al. 2018). Additionally, we also observed the trend that Si accumulation tended to develop at the ends of transpiration flows. As shown in Figs. 2 and 3, foliage from the outside of the crowns and the top of the crowns had high total Si content,

which displays a transpiration-dependent silica accumulation (Cornelis et al. 2010). Thus, we believe that the accumulation of foliar Si is not solely dependent on the regulation of transpiration rate but could also be related to the regulation of available light, which is associated with crown orientation. We concluded that the part accumulation of Si is independent of the regulation of transpiration but may be important for plant adaptations to low light conditions.

The total Si and total mineral contents of foliage from the shaded sides of the trees were higher than those of foliage from the sunny sides, although the differences between the shaded and sunny sides were statistically significant only for the total Si contents ($p < 0.05$) (Figs. 1 and 2). This discrepancy provided compelling evidence that foliar Si accumulation depended on the available light more than total minerals in different crown positions. The discrepancy in how they reacted to available light could be attributed to their physiological functions. Since Si is mostly used for structural support in extracellular (Currie and Perry 2009), it is also stable and not easy to reuse after deposition in plants. It is believed that Si accumulation responding to environmental conditions is more stable than those of other mineral elements in various environments (Zhang et al. 2019). Additionally, shaded foliage has less water potential than sunward foliage (Pereira and Kozlowski 1997) and more water and mineral elements are easily taken into cells in shaded foliage along water potential gradients at night. This could reasonably explain why the Si and total mineral contents in foliage from the shaded sides were higher than those in foliage from the sunny sides. Hence, mineral transport at night could be another factor when there is no stomatal transpiration. Finally, compared to total Si accumulation, the total mineral accumulation showed a larger dependence on the transport distance in the xylem (Fig. 3). These underlined how different the Si and total mineral accumulation were as physiological indicators.

As is well-established, shaded foliage is easily affected by the limitation of available light intensity or duration, which leads to decreases in photosynthetic carbon suppliers (Cai 2011; Catoni et al. 2015). Additionally, photosynthetic carbon supplies are usually preferentially used for defense metabolism rather than growth under limited resource conditions (Imaji and Seiwa 2010). Cell walls, as the largest carbon sinks for growth, are limited by reductions in carbon allocation under shaded conditions. Considering the metabolic costs, the incorporation of Si into cell walls is considered to be an energy-saving alternative to cell wall components (Raven 1983; Neu et al. 2017). Thus, increased Si in shaded foliage can counteract the lack of carbon or energy in limited available light, which is supported by the result that branch Si variation, a non-photosynthetic organ, does not depend on available light (Fig. 4) and is consistent with the optimal allocation theory (McKey 1974). Similar results have confirmed the negative correlation between foliar Si and carbon concentrations (Klotzbücher et al. 2018) and the reduced carbon content in Si applications (Mastalerczuk et al. 2022). In addition, plants also adapt to minimize available light through the enhancement of light capture, for example, via the increased synthesis of chlorophyll and protein (Atanasova et al. 2003). This synthesis also increases carbohydrate consumption, which also arises the potential risk of carbon deficiency. Thus, our data suggested that an increased Si accumulation is a non-negligible factor in the trade-off with potential carbon deficiency in tree crowns. Of course, the fact that an increase in the total mineral concentration in shaded leaves is also conducive to the supplement of osmotic adjustments under shaded conditions cannot be ignored.

This study offered evidence that increased Si accumulation is associated with shade caused by crown orientation and position. In shaded foliage from tree crowns, an increased Si concentration is useful for offsetting a lower carbon supply as an energy-saving alternative for growth, which provides a novel understanding of the energy-saving function of Si under unfavorable conditions. This also clarifies how Si helps plants to survive (particularly under unfavorable environmental conditions) (Guntzer et al. 2012), our understanding of shade-induced responses in plants (Zhang et al. 2022), and the trade-offs between crown architecture and foliar morphological traits (Pearcy et al. 2005). However, this research focused on explaining the changes in Si accumulation that are caused by long-term available light variations. In the future, the effects of short-term variations in light intensity and quality on Si accumulation need further study to examine the energy consumption balance that is regulated by silicon and carbon metabolism. Additionally, there is a lack of evidence regarding whether Si transporters actively regulate Si accumulation on the sunny and shaded sides of tree crowns, and whether there is a dilution effect due to the difference in growth rate caused by light. To better understand the potential roles of Si in physiology and ecology, follow-up research must also pay attention to the relationship between Si and carbon metabolism at the cellular level under environmental changes (Hodson and Guppy 2022) and differences in the transport process of silicon-water in the xylem.

Conclusions

In the shaded foliage of tree crowns, Si and total mineral concentrations exhibited a preferential accumulation tendency. However, foliar total Si content was more sensitive to changes in available light than total mineral content, whereas the total mineral content was more dependent on transport distance in the xylem than total Si content. Since Si is an energy-saving alternative for supplementing cell walls, it has been speculated that preferential Si distribution in shaded foliage could improve the carbon balance of metabolic energy use in terrestrial plants, thereby increasing their tolerance to shade or a lack of light. Thus, in this study, the energy-saving function of Si was proposed as an explanation of its adaptive mechanism against shade. In the future, the universality of Si in its energy-saving role under various stresses should be further verified through metabolic energy tests and the energy-saving function of Si under abiotic environmental conditions needs to be explored further.

Declarations

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Author Contributions

Y.Z. and C.C. prepared the original draft and edited the manuscript; R.Z carried out the data analysis; T.C. designed the experiments and reviewed the manuscript. All the authors have read and agreed to the published version of the manuscript.

Data Availability Statement:

All data in this study are available from the corresponding author upon reasonable request.

Conflict of interest:

The authors declare no conflicts of interest.

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Figures

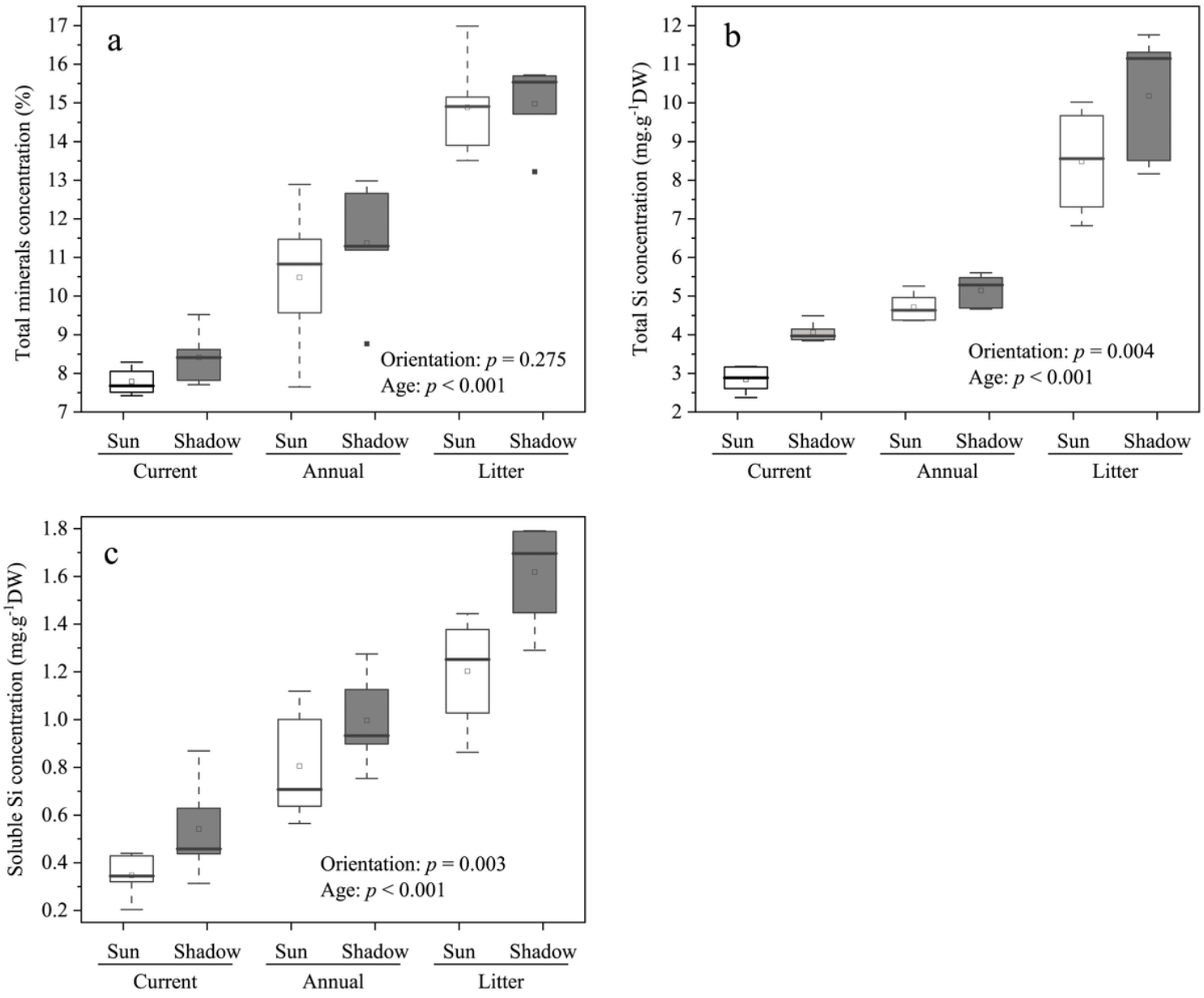

Figure 1

The concentrations of total minerals (a), total Si (b), and soluble Si (c) in foliage of different ages (current, annual, and litter) from different orientations of the crowns (sunny and shaded sides): ■ indicates the outliers.

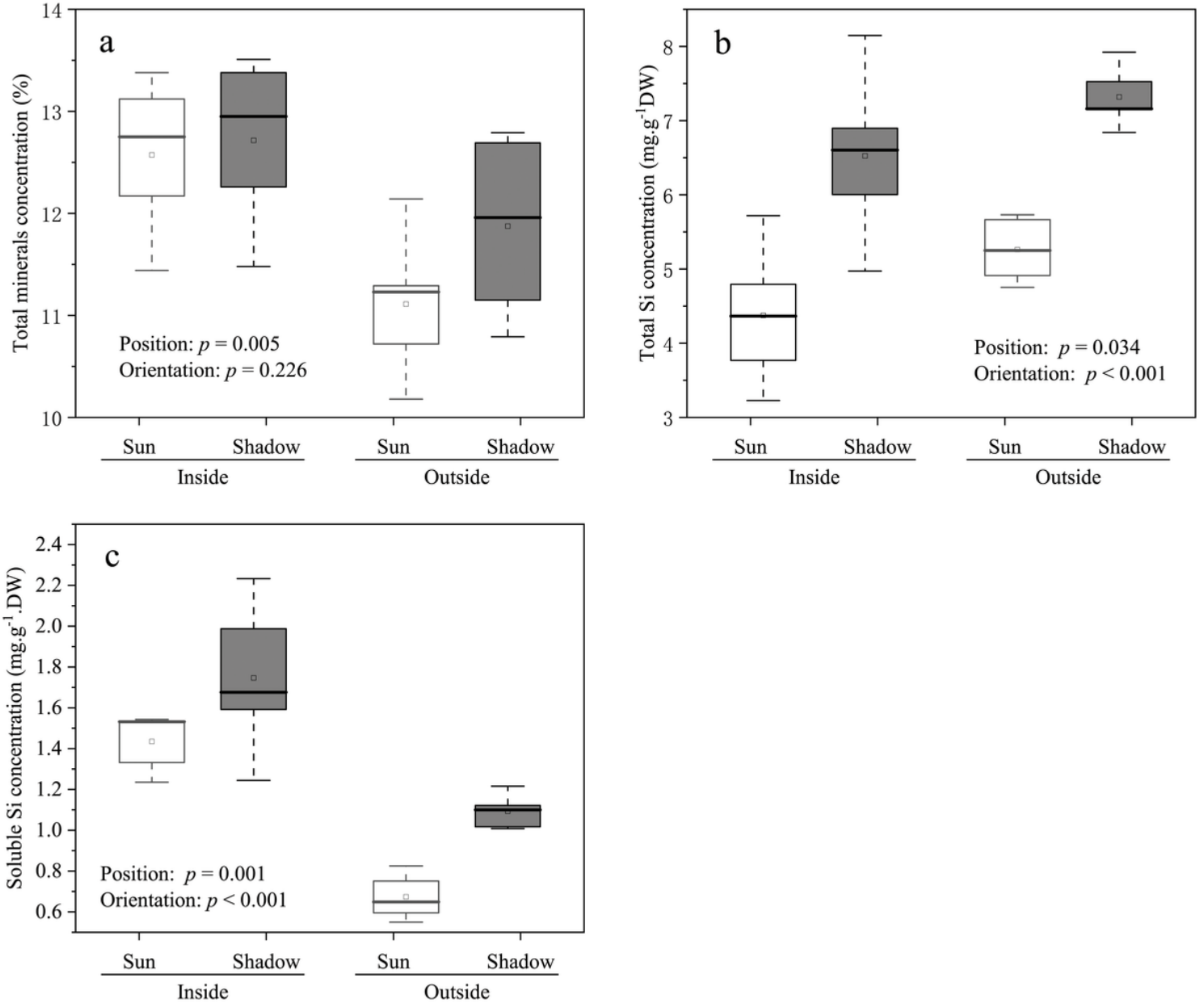

Figure 2

The concentrations of total minerals (a), total Si (b), and soluble Si (c) in foliage from different positions (inside and outside) and orientations (sun and shadow) of the crown.

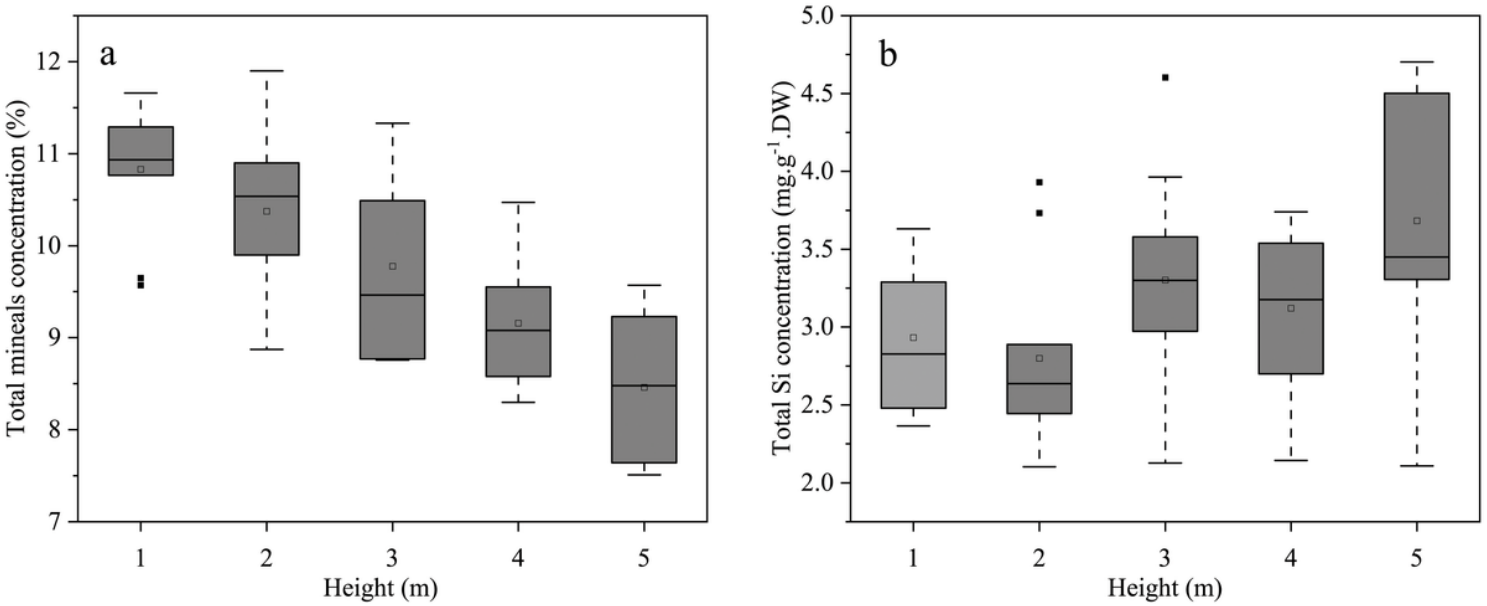

Figure 3

The concentrations of total minerals(a) and Si(b) at different crown heights (1 m, 2 m, 3 m, 4 m, and 5 m): ■ indicates the outliers.

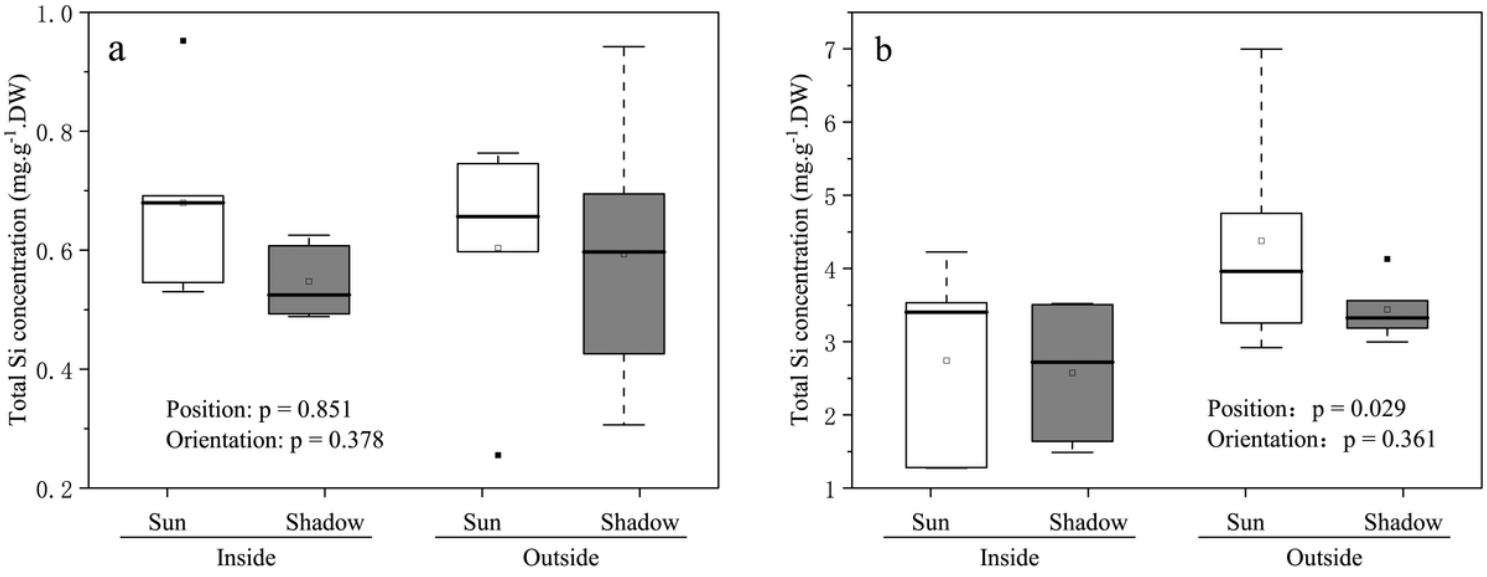

Figure 4

Total Si concentrations in xylem (a) and phloem (b) of the inside and outside branches of the same crown, ■indicates the outliers.