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Seed dispersal

Directed deterrence by capsaicin in chillies

The primary function of ripe, fleshy fruit is to facilitate seed dispersal by attracting consumers^{1,2}, yet many fruits contain unpleasant-tasting chemicals that deter consumption by vertebrates³. Here we investigate this paradox in the chilli (*Capsicum*) and find that capsaicin, the chemical responsible for the fruit's peppery heat⁴, selectively discourages vertebrate predators without deterring more effective seed dispersers.

The worldwide popularity of chillies has prompted numerous investigations of the biological properties of capsaicin^{5,6}, yet its evolutionary significance in the plants that produce it has not been examined. Chillies are low shrubs with fruit that is accessible to mammals as well as birds. However, capsaicin in the fruit has been found to repel or poison mammals, but not birds, in laboratory studies^{7,8}. This taxonomic distinction is predicted by the 'directed deterrence' (toxicity) hypothesis, whereby chemicals in ripe fruit function selectively to discourage seed predators without deterring beneficial seed dispersers^{9,10}.

To test the value of capsaicin as a directed deterrent, we used a native population of chiltepine chillies (*Capsicum annuum* var. *glabrusculum*) in southern Arizona¹¹ and determined which of the local animal species consumed chillies and which were put off by capsaicin. We then investigated the fitness consequences to the plant of seed consumption by both types of potential consumer.

Video observation of chilli plants (146 h in total) revealed that only birds fed on chillies diurnally, with curve-billed thrashers (*Toxostoma curvirostre*) being responsible for 72% of all fruit removal. To assess

nocturnal consumption, we presented fruits of both chilli and desert hackberry (*Celtis pallida*, the most common fruiting plant at our study sites) on microsites available to birds and mammals. During the day, both fruit types were removed in equal amounts (paired- $t_{26} = 0.71$, $P = 0.483$); at night, only hackberry fruits were taken (paired- $t_{20} = 3.11$, $P = 0.006$). Wild chillies thus seem to be consumed exclusively by birds and avoided by small mammals.

To determine whether small mammals avoid chillies because of their capsaicin content, we captured cactus mice (*Peromyscus eremicus*) and packrats (*Neotoma lepida*), the most abundant fruit-consuming mammals, and curve-billed thrashers from the chilli site and studied them in laboratory feeding trials. Animals received three fruit types simultaneously: *Capsicum annuum* from the study site; a non-pungent mutant variety of *Capsicum chacoense*, a chilli that is similar in size, colour and nutritive content to *C. annuum* but lacking in capsaicin as the result of a developmental mutation; and hackberry fruit as a control. Both mammal species consumed all hackberry, an intermediate amount of non-pungent chilli, and no pungent chilli; in contrast, thrashers consumed virtually all fruits and were not deterred by the presence of capsaicin (Fig. 1a). Thus, capsaicin selectively influences the feeding preferences of consumers.

Under the directed-deterrence hypothesis, deterred species (mammals) should be seed predators or ineffective seed dispersers, whereas undeterred consumers (thrashers) should increase the fitness of the chilli plant. We therefore examined the effects of fruit ingestion on seed germination by using non-pungent *C. chacoense*, as mammals will not eat hot chillies. Consumption of *C. chacoense* by both mammal species resulted in zero germination, whereas consumption by thrashers resulted in germination rates similar to those of control seeds planted directly from fruit (Fig. 1b). When pungent chillies were fed to thrashers, these seeds also germinated at the same rate as control seeds ($F_{1,10} = 0.233$, $P = 0.64$). These findings indicate that fruit-consuming small mammals are seed predators, whereas thrashers are not.

The benefit to the plant of fruit consumption by thrashers depends on whether thrashers deposit seeds in places that are suitable for germination, establishment, fruit maturation and dispersal. Although less than 40% of our study area was shaded, 86% of adult chilli plants ($n = 309$) and all seedlings ($n = 22$) were found under the shade of other shrubs, as a result of directed dispersal by thrashers and increased seedling survival in shaded areas¹¹.

However, not all shade is equal: shrubs and trees producing bird-dispersed fruits contributed less than 5% of all shade at our

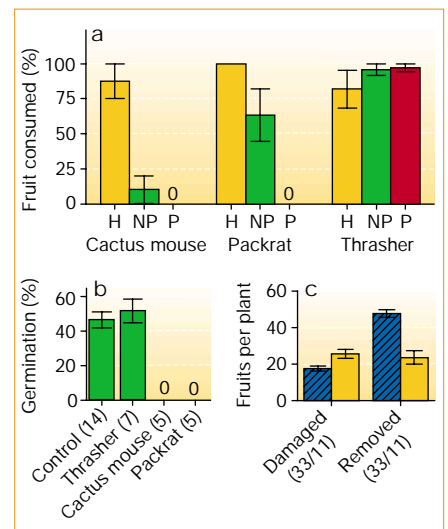


Figure 1 The effects of capsaicin on consumers and of consumers on chillies. **a**, In captive feeding-preference trials, the two most common mammals (five animals per species) readily consumed hackberry fruit (H); consumed non-pungent chillies (NP) only if they had not first sampled pungent chillies; and always avoided pungent chillies (P) (cactus mouse, $F_{2,12} = 8.05$, $P = 0.008$; packrat, $F_{2,12} = 22.29$, $P < 0.0005$). Thrashers (ten birds) ate virtually all pungent chillies that they were offered ($F_{2,15} = 1.68$, $P = 0.219$) and showed no aversion to capsaicin. **b**, Non-pungent chilli seeds from fruit ingested by thrashers germinated at the same rate as controls, whereas seeds from fruit ingested by cactus mice or packrats did not germinate, primarily because both mammal species rarely passed whole seeds ($F_{2,25} = 19.0$; thrashers vs control $P = 0.593$, mammals vs control $P < 0.0005$). The number of animals used is shown in parentheses. **c**, Chilli plants growing under shrubs with bird-dispersed fruit (striped bars) had fewer damaged fruits ($F_{1,41} = 8.2$, $P = 0.006$) and more fruit removed ($F_{1,41} = 32$, $P < 0.0005$) than chillies growing in the shade of plants that do not produce bird-dispersed fruit (orange bars), after controlling for total fruit production. The respective numbers of plants surveyed are shown in parentheses.

study sites, yet 53% of chilli plants were growing under these plants ($\chi^2 = 24.9$, $P < 0.0005$). Chillies under these plants gain two fitness advantages. First, they suffer significantly less insect damage to their immature fruit than do chillies that are shaded by other species (Fig. 1c). Damaged fruits are not released from the petiole and so the seeds are not dispersed; also, only 11% of seeds from damaged fruit germinate, compared with 70% of seeds from healthy fruit (paired- $t_{1,9} = 4.4$, $P = 0.002$). Second, because thrashers primarily forage in the canopies of fruiting trees and shrubs, removal and dispersal of healthy fruit from chillies growing beneath these species is higher than that from chillies under non-bird-dispersed plants (Fig. 1c). In short, directed dispersal by thrashers to sites under bird-dispersed plants is highly beneficial to chillies.

The capsaicin-mediated dispersal of chillies described here provides the first evidence, to our knowledge, that directed deterrence in a ripe fruit may shape plant-vertebrate interactions. The combination of chemical-mediated 'filtering' of

vertebrate seed predators¹⁰, together with directed dispersal by thrashers, creates a pattern of plant recruitment that is beneficial to wild chilli plants: mammalian seed-predation is eliminated and seeds are disproportionately dispersed to specific shaded areas where seedlings can be more easily established, predispersal fruit predation is lower, and seed dispersal is greater.

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Nanostructure

Epitaxial diamond polytypes on silicon

Carbon is unique in the variety of configurations it can adopt with itself and other elements. Here we show how ion beams can be used to nanostructure various diamond polytypes, epitaxially aligning them to a silicon substrate. The ready controllability of ion beams, which are already used to manufacture submicrometre-scale devices, means that our findings should enable new carbon and non-carbon materials to be nanostructured for a host of applications.

Metastable phases (including carbon) can be deposited using hyperthermal species (10–100 eV) by a ‘shallow-implantation’ process¹. The energy barrier for their formation is overcome by trapping energetic species in subsurface positions of a ‘mould’ host matrix. Examples include amorphous, diamond-like carbon films with a local tetrahedral configuration²; transformation of carbon nanotubes to cubic diamond by electron bombardment³; and ion-beam nanostructuring of multi-walled, small-diameter carbon nanotubes⁴.

Diamond polytypes are formed by changing the stacking sequence of the closed-packed plane of the diamond crystal. We used ion beams to form diamond poly-

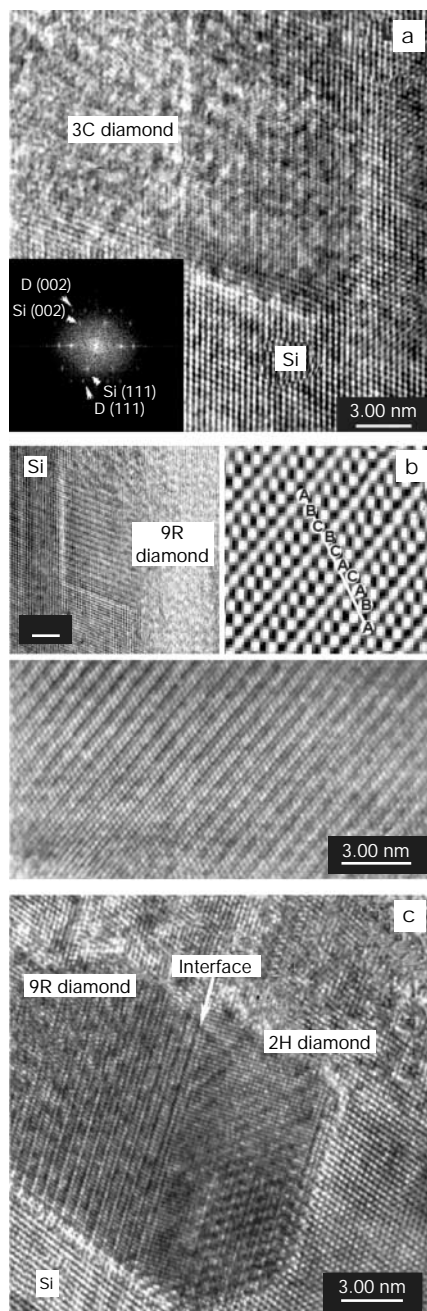


Figure 1 High-resolution transmission electron microscopy (Philips CM200) cross-sectional images of diamond polytypes. **a**, Cubic-diamond crystallite grown epitaxially on a silicon step; inset, crystallite diffractogram (Fourier transform). There is no misorientation between the diamond and silicon. **b**, Top left, 6-nm 9R diamond crystallite grown epitaxially on a Si step; bottom, part of a 60-nm 9R crystallite; top right, filtered image of 9R diamond showing the 9R repeat ‘ABCBCACAB’ sequence. **c**, Another diamond crystallite, also grown epitaxially on a Si step. Note the different symmetry of the 2H crystallite (right) and the sharp boundary with the 9R crystallite (left).

types (cubic, 3C; hexagonal, 2H; and rhombohedral, 9R, where the number denotes the number of closed-packed planes in a unit cell⁵) differing in the stacking order and periodicity of their closed-packed planes. The stacking sequence is controlled by the mould provided by the nucleation site^{1,6} and by the deposition conditions.

Films were prepared using a (CH₄ or C₂H₂)/Ar/H₂-fed Kaufmann source to bombard a Si(100) sample held at 600 or 700 °C with ions at 80 or 200 eV. The Fourier transform diffractogram of a cubic diamond crystal nucleated on a silicon step indicates the high-quality cubic-to-cubic epitaxial relationship between the Si and diamond, with a (111) diamond/Si interface and the absence of misorientation (Fig. 1a).

Figure 1b shows an epitaxial crystal and part of a similar large crystal, with its filtered image: the 9R registry is evident. Orientation relations for this phase are: [0001]_{9RDia}//[-111]_{Si}, [10-10]_{9RDia}//[110]_{Si}, [01-10]_{9RDia}//[0-11]_{Si} (hexagonal indexing).

The left part of a third crystallite (Fig. 1c) is 9R diamond, but its right part has a different stacking sequence and symmetry from 9R and cubic diamond (Fig. 1a, b). The lower-right portion of this crystallite gives a complex image (Moiré fringes, resulting from interference between beams diffracted from both the silicon and the diamond lattices). The upper-right part shows a grid of lines normal to each other, in contrast to the 109.5° angle seen in the high-resolution transmission electron micrographs of cubic diamond (Fig. 1a) and silicon (Fig. 1a, c). Comparison with image simulations for possible diamond polytypes indicates that this crystallite is a hexagonal polytype; the nucleation on a silicon step and the strong epitaxial relations (the same as those of the 9R polytype) are evident. Although these crystallites may contain defects, we have shown that different diamond polytypes can be structured, sometimes with sharp transition from one polytype to another (Fig. 1c).

Polytypes have similar properties with variations that may be useful⁷. Heterojunctions are an example of an application that can involve different polytypes⁷. Our findings indicate that metastable phases can be manipulated by using low-energy ion beams, offering new opportunities to control material synthesis.

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