PERSPECTIVES: ECOLOGY

The Enemy of My Enemy Is My Ally

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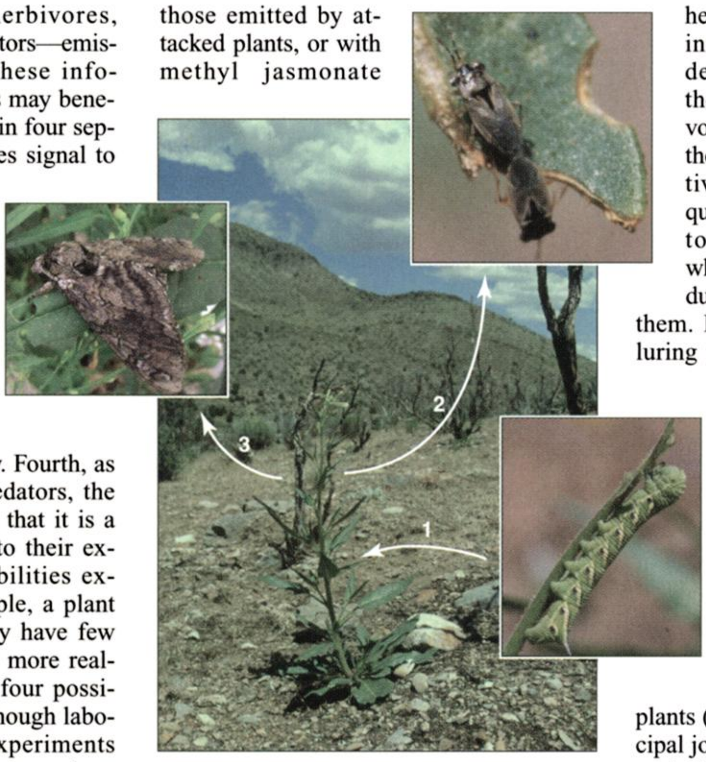
When attacked by insects or other herbivores, plants release airborne chemical information in the form of volatile organic compounds. Assuming that there are no more than three trophic levels in the food chain—plants, herbivores, and predators—emission of these infochemicals may benefit plants in four separate ways. First, these volatiles signal to other herbivores that the plant's defense system has been switched on. Second, volatiles let other herbivores know that the plant is already under attack and so, to avoid competition, they may prefer to feed elsewhere. Third, they signal to the predators of herbivores that their prey is in the vicinity. Fourth, as a by-product of attracting predators, the plant alerts hungry herbivores that it is a well-guarded fortress. Taken to their extremes, some of these possibilities exclude one another—for example, a plant that is toxic to herbivores may have few prey to offer predators. Under more realistic conditions, however, all four possibilities may act in concert. Although laboratory (*1*) and field (*2, 3*) experiments have amply demonstrated pronounced responses of herbivorous and predaceous insects to herbivore-induced plant volatiles, all of these experiments have been conducted in agricultural settings (*4, 5*). On page 2141 of this issue, Kessler and Baldwin (*6*) present evidence that herbivore-induced plant volatiles are both a direct and an indirect plant defense in nature as well. They show that plants under attack by herbivorous insects release volatiles that both repel new herbivores and attract insect predators.

In a series of elegant experiments conducted in the Great Basin desert of southwestern Utah in the United States, Kessler and Baldwin first established that wild tobacco plants release volatiles when fed upon by three species of herbivorous insects (see the figure). Next, they studied the degree of predation of herbivore eggs by native heteropteran leaf bugs. The eggs were glued onto tobacco leaves that had been treated either with a single synthetic volatile identical to those emitted by attacked plants, or with methyl jasmonate (MeJA), a chemical that induces plants to release a blend of volatiles similar to that induced by herbivory (*7*). Finally, they assessed how many eggs were laid by one of the herbivorous insect species on tobacco plants treated with a single volatile or with MeJA. When tobacco plants were treated with different single synthetic volatiles, herbivores avoided laying their eggs in response to some volatiles and predators ate more of the test prey (glued-on herbivore eggs) in response to others. Application of either MeJA or linalool (a synthetic volatile) induced both effects simultaneously. So, the double-edged defense system of plants can be elicited by either a single volatile or a blend of volatiles.



Plant perfumes, hungry herbivores, and biting bugs. Pictured is a natural ecosystem in the Great Basin desert of southwestern Utah (*6*). **(1)** Wild tobacco plants are attacked by caterpillars of the moth *Manduca quinquemaculata*. **(2)** This attack induces the tobacco plants to emit volatile organic compounds that attract natural enemies of the caterpillars such as big-eyed bugs (*Geocoris pallens*). **(3)** The airborne volatiles also stop adult *M. quinquemaculata* moths from laying their eggs on tobacco plant leaves.

The Kessler and Baldwin results strongly support the notion that herbivore-induced plant volatiles not only deter herbivores but also attract predators that act as bodyguards. It is not yet clear whether individual volatiles enable predators to identify the species and abundance of herbivores on a particular plant [but see (*8*)]. It is also not known why volatiles repel herbivores and whether they convey information about the plant's well-defended state. It is possible that these versatile volatiles alert herbivores to one or more of the following: the plant harbors competitors, has activated its direct defenses, has acquired indirect protection from predators. Finally, it remains unclear whether volatiles promote the reproductive success of the plant that emits them. Kessler and Baldwin estimate that luring predators and repelling herbivores results in about a 90% reduction in the number of herbivorous insect eggs laid on volatile-treated tobacco leaves. Of course, it is not the eggs themselves but rather the insect larvae that induce plants to release volatiles, and so plants will attract predators only after the eggs have hatched. Because one hornworm larva is enough to completely defoliate several wild tobacco plants (*6*), one might ask whether the principal job of volatiles is to reduce herbivory such that the plant is not completely defoliated and is still able to reproduce.

To find out why natural selection favors plants that emit an airborne signal upon attack, a cost-benefit analysis should be undertaken. Such an analysis would monitor not only interactions among plants, herbivores, and their predators, but also those between members of the entire food web (*5, 9, 10*). The reason for this is that herbivore-induced plant volatiles may not only lure predators and repel herbivores, but also may attract competitively superior herbivores or predators that also eat plants (omnivores) or hyperpredators, or hyperparasitoids (*9*). Potentially, volatile emission could cause the plant to incur more damage or to lose its bodyguard protection. Moreover, competing nearby plants may profit from the predators lured by a volatile-releasing plant, saving their own energy for other purposes (*10*). Because Kessler and Baldwin's experiments were

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conducted in low-density, pioneer vegetation in the desert, such tests need to be repeated in regions with more diverse, dense vegetation. Also, the time scale of future studies should be longer. Kessler and Baldwin's experiments were probably conducted over too short a period to enable them to observe the full behavioral repertoire of all organisms in the food web and the complete range of interspecific interactions. Indeed, anyone undertaking a critical cost-benefit analysis needs to be aware that apparently beneficial interactions are never foolproof and that their outcome may vary between parasitism at one extreme and mutualism at the other, depending on the conditions (*11*). Nevertheless, Kessler and Baldwin have taken an important first step toward unraveling the nature of direct and indirect plant defense.

References

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PERSPECTIVES: CHEMISTRY

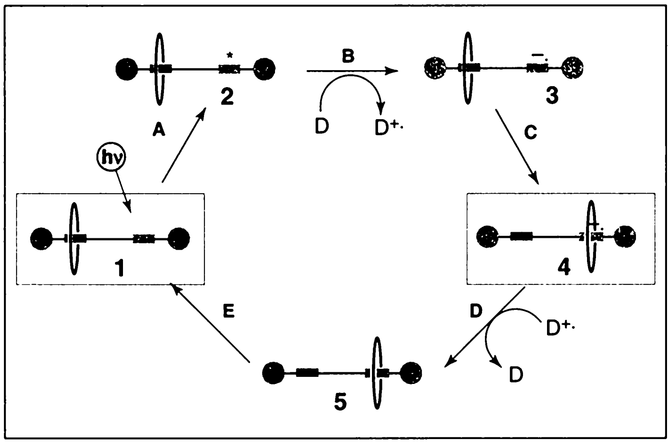
A Light-Driven Linear Motor at the Molecular Level

Jean-Pierre Sauvage

Molecules called catenanes (interlocking rings) and rotaxanes (a dumbbell threaded through a ring) have experienced a spectacular revival during the past 15 years. Until the beginning of the 1980s, they were considered interesting laboratory curiosities but suffered from the fact that they could be prepared in tiny amounts only (*1*), thereby precluding their detailed study or application.

The introduction of templated strategies to construct catenanes and rotaxanes dramatically changed their fate. Within a few years, they became synthetically quite accessible compounds, typically made on a scale of 0.1 to 1 g (*2*). Synthetic chemists could tune their properties by introducing appropriate functions and began to envision a bright future for materials made from these molecules. The post-1980s catenanes and rotaxanes display interesting properties, such as transition metal complexation, photochemistry, photoinduced electron transfer and luminescence, electrochemistry, and electrochromism. A second revolution occurred at the beginning of the 1990s, when chemists proposed that these compounds could form the basis of molecular machines and motors; the time for setting them into motion was ripe (*3*, *4*). New concepts were introduced, such as molecular "shuttles" (*5*), in which a ring moves at will along the string on which it is threaded, and controllable catenanes (*6*), in which a ring undergoes circumrotation within another ring with which it is interlocked. Soon, molecules other than catenanes and rotaxanes were used to build fascinating molecular machines made from synthetic organic compounds or DNA (*7*). Recent examples include rotary motors (*8*, *9*).

On page 2124 of this issue, Brouwer *et al.* show that an asymmetrical rotaxane, based on hydrogen bonding, behaves like a linear motor, reminiscent of the way a piston moves within a cylinder (*10*). The translational motions of the ring along the axle through which it has been threaded can be regarded as the power stroke of a piston in a given direction, followed by a recovery stroke in the opposite direction. The system is particularly remarkable because the "motor" is entirely driven by light (see the figure).



Light-driven "power stroke" of Brouwer *et al.*'s molecular linear motor. In the resting state of the rotaxane (**1**), the ring preferentially interacts with the station on the left through hydrogen bonds. In step **A**, energy input in the form of light generates an excited state on the station on the right (**2**). The excited state has a strong electron-accepting character. In step **B**, it accepts an electron from an external electron donor D to afford **3**, with an extra electron on the station on the right. This negative charge enhances the affinity of the ring for this station. The ring moves to the right (step **C**) to afford **4**. By analogy with a piston, steps **A** to **C** can be considered as the "power stroke." This takes about 1 μs, after which the system returns to its original state ("recovery stroke"). The oxidized donor D$^{+\cdot}$ generated in step **B** is reduced back to D in step **D**, and the unstable species **5** thus generated leads to the starting form **1** by shuttling the ring back to the left. The recovery process is complete within about 100 μs.

The motion has been demonstrated with a set of various physical techniques, the most important of which is time-resolved transient absorption spectroscopy, which almost allows the "visualization" of the shuttling process as a function of time. Until now, the "fuel" used to set molecular machines in motion was mostly electrochemical, chemical, or photochemical, the latter requiring the consumption of an added compound used as a "sacrificial" agent. In the previous studies, one could also isolate the different states of the machine. The beauty of the present system is that nothing but light is consumed. If the shuttle is pumped with laser pulses at the right frequency, the molecular machine can, in principle, generate mechanical power.

There are at least two reasons for designing, constructing, and studying molecular machines. First, such systems may be able to mimic essential biological processes involving motion, such as the rotary motor adenosine triphosphatase (*11*) or linear motors involved in muscle contraction and stretching (actin/myosin). Second, artificial systems may act as switches or as information storage and processing devices at the molecular level. Remarkable recent

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