Grasses bite back

How do grasses protect themselves from attack by herbivores? When **Fergus Massey** and **Sue Hartley** asked this question they uncovered an effective secret defence mechanism.

'Sheep may safely graze', thought Johann Sebastian Bach, and after all what could be more harmless than grass? It is not poisonous and has no spines or thorns like other plants. But our recent work suggests that it may be time to reassess this view – eating grass is a lot trickier than it first appears.

Grasses contain silica which they take up from the soil and deposit in their leaves. Some of these deposits are almost spherical, but other have such complex shapes they look and, if our findings are correct, feel like mini razor blades. Our studies provide the first experimental evidence of the dramatic effects these silica bodies can have on herbivore performance, reducing their ability to extract essential nutrients from their food, slowing down their growth and reproduction and hence potentially even influencing their abundance. Could silica defences be the key to understanding what causes the dramatic cyclic fluctuations in abundance in some grass-feeding mammals, such as voles? If so this would be a major step forward: for eight decades population ecologists have tried to understand what causes these cycles.

Silica levels are twice as high in areas where vole populations are beginning to decline.

Over 40 years ago, researchers first suggested silica could act as an anti-herbivore defence in grasses, but until recently there was little experimental evidence to support this idea because no one had measured its effects on herbivore performance. Our work has revealed that silica has wide-ranging impacts on many groups of grass feeding herbivores, including caterpillars, locusts, voles and sheep. Silica deposits within grass leaves increase the abrasiveness of the leaves; for the majority of herbivores this deters feeding. However, silica has even more dramatic effects on herbivores than changing their feeding behaviour: it is able to reduce their digestive efficiency. This means herbivores grow more slowly and can even lose weight when they are fed high-silica diets.

Field voles fed on silica-rich grass leaves displayed growth rates that were almost half the rate of voles feeding on grass leaves low in silica. We found this massive reduction in growth rate was down to the voles' reduced ability to absorb nitrogen from the grass when silica was present. These reductions in digestive efficiency occurred both in mature adult female voles and juvenile females and so have implications for population growth.

Vole population growth rate is predominantly determined by two factors: how early in the year voles begin breeding, which is dependent upon females maintaining their body weight through winter; and how quickly juvenile voles reach sexual maturity in the spring, which again largely depends on their growth rate. Therefore, any factor, such as silica, which reduces the growth rate and body mass of female voles can have a major effect on population growth and hence, potentially, on population cycles.

But for a factor to influence population cycles, it must increase in its effect when vole populations increase, to drive populations down from a peak to a trough, and decrease in effectiveness when vole populations are low, to allow the populations to recover back up to a second peak. Could silica work in this way? Researchers have known for some time that grasses from highly grazed areas often contain higher levels of silica than grasses from areas of low grazing intensity. Our studies are the first to demonstrate experimentally that silica is an inducible defence, that is, one whose levels are dramatically increased after damage by herbivores in a similar way to many chemical defences. Silica levels of grasses grazed by voles quadrupled compared with levels in undamaged plants. Interestingly, grasses clipped with scissors did not respond in the same way, suggesting that it is a specific cue from herbivore feeding that elicits the induction response. This may sound unusual, but it is well known that induction of chemical defences often relies on cues in the saliva of insects. Most importantly, in terms of a possible effect on population cycles, we only found the silica induction response when plants suffered intense grazing damage over a prolonged period. At lower levels of damage or over short time periods we found no induction response. In other words, there is a mechanism by which changing silica levels could track changing vole populations over the sort of timescales required for cycles.

Vole populations oscillate on a three-to-five year cycle in many areas throughout Europe, with very large differences between population peaks and troughs. When voles are abundant, they can reach densities of up to 500 per hectare, but these populations may crash to only 50 per hectare the following year. We suggest that silica may play a role in driving these population changes. During years of rapid population growth, grazing intensity increases on grasses, the main food of field voles, causing induction of silica defences over several months. The increased silica levels in grass leaves reduce vole performance and population growth slows. As the population declines so does the grazing pressure, leading to a relaxation of silica defence levels in new grass tissues. Our preliminary observations from a long-term study site of field vole populations in Keilder Forest, Northumberland, support these ideas: silica levels are twice as high in areas where vole populations are now beginning to decline than they are in areas where vole populations are still increasing. We've started work to assess the timescale over which grasses induce and relax silica defences in response to variation in vole grazing intensity. ■

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The field vole.

Silica is an inducible defence.