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Wade, R.N., Donaldson, S.M., Karley, A.J. et al. (2 more authors) (2022) Uptake of silicon in barley under contrasting drought regimes. Plant and Soil. ISSN 0032-079X

https://doi.org/10.1007/s11104-022-05400-w

Plant Soil
https://doi.org/10.1007/s11104-022-05400-w

REGULAR ARTICLE

Uptake of silicon in barley under contrasting drought regimes

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Received: 1 December 2021 / Accepted: 20 March 2022

Abstract

Purpose Silicon (Si) accumulation in plant tissues plays a vital role in alleviating biotic and abiotic stresses, including drought. Temperate regions are predicted to experience reductions in the quantity and frequency of rainfall events, potentially impacting plant Si uptake via the transpiration stream. Despite the importance for predicting plant responses to Si amendments, the effects of changes in rainfall patterns on Si uptake in cereals have not been characterised.

Methods Five watering regimes were applied based on predicted precipitation scenarios, varying the quantity of water delivered (ambient, 40% or 60% reduction) and watering frequency (40% reduction in quantity, applied 50% or 25% of ambient frequency), and the effects on growth and leaf Si concentrations of a barley landrace and cultivar were determined.

Results Reductions in the quantity of water reduced plant growth and yield, whereas reducing the watering frequency had little impact on growth, and in some cases partially ameliorated the negative effects of drought. Reductions in quantity of water lowered leaf Si concentrations in both the cultivar and landrace, although this effect was alleviated under the drought/deluge watering regime. The landrace had greater leaf Si concentration than the cultivar regardless of watering regime, and under ambient watering deposited Si in all cells between trichomes, whereas the cultivar exhibited gaps in Si deposition.

Responsible Editor: Christopher Guppy.

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Conclusion The impact of future reductions in rainfall on barley productivity will depend upon how the water is delivered, with drought/deluge events likely to have smaller effects on yield and on Si uptake than continuous drought.

Keywords Landrace · Climate change · Drought/deluge · Defence · Silicon · Rainfall patterns

Introduction

Silicon (Si) plays a significant role in a range of plant physiological processes (Souri et al. 2021) and particularly in alleviating biotic and abiotic stresses (Debona et al. 2017) including drought (Rizwan et al. 2015; Thorne et al. 2020). Recently there has been interest in the potential of Si amendments improving the performance of a wide range of crops in soils depleted of bioavailable Si (Artyszak 2018; Brahma et al. 2020; Zhou et al. 2021). However, the beneficial impacts of Si on crop performance could be constrained by changes in water availability (Grašič et al. 2019; Mandlik et al. 2020) under climate change, as Si uptake and transport is influenced by the transpiration stream (Ma et al. 2006; Ma and Yamaji 2006). Therefore it is critical to understand how future changes in rainfall patterns will impact Si uptake if the potential benefits of Si amendments on crop yield are to be realised.

Silicon uptake has been reported to improve the tolerance of plants, including crop species, to water stress by a range of mechanisms (Rizwan et al. 2015; Thorne et al. 2020). These include increasing antioxidant defence, increasing net CO_2 assimilation of leaves under drought (Gong et al. 2005), decreasing transpiration by forming cuticle-Si double layer of epidermal cells affecting the permeability of the cell and providing structural support to plant tissues to prevent lodging (Ma 2004; Fallah 2012). Ability to accumulate Si as a mechanism to alleviate the adverse impacts of drought on crops is of increasing interest given the predictions of reduced water availability under climate change (Arneth et al. 2019) and the potential of Si application in mitigating the impacts of drought on crop performance (Thorne et al. 2020). Temperate climates like that of the UK are predicted to experience reductions of up to 40% in the quantity of summer precipitation by 2080, concomitant with increases in the frequency of extreme drought and heavy rainfall events (Bates et al. 2008; Murphy et al. 2009; Bouwer et al. 2014). Plants growing in these conditions are likely to suffer from periods of extreme stress and recovery, with an increase in the duration of dry periods between heavy rainfall events (McCracken and Stoate 2011). Research is needed to establish the effects of these 'drought/deluge' conditions on plant Si accumulation, as they have the potential to severely reduce Si uptake and transport in the plant, and therefore diminish the positive effects of Si amendments on plant performance.

Si is taken up from the soil as silicic acid via the transpiration stream and accumulated by plant tissues to variable concentrations depending on factors including plant species and variety (Mitani and Ma 2005; Ma et al. 2007) and soil Si availability (Garbuzov et al. 2011). The process involves both passive uptake via aquaporin channels and the transpiration stream, and active efflux transporters (Ma and Yamaji 2015; Deshmukh and Bélanger 2016). The relative contribution of passive and active processes to Si uptake and transport remains unclear (Hartley et al. 2015), although variation in Si uptake and accumulation between plant species and varieties is now known to reflect differences in stomatal density and conductance, and in transporter abundance and expression (Ma et al. 2007; McLarnon et al. 2017).

Low water availability in the soil during periods of reduced rainfall will reduce transpiration rates and could, therefore, reduce Si uptake (McLarnon et al. 2017) and transport in the plant, limiting the potential benefits of Si. Although the impact of reduced water availability on Si uptake has been demonstrated (Quigley and Anderson 2014; Quigley et al. 2017; Grašič et al. 2019), future changes in precipitation as a result of climate change will include changes in the frequency as well as quantity of rainfall. The effect of these contrasting precipitation scenarios on Si accumulation in plant leaves has not yet been assessed.

Barley (*Hordeum vulgare* L.) is one of the main cereal crops grown throughout the UK (DEFRA et al. 2022). In the UK, most barley cultivation uses modern cultivars, which have been exposed to intensive agronomic selection for increased yield with high input levels. However, landraces, with a long history of localised seed saving and cultivation by traditional farming practises, are increasing in popularity, in part because they are considered more resilient to abiotic and biotic stress (Newton et al. 2010). Silicon uptake in landraces compared with modern cultivars remains relatively under studied, although the impact of agronomic selection on Si-based defences has been demonstrated (Simpson et al. 2017) and recently wheat landraces have been shown to differ in their Si accumulation under a continuous drought treatment (Thorne et al. 2021). As yet there has been no study on how barley landraces and cultivars differ in their allocation to Si defence and the patterns of Si deposition on their leaf surfaces have never been investigated, though this is key to determining the effectiveness of Si defences against herbivores (Massey and Hartley 2009; Hartley et al. 2015). Significantly, there have been no studies on how Si uptake in cereals is affected by contrasting drought scenarios that incorporate the predicted changes in rainfall frequency under climate change, rather than just changes in total rainfall.

The effect of predicted changes in both the water quantity and watering frequency under future climates on the growth, yield and leaf Si uptake and patterns of deposition was assessed for a modern UK cultivar of spring barley (Optic) and for a UK barley landrace (Bere), which might be expected to have greater resilience to water shortage. We hypothesised that reductions in water quantity and watering frequency would reduce barley growth, yield and leaf Si concentration. We also predicted that the most severe reductions in water quantity and frequency would have the largest negative impacts on these traits, and that there would be contrasting responses of barley to prolonged drought as compared with drought followed by deluge.

Materials and methods

Plants of the barley cultivar Optic (supplied by Syngenta 2010) and landrace, Bere (from the Orkney Isles, supplied by SASA 2010) were grown in three controlled environment cabinets with 16 h daylight (av. light intensity across the three cabinets was 262.1 ± 3.7 µmol m^{-2} s^{-1} [mean ± standard error], 57 w/m^2 at pot height), 50% RH, at 20 °C/ 18 °C day/night.

All barley plants were grown individually in 2.4 L pots filled with 3 kg of dried, sieved (10 mm) topsoil (A1 Plant, Elvington) mixed in a 3:1 ratio with washed sharp horticultural sand (Keith Singleton, UK) to give a sandy loam soil substrate. The saturation and desiccation (dried at 105 °C for 7 d) masses of the soil were measured and from these values the total water holding capacity was calculated. Two seeds of each barley variety were placed in the centre of each pot c. 2 cm from the soil surface. Pots were initially watered to ensure soil moisture content was 60% of the total soil water holding capacity, after which they were watered from the top of the pot twice per week for two weeks with 150 ml of deionised water per pot. Saucers placed under each pot captured any water draining through the soil. Following germination, seedlings were thinned to a single plant per pot of consistent height and development stage. After two weeks, plants were subjected to one of five watering regimes (see Fig. 1), as described below:

- Ambient: plants were watered 200 ml per watering event (based on 10 year av. weekly rainfall during June, July and August measured at The James Hutton Institute, Invergowrie, Dundee, Scotland), delivered twice per week;
- Drought (D): 40% reduction in volume of water added compared to ambient, watered twice per week;
- Severe drought (SD): 60% reduction in volume of water added compared to ambient, watered twice per week;
- Drought deluge (D/del): 40% reduction in volume of water added compared to ambient, watered once per week i.e. 50% as frequent as the ambient treatment;
- Drought with extreme deluge (D/Edel): 40% reduction in volume of water added compared to ambient, watered once per fortnight i.e. 25% as frequent as the ambient treatment.

These watering regimes allowed comparison of the effects of changes in water quantity (40% and 60% reduction in volume of water added compared to the ambient) and changes in watering frequency under the 40% reduction regime (water provided twice per week, once per week or once per fortnight). Experiments comprised a randomised complete block design. Within each block, one replicate of each watering regime x variety combination was assigned at random to each pot position. The nine blocks were

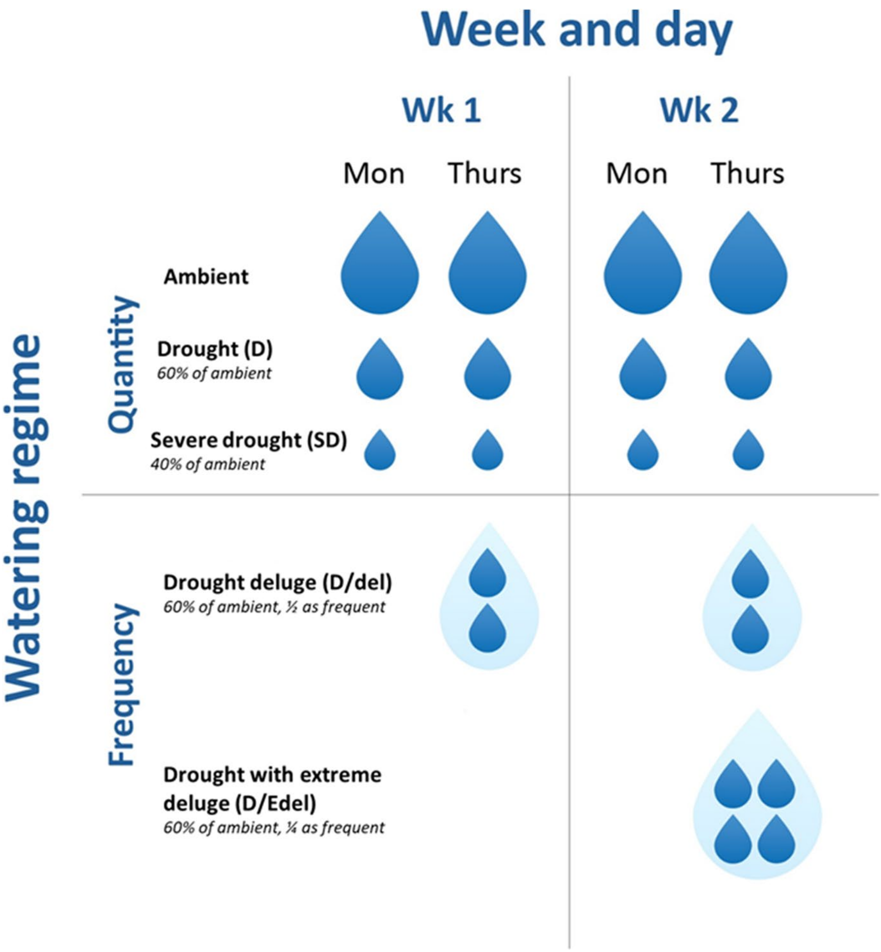


Fig. 1 Diagram illustrating the different watering regimes, showing water quantity delivered at each watering event and the frequency of the events

staggered temporally by two to three weeks between each block to facilitate harvesting.

Transpiration rate (mmol m^{-2} s^{-1}) was measured using a portable gas exchange analyser (LCA-4; ADC BioScientific Ltd., Hoddesdon, UK) equipped with a broadleaf chamber (cuvette window area, 6.25 cm^2). Measurements were taken between 14:00 and 15:30 h on the second fully expanded leaf, 51 days after sowing, one day after ambient, D, SD and D/del treated plants and eight days after D/Edel treated plants were last watered. Photosynthetic active radiation (PAR), relative humidity (RH), and carbon dioxide concentrations were set at ambient value.

All barley plants in each block were harvested on the same day when the ear on the main stem of the ambient treatment for each variety reached Zadok's growth stage 71 (Zadoks et al. 1974). Watering regime had no effect on the time to maturity of the ear on the main stem. At harvest, the fourth youngest fully expanded leaf on the main stem was removed, leaf area measured (cm^2) using a portable area meter (Li-cor model LI-3000A), dried and weighed to calculate specific leaf area. Plant material was then separated into roots, stems, leaves and ears, weighed for fresh mass (g FM) and dried at 70 °C for c. 4 d, after which total dry biomass was recorded (g DM), and water content (g) and root: mass ratio (RMR) calculated. Grains were manually threshed, counted, dried and weighed. Harvest Index (HI) was calculated by dividing total ear mass by total above-ground dry mass.

Elemental analysis was conducted on dried milled green leaf material (c. four green leaves per plant) from separate plants. Silicon concentration (% dry mass) was determined using a commercial P-XRF instrument (Niton XL3t900 GOLDD analyser: Thermo Scientific Winchester, UK) (Reidinger et al. 2012). The carbon (C) and nitrogen (N) concentrations of leaf (% dry mass) were determined by flash combustion and chromatographic separation of ~1.5 mg milled leaf using an elemental analyser (Elemental combustion system 4010 CHNS-O Analyser, Costech Analytical Technologies, Inc., Milan, Italy), calibrated against a standard ($C_{26}H_{26}N_2O_2S$). Percentage C and N of the leaves was used to calculate the C/N ratio.

To investigate the pattern of Si deposition and presence of trichomes on the leaves of barley, surface analysis was carried out by scanning electron microscopy (SEM) and energy dispersive X-ray spectroscopy (EDX). Two replicate plants of Optic and Bere were grown under ambient watering for eight weeks in a greenhouse (253 µmol m^{-2} s^{-1}, 55 w/m^2 at pot height) with 16 h daylight at 20 °C/ 15 °C day/night, 50% RH, in the same soil and pots as described above. Three square sections (~5 mm^2) of material were excised either side of the midrib from a mature, expanded leaf blade from each plant and prepared for analysis using the acetone graduation series described by Hartley et al. (2015). SEM images of the leaf surface were obtained using FEI Sirion S-FEG FESEM (Oxford Instruments, Abingdon, Oxfordshire) and EDX was used to determine the distribution of elemental Si on the leaf surface in relation to the leaf surface structures observed using SEM (Goldstein et al. 2003). The EDX analysis was performed using an Oxford INCA analysis system FESEM (Oxford Instruments), using a 10 mm working distance. Voltages were 5–10 kV and 12 kV, respectively, for the SEM and EDX analysis.

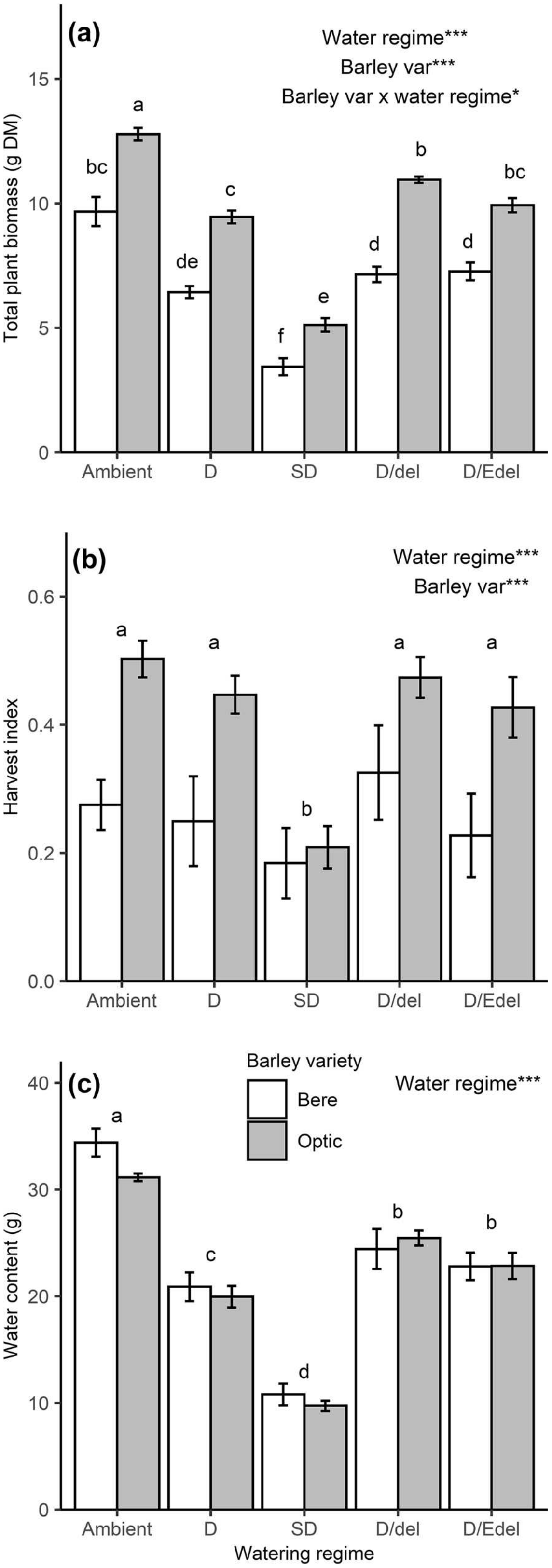
Analyses were performed in R studio (version 1.1.456). Linear mixed effect models (*lme4* package) (Bates et al. 2014) were used to test the interactive effects of barley variety and watering regime on the measured variables. Block was included as a random term in the model. Data were checked for normality and homogeneity of variance (shapiro.test) and where appropriate, data were log or arcsine square root transformed. Statistical significance was set at a 95% confidence interval ($P < 0.05$) for all analyses. Models were simplified using AIC values (calculated using '*AIC'* function) to find the minimum adequate model (Crawley 2007). ANOVA was used to test the main and interactive effects of barley variety and watering regime on leaf silicon concentrations and plant growth. Estimated marginal means using package emmeans (Russell et al. 2018), was used to determine differences between treatments. All measured growth parameters were assessed on nine replicates (plants) for each treatment. Leaf Si concentrations were assessed on three to eight replicates depending on the availability of sufficient green plant material for analysis. Transpiration rate was measured on five replicates (plants) for each treatment. Correlations were performed using cor.test.

Results

Bere plants treated with ambient watering reached maturity on average 22 d earlier than Optic, therefore Bere plants were harvested after a shorter growing period. Optic plants had significantly greater (c. 30%) total plant biomass than Bere plants regardless of watering regime (Fig. 2a). Optic and Bere plants responded in the same way to a reduction in water quantity: 40% (D) and 60% (SD) reductions in water quantity caused a significant reduction in total plant biomass (c. 30% and c. 60% reduction respectively). In contrast, there were differences between the genotypes in the response to watering frequency: Bere did not respond to changes in the watering frequency, whereas Optic plants watered once per week (D/Del) had significantly larger (c. 14%) total plant biomass compared to plants receiving the same total amount of water twice per week (D; Fig. 2a). Optic plants had a larger increase in biomass per day than Bere plants and the biomass increase per day was similarly affected by the watering regimes for both barley varieties. Reduction in the water quantity reduced biomass increase per day whereas plants watered once per week had a significantly larger increase in biomass per day compared to plants receiving the same total amount of water twice per week (Table 1).

Optic plants had a significantly larger grain mass, more grains (Table 1) and HI compared to Bere regardless of watering regime (Fig. 2b). D and SD treated plants exhibited c. 30% and c. 70% decreases, respectively, in total ear biomass and number of grains at harvest compared to ambient plants. However, harvest index was unaffected by a reduction in the watering frequency. Optic plants had a smaller specific leaf area (SLA) compared to Bere plants (Table 1): the difference between Optic and Bere plant SLA was greatest under ambient watering regime. With increasing drought there was a trend

Fig. 2 **a** Total plant biomass (g dry mass (DM)), **b** harvest index and **c** water content (g) of barley Optic and Bere plants at harvest treated with different watering regimes. Values represent mean ± standard error bars of nine replicates. Bars sharing the same letter were not significantly different as determined by estimated marginal means (package emmeans). Letters on total plant biomass bars (**a**) show results of *Post-hoc* test of the interaction between barley variety x watering regime. The interaction between barley variety x watering regime was not significant for harvest index (**b**) and water content (**c**), therefore the letters on these bars show which watering regimes significantly differed from one another. $P < 0.001$***, $P < 0.05$* ▶



towards a reduction in SLA for Bere but an increase in SLA for Optic plants (Table 1). RMR ratio was unaffected by the different watering regimes; however, Bere had a larger RMR ratio than Optic regardless of the watering regimes (Table 1).

Bere and Optic plants did not significantly differ in total plant water content (Fig. 2c) and the barley varieties responded similarly to the watering regimes: reductions in water quantity significantly reduced total plant water content, whereas reductions in watering frequency increased total plant water content. Optic plants had a higher C:N ratio than Bere: reducing the quantity and frequency of watering regimes significantly reduced C:N ratio of both barley varieties with the severe drought treatment causing the largest decrease in C:N (Table 1). Bere plants also had a significantly higher transpiration rate compared to Optic plants regardless of watering regime (Table 1). The barley varieties showed a similar transpiration rate under the different watering regimes. There was no significant difference in transpiration rate between ambient, D, SD and D/del treated plants, but plants watered once per fortnight (D/Edel)had a significantly lower (c. 27% reduction) transpiration rate compared to plants receiving the same total amount of water twice per week (D) or once per week (D/Del; Table 1).

Bere plants accumulated higher leaf Si concentrations (%) compared to Optic plants regardless of watering regime, although the difference was less apparent under drought/ extreme deluge watering (Fig. 3a). Leaf Si concentrations were reduced in D and SD plants compared to ambient watered plants, but leaf Si increased under the reduced watering frequency treatments in both barley varieties. Bere and Optic plants deposited Si in trichomes and in the sclerenchyma cells between the trichomes, but there were

Table 1 The effect of changing the water quantity and watering frequency on growth and chemical composition parameters of barley cultivar (Optic) and landrace (Bere). Results of linear models testing the effect of barley variety, changes in watering regime and their interaction on the measured parameters. $P<0.05$*, $P<0.01$**, $P<0.001$***. For each measurement, rows sharing the same letter were not significantly different as determined by estimated marginal means (package emmeans)

Measurement	Watering regime	Bere Av. ± SE	Optic Av. ± SE		ANOVA Stats (F values)
Total plant biomass (mg DM) per day	Ambient	130 ± 8.9	133 ± 9.8	a	Watering regime $134.2_{4,84}$***
	D	88 ± 10.7	99 ± 8.8	b	Barley variety $13.6_{1,84}$***
	SD	46 ± 11.4	53 ± 8.7	c	
	D/del	97 ± 9.6	114 ± 4.7	d	
	D/Edel	99 ± 14.6	104 ± 8.4	bd	
Grain mass (mg DM)	Ambient	19.9 ± 3.4	30.8 ± 2.3	ab	Watering regime $3.16_{4,74}$*
	D	18.7 ± 4.9	31.9 ± 3.7	a	Barley variety $34.44_{1,74}$***
	SD	13.3 ± 3.5	26.0 ± 3.1	ab	
	D/del	18.4 ± 2.7	25.0 ± 2.4	ab	
	D/Edel	13.1 ± 2.5	22.3 ± 2.1	b	
Specific leaf area (cm^2)	Ambient	309.0 ± 9.57a	110.7 ± 8.98b		Watering regime $0.11_{4,80}$***
	D	278.7 ± 19.40a	156.1 ± 10.68b		Barley variety $198.26_{1,80}$^{NS}
	SD	263.2 ± 8.85a	171.6 ± 8.75b		Barley variety x watering regime $5.17_{4,80}$***
	D/del	273.3 ± 14.39a	156.3 ± 17.65b		
	D/Edel	256.9 ± 11.98a	169.2 ± 21.03b		
Root: mass ratio	Ambient	0.26 ± 0.013	0.16 ± 0.007	a	Barley variety $131.81_{1,80}$***
	D	0.28 ± 0.030	0.16 ± 0.007	a	
	SD	0.25 ± 0.022	0.16 ± 0.007	a	
	D/del	0.24 ± 0.010	0.16 ± 0.008	a	
	D/Edel	0.22 ± 0.021	0.16 ± 0.010	a	
No. grain	Ambient	105 ± 10.7	113 ± 5.1	a	Watering regime $36.9_{4,76}$***
	D	65 ± 7.9	78 ± 4.4	b	Barley variety $7.3_{1,76}$**
	SD	35 ± 5.2	31 ± 3.3	c	
	D/del	84 ± 7.7	99 ± 2.5	ad	
	D/Edel	67 ± 11.2	89 ± 4.4	bd	
C:N	Ambient	26.7 ± 0.49	40.7 ± 2.38	a	Watering regime $11.07_{4,57}$***
	D	26.0 ± 2.36	42.5 ± 7.36	ad	Barley variety $143.57_{1,57}$**
	SD	16.6 ± 1.30	27.9 ± 2.95	b	
	D/del	22.5 ± 1.26	45.3 ± 4.07	ad	
	D/Edel	19.6 ± 0.93	38.5 ± 4.53	d	
Transpiration (mmol m^{-2} s^{-1})	Ambient	0.22 ± 0.07	0.22 ± 0.05	ab	Watering regime $4.80_{4,40}$**
	D	0.28 ± 0.06	0.23 ± 0.08	a	Barley var. $4.30_{1,40}$*
	SD	0.22 ± 0.05	0.18 ± 0.04	ab	
	D/del	0.34 ± 0.04	0.23 ± 0.05	a	
	D/Edel	0.16 ± 0.05	0.15 ± 0.05	b	

slight differences in the deposition pattern: Bere filled all the sclerenchyma cells between the trichomes with Si, whereas there were some gaps in Si deposition in the sclerenchyma cells between trichomes in Optic (Fig. 3b). Si did not accumulate in all ridges, only those with trichomes.

There was a significant negative correlation between leaf Si (%) and C (%) concentration (Fig. 4a), as well as between leaf Si (%) and transpiration rate (mmol m^{-2} s^{-1}) ($r=-0.46$, $P=0.0194$), whilst leaf Si (%) was positively correlated with both leaf water content (g) (Fig. 4b) and root mass (g DM) (Fig. 4c).

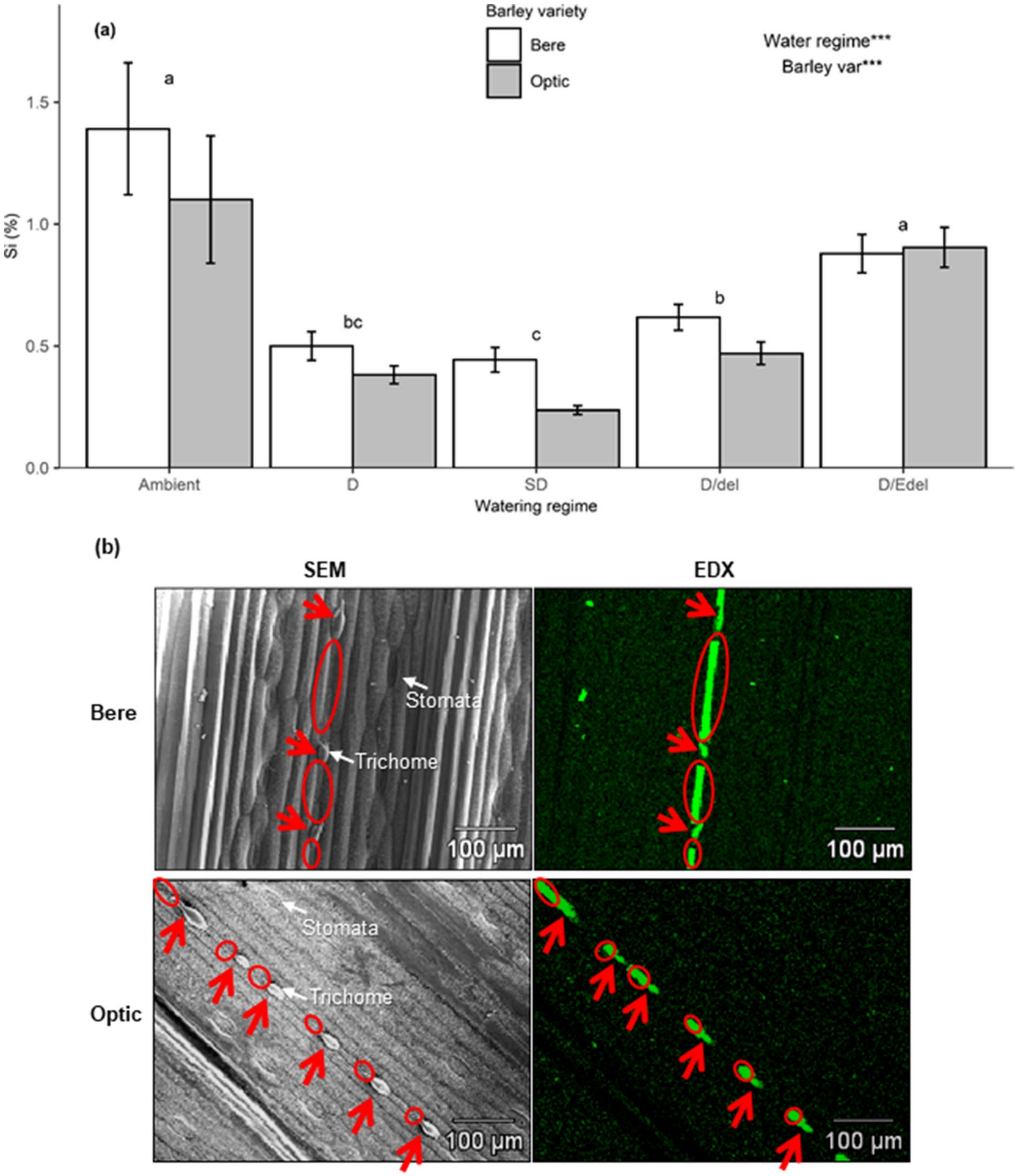


Fig. 3 **a** Total Si concentration (% dry mass) of barley Optic and Bere plants at harvest treated with different watering regimes. Values represent mean ± standard error bars of three to eight replicates for leaf. Bars sharing the same letter were not significantly different as determined by estimated marginal means (package emmeans). The interaction between barley variety x watering regime was not significant for total Si concentration, therefore letters on these bars show which watering regimes significantly differed from one another. **b** Abaxial leaf surface of ambient watered barley landrace, Bere, and cultivar, Optic, (× 60 magnification), showing stomata, trichomes and sclerenchyma cells. Red arrows indicate trichomes with Si deposition and red circles indicate cells filled with Si; green intensity indicates Si concentration. SEM = Scanning electron microscope; EDX = Electron density X-ray spectroscopy

There was no correlation between Si (%) and SLA ($r = 0.12$, $P > 0.05$).

Discussion

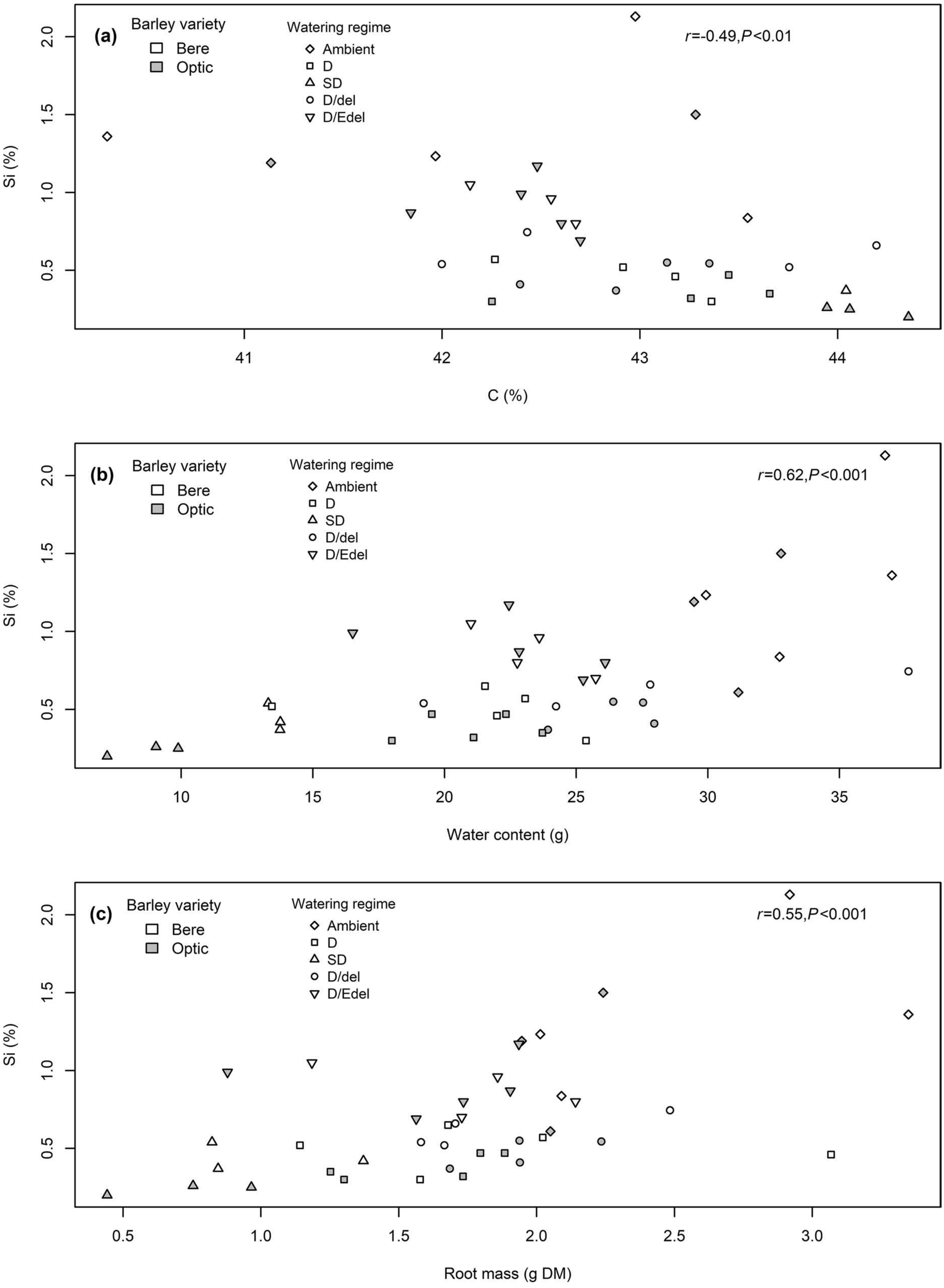
Drought significantly reduced the growth and yield of the barley varieties. However, reducing watering frequency in most cases either had no effect or small positive effects on barley growth when compared to the drought treatment delivering the same quantity of water but in more frequent events. Therefore there were much smaller adverse impacts on barley of reductions in watering frequency, compared with the impacts of reductions in water quantity, although growth did not fully recover under drought/deluge to the values shown by plants grown under ambient conditions. A 40% reduction in water quantity, which equates to the predicted decrease in UK summer precipitation by 2080, caused significant reductions in total plant biomass and yield of the barley varieties. These findings suggest that future changes in precipitation are likely to have severe consequences for barley production in the UK with reductions in the capacity of plants to take up Si, but that continuous small reductions in rainfall will be more adverse for barley growth and yield than periods of drought followed by deluge.

Barley leaf Si concentration was reduced under drought conditions, i.e. reductions in water quantity, with more severe reductions under greater water limitation. Similar findings have been reported for leaf Si of native grasses under reduced water availability (Quigley and Anderson 2014; Xu et al. 2017), demonstrating the importance of water availability and the transpiration stream for Si uptake (McLarnon et al. 2017). However in contrast to our hypothesis, and a novel finding of this study, Si accumulation under reductions in watering frequency showed a different pattern, with more severe reductions in frequency showing higher levels of Si uptake, such that plants under the drought/extreme deluge treatment contained the same levels of Si as those grown under ambient conditions. The enhanced uptake of Si under the reduced watering frequency may have been due to the large quantity of water delivered in one event penetrating deeper into the soil (Wade et al. 2017), allowing this part of the soil profile to remain wetter for longer and facilitating Si uptake by deeper roots. Si uptake by plants is known to be influenced by changes in root biomass allocation to different rooting zones and by root architecture (Barati et al. 2015). The importance of maintaining root biomass for Si uptake under the drought treatments is demonstrated by our finding of a significant correlation between these two parameters (Fig. 4c).

A soil structure that enables water drainage through the soil profile as well as supporting water pore filled spaces and soil organisms, such as arbuscular mycorrhizal fungi, which aid water retention (Rabot et al. 2018) may also play a significant role in maintaining plant Si uptake. Soil water has previously been shown to be a major driver of Si uptake (Quigley and Anderson 2014) and the positive correlation between leaf Si and leaf water content in this study (Fig. 4b) supports the idea that water and Si uptake are closely linked. These findings are particularly important when considering the impact and timing of soil Si amendments: under drought conditions and/or when plants have low transpiration rates the ability of plants to take up Si are likely to be significantly reduced. However, the relationship between Si uptake and transpiration rates is clearly complex (Thorne et al. 2020); here we found that although transpiration rates were lower in plants receiving the drought/deluge treatment than those under ambient conditions, their Si concentrations were higher. This reflects the fact that other mechanisms in addition to transpiration rate affect the rate of Si uptake (Ma et al. 2001), such as increased transporter density and activity (Hartley et al. 2015; McLarnon et al. 2017). Whatever the mechanism, the increased leaf Si concentrations under future predicted drought/deluge events could allow barley to maintain an erect canopy (Isa et al. 2010) and resist herbivory (Massey and Hartley 2006), although this benefit is known to depend on how Si is deposited at the leaf surface (Hartley et al. 2015).

In addition to the significant relationships between leaf Si and both water content and root biomass, we found a significant negative relationship between Si and C content. Several studies have found such a relationship, which is thought to arise as C-derived structural support may be substituted with metabolically cheaper Si (Schoelynck et al. 2010) (Fig. 4a).

The barley varieties tested in this study differed in plant growth, development and biomass. For example, the modern cultivar Optic, had a larger total plant


(a)
Barley variety
Bere
Optic
Watering regime
Ambient
D
SD
D/del
D/Edel
r=-0.49,P<0.01
Si (%)
0.5
1.0
1.5
2.0
41
42
43
44
C (%)
(b)
Barley variety
Bere
Optic
Watering regime
Ambient
D
SD
D/del
D/Edel
r=0.62,P<0.001
Si (%)
10
15
20
25
30
35
Water content (g)
(c)
Barley variety
Bere
Optic
Watering regime
Ambient
D
SD
D/del
D/Edel
r=0.55,P<0.001
Si (%)
0.5
1.0
1.5
2.0
2.5
3.0
Root mass (g DM)

◂**Fig. 4** The relationship between total leaf Si concentration (%) and (**a**) carbon (%), (**b**) water content (g) and (**c**) root mass (g) of barley Bere and Optic plants treated with different watering regimes

biomass at harvest compared to the landrace Bere, and developed more slowly, reflecting its more intensive and rigorous selection for traits such as shorter stems to reduce lodging, high yield and malting qualities (Madic et al. 2009; HGCA 2014). Barley varieties differed in deposition pattern but both varieties deposited Si in trichomes and sclerenchyma cells between trichomes. Hayward and Parry (1973) also reported Si deposition as "rod-shaped opals" in the walls of trichomes and sclerenchyma fibres in barley leaves. Rosen and Weiner (1994) also reported Si deposition as "rod-shaped opals" in the walls of trichomes and sclerenchyma fibres in barley leaves. Rosen and Weiner (1994) reported that irrigation impacted Si deposition through changes in the number of cells per silica skeleton in the cereal crop emmer wheat: a higher percentage of four or more celled phytoliths were found in inflorescence bracts from irrigated compared to rain-fed wheat plants, with similar trends also reported in barley plants. Barley varieties differed in leaf Si concentration under ambient watering conditions, with the cultivar having lower leaf Si concentration than the landrace possibly due to different physiological traits contributing to Si uptake and accumulation, for example differences in stomatal density, and the density and activity of transporters for active transport (Ma and Yamaji 2006; McLarnon et al. 2017). The barley landrace and cultivar showed the same epidermal cell types at the leaf surface, but Bere exhibited more pronounced ridges of epidermal cells and longer cells between each trichome. Domestication in wheat has also been shown to affect cell size due to selection for dwarf varieties (Peng et al. 2011), although the impact of domestication on trichome density is less clear and differs between crops (Chen et al. 2015).

This study shows for the first time that the pattern of watering events under drought conditions determines the impact of reduced water availability on Si uptake by a crop. Our findings suggest that, although some precipitation scenarios predicted under climate change will reduce leaf Si concentration, with potential consequences for growth, yield and defence in the future, when drought is followed by a deluge the impact on Si uptake is far less, or even non-existent. In terms of maintaining Si uptake and its associated benefits in resisting biotic and abiotic stresses, sustained decreases in rainfall might be more damaging to the crop, than equivalent reduction in water availability through more episodic droughts followed by heavy rainfall events. Increased frequency of heavy rainfall events are also predicted under climate change, so our findings are significant for predicting plant Si accumulation in response to Si amendments under future rainfall patterns. Future research should consider the impact of likely changes in extreme rainfall events when assessing the potential benefits of Si amendments for crop production.

Acknowledgements For their assistance with growing the plants, and SEM, we thank the horticultural staff at the University of York, Jerry Thomas and Meg Stark from the University of York technology facility and Ian Wright from The York JEOL Nanocentre. We also thank Syngenta and John Innes for providing the seeds.

Author's contributions RW, AK, SJ and SH conceptualised and designed the study. RW and SD generated the data. RW analysed the data. RW wrote the paper with the help of SD, AK, SJ and SH. Funding: RW was funded by a studentship from The James Hutton Institute and University of York. AK was supported by the strategic research programme funded by the Scottish Government's Rural and Environment Science and Analytical Services Division.

Declarations

Conflict of interest Authors have no conflict of interest to declare.

Data depository The datasets generated during this study will be available at repository.

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