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Article:

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

Journal:	*Functional Ecology*
Manuscript ID	Draft
Manuscript Type:	Standard Paper
Date Submitted by the Author:	n/a
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Key-words:	crop protection, grasses, growth-defence trade-offs, herbivory, silica, wild ancestors, landraces, modern cultivars

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1   *Title page*

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

4   anti-herbivore defences in cereals

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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; Wieczorek *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; Wieczorek *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 μmol m^{-2} 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_{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*

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-Ciocalteau 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-Ciocalteau 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^{-1} day^{-1}), landraces

272   (0.32 g g^{-1} day^{-1}) and modern cultivars (0.26 g g^{-1} day^{-1}). 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 boeticum)* was predicted

285   to have 18% lower maximum relative growth rate (0.235 vs. 0.288 g g^{-1}day^{-1}) and

286   15% lower final plant size (taken at 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 g g^{-1}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

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)

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

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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 = ± 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 ± 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-

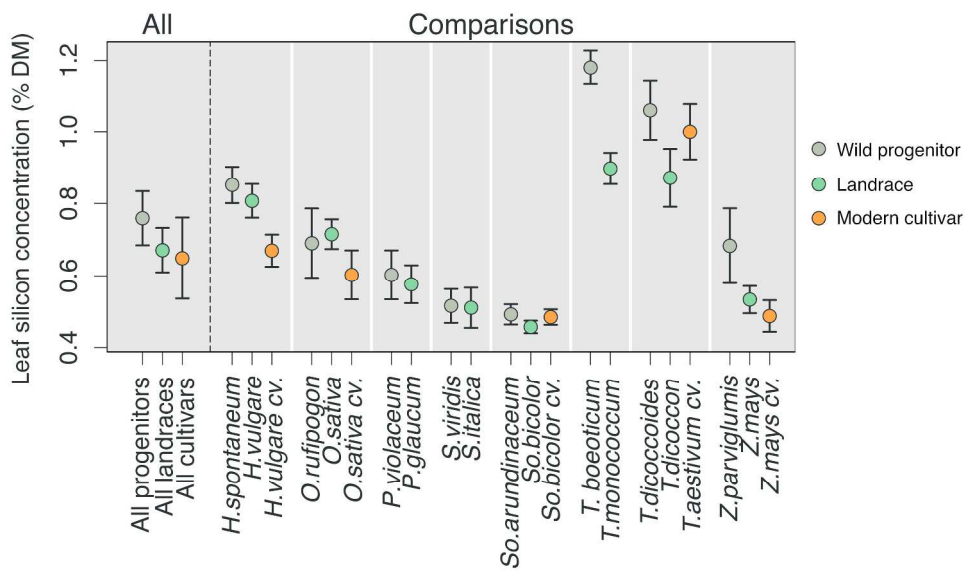677   transformation to ensure positive end values.

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 = ± standard error. DM = dry mass; cv = cultivar.
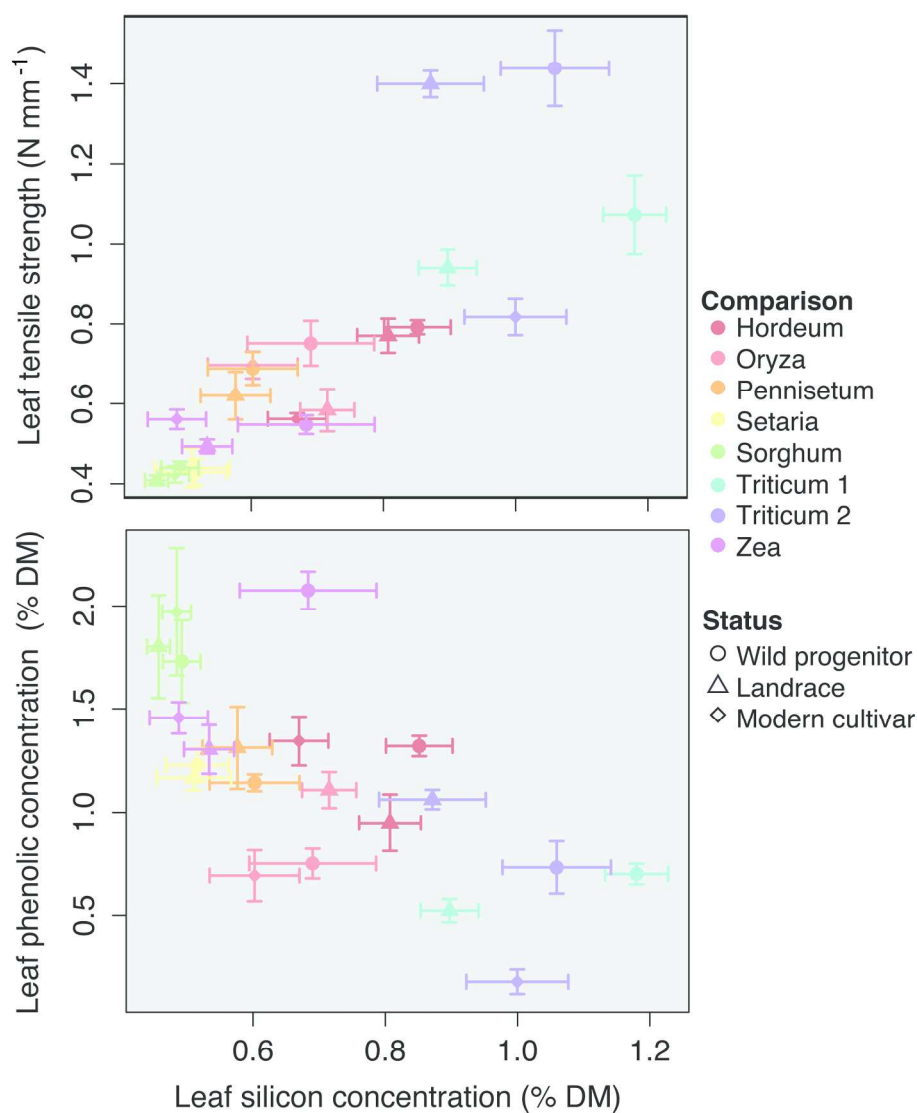
268x162mm (300 x 300 DPI)

Figure 2. The relationships of leaf silicon concentration with leaf tensile strength (top) and leaf phenolic concentration (bottom). Values represent means ± 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.
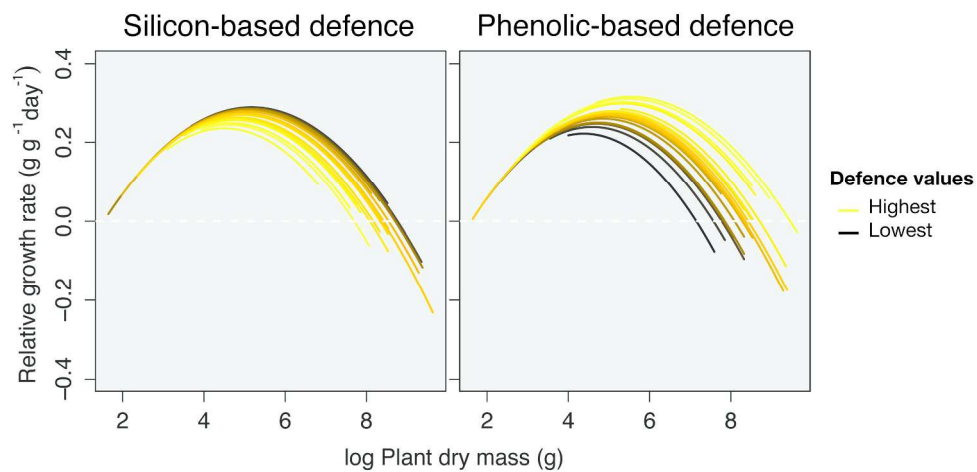
178x226mm (300 x 300 DPI)

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 (mmax) 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

Kimberley J. Simpson, Ruth N. Wade, Mark Rees, Colin P. Osborne, Sue E. Hartley

Supplementary Tables

Table S1. Accession and seed source details.

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

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

Table S2. Species average values of leaf silicon concentration, phenolic concentration and tensile strength. Average values ± 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^{-1})	Average leaf phenolic content (%DM)
Hordeum spontaneum	W	0.851 ± 0.050	0.792 ± 0.018	1.319 ± 0.049
Hordeum vulgare	L	0.807 ± 0.047	0.770 ± 0.043	0.949 ± 0.137
Hordeum vulgare cv. 'Perga'	C	0.670 ± 0.044	0.562 ± 0.014	1.343 ± 0.117
Oryza rufipogon	W	0.690 ± 0.096	0.751 ± 0.056	0.751 ± 0.072
Oryza sativa	L	0.715 ± 0.041	0.584 ± 0.053	1.107 ± 0.087
Oryza sativa cv. 'IR72'	C	0.607 ± 0.054	0.697 ± 0.034	0.692 ± 0.124
Pennisetum violaceum	W	0.576 ±0.053	0.689 ± 0.041	1.142 ± 0.040
Pennisetum glaucum	L	0.602 ± 0.068	0.620 ± 0.060	1.311 ± 0.198
Setaria viridis	W	0.516 ± 0.047	0.429 ± 0.033	1.227 ± 0.080
Setaria italica	L	0.511 ± 0.056	0.439 ± 0.048	1.166 ± 0.060
Sorghum arundinaceum	W	0.492 ± 0.028	0.439 ± 0.016	1.729 ± 0.200
Sorghum bicolor	L	0.457 ± 0.017	0.409 ±0.012	1.802 ± 0.250
Sorghum bicolor cv. 'Tech8'	C	0.485 ± 0.022	0.423 ± 0.021	1.971 ± 0.308
Triticum boeticum	W	1.180 ± 0.048	1.072 ± 0.094	0.700 ± 0.050
Triticum monococcum	L	0.897 ± 0.044	0.941 ± 0.045	0.523 ± 0.056
Triticum dicoccoides	W	1.059 ±0.082	1.439 ± 0.094	0.732 ± 0.127
Triticum dicoccon	L	0.871 ± 0.080	1.399 ± 0.033	1.062 ± 0.047
Triticum aestivum cv. 'Hereward'	C	1.000 ± 0.077	0.817 ± 0.045	0.177 ± 0.060
Zea mays subsp. *parviglumis*	W	0.683 ± 0.103	0.547 ± 0.023	2.075 ± 0.091
Zea mays	L	0.533 ±0.038	0.493 ± 0.017	1.303 ± 0.117
Zea mays cv. 'KAT_369'	C	0.488 ± 0.044	0.561 ± 0.024	1.456 ± 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.