What should goldenrod do to avoid an insect attack? Duck

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Plants employ a large arsenal of defenses against natural enemies. The most familiar defenses are chemicals, such as alkaloids, or mechanical structures, such as thorns and trichomes. In their studies of goldenrods, Michael Wise and colleagues have identified a novel defense in which plants essentially duck their apex to hide from would-be herbivores. Most individuals of tall goldenrod (*Solidago altissima*) have erect stems from emergence to senescence, but some individuals temporarily nod in early spring, effectively hiding their apical-leaf bud when apex-attacking herbivores are on-the-wing. These herbivores include the familiar ball-gall-making fly, *Eurosta solidaginis*, pictured here. The short-lived adults do not feed, and a female's main task after mating is to lay eggs in as many apical-leaf buds as it can. This female gall fly sits on a leaf near the top of the plant, seemingly oblivious to the nodding apical-leaf bud just centimeters below. Goldenrod individuals with nodding stems (aka, "candy-cane" stems) have proven much less likely to suffer ovipositions from gall-inducing insects than individuals with erect stems. Thus, "defense by ducking" appears to be an effective strategy in *S. altissima*, and it is likely to turn out to be important in other species as well. Courtesy of Michael Wise.

A field of golden-flowered stems swaying in an autumn breeze may evoke a peaceful scene. But this tranquility belies serious battles between natural enemies that took place in the spring. In particular, young goldenrod stems are subjected to attack by several species of insects that lay eggs in their apical-leaf buds, inducing growths called galls that can reduce or even completely prevent goldenrod from flowering and producing seeds.

It has long been recognized that plants and herbivores are involved in a sort of arms race, and plants' defensive strategies commonly involve thorns, spines, and chemical toxins. However, Michael Wise (formerly of Blandy Experimental Farm in Virginia) and colleagues have identified a completely different form of defense employed by some individuals of the tall goldenrod, *Solidago altissima*. They published their findings in the March issue of the American Journal of Botany.

Wise explains the defense this way: "When gall-inducing flies are out looking for goldenrod apices to lay their eggs on, some goldenrod plants react in a seemingly rationale way: they duck."

This ducking "behavior" is actually a gradual growth response, wherein the stem of a young plant begins to nod in early spring until the apical-leaf bud is facing downward instead of upward. Wise says that these nodding stems are reminiscent of green candy-canes. The "candy-cane" stems remain nodding during the egg-laying period of apex -attacking gall flies, but straighten again by late summer in time for flowering. Wise and colleagues have previously shown that candy-cane stems are roughly twice as resistant to three common species of gall flies as are the more common non-ducking, or "erect," stems.

"While we were confident that the candy-cane stems enjoyed a

resistance advantage over erect stems," Wise explained, "we could not say for sure that it was the ducking behavior itself that led to this advantage. It made sense, but we needed a way to test whether the advantage would go away if a plant with a candy-cane genotype did not duck."

Wise and colleagues caught a break when they observed that strong shade causes a ducking plant to become erect. They used this straightening response to test the "ducking hypothesis."

In a greenhouse experiment at Bucknell University in Pennsylvania, the authors used four sets of plants: ducking candy-cane plants grown in full sun, candy-cane plants with stems straightened by a shade treatment, erect plants grown in full sun, and erect plants grown in the shade treatment. The four sets of plants (128 total) were then randomized in a grid on a greenhouse bench, and the authors released adults of the goldenrod ball-gall-making fly, *Eurosta solidaginis*, amid the plants.

The results were striking. The flies did not lay an egg on a single ducking plant. However, they laid eggs on just as many straightened candy-cane plants as they did on both groups of erect plants. Because the straightened candy-cane plants completely lost their resistance, and because there were no differences between the straightened and nodding candy-cane stems other than ducking, the authors concluded that it is indeed the ducking that confers the resistance advantage.

The experiment also shed insight into why the gall flies did not lay eggs in ducking stems. Female flies were able to find the ducking plants well enough, but they seemed to be confused once they landed on a ducking plant. Wise suggests that the flies either do not see the apical leaf bud, or are confused by its upside-down orientation. "Rather than waste too much time, the flies leave the ducking plants to lay eggs on more accommodating hosts," Wise explains. He states that the next challenge

is to figure out why, given their resistance advantage, ducking plants are always in the minority in goldenrod populations.

More information: http://www.amjbot.org/cgi/content/full/97/3/525

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