New Phytologist

Research

Across 33 broad-leaved deciduous woody species, silicon enhances leaf lamina stiffness but not tensile strength whereas cellulose enhances both

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Received: *27 December 2024*
Accepted: *24 February 2025*

New Phytologist (2025) **246:** 2075–2083
doi: 10.1111/nph.70079

Key words: biomechanics, cell wall components, leaf mechanical properties, silicon, trade-off.

Summary

- Silicon (Si) has been hypothesized to be a metabolically cheaper substitute for carbon-based cell wall components to support leaves. However, how the biomechanical function of Si, deposited as amorphous silica, differs from cell wall components remains untested. Here, we tested the hypothesis that species with higher leaf Si concentrations have stiffer but more brittle leaf lamina.
- We measured the mechanical properties, including modulus of elasticity (E), tensile strength (σ_{max}), and maximum strain (ε_{max}), tissue density, and the concentrations of Si and cell wall components for 33 deciduous broad-leaved woody species.
- Multiple regression results showed that tissue density, Si concentration, and cellulose concentration contributed positively to E and negatively to ε_{max}. By contrast, tissue density and cellulose concentration, but not Si concentration, contributed to σ_{max}. No significant contribution of lignin concentration to mechanical properties was detected.
- These results suggest that Si might function as a substitute for cellulose to increase stiffness but not the strength of a lamina. Greater Si concentration decreased ε_{max} without increasing σ_{max}, which made the lamina more brittle. The brittleness associated with Si might explain a potential cost or disadvantage of using Si, which would elucidate the trade-offs between species with different leaf Si concentrations.

Introduction

Leaves are subjected to destructive forces incurred by herbivory (Coley, 1983), wind, and rainfall (Niklas, 1992). Hence, for leaves to achieve a longer lifespan, they must have greater strength and toughness (force and energy to fracture, respectively) (Reich *et al.*, 1991; Wright & Westoby, 2002; Onoda *et al.*, 2011; Westbrook *et al.*, 2011; Kitajima *et al.*, 2012; He *et al.*, 2019). Previous studies have shown that the strength and toughness of leaf lamina primarily reflect the dry mass density and mass-basis concentrations of the cell wall components (Onoda *et al.*, 2008; Kitajima *et al.*, 2016) and that species with longer leaf lifespans have stronger leaves (Wright & Cannon, 2001; Onoda *et al.*, 2004; Mediavilla *et al.*, 2008; Kitajima & Poorter, 2010; Kitajima *et al.*, 2013). Studies comparing tropical trees have revealed that, among cell wall components, the concentration of cellulose, but not hemicellulose and lignin, explains the leaf fracture toughness and leaf lifespan (Westbrook *et al.*, 2011; Kitajima *et al.*, 2016).

In addition to carbon (C)-based components in the plant cell wall, silicon (Si) deposited in the cell wall as opal (i.e. amorphous $SiO_2 \cdot nH_2O$) can also contribute to the mechanical properties. For example, in rice with extremely high leaf Si concentrations (often > 10% of dry mass, Ma & Takahashi, 2002), Si contributes to the mechanical support of the leaf blade to keep the leaf at optimal angles to reduce self-shading (Yoshida *et al.*, 1969) by increasing the stiffness of the cell wall (He *et al.*, 2015) and the whole leaf (Yamamoto *et al.*, 2012). As the metabolic cost to absorb Si from the soil solution and to deposit it as SiO_2 is considered to be a small fraction of the biosynthetic cost of C-based cell wall components (6.7% and 3.7% of the energetic costs for polysaccharide and lignin, respectively; Raven, 1983), Si has been hypothesized to be a cheaper substitute for C (Raven, 1983; Cooke & Leishman, 2011; but see de Tombeur *et al.*, 2021, who proposed the metabolic cost may be larger when soil Si availability is low). Cooke & Leishman (2011) found a negative correlation between leaf Si concentration and leaf longevity across species by analyzing leaf Si concentration data assembled by Hodson *et al.* (2005) with the leaf longevity data assembled by Wright *et al.* (2004) and suggested that Si might be a good substitute for C for the species with short leaf lifespans. From the point of view of the specific function of Si, silica in leaf cell walls ($SiO_2 \cdot nH_2O$) might act similarly to lignin, because both are expected to increase compression strength (Raven, 1983).

Negative correlations reported between the concentrations of Si and lignin observed within species (Suzuki *et al.*, 2012; Yamamoto *et al.*, 2012; Klotzbücher *et al.*, 2018; Schaller *et al.*, 2019) and across species (Schoelynck *et al.*, 2010) might support this view. Similarly, some studies have reported negative correlations between Si and cellulose, although such correlations differ among functional types or plant organs (Schoelynck *et al.*, 2010; Schaller *et al.*, 2012, Yamamoto *et al.*, 2012; de Tombeur *et al.*, 2020).

While some plants, such as rice and maize, absorb Si with an active transport mechanism from the soil and accumulate Si in their leaves (Ma *et al.*, 2006, 2007; Mitani *et al.*, 2009), most land plants show lower Si concentrations in leaves (e.g. Hodson *et al.*, 2005) than would be explained by a passive entry of Si into the xylem water stream (Takahashi *et al.*, 1990). This suggests a mechanism to prevent Si uptake in many land plants (Raven, 2003). Indeed, the Si concentration in the xylem sap of tomatoes is lower than the external solution around the root (Mitani & Jian, 2005) because Lsi2, a homolog of a Si efflux transporter in rice, in tomatoes lacks the function to transport Si (Sun *et al.*, 2020; Mitani-Ueno & Ma, 2021). In addition, a comparison of leaf Si concentrations among 494 species of land plants, including moss, ferns, gymnosperms, and angiosperms, suggests that the ancestral gymnosperms once established a mechanism to prevent Si absorption (Takahashi *et al.*, 1981; reviewed by Epstein, 1999; Ma & Takahashi, 2002). Such macroevolutionary trends suggest that there may be certain disadvantages or constraints associated with Si uptake and accumulation in leaves, or the cost of absorbing and using Si can be much higher than it has been estimated (e.g. de Tombeur *et al.*, 2021, 2022). However, while many studies have reported the positive aspects of Si accumulation (Ma, 2004; Cooke & Leishman, 2016; Coskun *et al.*, 2019), the disadvantages of Si accumulation have not been demonstrated quantitatively (Hodson & Guppy, 2022; de Tombeur *et al.*, 2022).

The relationship between leaf mechanical properties and the concentration of Si, which exists as amorphous SiO_2 in the plant body, could be key to understanding the potential disadvantage of accumulating Si in the leaf, as speculated in several papers (e.g. Minden *et al.*, 2021). Yamamoto *et al.* (2012) found that Si makes the rice blades stiffer (i.e. more force is required to cause a unit of deformation) but more brittle (i.e. fractured at smaller deformation). To withstand destructive forces from wind or water, plants may employ either of the two contrasting strategies: The first is to create a stiff body that is deformed less by a unit force, and the second is to have a flexible body that deforms easily without breaking (Bouma *et al.*, 2005). Leaves are generally thin and, to some extent, stiff for efficient light capture, but they must also flutter without breaking against strong wind. Thus, most land plants must produce a leaf that is both flexible and strong enough to withstand destructive forces. Silicon-derived brittleness could be disadvantageous, even if Si contributes to the stiffness. However, few previous studies evaluated the relationship between leaf mechanical properties, such as stiffness, brittleness, and strength, and Si concentration across species (Massey *et al.*, 2007; Simpson *et al.*, 2017). In addition, a recent study by de Tombeur *et al.* (2022) found that Si concentration positively correlates with leaf dry matter content (LDMC, leaf dry mass divided by fresh mass), which correlates with tissue density, across 469 nonwoody species. As LDMC is a known leaf trait associated with leaf strength (Kitajima *et al.*, 2012), it is necessary to evaluate the relationship of leaf mechanical properties with Si concentration and other factors, such as tissue density and concentrations of cell wall components simultaneously.

In the present study, we used a tensile test to evaluate how stiffness, strength, and extensibility (i.e. to what extent a material can be stretched without breaking) of leaves would covary with the concentrations of Si and cell wall components across 33 deciduous broad-leaved woody species. We chose broad-leaved woody species as a life form that includes species with both high and low leaf Si concentrations (Raven, 1983; Hodson *et al.*, 2005). In addition, as most previous studies on Si utilization have been done in nonwoody species (but see Korndörfer & Del-Claro, 2006; Klotz *et al.*, 2023a, 2023b, 2024 for the studies on woody plants), exploring the function of Si in woody plants might expand our understanding of how plants utilize Si. As leaf mechanical properties are well known to covary with leaf lifespan (e.g. Kitajima & Poorter, 2010; Kitajima *et al.*, 2012) and comparison among species with a wide range of leaf lifespans could make the relationship between leaf mechanical properties and Si concentration unclear, we used only deciduous species with relatively short leaf lifespans (*c.* 3–7 months) as a first step. Specifically, we tested the following hypothesis: Leaves with higher Si concentrations are stiff but more brittle (i.e. breakable with a smaller deformation). We also explored the difference in the functions of Si and cell wall components for the mechanical support of the leaf lamina.

Materials and Methods

Collection of leaves

We used 33 deciduous broad-leaved woody species (31 trees and 2 shrubs; Table 1, Supporting Information Table S1) growing mainly on natural or seminatural soils around the Yoshida Campus of Kyoto University (35°03N, 135°78E) between 12 September and 3 October 2019. The mean annual precipitation is 1522.9 mm, and the mean annual temperature is 16.2°C from 1991 to 2020 (Japan Meteorological Agency). Approximately two-thirds of the species in the study were native or naturalized species in Japan.

From five individuals of each species (165 individuals in total), we collected more than five leaves that were fully developed and showed no damage or signs of senescence. Leaf samples taken from each individual were separately wrapped in a moistened paper towel and stored in a sealed plastic bag at 4°C to keep them turgid until the mechanical test. We used one leaf for mechanical tests per individual and stored the rest for chemical analysis to ensure sufficient quantity was available for chemical analysis.

Mechanical test

As the Si concentration of the leaf vein is negligibly low in broad-leaved trees (Kajino & Kitajima, 2023), we measured the

Table 1 Thirty-three broad-leaved woody species, including two shrub species, *Kerria japonica* and *Stephanandra tanakae*, used for the study along with their key traits (mean values ± SD of three to five individuals per species).

Species	Family	Tissue density (g cm^{-3})	Si (%)	Cellulose (%)	Hemicellulose (%)	Lignin (%)	E (N mm^{-2})	σ_{max} (N mm^{-2})	ε_{max} (%)
Liquidambar formosana	Altingiaceae	0.37 ± 0.06	2.86 ± 0.72	21.98 ± 2.67	11.52 ± 3.59	23.29 ± 3.62	112.2 ± 42.43	1.86 ± 0.79	3.04 ± 1.4
Ilex macropoda	Aquifoliaceae	0.21 ± 0.03	0.2 ± 0.02	6.55 ± 0.67	12.71 ± 3.38	16.87 ± 1.38	11.99 ± 4.9	0.98 ± 0.22	11.36 ± 1.61
Gamblea innovans	Araliaceae	0.2 ± 0.02	0.16 ± 0.08	10.17 ± 2.02	8.37 ± 0.33	19.72 ± 0.94	25.73 ± 3.51	1.6 ± 0.12	9.19 ± 1.07
Ehretia dicksonii	Boraginaceae	0.11 ± 0.02	0.69 ± 0.14	12.55 ± 5.96	11.63 ± 0.45	24.54 ± 5.87	8.29 ± 4.05	0.91 ± 0.18	18.61 ± 3.81
Aphananthe aspera	Cannabaceae	0.27 ± 0.09	2.74 ± 0.72	10.12 ± 0.3	10.47 ± 2.08	30.04 ± 1.66	38.81 ± 31.37	1.94 ± 0.57	11.14 ± 4.8
Celtis sinensis	Cannabaceae	0.28 ± 0.11	2.13 ± 0.75	7.68 ± 1.2	10.08 ± 3.92	19.41 ± 0.87	30.97 ± 19.6	1.12 ± 0.36	6.05 ± 2.92
Clethra barbinervis	Clethraceae	0.23 ± 0.06	0.42 ± 0.03	17.79 ± 1.05	13.7 ± 2.77	26.13 ± 5.14	17.87 ± 3.71	1.39 ± 0.2	9.5 ± 1.74
Lyonia ovalifolia	Ericaceae	0.27 ± 0.04	0.26 ± 0.04	23.04 ± 1.75	12.59 ± 3.97	20.64 ± 2.11	36.68 ± 5.57	1.81 ± 0.13	7.12 ± 0.73
Mallotus japonicus	Euphorbiaceae	0.19 ± 0.01	0.57 ± 0.06	12.67 ± 0.86	10.66 ± 1.41	6.66 ± 1.47	15.37 ± 3.68	1.04 ± 0.13	8.87 ± 0.9
Triadica sebifera	Euphorbiaceae	0.28 ± 0.06	0.67 ± 0.15	8.51 ± 0.77	12.91 ± 2.82	4.49 ± 1	17.44 ± 2.07	1.58 ± 0.22	13.8 ± 2.05
Styphnolobium japonicum	Fabaceae	0.27 ± 0.03	0.35 ± 0.09	7.1 ± 1.33	25.86 ± 1.19	7.61 ± 1.31	13.47 ± 5.84	0.83 ± 0.11	11.63 ± 5.61
Robinia pseudoacacia	Fabaceae	0.2 ± 0.02	0.22 ± 0.01	11.33 ± 1.43	13.62 ± 1.83	36.97 ± 3.14	5.98 ± 1.97	0.84 ± 0.12	17.78 ± 5.09
Quercus serrata	Fagaceae	0.38 ± 0.05	1.2 ± 0.14	15.04 ± 2.48	11.07 ± 0.91	17.34 ± 4.1	60.4 ± 10.4	1.8 ± 0.39	4.89 ± 1.43
Clerodendrum trichotomum	Lamiaceae	0.12 ± 0.01	0.25 ± 0.02	8.71 ± 1.2	10.01 ± 0.86	32.07 ± 1.22	6.54 ± 1.11	0.91 ± 0.14	16.95 ± 4.1
Magnolia kobus	Magnoliaceae	0.27 ± 0.04	2.62 ± 0.34	16.16 ± 1.59	9.52 ± 3.1	23.02 ± 3.95	90.02 ± 12.55	1.9 ± 0.2	3.41 ± 0.91
Magnolia obovata	Magnoliaceae	0.24 ± 0.05	1.55 ± 0.52	17.21 ± 2.46	11.75 ± 2.54	26.15 ± 3	55.12 ± 20.5	1.35 ± 0.19	4.19 ± 2.55
Liriodendron tulipifera	Magnoliaceae	0.28 ± 0.05	0.2 ± 0.04	13.91 ± 0.42	10.37 ± 2.28	21.09 ± 2.77	35.98 ± 9.72	1.9 ± 0.21	10.63 ± 1.41
Firmiana simplex	Malvaceae	0.24 ± 0.06	1.1 ± 0.39	19.93 ± 1.43	15.89 ± 1.45	9.82 ± 0.89	49.93 ± 13.91	1.84 ± 0.4	5.86 ± 0.99
Broussonetia papyrifera	Moraceae	0.23 ± 0.02	1.2 ± 0.19	11.99 ± 0.38	15.77 ± 2.69	14.57 ± 0.55	12.91 ± 3.21	1.24 ± 0.18	13.7 ± 2.36
Ficus erecta	Moraceae	0.27 ± 0.02	1.94 ± 0.28	11.9 ± 1.34	8.86 ± 1.13	7.24 ± 0.88	38.08 ± 1.19	1.5 ± 0.2	6.19 ± 1.35
Morus australis	Moraceae	0.16 ± 0.02	1.21 ± 0.11	8.13 ± 1.41	12.96 ± 1.87	12.49 ± 2.41	5.68 ± 1.12	0.71 ± 0.12	16.71 ± 3.27
Rhamnella franguloides	Rhamnaceae	0.24 ± 0.03	0.45 ± 0.05	7.55 ± 1.21	12.6 ± 2.39	11.45 ± 1.87	17.37 ± 2.55	1.32 ± 0.14	11.12 ± 1.7
Kerria japonica	Rosaceae	0.19 ± 0.05	0.56 ± 0.16	8.41 ± 1.71	16.42 ± 3.22	7.83 ± 2.13	10.51 ± 3.51	0.93 ± 0.13	9.23 ± 2.19
Pseudocydonia sinensis	Rosaceae	0.3 ± 0.03	0.45 ± 0.07	12.27 ± 2.15	15.38 ± 3.2	11.76 ± 2.45	46.64 ± 1.96	1.4 ± 0.12	5.39 ± 0.6
Prunus jamasakura	Rosaceae	0.35 ± 0.05	0.34 ± 0.06	5.14 ± 0.7	10.94 ± 2.21	27.8 ± 3.15	23.8 ± 3.07	1.55 ± 0.22	9.96 ± 2.02
Stephanandra tanakae	Rosaceae	0.35 ± 0.03	0.23 ± 0.03	4.88 ± 0.58	10.39 ± 5.41	16 ± 2.7	17.66 ± 3.89	1.71 ± 0.15	12.82 ± 1.74
Acer palmatum	Sapindaceae	0.42 ± 0.05	2.25 ± 0.24	17.84 ± 0.52	12.97 ± 0.53	10.87 ± 0.43	63.87 ± 15.42	2.44 ± 0.32	4.93 ± 1.49
Acer rufinerve	Sapindaceae	0.25 ± 0.04	0.9 ± 0.31	14.29 ± 3.02	6.68 ± 0.76	29.98 ± 3.86	24.66 ± 4.06	1.65 ± 0.27	11.43 ± 1.07
Koelreuteria paniculata	Sapindaceae	0.33 ± 0.04	0.33 ± 0.01	12.02 ± 2.11	11.76 ± 2.16	9.85 ± 0.51	17.4 ± 0.98	1.15 ± 0.1	8.88 ± 1.33
Ailanthus altissima	Simaroubaceae	0.24 ± 0.02	0.52 ± 0.07	10.06 ± 1.48	14.09 ± 1.23	8.54 ± 1.03	15.62 ± 1.96	0.83 ± 0.1	7.39 ± 1.19
Styrax japonica	Styracaceae	0.32 ± 0.03	0.49 ± 0.08	11.17 ± 6.07	11.68 ± 4.69	12.79 ± 3.33	38.36 ± 7.92	2.11 ± 0.28	9.19 ± 1.53
Styrax obassia	Styracaceae	0.19 ± 0.06	0.26 ± 0.03	25.99 ± 1.9	14.64 ± 3.15	17.69 ± 1.73	22.33 ± 4.18	1.23 ± 0.17	8.76 ± 1.4
Zelkova serrata	Ulmaceae	0.28 ± 0.03	2.77 ± 0.22	14.91 ± 4.29	11.36 ± 0.81	21.18 ± 4.11	41.68 ± 5.65	2.14 ± 0.29	7.51 ± 2.11

Cellulose, dry weight basis cellulose concentration (%); E, Young's modulus of elasticity of the lamina (N mm^{-2}); hemicellulose, dry weight basis hemicellulose concentration (%); lignin, dry weight basis lignin concentration (%); Si, dry weight basis Si concentration (%); tissue density, dry weight of the lamina per volume (g cm^{-3}); ε_{max}, the maximum strain of the lamina (%); σ_{max}, the tensile strength of the lamina (N mm^{-2}). Mean values ± SD of leaf mass per area (LMA, g m^{-2}), lamina thickness (mm), and cell wall concentration (%) are shown in Supporting Information Table S1.

leaf blade, excluding primary and secondary veins. A small strip of leaf lamina (*c.* 0.5 × 5 cm) was cut with a razor, and the width and thickness of the strip were measured with a caliper and a custom-made thickness gage that held a compressive force of < 0.7 N (547-401-421FAS381; Mitutoyo, Kawasaki, Japan). Lamina thickness measurement avoided visible veins within the strip as much as possible.

The mechanical properties of the lamina strips were measured with a tensile test, as immediately as possible after cutting the strip, following the method used by Onoda *et al.* (2015). The two ends of the rectangular strips were clamped and stretched slowly (10 mm min^{-1}) until the strips were torn with a universal tester (EZ-LX; Shimadzu, Kyoto, Japan). We measured force and displacement every 100 milliseconds. Stress (σ, N m^{-2}) was calculated as force per cross-sectional area (= thickness × width of the strip), whereas strain (ε, %) was calculated as the ratio of the length change in the test strip relative to its original length. To evaluate stiffness, we measured Young's modulus of elasticity (E, N m^{-2}) as the initial slope of stress plotted against strain. The maximum stress when the strip was torn (σ_{max}) was defined as the ultimate tensile strength (hereafter 'strength'). The maximum strain (ε_{max}) was interpreted as the measure of lamina extensibility. After the tensile test, we scanned the leaf strips with a flatbed scanner (CanoScan LiDE 400; Canon, Tokyo, Japan) and measured the dry weight after drying in an oven at 65°C for > 3 d. We measured the area of the strip from the scanned data and calculated leaf mass per area (LMA; g m^{-2}) and tissue density (g cm^{-3}) by dividing the dry weight of the strip by the area and volume (= area × thickness), respectively. We confirmed that increases in the area of the strips before and after tensile testing were negligible (0.17% on average). We also calculated silica-free tissue density (i.e. tissue density without SiO_2), as silica deposited in the leaves could occupy substantial proportions of dry mass and affect the relationships between tissue density and other traits.

Chemical analysis

The rest of the leaves that were not used for the mechanical test were washed with running water before petiole removal, oven drying, and grinding into a fine powder with a mill (MM 400; Retsch, Haan, Germany) separately by individuals. Though these leaf samples contain midribs and other thicker veins, we assumed the chemical properties of these samples should be similar to those in the mechanical tests as the mass proportions of midribs in deciduous broad-leaved trees are relatively small. For chemical analysis, we used the leaves of three individuals out of the five of each species. Silicon concentration (%) was measured by the molybdate blue colorimetry (Sauer *et al.*, 2006) after alkaline extraction with 1% Na_2CO_3 solution at 85°C (Conley & Schelske, 1993; Nakamura *et al.*, 2020). Absorbance at 650 nm was measured with a spectrophotometer (UV-1650PC; Shimadzu). The concentrations of cell wall components (%) were measured with a modified method by Van Soest (1963). Briefly, nonpolar fractions, including fats, oils, carbohydrates, and proteins not bound to the cell wall, were removed by treating in a neutral detergent solution (ANKOM Technology, Macedon, NY, USA) at 90°C for 1 h. The neutral detergent fiber (i.e. the sum of hemicellulose, cellulose, and lignin) was determined from the residue as the measure of the bulk cell wall (% of dry mass). Next, hemicellulose was removed by washing with acid detergent (ANKOM Technology) at 90°C for 1 h. Finally, 72% H_2SO_4 was used to remove cellulose at room temperature for 3 h. The residue after washing with 72% H_2SO_4 was regarded as lignin.

Statistical analysis

Concentrations (% of leaf dry mass) of Si and cell wall components, leaf mechanical properties, and LMA, but not tissue density, were log-transformed to meet normality assumptions before statistical analysis. Analysis of variance on traits by species was tested to calculate the percentages of the trait variance that were explained by interspecific variation (five individuals for mechanical and morphological traits and three for chemical traits). The correlations among leaf mechanical properties, chemical properties, and morphological traits were tested by least squares regression. To test the relative contributions of Si and cell wall components to the mechanical properties, we used multiple regression models, with the leaf mechanical properties as the dependent variable, and tissue density and concentrations of Si, cellulose, hemicellulose, and lignin as independent variables. The model with the lowest Akaike information criterion (Akaike, 1974) was selected as the best model to predict the relative contribution of Si and cell wall components to the mechanical properties. Principal component analysis (PCA) was conducted to describe the multivariate relationships among the leaf traits (morphological traits, chemical traits, and mechanical properties). All statistical analyses were conducted by R v.4.2.2 (R Core Developmental Team, 2022).

Results

The percentages of the trait variance that were explained by interspecific variation were large in all traits tested (from 63.3% in hemicellulose concentration to 96.2% in Si concentration; Table S2). Among the morphological and chemical traits examined as potential correlates of leaf mechanical properties, tissue density exhibited the strongest correlation (Fig. 1; Table 2). Leaves with greater tissue density, that is more dry mass per unit leaf volume, had greater rigidity (E, r^2 = 0.48; Fig. 1a), greater stress for breaking the leaf lamina (σ_{max}, r^2 = 0.47; Fig. 1b), and less stretching before breaking (ε_{max}, r^2 = 0.31; Fig. 1c). Tissue density was not correlated with mass-based concentrations of Si and cell wall components, which were not correlated with each other (all $P > 0.05$; Figs S1, S2; Table 2) except for a negative correlation between hemicellulose and lignin concentrations (Fig. S2f). Silica-free tissue densities were almost equal to the tissue densities (94.3–99.7%), and relationships between silica-free tissue densities and other traits were quite similar to those of tissue densities (data not shown). Leaf mass per area (= tissue density × leaf thickness) was correlated positively with E ($P < 0.01$) and negatively with ε_{max} ($P < 0.05$), but not with σ_{max} and the

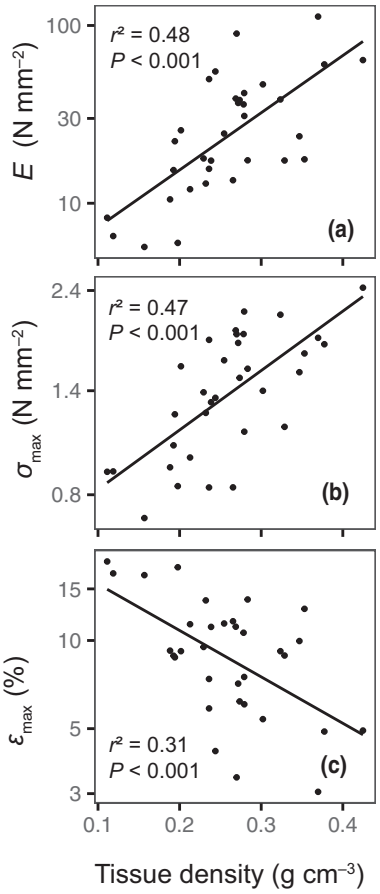

Fig. 1 Relationship of tissue density with Young's modulus of elasticity (E) (a), the tensile strength of the lamina (σ_{max}) (b), and the maximum strain (ε_{max}) (c) of the lamina across the 33 species studied.

concentrations of Si and cell wall components ($P > 0.05$, data not shown). In the PCA of these traits together (Fig. S3; Table S3), the first axis principal component 1 (PC1) explained 40.8% of the variation and showed positive loadings with E, σ_{max}, tissue density, Si concentration, cellulose concentration, and LMA, and negative loading with ε_{max} ($P < 0.05$). Principal component 2 showed positive loadings with tissue density and negative loadings with cell wall concentration, lignin concentration, and cellulose concentration ($P < 0.05$), explaining 20.6% of the variance. In multiple regression models for E, the best model included positive effects of tissue density, Si concentration, and cellulose concentration, and a negative effect of hemicellulose concentration. The best model for σ_{max} included positive effects of tissue density and cellulose concentration and a negative effect of hemicellulose concentration. The best model for ε_{max} included the negative effects of tissue density, Si concentration, and cellulose concentration (Table 3). Lignin concentration was not selected in these models.

Silicon and cellulose, but not lignin and hemicellulose, were significantly related to mechanical properties in most combinations of mechanical and chemical properties (Table 2). To evaluate the specific contribution of Si and cellulose in addition to the effect of tissue density, we examined how the residuals of the linear regressions of mechanical properties against tissue density were related to the concentration of Si and cellulose. Mass-based concentrations of Si and cellulose were positively correlated with the residual of the regression of E against tissue density ($P < 0.01$ and < 0.001; Fig. 2a,b). Hence, greater Si concentration and cellulose concentration both enhanced leaf rigidity at a given value of tissue density. A similar analysis for σ_{max} showed that cellulose had positive contributions to σ_{max} ($P < 0.01$; Fig. 2d). By contrast, no significant contribution of Si to σ_{max} was detected ($P > 0.05$; Fig. 2c). In terms of the degree of deformation at breaking, both Si and cellulose were negatively correlated with ε_{max} ($P < 0.05$ and < 0.001; Fig. 2e,f). Similar analyses for hemicellulose and lignin did not yield significant trends except for a negative correlation between σ_{max} and hemicellulose concentration (Fig. S4).

Discussion

Our prediction that Si should make leaves stiffer and more brittle was supported, regardless of whether we simultaneously considered the tissue density effect or not (Fig. 2; Tables 2, 3). We also explored how Si, cellulose, hemicellulose, and lignin contributed to the mechanical properties of the leaf lamina. Silicon contributed to E but not σ_{max}, while cellulose enhanced both E and σ_{max} (Fig. 2; Tables 2, 3). Thus, Si cannot substitute for cellulose as a material to help a leaf resist breaking forces, even though it helps lamina stiffen to hold the leaf at an optimal angle. On the other hand, somewhat surprisingly, we did not detect the effect of lignin on leaf mechanical properties (Fig. S4; Tables 2, 3). We found neither significant correlations between Si concentration and cell wall component concentrations that would indicate a trade-off between Si and cell wall components nor correlations between tissue density and concentrations of Si and cell wall components across the species studied (Table 2; Figs S1, S2). These results were similar to the analysis of 197 tropical tree species (Westbrook *et al.*, 2011, and unpublished data of the same authors on Si) but differed from previous studies on nonwoody species (e.g. Klotzbücher *et al.*, 2018; de Tombeur *et al.*, 2022).

The differences in the effects of Si vs cellulose on the mechanical properties may be summarized in a conceptual diagram (Fig. 3). Silicon increases lamina stiffness but not strength, as Si reduces lamina extensibility (Fig. 3a). On the other hand, cellulose increases both stiffness and strength even though cellulose reduces lamina extensibility to a certain extent (Fig. 3b). As shown in Fig. 3a, the tensile work (i.e. the area under the stress–strain curve in the figure, mJ mm^{-2} for a unit length of test strip) should decrease with Si concentration if Si decreases lamina extensibility without increasing tensile strength. The support for this prediction was marginal (negative correlation at $P = 0.08$), but this idea may deserve further analysis. The negative correlation between the tensile work to fracture and Si concentration suggests the overall brittleness of Si-rich leaves. By contrast, cellulose concentration did not correlate with the tensile work to tear across species studied ($P = 0.15$, data not shown), supporting the hypothetical relationship shown in Fig. 3b.

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Table 2 Pairwise correlations among leaf mechanical properties, tissue density, and chemical traits across 33 study species.

	E	σ_{max}	ε_{max}	Tissue density	Si	Cellulose	Hemicellulose	Lignin
E								
σ_{max}	***0.82***							
ε_{max}	***−0.88***	***−0.52***						
Tissue density	***0.69***	***0.69***	***−0.56***					
Si	**0.53**	0.34	**−0.53**	0.29				
Cellulose	**0.52**	*0.39*	**−0.52**	0.07	0.30			
Hemicellulose	−0.24	*−0.37*	0.09	−0.07	−0.15	−0.02		
Lignin	0.07	0.14	0.05	−0.11	−0.02	0.17	*−0.41*	

Cellulose, cellulose concentration (%); E, Young's modulus of elasticity (N mm^{-2}); hemicellulose, hemicellulose concentration (%); lignin, lignin concentration (%); Si, Si concentration (%); tissue density, the dry weight of the lamina per unit volume (g cm^{-3}); σ_{max}, maximum stress (N mm^{-2}); ε_{max}, maximum strain (%). All variables, except tissue density, were $\log_{10}$ transformed before the analysis to achieve a normal distribution. The significance of correlations is indicated by bold italic ($P < 0.001$), bold nonitalic ($P < 0.01$), and italic ($P < 0.05$).

Table 3 Coefficients and P-values of the best model which predict leaf mechanical properties (Young's modulus of elasticity (E, N mm^{-2}), the tensile strength (σ_{max}, N mm^{-2}), and the maximum strain (ε_{max}, %)) with tissue density (g cm^{-3}) and the concentrations of Si and cell wall components (%).

	Tissue density		Si		Cellulose		Hemicellulose		Lignin	
Responsive values	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
E	2.74	< 0.001	0.18	< 0.05	0.76	< 0.05	−0.49	ns	–	ns
σ_{max}	1.29	< 0.001	–	ns	0.27	< 0.01	−0.53	< 0.01	–	ns
ε_{max}	−1.27	< 0.001	−0.14	< 0.05	−0.54	< 0.01	–	ns	–	ns

All variables, except tissue density, were $\log_{10}$ transformed before the analysis to achieve a normal distribution.

While Si has been hypothesized to work as a cheaper substitute for C-based cell wall components for a long time (e.g. Raven, 1983; Cooke & Leishman, 2011), we found that Si cannot fully substitute cellulose in terms of mechanical properties. Si might help lamina resist deformation but does not increase the resistance against breakage. Because lamina strength and toughness are required to keep a leaf alive for a long time (Wright & Cannon, 2001; Kitajima *et al.*, 2012), Si might not be a suitable material for species with long leaf lifespans. In addition, the negligibly low Si concentrations in leaf veins reported in bananas (Henriet *et al.*, 2006) and eudicot trees (Kajino & Kitajima, 2023) and the sparse deposition of Si in vascular bundles observed in dwarf bamboos (Motomura *et al.*, 2004) also suggest that the function of Si to support leaves is somewhat limited. Because leaf veins, which primarily support the leaf, should be strong and elastic, brittleness associated with Si deposition might be undesirable for optimizing the function of leaf veins.

A trade-off between cheap-and-brittle vs. costly-but-durable could be key to understanding the selective pressures for and against Si accumulation. Using Si enables plants to increase lamina stiffness at a given cellulose concentration (Table 3), suggesting that plants can support their leaves with lower energy costs by using Si. On the other hand, the brittleness associated with Si-rich leaves itself could be disadvantageous when a long leaf lifespan is required. The longer the leaf remains, the greater the chance that it experiences gusts and storms with destructive forces. In such events, leaves need to flutter without breaking, so species with a long leaf lifespan might require not only lamina strength but also some lamina elasticity (lower brittleness). In addition, as we mentioned above, the reduction in elasticity for a given strength (Fig. 3a) must decrease the work to tear. Whereas many studies have examined the relationships of leaf lifespan with mechanical strength or toughness (e.g. Onoda *et al.*, 2011; Kitajima *et al.*, 2012; He *et al.*, 2019), few have considered lamina brittleness. This trade-off between stiffness and brittleness associated with Si is a new kind of trade-off that has not been quantified in published studies. Still, we should be careful when we consider how these trade-offs relate to the frequency and intensity of destructive forces, as leaf Si concentration correlates positively with wind speed across Chinese herbaceous communities (Song *et al.*, 2020), suggesting that Si accumulation can be adaptive under strong winds.

Others have also proposed potential disadvantages associated with Si accumulation in leaves. De Tombeur *et al.* (2021, 2022) proposed that the metabolic cost to absorb Si could be higher under low Si availability than often assumed. Si accumulation may interfere with certain physiological processes, such as photosynthesis (e.g. Motomura *et al.*, 2008) or water transportation (Cooke & Carey, 2023), but there have been no conclusive tests of these possibilities. Another potential disadvantage is that Si-rich tissues can be heavier and more difficult to support as the density of SiO_2 is higher than that of organic matter (Raven, 1983). Indeed, de Tombeur *et al.* (2022) found that species with Si-rich leaves tended to show high tissue density. However, to what extent such an increase in tissue density makes the leaves more difficult to support has not been tested. Hence, our

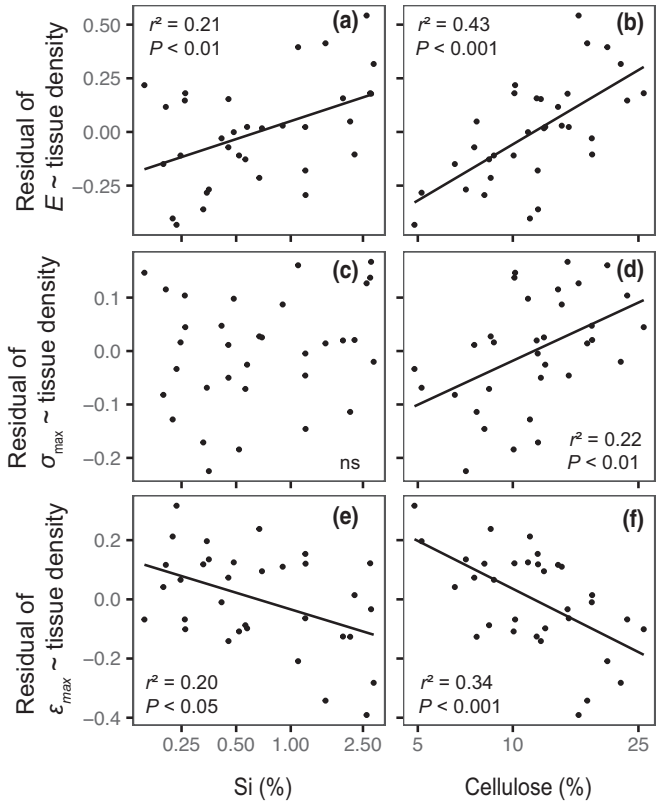

Fig. 2 Relationship of silicon and cellulose concentrations with the residuals of the regressions of Young's modulus of elasticity (E) (a, b), the tensile strength of the lamina (σ_{max}) (c, d), and the maximum strain (ε_{max}) (e, f) with tissue density of the lamina across the 33 study species.

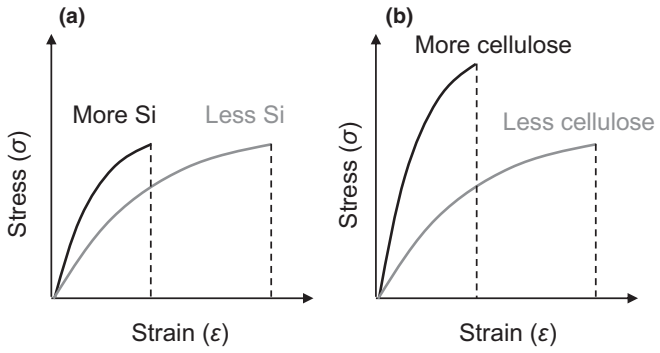

Fig. 3 Conceptual diagrams of the contributions of silicon (Si) (a) and cellulose (b) to the stress–strain curve of leaf lamina, summarizing the results of this study. More Si in leaves increases the modulus of elasticity (E, the initial slope of the stress–strain curve), with no change in the maximum stress (σ_{max}) but reduced maximum strain (ε_{max}), resulting in less area under the curve (the work to fracture). By contrast, more cellulose in leaves increases both E and σ_{max}, with a similar area under the curve.

study focusing on biomechanical properties is the first to demonstrate a potential disadvantage associated with accumulating Si in leaves. One caveat is that we used deciduous woody species with a narrow range of leaf lifespans to focus on the relationship between leaf mechanical properties and Si concentration. Studies that compare leaf mechanical properties and Si concentration across species with a wider range of leaf lifespans (e.g. evergreen and deciduous woody species) should be conducted in the future to understand how leaf Si concentration relates to leaf lifespan via leaf mechanical properties.

Unlike cellulose or Si, lignin concentration did not correlate with the mechanical properties across the 33 species tested (Fig. S4; Tables 2, 3). This may be surprising because 'lignification' gives an impression of stiff and strong materials. On the other hand, our results were consistent with findings from a cross-species comparison of leaves by Kitajima *et al.* (2012, 2016) who found that cellulose, but not lignin, contributes to leaf fracture toughness. Similarly, Kurokawa & Nakashizuka (2008) found that leaf lignin concentration does not correlate with the force to punch the lamina across species. In addition, a study in horsetail (Yamanaka *et al.*, 2012) suggests that lignin does not contribute to biomechanical support while Si does, using a biomechanical simulation. As lignin is a compression-resistant material, other mechanical tests, such as a compression test or a bending test, might be able to detect the contribution of lignin to mechanical supports. Indeed, seedling stems of the species with greater stem lignin concentrations had a higher modulus of elasticity measured by a bending test (Alvarez-Clare & Kitajima, 2007).

In the current study, we analyzed chemical traits as bulk concentrations. However, leaf mechanical properties should also be affected by how cell walls of different chemical properties are arranged within the leaf (e.g. Onoda *et al.*, 2015). Similarly, Hodson & Guppy (2022) argued the importance of considering the specificity of Si deposits in plant tissues and cells to understand the function of Si. A recent study by de Tombeur *et al.* (2025) reports that Si deposits mainly in the cells where phenolics do not accumulate within the epidermis tissues of sedge plants. However, the ecological significance of Si distribution in plant tissue is still unclear. Hence, future studies should address how the three-dimensional distribution of Si and cell wall components within the leaf affect mechanical properties and ecological differences.

Conclusion

This study demonstrated for the first time that leaf Si increases lamina stiffness but not strength across broad-leaved tree species. Overall, Si and cellulose contribute to lamina stiffness in an additive manner to tissue density. Unlike cellulose, which increases both stiffness and strength, Si might not be suitable to construct leaves with a long lifespan because Si reduces the lamina extensibility without increasing the lamina strength. These results would help us to understand the selective pressures for and against Si accumulation in broad-leaved tree leaves with short and long leaf lifespans.

Acknowledgements

We appreciate the Kyoto University Botanical Garden and the Kitashirakawa Experimental Station of Kyoto University for

permission to harvest leaf samples. We also thank Dr. Natsuki Komada for species identification and Dr. Ryosuke Nakamura for valuable comments on the draft of the manuscript. This study is partly supported by JSPS KAKENHI no. 19H05365 to YO.

Competing interests

None declared.

Author contributions

HK, YO and KK conceived the ideas and designed the methodology. HK conducted the field survey, mechanical test, chemical analysis, and data analysis, and wrote the first manuscript. All authors reviewed, revised, and approved the article.

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Data availability

Data are available in Tables 1 and S1.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Relationship of the concentrations of silicon and cell wall components with tissue density of the lamina across the 33 species studied.

Fig. S2 Relationship among concentrations of silicon and cell wall components.

Fig. S3 The result of the principal component analysis.

Fig. S4 Relationship between leaf mechanical properties and concentrations of hemicellulose and lignin.

Table S1 Mean ± SD of leaf mass per area, lamina thickness, and cell wall concentrations.

Table S2 The percentage of variances of traits that were explained by interspecific variation.

Table S3 The loadings of each trait in the principal component analysis.

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