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1 **Consistent alleviation of abiotic stress with silicon addition: a meta-analysis**

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14 Running title: Abiotic stress alleviation by silicon

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16

17 **ABSTRACT**

- 18 • Hundreds of single species studies have demonstrated the facility of silicon (Si) to alleviate diverse  
19 abiotic stresses in plants. Understanding of the mechanisms of Si mediated stress alleviation is  
20 progressing, and several reviews have brought information together. A quantitative assessment of the  
21 alleviative capacity of Si, however, which could elucidate plant Si function more broadly, was lacking.
- 22 • We combined the results of 145 experiments, predominantly on agricultural species, in a meta-  
23 analysis to statistically assess the responses of stressed plants to Si supply across multiple plant  
24 families and abiotic stresses. We interrogated our database to determine if: stressed plants increased  
25 in dry mass and net assimilation rate, oxidative stress markers were reduced, anti-oxidant responses  
26 were increased and if element uptake showed consistent changes when supplied with Si.
- 27 • We demonstrated that across plant families and stress types, Si increases dry weight, assimilation rate  
28 and chlorophyll biosynthesis and alleviates oxidative damage in stressed plants. In general, results  
29 indicated that plant family (as a proxy for accumulator type) and stress type had significant  
30 explanatory power for variation in responses. The consistent reduction in oxidative damage was not  
31 mirrored by consistent increases in anti-oxidant production, indicative of the several different stress  
32 alleviation mechanisms in which Si is involved. Silicon addition increased K in shoots, decreased As and  
33 Cd in roots and Na and Cd in shoots. Silicon addition did not affect Al, Ca or Mn concentration in  
34 shoots and roots of stress plants. Plants had significantly lower concentrations of Si accumulated in  
35 shoots but not in roots when stressed.
- 36 • Meta-analyses showed consistent alleviation by Si of oxidative damage caused by a range of abiotic  
37 stresses across diverse species. Our findings indicate that Si is likely to be a useful fertilizer for many  
38 crops facing a spectrum of abiotic stresses. Similarities in responses across families provides strong  
39 support for a role of Si in the alleviation of abiotic stress in natural systems, where it has barely been  
40 explored. We suggest this role may become more important under a changing climate and more  
41 experiments using non-agricultural species are now needed.

42

43 **Keywords:** stress alleviation, silica, agriculture, silicon fertiliser, oxidative stress, heavy metal toxicity

44

45

## 46 INTRODUCTION

47 Plants can use silicon (Si), acquired as a nutrient through their roots, to alleviate the impacts of an  
48 impressive range of abiotic stresses including salinity, metal toxicity, nutrient imbalance, temperature and  
49 water stress (Ma 2004). Our knowledge of these functions comes from predominantly agricultural studies and  
50 in comparison, a role for Si in abiotic stress elevation in natural ecosystems has been little considered (Cooke &  
51 Leishman 2011). Abiotic stress is estimated to reduce the yield of crops by 51-82% (Bray, Bailey-Serres &  
52 Weretilynk 2000). Plants in natural systems contend with abiotic stress with seasonal variations, unusual  
53 weather, environmental gradients and at the edge of their ranges, as examples (Hirt & Shinozaki 2004).  
54 Impacts of abiotic stress are increasing; in response to rising demand, agriculture has expanded into sub-  
55 optimal areas, causing a need to ameliorate the resultant plant stresses to improve crop yield (Tilman *et al.*  
56 2001) and a changing climate means both agricultural and native species experience altered rainfall and  
57 temperature regimes (IPCC, 2014). Abiotic stresses disrupt cellular homeostasis and increase the production of  
58 reactive oxygen intermediates (ROIs). High levels of these toxic compounds can induce cell death due to  
59 membrane, RNA and DNA damage (Mittler 2002).

60 The wide-ranging benefits of Si for stressed plants are exploited for agricultural gain (Datnoff, Snyder  
61 & Korndorfer 2001). Si is routinely added to a variety of crops, most notably rice and sugarcane (Korndorfer &  
62 Lepsch 2001), to increase yield (Datnoff *et al.* 2001). Using agricultural studies, Liang *et al.* (2007) identified four  
63 main mechanisms of Si use for abiotic stress alleviation: (a) stimulation of stress response systems through  
64 increased anti-oxidant production; (b) binding of Si to toxic metal ions resulting in co-precipitation and  
65 complexation; (c) changing uptake rates of toxic or scarce elements; and (d) changing the deposition or storage  
66 location of metal ions in plants, as well as (e) immobilising metal ions in the growth media, before uptake by  
67 the plant (*ex planta*). Ma and Yamaji (2008) have identified additional functions including reducing water loss  
68 through cuticular transpiration via deposition of silica beneath the cuticle and increasing the strength of stems  
69 through silica deposition. Silicon has also been shown to reduce UV-B stress (Schaller *et al.* 2013).

70 Hundreds of studies have now assessed the capacity of Si to alleviate abiotic stresses in single species  
71 by single stress experiments. While the responses and mechanisms of stress alleviation by Si have been  
72 qualitatively reviewed (Ma, Miyake & Takahashi 2001; Ma 2004; Liang *et al.* 2007; Balakhnina & Borkowska  
73 2013; Adrees *et al.* 2015; Pontigo *et al.* 2015), a numerical assessment is lacking and it is not known if  
74 predictable plant use of Si in stress alleviation occurs across plant groups and different stresses. Determining if  
75 stressed plant responses to Si application are consistent and which factors explain variation in plants, may  
76 stimulate better farming practices or more efficient Si fertiliser use. From an ecological perspective,  
77 consistency of responses to Si across families could allow predictions about how plants use Si to alleviate  
78 stress in natural systems. Meta-analyses allow statistically robust comparisons across multiple studies and  
79 hypothesis testing of data combined from many experiments (Gurevitch, Curtis & Jones 2001). Here, we  
80 quantitatively assess if Si consistently alleviates abiotic stress in plants through the reduction of oxidative  
81 stress.

82 Most research examining the effect of Si on alleviation of abiotic stress involves single species, single  
83 stress, often factorial experiments with four treatments arising from different combinations of stressed

84 (+Stress) and unstressed (-Stress) plants that are treated (+Si) or untreated (-Si) with Si fertiliser, although a  
85 subset with stressed plants +/- Si is also frequent. Stresses examined include water, salinity, metal and heavy  
86 metal, low nutrient, UV, heat and cold stress. A large number of measured plant responses are reported  
87 including changes in element concentration (including Si), biomass, yield, stress indicators (especially for  
88 oxidative stress), enzymatic and non-enzymatic anti-oxidant responses, and photosynthetic and transpiration  
89 rates. Common markers of oxidative stress include hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), malondialdehyde (MDA) and  
90 proline (PRO) concentration. The dominant ROI-scavenging enzymes in plants to combat oxidative stress  
91 comprise superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) and peroxidase (POD).

92 Silicon is acquired through the roots of plants as silicic acid and transported up through the plant in  
93 the xylem (Raven 1983). Nodulin 26-like intrinsic proteins and other aquaporins facilitate increased Si uptake in  
94 some species, and active uptake occurs through co-operation of influx and efflux transporters (Ma *et al.* 2006;  
95 Ma & Yamaji 2015; Deshmukh & Belanger 2016). The majority of Si is ultimately deposited as amorphous silica  
96 within and between cells and once deposited silica is not remobilised (Currie & Perry 2007). There is much  
97 variation in Si accumulation among families (Hodson *et al.* 2005; Trembath-Reichert *et al.* 2015) and the  
98 differential uptake is attributed to different expression rates and locations of the aquaporins (Ma & Yamaji  
99 2015). The Poaceae is well known as a high Si accumulating family (accumulating up to 10% Si in dry mass),  
100 while the Fabaceae and Brassicaceae are considered lower Si accumulators often accumulating <1% (Datnoff *et*  
101 *al.* 2001; Ma 2003).

102 Si accumulation capacity, or plant family as a surrogate, could an important factor affecting how  
103 stressed plants use Si to alleviate abiotic stress. Silicon is considered most important for high accumulating  
104 families, despite acknowledgment of functional roles in species that accumulate little Si (Katz 2014). The  
105 physical functions of Si, such as cuticular deposition to reduce transpiration, may be limited to high  
106 accumulating species as a build-up of silica is required (Raven 1983; Ma & Yamaji 2006; Massey & Hartley  
107 2009). In contrast, the impact of Si accumulation capacity on biochemical functions associated with abiotic  
108 stress alleviation, may be lower with a smaller but concurrent supply of Si may be needed (Iwasaki *et al.*  
109 2002a). Tomatoes (*Solanum lycopersicum*), for example, are considered low-moderate accumulators of Si, but  
110 Si fertiliser alleviates salt stress, boron toxic soils and fungal infections in this species (Al-Aghabary, Zhu & Shi  
111 2004; Heine, Tikum & Horst 2005; Romero-Aranda, Jurado & Cuartero 2006; Gunes *et al.* 2007).

112 Stress type could also be a factor explaining variation in how Si ameliorates abiotic stress in plants. As  
113 described above, Si is involved in multiple mechanisms of stress alleviation depending on the type of stress  
114 (Liang *et al.* 2007). An example of this is anti-oxidant activity, which shows both significant increases and  
115 decreases in production when stressed plants are supplied with Si (eg. Liang *et al.* 2003; Ma *et al.* 2004; Gunes  
116 *et al.* 2007b). Increased anti-oxidant production can be induced by Si supply, but reduced anti-oxidant  
117 production could arise from reduction of the stress through another mechanism as described above. Using  
118 tomatoes as an example again, when supplied with Si, the alleviation of salt stress was associated with a  
119 significant stimulation of anti-oxidant production (Shi *et al.* 2014), while the alleviation of boron stress was  
120 associated with reduced B uptake which resulted in a reduction of anti-oxidant production (Gunes *et al.*  
121 2007a).

122 A third factor that is potentially important to consider in assessing the consistency in alleviation of  
123 abiotic stresses by Si is plant part. Differences have been noted between shoot and root responses when Si is  
124 applied to stressed plants (eg. Cocker, Evans & Hodson 1998a; Zsoldos *et al.* 2003a). For example Zsoldos *et al.*  
125 (2003b) report that Si supply to aluminium-stressed wheat led to increased accumulation of Si in roots  
126 compared with shoots. Knowledge of shoot and root responses may allow further understanding of the  
127 mechanisms by which Si alleviates such a broad range of biotic stresses, particularly in terms of storing toxic  
128 levels of metals and salts.

129 In addition to abiotic stress alleviation, Si is used by plants to defend against biotic stresses,  
130 particularly herbivory. In some Poaceae, sustained herbivory can induce the uptake of additional Si in both  
131 natural and agricultural systems (Reynolds, Keeping & Meyer 2009; Hartley & DeGabriel 2016). It is not known  
132 if abiotic stress induces plants to take up more Si in a similar way.

133 The many single species studies provide the opportunity to test for consistency across a diverse range  
134 of species and stress types. Through quantitative analysis, we first sought to definitively determine if plant  
135 biomass and photosynthesis is increased following Si supply to stressed plants, and if this consistently occurs  
136 through the alleviation of oxidative stress (ie. a reduction in oxidative stress markers). In addition, we asked if  
137 responses vary with stress type but predicted that because all stress types are likely to cause oxidative damage,  
138 stress type will not be a significant explanatory factor. We also asked if plant family, as a surrogate for Si  
139 accumulation capacity, is an important explanatory factor. Subsequently our goal was to test if there are  
140 consistent anti-oxidant responses across experiments assessing the addition of Si to stressed plants. We  
141 predicted that due to different alleviation mechanisms, there would be no clear overall signal in changes in  
142 anti-oxidant activity when stressed plants are supplied with Si. However, we anticipated that plants stressed  
143 by metals and heavy metals show a reduction in anti-oxidant production, and other stresses show a significant  
144 increase. Next we sought to test if element uptake, including toxic elements, was consistently increased or  
145 decreased in plants, across species, and if there are differences in root and shoot allocation of these elements.  
146 We predicted reduced uptake of Na and metals, with no difference between roots and shoot allocation and no  
147 impact of plant family. Finally, given that herbivory can induce increased Si uptake, we predicted that plants  
148 would take up more Si when stressed, with a stronger signal in higher Si accumulators. In summary we tested  
149 the following hypotheses:

- 150 1. Plant biomass and net assimilation rate are consistently increased following Si supply to stressed  
151 plants, with family but not stress type significant explanatory factors
- 152 2. Oxidative stress is consistently alleviated (ie. a reduction in oxidative stress markers) with family but  
153 not stress type a significant explanatory factor
- 154 3. Anti-oxidant responses are not consistent across experiments assessing the provision of Si to stressed  
155 plants, and stress type will be a significant explanatory factor because plants stressed by metals and  
156 heavy metals will show a reduction in anti-oxidant production, while other stresses will show an  
157 increase
- 158 4. Element uptake is consistently increased or decreased across plants dependent on the element, with  
159 differences in root and shoot allocation of these elements and no impact of plant family

160 5. Plants take up more Si when exposed to abiotic stress

161

## 162 **MATERIALS AND METHODS**

163 Identification of papers, selection of data and analysis followed a consistent approach (Koricheva &  
164 Gurevitch 2014, see Supplementary Information Table S1). To identify studies in which stressed plants were  
165 grown with and without Si fertiliser, a tailored Web of Science, BIOSIS Citation Index search was carried out on  
166 15 August 2015 using ((alleviat\* or ameliorat\* or amend\* or contaminat\* or deficien\* or drought or enhance\*  
167 or excess\* or imbalance or induc\* or mediat\* or modifi\* or modulat\* or resistance or salin\* or stress\* or  
168 tolerance or toxic\*) not blast not borer not disease not fung\* not grazing not herbiv\* not infection not insect  
169 not mildew not root rot) AND (silicon or silica or "Si" or silicification or silicate or silicic) in the title AND (plant  
170 or leaf or leaves or shoot or root or stem or grass) in the topic. The search was further refined by selecting only  
171 journal articles and conference proceedings and including only journals likely to be relevant (including plant  
172 sciences or food science technology or chemistry physical or agronomy or biology or environmental science or  
173 ecology or soil science or chemistry multidisciplinary or chemistry analytical or agriculture multidisciplinary or  
174 biochemistry molecular biology or horticultural or forestry or agricultural engineering).

175 The search identified 504 papers, of which after inspection of titles and abstracts 352 were considered  
176 potentially relevant and 93% of these papers could be obtained. Papers were excluded where experimental  
177 design was not suitable for comparison (ie. did not follow experimental design of stressed plants +/- Si  
178 addition), foliage rather than root application of Si was employed, and replication details and/or measures of  
179 variance were not supplied (including by authors on request). In total, information from 145 papers was  
180 accessible, suitable, and collated for analyses. Data were extracted from figures using DataThief (Tummers  
181 2006) and Web Plot Digitizer (Rohatgi 2015) where necessary. Only the maximum stress and Si treatment levels  
182 were selected where multiple levels were included in the experimental design, and all cultivars listed were  
183 included separately.

184 For each experiment, details for as many of the four potential treatments reported (-Si-Stress, +Si-  
185 Stress, -Si+Stress, +Si+Stress) were recorded, together with the sample size. Measures of variance were  
186 recorded as standard deviations, converting other measures where possible. Not all of the responses could be  
187 used in the analyses due to small sample sizes. Subsets of data, isolating the most frequently measured  
188 responses, were extracted to test specific hypotheses. Shoot or leaf responses were used in analyses of net  
189 assimilation rate, chlorophyll content, oxidative stress markers (MDA, H<sub>2</sub>O<sub>2</sub>, proline concentration) and anti-  
190 oxidant activity (SOD, CAT, POD and APX) and both shoot and root responses were use in analyses of dry  
191 weight (DW) and element content (Al, As, Ca, Cd, K, Mn, Na, Si). Although cultivars play an important role in  
192 crop selection and vary in tolerance to stresses, it was considered that species and family (a proxy for  
193 accumulator type) would have a much larger effect; hence cultivars were not included in the analyses as a  
194 factor. Values were predominantly reported for shoots of non-woody and leaves of woody species and we  
195 considered these analogous, referring to them all as shoots.

196 After selecting subsets of data to analyse the variables above, of the 145 studies from which we  
197 extracted information, we used data from 125 published papers (Matoh, Kairusmee & Takahashi 1986; Ma &

198 Takahashi 1990; Bradbury & Ahmad 1990; Ahmad, Zaheer & Ismail 1992; Barceló & Guevara 1993; Hammond,  
199 Evans & Hodson 1995; Liang *et al.* 1996, 1999, 2008; Corrales, Poschenrieder & Barceló 1997; Nowakowski &  
200 Nowakowska 1997; Cocker *et al.* 1998a; Liang 1998; Rahman *et al.* 1998; Yang *et al.* 1999; Yeo *et al.* 1999; Hara,  
201 Gu & Koyama 1999; Iwasaki & Matsumura 1999; Iwasaki *et al.* 2002b; Rogalla & Roemheld 2002; Zsoldos *et al.*  
202 2003a; b; Gong *et al.* 2003, 2005; Gong, Randall & Flowers 2006; Gong *et al.* 2008; Al-Aghabary *et al.* 2004; Zhu  
203 *et al.* 2004; Shi *et al.* 2005b, 2010, 2013, 2014; Eneji *et al.* 2005; Guo *et al.* 2005, 2007, 2013; Hattori *et al.*  
204 2005, 2008; Shi *et al.* 2005a; Treder & Cieslinski 2005; Tahir *et al.* 2006, 2010; Moussa 2006; Romero-Aranda *et al.*  
205 *et al.* 2006; Wang & Han 2007; Gunes *et al.* 2007b; c; da; e, 2008; Maksimovic *et al.* 2007, 2012; Savvas *et al.*  
206 2007; Murillo-Amador *et al.* 2007; Tuna *et al.* 2008; Nwugo & Huerta 2008a; b, 2011; Saqib, Zörb & Schubert  
207 2008; Vaculík *et al.* 2009, 2012; Feng, Shi & Wang 2009; Feng *et al.* 2010; Inal, Pilbeam & Gunes 2009;  
208 Doncheva *et al.* 2009; Pei *et al.* 2009; He *et al.* 2009; Song *et al.* 2009, 2011; Ashraf *et al.* 2010b; a; Lee *et al.*  
209 2010; Miao, Han & Zhang 2010; Chai, Shao & Zhang 2010; Shen *et al.* 2010a; b, 2014a; b; c; Hashemi,  
210 Abdolzadeh & Sadeghipour 2010; Singh *et al.* 2011; Chen *et al.* 2011; Yao *et al.* 2011; Zeng *et al.* 2011; Frantz,  
211 Khandekar & Leisner 2011; Kafi & Rahimi 2011; Tripathi *et al.* 2012a; b, 2013; Fu *et al.* 2012; Gong & Chen  
212 2012; Gu *et al.* 2012; Li *et al.* 2012, 2015; Masarovič *et al.* 2012; Yin *et al.* 2013, 2014; Zhang *et al.* 2013a; b;  
213 Farooq *et al.* 2013; Habibi & Hajiboland 2013; Hu *et al.* 2013; Liu *et al.* 2013, 2014, 2015; Lukačová *et al.* 2013;  
214 Mateos-Naranjo, Andrades-Moreno & Davy 2013; Mateos-Naranjo *et al.* 2015; Pavlovic *et al.* 2013; Chalmardi,  
215 Abdolzadeh & Sadeghipour 2014; Siddiqui *et al.* 2014; Soundararajan *et al.* 2014; Dufey *et al.* 2014; Habibi  
216 2014; Hajiboland & Cheraghvareh 2014; Kang *et al.* 2014; Khoshgoftarmansh, Khodarahmi & Haghghi 2014;  
217 Kim *et al.* 2014a; b; Kostopoulou & Therios 2014; Bokor *et al.* 2014; Mihaličová Malčovská *et al.* 2014; Sanglard  
218 *et al.* 2014; Sayed & Gadallah 2014; Tang *et al.* 2015; Wu *et al.* 2015; Anwaar *et al.* 2015; Gengmao *et al.* 2015;  
219 Greger *et al.* 2015; Balakhnina *et al.* 2015; Mbonankira *et al.* 2015).

220 Meta-analyses were conducted in Metafor in R (Viechtbauer 2010). For subsets of the data, the effect  
221 size, Hedges'  $d$ , for individual studies was calculated for the relevant pair of responses (-Si+Stress vs +Si+Stress  
222 for all comparisons except Si accumulation which used +Si-Stress vs +Si+Stress). This effect size measure  
223 compares two means using a pooled standard deviation and bias correction, and is a measure of the number of  
224 standard deviations by which the means differ (Hedges & Olkin 1985). A positive value indicates that the  
225 response measure was higher in the experimental versus control treatment, while a negative value indicates  
226 the response measure in the experimental treatment was lower. The data were checked for outliers and  
227 normality of residuals.

228 Models were analysed with the `rma.mv` function in the `metaphor` package, with a maximum likelihood  
229 "ML" model fit. Overall effect sizes ("Overall") across studies were determined using a (null) model with  
230 publication (reference) as a random factor, which accounted for similarities of results within studies. Including  
231 species as a random factor did not have additional explanatory power and hence was not included in models.  
232 To further explore the sources of heterogeneity among responses, a combination of fixed and random effects,  
233 in mixed models, were used. In these models publication as a random factor was retained and either plant  
234 family or stress type was the fixed effect. Plant family can be considered a surrogate for variation in Si  
235 accumulation capacity (Hodson *et al.* 2005). We did not assign families to specific accumulation groups as there



236 are not yet definitive classifications (Deshmukh & Belanger 2016), but shoot Si content from our database was  
237 compared to a larger dataset of Si accumulation for relevant families (Trembath-Reichert *et al.* 2015) to allow  
238 interpretation of the results according to accumulation potential (Supporting information Fig S1).

239 Interactions between family and stress type are possible and ideally we would test for the interaction  
240 of these two moderators in the same model. However, this was not possible because the data compilation did  
241 not include multiple stress types applied to the same families with sufficient numbers of samples. Instead we  
242 tested the importance of stress type as a moderator in a single family, the Poaceae, for which the most data  
243 had been collected. When stress type explained significant heterogeneity in analysis of both the full data set  
244 and the Poaceae subset, we could be more confident of a true effect of stress type. Differences among families  
245 could not be tested in the same way as there were insufficient data.

246 Null model results indicated if there were significant overall effects of Si addition. Mixed-effect model  
247 results indicated if family or stress type explained a significant proportion of variation (heterogeneity) among  
248 studies. If the heterogeneity explained by the model including a moderator ( $Q_M$ ) was significant, we  
249 considered the moderator likely to be an important factor. Log ratio tests, comparing null and mixed models  
250 yielded almost identical findings (data not shown). The 5-95% confidence intervals in figures were used to  
251 determine if overall effect sizes for each factor (plant family or stress type) were significantly different from  
252 zero (ie if 95% confidence intervals do not overlap zero then there is a significant overall positive or negative  
253 effect) or each other.

254

## 255 **RESULTS**

### 256 *Data set*

257 The dataset used across all meta-analyses included 16 families comprising 48 plant species  
258 (Supplementary information, Table S2). Poaceae was best represented with 15 species, Fabaceae with 10, and  
259 Asteraceae, Cucurbitaceae and Solanaceae with 3 and two species in each of Amaranthaceae and Brassicaceae.  
260 Silicon content varied between families, with the Poaceae the highest (Supplementary information, Fig. S1).  
261 The majority of species were agricultural plants, often domesticated (Supplementary information, Table S2).  
262 The majority ( $\approx 75\%$ ) of experiments used hydroponic systems while others used sands, soils, vermiculite or  
263 contaminated soils in the field. Differences between growing media, study duration and stress intensity were  
264 not tested, as there were not enough studies from the same family and same stress type to allow this.

265 The most frequently imposed stresses across studies were salinity ( $n=44$  papers) and water stress  
266 ( $n=22$ ) with metal (Al ( $n=17$ ), B ( $n=7$ ), Cu ( $n=3$ ), Mn ( $n=8$ )) and heavy metal stresses (As ( $n=6$ ), Cd ( $n=17$ ) and Cr  
267 ( $n=3$ )) also popular. Cold temperature, acid rain, UV-B, heat and high and low phosphorus stress were  
268 represented by 1 to 3 experiments each.

269 There was some evidence of publication bias, as shown by funnel plots (Supplementary Information,  
270 Fig S3) mainly for shoot and root biomass measurements, but plotting residuals of models including  
271 moderators showed less bias. Four of the 27 responses showed significant, but generally weak temporal  
272 trends (Supplementary Information, Table S3). Small sample sizes (ie few studies) for some families and stress  
273 types resulted in large confidence intervals that meant for some groups the results were not significant despite

274 potentially large effect sizes. In part, this illustrates the benefits of meta-analyses as the quantitative  
275 combination of studies provided more statistical power. However, methodological heterogeneity and  
276 interactions between moderators, were difficult to explore conclusively, though causes of heterogeneity were  
277 explored (Supplementary Information, Tables S1,S4). The magnitude of the stress was significantly correlated  
278 with the magnitude of recovery (Supplementary Information, Fig. S1) which has the potential to impact  
279 magnitude but not sign of effect sizes.

280

### 281 *Plant biomass and photosynthesis*

282 Overall, combining experiments across 18 stress types and 14 families, supplying Si to stressed plants  
283 significantly increased the dry weight of both shoots and roots (Fig. 1, Table 1), supporting hypothesis 1. Not all  
284 groupings showed a significant dry weight (DW) increase (Fig 1), though most of the 8 stress types and 7  
285 families that did not had small samples sizes. Both stress type and family were significant moderators in  
286 explaining variation in both shoots and roots (Table 2), though there could be an interaction between stress  
287 type and plant family. However, using only experiments from a single family (Poaceae), stress type was still a  
288 significant moderator (Table 1). Several families showed significant DW increases with Si supply for both  
289 shoots and roots (Fig. 1), though contrary to expectations, the high accumulating Poaceae did not show a  
290 stronger response than other families. No significant DW decreases were found in any stress type or family  
291 after merging studies.

292 Meta-analyses showed that addition of Si to stressed plants significantly increased photosynthetic rate  
293 ( $A_{net}$ ) and total chlorophyll concentration (Table 1, Fig. 2A-B). Plant family was a significant explanatory factor  
294 in models of  $A_{net}$  (Table 1) and 7 of 9 families showed a positive response to Si supply. Stress type was not an  
295 important moderator overall, but did explain significant heterogeneity within Poaceae. Plant family did not  
296 have explanatory power in models of total chlorophyll content (Table 2), and neither did stress type across  
297 families, though it was a significant moderator when considering only Poaceae (Fig. 2B, Table 1). Our  
298 hypothesis (hypothesis 1) that plant biomass and photosynthesis is increased with Si addition to a stressed  
299 plant was supported, with some apparent impacts of family and stress type. The high Si-accumulating Poaceae  
300 was not different to other families.

301

### 302 *Oxidative stress markers*

303 Overall, Si addition to stressed plants reduced oxidative damage, as shown by significant reductions in  
304 2 of 3 markers of oxidative stress ( $H_2O_2$  and MDA; Fig. 3A-C, Table 1). Including either family or stress type  
305 increased the explanatory power for  $H_2O_2$  and Proline (Table 1), and stress type explained significant  
306 heterogeneity for all markers when looking at studies within Poaceae. The oxidative stress marker  $H_2O_2$  was  
307 reduced by Si addition for 7 of 10 families, including the Poaceae, Fabaceae, Solanaceae and Cucurbitaceae.  
308 These are families in which Si aquaporins have specifically been identified, while the lower Si accumulating  
309 families of Brassicaceae and Asteraceae did not show significant responses (Fig. 4A). The marker MDA was also  
310 significantly reduced following Si addition in 6 of 10 families (Fig. 3B). Proline was only significantly reduced in

311 Poaceae, showed no change in Asteraceae and Fabaceae, despite including 12 replicates each. It showed a  
312 positive response in Cucurbitaceae, but represented one sample only (Fig 3C).

313 Silicon addition significantly reduced H<sub>2</sub>O<sub>2</sub> concentration across all 11 stress types (Fig 4A), MDA  
314 concentration was significantly reduced for 9 stress types but not As or waterlogging stress (Fig 4B) but proline  
315 concentration was varied between negative and no effect of Si addition to stressed plant among stress types.  
316 Overall, there was support, therefore, for our hypothesis 2 that Si consistently alleviates oxidative stress and  
317 that responses differed among plant families, with stress type also an explanatory factor.

### 318 319 *Anti-oxidant responses*

320 There was no significant overall positive or negative effect on any of the four anti-oxidant  
321 concentrations in shoots with Si supply to stressed plants (Fig. 4, Table 1). Including stress type in meta-analysis  
322 models increased the explanatory power for SOD concentration and CAT and POD activity, but not APX activity,  
323 both for the whole dataset and the Poaceae subset (Table 1). We did not find that responses to heavy metal  
324 stress were consistent. Indeed, across the 14 stress types in the analyses, no two stresses showed the same  
325 pattern in anti-oxidant changes with Si addition (Fig. 5). For example, in B stressed plants, adding Si showed  
326 significantly reduced CAT activity (no data for POD), while in water stressed plants, SOD concentration  
327 increased with no effect on the other anti-oxidants with Si addition. Therefore, these findings supported of our  
328 third hypothesis of no consistent responses in anti-oxidant levels in stressed plants supplied with Si as it is  
329 strongly dependent on stress type. Although we made no predictions about the explanatory power of plant  
330 family, it was also a significant predictor explaining heterogeneity in Si induced anti-oxidant responses to  
331 abiotic stress.

### 332 333 *Element accumulation*

334 The overall effect sizes showed Si addition consistently increased K, and decreased Cd and Na  
335 concentrations in shoots. Similarly, it decreased As and Cd concentration in roots of stress plants, with no  
336 significant responses for Al, Ca and Mn accumulation (Fig. 5A-G). Including plant family in models of element  
337 accumulation had significant explanatory power for about half of the groups tested, predominantly those with  
338 larger sample sizes and multiple families (Table 1). The meta-analysis supported our hypothesis 4 that there are  
339 consistent changes in uptake of some elements when stressed plants are supplied with Si. Contrary to  
340 predictions, including family as a factor did increase explanatory power for the majority of elements. In  
341 addition, there were shoot and root differences, though not formally tested here. Metal concentration was not  
342 routinely reduced, though Na concentration was consistently reduced overall.

### 343 344 *Abiotic stress induced uptake of silicon*

345 Overall when Si supplied plants were stressed, Si accumulation in shoots was significantly reduced  
346 across studies, though accumulation in roots was not affected (Fig. 5E). For Si accumulation in shoots, both  
347 family and stress type were significant moderators, and stress type remained a significant factor when the  
348 Poaceae were analysed alone. No moderators explained substantial heterogeneity in root Si concentration in

349 the whole dataset or the Poaceae. The significant decrease of Si accumulation was maintained within  
350 Asteraceae and Brassicaceae, but other families did not have mean effect sizes significantly different to zero.  
351 No family showed a significant change in the accumulation of Si in roots with Si addition. We therefore rejected  
352 our final hypothesis, number 5, that plants accumulate more Si when subjected to abiotic stresses as our  
353 analysis suggests that if anything Si uptake is reduced.

354

## 355 **DISCUSSION**

356         Compilation and analysis of 125 single species and single stress studies has demonstrated consistent  
357 responses to Si addition across a broad range of plant families – with Si supply significantly alleviating oxidative  
358 stress and increasing growth. Significant stress alleviation was not limited to high Si accumulating species.  
359 Responses varied between stress types, reinforcing that Si functions through multiple stress alleviation  
360 mechanisms. Increased accumulation of Si can be induced by herbivory in some Poaceae (Reynolds *et al.* 2009;  
361 Hartley & DeGabriel 2016), but there is no evidence that abiotic stress induces additional Si accumulation and  
362 in fact could do the opposite.

363         Silicon consistently increases productivity in diverse plant families challenged by a range of stresses  
364 (Fig. 1, Table 1) and reduces oxidative damage (Fig. 3). The pattern is upheld in a range of families, including  
365 both the high Si accumulating Poaceae, and also in Brassicaceae, Cucurbitaceae and Fabaceae which  
366 accumulate Si to lesser extents, which indicates that the benefits of Si for the alleviation of abiotic stresses are  
367 not limited to high accumulating groups. Similarly consistent increases in productivity in plants subjected to  
368 diverse stresses following Si supply (both across families and within Poaceae) reinforces that the beneficial  
369 function of Si for plants is general in nature, as championed by other researchers (Datnoff *et al.* 2001; Ma 2004;  
370 Liang *et al.* 2007).

371         Meta-analyses should allow comparison between families, given sufficient samples sizes within  
372 groupings, and if 95% confidence intervals among treatments do not overlap they can be considered  
373 significantly different (Gurevitch *et al.* 2001). However, due to potential interactions between plant families  
374 and stress type and because not all family-stress type combinations were included in the meta-analysis, we are  
375 cautious about drawing conclusions about among-family differences in cases with small sample sizes. Silicon  
376 uptake is strongly associated with phylogeny (Hodson *et al.* 2005), but plants also respond to silicic acid  
377 availability with uptake increasing with availability (Ma *et al.* 2001). The amount of Si required for significant  
378 stress alleviation through biochemical mechanisms has not been established, but the significant responses by  
379 low accumulators of Si shown here, suggests that a small supply of concurrent silicic acid may be sufficient (Fig.  
380 4).

381         The significant Si-induced increase in the dry weight of stressed plants can be attributed at least in  
382 part to increased chlorophyll biosynthesis and photosynthetic rates (Fig. 3A and B), however it is not clear if  
383 stress-induced suppression has been relieved or if Si stimulates these processes directly. In a proteomic assay,  
384 Nwugo and Herta (2011) showed 50 Si related changes in 50 protein spots, including those associated with  
385 photosynthesis, redox homeostasis and protein synthesis, but could not determine if Si was the signaling  
386 molecule, or if these changes were secondary to other impacts of Si. Similarly, in a review of heavy metal

387 alleviation by Si, Wu *et al* (2013) highlighted that it can be difficult to separate interacting avoidance and  
388 tolerance responses, and the signaling and molecular role of Si in stress alleviation warrants further  
389 investigation.

390 The highly consistent reduction in two oxidative stress markers across families and stress types found  
391 in this analysis (Fig. 3), was not simply reflected by an increase in the production of anti-oxidant enzymes which  
392 showed much more complicated patterns among families and stresses (Fig. 4). Several mechanisms of stress  
393 alleviation by Si aside from stimulation of anti-oxidant production have been demonstrated, so lack of  
394 significant changes in SOD, CAT, POD and APX activity with Si supply to stressed plants is suggestive that  
395 another function of Si has been employed. The reduction in anti-oxidant production for Si supplied plants  
396 subjected to Al stress, for example, is compatible with Al co-precipitating with Si either in the substrate or  
397 plant, thereby removing the stress and the need for anti-oxidants (though only represented by one study).  
398 There is strong evidence for Si amelioration of Al toxicity in the soil (by the formation of alumino-silicates which  
399 are not absorbed by plants, Liang *et al.* 2007) but studies demonstrated that the addition of Si was not altering  
400 the external solution or soil properties or provided some evidence for *in planta* mechanisms (Cocker *et al.*  
401 1998a; Cocker, Evans & Hodson 1998b; Wang, Stass & Horst 2004). Although this meta-analysis reveals  
402 patterns in plant responses, the impact of Al stress across families and any role of anti-oxidants remains  
403 elusive.

404 The response in accumulation of the seven elements other than Si that were considered here (Al, As,  
405 Ca, Cd, K, Mn, Na), showed no apparent differences between shoots and roots overall (non-overlapping  
406 confidence intervals, Fig. 5A-E). Across plant families, Na content was significantly reduced in shoots but not  
407 roots (Fig. 5C). The reduction in Na concentration is attributed to a suppression of transpiration rates by Si  
408 deposition of the leaf epidermis and by partial blockage of the transpiration bypass flow (Matoh *et al.* 1986).  
409 Potassium uptake is increased in shoots with Si supply to stressed plants which supports the idea that  
410 mechanisms other than changed transpiration rates are responsible for differences in ion uptake rates.  
411 Evidence of multiple alleviation mechanisms is further provided by the uptake of Mn, which is not affected by  
412 Si supply to stressed plants (Fig. 5F). Individual studies record changes in other anti-oxidants and enzymes, such  
413 as guaiacol-peroxidase activity, not examined here, together with a change in Mn distribution within the plant  
414 (Ma *et al.* 2001; Iwasaki *et al.* 2002a; Fühns *et al.* 2009).

415 It is well recognised that plants provided with Si in experiments increase Si concentration (Epstein  
416 1994), and increased Si accumulation can be induced by vertebrate and invertebrate herbivory (McNaughton &  
417 Tarrant 1983; Massey, Ennos & Hartley 2007; Reynolds *et al.* 2009). In contrast dehydration or ABA treatment  
418 induces rapid reduction of Si uptake and also down regulation of Si transporter genes in rice (Yamaji & Ma  
419 2007, 2011). However, it had not been investigated whether plants take up additional Si when suffering abiotic  
420 stresses beyond this. In contrast to our prediction, when supplied with ample Si, stressed plants compared to  
421 unstressed plants accumulate less Si in shoots with no change in root Si concentration (Fig. 5F). It appears that  
422 abiotic stresses do not induce increased uptake, and it is worth noting that no increase was found in the high Si  
423 accumulating Poaceae where induced responses have been shown in response to biotic stress (Hartley &  
424 DeGabriel 2016).

425           Importantly, this study found consistent patterns, despite much variation in experimental conditions of the  
426 studies examined, including substrate used (hydroponics or soil), stress application method and severity, Si  
427 application quantities and methods, and experiment duration. The consistent responses, given the variation in  
428 experimental methods, suggest that these overall responses are conserved within plant parts and potentially  
429 within families. It was assumed that the direction of the effect of Si supply to stressed plants (ie. increases or  
430 decreases in response measure) would not be impacted by experiment differences, but at worst the variation  
431 between methods would lead to broad confidence intervals and lack of significance. Although the model  
432 moderators explained significant parts of the heterogeneity in the effect size, much remained unexplained  
433 (Table 1). Methodological heterogeneity is a likely source of variation, as noted above, together with other  
434 factors not tested here, such as cultivar and domestication status. The range of stresses that Si can alleviate,  
435 and the diversity of species tested is impressive, but hampers analyses because so many combinations need  
436 replications for statistical rigour.

437           Although the majority of these studies have been undertaken with agricultural or horticultural species,  
438 they represent taxonomically diverse groups including Poaceae, Cucurbitaceae, Brassicaceae, Solanaceae,  
439 Amaranthaceae, and nitrogen fixing Fabaceae (Supporting Information, Table S2). Consistency in responses  
440 across this phylogenetic diversity suggests that the ability of plants to use Si is widespread. Given that Si can  
441 ameliorate stress in high and low accumulators of Si, this meta-analysis provides strong evidence that in nature  
442 there are likely to be many species for which Si is an important nutrient for stress relief. While there are  
443 ecological studies exploring the function of Si and biotic stress – predominantly herbivore stress (Massey &  
444 Hartley 2006, for example) - studies of abiotic stress amelioration in nature are limited (Cooke & Leishman  
445 2011) but have increased in recent years.

446           The few studies on non-agricultural species included in this meta-analysis, however, provide  
447 tantalising evidence of the role of Si in abiotic stress alleviation in ecology. Bradbury and Ahmad (1990)  
448 demonstrated that Si increased salinity tolerance in *Prosopis juliflora*. Si was shown to reduce impacts Cd  
449 stress on mangroves, where the high availability of Si in the sea-water could play a key role in the tolerance of  
450 heavy metals of mangroves (Zhang *et al.* 2013b). Kang *et al.* (2014) demonstrated a positive impact of Si on the  
451 growth of *Haloxylon ammodendron*, a woody C4 arid-zone species, in drought conditions, but in a complicated  
452 association with NaCl. Si contributes to the salt tolerance of the marsh grass *Spartina densiflora*, despite its  
453 other adaptations to salinity and may contribute to the invasive success of this weed (Mateos-Naranjo *et al.*  
454 2013). Si also ameliorated Cu stress in the same species (Mateos-Naranjo *et al.* 2015), an illustration of the  
455 capacity of Si to alleviate multiple abiotic stresses in natural systems. In another invasive species, *Solanum*  
456 *nigrum*, Si was similarly shown to reduce the impacts of Cu toxicity (Liu *et al.* 2013). The benefits of Si  
457 accumulation in wetland environments have been studied in terms of increased ability to resist water currents  
458 and allow roots to better penetrate mud (Ernst, Vis & Piccoli 1995; Struyf & Conley 2008, not included in the  
459 meta-analysis). Also Querné *et al.* (2012) investigated the potential of Si to alleviate storm, salinity, heavy  
460 metal, grazing and disease stress in *Spartina alterniflora* in an ecological study, but showed that unravelling the  
461 interactions between Si accumulation and its role in alleviating simultaneous stresses is difficult. There is a  
462 clear need for more controlled experiments involving non-agricultural species.

463           Meta-analyses allow outcomes of multiple studies to be collated and analysed in a quantitative  
464 fashion. With hundreds of single species, single-stress studies, this field is ripe for such an evaluation. Here we  
465 analysed the 18 response variables that were among the most frequently reported, but over 200 response  
466 types were reported in the literature (Supplementary information, Table S5). Given the consistent responses  
467 found here, across families and stresses, this approach shows potential. As more data become available, it may  
468 be possible to tease apart interactions between stress types and plant family, and incorporate the severity of  
469 stress to better understand responses. This study highlights where family by stress type data are missing for  
470 different plant responses. Changes in gene expression with Si supply found only when plants are stressed  
471 (Fauteux *et al.* 2006) and proteomics analysis also offer new ways to explore how stressed plants use Si (Nwugo  
472 & Huerta 2011), through both individual and meta-analysis studies.

473           Time is also ripe to better understand the function of silicon in plants, particularly in the alleviation of  
474 abiotic stress. Environmental stress causes huge losses in agricultural productivity worldwide, and expanding  
475 cropping into sub-optimal areas, emission from industry, use of wastewater for irrigation and misuse of  
476 fertilisers and pesticides are increasing the stresses crops experience (Nagajyoti, Lee & Sreekanth 2010),  
477 together with a rapidly changing climate (Challinor *et al.* 2009). Silicon may be a more environmentally-friendly  
478 alternative or complementary option to the addition of conventional fertilisers (Beman, Arrigo & Matson  
479 2005). In addition, many Si fertilisers are made from mining waste (ie. slag) or natural products such as  
480 diatomaceous earths (Datnoff *et al.* 2001), and there is no record of too much Si causing damage to plants (Ma  
481 *et al.*, 2001). However, the increasing scale of high-Si accumulating crops means that Si use in agriculture will  
482 not be without some environmental consequences. Silicon accumulation in crops is projected to increase by up  
483 to 35% by 2050, with potential impacts on Si cycles, including increases in the relatively labile plant Si pool  
484 causing changes in dissolved Si in rivers, for example (Carey & Fulweiler 2015).

485           Similarly this topic and meta-analysis are timely given concerns about the adaptive potential of plants  
486 in a changing climate (Jump & Penuelas 2005). The capacity of Si to alleviate a range of abiotic stresses,  
487 including climate related stresses such as drought, high and low temperatures, could mean that Si plays an  
488 increasing role in ecological systems. We have shown that silicon consistently increases growth through the  
489 reduction of oxidative damage in plants facing abiotic stresses, and the many studies qualitatively combined  
490 here suggest that Si plays a more significant role in plant abiotic stress alleviation in ecology than currently  
491 appreciated. Controlled experiments examining these functions are likely to be illuminating and valuable.

492

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499

500

501 **DATA ACCESSIBILITY**

502 Effect sizes for data used in these analyses are deposited in the Dryad repository

503 (<http://datadryad.org/resource/doi:10.5061/dryad.538f8>) (Cooke and Leishman 2015)



504 **Table 1. Meta-analysis results for plant responses to Si supply in stressed plants, and stress effects on Si**  
505 **content (last lines).** For the null models (no fixed factor), study ID is included as a random factor, and a z-score  
506 with a significant result (p-value, bold) indicates an overall effect on the response measure of Si addition to  
507 stressed plants. The number of data points in each analysis is given (*k*) and  $Q_E$  is the amount of unexplained  
508 heterogeneity. Subsequent models with (Family) or stress type (Stress) as fixed factors are reported and  $Q_M$  is  
509 indicative of the heterogeneity explained by the structured model, with a significant p-value (bold) showing the  
510 amount of variation explained is more than the null model. Models exploring the impact of stress type were  
511 repeated on a subset of data on the family with the most data (Poaceae). The studies used in the analyses are  
512 listed in Table S6.

Response	Fixed factors	K	df	AIC	$Q_E$	<i>p</i>	<i>z</i>	<i>p</i>	$Q_M$	<i>p</i>
<i>Growth and photosynthesis</i>										
<b>Dry weight</b> (shoot)	NA	175	1,174	914	687	<0.001	<b>10.6</b>	<b>&lt;0.001</b>		
	Family	175	13	924	649	<0.001			14	0.29
	Stress	175	18	912	614	<0.001			<b>38</b>	<b>0.002</b>
	(Poaceae) NA	93	1,92	611	506	<0.001	<b>8.0</b>	<b>&lt;0.001</b>		
	(Poaceae) Stress	93	17	601	417	<0.001			<b>43</b>	<b>&lt;0.001</b>
	<b>Dry weight</b> (root)	NA	143	1,142	736	619	<0.001	<b>6.9</b>	<b>&lt;0.001</b>	
	Family	143	13	752	585	<0.001			8	0.76
	Stress	143	16	796	553	<0.001			22	0.12
	(Poaceae) NA	72	1,71	447	416	<0.001	<b>4.5</b>	<b>&lt;0.001</b>		
	(Poaceae) Stress	72	14	457	383	<0.001			11	0.40
<b>A<sub>net</sub></b>	NA	51	1,50	258	155	<0.001	<b>8.5</b>	<b>&lt;0.001</b>		
	Family	51	9	231	118	<0.001			15	0.05
	Stress	51	8	256	139	<0.001			4	0.74
	(Poaceae) NA	32	1,31	123	66	<0.001	<b>8.3</b>	<b>&lt;0.001</b>		
	(Poaceae) Stress	32	7	121	51	0.003			<b>15</b>	<b>0.004</b>
	<b>Chlorophyll concentration</b>	NA	51	1,51	248	180	<0.001	<b>4.4</b>	<b>&lt;0.001</b>	
Family		51	8	226	145	<0.001			8	0.196
Stress		51	9	220	136	<0.001			<b>18</b>	<b>0.013</b>
(Poaceae) NA		35	1,34	156	119	<0.001	<b>4.4</b>	<b>&lt;0.001</b>		
(Poaceae) Stress		35	6	159	106	<0.001			9	0.168
<i>Oxidative stress indicators</i>										
<b>H<sub>2</sub>O<sub>2</sub> concentration</b> (shoots)	NA	70	1,54	368	259	<0.001	<b>-6.8</b>	<b>&lt;0.001</b>		
	Family	70	10	368	190	<0.001			<b>58</b>	<b>&lt;0.001</b>
	Stress	70	11	367	190	<0.001			<b>38</b>	<b>&lt;0.001</b>
	(Poaceae) NA	26	1,25	132	76	<0.001	<b>-5.0</b>	<b>&lt;0.001</b>		
	(Poaceae) Stress	26	7	113	31	0.025			<b>45</b>	<b>&lt;0.001</b>
	<b>MDA concentration</b> (shoots)	NA	84	1,83	363	282	<0.001	<b>-7.8</b>	<b>&lt;0.001</b>	
Family		84	9	374	195	<0.001			10	0.383
Stress		84	11	375	211	<0.001			11	0.394
(Poaceae) NA		29	1,28	126	67	<0.001	<b>-7.9</b>	<b>&lt;0.001</b>		
(Poaceae) Stress		29	8	129	50	<0.001			17	<b>0.03</b>
<b>Proline concentration</b> (shoots)		NA	51	1,50	351	244	<0.001	-1.5	0.122	
	Family	51	6	247	201	<0.001			<b>12</b>	<b>0.035</b>
	Stress	51	6	243	195	<0.001			<b>14</b>	<b>0.014</b>
	(Poaceae) NA	20	1,19	117	156	<0.001	-1.8	0.08		
	(Poaceae) Stress	20	5	104	68	<0.001			<b>37</b>	<b>&lt;0.001</b>
	<i>Anti-oxidant enzymes</i>									

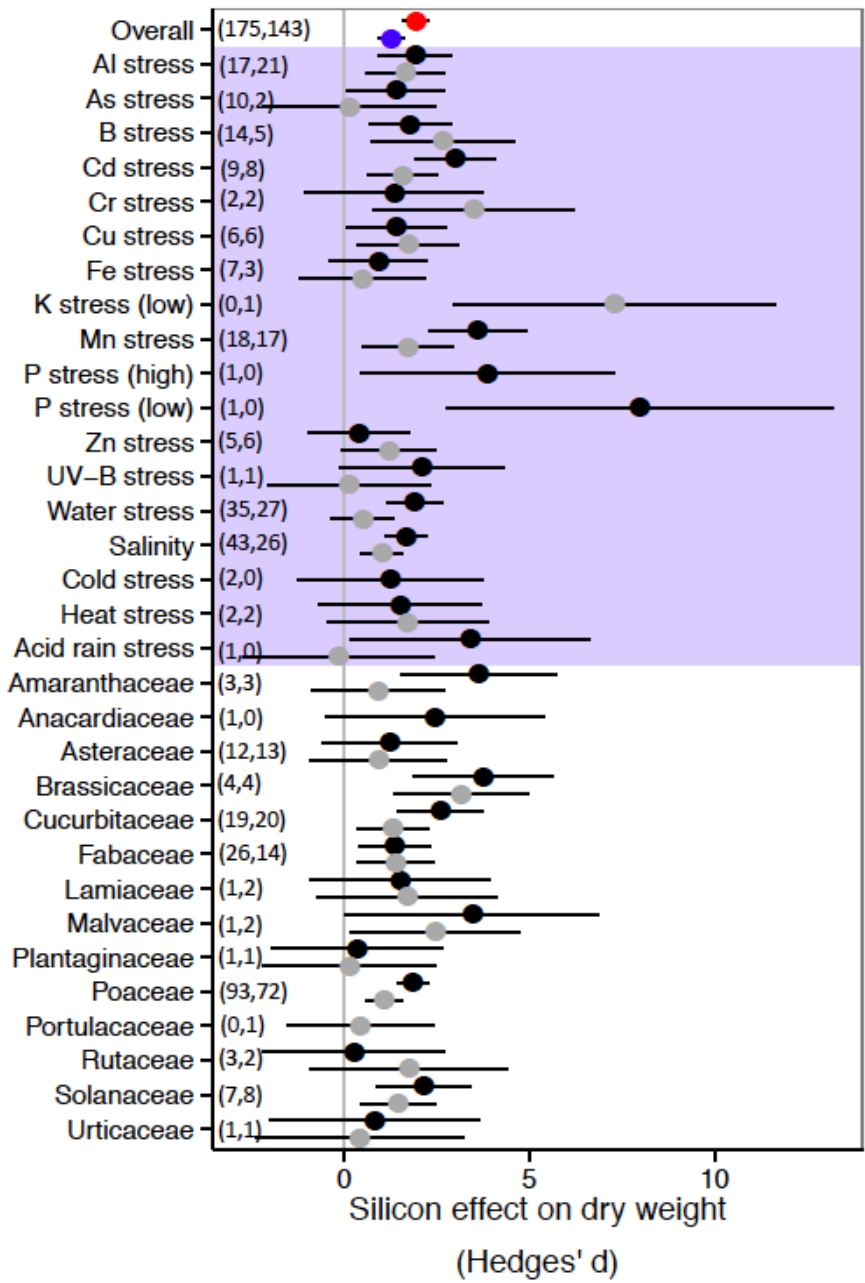
<b>SOD concentration</b> (shoots)	NA	82	50	401	453	<0.001	0.7	0.494			
	Family	82	10,71	395	332	<0.001			<b>29</b>	<b>0.001</b>	
	Stress	82	11,70	405	333	<0.001			<b>22</b>	<b>0.025</b>	
	(Poaceae)	NA	28	1,27	129	164	<0.001	7.7	0.401		
	(Poaceae)	Stress	28	7,20	135	94	<0.001			8	0.293
<b>CAT activity</b> (shoots)	NA	86	1,85	578	411	<0.001	0.61	0.543			
	Family	86	9,76	446	345	<0.001			39	<b>&lt;0.001</b>	
	Stress	86	13,72	454	286	<0.001			52	<b>&lt;0.001</b>	
	(Poaceae)	NA	33	1,32	158	139	<0.001	0.8	0.438		
	(Poaceae)	Stress	33	9,23	143	62	<0.001			77	<b>&lt;0.001</b>
<b>POD activity</b> (shoots)	NA	20	1,19	126	143	<0.001	-1.5	0.123			
	Family	20	5,14	121	91	<0.001			22	<b>0.004</b>	
	Stress	20	8,11	109	50	<0.001			61	<b>&lt;0.001</b>	
	(Poaceae)	NA	9	1,8	44	46	<0.001	-1.2	0.226		
	(Poaceae)	Stress	9	4,4	31	5	0.342			41	<b>&lt;0.001</b>
<b>APX activity</b> (shoots)	NA	66	1,65	323	346	<0.001	1.8	0.080			
	Family	66	8	307	231	<0.001			32	<b>&lt;0.001</b>	
	Stress	66	10	332	263	<0.001			10	0.323	
	(Poaceae)	NA	27	1,26	142	165	<0.001	<b>2.4</b>	<b>0.014</b>		
	(Poaceae)	Stress	27	8,18	152	135	<0.001			8	0.419
<i>Element accumulation</i>											
<b>Al</b> (shoots)	NA	18	1,17	201	152	<0.001	-1.2	0.128			
	Family	18	2,16	183	131	<0.001			.04	0.84	
<b>Al</b> (roots)	NA	26	1,25	174	258	<0.001	-1.5	0.634			
	Family	26	2,24	170	222	<0.001			<b>7.8</b>	<b>0.005</b>	
<b>As</b> (shoots)	NA	15	1,14	76	64	<0.001	-1.7	0.091			
	Family	15	1,13	77	57	<0.001			7.3	0.240	
<b>As</b> (roots)	NA	11	1,10	52	38	<0.001	<b>-2.7</b>	<b>&lt;0.001</b>			
	Family	11	1,9	52	24	0.005			3.3	0.069	
<b>Ca</b> (shoots)	NA	17	1,16	71	54	<0.001	1.2	0.224			
	Family	17	5,11	66	31	<0.001			<b>11</b>	<b>0.002</b>	
<b>Ca</b> (roots)	NA	15	1,14	72	53	<0.001	0.98	0.327			
	Family	15	4,10	77	50	<0.001			4.0	0.450	
<b>Cd</b> (shoots)	NA	26	1,25	131	107	<0.001	<b>-3.0</b>	<b>0.003</b>			
	Family	26	7,9	125	63	<0.001			<b>26</b>	<b>0.001</b>	
<b>Cd</b> (roots)	NA	17	1,16	113	114	<0.001	<b>-2.4</b>	<b>0.017</b>			
	Family	17	9,17	97	57	<0.001			<b>33</b>	<b>0.001</b>	
<b>K</b> (shoot)	NA	38	1,37	198	261	<0.001	<b>3.2</b>	<b>0.001</b>			
	Family	38	8,29	207	219	<0.001			7.7	0.486	
<b>K</b> (root)	NA	25	1,24	163	194	<0.001	1.3	0.204			
	Family	25	7,18	161	134	<0.001			<b>19</b>	<b>0.007</b>	
<b>Mn</b> (shoots)	NA	33	1,32	184	131	<0.001	0.22	0.801			
	Family	33	3,29	189	115	<0.001			1.5	0.683	
<b>Mn</b> (roots)	NA	22	1,21	127	77	<0.001	-1.5	0.142			
	Family	22	2,19	130	75	<0.001			0.5	0.768	
<b>Na</b> (shoot)	NA	52	1,51	271	276	<0.001	<b>-3.4</b>	<b>&lt;0.001</b>			
	Family	52	8,42	271	185	<0.001			<b>23</b>	<b>0.001</b>	
<b>Na</b> (root)	NA	20	1,19	85	82	<0.001	-1.1	0.281			
	Family	20	6,12	91	55	<0.001			7.4	0.281	
<b>Si</b> (shoots)	NA	77	1,76	450	459	<0.001	<b>-2.0</b>	<b>0.040</b>			
	Family	77	8,68	442	409	<0.001			<b>26</b>	<b>0.001</b>	
	Stress	47	10,36	282	237	<0.001			<b>41</b>	<b>&lt;0.001</b>	
	(Poaceae)	NA	47	1,46	296	333	<0.001	-0.9	0.346		
	(Poaceae)	Stress	47	10,36	282	236	<0.001			<b>40</b>	<b>&lt;0.001</b>
<b>Si</b> (roots)	NA	54	1,53	270	239	<0.001	-0.7	0.481			
	Family	54	7,46	277	201	<0.001			8	0.330	

	Stress	54	9,44	281	213	<0.001		7	0.630
(Poaceae)	NA	38	1,36	188	165	<0.001	-	0.888	
							0.14		
(Poaceae)	Stress	38	9,28	196	130	<0.001		11	0.281

513 Hydrogen peroxide concentration (H<sub>2</sub>O<sub>2</sub> concentration), malondialdehyde (MDA) concentration, non-enzymatic  
514 antioxidants (AA) activity, lipoxygenase (LOX) activity, ascorbate peroxidase (APX) activity, catalase (CAT)  
515 activity and superoxide dismutase (SOD) concentration.

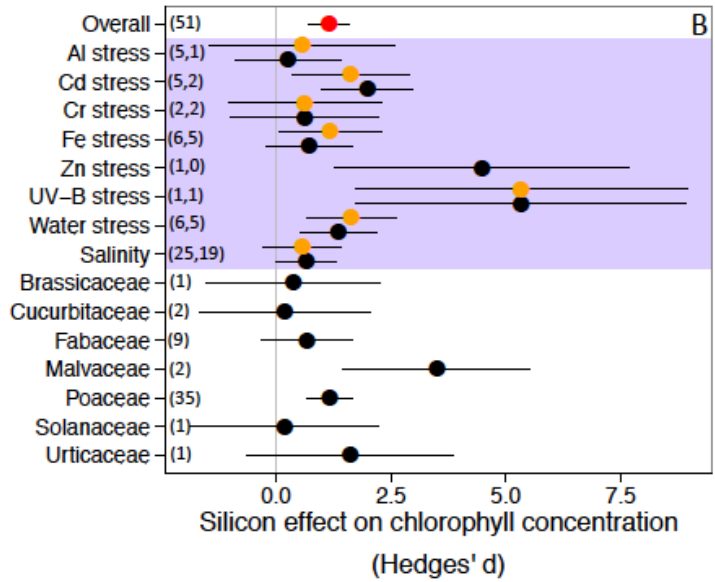
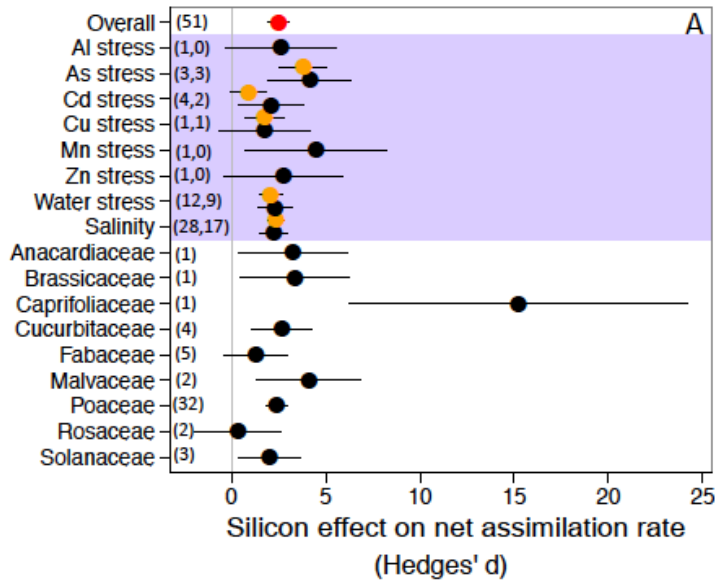
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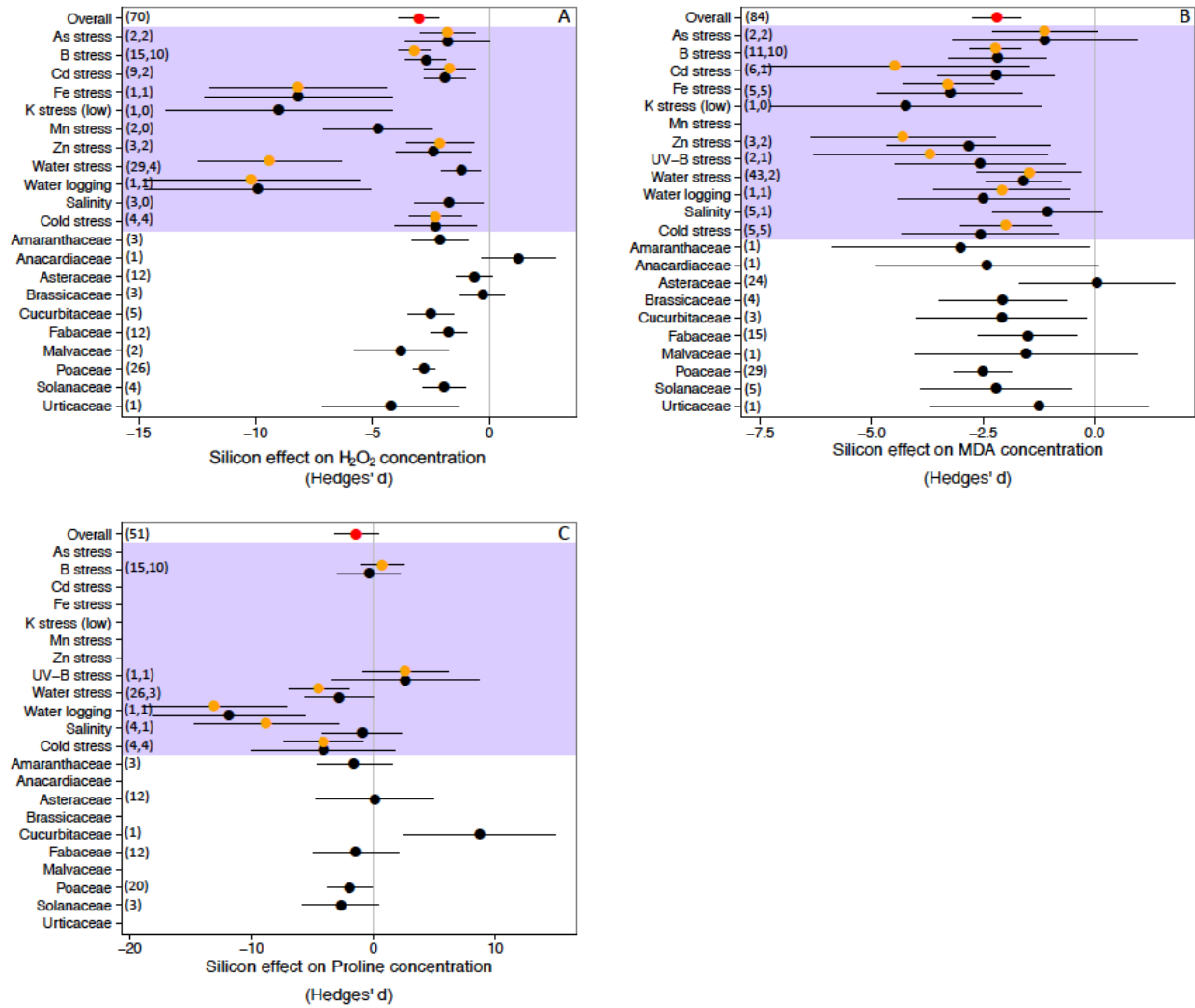


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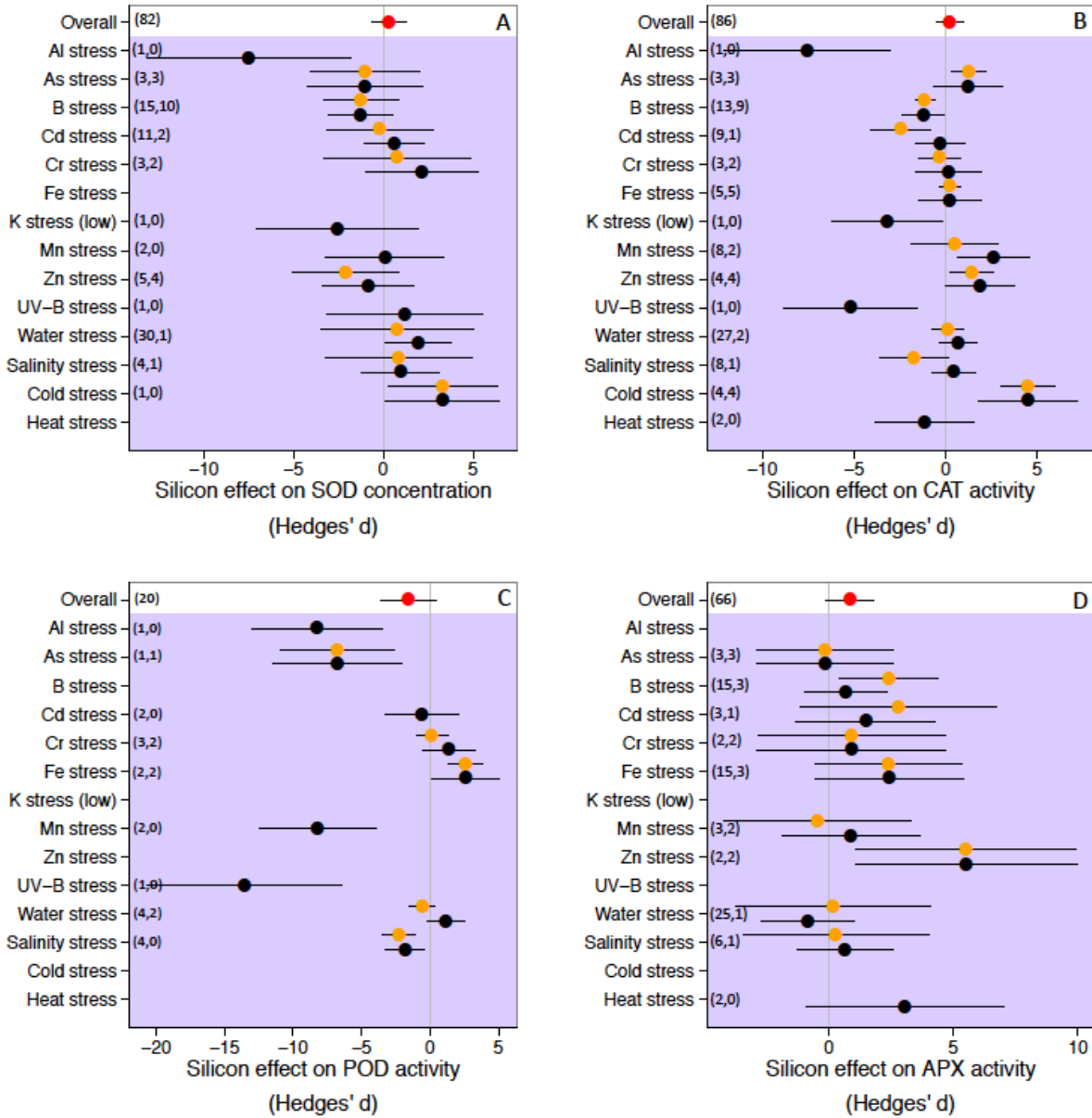
**Figure 1:** Plot of standardized effect sizes for the Si effect on dry weight. Red and blue dots indicate the mean (summary) effect size of all studies for shoot and root responses respectively. Black and grey dots indicate the mean effect sizes for factor groups of shoot and root responses respectively. Lines are 95% confidence intervals and the grey vertical line shows zero effect. Blue boxes indicate responses categorized by stress type. Samples sizes are given (shoots, roots).



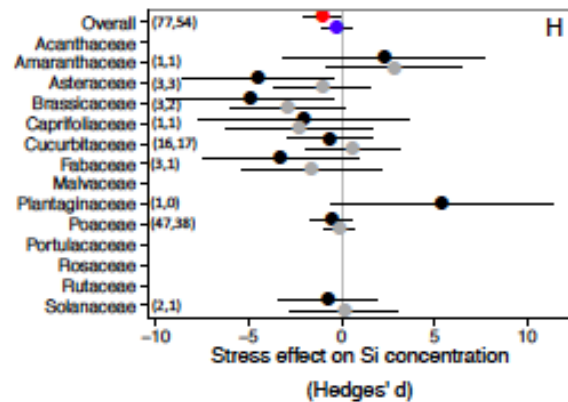
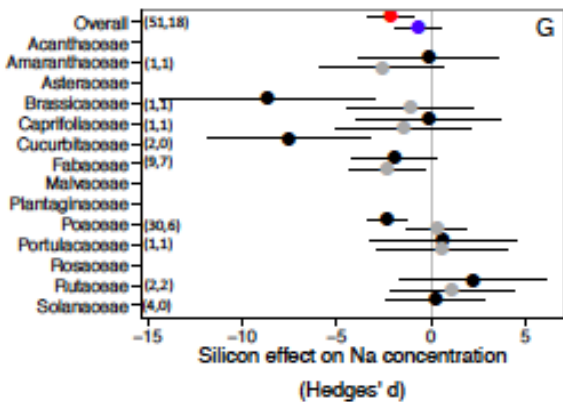
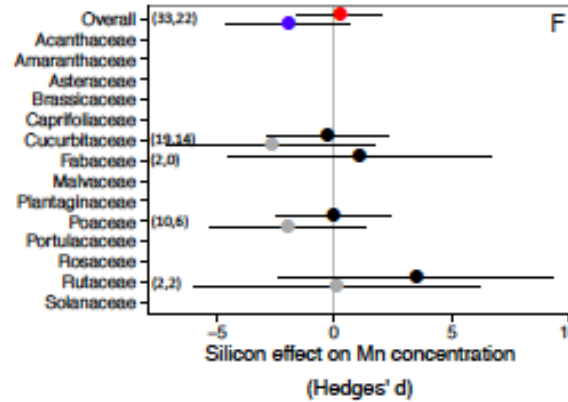
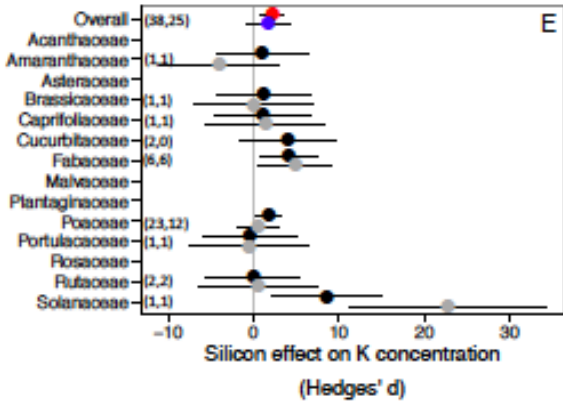
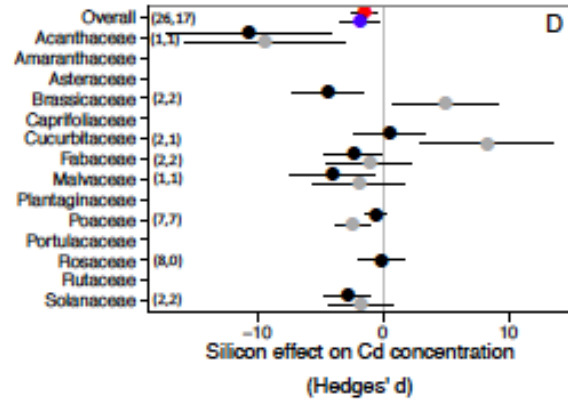
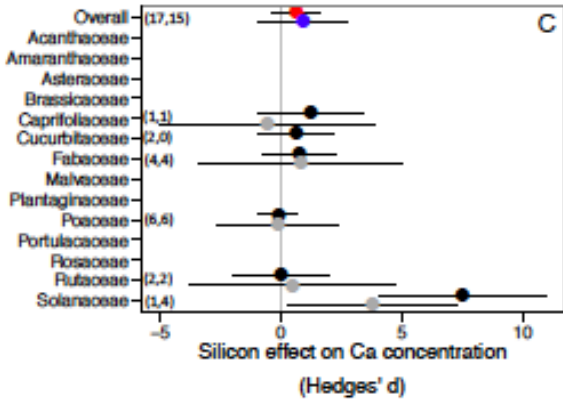
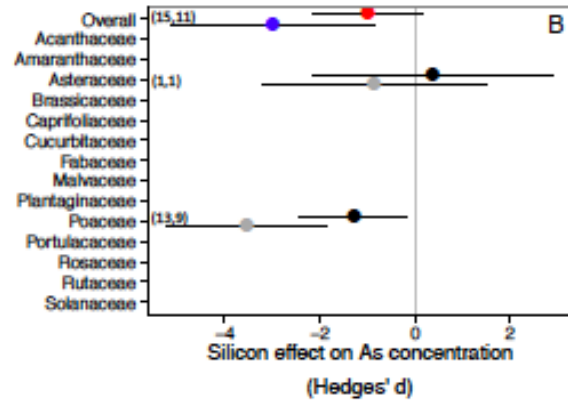
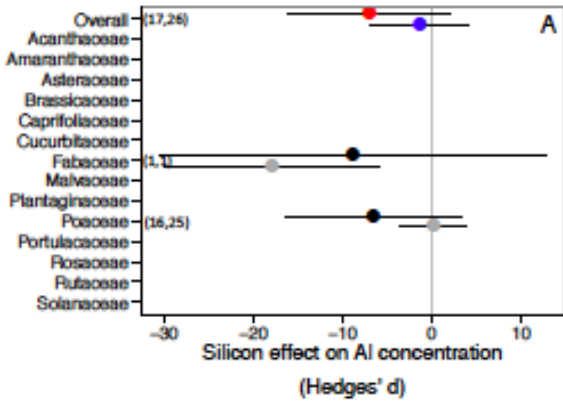
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 528 **Figure 2:** Plots of standardized effect sizes for the Si effect on (a) net assimilation rate and (b) total chlorophyll  
 529 concentration in stressed plants. Red dots indicate the mean (summary) effect size of all studies, black are subsets  
 530 as shown, and orange for subsets of Poaceae only. Lines are 95% confidence intervals and the grey vertical line  
 531 shows zero effect. Samples sizes are given (all groups, Poaceae only).



532  
 533 **Figure 3:** Plots of standardized effect sizes for the Si effect on oxidative stress markers in stressed plants including  
 534 (a) H<sub>2</sub>O<sub>2</sub> concentration; (b) MDA concentration; and (c) proline concentration. Red dots indicate the mean  
 535 (summary) effect size of all studies for shoot responses. Black dots indicate the mean effect sizes for factor groups  
 536 of shoot responses, and orange for subsets of Poaceae only. Lines are 95% confidence intervals and the grey  
 537 vertical line shows zero effect. Blue boxes indicate responses categorized by stress type. Samples sizes are given (all  
 538 groups, Poaceae only).



539  
 540 **Figure 4:** Plots of standardized effect sizes for the Si effect on anti-oxidant activity of stressed plants including (a)  
 541 SOD concentration; (b) CAT activity; (c) POD activity and (d) APX activity. Red dots indicate the mean (summary)  
 542 effect size of all studies for shoot responses. Black dots indicate the mean effect sizes for factor groups of shoot  
 543 responses. Lines are 95% confidence intervals and the grey vertical line shows zero effect. Blue boxes indicate  
 544 responses categorized by stress type.





546 **Figure 5:** Plots of standardized effect sizes for the Si effect on element accumulation of stressed plants (a) Al; (b) As;  
547 (c) Ca; (d) Cd; (e) K; (f) Mn; and (g) Na. Plot (h) shows the standardized effect sizes for the stress effect of Si  
548 accumulation in plants. Red and blue dots indicate the mean (summary) effect size of all studies for shoot and root  
549 responses respectively. Black and grey dots indicate the mean effect sizes for factor groups of shoot and root  
550 responses respectively. Lines are 95% confidence intervals and the grey vertical line shows zero effect.  
551

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992

993 **SUPPORTING INFORMATION Additional supporting information may be found in the online version of this**  
994 **article.**

995

996 Table S1: Description of how the criteria for meta-analyses in ecology (Koricheva & Gurevitch 2014) were addressed  
997 in this study.

998 Table S2: Species and families included in the meta-analyses

999 Table S3: Relationships between effect size and year of publications for any of the plant responses explored in the  
1000 meta-analysis.

1001 Table S4:  $I^2$  values (%) from the null models and models with stress and family as moderators.

1002 Table S5: Plant responses measured in the studies and collated for meta-analysis. All responses are shown to  
1003 illustrate the range and diversity of information available, however not all responses were considered in the  
1004 analyses.

1005 Table S6: Studies used in the meta-analyses described in Table 1 in the main text.

1006 Figure S1: Comparison of shoot Si content by family where given in studies compiled (filled boxes), compared to the  
1007 same families from the largest current dataset of Si accumulation (open boxes), compiled by Trembath-Reichert *et*  
1008 *al.* (2015).

1009 Figure S2: There was a significant relationship between the impact of the stress (-Si+Stress compared to -Si-Stress,  
1010 y axis) and the response to Si addition to stressed plants (+Si+Stress compared to -Si+Stress, x axis) on shoot DW,  
1011 (n=155,  $R^2=0.799$ ,  $p<0.001$ ).

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