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Title page

Still armed after domestication? Impacts of domestication and agronomic selection on anti-herbivore defences in cereals

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Running headline: Anti-herbivore defences through cereal domestication

Summary

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

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

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

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

Introduction

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

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

In crop systems, a strong directional selection for faster growth is predicted through domestication, so that a reduction in resources available for defence investment is expected to have occurred concurrently (Massei & Hartley 2000). In general, domestication has led to a reduction in defences in many crops (Rosenthal & Dirzo 1997; Massei & Hartley 2000; Mondolot *et al*. 2008; Mayrose *et al*. 2011; Rodriguez-Saona *et al*. 2011; Meyer, Duval & Jensen 2012; Bellota, Medina & Bernal 2013; Chen, Gols & Benrey 2015). However, the increase in growth rate through domestication and agronomic selection assumed to be driving this reduction has not been found in several studies (Cook & Evans 1983; Evans 1993; Welter 2000; Preece *et al*. 2017), suggesting that changes in defence investment through domestication may not result from a trade-off with growth rate. Additionally, some studies have not found a defence reduction through domestication (Turcotte, Turley & Johnson 2014), suggesting that the phenomenon of plants being 'disarmed by domestication' may not be as widespread as first thought.

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

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

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

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

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

Materials and methods

Species selection and plant growth conditions

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

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

Growth rate analysis

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

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

Plant defence measurements

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

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

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

Statistical analysis

The effects of domestication and agronomic selection on SGR, leaf silicon concentration, phenolic concentration and tensile strength were determined by fitting linear mixed-effects models to the trait data ("lme4" package, Bates *et al*. 2014). The fixed effect was "domestication status", and "comparison" was added as a random effect to account for the phylogenetic non-independence of species within each comparison. "Species" was an additional random effect in the silicon, phenolic and tensile strength models to account for multiple measurements per species. The effects that domestication status had on SGR, leaf silicon concentration, phenolic concentration and tensile strength were determined through model comparison (complete model vs. grand mean model) using a parametric bootstrapping method ("pbkrtest" package, Halekoh & Højsgaard 2015) with 10,000 simulated generations. As there was a significant effect of domestication status on leaf silicon concentration, the same model comparison approach was used to determine where in the domestication/agronomic selection process this significant change occurred.

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

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

Results

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

Domestication status had no effect on SGR (LRT=2.80; df=2; *P*=0.24), with average values differing little between wild progenitors (0.29 g g^{-1} day^{-1}), landraces (0.32 g g^{-1} day^{-1}) and modern cultivars (0.26 g g^{-1} day^{-1}). Domestication status also had a marginally significant influence on the minimum mass (m_{min}), consistent with the larger seed size of domesticated crops than their wild progenitors, but there was no effect on the other parameters used to fit the growth curves *(P*>0.05; Figure S1).

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

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

Discussion

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

A high level of accumulated silicon acts as an effective plant anti-herbivore defence. Multiple detrimental impacts on herbivore performance are well-documented (Ma & Takahashi 2002; Hunt *et al*. 2008; Massey & Hartley 2009). In addition, we found that species with high leaf silicon concentrations also tended to have high tensile strength. Like silicon, this leaf trait is an important physical defence against herbivores, reducing their performance by increasing the metabolic costs of leaf digestion (Roces & Lighton 1995; Clissold *et al*. 2009). Interestingly, within species there is little evidence of significant correlations between leaf silicon concentration and tensile strength, and neither was there evidence of changes in leaf tensile strength through domestication and agronomic selection as found elsewhere (Maag *et al*. 2015). The 10% reduction in silicon concentration through domestication we detected could imply that cereal landraces may be more susceptible to herbivory than their wild progenitors. However, whether such changes in silicon are sufficient to influence herbivore behavior is unknown; studies demonstrating impacts on herbivore preference and performance have involved much larger changes in silicon concentration (e.g. Massey, Ennos & Hartley 2006, 2007a).

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

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

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

We found no consistent change in size-standardised growth rate through cereal domestication or agronomic selection. This adds to a growing body of studies that have failed to find growth rate alterations through domestication (Cook & Evans 1983; Welter 2000; Preece *et al*. 2017). For example, Evans (1993) found no consistent trends in growth rate between wild and domesticated wheats, whilst Preece *et al*. (2017) attributed the greater yield in domesticated wheat and barley landraces to larger initial and final sizes, and changes in allocation, compared with their wild relatives. Some differences in traits relating to seed size and dormancy were consistent with the domestication syndrome (i.e. an increase in initial plant mass and shorter seedling emergence times); however these traits are not directly related to growth rate. In our SGR analysis, we therefore find no direct evidence that the small reduction in silicon-based defence through domestication was caused by a reallocation of resources towards faster growth despite our modeled prediction that higher silicon concentrations are associated with lower growth rates and smaller final plant sizes. Through our modelling approach, we found that the adverse effect of allocation to silicon defences on growth rate increases with plant size, implying that the costs of silicon defences are relatively greater for larger plants. This could be due to the greater costs of uptake, mobilization and deposition of silicon in larger plants, or because plants with higher potential maximal growth rate and asymptotic size suffer most from the costs associated with silicon uptake. The predictions from our model may contrast with the results from the SGR analysis because we conducted this species comparison with plants of only 0.2g, possibly too small to show any effects of silicon on growth rate. However, as the plants increase in size, the effect is predicted to become more pronounced.

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

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

Author Contributions Statement

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

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Data Accessibility

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

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Tables

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)

Figures

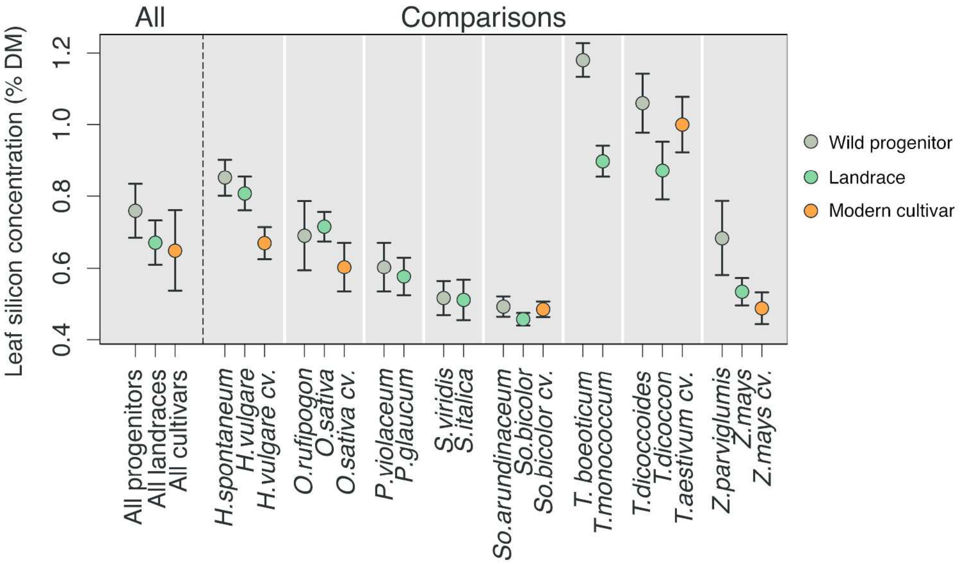
Figure legends

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.

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.

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.



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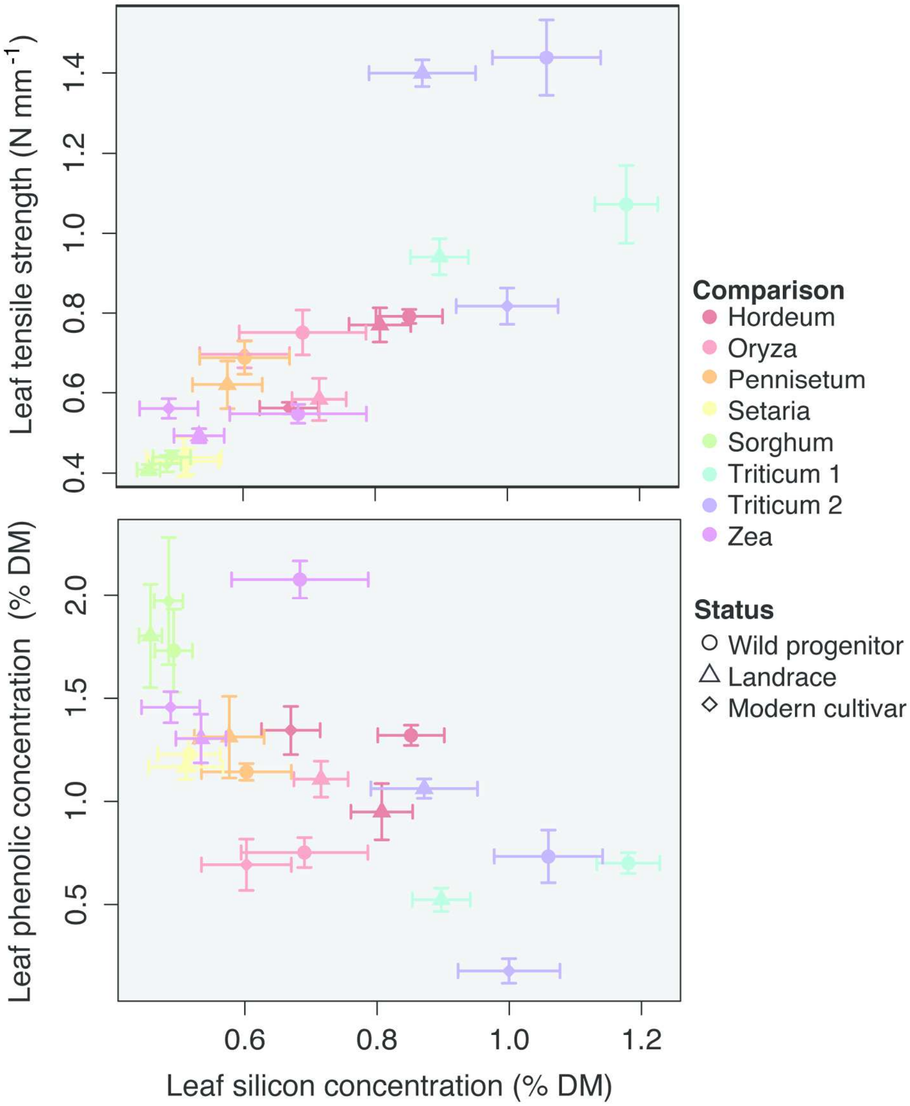

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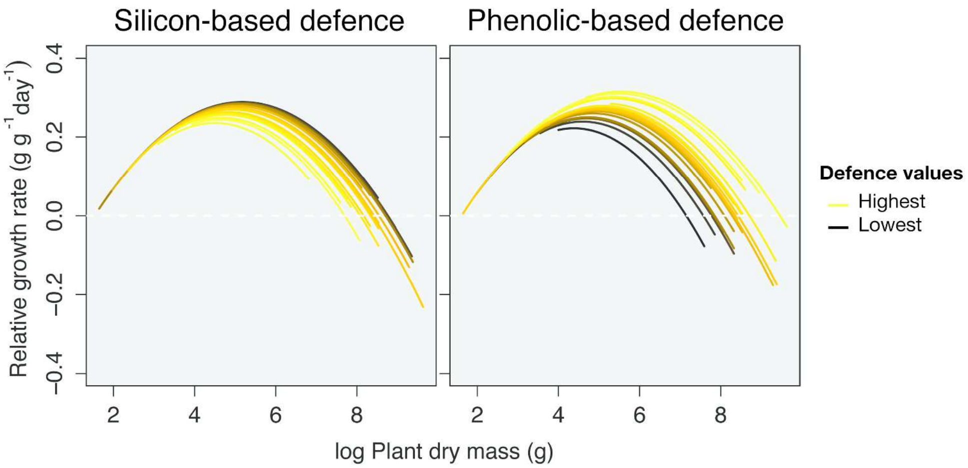

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Supporting information for:

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.