

Delayed induced silica defences in grasses and their potential for destabilising herbivore population dynamics

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Abstract Some grass species mount a defensive response to grazing by increasing their rate of uptake of silica from the soil and depositing it as abrasive granules in their leaves. Increased plant silica levels reduce food quality for herbivores that feed on these grasses. Here we provide empirical evidence that a principal food species of an herbivorous rodent exhibits a delayed defensive response to grazing by increasing silica concentrations, and present theoretical modelling that predicts that such a response alone could lead to the population cycles observed in some herbivore populations. Experiments performed under greenhouse conditions revealed that the rate of deposition

of silica defences in the grass *Deschampsia caespitosa* is a time-lagged, nonlinear function of grazing intensity and that, upon cessation of grazing, these defences take around one year to decay to within 5 % of control levels. Simple coupled grass–herbivore population models incorporating this functional response, and parameterised with empirical data, consistently predict population cycles for a wide range of realistic parameter values for a (*Microtus*) vole–grass system. Our results support the hypothesis that induced silica defences have the potential to strongly affect the population dynamics of their herbivores. Specifically, the feedback response we observed could be a driving mechanism behind the observed population cycles in graminivorous herbivores in cases where grazing levels in the field become sufficiently large and sustained to trigger an induced silica defence response.

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Introduction

Unstable consumer–resource interactions are hypothesised to drive multi-year population cycles (Turchin 2003), such as those observed in some populations of moths, hares and rodents (Turchin and Batzli 2001). The general consensus is that, unlike predator–prey or host–parasite interactions, plant–herbivore interactions alone are unlikely to be the cause of the delayed density dependence that characterises such cycles. A sufficiently strong and time-lagged negative feedback is required for coupled trophic interactions alone to generate population cycles (Berryman 2002; Turchin 2003) and, to date, there has been a general lack of empirical support to suggest that the negative feedback

between density-dependent grazing intensity and grazing-dependent food availability meets this requirement (Turchin and Batzli 2001). Previous studies examining whether grazing-induced changes in food quantity provide a potential negative feedback mechanism have rarely observed a sufficient depletion of plant biomass, and many plant species regrow rapidly following grazing (e.g. Krebs and Myers 1974; Ostfeld and Canham 1993), although there are some possible exceptions, such as studies of Norwegian and brown lemmings in colder climates feeding on slow-growing mosses (Turchin et al. 2000; Krebs et al. 2010). Hence, the quantity of food available is currently believed to play a secondary role in shaping the population cycles of herbivores, being limited to interactions with other destabilising mechanisms such as physiological condition or susceptibility to predators or pathogens (Huitu et al. 2003; Boonstra and Krebs 2006).

However, a decrease in plant biomass is not the only way food can become limiting for herbivores (Batzli 1992): in addition, the availability of high-quality food can be reduced by the production of grazing-induced plant defences. Increases in the levels of plant defences following grazing have been demonstrated in many plant species (Karban and Baldwin 1997). There are also a substantial number of theoretical studies suggesting that grazing-induced plant defences may provide a sufficient negative feedback to drive population cycles. These mostly involve generic models (Edelstein-Keshet and Rausher 1989; Lundberg et al. 1994; Underwood 1999; Turchin 2003), although a few have been parameterised for particular insect systems (Haukioja 1980; Underwood and Rausher 2002). This theoretical work has highlighted the characteristics of a negative feedback between grazing intensity and levels of induced defences that could potentially generate population cycles. These include: (a) the time elapsing between herbivore damage and the onset of induction relative to the potential rate of increase of the herbivore population in that time (Haukioja 1980; Bryant 1981; Myers and Williams 1984; Haukioja 1991) and (b) the magnitude (in terms of demographic impact on the herbivore) and persistence of the induced response (in terms of decay rate or “relaxation”) (Edelstein-Keshet and Rausher 1989; Turchin and Taylor 1992; Lundberg et al. 1994; Underwood 1999; Underwood and Rausher 2002). Several inducible defence mechanisms of a magnitude and persistence that are appropriate to give them the potential to generate cycles have been considered (Karban and Baldwin 1997), some of which—known as delayed inducible resistance mechanisms—can occur over timescales of months or even years (Haukioja 1991). Despite this, it has proven difficult to demonstrate empirically that induced defences affect herbivore population cycles (e.g. Haukioja 1980; Underwood 1999; Klemola et al. 2000a; Ruohomaki

et al. 2000; Turchin 2003; Huitu et al. 2003; Kent et al. 2005).

Current explanations for population cycles of voles in Fennoscandia invoke a predator–prey interaction between voles of the genus *Microtus* and their specialist predators, with other small mammal species, including *Myodes* folivorous voles, being entrained by “spill over” predation (Hanski and Henttonen 2002; Oksanen et al. 2000). In these systems, induced plant defences do not seem to play a role in driving the cycles of folivorous voles. Indeed, several studies have provided convincing evidence against the induction of plant defences in response to grazing by those rodents. For example, ericaceous plants subjected to grazing by *Myodes* voles in northern Fennoscandia (Oksanen et al. 1987; Rammul et al. 2007) showed no inducible defences, and the sedge *Carex bigelowii* showed no induced defensive response to simulated grazing by lemmings (*Lemmus lemmus*) (Lindgren et al. 2007). However, there may be important contrasts between populations in Fennoscandia and other regions, and between forb- and grass-feeding species. Although no populations of forb-eating *Myodes* voles display cyclic dynamics outside Fennoscandia and in allopatry with graminivorous *Microtus* voles (Oksanen et al. 2000), numerous grass-eating *Microtus* vole populations display cyclic dynamics outside Fennoscandia (Lambin et al. 2000, 2006; Mackin-Rogalska and Nabaglo 1990; Tkadlec and Stenseth 2001; Zub et al. 2012).

Grasses are the main food for several herbivores exhibiting cyclic populations, including *Microtus* vole populations across much of Europe. Unlike the *Myodes* vole populations mentioned above, some of the *Microtus* vole populations reach sufficiently high densities to significantly damage grasses through sustained grazing, especially in winter (Jedrzejewska and Jedrzejewski 1998; Lambin et al. 2000, 2006; Myllymäki 1977; Tkadlec and Stenseth 2001). Despite using similar experimental designs, three previous studies using *Microtus* voles reached contradictory conclusions on the impact of past grazing on herbivore population performance. Through manipulation of vole densities within enclosed wet meadow areas, Agrell et al. (1995) observed that reproduction, recruitment, and body growth rate in introduced *Microtus agrestis* populations were negatively affected by high previous density. In contrast, working with the same species in abandoned farmland colonised by grasses, Klemola et al. (2000b) only found weak delayed effects of past overgrazing on vole reproduction, and no effect on population growth rates. A third study with meadow voles (*Microtus pennsylvanicus*) in old fields detected effects of past density on adult survival rates but not on other traits (Ostfeld and Canham 1995). The indices of plant quality (sugar, fibre and protein content) measured in the two former studies were also inconclusive.

Traditionally, it has been thought unlikely that induced defences in grasses would affect population growth rates of grazing herbivores, because—particularly in comparison to woody plants (Bryant et al. 1983)—grasses were thought to respond to herbivory by instigating rapid regrowth from their basal meristems rather than investing in chemical defence (McNaughton 1979). Many of the plant defences involved in delayed induced resistance in trees, such as some types of phenolic compounds, resins and tannins (Bryant et al. 1983; Kaitaniemi et al. 1998), are not present in grasses. However, it has long been suggested that grasses may in fact “fight back” (Vicari and Bazely 1993). Grasses contain silica-based physical defences, which have been shown to be an effective deterrent against mammalian herbivores (Gali-Muhtasib et al. 1992; Cotterill et al. 2007; but see Vicari and Bazely 1993). Silica (SiO_2) is taken up from the soil as silicic acid and deposited in the leaves as hard granules known as phytoliths, which make grasses abrasive. Concentrations of silica are related to previous grazing history (McNaughton et al. 1985; Brizuela et al. 1986), and so are potentially inducible.

Recent empirical studies performed under greenhouse conditions have demonstrated silica induction experimentally (Massey et al. 2007a) and suggested that inducible silica-based defences in grasses could have important consequences for the dynamics of herbivore populations. The presence of silica in plants can alter both the preference and performance of mammalian herbivores (Massey and Hartley 2006; Massey et al. 2007b, 2009). For example, silica-enriched grass has been shown to be poorly digested by field voles (*Microtus agrestis*), leading to declines in the growth rates of both adults and juveniles, particularly on winter forage (Massey and Hartley 2006; Massey et al. 2008). In addition, there is both laboratory and field evidence that grasses vary their uptake of silica in response to sustained grazing, indicating the potential for reciprocal feedback between herbivores and their food (Massey et al. 2007a, 2008). Despite this, we still lack sufficient data on the nature of the response to test whether inducible silica defences could play a role in generating the population cycles observed in some herbivore populations. Specifically, our previous work only generated a relatively imprecise estimate (between 3 and 14 months) of the rate of silica induction in grasses in response to grazing (Massey et al. 2007a), and to date we have no knowledge of whether, and for how long, such a response persists once grazing is removed.

The effect that inducible silica-based defences in grasses have on the population dynamics of herbivores is therefore akin to a jigsaw puzzle in which some of the pieces are already in place: silica is an inducible defence; grazing can trigger this induction; and the silica level in grass does affect the performance of mammalian herbivores.

However, two vital pieces of this jigsaw puzzle are currently missing, both related to the timescale of silica-based defences, which is crucial to their potential to cause cycles. Firstly, what is the timescale of silica induction after grazing in grasses, and how quickly do these defences “relax” once grazing has stopped? And secondly, is the timescale of induction and relaxation compatible with the generation of herbivore population cycles?

In this paper we answer the first of these questions by performing a greenhouse experiment that yields, for the first time, specific data on silica induction and relaxation in a grass species. Though herbivore-induced increases in leaf silica concentrations are a common feature of many, if not most, grasses (McNaughton et al. 1985; Brizuela et al. 1986; Massey et al. 2007a, b), we chose *Deschampsia caespitosa* (L.) P. Beauv. as our model species because its leaves stay green throughout winter and early spring, the time when food quality is particularly important for voles, whereas leaves of most other grass species quickly die off under prolonged periods of snow cover. We then address the second question by using our data to parameterise models for the specific case of field voles (*Microtus agrestis*) in Kielder Forest (Northumberland, UK), whose diet—especially in winter and early spring—is dominated by *D. caespitosa* (Stenseth et al. 1977; Klemola et al. 2000a). Like many other *Microtus* voles, populations of *M. agrestis* are renowned for exhibiting large amplitude cycles in abundance (Lambin et al. 2000), and in some cases these cycles can occur in the absence of obvious top-down regulation (Ergon et al. 2001; Graham and Lambin 2002). Our results suggest that silica-based defences in grasses may be a key causal factor for the cycles in such cases.

Materials and methods

Timing and nature of silica defence induction and relaxation

Seeds of *D. caespitosa* were germinated on vermiculite before being individually transferred to 1 l pots of a standard compost mix (5:1:1:1 of peat:grit:potting sand:perlite), grown under greenhouse conditions (18:6 h light:dark photoperiod, 10–20 °C) and watered with 150 ml of half-strength Hoagland’s solution containing 150 mg l⁻¹ silica (as $\text{NaSiO}_3 \cdot 9\text{H}_2\text{O}$) every three days for six months prior to the experiment.

The plants, which by then typically had several hundred leaves, were then randomly allocated to one of three damage treatments, with 72 plants per treatment:

1. Approximately 5 % of leaves eaten by voles per month

2. Approximately 20 % of leaves eaten by voles per month
3. Undamaged control.

Damage levels were achieved by placing 6 mm wire mesh enclosures over each plant, then pulling the desired proportion of the total number of leaves through the mesh so that they were exposed to voles. The pot along with the mesh cover was then placed in a glass tank with a vole that had been deprived of green food for 3 h, and left until all exposed foliage had been eaten. This took 20–40 min per plant, depending on vole activity. Control plants were treated in the same manner; however, no foliage was pulled through the mesh while the vole was in the glass tank.

The experiment was conducted in two parts: defence induction and then defence relaxation. For the defence induction phase, each plant was damaged monthly by voles in accordance with the specific damage treatment for six months. Following this, all damage events were stopped but each plant retained its treatment identity. Plants were grown for a further six months to test for a “defence relaxation” phase: the time required following the last damage event for a plant to cease producing elevated levels of silica. During both phases, samples of newly expanded leaves from plants of each treatment were removed at monthly intervals (approximately ten leaves per plant, ~1 g dry mass), dried at 80 °C, ground (MM2 ball mill, Retsch, Germany) and stored for analysis of silica concentration. Six plants per treatment were sampled at each time point, and sampled plants were removed from the study to prevent subsequent induction results being influenced by any effect of sampling. Therefore, six plants from all treatments were lost each month from the study, and the data obtained were not repeated measures on individual plants.

Silica analysis

The silica concentrations of samples were analyzed using a Niton XL3t portable XRF analyzer (Thermo Fisher Scientific, Inc.). To calibrate the instrument for silicon (Si) measurements in plant material, we used synthetic methyl cellulose to simulate the plant matrix and precipitated silica powder to spike the matrix with Si. We used two types of calibration materials, one containing 0 % Si (no Si added) and one containing 10 % Si; these levels cover the whole range of Si concentrations in foliage. A calibration curve was established by measuring 15 spiked and 15 unspiked methyl cellulose pellets, and a linear regression analysis was applied to the data set. This was used to model the Si fluorescence intensity, in conjunction with the Niton data analysis software. Four herbal certified reference materials were employed to measure the bias and repeatability of the

technique. All analyses were performed in a helium atmosphere to avoid signal loss by air absorption. The samples were exposed to X-rays for a measurement time of 40 s.

To account for seasonal variation in silica levels which was unrelated to damage treatment (see control data in Fig. 1a, b), we subtracted the mean silica concentration of the control plants from both of the other treatments at each time point prior to statistical analysis. The resulting silica concentrations (Fig. 1c) were thus those resulting directly from the damage treatments imposed, rather than the date during the growing season.

Experimental results

Silica concentrations in this greenhouse study were similar to the ones previously reported from field-collected *D. caespitosa* plants (Massey et al. 2008). Concentrations in young *D. caespitosa* leaves exposed to the high-grazing treatment (20 % leaf area removed per month) increased nonlinearly with time (Fig. 1). In contrast, the low-grazing treatment (5 % leaf area removed per month) did not induce a persistent increase in silica over the six-month period, although the data imply that there might have been an initial small increase in silica concentrations by month 4 relative to the control (Fig. 1), which subsequently ceased. Following the cessation of the grazing treatments, silica concentrations in the newly expanded leaves from plants in the high-damage treatment decreased over the subsequent seven-month period. However, even after seven months without damage, the higher silica concentrations in new leaves in the high-grazing treatment imply that the relaxation of past induction was not complete (Fig. 1). Silica concentrations in the low-grazing treatment remained at control levels over the same period.

Theoretical modelling of silica dynamics

We developed a simple mechanistic model of grazing-induced silica defences, with relaxation in the absence of grazing, and fitted it to our empirical data. We assumed that silica induction is an increasing saturating function of damage (implied from Fig. 1), but that there is some time delay in this response (Fig. 1)—presumably related to the time required for leaf regrowth—between damage and the occurrence of elevated silica levels in new leaves. We also assumed that after the cessation of damage, silica concentrations decay exponentially back to their pre-treatment levels (strongly suggested by Fig. 1). To enable us to later combine this model with a model of vole population dynamics, we made the simple assumption that the levels of damage by voles in a given area are directly proportional

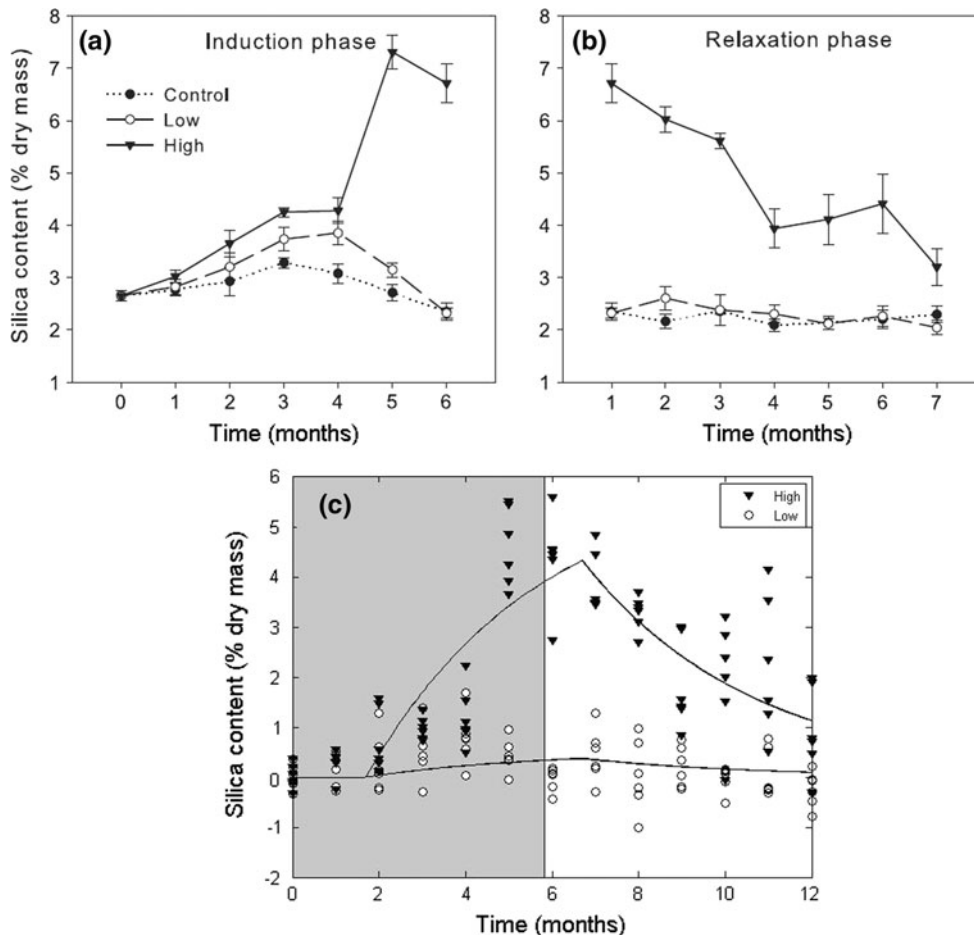


Fig. 1 **a, b** Silica concentrations (mean ± SE) in *D. caespitosa* leaves from plants under three damage treatments (low: 5 % leaf area removed per month; high: 20 % leaf area removed per month; undamaged controls) plotted against **a** time since starting monthly damage events (defence induction phase), and **b** time since cessation of monthly damage events (defence relaxation phase). Note that the data at six months in the induction phase are the same as those at one month of the relaxation phase. **c** Silica concentrations of individual *D. caespitosa* leaves under the same treatments (after subtracting control means from each data point) compared to our

fitted solutions of Eq. 1 for the two damage regimes, with parameter values as given in the main text. Note that the induction phase and the relaxation phase are shown together here. In the grey-shaded region, the leaves were exposed to monthly damage events. We assessed the fit between the model and the data by analyzing the standardised residuals (one for each data point). Visual inspection of residuals plotted against time indicated no bias, making a chi-squared goodness of fit test appropriate. With 20 goodness of fit bins, this gave a significance probability of 0.33

to vole density, and used vole density to represent grazing rate. Denoting the vole density (voles ha⁻¹) and silica concentration (% dry mass) at time *t* (years) by *V(t)* and *S(t)*, respectively, our model is

$$\begin{aligned}
 dS/dt &= \text{induction} - \text{decay} \\
 &= \frac{KV(t - T)^n}{V_0^n + V(t - T)^n} - c(S(t) - S_{\text{control}}), \quad (1)
 \end{aligned}$$

where *S*_{control} is the mean silica concentration in the absence of damage, (*cS*_{control} + *K*) is the maximum possible rate of silica production (year⁻¹), *n* (the Hill coefficient, unitless) scales the shape of the functional response of silica induction rate to vole density (grazing intensity), *V*₀ is the vole density at which damage-induced production

is half of the maximum possible (ha⁻¹), *T* is the time delay in silica induction (years), and *c* scales the background exponential decay rate of silica (year⁻¹).

Parameterising the model

Our measurements of the silica concentrations in control plants (see Fig. 1a, b) were used to estimate *S*_{control} = 2.54 % dry mass. We assumed that the two damage treatments corresponded to two different values of *V* in the first five months of the experiment; specifically, we assume a direct proportionality between vole density and grazing intensity. Equation 1 is linear in *S*, so it can easily be rewritten in terms of *S**(*t*) = *S(t)* - *S*_{control}:

$$dS^*/dt = -cS^*(t) + 0, \quad 0 < t < T \text{ and } t > T + 5 \text{ months} \quad (2a)$$

$$dS^*/dt = -cS^*(t) + P_{\text{low}}, \quad T < t < T + 5 \text{ months, low damage (low } V) \quad (2b)$$

$$dS^*/dt = -cS^*(t) + P_{\text{high}}, \quad T < t < T + 5 \text{ months, high damage (high } V). \quad (2c)$$

Here, P_{low} and P_{high} are the production rates of silica at low and high levels of vole damage, respectively; they depend on K , V_0 , n , and the two damage levels. To fit the four parameters c , T , P_{low} and P_{high} , we minimised the sum of the squared differences between the numerical solution of (2a–c) and the empirical data: both the model solutions and the minimisation were done using the software package Matlab (<http://www.mathworks.com>). This gives $c = 3.0$ per year, $T = 1.7$ months, $P_{\text{low}} = 1.6$ % dry mass per year, and $P_{\text{high}} = 18.4$ % dry mass per year. From the fitted values of P_{low} and P_{high} , we must determine K , V_0 and n . Positivity of K and V_0 requires $n > 1.8$, implying that silica induction is fundamentally a threshold phenomenon. However, beyond this constraint there are insufficient data to independently determine all three parameters, and we fix $n = 2$ (but examine the sensitivity of the results to changes in n later); this allows us to obtain values for K and V_0 in terms of the effective vole densities in the two treatment regimes.

Model solutions

We superimposed the solution of Eq. 1 onto the empirical data (Fig. 1c) using parameters obtained from our experiments via nonlinear least squares regression, with vole densities corresponding to the experimental damage treatments. The predictions of this fitted model are consistent with the empirical data, and the standardised residuals show no evidence of bias (see the legend to Fig. 1c for details). Overall, this model clearly captures the qualitative dynamics of the induction and decay phases of the silica dynamics under both high- and low-grazing treatments. The fitted parameters imply that there is a time lag of around 1.7 months in the response of silica to grazing, that the silica induction response is a saturating (sigmoidal) function of cumulative vole grazing intensity, and that there is a background exponential decay rate of induced defences of 3 year^{-1} , which translates to a decay of around 22 % per month, or 95 % per year.

Model extension: incorporating vole dynamics

The next stage in our study was to couple the silica induction and decay model fitted to our experimental results to a simple model of *M. agrestis* population

dynamics in order to investigate whether the feedback between the functional response and the rodent population dynamics is sufficient to generate population cycles if silica only affects vole reproductive rate. We modelled the vole population dynamics using

$$dV/dt = \text{birth} - \text{death} \\ = [B_{\text{min}} + (B_{\text{max}} - B_{\text{min}})F(S(t))]V(t) - dV(t), \quad (3)$$

where d is the vole death rate, assumed to be constant and independent of silica, and B_{min} and B_{max} are the minimum and maximum vole birth rates. In the absence of relevant data, we took $B_{\text{min}} = 0.1B_{\text{max}}$, but the precise scaling between the minimum and the maximum birth rates only affects the quantitative details of the results. The function $F(S(t))$ is the functional response of vole birth rates to silica concentrations. Caged voles fed on a controlled diet start to lose weight rather than gain it at a silica level of 6.6 % dry mass (Massey et al. 2008). Therefore, we took $F = 0$ for $S > 6.6$ % dry mass, with $F = 1$ for $S < S_{\text{control}}$ and with a linear decrease between these two levels (see Fig. 2a). We parameterised d and B_{max} for the *M. agrestis* populations in Kielder Forest, the site of our long-term field studies on vole populations in northern UK. At this upland site, voles show 3–5 year population cycles and live in grass-dominated clear cuts within large stands of spruce plantation. In a previous study at Kielder, we detected an association between silica concentrations in *D. caespitosa* plants and the rate of change of the rodent populations (Massey et al. 2008), and we have also demonstrated that changes in the timing of reproduction, rather than survival, co-vary strongly with past vole density (Ergon et al. 2011). Monthly survival probabilities implied by field data (Graham and Lambin 2002; Burthe et al. 2008)

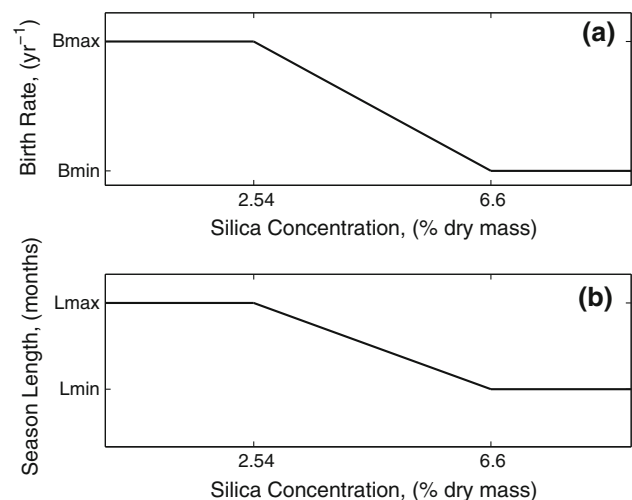


Fig. 2 **a** The relationship between the birth rate, which equals $[B_{\text{min}} + (B_{\text{max}} - B_{\text{min}})F(S(t))]$, and silica concentration for the non-seasonal model: coupling Eqs. 1 and 3. **b** The relationship between season length, which equals $[L_{\text{min}} + (L_{\text{max}} - L_{\text{min}})F(S(t^*))]$, and silica concentration for the seasonal model: coupling Eqs. 1, 4a, and 4b

led us to estimate a death rate of $d = 2.7$ per year (Smith et al. 2006). The maximum per capita birth rate of voles, B_{\max} , is a more difficult parameter to estimate. Time series data from Kielder imply a maximum per capita birth rate of at least 4.1 per year (Smith et al. 2006), whereas trapping data implies a figure of 10.6 (Smith et al. 2008) and studies of similar rodent taxa have suggested values of 13.8, or even values as high as 16 (Turchin and Ostfeld 1997). We therefore regarded the maximum birth rate as a free parameter and investigated the form of the model solutions as it was varied. With a value of 4.1 per year, the model predicts constant population levels. However, at maximum birth rates above 8.4 per year, population cycles occur (Fig. 3).

The key driver for these cycles is the delayed nonlinear induction of silica due to grazing (see Eq. 1). Figure 4 illustrates the sensitivity of the vole dynamics to changes in the four parameters that determine this induction term and also to the silica decay rate. We varied each parameter by $\pm 70\%$ of the values used in Fig. 3, with the other parameters fixed. Throughout this range, changes in the parameter values mainly have quantitative effects on the amplitude of the population cycles, with changes in the value of the delay parameter, T , and the Hill coefficient, n , having the largest effects. In addition, a qualitative difference in the dynamics is predicted for sufficiently small values of T , n , and K , which is proportional to the maximum rate of silica production. Specifically, the dynamics

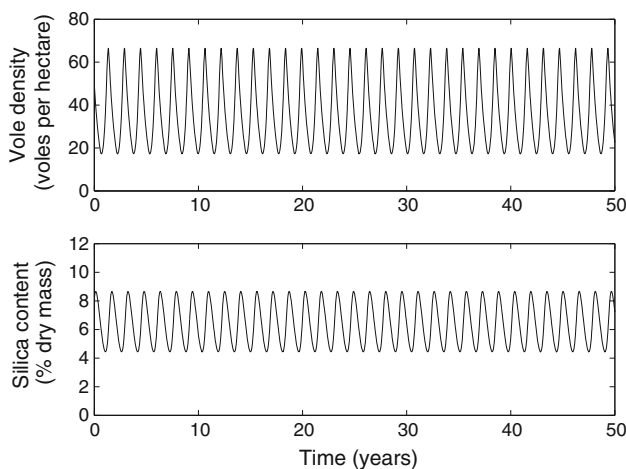


Fig. 3 Vole population cycles driven by silica induction in grass, as predicted by the nonseasonal model: coupling Eqs. 1 and 3. We assumed a maximum birth rate of 12.0 year^{-1} ; other parameters are as given in the main text. Solutions after 50 years are shown, which removes the effects of our initial conditions ($S = 5\%$ dry mass, $V = 25 \text{ ha}^{-1}$ for $t \leq 0$). In order to label the vole density axis, it is necessary to assign a value to V_{high} , the effective vole density corresponding to the high damage level, and we use $V_{\text{high}} = 50 \text{ ha}^{-1}$. This implies that the effective vole density corresponding to the low-damage level is $V_{\text{low}} = 50/4 = 12.5 \text{ ha}^{-1}$. (These values of V_{high} and V_{low} give parameter values of $K = 65.0 \text{ year}^{-1}$ and $V_0 = 79.8 \text{ ha}^{-1}$)

change from cyclic to non-cyclic when T , n and K are decreased by 41, 40 and 69 % of their reference values, respectively. Cyclic behaviour is lost when c is increased by 192 % of its reference value; we have never found non-cyclic behaviour when changing V_0 .

Further model extension: incorporating seasonality

Given the known destabilising role of seasonality on trophic interactions (Hanski and Korpimäki 1995; Altizer et al. 2006), we investigated coupling our silica induction and decay model to an alternative model of vole population dynamics in which each year was divided into a reproductive and nonreproductive season, with plant silica concentration determining the relative lengths of those seasons. Field studies have shown that the timing of seasonal reproduction in overwintered female rodents can vary in a delayed density-dependent manner in some cyclic populations (Ergon et al. 2011), and theoretical studies have provided evidence that the phenomenon of delayed density-dependent reproductive timing can generate population cycles (Smith et al. 2006). Thus, it is hypothesised that, rather than the birth rate being modified by silica levels, it is the onset of reproduction that is delayed as a result of a high-silica diet, and this affects the total births in a season by reducing the breeding season length (Smith et al. 2006). We therefore explored whether making the onset of the reproductive season a function of past silica concentrations could lead to cyclic dynamics. To do this we replaced the silica-dependent birth rate with a rate that is constant over a breeding season, and incorporated seasonality by setting the breeding season length (in months) to be a function of the silica level in the early spring. Therefore, we modelled the vole population dynamics as

$$dV/dt = B_{\max} V(t) - dV(t) \quad \text{in the breeding season} \tag{4a}$$

$$dV/dt = -dV(t) \quad \text{in the non-breeding season.} \tag{4b}$$

We assumed that the date of onset of the breeding season is a simple function of the plant silica concentration at the beginning of spring, of the form season length = $L_{\min} + (L_{\max} - L_{\min})F(S(t^*))$, where $L_{\min} = 4$ months and $L_{\max} = 10$ months are the shortest and longest possible breeding seasons, respectively (Smith et al. 2006; Ergon et al. 2011). We assumed $F = 1$ when $S < S_{\text{control}}$, and $F = 0$ when $S > 6.6\%$ dry mass, with F decreasing linearly as a function of silica between these two levels (see Fig. 2b). Here t^* is a fixed ‘‘census point’’, and represents the earliest possible start to breeding (in spring). Thus, the breeding season starts at time $t^* + (L_{\max} - L_{\min}) [1 - F(S(t^*))]$ and ends at time $t^* + L_{\max}$.

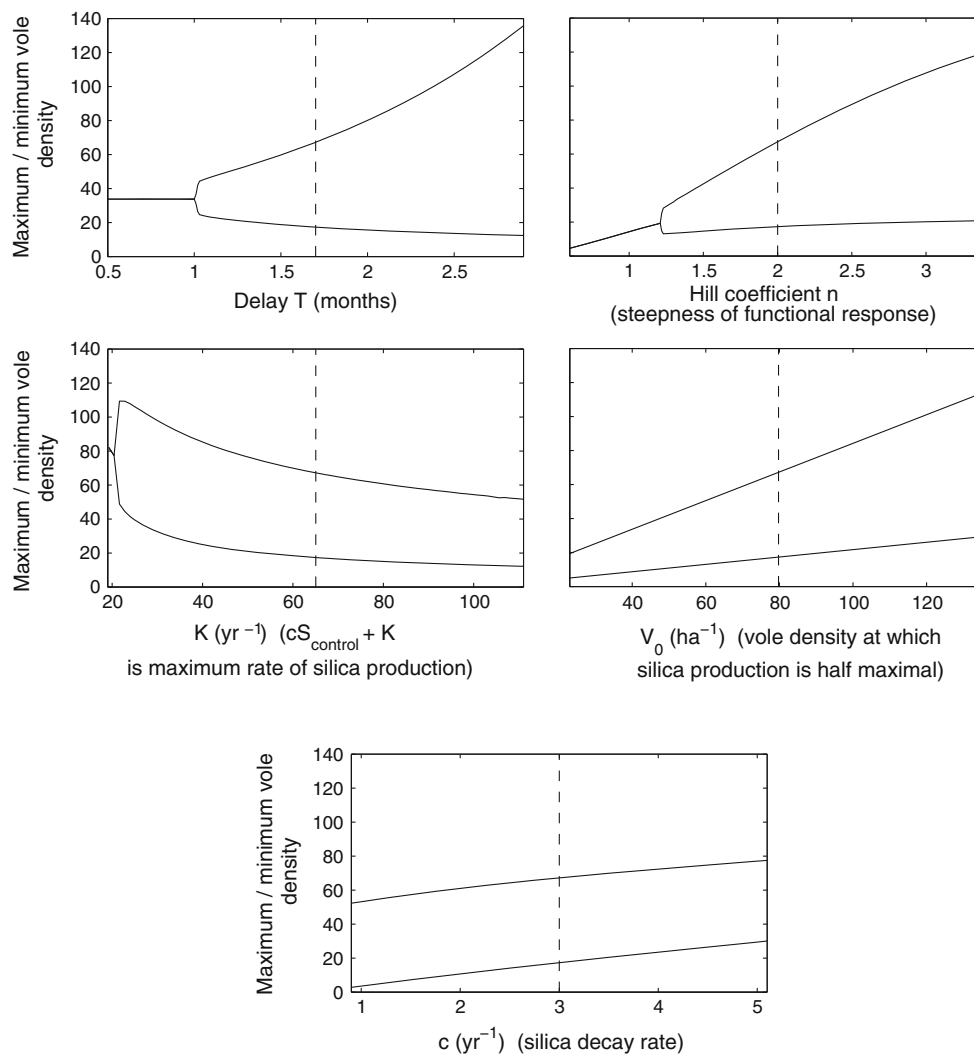


Fig. 4 Sensitivity of vole population cycles to changes in the parameters in the silica equation (1). The five parameters are T , n , K , V_0 and c . In each panel we fixed four of the five parameters at the values used in Fig. 3, and varied the fifth by $\pm 70\%$ (chosen arbitrarily). For a sequence of values of the varying parameter, we solved the nonseasonal model equations (1) and (3) for 500 years

The nonseasonal model framework and sensitivity analysis outlined above highlights the potential for silica effects on reproduction to drive cycles in natural systems. The seasonal model, more reflective of our particular vole system, predicts multi-year population cycles for lower and more realistic birth rates than the previous model (above 5.2 per year) and emphasises that the results are robust to the manner in which the silica effect is represented. The model solutions show intervals of irregular cycles separating periodic behaviour (Fig. 5); dynamics of this type are characteristic of systems on the edge of chaos. The cycle periods are typically three or four years, with the breeding season lengths implied by the silica solutions varying between 4 and 7.5 months. Both of these properties

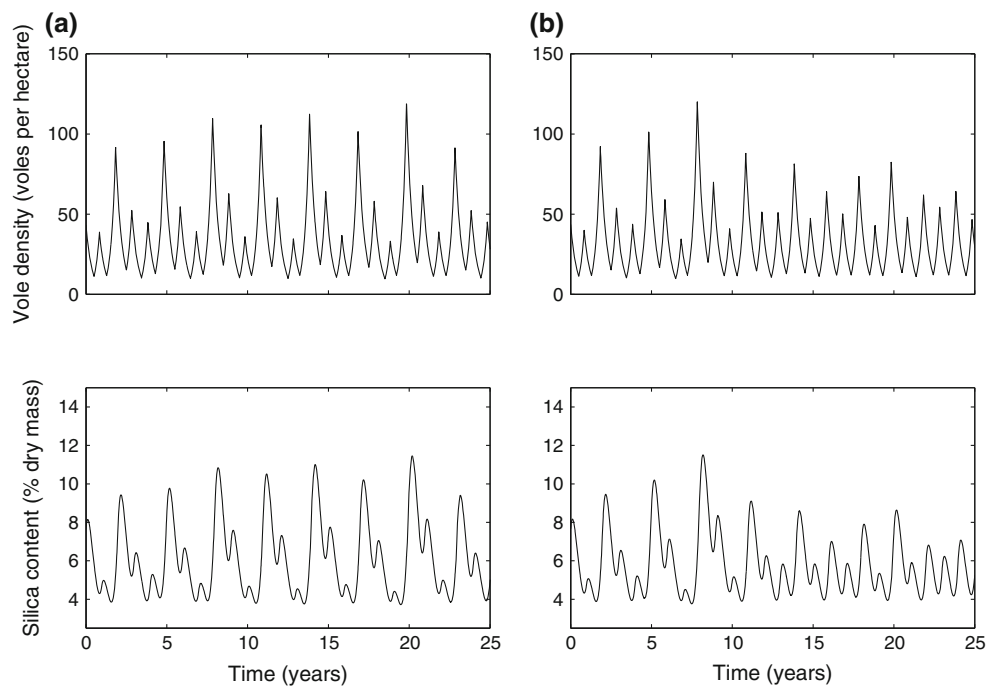
starting from the initial conditions as in Fig. 3, and then recorded the maxima and minima of the solutions over the next 100 years. Cases for which these two curves coincide correspond to non-cyclic dynamics. The *dashed lines* indicate the reference values of the five parameters, i.e. the values used in Fig. 3

and also the overall form of the simulated dynamics are highly reminiscent of field data on vole population cycles in general, and of the *M. agrestis* populations in Kielder Forest in particular (Lambin et al. 2000).

Discussion

In this study, we have empirically characterised the induction of silica-based defences in *D. caespitosa* following grazing. Furthermore, we have provided theoretical evidence that if this response alone is driving vole population dynamics through its impact on reproduction, then it could generate multi-year cycles in their populations. We restricted

Fig. 5 Vole population cycles driven by silica induction in grass, as predicted by the seasonal model: coupling Eqs. 1, 4a, and 4b. We assumed a birth rate of 6.42 year^{-1} in **a** and 6.48 year^{-1} in **b**; other parameters are as given in the main text. Solutions are shown after 960 years, which removes the effects of our initial conditions. The initial conditions, and the assumed value of V_{high} , are as for Fig. 3. In both **a** and **b**, the breeding season length varies between 4 months and 7.5 months, in line with field data (Ergon et al. 2011)



ourselves to a minimalist model grounded in empirical evidence: a variety of other factors are also likely to influence the delayed density dependence, even if induced silica defences are found to be a key mechanism driving cycles in some herbivore populations. For example, silica-induced reductions in the assimilation of nutrients by voles—which we hypothesise would delay reproduction further—could also reduce survivorship, fecundity, immune responses (Kapari et al. 2006) and/or susceptibility to predators. It is important to note that silica defence induced cycles, if they do occur, are likely to be restricted to herbivores in which grasses form an important component of their diet, either as a dominant source of nutrition in general, or at specific time periods (e.g. over the winter). During times with relatively high population densities (~ 200 voles/hectare), around one-third of all *D. caespitosa* leaves within a tussock are clipped by field voles (unpublished data). This suggests that *D. caespitosa* leaves are a major food source, and that damage levels imposed in the field are high enough to cause an induction of silica defences. There is little empirical evidence for such induced plant defences operating in forb-eating cyclic *Myodes* vole populations in Fennoscandia. However, in the specific field study system modelled here, and in a wide range of other herbivore populations, grasses form a major component of the diet and may become the only source of nutrition during the winter. For example, Hansson (1971) found that grasses and graminoids were the dominant food source (together comprising between 44 and 60 % of the annual intake) for *M. agrestis* voles in Sweden. Whilst we have characterised the induced silica responses of just one

grass species, itself an important food source for *Microtus* voles, particularly over the winter months when it constitutes more than 50 % of all available green matter (unpublished data), Massey et al. (2007a, b) demonstrated that several other grasses eaten by voles (e.g. *Festuca*) induce silica in response to vole grazing, and that silica level was an important determinant of vole preference in experiments using 18 different grass species. Therefore, even if several different grasses are eaten in the field, as reported by Hansson (1971), we believe it is highly likely that silica defences are present in many of them and will be induced if herbivory is sustained.

While our model predictions are general, when parameterised by empirical data they are similar to multi-annual cyclic population trajectories observed at least in the southern European cyclic *Microtus* vole populations (where both peak and trough densities are higher than in Fennoscandia). Similarities include cycle period length, the variable breeding season length, and associated summer declines in density following extended nonbreeding seasons, a feature shared by virtually all cyclic vole populations (Hansson and Henttonen 1985). Moreover, both in model predictions and in field data from Kielder Forest, vole abundance in the trough of the cycles is relatively high, a feature implying that vole cycles in this location are unlikely to be caused by predator–prey interactions.

There are four features of the observed functional response of *D. caespitosa* to grazing that we predict would contribute to it having a destabilising effect on rodent population dynamics:

1. The time lag between initial damage and an induced response
2. The nonlinear response of the rate of silica induction to grazing intensity
3. The relatively slow relaxation rate of the response in the absence of grazing
4. The overall magnitude of the silica response and the assumed associated impact on vole reproduction.

Our sensitivity analysis (Fig. 4) describes how variation in each of these features might influence the interaction, and also suggests that the cycles predicted by our models are not restricted to narrow or unrealistic ranges of parameter values. The emergence of new leaves is clearly influenced by seasonality, and may be coupled with changes in herbivore pressure. A more detailed study of the dynamics of leaf cohorts as a function of both seasonality and grazing may thus provide a natural extension to this work.

The time lag between initial damage and the observed induced response in our experiment is within the (wide) range of induced physical responses seen in other plant species (e.g. Molano-Flores 2001; Dalin and Bjorkman 2003), but is slow relative to the induction of many chemical defences (e.g. Hartley and Firn 1989; Underwood 1998). On that basis, we predict that induced physical defences are more likely to have a destabilising effect on herbivore populations than most types of chemical defences. The shape of the functional response of silica induction to grazing intensity implies some mechanism through which, above a threshold level of cumulative grazing, plants rapidly increase silica uptake and deposition. This is consistent with a previous study using two other grass species, in which repeated damage was required for silica induction, and a single high-damage event had no detectable effects on silica concentration in regrowth tissues (Massey et al. 2007a). Overall, this finding implies that the grazing-induced silica defence mechanism is an active response which can be “switched on” by some stimulus induced by sufficient grazing. Our theoretical findings confirm that the existence of this threshold-like induced silica response significantly increases the likelihood of an unstable plant–herbivore interaction (Fig. 4).

The observed relaxation of silica defences after the cessation of grazing occurs over a relatively long period of time; it is predicted to take around one year to decline to within 5 % of control levels. This rate is likely to be significantly slower under colder field conditions because the rate of silica uptake is affected by temperature (as are many other transport processes in plants; Tamai and Ma 2003); also, leaf lifetime is likely to be longer in the field than under greenhouse conditions. Once silica is deposited as phytoliths within the leaves, it is highly immobile and likely to remain there for the lifetime of the leaf (Epstein

1999). Furthermore, in perennial grasses like *D. caespitosa*, which have relatively slow leaf turnover, much of the standing leaf biomass will retain the “memory” of past induction, although old leaves may only be eaten by voles at times of acute food stress. Similar slow relaxation rates in physical defences have been observed in other systems (Bryant et al. 1985; but see Sinclair et al. 1988; Huntzinger et al. 2004). We only measured silica concentrations in newly expanded leaf blades, so we do not know whether silica deposition also takes place in basal plant parts or extant leaves that survive herbivore damage events, or whether induction is restricted to the plant growing season. However, in a recent field study, we found silica levels of newly expanded *D. caespitosa* leaves to be around 75 % of those in old leaves (see also Cid et al. 1990; de Melo et al. 2010), and that silica concentrations in old and new leaves were closely correlated within a plant (Pearson correlation coefficient = 0.75, $P < 0.001$). In addition, Handreck and Jones (1968) demonstrated that differences in the availability of soil silicon can cause tenfold differences in total plant silica concentrations without affecting its relative distribution between plant parts. This suggests that all parts of the damaged plant, irrespective of age, respond to damage with increased silica levels.

Although silica has long been thought to be a potentially inducible defence mechanism in grasses (McNaughton and Tarrants 1983), the main mechanism by which silica was thought to deter herbivores was a constitutive one, namely increased abrasion and physical resistance by phytoliths (Reynolds et al. 2009). Attempts to demonstrate that silica is inducible by experimental damage have produced conflicting results (Kindomihou et al. 2006), possibly because many studies use artificial defoliation, which does not cause the same defence induction response as real herbivory (Massey et al. 2007a). This distinction between plant responses to real and artificial herbivory is long established (e.g. Hartley and Firn 1989), and the mechanisms responsible are now elucidated (Halitschke et al. 2001). Here, we demonstrate a more dynamic aspect of silica defences, whereby herbivory itself is shown to alter the rate of silica uptake by the plant, and this response decays once herbivory stops. Our work adds to a growing body of evidence that shows physical defences to respond to external stimuli in a similar way to many inducible chemical ones. By characterising the dynamics of both induction and relaxation, this work adds a new dimension to our understanding of the evolution of plant defences. Manipulative field experiments are required to further understand the mechanistic links between silica induction and relaxation responses and vole population dynamics.

In conclusion, our study provides clear evidence that a principal food species of an herbivorous rodent exhibits a delayed defensive response to grazing, and provides

empirical data on the details of this induction and of the subsequent relaxation. Our modelling further predicts that this induction—relaxation response alone is sufficient to drive the population cycles both in the specific system of *M. agrestis* voles in Kielder Forest and more generally in other graminivorous rodent populations in which populations reach densities that are sufficiently high to induce silica defences in their food supply. These results argue strongly for a more widespread assessment of the extent and role of silica defences in natural communities, in particular those with cyclic populations of herbivores.

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