

## Plant defences - the mystery deepens

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New research has brought us a step closer to untangling the complex reasons why certain plant species triumph over others.

A recent experiment shows that the interplay between the amount of silicon in the soil and the presence of herbivores can have a big effect on which <u>plants</u> come out on top in the struggle for dominance. But it also shows that the relationship between these variables is much more complicated than previously thought.

Silicon is important for some plants because they take it up from the soil and deposit it in their leaves to make them tougher and less attractive to plant-eating <u>animals</u>. Researchers found that when growing in siliconpoor soil, a grass species that can usually become tough and indigestible because of the silicon in its leaves suffers more attack by herbivores than a supposedly softer, more palatable <u>competitor</u> grass. Once it gets access



to more silicon in the soil, though, it turns the tables on its more palatable competitor and returns to <u>dominance</u>.

This wasn't very shocking in itself. Yet the researchers were surprised to find that when silicon is available, the supposedly softer grass packs even more into its leaves than its tougher relative does – but that doing so doesn't seem to give it much protection against being eaten.

'Our results were a little unexpected - we thought the plants we looked at would differ in quite predictable ways, but it turns out their response to different conditions is very complex,' says Professor Sue Hartley, a plant biologist at the University of York and one of the authors of the paper, published in *Annals of Botany*. 'But overall we certainly do see differences in these plants' competitive success arising from the presence of herbivores and the availability of soil silicon.'

Many grasses use silicon taken up from the soil to defend themselves against herbivores. Once taken up they turn it into tiny granules called phytoliths, which are stored in their leaves. By making leaves tougher and harder for animals to digest, and by wearing down their teeth, phytoliths can persuade most herbivores – anything from locusts and voles to sheep – to find something else to eat.

This defence can come at a cost, though. Taking up silicon and turning it into phytoliths uses energy that the plant could otherwise use for growth and reproduction. The theory is that if there are herbivores about, this defensive investment should be worthwhile, but if there aren't, heavily-defended plants will find themselves at a competitive disadvantage. This idea has so far received little confirmation from experiments, though. The scientists behind this research set out to change that by investigating the ecological costs and benefits of silicon defences.

They grew two different grass species under a variety of different



conditions: alone and mixed in with each other, with and without silicon added to the soil, and with and without the presence of herbivores - in this case, desert locusts. To test how each plant was performing, they measured its biomass after six months.

The first species was Poa annua, a short-lived, relatively soft grass that usually lives on newly-disturbed ground and is thought to accumulate relatively little silicon in its leaves, through purely passive mechanisms that don't respond to its changing environment. The other was Lolium perenne, a much tougher customer - a perennial grass that competes vigorously in established grassland habitats and that typically takes up much more silicon to defend itself, particularly after it has been attacked by herbivores. Moreover, it does so actively, using special transporter systems in its roots to move silicon from the soil into the plant – an energy demanding process.

At first glance, the results were as expected – when herbivores were present, adding more silicon to the soil made the silicon accumulator Lolium even more competitive, as the herbivores switched their diet from Lolium to Poa. In their absence, silicon addition benefited Poa, and Lolium became less dominant.

This fits the idea that actively taking up silicon has a cost for Lolium, and that this is an unnecessary expense if herbivores aren't present. The team found a surprising twist, though – silicon addition increased leaf concentrations in both species by more than 400 per cent, and Poa even ended up with slightly higher leaf silicon concentrations than Lolium. Poa was not previously thought to have the ability to increase its silicon uptake so dramatically. And while Lolium suffered far less from herbivores after this increase in silicon content Poa didn't seem to get much protection, continuing to lose more of its biomass to locusts than Lolium did.



But if Poa accumulates even more silicon than Lolium, why doesn't this deter the locusts? 'It could be that the two species make different kinds of phytolith,' Hartley suggests. 'We don't know exactly what these plants do with the silicon when they have taken it up, and it may well be that Loliummakes much rougher, sharper phytoliths than Poa does, which are more abrasive and so better at deterring herbivores.'

Her group is now examining the different shapes of phytoliths made by different plants. 'Some grass species seem to be far more tough and abrasive than you might think from looking only at the silicon concentration in their leaves,' she explains. 'Poa's defences against herbivores are clearly not so effective as Lolium's when soil silicon is readily available, though when the silicon runs out the palatability of the species, and the competitive balance between them, can change. So plants face a complex and ever-changing battle against their neighbours!'

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