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RESEARCH PAPER

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Association of leaf silicon content with chronic wind exposure across and within herbaceous plant species

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Abstract

Aim: High foliar silicon (henceforth Si) concentration protects plant tissues against herbivory, but protection against several abiotic stressors has also been proposed, although the adaptive significance of these functions is still being debated. We aimed to explore the potential relationships between foliar Si content and chronic wind exposure across a large scale and multiple species and to analyse an overlooked alternative or complementary function of silicon in leaves: mechanical protection against wind.

Location: Mainland China.

Time period: From July to September during 2012–2014.

Major taxa studied: Two hundred and eighty-two vascular plant species in predominantly herbaceous communities.

Methods: We compiled a dataset for leaf silicon concentration ([Si]) across 27 sites and 153 herbaceous plots within the major climate zones of China. We hypothesized that evolutionary lineages that generally have high [Si] should show positive relationships between leaf [Si] and mean annual wind speed.

Results: Within major families with generally high [Si] (especially grasses, sedges and composites), leaf [Si] exhibits a consistently positive correlation with mean wind speed among species across China. For the seven widespread monocot species with high leaf [Si], including the globally distributed common reed (*Phragmites australis*), intraspecific variation in leaf [Si] exhibits the same consistent positive correlation with mean wind speed.

Main conclusions: Our findings suggest that high leaf [Si] is likely to have widespread adaptive value for wind exposure of leaves, at least in several very widespread families and species of herbaceous plants. Damage from wind is a danger for plants in many ecosystems, hence these findings are of global significance and indicate that further research into large-scale variation of leaf Si and mechanical traits in relationship to wind exposure is likely to be illuminating.

KEYWORDS

leaf functional traits, mechanical protection, phylogeny, silica, wind speed, wind stress

Yao-Bin Song and Yu-Kun Hu contributed equally to this work.

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1 | INTRODUCTION

Silicon is among the most common soil elements on Earth (Sommer, Kaczorek, Kuzyakov, & Breuer, 2006) and its biogeochemical cycling is considered important for the functioning of ecosystems worldwide (Blecker, McCulley, Chadwick, & Kelly, 2006; Carey & Fulweiler, 2012; Cooke, DeGabriel, & Hartley, 2016; Coskun et al., 2019; Katz, 2019; Ma & Takahashi, 2002; Schaller et al., 2018; Street-Perrott & Barker, 2008). The annual fixation of biogenic silica ranges from 60 to 200 Tmol/year in global Si cycling (Conley, 2002) and from 55 to 113 Tmol/year in the terrestrial biosphere (Carey & Fulweiler, 2012). Rivers transport soluble silicic compounds from weathering or biogenic processes to the oceans, which could be used in marine ecosystems (Street-Perrott & Barker, 2008). Furthermore, the silicate weathering process is an important sink for atmospheric CO_2 (Struyf, Smis, Van Damme, Meire, & Conley, 2009), and the growth of diatoms could assimilate dissolved CO_2 in oceans (Tréguer & Pondaven, 2000). Consequently, silicon biogeochemical cycling could interact with global carbon cycling, which might have a large impact on the global climate (Struyf et al., 2009).

A key aspect of Si cycling is that significant amounts of Si are taken up by plants from the soil and built into their tissues, including leaf tissues (Cooke et al., 2016; Strömberg, Di Stilio, & Song, 2016). Silicon in plants has been found to provide resistance to many adverse biotic and/or abiotic environmental conditions, including, for example, nutrient deficiency, drought and toxic metal stress, pathogen intrusion, antiherbivory and mechanical stress (Cooke & Leishman, 2011; Coskun et al., 2019; Frew, Weston, Reynolds, & Gurr, 2018; Guntzer, Keller, & Meunier, 2012; Strömberg et al., 2016). The common view has been that the main function of foliar Si accretions in solid form (e.g., phytoliths) is to protect plant tissues from herbivory (Cooke et al., 2016; Epstein, 1994; Hartley & DeGabriel, 2016; Hartley, Fitt, McLarnon, & Wade, 2015), especially from being eaten by (mostly mammalian) vertebrates (Massey & Hartley, 2006; Massey, Massey, Ennos, & Hartley, 2009; Strömberg et al., 2016; Teaford, Lucas, Ungar, & Glander, 2006; Wieczorek, Zub, Szafrańska, Książek, & Konarzewski, 2015) or invertebrates (Garbuzov, Reidinger, & Hartley, 2011; Hunt, Dean, Webster, Johnson, & Ennos, 2008; Johnson et al., 2019; Massey & Hartley, 2009; Reynolds, Keeping, & Meyer, 2009; Ryalls, Hartley, & Johnson, 2017; Soininen, Bråthen, Jusdado, Reidinger, & Hartley, 2013), and to act as a potentially cheap alternative to cellulose or lignin (Cooke & Leishman, 2011; Raven, 1983; Schoelynck et al., 2010). Silicon is even thought to have played a central role in the co-evolution of grasses and their mammalian grazers, which had to evolve teeth that could withstand chronic erosion by foliar phytoliths, although this role is still under active debate (Calandra, Zub, Szafrańska, Zalewski, & Merceron, 2016; Hartley & DeGabriel, 2016; Strömberg et al., 2016). However, horsetails (Equisetopsida), which generally have a very high tissue Si concentration ([Si]; in milligrams per gram dry weight; Hodson, White, Mead, & Broadley, 2005), are known to have been abundant as early as the Carboniferous (Trembath-Reichert, Wilson, McGlynn, & Fischer, 2015), when herbivorous vertebrates had hardly evolved or not yet evolved (Sues, 2000). Limited available data have shown that several other pteridophyte families within Pteropsida (true ferns), another predominant clade in the Carboniferous, also have high foliar Si concentrations compared with seed plants (Trembath-Reichert et al., 2015). Thus, it is not unthinkable that high [Si] in extant pteridophytes is an evolutionary legacy of high [Si] of their carboniferous ancestors.

This then raises the question of whether high tissue [Si] is, at least in some lineages, an adaptation (i.e., exaptation) or phenotypic response to protect against other physical forces rather than solely being a direct adaptation (Cooke & Leishman, 2011) by plants to defend themselves against herbivory. As mentioned above, such adaptations may involve physical protection against abiotic stressors, such as mechanical forces; for example, preferentially silicified fibres in grasses and sclereids in eudicotyledonous tree leaves (Cooke et al., 2016; Strömberg et al., 2016). However, compared with the growing body of evidence in support of the adaptive significance of high foliar [Si] as an anti-herbivore defence, especially in grasses (Schoelynck & Struyf, 2016; Strömberg et al., 2016), empirical evidence for parallel or alternative functions of Si in fortifying plant tissues against abiotic stressors is rare, even rarer in natural ecosystems and across multiple species at a large scale (Epstein, 1999). However, some empirical and experimental evidence has shown that application of Si could enhance the strength of the rice cell wall, consequently improving the lodging resistance of stems and yield (Dakora & Nelwamondo, 2003; Isa et al., 2010; Kashiwagi & Ishimaru, 2004; Liang et al., 2013; Ma, 2004; Ma & Takahashi, 2002; Ma & Yamaji, 2006; Savant, Snyder, & Datnoff, 1996) or mechanical strength of leaves (e.g., erectness; Epstein, 1999; Ma & Takahashi, 1993; Ma & Yamaji, 2006; Yoshida, Navasero, & Ramirez, 1969) of some crops (e.g., rice) in managed ecosystems. A possible role of leaf Si for protection against wind or wave stress was mentioned for emergent macrophytes (Schoelynck & Struyf, 2016) and tidal wetland plants (Sloey & Hester, 2018), but this link with wind has, to our knowledge, not been tested outside agricultural systems and certainly not in natural ecosystems on a large scale. Given that chronic wind stress can affect plant growth, morphology and physiology within the lifetime of a plant (Gardiner, Berry, & Moulia, 2016; Grace, 1977; Vogel, 2009) or on an evolutionary time-scale (Niklas, 1998), we predict selection for high tissue [Si] associated with windy environments, that is, well above a minimum concentration needed for physiological function in the absence of wind. However, only species/families with the capacity to take up sufficient Si to allocate substantial amounts for physical protection may be expected to use silicon in this function, whereas non-accumulators would adopt other strategies to cope with wind stress, hence a relationship between wind stress and Si might be evident only in high-accumulating species/families. This led us to propose the following hypothesis: Plant families that generally have high [Si] will show positive relationships between leaf [Si] and mean annual wind speed as a key variable representing chronic wind stress to plants (Royer, McElwain, Adams, & Wilf, 2008; Wooldridge, Musselman, Sommerfeld, Fox, & Connell, 1996), both across and within plant species.

Mainland China, at >9.6 million km^2, spans a range in latitude of 20.26° to 53.55°N and longitude of 73.67° to 135.04°E, which includes several climate zones. Diverse levels of windiness (measured as average windspeed) are present (ranging from 1 to 12 m/s) and well

characterized through a network of meteorological stations in China. Together with a diverse flora of *c*. 350,000 species (*c*. 312 families) of vascular plants (Lu & He, 2017; Wu, Raven, & Hong, 2013) (including some high Si families), the varied and well-characterized climate variables make China an ideal country in which to test the hypothesis of a relationship between leaf [Si] and wind stress. A large survey involving the collection of leaves of many populations and species from across China, to assess variation in plant traits between terrestrial and wetland habitats (currently unpublished), provided samples with the appropriate species diversity and range of environmental conditions to test the hypothesis in this study. Leaf mass per area (LMA) broadly reflects carbon-based investments in foliar defense (Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Wright & Cannon, 2001), bigger leaves are expected to be more vulnerable to wind stress for biomechanical reasons (Niklas, 1996), and the amount of plant availability of Si in the soil affects plant uptake (Garbuzov et al., 2011; Ma & Yamaji, 2006); hence, these three factors must be taken into account, because they might confound or mask any relationship between wind stress and Si accumulation.

2 | MATERIALS AND METHODS

2.1 | Sampling

In total, 27 sites of nearly even distribution across Mainland China were selected, with geographical distribution ranging by >22° in latitude, 37° in longitude and 4,700 m in elevation, that is, from 24.92° to 46.31°N, from 83.33° to 123.03°E and from 3 to 4,778 m, respectively (Figure 1). This sampling area occupied most of the

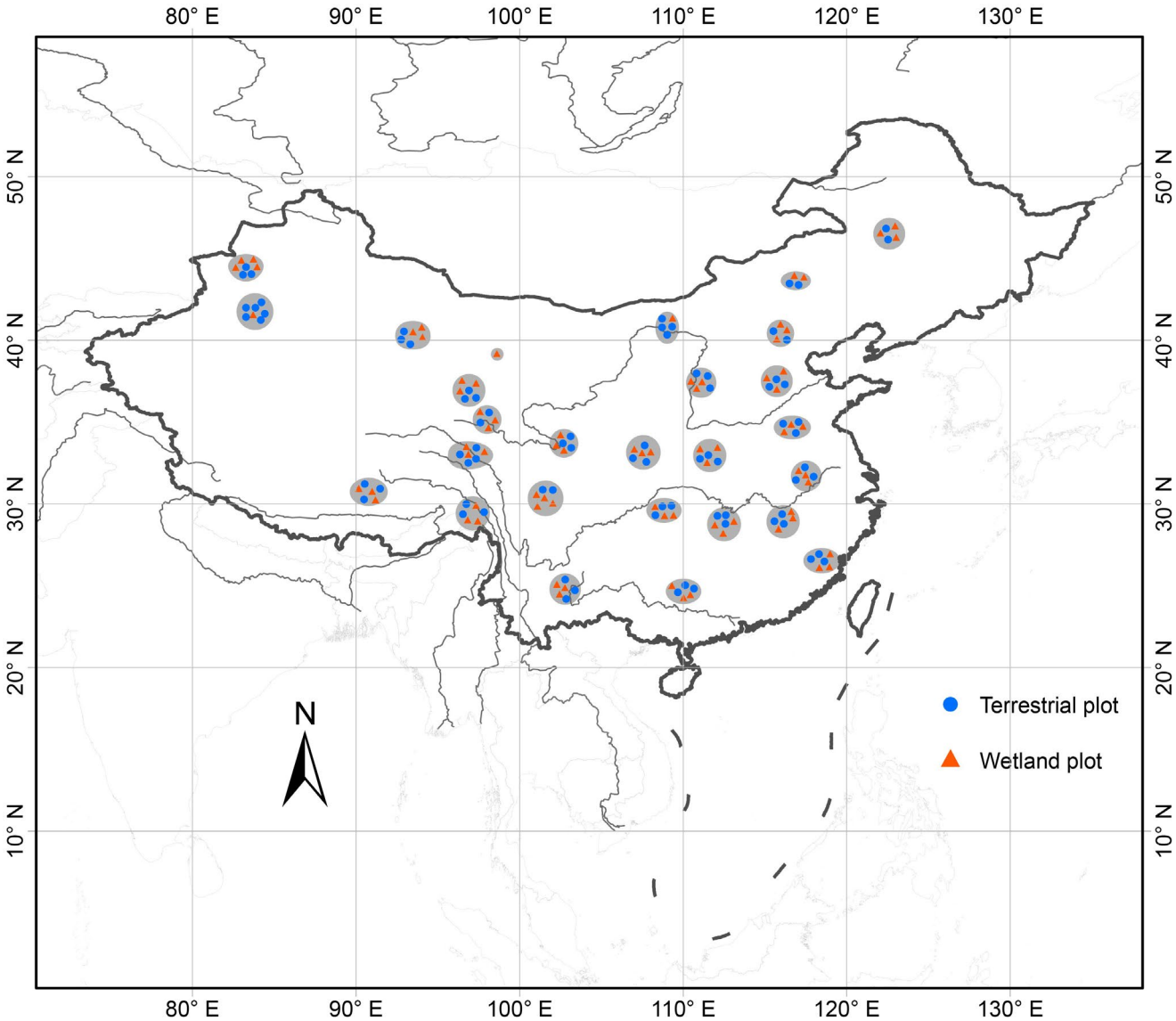

FIGURE 1 The geographical locations of the total of 27 sampling sites [grey shaded ares, including 75 terrestrial (blue circles) and 78 wetland plots (red triangles)] of this study across China. Please note that the locations of each plot do not represent the exact geographical coordinates [Colour figure can be viewed at wileyonlinelibrary.com]

climatic space of China from the subtropical to the cold-temperate zone. Their mean annual temperature (MAT) ranged from −4.6 to 19.8°C, mean annual precipitation (MAP) from 26 to 1,811 mm, and mean annual wind speed from 1.0 to 5.6 m/s. In each site, we selected one wetland and a paired terrestrial sub-site (generally within 10–30 km distance); in each sub-site, with few exceptions, we set up three 20 m × 20 m plots for community composition survey and leaf sampling. In closed woody canopies, the wind speed experienced by leaves may not represent that measured nearby in open terrain and thus cannot be derived from meteorological stations (see Measurement); therefore, we tried to exclude the effects of major human disturbances and woody plants. The selected plots generally hosted natural or semi-natural, herbaceous plant communities. Altogether, 153 plots (78 in wetlands and 75 terrestrial) were investigated. Within each plot, we focused on only adult dominant and subordinate species based on their relative coverage. For each target species, we randomly selected three to 10 individuals, depending on their abundance; we sampled three healthy, fully expanded and hardened leaves from each individual and stored them cool in sealed plastic bags until measurement (Pérez-Harguindeguy et al., 2013; for further details of sampling, see Hu et al., 2015). Three soil samples were randomly collected from 0–15 cm depth in each plot. Soil samples were air dried and passed through a 1 mm sieve before measurement.

2.2 | Leaf measurements and climate data

In wetland plots, truly aquatic species (submerged or floating-leaf plants) were excluded from our trait analysis, and for riparian species only those with most foliage emerging above the water level (i.e., helophytes) were measured. Submerged or floating-leaf plants are exposed more to the water current or waves, and they would suffer less wind stress compared with emergent macrophytes. Leaf samples were scanned while still fresh with a photographic scanner (CanoScan LiDE210; Canon, Japan), oven dried at 70°C for 72 hr and weighed. The leaf area (LA; in square millimetres) of each sample was derived from the scanned photograph with ImageJ software (http://imagej.nih.gov/ij/) (Hu et al., 2015). Leaf mass per area (LMA; in grams per square metre) was calculated as the ratio of dry mass to fresh leaf area for each sample. Leaf silicon concentration [Si] was measured with the molybdenum blue colorimetric determination method according to Wang, Wang, Zhang, and Mao (2004). Briefly, 0.3 g dried and ground leaf samples were combusted in a Muffle furnace at 550°C for 4 hr before pre-ashing at 300°C for 3 hr. The ashed samples were dissolved in 50 mL of 0.08 mol/L H_2SO_4 with 2 mL of (40%) hydrofluoric acid solution. After adding 0.08 mol/L H_2SO_4 with 2% $(NH_4)_6Mo_7O_{24}.4H_2O$ (v:v, 1:1), tartaric acid and ascorbic acid solution sequentially to color at 25°C, the mixed solution was analysed colorimetrically at 811 nm with a spectrophotometer. The standard curve was validated with a silica standard solution (Sinopharm Chemical Reagent Co., Ltd). Results were expressed as the foliar silicon concentration on a dry mass basis (in milligrams per gram). The available silicon concentration in soil (in milligrams per kilogram) was determined by the same molybdenum blue colorimetric determination method with citric acid extraction (Bao, 2005).

The MAT and MAP were obtained from the WorldClim database (http://www.worldclim.org/) according to geographical coordinates of each site. The mean annual wind speed was accessed from the dataset of daily surface observation values in individual years (1981–2010) in China (http://data.cma.cn/en/) based on the nearest meteorological station to each of our studied sites. Although we assumed mean wind speed to be the most meaningful variable related to chronic wind stress to plants, key to our hypothesis (see Introduction), we also collected data for maximum wind speed from the same weather stations, because particularly strong wind speed can also be damaging to plants (Grace, 1977). However, given that we did not find any strong or consistent relationships between maximum wind speed and leaf [Si] (results not shown here), we do not refer to this variable below.

2.3 | Data analysis

The phylogeny was obtained from the online program PHYLOMATIC (Webb & Donoghue, 2005) and based on the Angiosperm Phylogeny Group III classification (Zanne et al., 2014), and branch-length estimates were included using the program PHYLOCOM v.4.1 (Webb, Ackerly, & Kembel, 2008). Visualization of the phylogeny and leaf [Si] plotted onto it was performed with the GGTREE package (Yu, Smith, Zhu, Guan, & Lam, 2017) using the program R (R Development Core Team, 2016), v.3.2.4. To approach normal distributions, leaf [Si] was [$\log_{10}$ + 1]-transformed, whereas LMA and leaf area were $\log_{10}$-transformed, and soil available silicon concentration was square-root transformed before analysis. We used a *t*-test to examine the differences in [Si] between the eudicots and monocots; the sample size for pteridophytes (i.e., *Equisetum*) was too small for any statistical analysis. Pearson's correlation coefficients were calculated to examine the relationships between leaf [Si] and mean annual wind speed, between LMA and mean annual wind speed and between LA and mean annual wind speed, both at the level of species within families and for populations within species with the condition that sampling size is ≥ 20. We also checked relationships between MAT, MAP, wind speed, soil available silicon concentrations and leaf [Si], and relationships between LMA and leaf [Si], between LMA and mean annual wind speed, between LA and leaf [Si] and between LA and mean annual wind speed for all species, family and species level for sampling size of ≥ 20, with Pearson's correlation tests. Silicon accumulators were previously defined as plants with Si levels > 10 mg/g (Ma, Miyake, & Takahashi, 2001; Ma & Takahashi, 2002). We doubled this threshold for the mean [Si] of given taxa (i.e., setting it at 20 mg/g), in order to ensure that most values within the range of each taxon would be above the literature-based accumulator level of 10 mg/g. For the data with sampling size ≥ 20, we calculated pooled correlation coefficients

(Fisher's *z* transformation) of accumulators (i.e., leaf [Si]>20 mg/g) and non-accumulators (i.e., leaf [Si] ≤20 mg/g) with the *meta* package in R (Schwarzer, 2007).

For the four families [i.e., Poaceae, Cyperaceae, Rosaceae and Asteraceae (composites)] and four species (*Cynodon dactylon*, *Phragmites australis*, *Poa annua* and *Xanthium sibiricum*) identified as accumulators (i.e., >20 mg/g), and with sufficient numbers of replicates for analysis, general linear regression analysis was used to describe the relationships between leaf [Si] and mean annual wind speed. To exclude potential extreme data effects, we also analysed the relationships between leaf [Si] and mean annual wind speed without the data points at the extremely windy sites (>5 m/s). We used SPSS v.17.0 software (SPSS, Chicago, IL, USA) for these analyses.

3 | RESULTS

The mean leaf [Si] varied greatly among species (Figure 2), ranging from 0.96 (*Ludwigia adscendens*) to 171.64 mg/g (*Equisetum palustre*). The three *Equisetum* species had much higher mean leaf [Si] than the mean for eudicot species or monocot species (Figure 2). Within the two angiosperm clades, monocot species on average

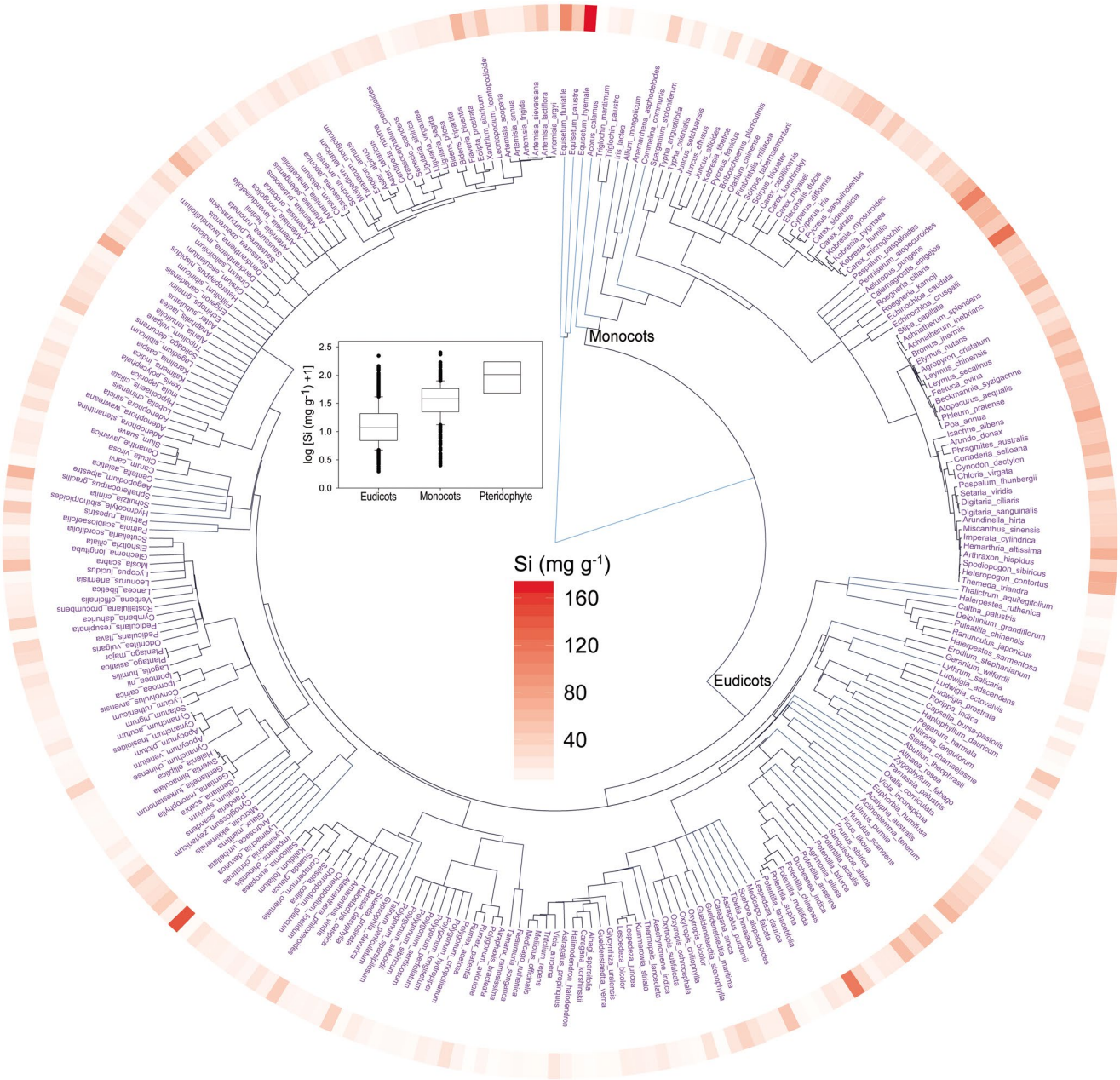

FIGURE 2 Phylogenetic tree of 282 vascular plant species and their mean leaf [Si] (in milligrams per gram). The denser the red shading of the outer circle, the higher the leaf [Si]. The phylogeny is based on the Angiosperm Phylogeny Group III classification (Zanne et al., 2014). The inset shows the logarithm of mean leaf [Si] for the three main clades [i.e., eudicots, monocots and pteridophytes (specifically, horsetails)] [Colour figure can be viewed at wileyonlinelibrary.com]

had much higher leaf [Si] than eudicot species (t_{1479} = 22.317, p < .001, for all samples; t_{277} = 7.402, p < .001, using species means; see Figure 2). The intraspecific variation in leaf [Si] among plots across China was substantial. For example, the coefficient of variation (CV) of leaf [Si] was high in most sampled species, that is, accumulators: *Cynodon dactylon*, *Poa annua* and *Phragmites australis* were 87.7% (n = 26), 90.0% (n = 38) and 81.5% (n = 57), respectively; non-accumulators: *Polygonum hydropiper*, *Potentilla anserine* and *Trifolium vulgare* were 74.0% (n = 35), 94.8% (n = 38) and 101.0% (n = 22), respectively.

Overall, for accumulators and non-accumulators together, MAT (r = 0.027, p = .229, n = 1,484) MAP (r = −0.003, p = .917, n = 1,484), soil available [Si] (r = 0.005, p = .849, n = 1,376) and mean annual wind speed (r = 0.011, p = .627, n = 1,484) were not correlated with leaf [Si] across sites in China, either at the family or at the species level (Supporting Information Figure S1). When accumulators and non-accumulators were separated, the leaf [Si] of accumulators exhibited a consistent significant positive correlation with mean wind speed both at the family (r_{pooled} = 0.2296, p = .002) and at the species (r_{pooled} = 0.3788, p < .001) level, whereas there were no significant relationships for non-accumulators at either the family (r_{pooled} = −0.0572, p = .353) or the species level (r_{pooled} = 0.0420, p = .613; Table 1). In contrast, the relationships of leaf [Si] with MAT, MAP or soil available [Si] were absent or inconsistent and, where significant, very weak compared with the relationships of [Si] with mean wind speed (Table 1), although there were some inconsistent and mostly weak significant r values within specific families and species for these relationships (Supporting Information Table S1). Leaf [Si] showed a significant but only very weak negative overall relationship to mean annual precipitation for accumulators at the family level (but not at the species level), whereas soil available [Si] showed a weak negative relationship with [Si] for non-accumulators at the family level and a weak positive trend for accumulators at the species level (Table 1). The overall positive relationships between leaf [Si] and mean wind speed for accumulators came about because of consistent positive relationships within all the individual accumulator families and species in the dataset (Table 1; Supporting Information Table S1). Indeed, three out of four individual accumulator families showed highly significant positive relationships between site mean wind speed and leaf [Si], with the highest correlation coefficients in the two monocot families, which also had the highest mean leaf [Si] values: Poaceae (grasses, mean leaf [Si] = 49.7 mg/g, Pearson's r = 0.321, p < .001) and Cyperaceae (sedges, mean leaf [Si] = 32.3 mg/g, r = 0.387, p < .001); see also Figure 3. Moreover, all seven accumulator species with sample size ≥ 20 across sites in China showed positive Pearson's correlation coefficients, ranging from 0.29 to 0.48, of which four were significant at p < .05 (Supporting Information Table S1; Figure 3).

Interestingly, leaf [Si] was unrelated to LMA across taxon levels and sites (Supporting Information Figure S2a), although LMA itself had a positive, albeit weak, relationship with mean wind speed (Supporting

TABLE 1 Pooled correlation coefficients [±95% confidence interval (CI)] between leaf traits {leaf [Si], leaf mass per area (LMA) and leaf area (LA)} and environmental factors {mean annual wind speed, mean annual temperature (MAT), mean annual precipitation (MAP) and soil [Si]} for accumulators (leaf [Si] > 20 mg/g) and non-accumulators (leaf [Si] < 20 mg/g) at the family and species levels

		Family level		Species level	
Comparison		Accumulators	Non-accumulators	Accumulators	Non-accumulators
Leaf [Si] versus mean annual wind speed	r	**.2296**	−.0572	**.3788**	.0420
	95% CI	**[.0850, .3648]**	[−.1761, .0634]	**[.2547, .4906]**	[−.1202, .2020]
	p-value	**.0020**	.3528	**< .0001**	.6128
LMA versus mean annual wind speed	r	**.1803**	.061	.0445	.0270
	95% CI	**[.1158, .2433]**	[−.1280, .2458]	[−.1269, .2132]	[−.1335, .1880]
	p-value	**< .0001**	.5282	.6122	.7462
LA versus mean annual wind speed	r	.0166	**−.2328**	.0411	**−.2277**
	95% CI	[−.0599, .0930]	**[−.3851, −.0681]**	[−.1029, .1834]	**[−.4061, .0327]**
	p-value	.6707	**.0059**	.5767	**.0225**
Leaf [Si] versus MAT	r	−.0072	−.0259	−.0793	.0415
	95% CI	[−.1493, .1352]	[−.1984, .1482]	[−.3197, .1707]	[−.2372, .3138]
	p-value	.9214	.7721	.5362	.7741
Leaf [Si] versus MAP	r	**−.1010**	.0950	−.1763	−.1467
	95% CI	**[−.1937, −.0064]**	[−.0430, .2295]	[−.3668, .0284]	[−.3675, .0898]
	p-value	**.0364**	.1769	.0910	.2233
Leaf [Si] versus soil [Si]	r	.1700	**−.1555**	.1703	−.0469
	95% CI	[−.0479, .3724]	**[−.2883, −.0168]**	[−.0030, .3336]	[−.2124, .1211]
	p-value	.1256	**.0282**	.0540	.5833

Note: Bold values indicate statistical significance at p < .05.

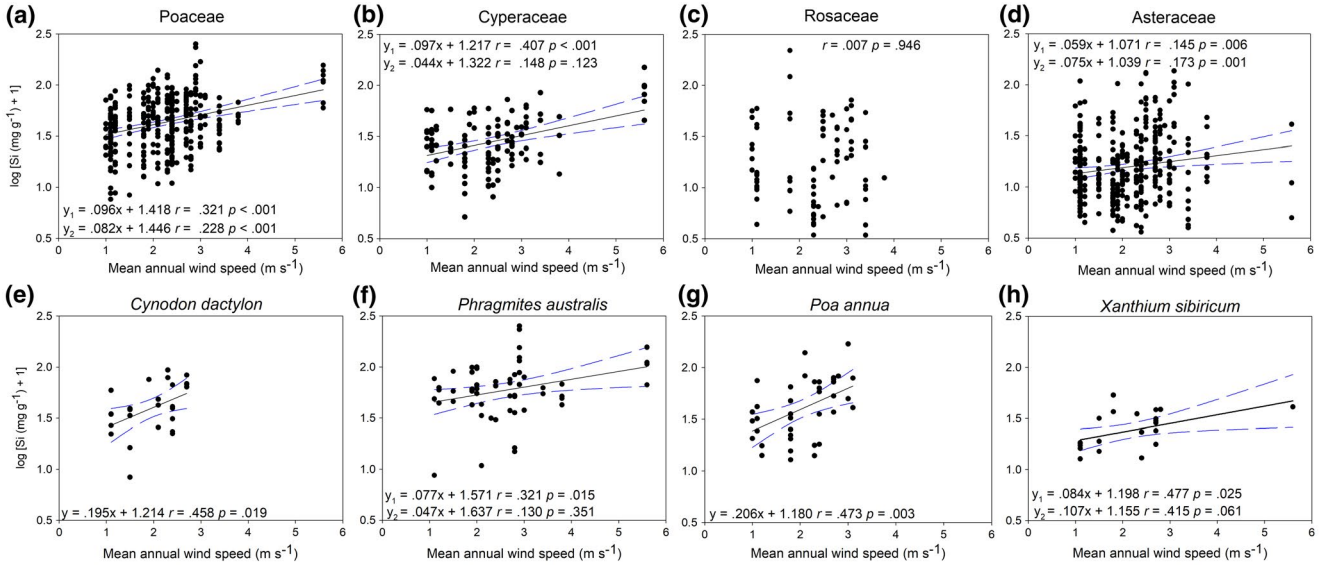

FIGURE 3 The relationship between leaf [Si] and mean annual wind speed. (a–d) Family level: (a) Poaceae, (b) Cyperaceae, (c) Rosaceae and (d) Asteraceae. (e–h) Species level: (e) *Cynodon dactylon*, (f) *Phragmites australis*, (g) *Poa annua* and (h) *Xanthium sibiricum*. Dashed lines show 95% confidence intervals around the regression line. In each panel, the upper equation represents the relationship across all data points, and the lower equation represents the relationship without the data points at the extremely windy (>5 m/s) sites [Colour figure can be viewed at wileyonlinelibrary.com]

Information Table S1; Figure S2b) for Si accumulators only at the family level (Table 1). The relationship between leaf [Si] and individual leaf area showed a virtually flat trend across species and sites (Supporting Information Figure S2c). However, although none of the other three families [Cyperaceae, Rosaceae and Asteraceae (composites)] showed a significant relationship between leaf [Si] and individual leaf area, Poaceae did, albeit a rather weak one (r = 0.133, p = .014). Within the species that had a positive relationship between leaf [Si] and mean wind speed, there was no consistent relationship between leaf [Si] and individual leaf area (*Cynodon dactylon*: r = −0.397, p = .044; *Phragmites australis*: r = 0.212, p = .113; *Poa annua*: r = 0.428, p = .007; and *Xanthium sibiricum*: r = −0.316, p = .152). Correspondingly, leaf area itself showed only a very weak, and negative, relationship with mean wind speed (Supporting Information Figure S2d), which might be attributable to some Si non-accumulators that showed a significantly negative relationship at the species level (Table 1; Supporting Information Table S1).

4 | DISCUSSION

In the present study, the consistent positive relationships between leaf [Si] and site mean annual wind speed, both across species within families and within plant species, for some plant groups, provides a strong indication of a potential new function of silicon in plant tissues. In addition, as hypothesized, these relationships were manifest only in taxa with higher mean leaf [Si]. Considering the weak relationships between leaf [Si] and MAT, MAP, mean annual wind speed or soil available [Si], we are confident that the consistent positive correlations between site mean annual wind speed and leaf [Si] within taxa with higher mean leaf [Si] reflect direct relationships rather than indirect relationships via confounding environmental variables. The mechanism underpinning this relationship might be attributable to higher transpiration rate caused by higher wind speed enhanced Si uptake (especially in wet environments) from the soil, leading to enhanced transportation and deposition of Si into leaves (Ma & Yamaji, 2006; Yoshida, Onishi, & Kitagishi, 1959). We also found that leaf [Si] was unrelated to LMA across taxon levels and sites, although LMA itself had a positive, albeit very weak, relationship with mean annual wind speed; LMA showed a positive correlation only with mean annual wind speed among accumulators at the family level. The LMA tends also to reflect protection against physical forces (Onoda et al., 2011), which is based on long-chain carbon-rich compounds, such as lignin and cellulose, deposited in cell walls (Poorter et al., 2009). Both lignin and Si are among the important structural compounds contributing to mechanical strength (Currie & Perry, 2007; Ma & Yamaji, 2006; Onoda et al., 2011). In a previous study, it was found that there was a negative correlation between the biogenic silica (BSi) concentration and the lignin concentration for wetland plants, but not for true aquatic plants (Schoelynck et al., 2010). However, it was also found that silicon could enhance the expression of the rice *CAD* gene, which could improve the accumulation of lignin and enhance the lodging resistance (Dorairaj, Ismail, Sinniah, & Tan, 2017). Overall, it seems that a high leaf [Si] and a high lignin concentration, as reflected here by LMA, could be alternative or complementary adaptive trait states in order to strengthen leaves as protection against physical damage. Direct comparison of leaf lignin and silicon concentrations across a large scale and multiple species would be an important next step in further studies.

The hypothesized positive relationship between leaf [Si] and individual leaf area, based on theoretical first principles of the mechanics of leverage, was not generally supported by our data,

alhough the leaf area of non-accumulators showed a negative trend (family level) or negative correlation (species level) with the mean annual wind speed (Table 1; Supporting Information Table S1). We speculate that the lack of a clear relationship between leaf [Si] and individual leaf area among accumulators can be attributed, at least in part, to the role of leaf petioles, which enable the entire leaf to bend and twist, thereby reducing the pressure of gravity (Cordero, Fetcher, & Voltzow, 2007; Ennos, Spatz, & Speck, 2000; Niklas, 1999), which should increase with leaf size. Related to this, it might be no coincidence that the families in which we find the strong relationships between leaf [Si] and mean annual wind speed (i.e., Poaceae and Cyperaceae) are the ones in which petioles do not occur. In families hosting species both with and without petioles, or with great variation in petiole form and function (Niklas, 1999), such variation might mask any contribution of leaf [Si] to mechanical protection against wind stress (Vogel, 2009). An alternative or complementary explanation for the lack of a clear relationship between leaf [Si] and individual leaf area, especially in dicot families, may be attributable to the important role of special leaf or foliage shapes for wind protection; for instance, the ability of individual leaves or leaf clusters to curl into cylinders (Vogel, 2009). At least for leaf clusters, such shapes have been reported within several dicot families (Vogel, 2009), but not in monocot families, such as Poaceae or Cyperaceae. Furthermore, such shapes also reduce transpiration owing to a decrease in exposure to wind, silicon uptake from the soil and silicon accumulation in leaves, which might be an adaptation to wind stress. Whether and how the investments of plants in petiole function or foliage shape versus leaf tissue reinforcement with silicon covary across plant families and within species across sites would be an important next step to elucidate further the role of leaf [Si] in wind protection.

We have demonstrated, across major climate zones, a consistent positive association of leaf silicon concentration with chronic wind exposure, both across and within species belonging to families that generally show stronger Si accumulation. Such a relationship suggests that further research to reveal the underlying mechanisms and wider ramifications would be valuable. Although this relationship is likely to reflect an adaptive value of leaf [Si] for wind exposure, our data cannot disentangle the extent to which it is the expression of genetic variation as a result of long-term evolutionary adaptation versus the phenotypic response of given species or populations to wind stress today. The fact that the relationship is seen in families from contrasting phylogenetic positions [e.g., monocots (grasses and sedges) versus eudicots (composites)] suggests that it has emerged repeatedly on a long evolutionary time-scale, based on its adaptive value. As implied above, we might even speculate that the well-established adaptive significance of leaf silicon as an anti-mammal herbivory defense (Massey & Hartley, 2006; Massey et al., 2009; Strömberg et al., 2016; Teaford et al., 2006; Wieczorek et al., 2015) is in some lineages an exaptation, with preadaptation to other physical forces, such as wind, already in place. In contrast, the strongest positive relationships are seen within monocot families, and here we also detect the strongest intraspecific associations between leaf [Si] and mean annual wind speed. This could indicate that high leaf [Si] reflects either genotypic variation among populations as an evolutionary response or a short-term phenotypic response to chronic wind stress, or both. The contribution of the phenotypic response of given species or genotypes to this positive relationship might be tested by growing plant populations experimentally at different wind speeds, and then comparing their leaf [Si] and fitness, or by using model plants or crops to elucidate the molecular, genetic and physiological mechanisms of such a relationship. Experiments in wind tunnels, for instance, would avoid the confounding effects of other abiotic or biotic factors that might also directly or indirectly influence foliar [Si] in outdoor experiments, such as reciprocal transplantation of plant populations among sites varying in windiness.

Another important development from our research would be to test whether the relationship we unveiled across herbaceous taxa is also seen among woody ones. On the one hand, we might expect a weaker relationship, if any, among shrubs and trees if mean annual wind speed data were derived from meteorological stations, as in our study, because in closed woody canopies the wind speed experienced by leaves may not represent that measured nearby in open terrain. On the other hand, among and within woody species, there might be a stronger contrast between wind exposure in plants growing in closed forest or shrubland canopies and plants growing in open land (e.g., savannah). At this stage, based on our findings, we can conclude that high leaf [Si] could be an adaptive functional trait for protection against chronic wind exposure of leaves, at least in several very widespread families and species of herbaceous plants.

4.1 | Conclusions

Our findings are of global significance, because chronic high wind speeds occur in many parts of the world, as do the plant families with high [Si], for which we show the consistent stronger positive relationships between leaf [Si] and mean annual wind speed across mainland China. Our findings also open up a new and important research agenda about, for instance: (a) the genetic basis versus phenotypic plasticity of strong Si accumulation in leaves in response to wind (warranting experimental study; e.g., in wind tunnels); (b) the possible trade-offs or coordination with other forms of leaf protection against chronic strong wind, such as cell walls reinforced with recalcitrant carbon-rich compounds, petiole presence and design, and foliage shape; and (c) possible application by selecting for the right genotypes of important and widely used plant species, such as the common reed (*Phragmites australis*), with respect to leaf mechanical strength.

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DATA AVAILABILITY STATEMENT

The data associated with this project are available for downloading from the Dryad Data Repository (https://doi.org/10.5061/dryad.gmsbcc2j6).

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BIOSKETCH

All authors are interested in the responses of plant functional traits along environmental gradients and their effects on environments.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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