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**Article:**

Simpson, Kimberley J., Wade, Ruth Nicola, Rees, Mark et al. (2 more authors) (2017) Still armed after domestication? Impacts of domestication and agronomic selection on silicon defences in cereals. *Functional Ecology*. pp. 2108-2117. ISSN 0269-8463

<https://doi.org/10.1111/1365-2435.12935>

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## Still armed after domestication? Impact of domestication and agronomic selection on silicon defences in cereals

Journal:	<i>Functional Ecology</i>
Manuscript ID	Draft
Manuscript Type:	Standard Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Simpson, Kimberley; University of Sheffield, Department of Animal and Plant Sciences Wade, Ruth; University of Sheffield, Animal and Plant Sciences; University of York, Biology Rees, Mark; Sheffield University, Department of Animal and Plant Sciences Osborne, Colin; Sheffield University, Dept of Animal and Plant Sciences Hartley, Susan (Sue); University of York, Department of Biology
Key-words:	crop protection, grasses, growth-defence trade-offs, herbivory, silica, wild ancestors, landraces, modern cultivars

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Manuscripts

1 ***Title page***

2

3 Still armed after domestication? Impacts of domestication and agronomic selection on

4 anti-herbivore defences in cereals

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14

15

16 *Running headline:* Anti-herbivore defences through cereal domestication

17

18 *Summary*

- 19 1. Plant phenotypes reflect trade-offs between competing resource-intensive  
20 physiological processes. A shift in resource allocation, away from anti-  
21 herbivore defences and towards growth and reproduction, is predicted through  
22 plant domestication, such that crops are faster growing and higher yielding  
23 than their wild ancestors. These changes are hypothesized to have come at the  
24 cost of defence investment, leaving crops ‘disarmed by domestication’. Silicon  
25 is the principal anti-herbivore defence in grasses, including many of our most  
26 important staple cereal crops, but the impact of domestication on silicon-based  
27 defences is unknown.
- 28 2. We measured the effects of both domestication and modern agronomic  
29 selection on growth rate and a suite of anti-herbivore defences, specifically  
30 leaf toughness, silicon and phenolic concentrations. Our comparison of wild,  
31 landrace and modern cultivated cereals spanned multiple cereal species,  
32 including wheat, barley and maize, sampling eight independent domestication  
33 events and five examples of modern agronomic selection.
- 34 3. Leaf silicon concentration showed a small, but significant, 10% reduction  
35 through domestication, but there was no effect of modern agronomic selection,  
36 and phenolic concentration was not affected by either factor. Silicon  
37 concentration correlated positively with leaf tensile strength, but negatively  
38 with foliar phenolic concentrations, suggesting a trade-off between chemical  
39 and physical defences. Size-standardised growth rate was independent of  
40 domestication status, and did not trade-off with silicon or phenolic defences.  
41 However, modeling showed that relative growth rate slowed more with  
42 increasing size in plants with higher silicon levels, so that they reached a

43 smaller asymptotic size, implying a cost of silicon-based defence. We found  
44 the opposite pattern for phenolic-based defence, with increasing phenolic  
45 concentrations associated with a greater plant size at maturity, and faster  
46 maximum relative growth rates.

47 4. Silicon-based defences have been reduced in cereals through domestication,  
48 consistent with our predicted costs of these defences to growth. However,  
49 modern agronomic selection has not influenced silicon defences in cereal  
50 crops and the small decrease in silicon concentration associated with  
51 domestication is unlikely to have a major effect on the ability of cereals to  
52 withstand a range of abiotic and biotic stresses. These findings have broad  
53 implications for crop protection and our understanding of plant trade-offs.

54

55 **Key words:** crop protection, cereals, growth-defence trade-offs, herbivory, silica, wild  
56 ancestors, landraces, modern cultivars, phenolics

57

58 ***Introduction***

59 Trade-offs between competing, energetically demanding traits are fundamental in  
60 shaping an organism's phenotype. The substantial phenotypic changes associated with  
61 plant domestication (Harlan 1971; Hammer 1984; Meyer *et al.* 2012) are thought to  
62 have resulted, in part, from changes in resource allocation between such traits, rather  
63 than an increase in productivity (Evans 1993). Strong directional selection by humans  
64 for traits of agronomic importance (Gepts 2004), such as enhanced seed production  
65 and growth rate, is predicted to have driven a re-partitioning of resources in  
66 domesticated landraces compared with their wild relatives. Modern crop cultivars,  
67 which have been shaped by recent agronomic selection and breeding (Lindig-  
68 Cisneros, Dirzo & Espinosa-Garcia 2002), are expected to be the product of an even  
69 greater reallocation of resources than domestication alone.

70 Life history theory predicts that a consequence of such a shift in resources  
71 through domestication and agronomic selection may be a reduction in other traits not  
72 of agronomic interest to humans (Evans 1993; Rosenthal & Dirzo 1997; Milla *et al.*  
73 2015). In particular, plant anti-herbivore defences may be metabolically costly and  
74 thus trade-off with traits such as growth (Herms & Mattson 1992; Coley, Bryant &  
75 Chapin 1985). Evidence from between-species comparisons shows that growth-  
76 defence trade-offs are common and widespread in natural ecosystems (Kneitel &  
77 Chase 2004, Lind *et al.* 2013), although they are not universally demonstrated (e.g.  
78 Siemens *et al.* 2002).

79 In crop systems, a strong directional selection for faster growth is predicted  
80 through domestication, so that a reduction in resources available for defence  
81 investment is expected to have occurred concurrently (Massei & Hartley 2000). In

82 general, domestication has led to a reduction in defences in many crops (Rosenthal &  
83 Dirzo 1997; Massei & Hartley 2000; Mondolot *et al.* 2008; Mayrose *et al.* 2011;  
84 Rodriguez-Saona *et al.* 2011; Meyer, Duval & Jensen 2012; Bellota, Medina &  
85 Bernal 2013; Chen, Gols & Benrey 2015). However, the increase in growth rate  
86 through domestication and agronomic selection assumed to be driving this reduction  
87 has not been found in several studies (Cook & Evans 1983; Evans 1993; Welter 2000;  
88 Preece *et al.* 2017), suggesting that changes in defence investment through  
89 domestication may not result from a trade-off with growth rate. Additionally, some  
90 studies have not found a defence reduction through domestication (Turcotte, Turley &  
91 Johnson 2014), suggesting that the phenomenon of plants being ‘disarmed by  
92 domestication’ may not be as widespread as first thought.

93 Cereals are grass species grown for their edible seed, and were among the first  
94 plants to be domesticated, around 12,000 yr ago (Zohary & Hopf 2000). There are  
95 ~30 cereal species (Bouchenak-Khelladi *et al.* 2008), which are grown worldwide at a  
96 huge scale, with an estimated production of over 2500 million tonnes for 2014/2015  
97 (FAO 2015). Three of these species (maize, rice and wheat) alone represent the  
98 world’s most important staple crops, together providing 60% of human food energy  
99 intake (FAO 1995). Through the domestication process, cereals developed a shared  
100 suite of traits that are strikingly different to their wild relatives (Harlan, Wet & Price  
101 1973). Traits associated with harvesting (non-shattering of mature seeds), seed  
102 production (increased seed size and yield), regeneration (loss of seed dormancy),  
103 development (reduced branching and synchronous maturation) and growth (increased  
104 seedling size and vigor) were selected for, consciously or unconsciously, through  
105 domestication.

106           The impacts of these major phenotypic changes on cereal resistance to  
107 herbivory have been explored in several studies (Rosenthal & Dirzo 1997; Bellota,  
108 Medina & Bernal 2013; Turcotte, Turley & Johnson 2014; Maag *et al.* 2015). Cereal  
109 anti-herbivore defences consist of chemical defences, including the presence of  
110 distasteful phenolic compounds in leaves and stems, and physical defences, such as  
111 tough leaves (Vicari & Bazely 1993). Domestication appears to have had mixed  
112 effects on these defences. For example, a reduction in leaf toughness through maize  
113 domestication was associated with lower resistance to a specialist herbivore (Bellota,  
114 Medina & Bernal 2013). However, in a comparison of 29 crops, including seven  
115 cereals, Turcotte, Turley and Johnson (2014) found that most domestication events  
116 did not cause differences in leaf phenolic concentrations or resistance to two common  
117 herbivores. However, none of these studies investigated the effect of domestication on  
118 the principal defence of grasses – silicon.

119           A widespread characteristic of grasses is tissue silicification, in which silicon  
120 is taken up in unusually large amounts from the soil and deposited in the leaves, in the  
121 form of spines and as sharp granules called phytoliths (Hodson *et al.* 2005; Hartley *et*  
122 *al.* 2015). Plant silicon has multiple functional roles in plants (Cooke, DeGabriel &  
123 Hartley 2016), including resistance to abiotic stresses, such as drought and salinity,  
124 and to biotic stresses such as pests and diseases (Ma & Yamaji 2008; Cooke &  
125 Leishman 2011). In addition, silicon may have important structural roles in plants, as  
126 a compression-resistant stiffening material (Schoelynck *et al.* 2010; Strömberg, Di  
127 Stilio & Song 2016). One key function of silicon is as the main physical anti-  
128 herbivore defence in grasses (Cooke & Leishman 2011; Hartley & DeGabriel 2016).  
129 By reducing digestibility and the absorption of essential nutrients, leaf silicon can  
130 detrimentally affect vertebrate and invertebrate herbivore performance (Massey &



131 Hartley 2006; 2009; Wiczorek *et al.* 2015; Reynolds, Keeping & Meyer 2009).  
132 Phytoliths also make leaves highly abrasive, which wears down the mouthparts of  
133 herbivores (Massey & Hartley 2009). In addition to being a constitutive defence,  
134 silicon-based defences can also be induced, with leaf silicon-levels being raised  
135 substantially in response to herbivore damage (Massey, Ennos & Hartley 2007a;  
136 Hartley *et al.* 2015; Wiczorek *et al.* 2015). This reactive increase in silicon levels  
137 implies active control over silicon uptake and/or allocation within the leaf, and hence  
138 a potential fitness cost of this defence. Although the relative contributions of active  
139 and passive processes to silicon uptake remain uncertain and are likely to vary  
140 between species (Faisal *et al.* 2012; Quigley & Anderson 2014; Hartley 2015; Kumar  
141 *et al.* 2016), the existence of an active proton pump required for efflux of silicon into  
142 the xylem in many crop species suggests an energetic cost to silicon uptake (Ma *et al.*  
143 2007; Ma & Yamaji 2015). However, costs associated with silicon-based defences  
144 have not been conclusively demonstrated, and whether these defences trade-off with  
145 growth or other physiological process is currently unknown.

146         This study aimed to determine how anti-herbivore defences were modified  
147 through cereal domestication and agronomic selection. Through comparisons of  
148 cereal landraces with their wild progenitors and with modern cultivars, we established  
149 the effects of domestication and agronomic selection on silicon- and phenolic-based  
150 constitutive defences. To determine whether any changes in leaf silicon or phenolic  
151 concentrations arose from resource reallocation, plant growth rate was measured as a  
152 performance trait that is expected to trade off against defence. We predicted that wild  
153 progenitors would be the best defended and slowest growing, modern cultivars would  
154 be the fastest growing and poorest defended, and landraces would have intermediate  
155 trait values.

156 ***Materials and methods***

157 Species selection and plant growth conditions

158 We chose 21 cereal species, representing eight independent domestication events,  
159 from multiple centres of domestication, and five periods of modern agronomic  
160 selection. Of these, eight species are landraces, and eight their wild progenitors (Table  
161 1). Modern cultivars were chosen for five major crops (excluding einkorn, *Triticum*  
162 *monococcum*, and the two millets, *Pennisetum glaucum* and *Setaria italica*). Seeds for  
163 all species were obtained from a variety of germplasm holdings (see Table S1 for  
164 details).

165 Seeds germinated in Petri dishes within a growth chamber set to 25°C and a 16-  
166 hour photoperiod. After 17 seeds of a species had germinated, the seedlings were  
167 transplanted into 1-litre pots filled with M3 compost (Levington Horticulture Ltd.,  
168 Ipswich, UK), supplemented with fertilizer (Scotts M3-4 Osmocote Exact Standard  
169 fertilizer, Maryville, OH, USA), so that nutrient supply was not limiting to growth.  
170 Plants were grown in a randomized block design within a controlled environment  
171 chamber (Conviron BDW 40, Winnipeg, Canada). Conditions were: 16 hour/8 hour  
172 day/night cycle, 25/16°C (day/night temperature), relative humidity of 80%, and  
173 photosynthetic photon flux density (PPFD) of 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Plants were top  
174 watered to saturation three times a week with deionised water and the blocks were re-  
175 randomized twice weekly.

176

177 Growth rate analysis

178 To examine the effect of domestication on plant growth, we determined the relative

179 growth rate for each species when plants were at a common mass (standardized  
180 growth rate, or SGR, Rees *et al.* 2010). Two randomly selected plants of each species  
181 were destructively harvested at 6 time points over a 30-day period. At each harvest,  
182 plants were removed from pots, washed clean of growth medium, and dried at 50°C  
183 for a week, before weighing using a four-point balance (PA413/1, Ohaus, NJ, USA).

184 Growth curves were fitted to log-transformed total dry mass data over time for  
185 each species in R (R Core Development Team 2013) using nonlinear mixed effects  
186 models (nlme package; Pinheiro *et al.* 2016). The four-parameter logistic growth  
187 function was used with a self-starting routine. Species-specific, independent random  
188 effects were fitted for asymptotic plant mass ( $m_{\max}$ ), minimum plant mass ( $m_{\min}$ ) and  
189 the time point when plant mass was midway between these ( $x_{\text{mid}}$ ). These species-  
190 specific growth curves were then used to estimate SGR (see Rees *et al.* (2010) for  
191 further details).

192

### 193 Plant defence measurements

194 We examined whether domestication and modern agronomic selection had  
195 consistently altered leaf phenolic and silicon concentrations in cereals, and how the  
196 latter trait relates to another physical defence, leaf tensile strength. Seven plants of  
197 each species were harvested 30 days after transplanting (five plants in addition to the  
198 two plants from the final harvest of the growth rate analysis). Leaf tensile strength  
199 was tested on freshly harvested leaf material following the methods of Cornelissen *et al.*  
200 *al.* (2003). The force required to tear two leaf sections of known width was  
201 determined for each plant, and an average value calculated. All leaf material was then  
202 oven dried at 60°C for 48 hours, before being ground into a fine powder.

203           The Folin-Ciocalteu method was used to determine total foliar phenolic  
204 content (Kerslake, Woodin & Hartley 1998). A sample (~10mg) from each individual  
205 was extracted in methanol at 80°C for 30 minutes, before being centrifuged. 100µl of  
206 the supernatant was added to 0.25ml Folin-Ciocalteu reagent and 1ml saturated  
207 sodium carbonate. After one hour, the absorbance of each sample was measured on a  
208 spectrophotometer at a wavelength of 760nm. Absorbance values were converted to  
209 tannic acid equivalents using a tannic acid standard curve (0-2mg tannic acid), and  
210 results were expressed in % per dry leaf mass.

211           For measurements of leaf silicon concentration, two oven-dried, ground  
212 samples (>0.1g) of leaf material from each individual were pressed into 13mm-  
213 diameter pellets. Following the methods of Reidinger, Ramsey and Hartley (2012),  
214 foliar silicon concentration (% dry mass) was determined using a Niton XL3t XRF  
215 analyzer (Thermo Fisher Scientific, Inc., MA, USA), for a measurement time of 30  
216 seconds. The machine was calibrated using a standard curve of methyl cellulose,  
217 validated with certified plant reference material of known silicon concentration  
218 (Garbuzov, Reidinger & Hartley 2011).

219

## 220 Statistical analysis

221 The effects of domestication and agronomic selection on SGR, leaf silicon  
222 concentration, phenolic concentration and tensile strength were determined by fitting  
223 linear mixed-effects models to the trait data (“lme4” package, Bates *et al.* 2014). The  
224 fixed effect was “domestication status”, and “comparison” was added as a random  
225 effect to account for the phylogenetic non-independence of species within each  
226 comparison. “Species” was an additional random effect in the silicon, phenolic and

227 tensile strength models to account for multiple measurements per species. The effects  
228 that domestication status had on SGR, leaf silicon concentration, phenolic  
229 concentration and tensile strength were determined through model comparison  
230 (complete model vs. grand mean model) using a parametric bootstrapping method  
231 (“pbkrtest” package, Halekoh & Højsgaard 2015) with 10,000 simulated generations.  
232 As there was a significant effect of domestication status on leaf silicon concentration,  
233 the same model comparison approach was used to determine where in the  
234 domestication/agronomic selection process this significant change occurred.

235       To determine whether silicon- and phenolic-based defences represent a  
236 metabolic cost to plants, two approaches were taken. Firstly, the relationships  
237 between growth and defence traits were investigated to see if they exhibited a trade-  
238 off. Linear mixed effects models were fitted to the species-level SGR and defence  
239 (leaf silicon and phenolic concentration) data, with “comparison” as the random  
240 effect. Model comparison was carried out as above. Secondly, the effect of varying  
241 leaf silicon and phenolic concentrations on relative growth rate (RGR) was modeled  
242 by allowing  $m_{\max}$  to be a linear function of silicon/phenolic concentration. Using this,  
243 the relationship between RGR and plant size was predicted for each species, based on  
244 the species-specific average silicon and phenolic concentrations.

245       To establish the relationships between the measured anti-herbivore defences  
246 across species, linear mixed effects models were fitted to the species-level leaf silicon  
247 concentration data, and both the leaf tensile strength and leaf phenolic concentration  
248 data in turn. Comparison was included as a random effect. To determine the  
249 relationships between silicon concentration and tensile strength/phenolic  
250 concentration within each species, linear models were fitted to these data for each

251 species.

## 252 **Results**

253 Domestication status had a significant effect on leaf silicon concentration (Likelihood  
254 ratio test (LRT=7.82, df=2,  $P=0.02$ ), but not on leaf phenolic concentration  
255 (LRT=0.90, df=2,  $P=0.64$ ) or leaf tensile strength (LRT=4.75, df=2,  $P=0.09$ ). Cereal  
256 domestication caused an average 10% reduction in leaf silicon concentration  
257 (LRT=4.78, df=1,  $P=0.03$ ), but agronomic selection did not reduce leaf silicon  
258 significantly (LRT=0.88, df=1,  $P=0.34$ ; Figure 1). Species average leaf silicon  
259 concentration ranged between 0.3 and 1.4% of leaf dry mass (Table S2), and was  
260 significantly positively correlated with leaf tensile strength between species  
261 (LRT=16.49, df=1,  $P<0.001$ ; Figure 2 and Table S2). Within species, the relationship  
262 between leaf silicon concentration and tensile strength was not significant for 19/21  
263 species ( $P>0.05$  in all cases). In the two cases where the relationship was significant,  
264 it was positive in one species (*Sorghum bicolor*, slope=0.692,  $P=0.007$ ) and negative  
265 in the other (*Triticum dicoccon*, slope= -0.253,  $P=0.01$ ). Leaf phenolic content ranged  
266 from 0.06 and 3.04% of leaf dry mass (Table S2), and was significantly negatively  
267 related to leaf silicon concentration across species (LRT=4.49, df=1,  $P=0.034$ ; Figure  
268 2), but was only significantly negatively correlated within one species (*Hordeum*  
269 *spontaneum*, slope=-0.693,  $P=0.006$ ).

270 Domestication status had no effect on SGR (LRT=2.80; df=2;  $P=0.24$ ), with  
271 average values differing little between wild progenitors (0.29 g g<sup>-1</sup> day<sup>-1</sup>), landraces  
272 (0.32 g g<sup>-1</sup> day<sup>-1</sup>) and modern cultivars (0.26 g g<sup>-1</sup> day<sup>-1</sup>). Domestication status also  
273 had a marginally significant influence on the minimum mass ( $m_{\min}$ ), consistent with  
274 the larger seed size of domesticated crops than their wild progenitors, but there was

275 no effect on the other parameters used to fit the growth curves ( $P>0.05$ ; Figure S1).

276 We found no direct evidence for a trade-off between SGR and leaf silicon  
277 concentration (LRT=0.64,  $df=1$ ,  $P=0.42$ ), or between SGR and leaf phenolic  
278 concentration (LRT=2.74,  $df=1$ ,  $P=0.12$ ), when SGR was compared among species at  
279 a common size of 0.2g. However, the modeled relationship between leaf silicon  
280 concentration and growth parameters throughout plant development provided  
281 evidence for a cost of silicon-based defences that emerged at larger plant sizes:  
282 increasing foliar silicon concentration was linked to a decrease in both the final plant  
283 size and the maximum relative growth rate ( $P=0.035$  for the fitted model, Figure 3).  
284 The species with the highest silicon concentration (*Triticum boeoticum*) was predicted  
285 to have 18% lower maximum relative growth rate (0.235 vs. 0.288  $\text{g g}^{-1}\text{day}^{-1}$ ) and  
286 15% lower final plant size (taken at  $\text{RGR}=0$ ; 7.47g vs. 8.81g), when compared to the  
287 species with the lowest silicon concentration (*Sorghum bicolor*).

288 In contrast, the modeled relationship between leaf phenolic concentration and  
289 growth parameters showed that increasing phenolic concentrations were associated  
290 with a greater plant size at maturity, and faster maximum relative growth rates  
291 ( $P=0.001$  for the fitted model, Figure 3). *Zea mays* subsp. *parviglumis*, the species  
292 with the highest average foliar phenolic concentration, was predicted to have a 25%  
293 greater final size (9.47g vs 7.15g) and a 30% higher maximum relative growth rate  
294 (0.315 vs 0.222  $\text{g g}^{-1}\text{day}^{-1}$ ) than *Triticum aestivum* cv. 'Hereward', the species with the  
295 lowest phenolic content.

296

## 297 **Discussion**

298 This study is the first to determine the impacts of domestication and modern

299 agronomic selection on silicon-based anti-herbivore defences in cereals, which  
300 include some of our most economically important staple crops. Whilst a handful of  
301 studies have explored the influence of domestication on other cereal defences  
302 (Rosenthal & Dirzo 1997; Bellota, Medina & Bernal 2013; Turcotte, Turley &  
303 Johnson 2014; Chen, Gols & Benrey 2015), none have investigated silicon, the key  
304 anti-herbivore defence in grasses (Vicari & Bazely 1993; Massey, Ennos & Hartley  
305 2007b; Reynolds, Keeping & Meyer 2009). The finding of a small but significant  
306 reduction in cereal silicon-based defence levels here suggests that this defence has  
307 been ‘disarmed’ by domestication, but to only a limited extent (Massei & Hartley  
308 2000; Meyer, Duval & Jensen 2012), whilst modern agronomic selection had no  
309 detectable effect on cereal silicon-based defences.

310         A high level of accumulated silicon acts as an effective plant anti-herbivore  
311 defence. Multiple detrimental impacts on herbivore performance are well-documented  
312 (Ma & Takahashi 2002; Hunt *et al.* 2008; Massey & Hartley 2009). In addition, we  
313 found that species with high leaf silicon concentrations also tended to have high  
314 tensile strength. Like silicon, this leaf trait is an important physical defence against  
315 herbivores, reducing their performance by increasing the metabolic costs of leaf  
316 digestion (Roces & Lighton 1995; Clissold *et al.* 2009). Interestingly, within species  
317 there is little evidence of significant correlations between leaf silicon concentration  
318 and tensile strength, and neither was there evidence of changes in leaf tensile strength  
319 through domestication and agronomic selection as found elsewhere (Maag *et al.*  
320 2015). The 10% reduction in silicon concentration through domestication we detected  
321 could imply that cereal landraces may be more susceptible to herbivory than their  
322 wild progenitors. However, whether such changes in silicon are sufficient to influence  
323 herbivore behavior is unknown; studies demonstrating impacts on herbivore



324 preference and performance have involved much larger changes in silicon  
325 concentration (e.g. Massey, Ennos & Hartley 2006, 2007a).

326         The negative relationship between silicon- and phenolic-based defences is  
327 consistent with several studies that have found that silicon accumulation is associated  
328 with reduced concentrations of phenolic compounds (Cooke & Leishman 2012; Frew  
329 *et al.* 2016). A proposed explanation for this trade-off is that plants partly substitute  
330 carbon- for silicon-based defences such that, when carbon is not limiting, it is  
331 deployed instead of silicon and associated with faster growth rates (Cooke &  
332 Leishman 2011; Schaller, Brackhage & Dudel 2012). This may result in a more  
333 efficient allocation of carbon, which would be consistent with the predicted positive  
334 association here between phenolic content, plant growth rate and final size. We found  
335 no reduction in phenolic concentration through cereal domestication, which mirrors  
336 the findings of other studies investigating cereal defences (Turcotte, Turley &  
337 Johnson 2014; Maag *et al.* 2015), possibly because allocation to phenolics is known  
338 to be particularly variable in response to a range of environmental and other  
339 parameters (Jones & Hartley 1999).

340         Agronomic selection has not significantly reduced constitutive chemical or  
341 physical defence levels in cereals, a result consistent with previous findings for maize  
342 (Rosenthal & Dirzo 1997) and cranberry (Rodriguez-Saona *et al.* 2011). An  
343 insufficient change in selection pressure between cereal landraces and modern  
344 cultivars may explain these non-significant results. Many modern cultivars are grown  
345 outside their natural range, so may experience reduced selection pressure for anti-  
346 herbivore defences, due to potential “escape” from herbivore attack (Keane &  
347 Crawley 2002; Müller-Schärer, Schaffner & Steinger 2004; Schaffner *et al.* 2011).

348 Alternatively, breeders may have selected for structural traits linked to high silicon  
349 concentrations through agronomic selection. Silicon-rich stiff straw and strong leaves  
350 may be associated with desirable properties such as resistance to lodging (Shimoyama  
351 1958) and enhanced photosynthesis (Okuda & Takahashi 1962). Silicon offers  
352 multiple, often unrelated, benefits to plants simultaneously, so distinguishing between  
353 the adaptive significance of increased structural support and resistance against  
354 herbivores is challenging. Indeed, the result of a recent attempt to do this in wild  
355 grasses was inconclusive and suggested that both herbivore pressure and structural  
356 support could be important evolutionary drivers of silicon accumulation (Strömberg,  
357 Di Stilio & Song 2016).

358 We found no consistent change in size-standardised growth rate through cereal  
359 domestication or agronomic selection. This adds to a growing body of studies that  
360 have failed to find growth rate alterations through domestication (Cook & Evans  
361 1983; Welter 2000; Preece *et al.* 2017). For example, Evans (1993) found no  
362 consistent trends in growth rate between wild and domesticated wheats, whilst Preece  
363 *et al.* (2017) attributed the greater yield in domesticated wheat and barley landraces to  
364 larger initial and final sizes, and changes in allocation, compared with their wild  
365 relatives. Some differences in traits relating to seed size and dormancy were  
366 consistent with the domestication syndrome (i.e. an increase in initial plant mass and  
367 shorter seedling emergence times); however these traits are not directly related to  
368 growth rate. In our SGR analysis, we therefore find no direct evidence that the small  
369 reduction in silicon-based defence through domestication was caused by a  
370 reallocation of resources towards faster growth despite our modeled prediction that  
371 higher silicon concentrations are associated with lower growth rates and smaller final  
372 plant sizes. Through our modelling approach, we found that the adverse effect of

373 allocation to silicon defences on growth rate increases with plant size, implying that  
374 the costs of silicon defences are relatively greater for larger plants. This could be due  
375 to the greater costs of uptake, mobilization and deposition of silicon in larger plants,  
376 or because plants with higher potential maximal growth rate and asymptotic size  
377 suffer most from the costs associated with silicon uptake. The predictions from our  
378 model may contrast with the results from the SGR analysis because we conducted this  
379 species comparison with plants of only 0.2g, possibly too small to show any effects of  
380 silicon on growth rate. However, as the plants increase in size, the effect is predicted  
381 to become more pronounced.

382       The deposition of silicon in plant tissues is an energetically expensive process  
383 involving active efflux transporters (Ma *et al.* 2007; Ma & Yamaji 2015). Our overall  
384 analysis is consistent with this: the species with the highest silicon concentration was  
385 modeled to be 15% smaller than the species with the lowest silicon concentration, and  
386 was predicted to grow more slowly, suggesting silicon uptake is costly. Silicon uptake  
387 in the roots occurs via a combination of passive uptake in the transpiration stream  
388 through aquaporin-type transporters and energy-demanding processes via proton  
389 pumps (Ma & Yamaji 2006; Cooke & Leishman 2011; Hartley 2015; Kumar *et al.*  
390 2016). The balance between active and passive processes, which may depend upon  
391 transpiration rates, plant silicon demands and soil silicon availability (Faisal *et al.*  
392 2012), could determine the impact of silicon uptake on plant growth rate. Despite  
393 such potential costs and associated impacts on growth, increased silicon concentration  
394 may also benefit plant growth under different abiotic and biotic stresses (Ma 2004;  
395 Gong *et al.* 2005; Cooke & Leishman 2011; Guntzer, Keller & Meunier 2012), such  
396 that the benefits from silicon uptake must sometimes outweigh the negative impacts  
397 of actively transporting additional silicon.

398 Our finding that silicon, the principal defence in grasses, has been unchanged or  
399 reduced by only a small degree through domestication and modern agronomic  
400 selection, suggests that cereal crops have not been ‘disarmed’ in this part of their  
401 armory (Massei & Hartley 2000). Silicon also has an important role in alleviating  
402 other biotic and abiotic plant stresses (Ma & Yamaji 2006; Zhu & Gong 2014); in  
403 grasses for example, silicon increases resistance to fungal and bacterial pathogens  
404 (Seebold *et al.* 2001; Rodrigues *et al.* 2015), and to drought (Hattori *et al.* 2005). The  
405 small decrease in silicon concentration associated with domestication is unlikely to  
406 have a major effect on the ability of cereal plants to withstand a range of abiotic and  
407 biotic stresses.

408

#### 409 *Author Contributions Statement*

410 KS, CO and SH conceived the ideas and designed methodology. KS collected the  
411 data. KS, RW, CO, SH and MR analysed the data. KS and SH led the writing of the  
412 manuscript. All authors contributed critically to the drafts and gave final approval for  
413 publication.

414

#### 415 *Acknowledgements*

416 We thank Georg Frenck, Catherine Preece, Rebecca Atkinson, Millie Mockford,  
417 Chris Bennett, Irene Johnson and Stefan Reidinger for their assistance in the lab.  
418 Seeds were kindly provided by a number of germplasm resources. Funding was  
419 provided by Natural Environment Research Council grants awarded to CO  
420 (NE/H022716/1) and SH (NE/F003137/1).

421

422 ***Data Accessibility***

423 Trait data: Species average values of leaf silicon concentration, phenolic  
424 concentration and tensile strength uploaded as online supporting information; raw  
425 data available in DRYAD entry doi: xx.xxxx/dryad.xxxx (TBC)

426

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645 University Press, Oxford, UK.

646 *Tables*

647 Table 1. Cereal wild progenitor and landrace comparisons.

Landrace	Wild progenitor	Centre of domestication	Reference
<i>Hordeum vulgare</i> (Barley)	<i>Hordeum spontaneum</i>	Southwest Asia	Zohary & Hopf (2000)
<i>Oryza sativa subsp. indica</i> (Asian rice)	<i>Oryza rufipogon</i>	South China	Cheng <i>et al.</i> (2003)
<i>Pennisetum glaucum</i> (Pearl millet)	<i>Pennisetum violaceum</i>	Africa (sub-Saharan)	De Wet (1995)
<i>Setaria italica</i> (Foxmail millet)	<i>Setaria viridis</i>	North China	Doust & Kellogg (2002)
<i>Sorghum bicolor</i> (Sorghum)	<i>Sorghum arundinaceum</i>	Africa (sub-Saharan)	Aldrich & Doebley (1992)
<i>Triticum monococcum</i> (Einkorn)	<i>Triticum boeoticum</i>	Fertile Crescent	Feldman, Lupton & Miller (1995)
<i>Triticum dicoccon</i> (Emmer wheat)	<i>Triticum dicoccoides</i>	Fertile Crescent	Feldman, Lupton & Miller (1995)
<i>Zea mays</i> (Maize)	<i>Zea mays subsp. parviglumis</i>	Meso-America	Doebley (2004)

648

649



650 *Figures*

651

652 *Figure legends*

653

654 **Figure 1. The effects of domestication and agronomic selection on cereal silicon-**

655 **based defence.** Points represent mean values of leaf silicon concentration for each

656 species, and these are grouped within comparisons. Silicon concentration was

657 significantly reduced through domestication ( $P=0.02$ ) but not modern agronomic

658 selection ( $P=0.34$ ). Error bars =  $\pm$  standard error. DM = dry mass; cv = cultivar.

659

660 **Figure 2. The relationships of leaf silicon concentration with leaf tensile strength**

661 **(top) and leaf phenolic concentration (bottom).** Values represent means  $\pm$  standard

662 error bars. Across species, leaf silicon concentration correlated positively with leaf

663 tensile strength ( $P<0.001$ ) but negatively with leaf phenolic concentration ( $P=0.034$ ).

664 Triticum 1 is the comparison between Einkorn wheat (*T. monococcum*) and its

665 progenitor (*T. boeoticum*); Triticum 2 is the comparison between Emmer wheat (*T.*

666 *dicoccon*), its progenitor (*T. dicoccoides*) and modern cultivar (*T. aestivum*). DM =

667 dry mass.

668

669 **Figure 3. Silicon-based defence is linked to slower growth whereas phenolic-**

670 **based defence is associated with faster growth.** The modeled effect of varying

671 levels of leaf silicon concentration (left) and phenolic concentration (right) on plant

672 relative growth rate. Final plant size ( $m_{\max}$ ) is modeled as a linear function of

673 silicon/phenolic concentration. Each line represents the predicted relationship

674 between relative growth rate and plant size for one species based on the species-

675 specific average silicon and phenolic concentrations. The line colour reflects defence  
676 concentration values. Plant dry mass values were multiplied by 1000 before log-  
677 transformation to ensure positive end values.

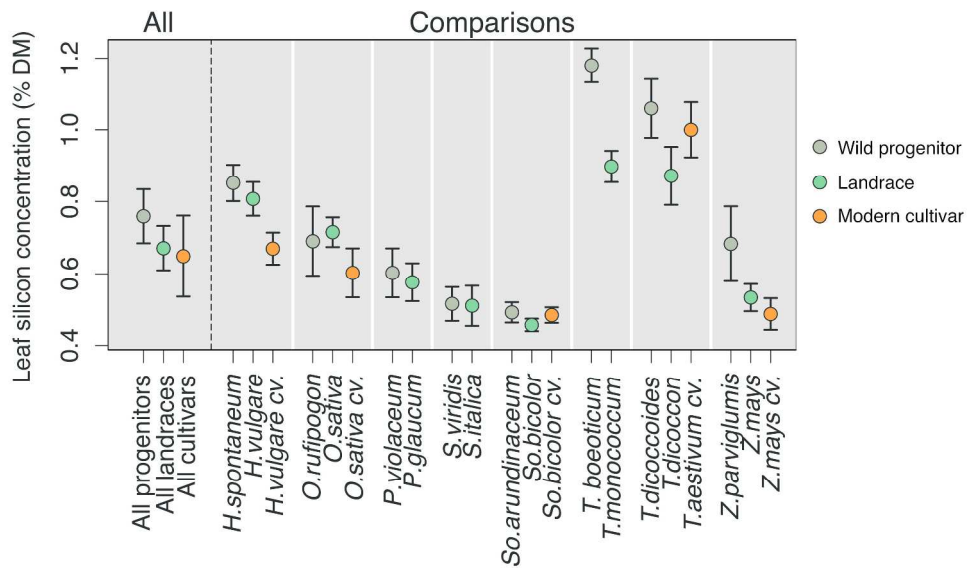


Figure 1. The effects of domestication and agronomic selection on cereal silicon-based defence. Points represent mean values of leaf silicon concentration for each species, and these are grouped within comparisons. Silicon concentration was significantly reduced through domestication ( $P=0.02$ ) but not modern agronomic selection ( $P=0.34$ ). Error bars =  $\pm$  standard error. DM = dry mass; cv = cultivar.

268x162mm (300 x 300 DPI)

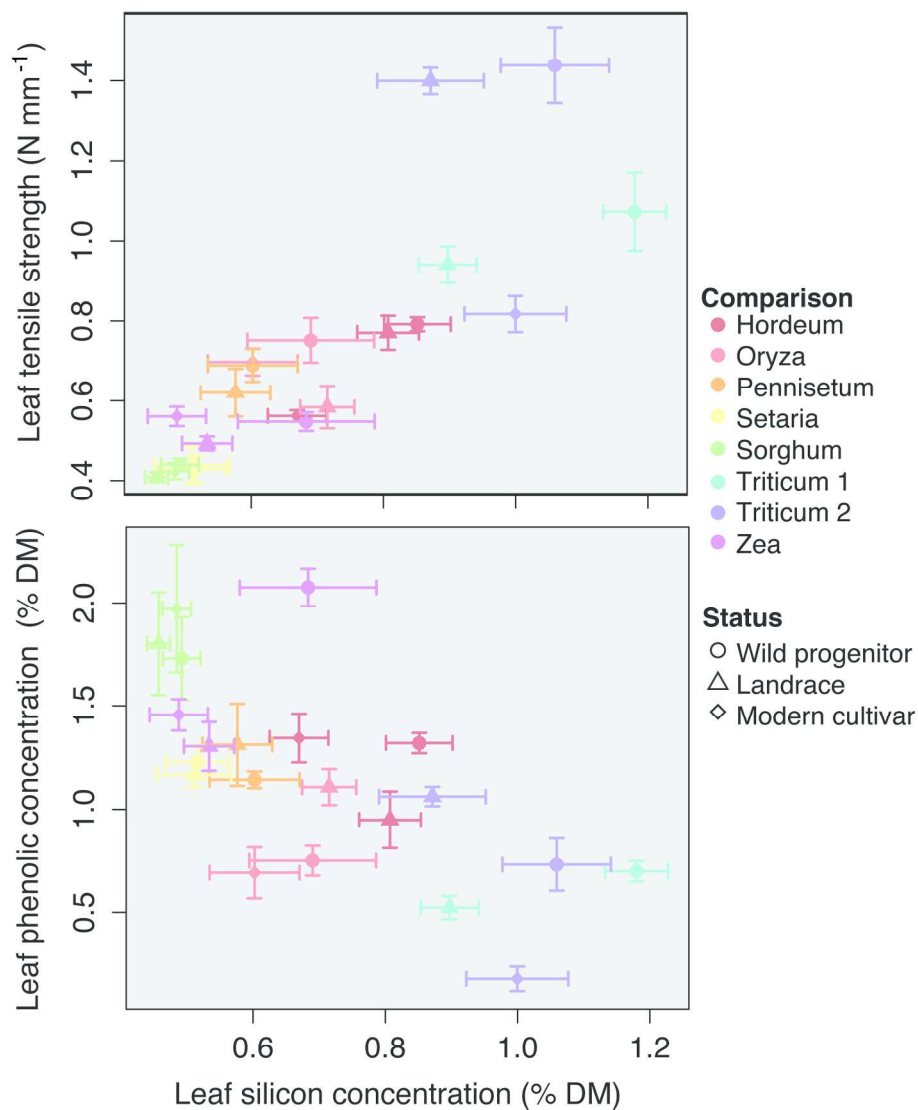


Figure 2. The relationships of leaf silicon concentration with leaf tensile strength (top) and leaf phenolic concentration (bottom). Values represent means  $\pm$  standard error bars. Across species, leaf silicon concentration correlated positively with leaf tensile strength ( $P < 0.001$ ) but negatively with leaf phenolic concentration ( $P = 0.034$ ). Triticum 1 is the comparison between Einkorn wheat (*T. monococcum*) and its progenitor (*T. boeoticum*); Triticum 2 is the comparison between Emmer wheat (*T. dicoccon*), its progenitor (*T. dicoccoides*) and modern cultivar (*T. aestivum*). DM = dry mass.

178x226mm (300 x 300 DPI)

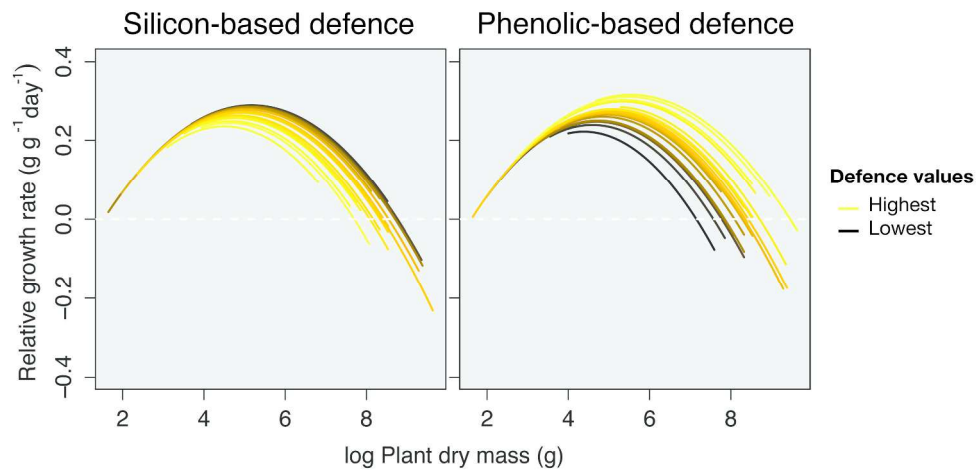


Figure 3. Silicon-based defence is linked to slower growth whereas phenolic-based defence is associated with faster growth. The modeled effect of varying levels of leaf silicon concentration (left) and phenolic concentration (right) on plant relative growth rate. Final plant size ( $m_{max}$ ) is modeled as a linear function of silicon/phenolic concentration. Each line represents the predicted relationship between relative growth rate and plant size for one species based on the species-specific average silicon and phenolic concentrations. The line colour reflects defence concentration values. Plant dry mass values were multiplied by 1000 before log-transformation to ensure positive end values.

250x128mm (300 x 300 DPI)

Supporting information for:

Still armed after domestication? Impacts of domestication and agronomic selection on silicon defences in cereals

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**Supplementary Tables**

**Table S1. Accession and seed source details.**

Species	Source	Accession number
<i>Hordeum spontaneum</i>	IPK Gatersleben, Germany	HOR 9473/88
<i>Hordeum vulgare</i>	United States Department of Agriculture, USA	GSHO 842
<i>Hordeum vulgare</i> cv. 'Perga'	IPK Gatersleben, Germany	HOR 3251
<i>Oryza rufipogon</i>	Australian Tropical Grains Germplasm Centre	JC2143
<i>Oryza sativa</i>	United States Department of Agriculture, USA	PI 503035
<i>Oryza sativa</i> cv. 'IR72'	University of Sheffield, UK	
<i>Pennisetum violaceum</i>	Kew Millenium Seed Bank, UK	0072964
<i>Pennisetum glaucum</i>	United States Department of Agriculture, USA	PI 521636
<i>Setaria viridis</i>	Herbiseed, Twyford, England	
<i>Setaria italica</i>	United States Department of Agriculture, USA	PI 408811
<i>Sorghum arundinaceum</i>	United States Department of Agriculture, USA	PI 153867
<i>Sorghum bicolor</i>	United States Department of Agriculture, USA	PI 533833
<i>Sorghum bicolor</i> cv. 'Tech8'	IPK Gatersleben, Germany	SOR 958
<i>Triticum boeoticum</i>	United States Department of Agriculture, USA	PI 427560
<i>Triticum monococcum</i>	United States Department of Agriculture, USA	PI 119423
<i>Triticum dicoccoides</i>	John Innes Centre, UK	552/2000

<i>Triticum dicoccon</i>	United States Department of Agriculture, USA	PI 470739
<i>Triticum aestivum</i> cv. 'Hereward'	University of Sheffield, UK	
<i>Zea mays</i> subsp. <i>parviglumis</i>	International Maize and Wheat Improvement Center, Mexico	SITI 3456 8781
<i>Zea mays</i>	United States Department of Agriculture, USA	
<i>Zea mays</i> cv. 'KAT_369'	University of Sheffield	

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**Table S2. Species average values of leaf silicon concentration, phenolic concentration and tensile strength.** Average values  $\pm$  standard error are shown. Status codes: W, wild progenitor; L, landrace; C, modern cultivar.

Species	Status	Average leaf silicon concentration (%DM)	Average leaf tensile strength (N mm <sup>-1</sup> )	Average leaf phenolic content (%DM)
<i>Hordeum spontaneum</i>	W	0.851 $\pm$ 0.050	0.792 $\pm$ 0.018	1.319 $\pm$ 0.049
<i>Hordeum vulgare</i>	L	0.807 $\pm$ 0.047	0.770 $\pm$ 0.043	0.949 $\pm$ 0.137
<i>Hordeum vulgare</i> cv. 'Perga'	C	0.670 $\pm$ 0.044	0.562 $\pm$ 0.014	1.343 $\pm$ 0.117
<i>Oryza rufipogon</i>	W	0.690 $\pm$ 0.096	0.751 $\pm$ 0.056	0.751 $\pm$ 0.072
<i>Oryza sativa</i>	L	0.715 $\pm$ 0.041	0.584 $\pm$ 0.053	1.107 $\pm$ 0.087
<i>Oryza sativa</i> cv. 'IR72'	C	0.607 $\pm$ 0.054	0.697 $\pm$ 0.034	0.692 $\pm$ 0.124
<i>Pennisetum violaceum</i>	W	0.576 $\pm$ 0.053	0.689 $\pm$ 0.041	1.142 $\pm$ 0.040
<i>Pennisetum glaucum</i>	L	0.602 $\pm$ 0.068	0.620 $\pm$ 0.060	1.311 $\pm$ 0.198
<i>Setaria viridis</i>	W	0.516 $\pm$ 0.047	0.429 $\pm$ 0.033	1.227 $\pm$ 0.080
<i>Setaria italica</i>	L	0.511 $\pm$ 0.056	0.439 $\pm$ 0.048	1.166 $\pm$ 0.060
<i>Sorghum arundinaceum</i>	W	0.492 $\pm$ 0.028	0.439 $\pm$ 0.016	1.729 $\pm$ 0.200
<i>Sorghum bicolor</i>	L	0.457 $\pm$ 0.017	0.409 $\pm$ 0.012	1.802 $\pm$ 0.250
<i>Sorghum bicolor</i> cv. 'Tech8'	C	0.485 $\pm$ 0.022	0.423 $\pm$ 0.021	1.971 $\pm$ 0.308
<i>Triticum boeoticum</i>	W	1.180 $\pm$ 0.048	1.072 $\pm$ 0.094	0.700 $\pm$ 0.050
<i>Triticum monococcum</i>	L	0.897 $\pm$ 0.044	0.941 $\pm$ 0.045	0.523 $\pm$ 0.056
<i>Triticum dicoccoides</i>	W	1.059 $\pm$ 0.082	1.439 $\pm$ 0.094	0.732 $\pm$ 0.127
<i>Triticum dicoccon</i>	L	0.871 $\pm$ 0.080	1.399 $\pm$ 0.033	1.062 $\pm$ 0.047
<i>Triticum aestivum</i> cv. 'Hereward'	C	1.000 $\pm$ 0.077	0.817 $\pm$ 0.045	0.177 $\pm$ 0.060
<i>Zea mays</i> subsp. <i>parviglumis</i>	W	0.683 $\pm$ 0.103	0.547 $\pm$ 0.023	2.075 $\pm$ 0.091
<i>Zea mays</i>	L	0.533 $\pm$ 0.038	0.493 $\pm$ 0.017	1.303 $\pm$ 0.117
<i>Zea mays</i> cv. 'KAT_369'	C	0.488 $\pm$ 0.044	0.561 $\pm$ 0.024	1.456 $\pm$ 0.076



## Supplementary Figures

**Figure S1. A comparison of growth rate parameters between wild progenitor, landrace and modern cultivar cereals.** The parameters are:  $m_{\min}$  (minimum plant mass; panel A),  $m_{\max}$  (asymptotic plant mass; panel B) and  $t_0$  (time when the plant mass is midway between  $m_{\max}$  and  $m_{\min}$ ; panel C). Domestication status had a marginally significant influence on  $m_{\min}$  ( $P=0.098$ ), but no significant effect on the other parameters.

