Plant communication – why should plants emit volatile cues?

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REVIEW ARTICLE

Plant communication – why should plants emit volatile cues?

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There are now approximately 10 documented examples of volatile plant communication that affect resistance to herbivores. For several of these cases, plants have been found to experience fitness benefits by responding to information (cues) released by experimentally damaged neighbors. However, it remains puzzling why plants might emit these cues following herbivore attack. One possibility is that release of cues is not adaptive for the emitter but rather cues leak out as a consequence of damage. Hypothetical benefits of emitting cues include: repelling herbivores; attracting predators of herbivores; suppressing germination of competitors; communicating with other branches of the same plant; and communicating with genetic relatives. Progress will be made in this field if we can find a system that is more tractable, allowing the nature of the cue to be identified and manipulated or allowing us to examine genetic constraints and influences on communication.

Keywords: plant fitness; signaling; resistance; herbivory; cost/benefit analysis

Plant tissues that are attacked by herbivores emit volatile organic compounds that can make unattacked tissues on the same or different plants more resistant to subsequent herbivory. This phenomenon of induced resistance that is stimulated by volatile cues has been controversial since its first reports in the 1980s (Baldwin and Schultz 1983; Rhoades 1983), although there are now approximately 10 widely accepted examples in the literature (reviewed by Heil and Karban 2010). Most of these examples involve either agricultural crops or long-lived woody species. These groups leave much to be desired as models that will yield answers to evolutionary questions about plant communication.

All communication systems have emitters that release information-rich cues and receivers that respond to them (Bradbury and Vehrencamp 1998). It makes intuitive sense for plants to respond to reliable cues from their abiotic and biotic environments and to change their phenotypes appropriately (Karban et al. 1999). For example, plants are well known to alter the direction and extent of stem elongation in response to the quality and quantity of light that they receive (Smith 2000). Plasticity in response to light can increase the fitness of plants that respond appropriately (Schmitt et al. 1999). We have several examples of plants that respond to volatile cues of herbivory to increase their defenses and appear to accrue fitness benefits. Wild tobacco plants growing in proximity to experimentally damaged sagebrush produced as many or more flowers and seed capsules as non-induced tobacco plants near unclipped sagebrush neighbors (Karban and Maron 2002). In this case, tobacco and sagebrush share many generalist herbivores although sagebrush is often attacked earlier in the season than tobacco. Similarly, lima bean tendrils that were exposed to volatiles from shoots damaged by herbivores produced more leaves and more inflorescences than non-induced control tendrils (Kost and Heil 2006).

The advantages of responding to cues released by herbivory pose few theoretical problems even though the evidence that plant fitness actually increases is limited. In contrast, it is not intuitive why plants would be favored to emit cues after they have been damaged. This problem becomes more puzzling if neighboring plants can use this information to appropriately adjust their phenotypes. This may give eavesdropping neighbors a competitive advantage relative to the damaged emitter. We have considered several non-exclusive hypotheses to explain the release of volatile cues in our work with sagebrush plants which we discuss below. These hypotheses are: (1) release of cues is not adaptive for the emitter; (2) volatile cues repel herbivores; (3) volatile cues attract predators and parasites of herbivores; (4) volatile cues suppress germination of competitors; (5) volatile cues allow plants to coordinate their own individual systemic responses; and (6) volatile cues allow plants to preferentially defend their kin.

There is a tendency to interpret plant traits that provide defense against herbivores in terms of their benefits against herbivory. However, those same traits may have many other undescribed consequences and these consequences may have been more influential than herbivory in shaping adaptations involved in

communication. In addition to correlations with other traits, physical laws, past evolutionary history, lack of variation, and other factors may constrain adaptation. Keeping these caveats in mind, it may still be useful to consider the fitness consequences of traits that are involved in complex processes such as communication between plants.

Many organisms are affected by the volatile organic chemicals that are released by foliar herbivory. In many cases, the volatiles released by damage are directly repellent to herbivores (Bernasconi et al. 1998; De Moraes et al. 2001; Bruinsma et al. 2008). Herbivore induced volatiles have also been reported to protect plants against pathogens and a variety of abiotic stresses (e.g. Shulaev et al. 1997; Behnke et al. 2007). However, there are also many examples in which volatiles are attractive to herbivores and pathogens so that their role as repellents is far from universal (e.g. Bolter et al. 1997; Carroll et al. 2008). We failed to find evidence that volatiles from experimentally clipped sagebrush were repellent to the generalist grasshoppers that feed on them (Karban and Baxter 2001).

Volatile chemicals that are emitted when herbivores attack plants can attract predators and parasitoids of the herbivores (Dicke and Sabelis 1988; Turlings et al. 1990). Considerable progress has been made in understanding the mechanisms of this process (reviewed by Arimura et al. 2009). There is mounting evidence that the carnivores attracted by volatiles increase rates of mortality to herbivores and even decrease levels of damage inflicted by herbivores under field conditions (Thaler 1999; Kessler and Baldwin 2001; Heil 2004). However, convincing evidence that volatile communication between plants and carnivores actually increases plant fitness under natural conditions is still lacking (Allison and Hare 2009; Kessler and Heil 2010). In our system, experimentally clipped sagebrush attracted more carnivores than unclipped controls although this produced no measurable reductions in leaf damage (Karban 2007a).

Volatile compounds that are emitted by herbivore damage may help the damaged adult plant by inhibiting its competitors. Plants that are attacked by herbivores are known to emit methyl jasmonate and this volatile plant hormone is a powerful germination inhibitor (Creelman and Mullet 1997). Ethylene has also been found to be capable of acting as a damage-induced inhibitor of root growth of neighbors (Inderjit et al. 2009) and other volatile chemicals may inhibit the growth of neighbors by still unexplained mechanisms (Barney et al 2009). Volatiles emitted by experimentally clipped sagebrush were effective germination inhibitors of neighboring seeds, particularly seeds of other species (Karban 2007b). Allelopathic effects of volatiles have been difficult to study for logistical and sociological reasons and we know very little about their potential benefits for plants that emit them.

Early reports of induced resistance being effective at reducing herbivore populations portrayed plants as responding systemically to herbivore damage (Karban and Carey 1984; Haukioja and Neuvonen1985; Pearce et al. 1991). However, subsequent work revealed that induced resistance was stronger in some parts of the plant, particularly those close to the site of damage (Tuomi et al. 1988; Orians et al. 2000). Indeed, many plants are highly sectored such that exchange of the nutrients, secondary chemicals, and hormones that mediate plant-herbivore interactions is limited to tissues that share active vascular connections. This is turn limits vascular communication and systemic induced resistance to those parts of the plant that share a common plumbing system (Viswanathan and Thaler 2004; Orians 2005; Rodriguez-Saona and Thaler 2005). Induced resistance that depends on vascular signaling may be further limited by a requirement for active transpiration making plants vulnerable to water stress and hydraulic failure (Waisel et al. 1972; Zanne et al. 2006; Schenk et al. 2008).

Recent work suggests that an important function of volatile communication is that it allows plants to coordinate physiological processes, including induced resistance, among tissues within an individual. Studies that have experimentally manipulated volatile communication have found that it is essential for systemic induced resistance (within an individual) for sagebrush and a variety of other plant species (Karban et al. 2006; Heil and Silva Bueno 2007; Frost et al. 2007; Rodriguez-Saona et al. 2009).

Volatile communication systems have many advantages over vascular communication although the volatile signals become 'public information' available for other organisms – other individuals of the same species, other plant species, herbivores, pollinators and other plant mutualists, and the predators and parasites of these species. Sagebrush was found to communicate more effectively between cloned cuttings that were genetically identical compared to different individuals (Karban and Shiojiri 2009). The volatile profiles of different sagebrush individuals vary considerably although the active components have not yet been identified (Ishizaki et al., unpublished). Regardless of the mechanism, these results suggest that plants respond differently to self- and non-self signals and they may also be able to respond differentially based on levels of relatedness. At the other extreme, communication has been found between individuals of different plant species (sagebrush and wild tobacco, Karban et al. 2000; thistles and barley, Glinwood et al. 2004). This lack of specificity may have been caused by signals that are highly conserved among species or by plants responding to the specific cues emitted by very abundant plants that they have coevolved with.

The sagebrush system has allowed us to elucidate some of the basic natural history of volatile communication between plants under natural conditions. In the future, we would like to identify the chemical

nature of the volatile cues, the fitness consequences of communication, and whether the effectiveness of communication is dependent upon genetic relatedness. Sagebrush may not be the best system to answer these questions because it produces a very large number of candidate volatiles that are difficult to analyze and manipulate, it is long-lived and slow-growing, and it is difficult to cross and clone. Some of the logistical problems can be solved by collecting and moving volatiles from one plant to another (Karban et al. 2010), although these procedures come with other potential side effects. Progress will be accelerated if communication can be demonstrated between plants that are more amenable to evolutionary, physiological, and genetic studies although to date no such systems have been identified. Experimental damage to *Arabidopsis thaliana* has been found to cause emission of volatiles (Godard et al. 2008) and both tomato and tobacco have been found to be useful as receivers but not emitters of cues (Farmer and Ryan 1990; Shulaev et al. 1997; Karban et al. 2000).

In summary, it makes sense that plants should respond to environmental cues to adjust their phenotypes but it is puzzling why they should emit cues when they have been attacked by herbivores. Several plant species appear to benefit by eavesdropping on the cues emitted by damaged neighbors. For sagebrush, emitting cues following damage may be favored as a means of reducing competition, signaling to achieve systemic induced resistance, or communicating with kin. Future work that takes an evolutionary perspective and uses a more tractable plant system will be required to resolve this puzzle.

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