Letter from the Desk of David Challinor
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Most of us consider plants to be relatively passive organisms. Once a fertile seed has formed and sprouted, we think the plant is stuck where it is growing and can do little to protect itself. Botanists and dendrologists (tree experts) know this is not the case at all and long-lived trees in particular possess extraordinarily varied defenses against assaults from insects, vertebrates and even fire. This month's letter will offer examples of how various kinds of trees can alter their growth to fit variant stages of growth and related degrees of vulnerability.

My first example is the oak and beech (*Fagaceae*) of the eastern United States. When the European gypsy moth was imported into Massachusetts in the late 1800's, entrepreneurs planned to cross it with the oriental silk worm to produce a hardy variety for a local silk industry. Sadly, the hybridization failed and, catastrophically, the gypsy moths escaped. Although they spread slowly at first, they rapidly expanded through the hardwood forests of the northeast and mid-Atlantic states.

By the late 1950's, gypsy moths became a major pest. Hordes of their three centimeter-long, hairy caterpillars in the last instar (have had their last molt and are ready to pupate or make a cocoon) of their larval stage voraciously devoured the foliage of favored oaks and beeches. When hungry enough, they would consume the evergreen leaves of mountain laurel and even conifer needles. I clearly remember walking through an oak forest outside New Haven in mid-June and hearing not only the leaves being chewed above me, but the gentle rain-like sound of caterpillar frass (faeces) falling on the dried hardwood leaves on the forest floor. Above me, the sky was incongruously visible through the stark winter-like, leafless canopy.

Although defoliated conifers always died, local deciduous trees retained enough stored energy from the previous summer of constant daytime photosynthesis that they reflushed with a whole new crop of leaves. By the 4th of July in Connecticut, the forest canopy was once again restored, with little evidence of the gypsy moth assault. Producing a second crop of leaves, however, is costly for a tree, and few hardwoods can withstand more than two consecutive defoliations. Trees are conservative organisms, and to protect themselves from having to double flush two years in a row, they take action to thwart an invasion the following year.

Oaks and beech produce tannins and in former times, tannic acid was extracted from the bark of certain trees—often oaks (especially tan bark oak (*Lithocarpus densiflorus*)) that grow among the coastal redwoods of California. During the summer after spring defoliation, Connecticut oaks, perhaps assisted by the fertilizing effect of the nitrogen-rich frass that passed through the guts of the caterpillar hordes eating their first leaf flush, marshaled their energy to produce their next year's initial flush. That leaf crop would have a higher tannic acid content than that of the previous year's and the leaves would, therefore, be considerably less tasty to the hungry larvae. That is why it is rare for oak groves to be defoliated for two consecutive summers. Gypsy moths merely move to an unprotected adjacent stand of trees and start eating their leaves. It was thus easy to observe the patchiness of defoliation.

Gypsy moth assault on the hardwoods of the northeastern USA seems to have abated somewhat in the last decades. Perhaps our native white-footed mice, a local forest-dwelling rodent, have adapted to eating gypsy moth egg masses in the winter. About 40 years ago, oak trunks in Connecticut forests commonly had pale tan felt-like splotches stuck to their bark. Inside the felt mass were hundreds of silvery-colored moth eggs, an ideal winter meal for a hungry mouse.

Trees not only have chemical defenses to protect themselves, as just described, but also physical ones. For example, in the juniper family, Virginia cedar (*Juniperus virginiana*), a common pioneer species frequently seen growing in their characteristic columnar form in abandoned pastures or along the sides of highways, protects its juvenile form (when the tree is only two or three feet tall) by having very prickly foliage; hungry deer will occasionally nibble the young trees, but cows and horses avoid them. When the tree reaches five or six feet, above the reach of many browsers, the foliage becomes softer and flatter. The lowest branches, however, retain their prickly juvenile characteristics throughout life, to deter deer.

Another common eastern tree, black locust (*Robinia pseudoacacia*), is one of the few temperate nitrogen-fixing trees. It has large rosebush-shaped thorns on its juvenile stem to deter deer. This tree grows quickly, however, and when the trunk is three or four inches in diameter, its bark is thick enough to protect the stem and the sharp needles drop off.

In the Zoo's Amazonia exhibit, there is a fiberglass replica of *Ceiba pentandra*, or the kapok tree. This tropical giant, whose crown often pierces the forest canopy, has wind-disseminated seeds that are borne aloft by a mass of fluffy fuzz, which at one time was harvested to fill life jackets. Today, synthetics have replaced kapok. Adjacent to this fiberglass replica (which also serves as an air duct for the exhibit) is a live juvenile kapok tree whose lower six-inch diameter stem is covered with thorns so sharp and thick that few monkeys or sloths would try to climb it. As in the case of black locust, the thorns disappear when the tree matures.

A more intriguing example of protective arboreal strategy is the use of ants to reduce browsing or canopy vine competition. Tropical acacias use this technique. Bull horn acacia in the dry parts of Central America has huge hollow, curved "horns" for its ants, and on the Smithsonian's Barro Colorado Island in Panama, *Acacia melanoceras* maintains biting ant colonies in its thorns.

A fascinating study by M. Huntzinger* on an African acacia *(Acacia drepanolobium*) was recently published. It sought to learn whether this tree would continue to maintain its ant colonies if it was artificially protected from browsing mammals. Huntzinger and colleagues conducted their work at Mpala ranch in Kenya, a research facility operated by the Smithsonian, Princeton and the National Museum of Kenya. This acacia has large hollow thorns in which any one of four biting species of ants live. When a mammal browses on its tasty nitrogen-rich foliage, resident ants rush from their thorns to bite the intruder. The tree, in turn, lures ants to its hollow thorns by providing nectaries (glands that secrete nectar) at the base of leaves. The swollen hollow thorns are modifications of smaller sharp spines and the ratio of hollow thorns to spines varies from tree to tree. How this ratio is determined remains unknown. As most of us realize, there is a cost to everything. Providing food and lodging to your own private army of ants is expensive in terms of energy the tree must expend to enjoy this protection.

To help understand the cost of this relationship between tree and ant, Huntzinger and colleagues sought to learn whether this acacia species would relax its efforts to provide food and housing for its ants if browsing herbivores were excluded. For seven years, the scientists monitored these trees in a series of fenced plots that effectively kept such browsers as elephants, giraffes and elands at bay.

What they found was that protected acacias invested less energy and thereby produced 25% fewer nectaries and swollen thorns than did neighboring unprotected trees. Observations showed that attacking ants significantly reduced the feeding time of juvenile giraffes and completely stopped foliage-browsing by goats. What is particularly interesting is that these acacias do not cut back on nectary and large thorn production until having at least a year of protection; by the end of seven fenced years, the trees could indeed relax and they produced significantly fewer nectaries and swollen thorns. This study is but one more example of how trees must be conservative in their strategy to survive. In other words, even after seven years of protection, they still had to maintain their guard in case conditions reversed, as in the case of broken fences. Humans can take heed from trees; boom times are not permanent and it is wise always to be ready for economic slumps.

Trees may modify their survival strategy slightly, but they seldom abandon it. For example, the tropical forest on Barro Colorado Island is classified as semi-deciduous, which means that many deciduous trees drop their leaves during the dry season. S.T.R.I. scientist Joe Wright experimented to learn whether he could alter the annual foliage loss of these dry season leaf droppers by pumping lake water on the forest floor during the dry season. After a few seasons of careful observation, he found that the species that normally dropped their leaves did so regardless of how much water was available. This

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* Huntzinger, M. *et al*. 2004. Relaxation of induced indirect defenses of acacias following exclusion of mammalian herbivores. *Ecology* 85(3): 609-614.

tells us that if you are a tree and your species has been growing on earth for a few hundred thousand years, you and your kin have evolved to handle most contingencies; in this case, you have to be ready for dry seasons when it sometimes rains as well as for unusual wet seasons. Non-adaptable individuals seldom survive.

When you next have time to look closely at a tree, try to imagine that among its leaves are myriad tiny foliavores chewing away. Warblers and other birds glean the foliage to reduce the damage. The tree itself can also often produce chemical compounds to protect all its parts—roots, trunk, foliage, fruit, etc. It is a dynamic process and a fascinating one to try to unravel. The interactions of prey and predator are so numerous and complex that future generations of scientists are unlikely ever to untangle them all.

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