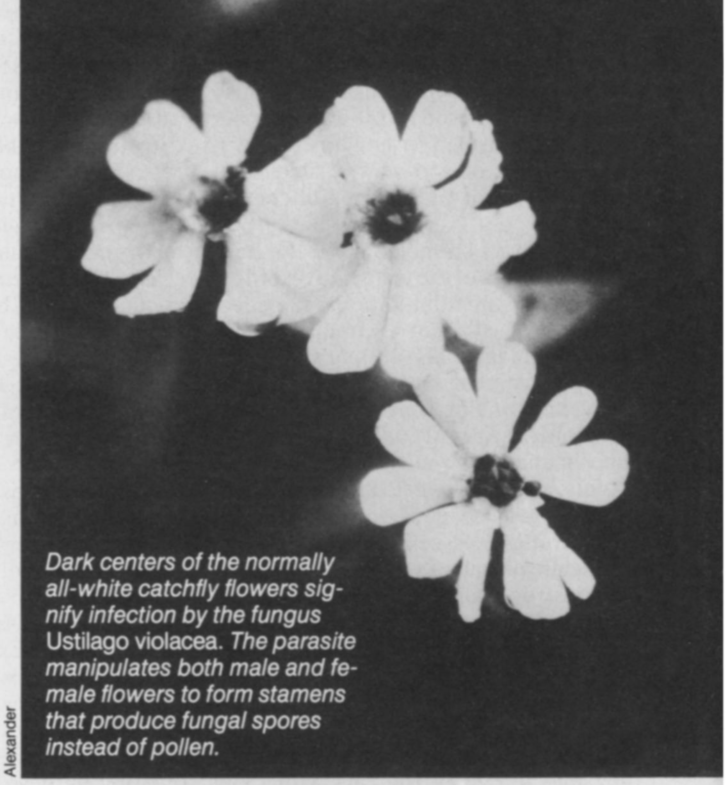
Parasite Power

In the perpetual race between parasite and host, evolution appears the winner



Dark centers of the normally all-white catchfly flowers signify infection by the fungus Ustilago violacea. *The parasite manipulates both male and female flowers to form stamens that produce fungal spores instead of pollen.*

Alexander

By RON COWEN

When the parasitic fungus *Ustilago violacea* infects a roadside weed called catchfly, casual observers might notice little difference in the plant. The abundant white blossoms do open a few weeks earlier in the growing season, and their centers take on a purplish tinge. Yet when bees, butterflies and other pollinators begin collecting the dusty grains on the flower's sex organs, business seems to proceed as usual.

Except that these grains aren't pollen.

In a bizarre scenario evoking the sci-fi films of the 1950s, the fungus performs a sex-change operation on female catchfly plants, causing them to abort their ovaries and develop stamens – male sex organs that normally produce pollen. And whatever the gender of its host, *U. violacea* secretly transforms stamens into spore factories. Dusted with spores instead of pollen, insects lured to the early, long-lasting blossoms unwittingly spread the fungal infection to the next cluster of catchfly they visit.

But the parasite's deception doesn't stop with this botanical masquerade. In its zeal to make the most of the takeover, *U. violacea* stimulates some plants to produce extra flowers, which attract more pollen-seeking insects, increasing the potential for spreading infection.

Helen M. Alexander of the University of Kansas in Lawrence, who has studied this fungal phenomenon for years, described her findings in July at the Fourth International Congress on Systematic and Evolutionary Biology, held in College Park, Md. She cites the maneuvers of *U. violacea* as a prime example of the parasitic potential for survival through manipulation.

Parasites are commonly written off as primitive, chemically simple organisms, incapable of such devious machinations. "That's a lot of rubbish," says Gerhard A. Schad, a parasitologist at the University of Pennsylvania in Philadelphia and president of the American Society of Parasitology. Indeed, Schad and others say mounting evidence suggests that parasite-host interactions may have profoundly influenced evolution, contributing to species diversity and perhaps fostering the emergence of sex itself.

In an attempt to elude parasitic control, hosts themselves have devised a variety of creative strategies. Some, such as aphids, turn to suicide when infected, sacrificing their lives in hopes of killing the parasite before it can spread to their relatives (SN: 4/15/89, p.231). Others switch from asexual reproduction – which yields genetically identical offspring – to sexual reproduction, mixing their genes with similar organisms nearby to create hybrids. Odds are that some of the hybrids will inherit natural resistance to the parasite.

These and other defensive ploys may in turn prompt the parasite to make adaptive changes so that it can maintain its foothold in the host species, says evolutionary biologist William D. Hamilton of Oxford University in England. Victories are only temporary in the never-ending race between parasite and host, yet each contender may profoundly change the course of its own evolution – and that of its opponent.

In 1973, Leigh Van Valen of the University of Chicago gave a formal name to the theory describing evolutionary changes triggered by interactions between antagonistic organisms. He called it the Red Queen hypothesis, after the character in Lewis Carroll's *Through the Looking Glass* who must run simply to stay in place. As Carroll put it:

> *Alice never could quite make out, in thinking it over afterwards, how it was that they began: all she remembers is, that they were running hand in hand, and the Queen went so fast that it was all she could do to keep up with her: and still the Queen kept crying "Faster! Faster!" but Alice felt she could not go faster, though she had no breath left to say so.*
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> *The most curious part of the thing was, that the trees and the other things round them never changed their places at all: however fast they went, they never seemed to pass anything. "I wonder if all the things move along with us?" thought poor puzzled Alice. And the Queen seemed to guess her thoughts, for she cried "Faster! Don't try to talk!"*

In the late 1970s, Hamilton and his colleagues began focusing on how that storybook concept applies specifically to parasites and their hosts. Today, researchers studying the flora and fauna of grasslands, lakes and tropical rain forests have a plethora of parasitic case histories to support the Red Queen theory. Such findings, says Schad, give scientists new respect for the power wielded by parasites.

At the July conference, biologist Keith Clay of Indiana University in Bloomington presented evidence that fungal parasites have gained the upper hand over certain wild grasses native to Indiana and sedges growing in the marshes of Louisiana. Normally, these plants can reproduce either sexually, through flowering, or asexually, by sending out genetically identical shoots. But Clay reports that natural infection with the fungus *Epichloe typhina* or its relatives destroys the flowering organs while leaving other parts unscathed. As a result, the plant can reproduce only by sending out shoots, which yield several square meters of equally vulnerable look-alikes.

By clamping down on sexual reproduction, the fungus ensures that if it can infect one generation, it can infect all others. "If sex is a defense by the host, then the parasite seeks to eliminate that defense," Clay suggests.

What's more, he says, infected grasses and sedges produce particularly lush, fast-growing offspring, providing the fungus with ample room for expansion. Many seed companies now take advantage of this effect, cultivating and marketing infected grass seeds as lawn starters.

At the same time, infection may offer the plants a protective benefit. In the February 1988 Ecology, Clay reported that several close relatives of *E. typhina* secrete toxic alkaloids while living in the tissues of the grasses they infect. The chemicals don't poison the plant; rather, they increase its resistance to insect pests and other natural enemies. In effect, the fungus defends its host, treating it as a valuable natural resource that must not die lest the invader lose its botanical sustenance. The parasite thus maintains control even while aiding the host.

Clay calls the parasite the winner in this interaction – for the time being, at least.

Sometimes, of course, the scale tips the other way. Curt M. Lively of Indiana University cites the apparent ability of a common freshwater snail of New Zealand to escape predation through reproductive versatility. Unlike most animals, the female *Potamopyrgus antipodarum* can generate offspring with unfertilized eggs. She can also reproduce sexually, with at least partial fertilization by a male snail.

This creature's nemesis is a worm known as the castrating trematode (genus *Microphallus*). Lively reports that the snail's asexual mode prevails in lakes where the trematode is rare, whereas sexual reproduction dominates in lakes with large populations of the worm. This suggests that trematode abundance triggers the snail to switch to sexual reproduction, producing a new generation of diverse offspring that may be less susceptible to the parasite, he says.

Observations such as these hint that in certain animals and plants, sexual reproduction originally evolved as a means of eluding parasitic attack, Clay asserts. Without the particularly potent and persistent influence of parasites, "it's hard to understand why, generation after generation, there are two sexes," he contends. "There's no inherent need to mate to produce offspring. If all species had just one sex, they could theoretically double their reproductive rates."

"Darwinian theory has yet to explain adequately the fact of sex," write Hamilton and several colleagues from the University of Michigan in Ann Arbor in the May Proceedings of the National Academy of Sciences (Vol.87, No.9). Their computer model of an evolving, human-like population indicates that sexual reproduction can endure only if it provides some added benefit beyond that of offspring. The researchers calculate that the "need to defeat various parasites" could offer that added benefit.

In any case, the give-and-take relationship between parasite and host appears to have had far-reaching consequences. Using fossil records and habitat studies, Brian D. Farrell and his colleagues at the University of Maryland in College Park have begun to sketch the broad evolutionary influence of insect herbivores and the plant species they parasitize – which together make up an astonishing 25 percent of all species on Earth. Farrell initially chose the leaf-eating beetles for their abundance and feeding habits, only later discovering that the fossilized shells of their ancestors hold a wealth of useful information.

He and his co-workers modeled their work on a hypothesis known as the co-evolutionary arms race, which was proposed in 1964 by Paul R. Ehrlich and Peter H. Raven, but has never been completely tested. According to the hypothesis, plant groups that temporarily escape herbivores through a newly evolved defense mechanism accelerate their own ability to diversify, creating a series of related species at a greater-than-normal rate. In turn, as parasites evolve to overcome that defense, they too diversify more rapidly, sometimes gaining the ability to exploit new host species. Thus, as plant and parasite continually break bonds and then reunite over the millennia, each presents the other with opportunities for gaining new evolutionary ground.

In an attempt to establish that diversity among host plants of the order Lamiales could have sparked diversity in the *Phyllobrotica* leaf beetles, the researchers first gathered data suggesting the beetles have had ample opportunity to interact with the same Lamiales hosts for extremely long periods of time. In the September Evolution, Farrell and Charles Mitter describe fossil records indicating that the oldest *Phyllobrotica* and Lamiales lineages date back to approximately the same period – about 30 million to 40 million years ago. And at last month's meeting of the American Institute of Biological Sciences in Richmond, Va., Farrell reported fossil evidence indicating that most of the beetle species remained faithful to the same host species for 1 million to 2 million years at a


White, spore-producing mass of Balansia cyperi, *a relative of the fungus* Epichloe typhina, *surrounds and smothers immature flowers of the sedge* Cyperus virens, *preventing flowering. By clamping down on the plant's ability to reproduce sexually, forcing it to generate genetically identical progeny, the parasite ensures that it can infect sedge offspring.*

Clay

time — long enough for significant interactions to occur, he says.

Small communities of plants and insects can persist over millions of years, Farrell explains, in part because the highly mobile insects can easily chase plants forced to migrate by climate changes or other disruptive events.

Farrell and Mitter went on to test a central concept of the parasitic arms race: that host plants evolving the most sophisticated defense systems would trigger the greatest diversity among their parasites. Working with University of Maryland colleague David D. Dussourd, they focused on a variety of plants (including poinsettia, milkweed and fig) that share a highly effective defense mechanism: leaves laced with tiny canals that ooze either latex or resin when leaf beetles and other herbivores chomp down. The gummy fluid serves to immobilize these trespassers at the first sign of attack.

The team matched each of the 16 host plant families with a control group — close relatives that seemed identical in every way, including age, shape and origin, except that they lacked the defensive canals. Then, using botanical data compiled by other researchers, they calculated species diversity for each group of plants. Farrell says the tabulation revealed that 14 of the canal-bearing plant groups had evolved into a significantly greater number of species — as many as 10 to 100 times more — than their sister groups.

Though preliminary, these findings offer some of the first quantitative evidence in plants that the arms race against insect parasitism leads to diversity, he says. A report on the work will appear in an upcoming AMERICAN NATURALIST.

Although researchers traditionally equate species abundance with the tropics, Farrell notes that the contrasting patterns of diversity seen in canal-bearing plants and their sisters persist in widely different climates, including both tropical and temperate zones. He suggests that the greater overall diversity in tropical rain forests stems from that ecosystem's greater age and not from climate conditions. Tropical plants have simply had a longer time to interact with parasitic insects, and thus more opportunity to diversify, he says.

In their most recent, unpublished work, Farrell and Mitter used fossil records and modern data to track the efforts of a particular host plant — the milkweed — to improve its leaf canals. By evolving a pressurized secretory system, the plant has gained the ability to respond more rapidly to wounding and to concentrate increasing amounts of defensive toxins in the latex.

But the plant's chief parasite, the milkweed beetle, did not remain idle as its host developed a more sophisticated defensive system. The researchers found that the beetle eventually gained the ability to sidestep the toxic defense by strategically cutting canal veins and then dining on leaves distant from the severed sites. Evolutionary changes also enabled many species of milkweed beetles to tolerate the toxins and incorporate them into their own bodies, where the chemicals serve to ward off the beetles' own predators, Farrell says.

Using modern methods of estimating species genealogy, the team concluded that diversity among milkweed beetles appears to have evolved in synchrony with diversity among milkweed plants. In other words, the number of beetle species rose after each jump in the variety of related host species. Farrell maintains that the same sort of synchronized diversification should appear among other parasites and their hosts.

Thus, he and others suggest, scientific efforts to keep score as the contenders take turns outwitting each other may miss the point. If evolutionary success is measured by an organism's ability to change and diversify, then simply perpetuating the race may be the real victory. Perhaps, in the long run, it's not whether you win or lose, but merely that you play the game. □