RESEARCH ARTICLE

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Plasticity of plant silicon and nitrogen concentrations in response to water regimes varies across temperate grassland species

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Abstract

1. Temperate grasslands exhibit strong spatial and temporal variation in water regimes. Thus, grassland plants experience potentially stressful water regimes, which may influence their tissue silicon (Si) and nitrogen (N) concentrations. Plant Si and N concentrations play important ecological roles in temperate grasslands, for example, by influencing plant performance and herbivory, yet comparisons of species' responses to a broad range of water regimes, including drought, waterlogging and flooding, are lacking.

2. We conducted a mesocosm experiment with 10 temperate grassland species of two life-forms (grasses and forbs) exposed to four different soil water regimes (drought, a benign control, waterlogged and flooded conditions), and analysed their Si and N concentrations.

3. Grasses showed lower Si concentrations under drought and flooding compared to the benign control and the highest concentrations emerged under waterlogging. Overall, plant Si responses of grasses were more uniform, while in forbs, responses varied both in direction and magnitude across species. For N concentrations, all species and life-forms showed the highest concentrations under drought compared to the benign control, while half of the species exhibited decreasing concentrations under waterlogging and/or flooding. The water regimes, especially waterlogging and flooding, induced changes in species rankings of plant Si and N concentrations, with stronger shifts in forbs than in grasses.

4. Our results indicate that spatial and temporal variation of water regimes may influence plant Si and N concentrations in temperate grassland species. Plant Si

responses to water regimes might be highly species-specific in forbs but more similar in grasses, whereas plant N responses are likely to be relatively uniform across species and life-forms.

5. The strong plasticity in plant Si and N concentrations we observed might have pervasive consequences for ecological processes, such as herbivory.

1 | INTRODUCTION

Temperate grasslands are species rich and offer essential ecosystem services (Dengler et al., 2014; Gibson, 2009). They exhibit strong spatial and temporal variation in water availability, ranging from dry to flooded conditions (Silvertown et al., 2015). Both ends of the water gradient impose stress on plants: under drought, plant performance is limited by a lack of water while under waterlogging and flooding, plants can be limited by anoxic conditions (Silvertown et al., 2015). Thus, water availability influences plant physiology, including silicon (Si) and nitrogen (N) concentrations (Brightly et al., 2020; He & Dijkstra, 2014; Lambers & Oliveira, 2019), which, in turn, influence essential ecological processes such as herbivory (Descombes et al., 2020; Loranger et al., 2012; Singh et al., 2020).

In plants, Si accumulation can alleviate multiple stressors, including drought and herbivory (Cooke & Leishman, 2016; Singh et al., 2020; Thorne et al., 2020). Therefore, understanding how plant Si concentrations respond to environmental drivers and the generality of these responses is pivotal. Water availability can influence Si concentrations in temperate and tropical grasses as well as crops (Brightly et al., 2020; Quigley et al., 2017, 2020; Quigley & Anderson, 2014; Ryalls et al., 2018; Thorne et al., 2020 and references therein). However, results have been inconsistent, with positive (e.g. Quigley & Anderson, 2014; Ryalls et al., 2018), negative (e.g. Brightly et al., 2020) or no (e.g. Quigley & Anderson, 2014) effects of water availability on Si concentrations.

Grassland species vary tremendously in Si concentrations, with monocots (e.g. grasses) commonly showing higher concentrations than dicots (e.g. most forbs; Hodson et al., 2005; Klotz et al., 2021; Strömberg et al., 2016). Physiological mechanisms in roots govern plant Si uptake and contribute to Si plasticity. Plants with low Si concentrations, for example, many forbs, take up Si largely via passive diffusion, driven by the transpiration stream (Faisal et al., 2012; Mitani & Ma, 2005). Additionally, many species, including most grasses and some forbs, take up Si actively mediated by energy-dependent transporters (Deshmukh & Bélanger, 2016; Ma & Yamaji, 2015), leading to high plant Si concentrations. As transpiration, energy (ATP) production and protein synthesis (e.g. for Si transporters) function optimally under ample water and oxygen supply (Lambers & Oliveira, 2019), plant Si concentrations should be highest under benign, nonstressing water regimes, and reduced under drought, waterlogging and flooding. Potential indirect effects of water regimes on plant Si concentrations

via changes in soil Si availability may occur (Schaller et al., 2021), but should be minimal, because plant Si uptake and responses to plant-available Si are thought to be strongly constrained by physiological factors (Deshmukh & Bélanger, 2016; Faisal et al., 2012; Klotz et al., 2021). Furthermore, substantial differences in stomatal regulation (Bartlett et al., 2016) as well as in the physiology of active Si uptake across species and life-forms (Deshmukh & Bélanger, 2016) suggest that species vary in how their Si concentrations respond to water regimes.

The physiological and ecological role of plant N concentrations has received a lot of attention with respect to leaf economics, plant performance and herbivory in temperate grasslands (e.g. Aerts & Chapin, 1999; Belluau & Shipley, 2018; Loranger et al., 2012). Plant N concentrations can be strongly affected by soil water regimes (Araya et al., 2013; meta-analyses of drought effects on plant N concentrations in He & Dijkstra, 2014 and Sardans et al., 2017). However, the responses observed in previous studies vary widely, for example, effects of drought on plant N concentrations ranged from positive to negative (He & Dijkstra, 2014). Processes of plant N provisioning, including decomposition and mineralization of organic matter, as well as N transport to and uptake by the root, require ample water as well as oxygen supply and are partly governed by plant transpiration (Lambers & Oliveira, 2019; Oyewole et al., 2014). These processes are impaired by drought, waterlogging and flooding (Araya et al., 2013; Sanaullah et al., 2012; Yeung et al., 2019), suggesting plant N concentrations should be—as with Si—highest under benign, nonstressing water regimes. However, plants can acclimate to adverse water regimes by regulating N uptake and leakage (Aerts & Chapin, 1999; He & Dijkstra, 2014) and these responses may vary across plant species due to variation in the preferred sources of N, root anatomy as well as type and density of N transporters located in root membranes, but also due to variation in stomatal regulation (Aerts & Chapin, 1999; Bartlett et al., 2016; Lambers & Oliveira, 2019).

Plant Si and N are the plant nutrients that are probably most important for influencing insect herbivory in grasslands (Awmack & Leather, 2002; Descombes et al., 2020; Loranger et al., 2012; Massey et al., 2006). Generalist insect herbivores preferably feed on plants with high N concentrations (Loranger et al., 2012; Pérez-Harguindeguy et al., 2003) as insect performance is largely N limited (Awmack & Leather, 2002; Elser et al., 2000). In contrast, high plant Si concentrations deter insect herbivores by decreasing the nutritional quality of plant tissues and the forming of physical barriers that protect plant cells against penetration and increase the abrasion of mouthparts (Massey et al., 2006; reviewed by Singh et al., 2020). Furthermore,

plant Si and N concentrations have been shown to jointly influence the nutritional quality of grassland species (Descombes et al., 2020; Massey et al., 2007) as well as rates of insect herbivory in a grassland community (Descombes et al., 2020). Thus, plasticity in tissue concentrations of both nutrients in response to water regimes might have major implications for insect herbivory and associated decreases in plant performance. Assessing Si and N plasticity in response to water regimes across plant species may contribute to better understand spatial and temporal patterns in insect feeding preferences and herbivory rates along gradients of water availability in temperate grasslands.

Multi-species experiments that directly assess the effect of different water regimes on plant Si and N concentrations and compare it across species are lacking for temperate grasslands. Studies on temperate species focussed on single crop or horticultural species, precluding cross-species comparisons, and/or considered the effects of drought only (Ryalls et al., 2018; Thorne et al., 2020 and references therein). To our knowledge, the only study that comparatively assessed the effects of water availability on plant Si across multiple species, focused on tropical grasses (Brightly et al., 2020; see Quigley & Anderson, 2014; Quigley et al., 2017 for comparisons of two grass species). For plant N concentrations in temperate grassland species, experimental studies that tested the effects of water regimes usually covered a rather limited gradient of water availability, focussing on drought but often disregarding waterlogging and flooding (see references in He & Dijkstra, 2014; Sardans et al., 2017). Studies including several water regimes did not compare species' plasticity across multiple species or life-forms but assessed community-level responses (e.g. Luo et al., 2018). In field experiments that assessed species plasticity (e.g. Ren et al., 2011) small-scale spatial variation in soil N availability may have confounded direct effects of water availability on N plasticity (Hodge, 2004).

Here, we experimentally assessed the effects of different water regimes on Si and N concentrations of plants in temperate grasslands. We grew 10 grassland species belonging to two life-forms (grasses and forbs) under four water regimes, ranging from dry to flooded conditions, in mesocosms with uniform substrate. We hypothesized that plant Si and N concentrations vary across water regimes, with the concentrations of both elements being highest under nonstressing, benign conditions and reduced under dry, waterlogged and flooded conditions. We further expected that plant Si and N responses to different water regimes vary across species and life-forms, reflecting species-specific nutrient uptake mechanisms, and that this results in changes of species rankings of Si and N concentrations across different water regimes.

2 | MATERIALS AND METHODS

2.1 | Experimental set-up

The experiment was conducted in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55′19″N, 11°34′55″E). The climate is temperate with a mean annual temperature of 8.7°C and 745 mm mean annual precipitation (1998–2007).

Mesocosms (round plastic containers, 67 cm diameter, 35 cm height, 90 L volume) with a homogenized soil mixture (see below) were exposed to four different watering treatments with five replicates each (i.e. 20 experimental units in total): (1) a 'control' treatment of benign, nonstressing water conditions, which consisted of a three-time weekly watering regime, initially applying the amount of water equivalent to average rainfall in the growing season (ca. 70 mm per month, based on monthly mean rainfall from May to September for the years 1998–2007), and increasing the amount as required to maintain the soil moist during hot and dry periods (assessed by finger probing); (2) a 'drought' treatment that, in total, received half the amount of water of the 'control' treatment by doubling the irrigation interval, but keeping the water supply constant at each watering; (3) a 'waterlogged' treatment that was waterlogged up to 15 cm below the soil surface; and (4) a 'flooded' treatment that was completely inundated to the rim of the mesocosm ca. 2–3 cm above soil surface (but plants emerged above the water level). For the drought and control treatments, soil water drainage was ensured through holes at the bottom of the containers, whereas in the waterlogged and flooded treatments holes were drilled in the sides of the containers, and water level was maintained through irrigation three times a week until overflow occurred from the holes. Treatments were maintained for 19 weeks from mid-May until the end of September 2016. Soil water potential in three randomly selected mesocosms of the drought, control and waterlogged treatment was monitored every 10 min using gypsum blocks (GB-1; Delmhorst, NJ) connected to a digital soil moisture tester (KS-D1; Delmhorst, NJ) at 10 cm depth. Soil water potential, aggregated into hourly values, differed strongly across water regimes (ANOVA: $p = 0.003$, Figure 1). In the drought treatment, soil water potentials remained below the permanent wilting point for most of the experimental period. In the control, soil water potentials stayed above the permanent wilting point, except for a short period end of June and beginning of July. Waterlogging consistently led to soil water potentials (near) zero, except for some brief reductions in June and July. All treatments were spatially randomized and implemented under transparent rain-out shelters, to assure similar light and temperature conditions. The substrate consisted of local topsoil (brown earth sensu IUSS with a sandy loam texture) mixed with 20% (v/v) crushed limestone to improve soil drainage, and had the following properties: pH = 7.0, 0.2% N, 2.9% C and 45% skeleton content.

2.2 | Study species

This study focussed on five grass species and five forb species (Table 1) typical for semi-natural grasslands of Central Europe with differing habitat associations to moisture (Ellenberg et al., 2001). In temperate grassland communities, plant species with a range of soil moisture associations often coexist due to small-scale variation of hydrological parameters (Silvertown et al., 2015).

Seeds were obtained from a commercial supplier (Rieger-Hofmann GmbH), and comprised a mixture of genotypes
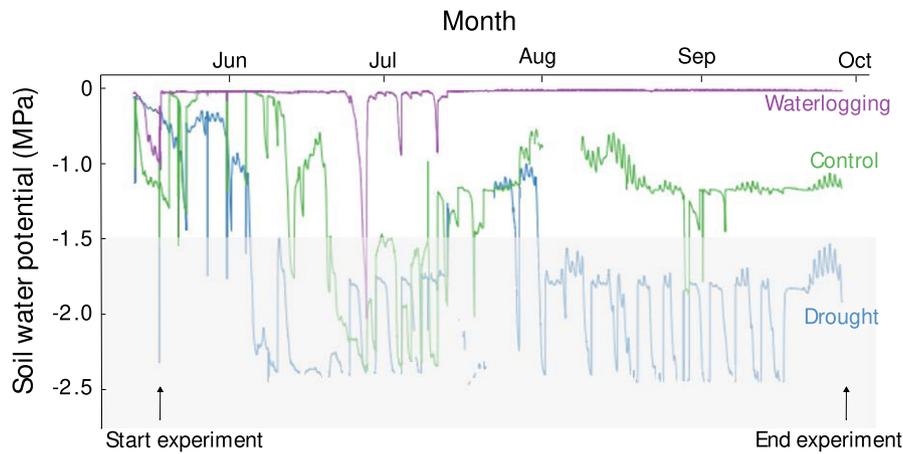
FIGURE 1 Soil water potentials during the mesocosm experiment in the drought, control and waterlogged treatment. Black arrows indicate start and end of the experiment and coloured lines represent different water regimes. No measurements were taken in the flooded treatments as water potentials in the fully submerged soil were assumed to be 0 MPa. The gypsum blocks used to monitor water potentials have a measurement range down to −1.5 MPa. Lower readings (grey area) therefore indicate water potentials below −1.5 MPa (considered the permanent wilting point) but do not represent the actual water potentials. For visualization values were aggregated into hourly values. See methods for details.

TABLE 1 Plant species included in the experiment with their scientific name, abbreviation, family, life-form and Ellenbergs' indicator value for moisture (M-value; Ellenberg et al., 2001)

Scientific name	Abbreviation	Family	Life-form	M-value
Artemisia campestris L.	AC	Asteraceae	Forb	2
Sanguisorba minor Scop., s. l.	SM	Rosaceae	Forb	3
Silene dioica (L.) Clairv.	SD	Caryophyllaceae	Forb	6
Silene flos-cuculi L.	SF	Caryophyllaceae	Forb	7
Silene vulgaris (Moench) Garcke	SV	Caryophyllaceae	Forb	4
Festuca pratensis Huds., s. l.	FP	Poaceae	Grass	6
Festuca valesiaca Schleich. ex Gaudin, s. l.	FV	Poaceae	Grass	2
Koeleria pyramidata (Lam.) P. Beauv.	KP	Poaceae	Grass	4
Poa angustifolia L.	PA	Poaceae	Grass	Indifferent
Poa palustris L.	PP	Poaceae	Grass	9

representing the genetic diversity of the species in southern Germany. Seeds were stratified and germinated in the greenhouse. Seedlings were then transplanted to the mesocosms in a concentric grid with ca. 6–8 cm distance between individuals (Figure S1), and with two individuals of each forb species, and four individuals of each grass species randomly assigned to each position. All plants were regularly watered until treatments were started, approximately 4 weeks after the plants were transplanted to the mesocosms.

2.3 | Chemical analysis

Plants (aboveground biomass) were individually harvested twice, once in summer (mid-July) and once in autumn (end of September), simulating two cuts in managed grasslands. The aboveground

biomass from the second harvest was dried at 70°C, ground to a fine powder and used for the analyses. One individual per species and mesocosm was used ($N = 5$).

Silicon was extracted from the leaves for 5 h by an alkaline method using 30 mg of plant material and 30 ml of 0.1 M sodium carbonate solution (Na_2CO_3) in a regularly shaken water bath following Katz et al. (2021). The solution was subsequently passed through a 0.2 μm syringe filter (ChromafilXtra CA-20/25). The Si concentration of the leaf extract was determined with inductively coupled plasma optical-emission spectrometry (ICP-OES) using a Varian Vista-Pro Radial element analyser (Varian Inc.).

Plant N concentrations were obtained with EA-IRMS coupling (Elemental Analyser NA 1108, CE Instruments; Interface ConFlo III, Finnigan MAT; Isotope ratio mass spectrometer: delta S, Finnigan MAT) and calculated from samples weights and peak areas as detailed by Liebel et al. (2010).

2.4 | Statistics

We analysed the effects of species (or life-form) and watering treatment, as well as their interactions separately for Si or N concentration using generalized least squares (GLS, for species) models or generalized linear mixed-effect models (GLMMs, for life-forms). Tukey post-hoc tests were applied to assess the significance of differences of Si or N concentrations across the watering regimes within each species and life-form. We ran models across all species, as well as for grasses and forbs separately. For graphic representation of the responses to the different water regimes, we calculated response ratios (RRs) of plant Si and N concentrations to the respective water regimes compared to control conditions as RR = log(treatment/control), compare Hedges et al. (1999).

In the models, we used variance structures allowing for heterogeneous residuals (Zuur et al., 2009), so that Si and N concentrations could be kept untransformed to retain valuable biological information on variability and to ease interpretability of the results. To find the appropriate variance structure for each model we built four competing models: one linear model and three GLSs for species as well as one linear mixed-effect model (LMM) and three GLMMs for life-forms, respectively, with each GLS and GLMM having different variance structures either allowing for heterogeneous residuals in species, watering treatment or both plus their interactions. We selected the model with the best fit based on AIC values. We ran graphical model diagnostics to ensure normality of ordinary residuals and homogeneity as well as independence in normalized residuals.

To fit the models we used the R-function *gls* for the GLSs and *lme* for the LMMs and GLMMs and included the variance structures by using the function *varIdent* from the R-package 'NLME' (Pinheiro et al., 2020). To conduct post-hoc tests we used the functions *emmeans* and *pairs* from the package 'EMMEANS' (Lenth et al., 2020).

In the flooded treatment the sample size of six species was reduced to N = 2–4 for both plant N and Si concentrations (*Artemisia campestris*, *Festuca valesiaca*, *Poa palustris*, *Sanguisorba minor*, *Silene dioica*, *Silene vulgaris*) and for plant Si concentrations one forb species (*Silene vulgaris*) was missing entirely because plant material for analyses was not sufficient due to low growth and/or high mortality. We therefore conducted the analyses for the complete dataset, and for a subset only containing data for the drought, control and waterlogging treatment. Results differed only marginally, so we present the results for the complete dataset in the main text. The missing data, however, led to rank deficient design matrices in all models fitted to plant Si concentrations that included forb species. To circumvent this issue, we tested the effect of the interaction term as a single factor in a separate model, using the *gls* function, in which all available species-treatment combinations were included as factor levels.

To assess how much of the total variation in plant Si and N concentrations is explained by species differences, water regimes and by species×water regime interactions, we partitioned the variance between these components. We fitted random intercept models

(see Messier et al., 2010) separately for grasses and forbs, with each model including species, treatment and the species×treatment interaction as random effects and no fixed effects. The percentage of variation explained by each random effect and the residuals was calculated based on their variance estimates. We ran graphical model diagnostics to ensure normality in residuals. Since we were interested in variance estimates instead of precisely calculated *p*-values, it was not necessary to fulfil the assumption of homogeneous variances of residuals and estimates within grouping variables. To fit the models we used the R-function *lmer* from the R-package 'LME4' (Bates et al., 2015).

2.4.1 | Species rankings across water regimes

To test for changes in species rankings of Si or N concentrations across water regimes, we calculated pairwise Spearman rank correlation coefficients between the control and the different watering treatments (control vs. drought, control vs. waterlogging, control vs. flooding). We conducted these analyses across all species and separately for grasses and forbs.

All statistical analyses were performed in R version 4.1.0 (R Core Team, 2021).

3 | RESULTS

3.1 | Differences of Si and N concentrations between life-forms and across species

Grasses showed significantly higher Si concentrations than forbs (8.95 mg g^{-1} vs. 0.67 mg g^{-1}), while N concentrations did not vary between life-forms (Table 2a). Si and N concentrations varied significantly across all species, as well as within forbs and grasses separately (Table 2b–d). Si concentrations varied ca. 42-fold across species, with species means ranging between 0.27 and 11.37 mg g^{-1}, while N concentrations varied ca. twofold between 12.32 and 22.80 mg g^{-1}.

3.2 | Effect of water regimes on Si concentrations

Water regimes significantly influenced Si concentrations across life-forms (Table 2a) and across all species, as well as across grasses and forbs separately (Table 2b–d). Significant effects of water regimes emerged within all species, except *Silene dioica* (Figure 2, Table S1), with up to a fourfold intraspecific variation of Si concentrations across treatments in forbs (*Artemisia campestris*) and up to sixfold in grasses (*Koeleria pyramidata*). The effect of water regimes on Si concentrations differed between grasses and forbs (life-form×treatment interaction, Table 2a), and across species, also within grasses and forbs separately (species×treatment interaction, Table 2b–d).

TABLE 2 Effects of water regime (treatment), life-form (or species) and their interaction on plant Si and N concentrations. Given are the results of generalized linear (mixed-effects) models including either life-form (a; two levels: Grasses and forbs; species included as random factor) or species identity (b, 10 species), and of separate models for forbs and grasses (c, d; five species each). For details see methods

|	Si			N		
	$df_{nom,den}$	F	p	$df_{nom,den}$	F	p
(a)						
Life-form	1, 8	114.30	**<0.001**	1, 8	2.40	0.160
Treatment	3, 167	13.53	**<0.001**	3, 175	111.87	**<0.001**
Life-form×treatment interaction	3, 167	97.66	**<0.001**	3, 175	2.27	0.082
(b)						
Species	9, 170	190.99	**<0.001**	9, 151	252.83	**<0.001**
Treatment	3, 170	11.75	**<0.001**	3, 151	271.92	**<0.001**
Species×treatment	38, 144	107.87	**<0.001**	27, 151	4.02	**<0.001**
(c) Within forbs						
Species	4, 79	46.78	**<0.001**	4, 72	315.23	**<0.001**
Treatment	3, 79	13.74	**<0.001**	3, 72	141.44	**<0.001**
Species×treatment	18, 68	36.44	**<0.001**	12, 72	2.25	**0.018**
(d) Within grasses						
Species	4, 76	17.52	**<0.001**	4, 79	24.47	**<0.001**
Treatment	3, 76	159.95	**<0.001**	3, 79	137.83	**<0.001**
Species×treatment	12, 76	10.39	**<0.001**	12, 79	4.95	**<0.001**
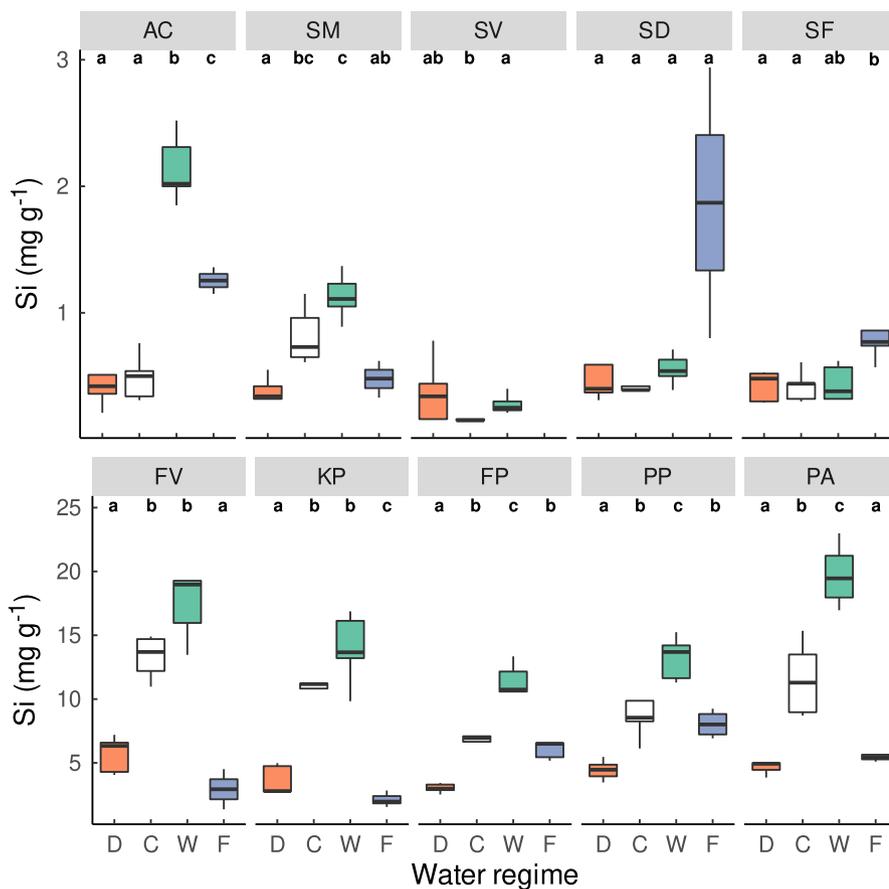
FIGURE 2 Plant Si concentrations of forbs (upper panel) and grasses (lower panel; five species each) under four water regimes (D = drought; C = control, i.e. benign conditions; W = waterlogging; F = flooding). Box plots show medians, 25th and 75th percentiles (interquartile range), and 1.5×interquartile ranges without outliers. Results of Tukey post-hoc tests conducted within each species are given as letters with each letter indicating groups which did not differ significantly. See Table 2 and Table S1 for details and Table 1 for species abbreviations.

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FIGURE 3 Plant N concentrations of forbs (upper panel) and grasses (lower panel; five species each) under four water regimes (D = drought; C = control, i.e. benign conditions; W = waterlogging; F = flooding). Box plots show medians, 25th and 75th percentiles (interquartile range), and 1.5× interquartile ranges without outliers. Results of Tukey post-hoc tests conducted within each species are given as letters with each letter indicating groups which did not differ significantly. See Table 2 and Table S1 for details and Table 1 for species abbreviations.
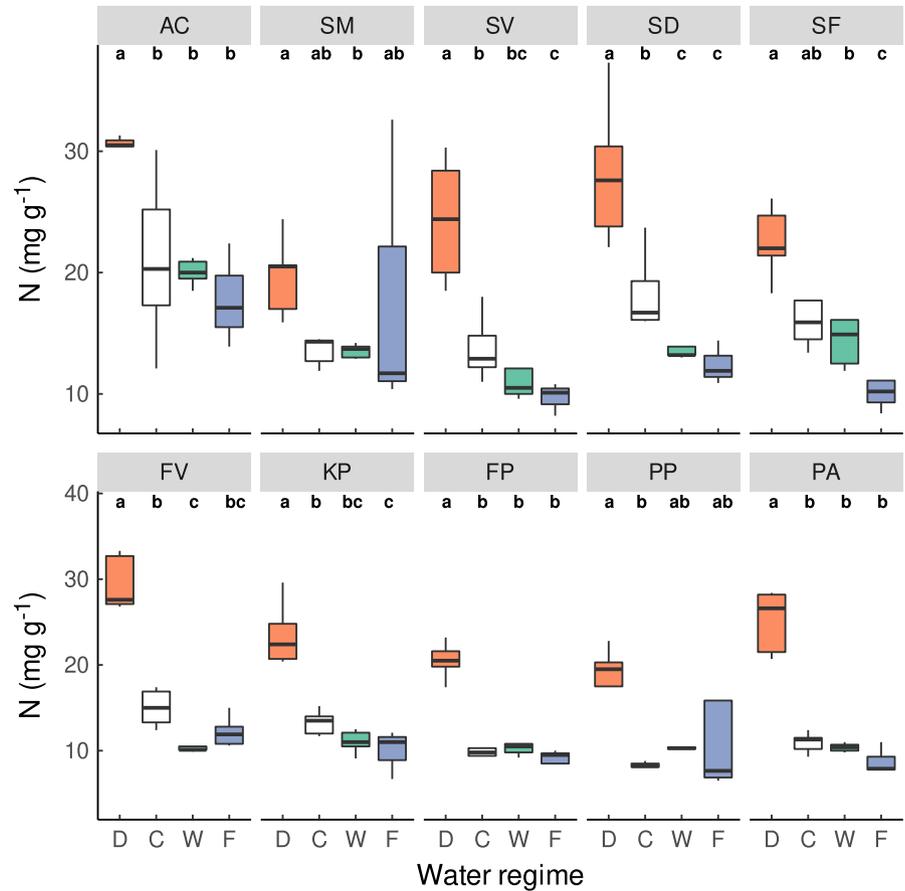
In all grasses, Si concentrations consistently decreased under drought and under flooded conditions relative to the control, consistent with our hypothesis, but they increased under waterlogging. The responses to the water regimes were strong and uniform in direction, but species responses varied in magnitude (species×treatment interaction, Table 2d), with most responses being significant (Figure 4a).

In contrast, in forbs, Si concentrations did not respond to water regimes as we had hypothesized. The responses differed across species in direction as well as in magnitude, with five responses being significant (Figure 4a): Relative to benign conditions, *Artemisia campestris* exhibited a strong increase in Si concentrations in response to both waterlogging and flooding (but no response to drought), and *Silene flos-cuculi* and *Silene vulgaris* exhibited a significant increase in response to flooding and waterlogging respectively (but no response to the remaining water regimes). In *Sanguisorba minor* Si concentrations decreased with drought, which was the only forb response supporting our hypothesis.

In grasses, the vast majority of the observed variation of Si concentrations was explained by plasticity due to different water regimes (73%), whereas species-specific plasticity and species differences accounted for 13% and 4% respectively. In contrast, in forbs, most of the observed variation in Si concentration was explained by species-specific plasticity in response to water regimes (i.e. species×treatment interaction, 54%, Figure 5), whereas the effect of water regimes and species differences explained only 13% and 7% respectively.

Species ranking of Si concentrations under flooded conditions was unrelated to that under control conditions, but it was maintained under drought and waterlogging (Table 3a). In grass species alone, the same pattern was observed (with correlation coefficients being marginally significant). In contrast, in forbs species ranking changed in all water regimes compared to the control conditions.

3.3 | Effect of water regimes on N concentrations

Water regimes significantly influenced plant N concentrations across life-forms (Table 2a) and species, also within grasses and forbs separately (Table 2b–d). Within each individual species, the effect of water regime was significant (Figure 3, Table S1), with up to threefold variation in N concentrations across all treatments (*Poa angustifolia*). The effect of water regime on N concentrations did not differ between grasses and forbs (no life-form×treatment interaction, Table 2a), but across species, also within grasses and forbs separately (species×treatment interactions, Table 2b–d).

Contrary to our hypothesis, under drought, all species consistently exhibited an increase in N concentration compared to control conditions, which was significant in nine of the 10 species (Figure 4b). Responses to waterlogging and flooding were less pronounced, but in line with our hypothesis: Most species showed a trend towards decreasing N concentrations in response to both waterlogging and
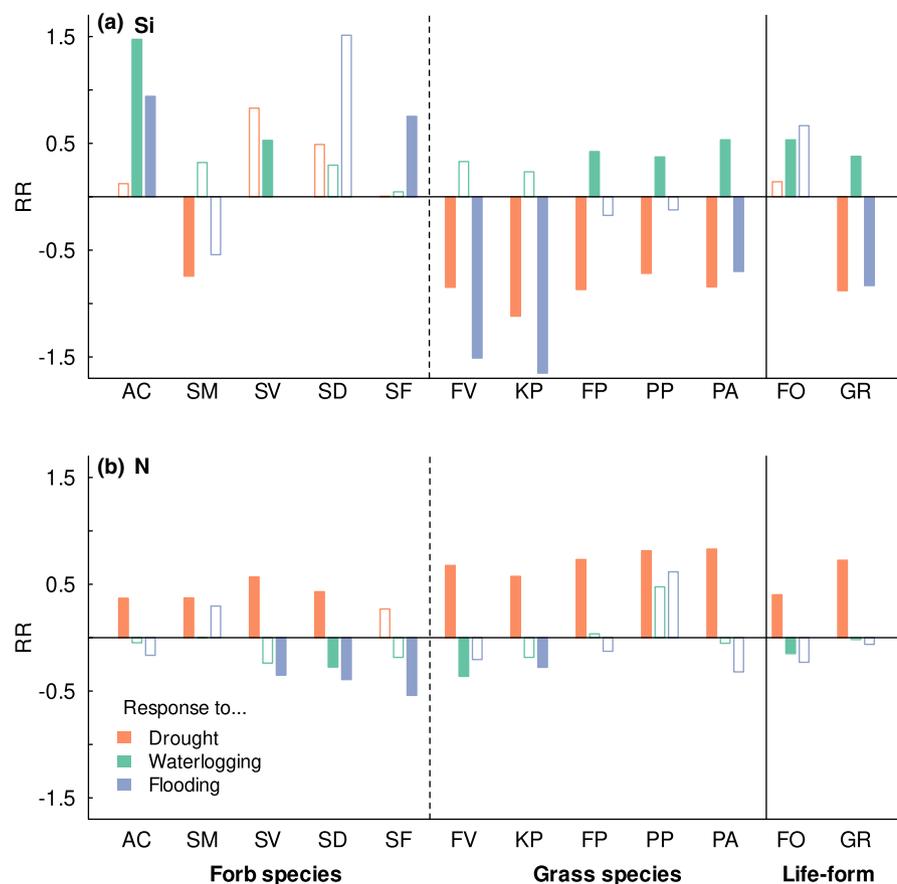
FIGURE 4 Responses of plant (a) Si and (b) N concentrations to different water regimes compared to benign control conditions in 10 grassland species and summarized for forbs (FO) and grasses (GR). Response ratios (RRs, compare Hedges et al., 1999) are given. Filled bars indicate significant ($p < 0.05$) responses based on Tukey post-hoc tests on the models for life-forms and species. See Table 2 and Table S1 for details and Table 1 for species abbreviations.

TABLE 3 Results of rank correlations between plant (a) Si concentrations and (b) N concentrations in the control versus the different water regimes (drought, waterlogging, flooding). Spearman rank correlation coefficients are given with the respective *p*-values in parentheses (significant values at $p = 0.05$ and $p = 0.10$ are given in regular and italic font respectively). No correlation (n.s.) indicates a change in species rankings in the respective water regimes relative to the control, while a significant positive correlation indicates that species ranking was maintained

	All species	Grasses	Forbs
	Control	Control	Control
(a) Si			
Drought	0.88 (0.002)	*0.90 (0.083)*	n.s.
Waterlogging	0.96 (<0.001)	*0.90 (0.083)*	n.s.
Flooding	n.s.	n.s.	n.s.
(b) N			
Drought	0.71 (0.028)	*0.90 (0.083)*	*0.90 (0.083)*
Waterlogging	0.67 (0.039)	n.s.	n.s.
Flooding	n.s.	n.s.	n.s.

FIGURE 5 Partitioning of the observed total variation of plant Si and N concentrations in five grass and five forb species under four water regimes ranging from dry to flooded conditions. Colours indicate the amount of variation explained by plasticity in response to water regimes (dark blue) and species-specific responses (interaction, light green), as well as species differences (dark green) and residual variation not explained by any of these factors (grey). Values were derived from variance estimates of random factors of random intercept models. For details see Section 2.

flooding. The effect was significant in two species for waterlogging and four species for flooding.

Most of the observed overall variation in plant N concentration was explained by plasticity due to the effects of water regimes both in f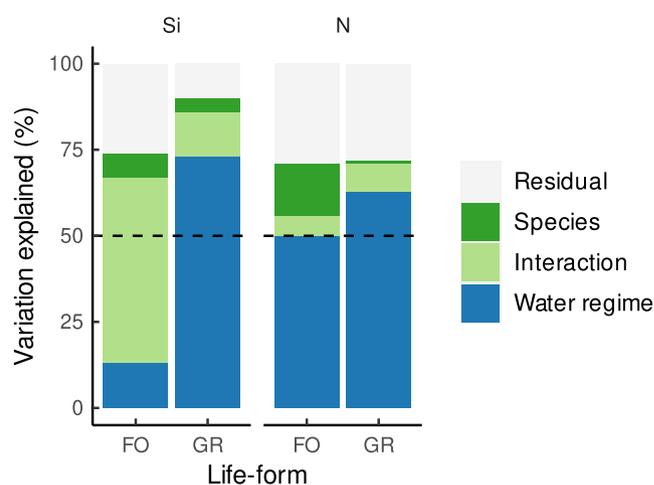orbs (50%) and grasses (63%). Species differences explained only 15% and 1% and species-specific responses explained 6% and 8% of the variation in forbs and grasses respectively (Figure 5).

Similar to Si concentrations, species rankings of N concentrations changed under flooding but were maintained under drought and waterlogging compared to control conditions (Table 3b). When analysed separately, species rankings of both grasses and forbs changed under waterlogging and flooding and were only maintained under drought (marginally significant correlation).

4 | DISCUSSION

Water regimes strongly influenced plant Si and N concentrations of temperate grassland species. Our hypothesis, that plant Si and N concentrations are highest under benign conditions and respond negatively to drought, waterlogging and flooding was only partially supported. Overall, plant Si responses differed strongly across species and life-forms, while plant N responses were more uniform, but still varied across species. Species plasticity, especially species-specific responses, rather than differences across species accounted for most of the variation found in plant Si and N concentrations across water regimes. By experimentally growing multiple plant species under different water regimes with standardized substrate, soil processes in the different treatments influenced all species similarly. Thus, the species-specific responses (and/or life-form specific responses) we observed reflect differences in the species' physiological capacity to respond plastically to different water regimes rather than differences in soil Si and N provisioning.

In grasses, drought and flooding consistently led to strong decreases in Si, as we had hypothesized, while waterlogging led to increases compared to benign control conditions. Drought and flooding can elicit similar plant stress responses, such as lowered transpiration rates and aquaporin expression, which ultimately reduce water uptake, photosynthesis and energy (ATP) supply (Bartlett et al., 2016; Lambers & Oliveira, 2019; Thorne et al., 2020; Yeung et al., 2019). This might have led to the downregulation of nonessential and energy-demanding physiological processes (Lambers & Oliveira, 2019), such as active Si uptake (see Coskun et al., 2019) and the production of Si-dissolving exudates (see de Tombeur et al., 2021). Additionally, reduced transpiration and aquaporin expression may have limited passive Si uptake via diffusion as well as Si transport from the roots to above-ground organs (Deshmukh & Bélanger, 2016; Mitani & Ma, 2005). In contrast, positive responses to waterlogging suggest that our treatment (waterlogged to 15 cm below the soil surface) did not lead to relevant oxygen limitation in the rooting zone, providing ideal conditions for grasses to maintain active Si uptake and high transpiration rates that resulted in high plant Si concentrations. Opposite responses of grasses to drought than we consistently observed in our study were shown in a recent study on tropical grasses, where most species (39 of 53) exhibited higher Si concentrations under drier than under well-watered conditions (Brightly et al., 2020). Different experimental conditions might have caused the conflicting pattern: very frequent irrigation may have led to Si leaching from the growth substrate in pots under well-watered conditions, while the drier conditions likely were less

intense (Brightly et al., 2020). Furthermore, previous studies suggest increased Si accumulation due to drought might reflect an adaptive response in grasses to mitigate detrimental effects of drought stress (Brightly et al., 2020; Quigley & Anderson, 2014; Strömberg et al., 2016), yet this was not supported by our data for temperate grasses. Instead, our results suggest energy availability and stomatal responses mediate the consistent decrease in plant Si concentrations under drought and flooding across temperate grass species.

In forbs, Si concentrations were not higher under benign than under stressful water regimes, as we had hypothesized. Compared to grasses, the responses of forbs were generally weaker (but still pronounced) and more species specific. Physiological differences in Si uptake might underlie these findings, as grasses and forbs exhibit varying degrees of passive and active uptake. Most grasses are considered to have functional, energy-dependent Si transporters that mediate active Si uptake (Deshmukh & Bélanger, 2016; Ma & Yamaji, 2015). In contrast, the relative contribution of active versus passive uptake varies strongly across forbs as Si transporters are often absent or less functional than in grasses; some forbs even reject Si (Deshmukh & Bélanger, 2016; Liang et al., 2006). Phylogenetic factors influence species differences in the genetic underpinnings of Si uptake (Hodson et al., 2005; Klotz et al., 2021; Strömberg et al., 2016), potentially explaining the uniform responses we observed across closely related grasses and the strong variation across forbs. Overall, the strong differences across forb species in their responses to water regimes suggest that differences in their active component of Si uptake (Deshmukh & Bélanger, 2016), in stomatal behaviour (Bartlett et al., 2016; Yeung et al., 2019) and/or in their physiological strategies to cope with flooding and drought (Mommer et al., 2006; Zwicke et al., 2015) might be important drivers of Si plasticity in forbs.

The direction of plant N responses exhibited a consistent pattern across species and life-forms. In all species, N concentrations were higher under drought compared to the unstressed control, not supporting our hypothesis. The responses to waterlogging and flooding were negative, consistent with our hypotheses, yet they were less pronounced than those to drought and differed stronger across species. The positive plant N response to drought we observed is in line with some previous studies (Sardans et al., 2017 and references therein), yet contradicts others, which reported negative or no effects of drought on plant N concentrations for grassland species (He & Dijkstra, 2014 and references therein; Naudts et al., 2011). Variation in the duration and intensity of drought and irrigation events can modulate plant N responses to drought (He & Dijkstra, 2014), potentially explaining the conflicting results. Soil processes affecting N availability cannot explain the increased plant N concentrations under drought, as soil N availability should be reduced under drought compared to benign conditions (Sanaullah et al., 2012). Instead, plant physiological processes are likely to be important: under drought, growth was substantially reduced in all species (unpublished data), a combined effect of stomatal closure limiting carbon assimilation and reduced cell turgor. Stronger limitation of growth than N availability and

uptake can eventually increase N concentrations in plant tissues (Aerts & Chapin, 1999; He & Dijkstra, 2014). Additionally, it is known that drought-resistant species can increase N allocation to leaves, enhancing their photosynthetic capacity and water-use efficiency (Lambers & Oliveira, 2019; Wright et al., 2003). The more species-specific plant N responses to waterlogging and flooding than to drought might be due to variation in root anatomy and N transporters located in root membranes and/or to variation in stomatal regulation (Aerts & Chapin, 1999; Bartlett et al., 2016; Lambers & Oliveira, 2019), but also due to strong differences in the physiological capacity to acclimate to excess water, with potential consequences for N metabolism (Mommer et al., 2006). Overall, we showed that N concentrations in grasses and forbs of temperate grasslands are influenced by water regimes and are particularly responsive to drought, leading to strong increases in plant N concentrations across species.

The strong plant Si and N responses to different water regimes across species may lead to shifts in species rankings of Si and N concentrations. We showed that species rankings based on Si concentrations changed across all water regimes in forbs, while in grasses shifts occurred only under flooding. For N concentrations species rankings changed under waterlogged and flooded conditions in both, forbs and grasses. As plants exhibiting higher N concentrations are generally preferred by insect herbivores (Loranger et al., 2012; Pérez-Harguindeguy et al., 2003), whereas plants accumulating more Si are more likely to be rejected (Massey et al., 2006; Singh et al., 2020), such shifts may lead to changes in feeding preferences of insect herbivores across water regimes, with implications for herbivore pressure and plant performance. In fact, effects of drought on plant nutritional quality and associated changes in insect feeding preferences are well studied for temperate herbaceous species. Changes in plant N concentrations, tissue hydration and secondary metabolites have been suggested to be important drivers (e.g. Gutbrodt et al., 2011; Huberty & Denno, 2004), yet results are conflicting, as increased and decreased feeding preferences were observed under drought (Gutbrodt et al., 2011; Huberty & Denno, 2004). Furthermore, the role of Si as well as waterlogging and flooding has been hardly considered in this context (but see Vandegeer et al., 2021). Our data suggest that, for forbs, highly species-specific effects of Si on herbivory damage across water regimes, including waterlogging and flooding, are likely. In most grass species, high Si concentrations under benign and waterlogged conditions might diminish their nutritional quality, potentially reducing herbivory damage. In contrast, low Si concentrations under drought and flooding might lead to higher herbivory damage. Furthermore, Si accumulation itself can increase plant N concentrations (Putra et al., 2022), reduce secondary metabolites in plants (Schaller et al., 2012) and improve tissue hydration under drought (Thorne et al., 2020). The species-specific plant Si responses to water regimes we observed, combined with the known defensive effect of Si, and its interaction with other plant traits which also affect herbivory imply that Si plasticity should influence insect herbivory across water regimes in temperate grasslands.

5 | CONCLUSIONS

We showed strong plasticity in plant Si and N concentration of temperate grassland plants in response to drought, waterlogging and flooding. The responses of plant Si concentrations were highly species specific in forbs, while plant N responses were more uniform across grassland species and life-forms. Our results suggest that spatial and temporal variation of soil water regimes, for example, with microtopography (Silvertown et al., 2015) or following severe drought and precipitation events as projected with climate change (IPCC, 2021), might influence plant Si and N concentrations differently across species. This might have pervasive consequences for plant performance and ecological processes, such as herbivory. Our results call for further multi-species experiments to elucidate the ecological consequences of changing plant Si and N concentrations in response to water regimes, including both excess and lack of water.

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