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Convergent evidence for temperature-dependent emergence of silicification in terrestrial plants

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Abstract

While research on terrestrial silicon (Si) biogeochemistry and its beneficial effects for plants has received significant attention in last decades, the reasons for the emergence of high-Si taxa remain unclear. Although the “arms race” hypothesis (i.e. increased silicification through co-evolution with mammalian grazers) has received some support, other studies have pointed to the role of environmental factors, such as high temperatures and low atmospheric CO_2 levels, which could have favored the emergence of silicification. Here, we combine experimentation and analysis of existing databases to test the role of temperature on the expression and emergence of silicification in terrestrial plants. We first show through experimental manipulations of rice that Si is beneficial for growth under high temperature stress, but harmful under low temperature. We then found that, globally, the average temperature of the distribution of high-Si plants was 1.2°C higher than that of low-Si plants. Moreover, within China, a notable positive correlation emerged between the concentrations of phytoliths in wheat and rice and air temperature. From an evolutionary perspective, 65–77% of high-Si families (> 10 mg Si g^{-1} DW) originated during warm geological periods, while 57–75% of low-Si families (< 1 mg Si g^{-1} DW) originated during cold geological periods. On average, Earth's temperatures during the emergence of high-Si families were 3°C higher than those during the emergence of low-Si families. A correlation was also observed between the divergence of proteins related to Si transport (Lsi1, Lsi2, Lsi3, and Lsi6) and historical climatic variability. Together, cumulative evidence suggests that plant Si variation is closely related to global and long-term climate change, with potential repercussions for global Si and C biogeochemical cycles.

Main

More than half of present-day terrestrial net primary productivity is produced by plants that actively accumulate silicon (Si)[1]. Plant silicification – that is, the deposits of hydrated amorphous silica between and within cells – has received increasing attention over the last two decades, with a particular focus on its role in plant defense against herbivores[2,3] and in alleviating various environmental stresses[4,5]. Although the role and functions of Si in plant biology have been extensively studied[6,7], the reasons for the up to hundred-fold variation in plant Si concentrations[8,9] and for the emergence of high-Si species over the course of evolution remain unclear[10–12]. Understanding this phenomenon is key since evolutionary phases of plant silicification might have impacted Si cycling and its coupling with the C cycle on different time and spatial scales[13].

The discovery of genes coding the expression of proteins facilitating Si uptake from soils and redistribution in plants provided some explanation for the variation in leaf Si concentrations[14–16]. Research has shown that the accumulation of Si is closely related to the expression levels, localization, and polarity of these transport proteins in different plant species[17]. These discoveries provided a molecular basis for our understanding of Si accumulation, but did not tell us why and when silicification emerged in plants. Many different hypotheses have been put forward (*e.g.*, increased silicification through co-evolution with mammalian grazers, the substitution of C by Si during periods of low atmospheric CO_2

levels, adapting to stressful habitats with seasonal aridity, low nutrient availability, or strong wind exposure)[11,12], but linking the emergence of high-Si taxa with one single environmental factor is not well supported by chronology[11].

One environmental factor that could have influenced the emergence of high-Si taxa is temperature[18]. The deposition of Si in the cell walls of leaf epidermis not only enhances the thermal stability of cell membranes and cell walls, but also cools the leaves through efficient mid-infrared heat emission[19,20]. As such, Si could play a key role in helping plants resisting high temperature stress[21], and therefore could have been selected during warm geological periods. Furthermore, lab experiments show that Si is highly plastic in response to increased temperature[18,22,23], although this could also be attributed to increased transpiration accelerating passive Si absorption[24,25]. Although interactions between temperature and Si have been suggested, we know very little about the role of long-term temperature shifts in the emergence of high-Si taxa. Yet, understanding whether the differentiation of high- and low-Si species and historical climate change are linked is essential to better understand plant Si variation, and the role of vegetation on global biogeochemical cycles.

To investigate relationships between long-term temperature changes and plant silicification, we integrated evidence from experiments and existing databases (see Fig. S1 for details about the databases). We first designed an experiment that investigated the effect of Si on rice – a model Si-accumulating species – experiencing high and low temperature stress. We then analyzed the present-day variation in Si concentrations in the plant kingdom to see whether this was related to current Earth's temperatures. We also used wheat and rice samples collected along climatic gradients to test whether Si intraspecific variation was linked to air temperature. Finally, we constructed evolutionary trees of plant Si transporter proteins and analyzed the relationship between periods of high- and low-Si species differentiation and corresponding Earth history temperatures.

Results

We first conducted an experiment testing the effect of Si on heat, cold and freeze-thaw cycling stress in an emblematic Si-accumulating species, namely rice (see Materials and Methods for details). After planting rice in a nutrient solution containing 1mM silicic acid for 15 days, no differences in shoot length, root length, and chlorophyll concentrations between the -Si and + Si groups were observed (Table S1). However, when rice plants were placed under three types of stress (heat, cold, and freeze thawing) for three days, a pronounced effect of Si fertilization was observed (Fig. 1a). Under heat stress, Si-fertilized rice had significantly higher shoot length, root length, and fresh weight than the -Si group (Fig. 1b-d). In contrast, root length and shoot fresh weight of the + Si group were lower than those of the -Si group under cold stress (Fig. 1). Under freeze thawing, the + Si group even showed significant wilting (Fig. 1).

Following this experiment, we used a recently published database with leaf Si concentrations in about 1800 species[12] that we combined with information on species distribution obtained from the GBIF (Global Biodiversity Information Facility) to check whether high-Si and low-Si plant orders were associated with locations with different climatic conditions (see Fig. S2 and Table S2 for details). Specifically, we selected 10 orders with high-Si concentrations (mean more than 2 mg g^{-1}) and 10 orders with low-Si concentrations (mean less than 1 mg g^{-1}). The high-Si orders were Poales, Saxifragales, Schisandraceae, Arecales, Boraginaceae, Fagales, Rosales, Nymphaeaceae, Asterales, Alismatales. The low-Si orders were Acorales, Brassicales, Liliales, Asparagales, Aquifoliales, Santalales, Pandanales, Celastraceae, Cornales, Bromeliaceae. We randomly selected the distribution information of 1000 occurences from each order (using rgbif package in R, see Table S2 for species information), and drew distribution maps of high-Si and low-Si plants. The data in Fig. 2a suggest that high-Si plants occur to a greater extent in areas of lower latitude while low-Si plants are more noticeably present in higher latitude regions. This is confirmed by the analysis in Fig. 2b: the average temperature of the distribution of high-Si plants was 1.2°C higher than that of low-Si plants. In addition, the distribution of the data indicated that high-Si plants were mainly concentrated in environments with a mean annual temperature near 17°C, while low-Si plants were predominantly concentrated in environments with a mean annual temperature near 11°C (Fig. 2b).

In addition to this global analysis, we conducted field sampling of two typical high-Si species, wheat and rice, in the main grain producing areas of China (Fig. 3). We found a significant positive correlation between both wheat and rice phytolith concentrations and air temperature, especially for wheat (Fig. 3). Samples from two regions were analyzed separately because of important differences in climate and soil types, but the results still showed that the phytolith concentrations were positively correlated with temperature (Fig. S3). Overall, this evidence suggests that present-day temperature influences both the distribution of high- and low-Si species worldwide, and also affects intraspecific variation in leaf Si concentrations.

We then constructed evolutionary trees of Si transporter proteins (encoded by the genes Lsi1, Lsi2, Lsi3, Lsi6)[16]. We searched for the homologous sequences of these proteins using NCBI BLASTp (Basic Local Alignment Search Tools for proteins)[26], and then downloaded the protein sequences of the top 15–20 species with the highest homology for evolutionary tree construction. Results showed that the Si transporter proteins of high-Si species evolved mainly during warm periods (Fig. 4a). However, the evolutionary trees include only a few species, and we still need evidence from more taxa.

Using data from Angiosperm Phylogeny Website, we investigated the occurrence of plant families with contrasted Si concentrations during warm and cold periods. We found that 77% of high-Si families (> 10 mg g^{-1}) emerged during warm periods, while 75% of low-Si families (< 1 mg g^{-1}) emerged during cold periods (Fig. 4b). The historical temperature of the Earth during the emergence of high-Si families was 3°C higher than that of low-Si families ($p < 0.001$) (Fig. 4c, see Table S3 for specific information on the plant families). In order to correct for species differentiation time, we selected another set of data from Li et al. (2019) for analysis. Unlike the evolutionary information collected from different literature sources on Angiosperm Phylogeny Website, Li et al. (2019) data was from their plastid phylogenomic tree based on 80 genes from 2881 plastid genomes and 62 fossil calibrations. A similar result was obtained, where high-Si families were more likely to appear during high temperature periods (65%), while low-Si families mainly appeared during cold periods (57%) (Fig. S4 and S5).

In addition, we analyzed the divergence times of different subfamilies in the five major families of angiosperms (Asteraceae, Orchidaceae, Fabaceae, Rubiaceae, and Poaceae). In Asteraceae, species with high Si concentrations (> 10 mg g^{-1}) are found in the Asteroideae subfamily, which emerged during the Middle Eocene Thermal Maximum[28,29], while low Si concentrations (< 2 mg g^{-1}) are typical of the Carduoideae and Cichorioideae subfamilies, which emerged in cooler periods[30,31]. In Orchidaceae, Si-rich species are found in the Apostasioideae and Cypripedoidoidae subfamilies, which thrived during a warm climate, whereas Si is notably absent in the Vanilloideae, Orchidoideae, and Epidendrioideae subfamilies that emerged during a cooler phase[32,33]. Fabaceae exhibits low Si concentrations (< 1 mg g^{-1}) in subfamilies like Caesalpinioideae and Cercidoideae that appeared during cold periods, while high-Si species are mainly in the Papilionoideae, particularly the Phaseoleae subclade that emerged during a warm period[34,35]. In Rubiaceae, high-Si species are found in the Rubioideae, which emerged in a warm era, while low-Si species appear in the Ixoroideae and Cinchonoideae, which emerged during a colder period[36]. Among Poaceae, low-Si species distributed among five subfamilies (Poodinae, Panicoideae, Poeae, Chloridoideae, and Paspaleae) all emerged during cold periods, except Chloridoideae. By contrast, high-Si species mainly belong to the Arundinarieae, Panicoideae, Cynodonteae, Andropogoneae, and Molinieae, of which all but the Cynodonteae emerged during warm periods. Detailed information on the emergence and mean leaf Si concentrations of these subfamilies is provided in Table S4. Overall, our analysis of the subfamilies from five different major families of angiosperms showed that the leaf Si concentrations in subfamilies seemed to closely relate to the Earth's temperature during their appearance period. This suggests that silicification might have been favored during warm and interglacial periods and/or avoided during glacial periods.

Discussion

Our research suggests that temperature and its long-term evolution on geological timescales play a significant role in plant Si accumulation. We first highlighted the beneficial effects of Si at high temperatures, and its harmful effects at low temperatures in an emblematic Si-accumulating species (i.e., rice). We then found that the average temperature of present-day high-Si species distribution is higher than that of low-Si, and that the intraspecific Si variation is positively correlated with temperature for two major crop species. Following that, we traced back through history and found that both the evolution of Si transporters and the differentiation of high-Si species were related to the warm periods of the Earth. In line with recent studies focused on grasses[18,37], our study suggests that climate is a key driver of present-day and possibly historical plant silicification, possibly more important than the presence of herbivores and grazing[11]. Plant Si uptake and accumulation are affected by a range of factors, including soil Si levels, water availability, altitude, soil fertility, CO_2 levels, grazing pressure or intraspecific genotypic differences[12,38–41], but it is clear from our findings that temperature plays a very significant role, both in current and historical time.

Silicon can help plants tolerate high temperature stress[42–44]. Numerous processes have been suggested to explain this beneficial effect[19,21]. The presence of silicified structures in leaf epidermis significantly could reduce heat load and prevent ultraviolet radiation through effective emission of thermal energy[6,20,45]. In addition, Si in rice leaves can prevent electrolyte leakage and maintain leaf water content by providing mechanical support to cell wall[44]. Silicon could also restore ultrastructural distortions of cellular organelles provoked by heat stress, particularly chloroplasts and the nucleus[46]. Moreover, the enhancement of plant antioxidant defense system in Si-treated plants has been reported to resist oxidative damage caused by high temperature[47,48]. Although our understanding of the role of Si in regulating heat stress remains incomplete, these mechanisms suggest that high temperatures might have favored the emergence of silicification.

Silicon can help plants resist high-temperature stress, but it could have an opposite effect on cold and freezing stress. Preserving cell integrity is critical for plants under freezing stress[49], but the thermal expansion of silica deposited on the cell wall is much lower than that of cellulose and lignin, which may damage the cell structure due to deformation differences caused by temperature effects[50,51]. In addition, intracellular ice formation poses a greater threat to plants than extracellular ice formation, and plants use a mechanism called "deep undercooling" to prevent it, enabling them to tolerate extremely low temperatures[52]. However, silica deposits in cell walls inhibit cellular water loss[53], which will interfere with "deep supercooling" and increase the risk of intracellular ice formation. In addition, ice formation in plants is a dynamic process. When the temperature is negative, water remains in a metastable liquid state until it turns into ice around an ice-nucleating substance, and then propagates longitudinally and radially[54]. Silicon has also been proven to act as an ice-nucleating substance to accelerate freezing[55], which may be one of the reasons why ice propagation is found to be more rapid in Poaceae (high-Si) than in Gymnosperms and Dicotyledons (low-Si)[56,57].

Perhaps due to the beneficial effects of Si in high-temperature environments and its adverse effects in cold environments, we found that the average temperature in the distribution area of high-Si species is higher than that of low-Si species. We also found that, regionally, wheat and rice Si concentrations increased with increasing temperatures. These observations echo results on grasses from Brightly et al.[18], who showed that high temperature treatments increased leaf Si concentrations, especially in taxa adapted to warm regions.

We also considered the relationship between the evolution of plant silicification and palaeoclimatic changes throughout history. First, we should note that plant leaf Si concentrations are closely linked to the Si uptake mechanisms[16]. The evolution of NIP-IIIs, serving as primary Si influx transporters, traces back to approximately 515 million years ago (Ma), during the Middle-late Cambrian period, characterized by a hot climate[58]. The evolutionary trees we constructed for the currently reported Si transporter proteins (Lsi1, 2, 3, and 6) collectively show that Si transporter proteins in high-Si taxa evolved mainly during warm climatic periods. Furthermore, we can draw similar conclusions from the perspective of species differentiation. Among the lower plant algae, the marine planktonic algae (Archaeplastida), which are low in Si, emerged between 659 and 645 Ma ago, during the "Snowball Earth" period[59]. However, diatoms, which are extremely rich in Si, originated at 200 Ma ago during the Triassic Hothouse[60]. In addition, both mosses and ferns exhibit high leaf Si concentrations (Fig. S2), and they also both occur during Cambrian–Ordovician Hothouse[61]. A transition from fern-dominated ecosystems (high Si) to gymnosperms-dominated landscapes (low Si) coincided with the Earth's shift from the Late Devonian Hothouse to the Late Paleozoic Icehouse[62]. Subsequently, Angiosperms rapidly diversified, dominating terrestrial ecosystems since the Lower Cretaceous period[63]. The emergence of early Angiosperm taxa, including Amborellales, Nymphaeales (low-Si), and Austrobaileyales (high-Si), has also been linked to climate, with Nymphaeales appearing in cooler intervals and Austrobaileyales during warmer times. Further, our analysis, based on two phylogenetic databases of angiosperms, supports the trend of high-Si species evolving in warm periods and low-Si species in cold periods (Fig. 4b, S4). Taken together, these results suggest that plant silicification is likely to be influenced by palaeoclimatic changes.

From a long-term evolutionary perspective, the beneficial effects of Si at high temperatures might have favored the emergence of high-Si taxa. Conversely, under cold conditions, the potential unfavorable effects of Si may have prevented the evolution of high-Si taxa. Some plants no longer use Si, possibly due to either the loss of capacity to take up Si (e.g., Si transporters) during evolution[64] or the development of mechanisms to excrete Si[65]. Alternatively, such loss may be related to the adjustment of certain cell wall polymers and proteins that affect Si deposition[66–68].

The Si cycle is crucial for regulating the Earth's carbon cycle[69]. Silicate weathering fixes CO_2 from the atmosphere; a process that is increasingly implemented in agroecosystems to provide benefits for both carbon sequestration and crop yields[70–72]. Plants enhance silicate weathering through various mechanisms[73], especially if Si demand increases, and our findings on the link between plant silicification and changes in the Earth's climate provide new clues regarding the interactions between Si and C cycling over geological timescales[13].

Materials and Methods

Effect of Si on rice's response to high and low temperature stress

We selected rice (*Oryza sativa* L. cv. Nipponbare), a typical high-Si species, for the experiment testing the effect of Si on high and low temperature stress. Seeds were surface-sterilized with 10% H_2O_2 (v/v) for 10 min then rinsed with deionized water five times. They were placed on moist filter paper and germinated at 30°C in the dark for three days. Seeds were then transferred to black plastic pots containing 1.2 L of deionized water for five days. Next, seedlings were grown in 1/4-strength Kimura B solution (adjusted to pH 5.6), renewed every five days in a growth chamber (at 30°C, 55% relative humidity, and using a 14/10 h light/dark period). Uniformly-sized 20-day-old rice seedlings were then selected for the experiment.

Rice seedlings were divided into two groups: the + Si group, for which 1mM of silicic acid (produced by passing sodium silicic acid solution through a column packed with ion exchange resin) was added to the nutrient solution, and the -Si group, which didn’t receive silicic acid. Apart from Si inputs, growth conditions were similar. The nutrient solution was renewed every five days. After 15 days, there was no difference in plant height or root length between the two groups (Table S1). We then changed the nutrient solution for both the + Si and -Si groups, and placed them under high temperature (40°C), low temperature (0°C), or freeze thawing (-2-2°C) stress. Three days later, we took photos for rice and measured the shoot height (the height of the highest shoot), root length (the length of the longest root), shoot fresh weight, root fresh weight, and chlorophyll concentration (using SPAD-502 chlorophyll meter) (five replicates per treatment). Data were expressed as mean ± standard error. Then, we use t-test method to evaluate whether there is a significant difference between groups for each stress treatment. Significant differences are indicated as follows: * $p < 0.05$, * * $p < 0.01$, *** $p < 0.001$.

Distribution temperature of high- and low-Si plants

We obtained information on leaf Si concentrations in different species, families and orders from de Tombeur et al.[12] – the largest database on leaf Si concentrations ever published. Taxonomic information was corrected using the NCBI database (www.ncbi.nlm.nih.gov). For each plant family within the pteridophytes, gymnosperms and angiosperms, we calculated the mean and standard errors of leaf Si concentrations. All analyses were performed in R 4.3.1[74].

From de Tombeur's database, we selected 10 orders with high (> 2 mg g^{-1}) and low (< 1 mg g^{-1}) mean leaf Si concentrations[12]. The high-Si orders include: Poales, Saxifragales, Schisandraceae, Arecales, Boraginaceae, Fagales, Rosales, Nymphaeaceae, Asterales, Alismatales. Low-Si orders include: Acorales, Brassicales, Liliales, Asparagales, Aquifoliales, Santalales, Pandanales, Celastraceae, Cornales, Bromeliaceae. We extracted the location of 1000 occurrences randomly selected within each order from the Global Biodiversity Information Facility, using the rgbif package in R (https://www.gbif.org/developer/occurrence#search, see Table S2 for details). After data cleaning, the final 19932 location will be used for subsequent analyses. We obtained mean annual temperatures (MAT) from CHELSA (High Resolution Climate Data for Earth's Land Surface Areas) to study the temperature distribution of high- and low-Si plants[75]. Finally, we mapped the world using R 4.3.1[74].

Effect of temperature on phytolith concentrations of wheat and rice

To also consider the intraspecific variation in leaf Si concentrations, a sampling campaign was conducted in China on two typical high-Si crops (wheat and rice). We collected 475 wheat individuals from 95 sampling sites and 279 rice individuals from 93 sampling sites (Fig. 4). The distribution of the sampling sites is 87.513–121.680 °E and 19.487–43.991 °N, which corresponds to the main harvesting regions of wheat and rice in China. Shoots were dried (105°C for 30 min, and then 75°C for 48 h) and ground through a 100-mesh (0.15 mm) sieve. Shoot phytoliths were extracted with HNO_3, HCl, and H_2O_2

by the microwave digestion method, following the potassium dichromate method to remove additional carbon residues[76]. Extracted phytoliths were washed with deionized water and dried in an oven at 75°C for 48 hours, and weighed. We analyzed the correlation between shoot phytolith concentrations and MAT (obtained from CHELSA). The linear regressions between the phytolith concentration in rice and wheat and the temperature at the sampling points were completed using Origin 2021[77]. The mapping of China was also done using R 4.3.1.

Differentiation of Si transporter proteins and historic climate change

To study the evolution of Si transporters in higher plants, we selected four proteins involved in Si absorption and transport in plants (Lsi1, Lsi2, Lsi3, Lsi6). Homologous sequences of Si uptake and transport proteins in *Oryza sativa* Japonica Group were searched by BLASTp on NCBI[26]. The protein sequences of the top 15–20 species with the highest homology were then downloaded (see Fig. 4a for species details). Sequence alignment was performed using MEGA[78] and the evolutionary tree was constructed using the Reltime and the Neighbor-Joining methods.

We used the dataset of historic climate change over the last 200 Ma reported by Scotese[27,79]. Since large polar icecaps can form when the global average temperature falls below 18°C, we referred to Scotese's methodology and characterized periods when the average temperature exceeds 18°C as warm periods, and periods below 18°C as cold periods. We then matched this historic climate dataset with the evolutionary tree in order to analyze the relationship between gene differentiation and temperature.

Differentiation time of high-Si and low-Si families and historic climate change

To test the link between the evolution of Si accumulation in plants and historic temperature fluctuations, we obtained evolutionary time data for both high- (> 10 mg g^{-1}) and low-Si (< 1 mg g^{-1}) families from Angiosperm Phylogeny Website (www.mobot.org/MOBOT/research/APweb/) (Table S3). We then compared Earth's historical temperatures during the emergence of high- and low-Si families. Given that the exact timing of species divergence may differ different databases, we conducted the same analysis using another phylogenetic database from Li et al.[63], and obtained similar results (Fig. S4).

Within the five families with the largest number of species among the angiosperms (Asteraceae, Orchidaceae, Fabaceae, Rubiaceae, and Poaceae), there was a large variation in leaf Si concentrations among the different subfamilies[12]. We first collected the divergence times of different subfamilies by searching for keywords of the five major families in the Web of Science database (www.webofscience.com/). We then analyzed the relationship between the mean leaf Si concentration of different subfamilies, their divergence dates and historic climate[27] (Table S4).

Declarations

Author contributions

Yongchao Liang and Nina Nikolic planned and designed the study with equal contributions. Zhihao Pang, Félix de Tombeur, Sue E. Hartley, Constantin M. Zohner, Miroslav Nikolic, Cyrille Violle, Lidong Mo, Thomas W. Crowther, Dong-Xing Guan, Zhongkui Luo, Yong-Guan Zhu, Yuxiao Wang, Ping Zhang, Hongyun Peng performed data analysis and writing.

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References

1. Carey, J. C. & Fulweiler, R. W. The Terrestrial Silica Pump. *PLoS One* **7** (2012). https://doi.org/10.1371/journal.pone.0052932.
2. Massey, F. P. & Hartley, S. E. Physical defences wear you down: progressive and irreversible impacts of silica on insect herbivores. *J. Anim. Ecol.* **78**, 281-291 (2009). https://doi.org/10.1111/j.1365-2656.2008.01472.x.
3. McNaughton, S. J. & Tarrants, J. L. Grass leaf silicification – natural-selection for an inducible defense against herbivores. *Proceedings of the National Academy of Sciences* **80**, 790-791 (1983). https://doi.org/10.1073/pnas.80.3.790.
4. Cooke, J., DeGabriel, J. L. & Hartley, S. E. The functional ecology of plant silicon: geoscience to genes. *Funct. Ecol.* **30**, 1270-1276 (2016). https://doi.org/10.1111/1365-2435.12711.
5. Thorne, S. J., Hartley, S. E. & Maathuis, F. J. M. Is Silicon a Panacea for Alleviating Drought and Salt Stress in Crops? *Front. Plant Sci.* **11** (2020). https://doi.org/10.3389/fpls.2020.01221.
6. Coskun, D. et al. The controversies of silicon's role in plant biology. *New Phytol.* **221**, 67-85 (2019). https://doi.org/10.1111/nph.15343.
7. Pang, Z., Peng, H., Lin, S. & Liang, Y. Theory and application of a Si-based defense barrier for plants: Implications for soil-plant-atmosphere system health. *Crit. Rev. Environ. Sci. Technol.* **54**, 722-746 (2024). https://doi.org/10.1080/10643389.2023.2267939.
8. Hodson, M. J., White, P. J., Mead, A. & Broadley, M. R. Phylogenetic Variation in the Silicon Composition of Plants. *Ann. Bot.* **96**, 1027-1046 (2005). https://doi.org/10.1093/aob/mci255.
9. Katz, O. Silica phytoliths in angiosperms: phylogeny and early evolutionary history. *New Phytol.* **208**, 642-646 (2015). https://doi.org/10.1111/nph.13559.

10. Katz, O. Silicon and Plant–Animal Interactions: Towards an Evolutionary Framework. *Plants* **9**, 430 (2020). https://doi.org/10.3390/plants9040430.
11. Strömberg, C. A. E., Di Stilio, V. S. & Song, Z. Functions of phytoliths in vascular plants: an evolutionary perspective. *Funct. Ecol.* **30**, 1286-1297 (2016). https://doi.org/10.1111/1365-2435.12692.
12. de Tombeur, F. et al. Why do plants silicify? *Trends Ecol. Evol.* **38**, 275-288 (2023). https://doi.org/10.1016/j.tree.2022.11.002.
13. Conley, D. J. & Carey, J. C. Silica cycling over geologic time. *Nat. Geosci.* **8**, 431-432 (2015). https://doi.org/10.1038/ngeo2454.
14. Ma, J. F. et al. A silicon transporter in rice. *Nature* **440**, 688-691 (2006). https://doi.org/10.1038/nature04590.
15. Ma, J. F. et al. An efflux transporter of silicon in rice. *Nature* **448**, 209-212 (2007). https://doi.org/10.1038/nature05964.
16. Ma, J. F. & Yamaji, N. A cooperative system of silicon transport in plants. *Trends Plant Sci.* **20**, 435-442 (2015). https://doi.org/10.1016/j.tplants.2015.04.007.
17. En, Y., Yamaji, N. & Ma, J. F. Linking root morphology and anatomy with transporters for mineral element uptake in plants. *Plant Soil* **484**, 1-12 (2023). https://doi.org/10.1007/s11104-022-05692-y.
18. Brightly, W. H., Hartley, S. E., Osborne, C. P., Simpson, K. J. & Strömberg, C. A. E. High silicon concentrations in grasses are linked to environmental conditions and not associated with C4 photosynthesis. *Glob. Change Biol.* **26**, 7128-7143 (2020). https://doi.org/10.1111/gcb.15343.
19. Saha, G., Mostofa, M. G., Rahman, M. M. & Tran, L. P. Silicon-mediated heat tolerance in higher plants: A mechanistic outlook. *Plant Physiol. Biochem.* **166**, 341-347 (2021). https://doi.org/10.1016/j.plaphy.2021.05.051.
20. Wang, G. et al. Extracellular Silica Nanocoat Confers Thermotolerance on Individual Cells: A Case Study of Material-Based Functionalization of Living Cells. *ChemBioChem* **11**, 2368-2373 (2010). https://doi.org/10.1002/cbic.201000494.
21. Bishnoi, A., Jangir, P., Shekhawat, P. K., Ram, H. & Soni, P. Silicon Supplementation as a Promising Approach to Induce Thermotolerance in Plants: Current Understanding and Future Perspectives. *J. Soil Sci. Plant Nutr.* **23**, 34-55 (2023). https://doi.org/10.1007/s42729-022-00914-9.
22. Johnson, S. N. et al. Climate warming and plant biomechanical defences: Silicon addition contributes to herbivore suppression in a pasture grass. *Funct. Ecol.* **33**, 587-596 (2019). https://doi.org/10.1111/1365-2435.13295.
23. Johnson, S. N. & Hartley, S. E. Elevated carbon dioxide and warming impact silicon and phenolic-based defences differently in native and exotic grasses. *Glob. Change Biol.* **24**, 3886-3896 (2018). https://doi.org/10.1111/gcb.13971.
24. McLarnon, E., McQueen-Mason, S., Lenk, I. & Hartley, S. E. Evidence for Active Uptake and Deposition of Si-based Defenses in Tall Fescue. *Front. Plant Sci.* **8** (2017). https://doi.org/10.3389/fpls.2017.01199.

25. Cornelis, J. T., Delvaux, B. & Titeux, H. Contrasting silicon uptakes by coniferous trees: a hydroponic experiment on young seedlings. *Plant Soil* **336**, 99-106 (2010). https://doi.org/10.1007/s11104-010-0451-x.
26. Boratyn, G. M. et al. BLAST: a more efficient report with usability improvements. *Nucleic Acids Res.* **41**, W29-W33 (2013). https://doi.org/10.1093/nar/gkt282.
27. Scotese, C. R., Song, H., Mills, B. J. W. & van der Meer, D. G. Phanerozoic paleotemperatures: The earth's changing climate during the last 540 million years. *Earth-Sci. Rev.* **215**, 103503 (2021). https://doi.org/10.1016/j.earscirev.2021.103503.
28. Bergh, N. G. & Peter Linder, H. Cape diversification and repeated out-of-southern-Africa dispersal in paper daisies (Asteraceae–Gnaphalieae). *Mol. Phylogenet. Evol.* **51**, 5-18 (2009). https://doi.org/10.1016/j.ympev.2008.09.001.
29. Panero, J. L. & Crozier, B. S. Macroevolutionary dynamics in the early diversification of Asteraceae. *Mol. Phylogenet. Evol.* **99**, 116-132 (2016). https://doi.org/10.1016/j.ympev.2016.03.007.
30. Herrando-Moraira, S. et al. Nuclear and plastid DNA phylogeny of tribe Cardueae (Compositae) with Hyb-Seq data: A new subtribal classification and a temporal diversification framework. *Mol. Phylogenet. Evol.* **137**, 313-332 (2019). https://doi.org/10.1016/j.ympev.2019.05.001.
31. Mandel, J. R. et al. A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *Proceedings of the National Academy of Sciences* **116**, 14083-14088 (2019). https://doi.org/10.1073/pnas.1903871116.
32. Ramírez, S. R., Gravendeel, B., Singer, R. B., Marshall, C. R. & Pierce, N. E. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. *Nature* **448**, 1042-1045 (2007). https://doi.org/10.1038/nature06039.
33. Prychid, C. J., Rudall, P. J. & Gregory, M. Systematics and Biology of Silica Bodies in Monocotyledons. *The Botanical review* **69**, 377-440 (2003). https://doi.org/10.1663/0006-8101(2004)069[0377:SABOSB]2.0.CO;2.
34. Lavin, M., Herendeen, P. S. & Wojciechowski, M. F. Evolutionary Rates Analysis of Leguminosae Implicates a Rapid Diversification of Lineages during the Tertiary. *Syst. Biol.* **54**, 575-594 (2005). https://doi.org/10.1080/10635150590947131.
35. Zhao, Y. et al. Nuclear phylotranscriptomics and phylogenomics support numerous polyploidization events and hypotheses for the evolution of rhizobial nitrogen-fixing symbiosis in Fabaceae. *Mol. Plant.* **14**, 748-773 (2021). https://doi.org/10.1016/j.molp.2021.02.006.
36. Bremer, B. & Eriksson, T. Time Tree of Rubiaceae: Phylogeny and Dating the Family, Subfamilies, and Tribes. *Int. J. Plant Sci.* **170**, 766-793 (2009). https://doi.org/10.1086/599077.
37. Quigley, K. M., Griffith, D. M., Donati, G. L. & Anderson, T. M. Soil nutrients and precipitation are major drivers of global patterns of grass leaf silicification. *Ecology (Durham)* **101**, 1-10 (2020). https://doi.org/10.1002/ecy.3006.
38. Johnson, S. N. et al. Climatic Drivers of Silicon Accumulation in a Model Grass Operate in Low- but Not High-Silicon Soils. *Plants-Basel* **12** (2023). https://doi.org/10.3390/plants12050995.

39. Soininen, E. M., Bråthen, K. A., Jusdado, J., Reidinger, S. & Hartley, S. E. More than herbivory: levels of silica-based defences in grasses vary with plant species, genotype and location. *Oikos* **122**, 30-41 (2013). https://doi.org/10.1111/j.1600-0706.2012.20689.x.
40. de Tombeur, F. et al. Nitrogen availability and plant-plant interactions drive leaf silicon concentration in wheat genotypes. *Funct. Ecol.* **36**, 2833-2844 (2022). https://doi.org/10.1111/1365-2435.14170.
41. Thorne, S. J., Stirnberg, P. M., Hartley, S. E. & Maathuis, F. The Ability of Silicon Fertilisation to Alleviate Salinity Stress in Rice is Critically Dependent on Cultivar. *Rice* **15** (2022). https://doi.org/10.1186/s12284-022-00555-7.
42. Deng, H. et al. Silicon (Si) Application Improved the Antioxidant Response and Grain Yield Formation in rice Under High Temperature Conditions. *Silicon* **15**, 4375-4385 (2023). https://doi.org/10.1007/s12633-023-02354-1.
43. Sharifi, P., Amirnia, R. & Shirani Bidabadi, S. Role of Silicon in Mediating Heat Shock Tolerance in Soybean. *Gesunde Pflanz.* **74**, 397-411 (2022). https://doi.org/10.1007/s10343-021-00617-8.
44. Agarie, S. K. U. F. et al. Effects of silicon on tolerance to water deficit and heat stress in rice plants (Oryza sativa L.), monitored by electrolyte leakage. *Plant. Prod. Sci.* **1**, 96-103 (1998). https://doi.org/10.1626/pps.1.96.
45. Wang, L. et al. Biosilicified structures for cooling plant leaves: A mechanism of highly efficient midinfrared thermal emission. *Appl. Phys. Lett.* **87**, 194105 (2005). https://doi.org/10.1063/1.2126115.
46. Younis, A. A., Khattab, H. & Emam, M. M. Impacts of silicon and silicon nanoparticles on leaf ultrastructure and *TaPIP1* and *TaNIP2* gene expressions in heat stressed wheat seedlings. *Biol. Plant.* **64**, 343-352 (2020). https://doi.org/10.32615/bp.2020.030.
47. Soundararajan, P., Sivanesan, I., Jana, S. & Jeong, B. R. Influence of silicon supplementation on the growth and tolerance to high temperature in *Salvia splendens*. *Hortic. Environ. Biotechnol.* **55**, 271-279 (2014). https://doi.org/10.1007/s13580-014-0023-8.
48. Muneer, S., Park, Y. G., Kim, S. & Jeong, B. R. Foliar or Subirrigation Silicon Supply Mitigates High Temperature Stress in Strawberry by Maintaining Photosynthetic and Stress-Responsive Proteins. *J. Plant Growth Regul.* **36**, 836-845 (2017). https://doi.org/10.1007/s00344-017-9687-5.
49. Takahashi, D., Willick, I. R., Kasuga, J. & Livingston III, D. P. Responses of the Plant Cell Wall to Sub-Zero Temperatures: A Brief Update. *Plant Cell Physiol.* **62**, 1858-1866 (2021). https://doi.org/10.1093/pcp/pcab103.
50. Sun, L. et al. Effects of SiO_2 Filler in the Shell and Wood Fiber in the Core on the Thermal Expansion of Core–Shell Wood/Polyethylene Composites. *Polymers* **12**, 2570 (2020). https://doi.org/10.3390/polym12112570.
51. Takahashi, D., Uemura, M. & Kawamura, Y. in *Survival Strategies in Extreme Cold and Desiccation: Adaptation Mechanisms and Their Applications* 61-79 (Singapore: Springer, 2018).
52. Wisniewski, M., Gusta, L. & Neuner, G. Adaptive mechanisms of freeze avoidance in plants: A brief update. *Environ. Exp. Bot.* **99**, 133-140 (2014). https://doi.org/10.1016/j.envexpbot.2013.11.011.

53. Liang, Y. et al. Role of silicon in enhancing resistance to freezing stress in two contrasting winter wheat cultivars. *Environ. Exp. Bot.* **64**, 286-294 (2008). https://doi.org/10.1016/j.envexpbot.2008.06.005.
54. Charrier, G. et al. Ultrasonic emissions during ice nucleation and propagation in plant xylem. *The New phytologist* **207**, 570-578 (2015). https://doi.org/10.1111/nph.13361.
55. Kumar, A., Marcolli, C. & Peter, T. Ice nucleation activity of silicates and aluminosilicates in pure water and aqueous solutions - Part 2: Quartz and amorphous silica. *Atmos. Chem. Phys.* **19**, 6035-6058 (2019). https://doi.org/10.5194/acp-19-6035-2019.
56. Hacker, J. & Neuner, G. Ice Propagation in Dehardened Alpine Plant Species Studied by Infrared Differential Thermal Analysis (IDTA). *Arct. Antarct. Alp. Res.* **40**, 660-670 (2008). https://doi.org/10.1657/1523-0430(07-077)[HACKER]2.0.CO;2.
57. Hacker, J. & Neuner, G. Ice propagation in plants visualized at the tissue level by infrared differential thermal analysis (IDTA). *Tree Physiol.* **27**, 1661-1670 (2007). https://doi.org/10.1093/treephys/27.12.1661.
58. Deshmukh, R., Sonah, H. & Belanger, R. R. New evidence defining the evolutionary path of aquaporins regulating silicon uptake in land plants. *J. Exp. Bot.* **71**, 6775-6788 (2020). https://doi.org/10.1093/jxb/eraa342.
59. Brocks, J. J. et al. The rise of algae in Cryogenian oceans and the emergence of animals. *Nature* **548**, 578-581 (2017). https://doi.org/10.1038/nature23457.
60. Bryłka, K., Alverson, A. J., Pickering, R. A., Richoz, S. & Conley, D. J. Uncertainties surrounding the oldest fossil record of diatoms. *Sci. Rep.* **13** (2023). https://doi.org/10.1038/s41598-023-35078-8.
61. Morris, J. L. et al. The timescale of early land plant evolution. *Proceedings of the National Academy of Sciences* **115** (2018). https://doi.org/10.1073/pnas.1719588115.
62. Smith & Alison, M. *Plant biology* (Taylor & Francis, 2010).
63. Li, H. et al. Origin of angiosperms and the puzzle of the Jurassic gap. *Nat. Plants* **5**, 461-470 (2019). https://doi.org/10.1038/s41477-019-0421-0.
64. Sun, H. et al. Tomato roots have a functional silicon influx transporter but not a functional silicon efflux transporter. *Plant, Cell & Environment* **43**, 732-744 (2019). https://doi.org/10.1111/pce.13679.
65. Nikolic, M., Nikolic, N., Liang, Y., Kirkby, E. A. & Römheld, V. Germanium-68 as an Adequate Tracer for Silicon Transport in Plants. Characterization of Silicon Uptake in Different Crop Species. *Plant Physiol.* **143**, 495-503 (2007). https://doi.org/10.1104/pp.106.090845.
66. Kido, N. et al. The Matrix Polysaccharide (1;3,1;4)-β-d-Glucan is Involved in Silicon-Dependent Strengthening of Rice Cell Wall. *Plant Cell Physiol.* **56**, 268-276 (2015). https://doi.org/10.1093/pcp/pcu162.
67. Kumar, S., Soukup, M. & Elbaum, R. Silicification in Grasses: Variation between Different Cell Types. *Front. Plant Sci.* **8** (2017). https://doi.org/10.3389/fpls.2017.00438.

68. Zexer, N., Kumar, S. & Elbaum, R. Silica deposition in plants: scaffolding the mineralization. *Ann. Bot.* **131**, 897-908 (2023). https://doi.org/10.1093/aob/mcad056.
69. Brantley, S. L., Shaughnessy, A., Lebedeva, M. I. & Balashov, V. N. How temperature-dependent silicate weathering acts as Earth's geological thermostat. *Science (American Association for the Advancement of Science)* **379**, 382-389 (2023). https://doi.org/10.1126/science.add2922.
70. Kelland, M. E. et al. Increased yield and CO_2 sequestration potential with the C4 cerealSorghum bicolor cultivated in basaltic rock dust-amended agricultural soil. *Glob. Change Biol.* **26**, 3658-3676 (2020). https://doi.org/10.1111/gcb.15089.
71. Beerling, D. J. et al. Potential for large-scale CO_2 removal via enhanced rock weathering with croplands. *Nature* **583**, 242-248 (2020). https://doi.org/10.1038/s41586-020-2448-9.
72. Beerling, D. J. et al. Enhanced weathering in the US Corn Belt delivers carbon removal with agronomic benefits. *Proceedings of the National Academy of Sciences* **121** (2024). https://doi.org/10.1073/pnas.2319436121.
73. Finlay, R. D. et al. Reviews and syntheses: Biological weathering and its consequences at different spatial levels – from nanoscale to global scale. *Biogeosciences* **17**, 1507-1533 (2020). https://doi.org/10.5194/bg-17-1507-2020.
74. Null, R. C. T. R. et al. R: A language and environment for statistical computing. *Computing* **1**, 12-21 (2011).
75. Karger, D. N. et al. Data Descriptor: Climatologies at high resolution for the earth's land surface areas. *Sci. Data* **4** (2017). https://doi.org/10.1038/sdata.2017.122.
76. Li, W. J. et al. The spatial distribution of phytoliths and phytolith-occluded carbon in wheat (Triticum aestivum L.) ecosystem in China. *Sci. Total Environ.* **850** (2022). https://doi.org/10.1016/j.scitotenv.2022.158005.
77. Seifert, E. Origin Pro 9.1: Scientific Data Analysis and Graphing Software-Software Review. *J. Chem. Inf. Model.* **54**, 1552 (2014). https://doi.org/10.1021/ci500161d.
78. Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. *Mol. Biol. Evol.* **35**, 1547-1549 (2018). https://doi.org/10.1093/molbev/msy096.
79. Scotese, C. R. An Atlas of Phanerozoic Paleogeographic Maps: The Seas Come In and the Seas Go Out. *Annu. Rev. Earth Planet. Sci.* **49**, 679-728 (2021). https://doi.org/10.1146/annurev-earth-081320-064052.

Figures

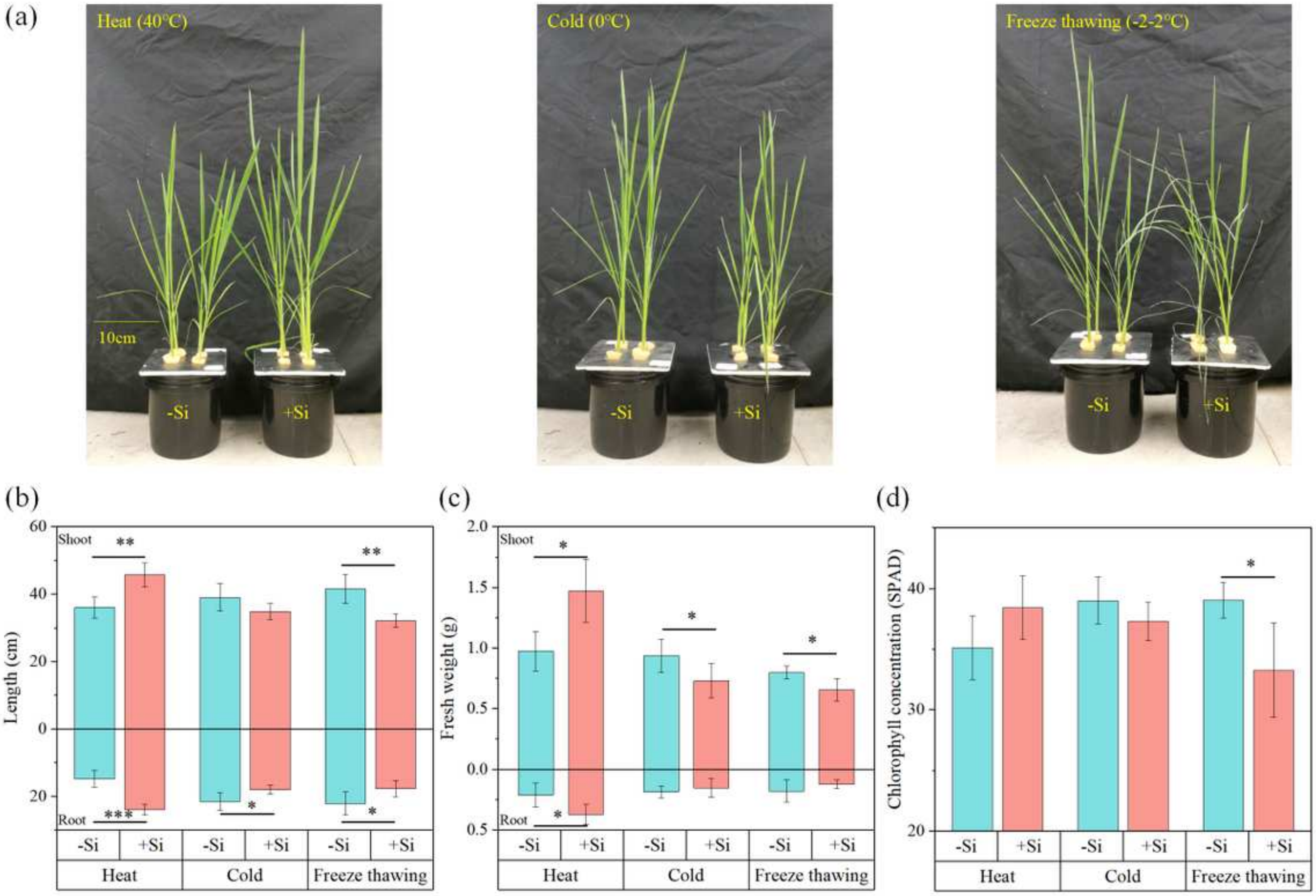

Figure 1

The effect of silicon on rice growth under high temperature, low temperature, and freeze thawing stress. a, Images of rice after three days of heat, cold or freeze stress. b, The length of rice shootsand roots. c, The fresh weight of rice shoots and roots. d, The chlorophyll concentration (using a SPAD-502 chlorophyll meter) of rice shoots and roots. The +Si group refers to the cultivation of rice in a nutrient solution containing 1mM silicic acid for 15 days prior to stress. The data represent the mean and standard deviation of five replicates. Significant differences between the groups without and with Si are indicated as follows: * $p < 0.05$, * * $p< 0.01$, *** $p < 0.001$.

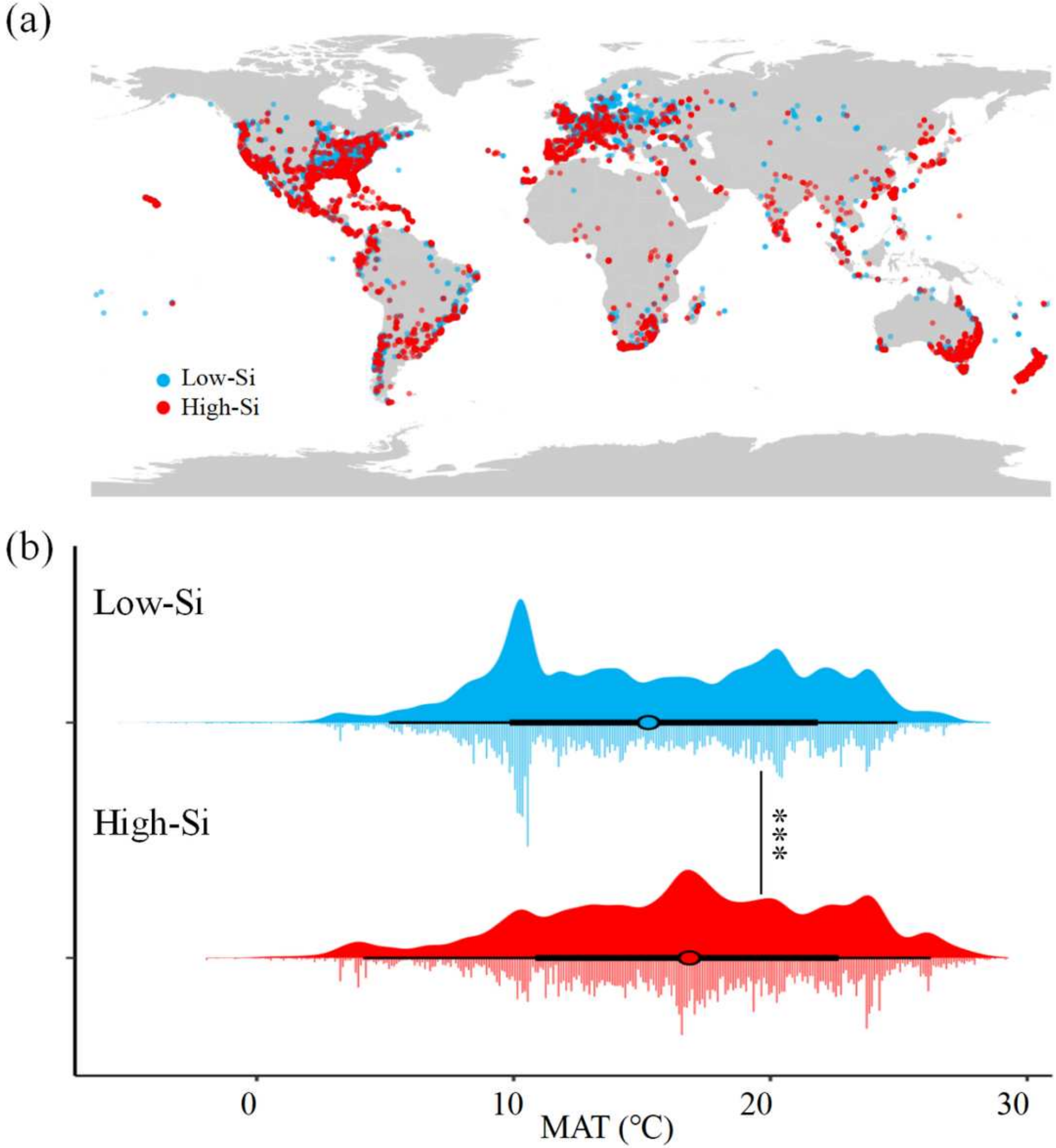

Figure 2

Relationship between temperature and the distribution of high- and low-Si plants a, Global distribution of sampling sites for high-(n=9972 occurrences) and low-Si (n=9990 occurrences) species. Data was obtained from GBIF. **b**, Temperature range of high- and low-Si plant distributions. The mean annual temperatures (MAT) were obtained from CHELSA (chelsa-climate.org). Significant differences between high- and low-Si plants are indicated as follows: *** $p< 0.001$.

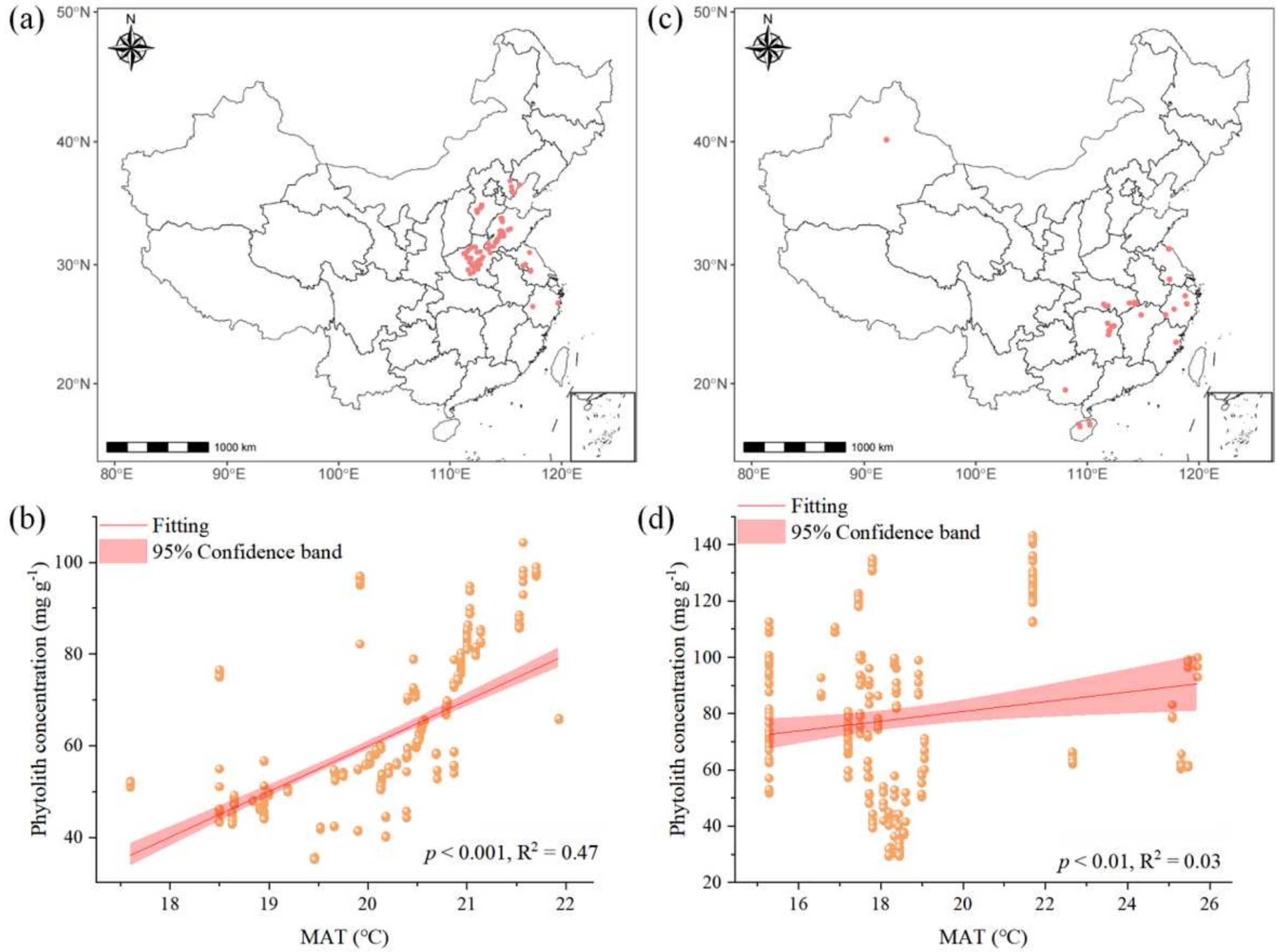

Figure 3

Correlation analysis of wheat and rice phytolith concentrations with mean annual temperatures. a and b, Distribution of wheat sampling sites and correlation of phytolith concentration with MAT (n=475 individuals). c and d, Distribution of rice sampling sites and correlation of phytoliths concentration with MAT (n=279 individuals). The Chinese map data is sourced from DATAV.GeoAltas (http://datav.aliyun.com/portal/school/atlas/area_selector).

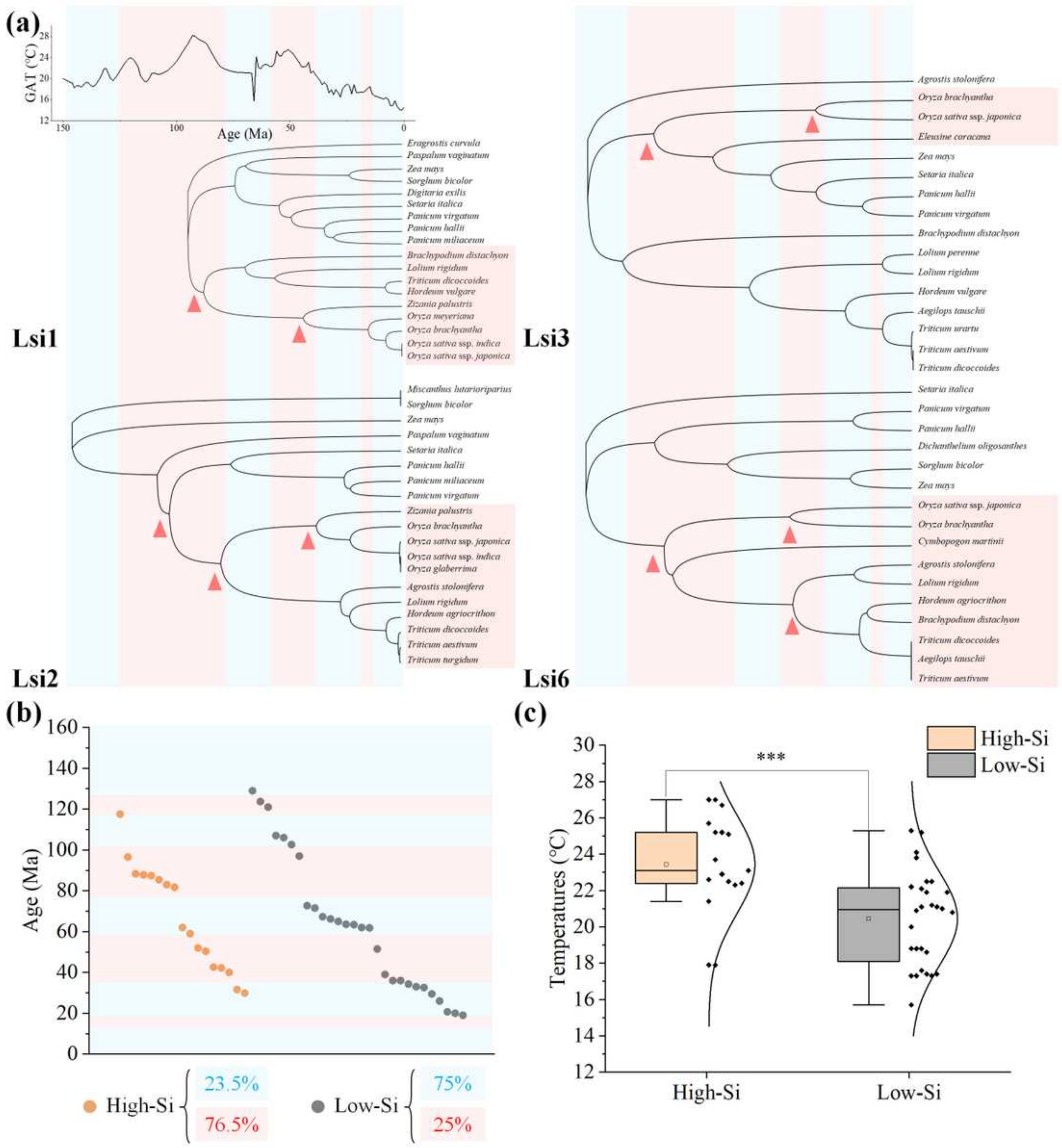

Figure 4

Differentiation times of Si transporter proteins and high-Si families. a, Evolutionary relationships between Si transporter proteins (Lsi1, Lsi2, Lsi3, Lsi6). Homologous sequences of Si transporter proteins in *Oryza sativa* Japonica Group were searched by BLASTp on NCBI. Protein sequences from the top 15-20 species with the highest homology were selected for the analysis. Sequence alignment was performed using MEGA and the evolutionary tree was constructed using the Reltime method and the Neighbor-Joining method. The evolutionary tree was computed using 2 calibration constraints. The upper left corner of the graph shows the changes in Earth's average temperature from 150 Ma to the present. The red area represents the warm period, and the blue area represents the cold period. The division is based on Scotese (2021). The results show that Si uptake and transport proteins of high-Si species (red shades) mainly diverged in warm periods (red arrows). **b**, Emergence of plant families with different leaf Si concentrations during warm and cold periods. Evolutionary information was obtained from Angiosperm Phylogeny Website (www.mobot.org/MOBOT/research/APweb/). Each point represents a family. Specific information about the plant families can be found in Table S3. Families with leaf Si concentrations above 10 mg g^{-1} are marked orange ($n = 17$), and families with leaf Si concentrations below 1 mg g^{-1} are marked gray ($n = 28$). Red areas indicate warm periods and blue areas indicate cold periods, and the division is based on Scotese[27]. **c**, Earth's temperatures during the emerging time of high- and low-Si families. The box plots show the medians and quartiles of the data. Significant differences are indicated as follows: *** $p < 0.001$.

Supplementary Files

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- SupplementaryMaterial.pdf
- TableS2.xls
- rs2.pdf