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To cite this article: M.W. Sabelis , A. Janssen & J. Takabayashi (2011) Can plants evolve stable alliances with the enemies' enemies?, Journal of Plant Interactions, 6:2-3, 71-75, DOI: [10.1080/17429145.2011.556262](https://doi.org/10.1080/17429145.2011.556262)

To link to this article: <https://doi.org/10.1080/17429145.2011.556262>



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Published online: 11 Mar 2011.



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REVIEW ARTICLE

Can plants evolve stable alliances with the enemies' enemies?

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(Received in final form 17 January 2011)

Rooted and unable to evade herbivores, plants gain by supporting the enemies of herbivores. They may provide food and refuge space to predators, but also release herbivory-induced chemical signals betraying herbivores to their predators. Can we expect such plant-predator alliances to resist invasion by mutants acting as saboteurs or cheaters? Examples of such mutants are 'stealthy' herbivores that do not alert the plant and 'cry wolf' plants that invest in acquiring predators even when they harbor no or only few herbivores? Mathematical models suggest alliances to build up and breakdown due to frequency-dependent selection. Hence, we predict that tritrophic systems are prone to exhibit waves of alliance build up and breakdown, and we point out the implications for pest control through crops with genetically engineered investments in alliances with predators.

Keywords: indirect plant defense; tritrophic interactions; induced defense; constitutive defense; herbivore; predator

Plant-predator alliances

Tripartite interactions offer the opportunity to combat an opponent by acquiring help from its enemy. This principle is expressed in the well-known proverb 'the enemy of your enemy is your ally,' which has a rich history of applications in international politics (Maoz et al. 2007) and ecological communities (Sabelis et al. 2001). However, the lesson from international politics is that such alliances are highly vulnerable to changes in the role of one or more parties: returns from helping wane if the enemy avoids interacting, yet may even turn out negative if the enemy of the enemy switches to become the main enemy. Such complete role changes are rare in ecological communities. Most organisms tend to retain their trophic position in the food web (some feed at more than one trophic level, but such omnivores usually do not switch their trophic position) and this may create better conditions for alliances between organisms one trophic level apart. However, we will argue that this does not necessarily render stability of such alliances because there are many ways to cheat or sabotage.

We will focus on the stability of alliances in tritrophic systems involving plants, herbivorous arthropods, and the herbivore's enemies. Rooted and unable to flee, plants have to defend themselves either directly against herbivorous arthropods or indirectly by acquiring help from predators of herbivorous arthropods (Price et al. 1980; Dicke and Sabelis 1988; Sabelis and de Jong 1988). Direct plant defenses involve all ways in which plants can intoxicate (e.g. cyanoglycosides) and immobilize herbivores (glandular

hairs) and in which their food content becomes indigestible (e.g. proteinase inhibitors), unpalatable, or unreachable (e.g. dense leaf hair mass, thick cuticle) to herbivorous arthropods, but also all ways in which plants can advertise their defendedness by releasing volatile chemicals (e.g. wild tomato sesquiterpenes, 7-epi-zingiberene, and R-curcumene, which upon ingestion by whitefly nymphs act as a toxin and upon emission from the plant as a volatile act as a repellent to whitefly adults; Bleeker et al. 2010). Indirect plant defenses involve all ways in which the plant can promote the effectiveness of the enemies of herbivorous arthropods. These include constitutive morphological plant structures (hollow thorns; hair-tuft, roof-like, pit-like structures where leaf veins branch; less compact and hairy plant apices) that act as a refuge (domatium) from abiotic (e.g. UV-B radiation; Onzo et al. 2010) and biotic (cannibalism, intraguild predation) conditions to predators (ants or predatory mites) (Jolivet 1996; Walter 1996; Faraji et al. 2002; Onzo et al. 2003, 2009; Sabelis et al. 2005; Ferreira et al. 2008), herbivore-induced morphological changes that help predators to get access to herbivorous arthropods otherwise concealed in plant tissues (Lesna et al. 2005; Aratchige et al. 2007), primary plant compounds (proteins, amino acids, and sugars) that become available as food packages (e.g. Beltian bodies, pollen), exudates or glandular secretions (e.g. from extrafloral nectar glands), either constitutively (i.e. independent of actual herbivory) or induced by herbivory, and that act as an alternative food supply to predators (Jolivet 1996; Van Rijn et al. 2002; Sabelis et al. 2005), and volatile secondary plant

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compounds that are induced by herbivory and signal the presence of prey to predators (Dicke and Sabelis 1988; Sabelis et al. 2007).

Herbivory-independent alliances

Constitutive modes of indirect plant defense have in common that the plant can exert no or limited direct control over which organisms make use or abuse of the support offered by the plant. For example, the most advanced domatia have an entrance that exactly fits the size of an ant or a mite, thereby excluding arthropods of larger, but not of smaller size. Although this does not guarantee the domatia – inhabitants are from the third trophic level, domatia are usually occupied by carnivorous (as well as fungivorous) arthropods (Walter 1996). This empirical observation may be explained as follows: any herbivore moving into domatia increases the probability of encountering predators seeking protection in domatia too, and this favors herbivores avoiding domatia (Sabelis et al. 1999a, 1999b). Much the same argument applies when the alternative foods provided by the plant are edible to both predators and herbivores (e.g. pollen is fed upon by western flower thrips and predatory mites alike). Usually these foods are provided locally (e.g. pollen in flowers or on leaves just below flowers), thereby allowing predators (and not herbivores) to monopolize this resource and reap the benefits (Van Rijn et al. 2002; Sabelis et al. 2005). In the (relatively rare) cases where herbivorous arthropods gain some profit from domatia (e.g. Kasai et al. 2002, 2005) or plant-provided foods (Sabelis et al. 2005), they do not necessarily cheat the plant if the benefit from boosting generalist predators offsets the costs of boosting herbivores (Van Rijn et al. 2002; Yamamura 2007). Whereas this may explain why ‘bed-and-breakfast for protection’ is a widespread mechanism in the plant kingdom, it does not occur in all plants (e.g. domatia occur in 30–70% of the plants and not all plants produce pollen edible to predatory arthropods; Walter 1996; Sabelis et al. 2005). One possible explanation is that plants do not need domatia when other defenses are sufficiently effective. Alternatively, plants saving investments in indirect defense may benefit from neighbors making such investments because carnivorous arthropods have a home range larger than an individual plant and therein they will go wherever the prey is. Thus, the benefits accruing to non-investing plants may depend on the frequency of investing plants. Moreover, since domatia are not induced by herbivory and thus represent constitutive investments, the benefits of the presence or absence of domatia may not be immediate, but become apparent only over one or even more generations. In theory this can give rise to cycles of frequency-dependent selection maintaining variability in investments in indirect plant defense (Sabelis and de Jong 1988). These predictions, however, still await rigorous experimental tests.

Herbivory-induced alliances

Plants can also limit misuse by providing their support only after herbivore attack. There is evidence for herbivore-induced secretion of extrafloral nectar to arrest predators (Heil et al. 2001), herbivore-induced morphological change promoting predator access to herbivores otherwise concealed in plant tissues (Lesna et al. 2005; Aratchige et al. 2007) and herbivore-induced release of volatiles chemicals by the plant, thereby signaling presence of prey to predators (Dicke and Sabelis 1988; Dicke et al. 1990). These plant responses to herbivory require herbivore-specific elicitors, which trigger a plant signaling cascade involving plant hormones, especially jasmonic acid (Heil et al. 2001; Ament et al. 2004; Kant et al. 2004) (but also salicylic acid and ethylene), which in turn results in transcription activity and enzymes promoting biosynthetic processes involved in indirect plant defense (Kessler and Baldwin 2002; Kant et al. 2009). Even when local, herbivory can induce plant-wide (systemic) responses and despite the long pathways involving very different biochemical processes somehow the plant manages to mount a specific response. For example, herbivory-induced plant volatiles are complex in composition (Yamane et al. 2010), vary with the herbivore species (Sabelis and van de Baan 1983; De Moraes et al. 1998) or even their genotype (Matsushima et al. 2006; Kant et al. 2008) and are usually released systemically, thereby increasing the downwind area over which they can be perceived (Dicke 1994). They elicit more or less specific responses in a wide range of natural enemies (parasitic nematodes, predatory mites, predatory insects, and insectivorous birds; see e.g. Sabelis et al. 2007) and they attract natural enemies, thereby reducing the ultimate damage to the plant due to herbivory (Drukker et al. 1995; Sabelis et al. 1999a, 1999b, 2002; Thaler 1999; Kessler and Baldwin 2001, 2004). Moreover, silencing the jasmonate signaling cascade has important consequences for the community structure of arthropods on plants (Kessler et al. 2004).

Once induced by herbivory, the signals and food produced by the plants is free to any organism using it to its own advantage. As argued in relation to plant domatia, plants cannot impose sanctions to ban unwanted visitors. For example, infestation by coconut mites increases the distance between perianth and coconut surface, thereby promoting access to predatory mites (Aratchige et al. 2007), but also to coconut moths that do not suffer from predation by these predators (Santana et al. 2009). How plants tune herbivore-induced morphological changes to balance increased predator access to the attacking herbivores against increased access by other noxious organisms, is an open question for future research. Free access to organisms other than the herbivore’s enemies seems even more of a problem when it comes to herbivore-induced release of alarm signals. Once

the chemical information is airborne, all organisms in the community can use it to their advantage (Janssen et al. 1998; Sabelis et al. 1999a, 1999b, 2007). For example, odors from infested plants may trigger or prime the antiherbivore defenses of their neighbors (and thus their competitors) (Ton et al. 2007). Also, other herbivores may use plant alarm signals to spot their host plant. For example, diamondback moths prefer to oviposit on plants infested by caterpillars of cabbage white butterflies and profit from the fact that their natural enemy, a parasitic wasp, does not innately recognize the odors from cabbage plants attacked by both herbivores whereas they do recognize odors from plants with the diamond caterpillars alone (Shiojiri et al. 2002; Takabayashi et al. 2006). It may be that there is no way out for an herbivore-attacked plant than to incur these side effects of releasing alarm signals, if the alternative is to be eaten.

Herbivores that feed stealthily

That herbivorous arthropods are not helpless bystanders when plants send out alarm signals is further illustrated by the observation that plant signals vary with herbivore genotype. Different color forms of the kanzawai spider mite, generating different damage symptoms to bean plants, were shown to induce different blends of volatiles (Matsushima et al. 2006). Thus, natural selection may act on herbivores to alter or even avoid alarm release by the plant. Indeed, 'saboteur' lines of two-spotted spider mites have been found that are morphologically indistinguishable, feed, and reproduce on tomato as well as lines resistant against direct plant defense, yet somehow manage to suppress the production of herbivore-induced volatiles from tomato (Kant et al. 2008). Moreover, a related spider mite species, known to be a specialist of tomato and capable of reducing proteinase inhibitors involved in direct defense below household levels, did not trigger the production of herbivore-induced terpenoids that are part of the alarm signals of tomato plants (Sarmiento et al. 2011). Probably, there is an arms race between plant and herbivore: the higher the frequency of plant-alarm-suppressing herbivores, the stronger the selection on plants to prevent herbivores from feeding stealthily, and vice versa (Kant et al. 2008).

Plants that 'cry wolf'

Plants may also manipulate communication with the herbivore's enemies. This is because the interests of sender and receiver only partially overlap: plants gain by acquiring the enemies of herbivores and these enemies gain by finding herbivores. Thus, in an environment with plants sending alarm only when induced by herbivory, a mutant plant may gain by sending the same alarm signal even when there are no or only few herbivores on that plant, thereby receiv-

ing early protection against herbivory. Indeed, such a 'cry wolf' strategy has been identified in a Japanese variety of cabbage. Whereas most plants, including other cabbage varieties, produce more herbivore-induced volatiles when there are more herbivores on the plant, this variety produces a maximal amount of these volatiles irrespective of the number of herbivorous larvae of the diamondback moth (Shiojiri et al. 2010). Since the parasitoids of these herbivores cannot assess the number of hosts on a plant from a distance, they have to rely on the alarm signals of the plant. If most plants send such alarms in amounts proportional to the herbivore damage incurred, this plant genotype gains by acquiring enemies of the herbivores because they need time to inspect the surface of the plant and then to ultimately find out that there are only few herbivores to feed on. Although the existence of such squeamish plant genotypes in natural populations still has to be shown, 'cry wolf' strategies are likely to have a tremendous impact on the communication between plants and the enemies of its herbivores. When the frequency of plants that send honest information on herbivore numbers is high, there is opportunity for 'cry wolf' plants to invade since they gain protection from the herbivore's enemies before they incur any damage from herbivory. The frequency of 'cry wolf' plants in the population may then increase, but the enemies of the herbivores responding to these cry wolf signals will find and search the plant in vain as there are no or only few herbivores. This will trigger selection favoring other plant genotypes that send a sufficiently different alarm odor that acts as an honest signal (i.e. the amounts of odor are proportional to the number of herbivores). This frequency-dependent selection process will proceed more readily in viscous plant populations because clusters of honest signalers provide an environment to the enemies of herbivores in which plant alarm signals are more reliable foraging cues. Once plants sending the honest signal dominate, new opportunities arise for 'cry wolf' plants mimicking this signal, yet harboring no or only few herbivores. Thus, frequency-dependent selection will give rise to alternating waves of plants sending 'honest' or 'cry wolf' signals (Van Baalen and Jansen 2001, 2003; Jansen and van Baalen 2006). This process is likely to increase the complexity of plant signals and theory on the evolution of cooperation has shown that the more complex the signal, the more likely it is that cooperative alliances evolve and persist (Traulsen and Nowak 2007). We therefore predict that chemical alarm 'languages' of plants change over generations and become complex due to frequency-dependent selection. Since the perception of odor blends seems not to be a simple sum of responses to individual components, but rather to be based on properties of the odor blend as a whole, small changes in the odor blend may allow the signal to be perceived as new and this may make plants with

new signals more easy to arise by mutation and more easy to be selected for (Van Wijk et al. 2008, 2010).

Conclusion and perspective

We predict frequency-dependent selection to play an important role in maintaining alliances between plants and the enemies of their enemies and we stress that the effect of plants providing food and/or refuge and the meaning of plant alarm signals changes over generations depending on food web structure and the strategies manifested at each trophic level (see also Kobayashi et al. 2006, 2011). This implies that genetic engineering of plant traits involved in indirect defense may work in the short run, but is doomed sooner or later: herbivores will be selected to become saboteurs of the plant-predator alliance and predators may become less reliant bodyguards.

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