# Mechanisms, ecological consequences and agricultural implications of tri-trophic interactions

## Anurag A Agrawal

Recent research bridging mechanistic and ecological approaches demonstrates that plant attributes can affect herbivores, natural enemies of herbivores, and their interaction. Such effects may be genetically variable among plants and/or induced in individual plants by herbivore attack, and are mediated by primary plant attributes (i.e. nutritional quality and physical structure) and defense-related products (i.e. secondary chemicals and plant volatiles), and may be modified by human activity (e.g. by the introduction of *Bacillus thuringiensis*). The study of tri-trophic interactions is important in order to understand natural species interactions and to manipulate these interactions in pest control.

### Addresses
Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada; e-mail: agrawal@botany.utoronto.ca

### Abbreviations
**Bt**    *Bacillus thuringiensis* toxin
**JA**    jasmonic acid
**PDA**    12-oxo-phytodienoic acid

## Introduction

For a long time, theoretical predictions have suggested that plants interact in complex ways with herbivores and pathogens that feed on plants, and with natural enemies of herbivores and pathogens [1] (Figure 1). For example, plant traits may be attractive or beneficial to some enemies of herbivores, but the same traits may be poisonous or otherwise detrimental to other enemies of herbivores [2••]. Studies of tri-trophic interactions aim to identify these interactions, understand their mechanistic basis, and document their consequences. Ultimately, manipulating these interactions may result in better pest control and the reduced use of pesticides. In the past year, rapid advances have been made and four edited books have appeared that cover various aspects of plant–herbivore/pathogen–natural-enemy interactions [3,4,5•,6•]. This review focuses on recent empirical advances that have improved our understanding of tri-trophic interactions.

## Plant volatiles and natural enemies of herbivores

Plants respond to initial attack by herbivores and pathogens by increasing their levels of defense [7]. For example, volatiles emitted by herbivore-infested plants that are attractive to natural enemies of herbivores are hypothesized to be an evolved response to herbivory. Although the net costs or benefits in plant performance of such induced volatile responses have not been identified, intricate and highly specific interactions between constituents of herbivore saliva and plant responses provide circumstantial evidence of their importance.

Recent physiological studies have linked the plant signal transduction pathways that result in induction of direct defenses in leaves to indirect defenses that act through the production of volatiles that attract natural enemies of herbivores. Jasmonic acid (JA) is a key component of the highly conserved octadecanoid pathway in plants that

## Figure 1

Tri-trophic interactions and the effects of plants on the natural enemies of plant parasites. Solid arrows indicate consumption, whereas the large clear arrow on the left indicates plant influences on the third trophic level. Plant chemistry, morphology, and resources (e.g. pollen and nectar) may positively or negatively affect the behavior, efficacy, and performance of natural enemies of plant parasites. Some tri-trophic interactions operate with a high degree of specificity between the interacting organisms, whereas others act more generally. The mechanisms and consequences of induced plant volatiles attracting herbivores [48•], predators eating predators [49], and pathogens infecting predators and parasitoids [50] deserve more attention.
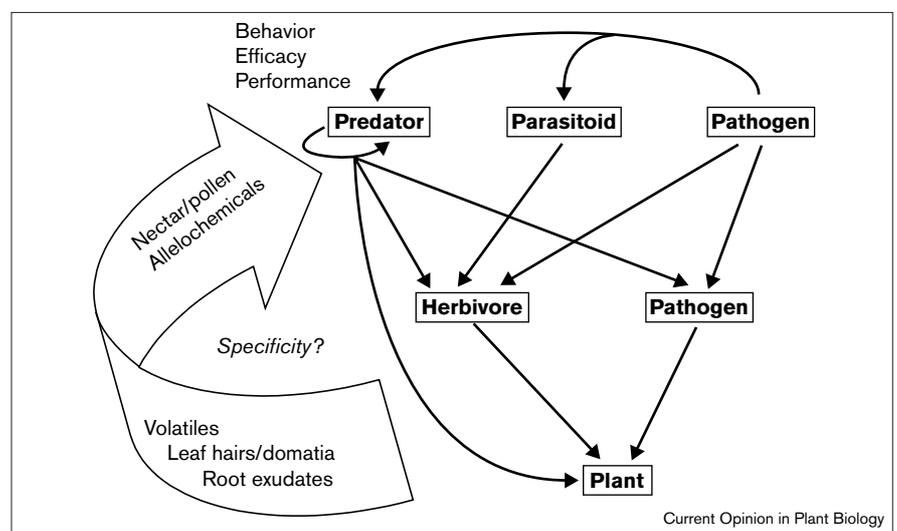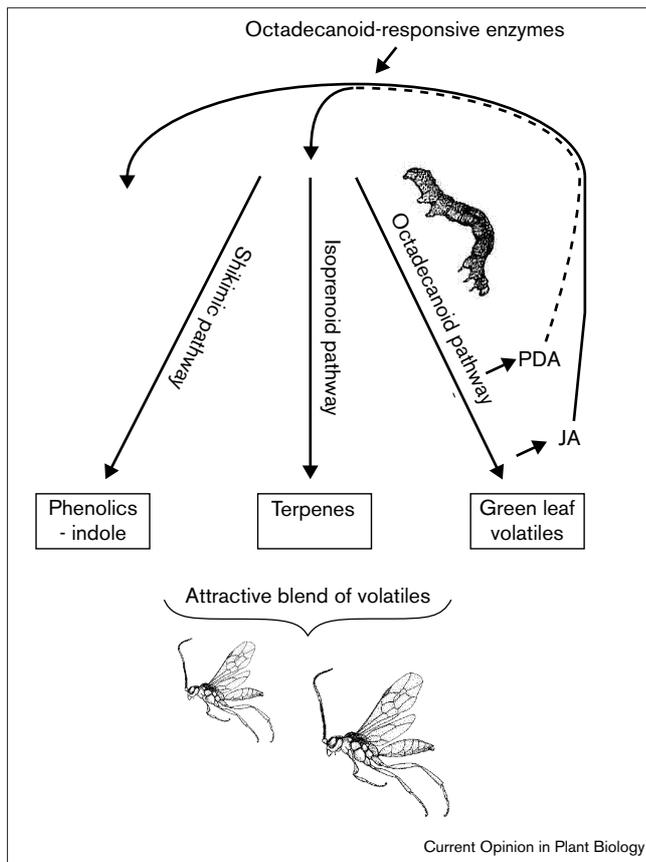


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**Figure 2**



Biosynthetic pathways resulting in the production of plant volatiles that are attractive to natural enemies of herbivores. JA and PDA are thought to be endogenous chemical signals that induce the production of these volatiles [8,13•]. JA- or PDA-responsive genes/enzymes upstream of the isoprenoid and shikimic pathways link the production of volatiles to the octadecanoid pathway, which is responsible for the expression of defensive genes, including those that result in the production of proteinase inhibitors.

mediates induction of direct foliar defenses [6•]. Boland *et al.* [8] have reviewed the evidence that JA plays a key role in the induction of volatiles that may attract natural enemies of herbivores. Specifically, lima bean leaves treated with inhibitors of JA biosynthesis did not produce the herbivore-induced volatiles that are implicated in indirect defense. Exogenous applications of JA to plants increase direct and indirect defenses [2••,6•,8]. JA is thought to work through a positive feedback mechanism in which precursors of JA are stimulated upstream, resulting in increased production of JA and subsequent downstream products *in planta*.

Thaler [2••] demonstrated that exogenous applications of JA to field-grown tomato plants cause an increase in the parasitism of naturally occurring beet armyworm larvae by a solitary ichneumonid parasitoid. This result was a direct effect of changes in plant quality, not an effect of changes in herbivore quantity or quality. JA-mediated

attraction of parasitoids was also shown to be associated with foliar defenses that negatively affected several herbivores by increasing their development time [2••,6•]. The pupal weights of the parasitoids of these herbivores were, however, also decreased. Thus, there were positive and negative effects associated with the JA induction, with the net benefits apparently being more important than the costs. Similar positive (i.e. parasitoid attraction) and negative effects (i.e. 40% fewer emerging parasitoid progeny) have been reported for a gregarious braconid parasitoid attacking gypsy moth larvae on induced poplar trees [9].

JA applications to gerbera and lima bean plants also resulted in induced volatile production and the attraction of natural enemies of herbivorous mites [10,11•]. The profiles of the volatiles emitted after application of JA were similar to those induced by natural herbivory, although not identical. In contrast to mite-induced plants, methyl salicylate, a well-known attractant of predatory mites, was conspicuously missing from JA-induced plants, which were consequently less preferred by predators than were mite-induced plants [10,11•]. The dose of JA and method of its delivery is likely to be an important determinant of some of the differences between the attraction of predators to JA-induced and mite-induced plants. A novel class of elicitors of volatiles, fungal peptaibols, induces both jasmonate products and methyl salicylate [12•]. Fungal peptaibols were previously shown to induce phytoalexins and are particularly intriguing because they appear to circumvent the typical antagonistic interaction between jasmonate and salicylate signaling in plants.

The bouquet of volatiles that are emitted from damaged plants come from at least three biosynthetic pathways: first, the fatty acid (or octadecanoid) pathway produces leafy green volatiles and jasmone; second, the shikimic acid (or tryptophan) pathway produces indole and methyl salicylate; and third, the isoprenoid-derived pathways produce terpenes [6•]. Given the essential role of JA in regulating volatile production, there must be a role for JA in activating the shikimic acid and isoprenoid pathways that is additional to its role in the octadecanoid pathway (Figure 2). JA-responsive enzymes are thought to catalyze the response of some terpenoids. Octadecanoid intermediates (which are present upstream of JA), including 12-oxo-phytodienoic acid (PDA), form a second group of signals that lead to the production of volatiles [13•]. JA and PDA induce different terpenoids in lima bean but the same terpenoids in corn [13•]. The identification and characterization of various octadecanoid-sensitive enzymes catalyzing volatile biosynthesis is just beginning. For example, (3S)-(E)-nerolidol synthase is induced in cucumber and lima bean after infestation by spider mites, but not after mechanical damage [14•]. The activity of this enzyme correlates with the release of the homoterpene 4,8-dimethyl-1,3(E),7-nonatriene, which is a major component

of the odor-blend released from many herbivore-infested plants. It is unclear whether (3S)-(E)-nerolidol synthase is responsive to JA or PDA, or both.

Until recently, little was known about how phloem-feeding aphids and their natural enemies respond to induced plant responses. Although induced direct defense to aphids is still poorly documented, a body of literature on the indirect attraction of natural enemies of aphids has emerged [15,16•,17,18••]. As demonstrated in studies of plant responses to lepidopteran and mite herbivores, volatiles induced in response to aphid attack are systemically released by the plant and appear to be positively dependent on the level of infestation. It was found that volatile extracts from host-infested plants are more attractive to parasitoids than extracts from plants infested with non-host aphids. This result exemplifies specificity in the response of plants to different aphid herbivores. Volatile isothiocyanates (produced from pre-formed glucosinolates) in the Brassicaceae attract aphid parasitoids. Bradburne and Mithen [18••] have shown that breeding for the release of specific volatiles from *Brassica napus* and *B. oleracea* result in the attraction of aphid parasitoids in the laboratory and field. The physical mapping and identification of the *GSL-ELONG* gene from *Arabidopsis thaliana*, which is involved in this volatile production, opens the door to genetically modifying plants to attract natural enemies of herbivores [19•]. Extreme caution will be needed when deploying such genetically modifying plants; natural enemies of herbivores are extremely good learners and the lack of prey at sites emitting volatiles causes natural enemies to negatively associate the odors with prey [6•].

Complex interactions between herbivores and plants continue to be revealed. Glucose oxidase is an important component in the saliva of many lepidopteran herbivores that attenuates JA-mediated direct resistance to herbivores in *Nicotiana* [6•], although it does not appear to affect the production of plant volatiles (GW Felton, personal communication). Constituents of the oral secretions of *Manduca sexta* also suppress JA-mediated production of nicotine (a direct defense) in *Nicotiana*, which is linked with plant production of ethylene. Unlike glucose oxidase, these oral secretions resulted in strong volatile responses [20]. In these variable interactions it is not clear whether it is the herbivore or the plant that controls the outcome of the interaction.

Ant–plant associations present a special case of mutualism between plants and predators of herbivores in which the plant provides the ants with food and/or shelter. These are perhaps the best-known cases of indirect defense with numerous examples of fitness benefits to plants that attract ants. Although not all ants benefit the plants [21•], herbivore damage may elicit induced recruitment of ants via the production of volatiles and/or extrafloral nectar rewards [22,23].

## Plant morphological traits affect tri-trophic interactions

Aspects of plant morphology may influence the performance of plant parasites, natural enemies of these parasites, and their interactions. Leaf domatia are small hair-tufts or pockets on the abaxial surface of leaves that have been found in nearly 300 plant families and 2000 species [24] (Figure 3). Over a century ago, a Swedish naturalist, Axel Lundströem, proposed that leaf domatia mediated a mutualism between plants (which provide shelter for arthropods) and predatory or fungivorous arthropods (which clean the leaf surface of plant parasites) (see [25]). Many crop plants, including coffee, grape, and walnut, are endowed with natural leaf domatia. These structures have apparently been lost (compared to their wild relatives) in crops such as avocado.

When artificial domatia were added to cotton plants, several species of predators increased in abundance, populations of three species of herbivores decreased, and cotton yield was enhanced compared to controls [26]. Although cotton plants do not possess leaf domatia, their close wild relatives do [27], and the quantitative trait loci for pubescence in cotton have been identified [28•]. Selective expression of pubescence in the vein axils could enhance the control of herbivores in cotton and other species.

Wild and cultivated grape plants show variation in the presence and size of leaf domatia that are inhabited by tydeid mites (Figure 3). Tydeid mites are voracious consumers of the phytopathogen powdery mildew, a major pest of grapes [29]. Norton *et al.* [30••] convincingly showed the importance of domatia for disease control using clonal variation and experimentally manipulated leaf domatia. Classical breeding as well as genetic enhancements of domatia could yield benefits for many crops. Leaf domatia benefit predators and fungivores by providing a refuge (from their own enemies) and a favorable microclimate. Domatia do not appear to have high costs in terms of energetic drain or ecological blunders, although this issue has not received much attention.

The morphological attributes of plants may also have a direct impact on herbivores. Leaf pubescence [31] and lack of cuticular waxblooms [32] can impair the development of herbivores. Of particular interest is the impact that these morphological traits can have on the natural enemies of herbivores. If morphological barriers interfere with the action of natural enemies, the benefits of these 'defenses' may be reduced. Understanding the compatibility of plant resistance factors with biological control and the interactions of biological control enhancing features, such as leaf domatia, with plant resistance remains an important challenge for plant biologists [26,31,32].

## Plant effects on omnivores: friend or foe?

Many arthropods are not strictly herbivores or predators, but feed on multiple foods, including leaf tissue, pollen, nectar, and other arthropods [33]. Generalist predators often rely on plants for alternative foods in times of prey

**Figure 3**
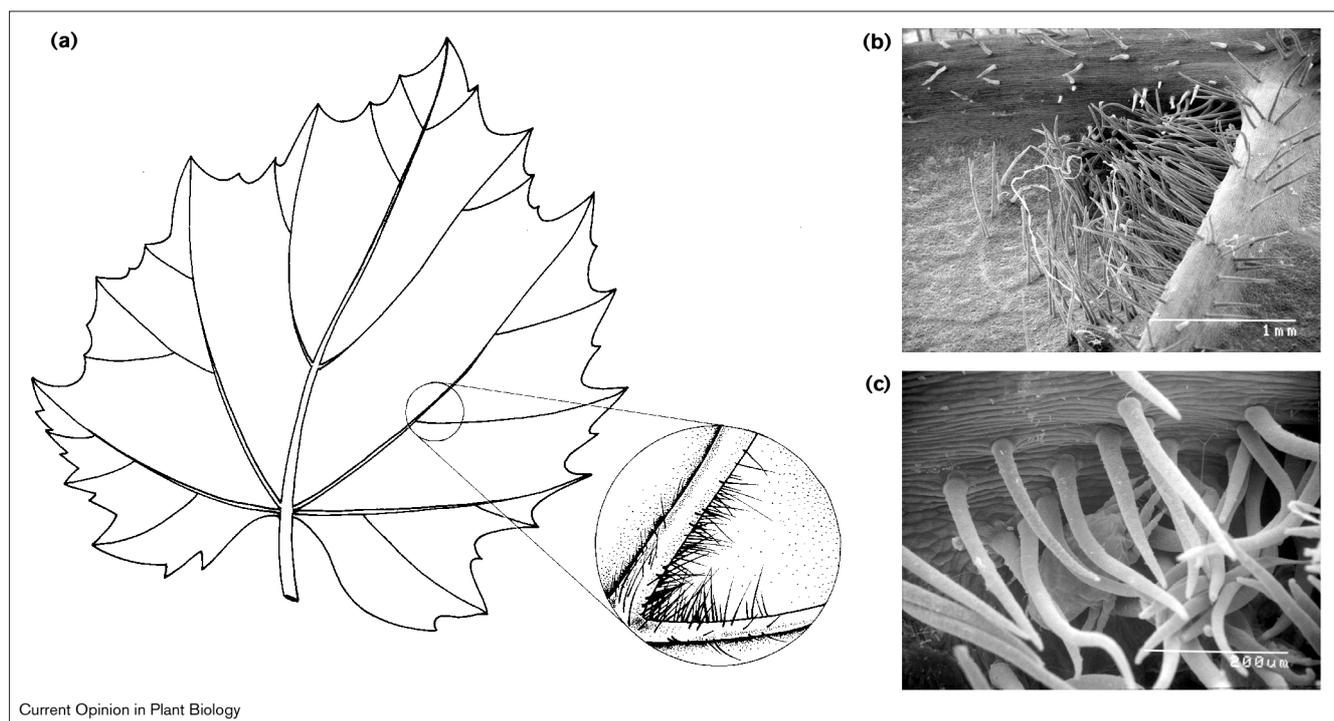


Leaf hair domatia. **(a)** and **(b)** The hair-tuft leaf domatium on a grape leaf. **(c)** The domatium is occupied by a tydeid mite, which has a voracious appetite for plant pathogens including powdery mildew [29,30••]. Tri-trophic interactions linking plant morphology with the control of plant parasites by natural enemies hold promise as a form of pest control. Line drawing courtesy of Karen English-Loeb, and scanning electron micrographs courtesy of Andrew Norton and Harvey Hoch.

scarcity. Big-eyed-bugs survive better and do not disperse when their diet of aphids is supplemented with high-quality plant material [34•]. The presence of alternative foods increases the retention of predators and may stabilize the interactions between predators and prey.

Omnivores may be either beneficial to plants because of their action as predators or detrimental to plants because of their action as herbivores. The factors that encourage predation and discourage herbivory could be exploited in pest control. In cotton plants, induced plant resistance has been shown to reduce herbivory by mites and thrips, and increase predation of mite eggs by thrips [35•]. Although thrips can be severe crop pests, manipulation of their feeding behavior can provide benefits to plants. Interactions between plant defenses, the quality of prey, and omnivory may obscure the costs and benefits of omnivory [36,37] and require further study. For example, the volatile odors of predators that eat thrips cause thrips to increase their occupancy of mite colonies (under mite webbing), thereby potentially increasing their consumption of herbivorous mites [38].

## Biotechnology, *Bacillus thuringiensis*, and beneficial insects

Genetic manipulation of plants can provide potent resistance against pests. Controversy has surrounded the current broad-scale use of transgenic plants with improved resistance to pests in agriculture because of their potential effects on the natural enemies of herbivores, other non-target organisms, gene flow to wild relatives, the rapid evolution of resistance in pests, and human health [39]. The consequences for tri-trophic interactions of expressing *Bacillus thuringiensis* toxins (*Bts*) in plants has been the subject of recent research. Parasitoids inside dead lepidopteran larvae that are exposed to *Bts* usually suffer the same fate as the larvae. Thus, death of herbivore larvae caused by *Bts* may be detrimental for populations of parasitoids. Two groups have found that herbivore larvae that were exposed to *Bts*, but were themselves resistant to its effects, however, supported the normal development of parasitoids [40,41•]. Because the strains of *Bts* currently in use are largely specific to lepidoptera, there may be no direct consequences of *Bts* for the predators and parasites of herbivores. Nevertheless, Hilbeck *et al.* [42•] report a dose-dependent effect of *Bts* on lacewing predators. This effect was mediated by the direct effects of *Bts* on the predators and the indirect effects of the predators feeding on caterpillars that had been fed *Bts*. Although many natural enemies of herbivores may not be directly affected by *Bts*, negative effects on their populations through the consumption of sick, dead, or dying herbivores may be a nasty indirect effect.

Do predators and parasitoids of herbivores avoid *Bts*-exposed prey? Could behavioral mechanisms in parasitoids potentially reduce the negative indirect effects of *Bt*? Because the feeding of susceptible caterpillars on *Bt* plants is severely reduced, and plant damage attracts parasitoids, parasitoids may preferentially be attracted to either resistant larvae or susceptible larvae on non-*Bt* plants [41•]. Thus, a potential tri-trophic benefit of employing *Bts* in agriculture is that parasitoids may be an agent for minimizing the evolution of resistance to *Bts* in pests. This possibility was demonstrated for the *Plutella* (diamondback moth)–*Cotesia* (parasitoid wasp) system in an elegant laboratory study [41•]. Unfortunately, diamondback moth was the first insect reported to have evolved resistance to *Bts* in the field. Thus, the relative importance of this tri-trophic interaction, which effectively sandwiches herbivores between toxic plants and virulent natural enemies, remains unclear.

The tri-trophic effects of other genetically engineered plant toxins have also been the subject of investigation. Contrary to the results of previous artificial diet studies, Ali *et al.* [43] showed that tobacco budworm feeding on transgenic tobacco plants that either under- or over-expressed phenylalanine ammonia-lyase (PAL) had higher mortality, caused by a nucleopolyhedrovirus, when feeding on lines with higher levels of PAL expression. Aphids grown on potatoes engineered with an anti-aphid plant protein (snowdrop lectin GNA), however, supported ladybird predators with reduced fecundity, egg viability and longevity [44]. The apparent specificity of *Bts* has made it more marketable than these other transgenic options. The benefits of *Bt* expression in plants are obvious for the short term; nevertheless, future research must address how the not-so-obvious negative aspects of such transgenics for trophic interactions can be minimized.

## Conclusions

In terrestrial environments, strong trophic interactions are modified by the chemistry, morphology, and behavior of each organism involved. Plants recruit natural enemies of herbivores using volatiles. The essential constituents of these interactions ranging from herbivore saliva to plant hormones and regulatory enzymes are now being isolated, and their genes cloned. It is unknown whether plants that are infested with microbial diseases or nematodes attract or facilitate natural enemies of these plant parasites. Such interactions are probably abundant, yet their natural history and applied potential are unexplored. Chemically mediated tri-trophic interactions have recently been described from marine ecosystems [45–47], indicating the prevalence of such interactions. Only a combination of natural history, molecular and genetic tools, and field experimentation can lead to a predictive understanding of tri-trophic interactions.

## References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1.  Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE: **Interaction between three trophic levels: influence of plants on interactions between insect herbivores and natural enemies.** *Ann Rev Ecol System* 1980, **11**:41-65.

2.  Thaler JS: **Jasmonate-inducible plant defences cause increased**
•• **parasitism of herbivores.** *Nature* 1999, **399**:686-688.
This work demonstrates that jasmonic acid, when applied exogenously to tomato plants, results in the attraction of wasps and increased parasitism of caterpillars in the field. This is one of the few studies linking biochemical mechanisms of induced defenses to ecological interactions in the field.

3.  Olff H, Brown VK, Drent RH (Eds): *Herbivores: Between Plants and Predators.* Oxford, UK: Blackwell Science; 1999.

4.  Tollrian R, Harvell CD: *The Ecology and Evolution of Inducible Defenses.* Princeton: Princeton University Press; 1999.

5.  Chadwick D, Goode J (Eds): *Insect–Plant Interactions and Induced*
• *Plant Defence.* New York: John Wiley & Sons; 1999.
A review of the biochemical and agricultural aspects of tri-trophic interactions that are influenced by induced plant responses.

6.  Agrawal AA, Tuzun S, Bent E (Eds): *Induced Plant Defenses Against*
• *Pathogens and Herbivores: Biochemistry, Ecology, and Agriculture.* St. Paul, Minnesota: American Phytopathological Society Press; 1999.
Recent advances in understanding interactions between plants, herbivores, pathogens, and natural enemies mediated by induced plant responses are reviewed. (Table of contents available at http://www.botany.utoronto.ca/ResearchLabs/agrawalLab/AA_book.html.)

7.  Agrawal AA: **Induced responses to herbivory and increased plant performance.** *Science* 1998, **279**:1201-1202.

8.  Boland W, Hopke J, Piel J: **Induction of plant volatile biosynthesis by jasmonates.** In *Natural Product Analysis: Chromatography, Spectroscopy, Biological Testing.* Edited by Schreier P, Herderich M, Humpf H-U, Schwab W. Braunschweig/Wiesbaden: Viehweg Verlag; 1998:255-269.

9.  Havill N, Raffa K: **Compound effects of induced plant responses on insect herbivores and parasitoids: implications for tritrophic interactions.** *Ecol Entomol* 2000, **25**:171-179.

10. Gols R, Posthumus MA, Dicke M: **Jasmonic acid induces the production of gerbera volatiles that attract the biological control agent** *Phytoseiulus persimilis.* *Entomologia Experimentalis Applicata* 1999, **93**:77-86.

11. Dicke M, Gols R, Ludeking D, Posthumus MA: **Jasmonic acid and**
• **herbivory differentially induce carnivore-attracting plant volatiles in lima bean plants.** *J Chem Ecol* 1999, **25**:1907-1922.
Two papers by Marcel Dicke's group [10,11•] show that the plant volatiles induced by the application of jasmonic acid and by spider mite herbivory are similar, although not identical. Methyl salicylate, in particular, is missing from jasmonate-treated plants, and predatory mites favored spider mite-infested plants over jasmonate-treated plants.

12. Engelberth J, Koch T, Kühnemann F, Boland W: **Channel-forming**
• **peptaibols are a novel class of potent elicitors of plant secondary metabolism and tendril coiling.** *Angew Chem* 2000, **39**:1860-1862.
This work shows that fungal peptaibols, which are known to induce phytoalexins, can induce both jasmonate and salicylate signaling in plants. This finding is particularly interesting because these pathways often exhibit a negative interaction.

13. Koch T, Krumm T, Jung V, Engelberth J, Boland W: **Differential**
• **induction of plant volatile biosynthesis in the lima bean by early and late intermediates of the octadecanoid-signaling pathway.** *Plant Physiol* 1999, **121**:153-162.
The authors show that early octadecanoid PDA may act as a signal for the production of some terpenoid volatiles and may mediate specificity in octadecanoid-mediated induced volatiles.

14. Bouwmeester HJ, Verstappen FWA, Posthumus MA, Dicke M: **Spider**
•   **mite-induced (3S)-(E)-nerolidol synthase activity in cucumber and lima bean. The first dedicated step in acyclic C11-homoterpene biosynthesis.** *Plant Physiol* 1999, **121**:173-180.
The authors describe a herbivore-induced enzyme that mediates the production of specific terpenoid volatiles; this enzyme is potentially responsive to jasmonate via the octadecanoid pathway.

15. Powell W, Pennacchio F, Poppy GM, Tremblay E: **Strategies involved in the location of hosts by the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae: Aphidiinae).** *Biol Control* 1998, **11**:104-112.

16. Guerrieri E, Poppy GM, Powell W, Tremblay E, Pennacchio F:
•   **Induction and systemic release of herbivore-induced plant volatiles mediating in-flight orientation of *Aphidius ervi*.** *J Chem Ecol* 1999, **25**:1247-1262.
Different aphid species are shown to induce specific volatiles in plants that are attractive to parasitoids. Such induction is systemic and dependent on the dose of attack.

17. Rao A, Vinson S, Gilstrap F, Michels GJ Jr: **Response of an aphid parasitoid, *Aphelinus asychis* to its host, plant, host–plant complex, and to malathion.** *Entomologia Experimentalis Applicata* 1999, **91**:449-456.

18. Bradburne R, Mithen R: **Glucosinolate genetics and the attraction**
••  **of the aphid parasitoid *Diaeretiella rapae* to *Brassica*.** *Proc R Soc Lond Series B* 2000, **267**:89-95.
Mithen and colleagues [18••,19•] show that breeding for specific glucosinolates results in the production of isothyocianates in two species of *Brassica* that are attractive to aphid parasitoids in the field. Cloning the gene for these glucosinolates in the related plant *Arabidopsis thaliana* could lead to genetic engineering of plants that are differentially attractive to natural enemies of herbivores.

19. Campos de Quiros H, Magrath R, McCallum D, Kroymann J,
•   Schnabelrauch D, Mitchell-Olds T, Mithen R: **Alpha-keto acid elongation and glucosinolate biosynthesis in *Arabidopsis thaliana*.** *Theor Appl Genet* 2000, in press.
See annotation [18••].

20. Kahl J, Siemens D, Aerts R, Gäbler R, Kühnemann F, Preston C, Baldwin I: **Herbivore-induced ethylene suppresses a direct defense but not a putative indirect defense against an adapted herbivore.** *Planta* 2000, **210**:336-342.

21. Stanton ML, Palmer TM, Young TP, Evans A, Turner ML: **Sterilization**
•   **and canopy modification of a swollen thorn acacia tree by a plant—ant.** *Nature* 1999, **401**:578-581.
The authors illustrate that among the several species of ants that inhabit an African *Acacia* tree, some are not mutualistic as traditionally thought; these 'parasitic' ants sterilize the tree by modifying the canopy structure to reduce competition from other ants.

22. Agrawal AA, Dubin-Thaler BJ: **Induced responses to herbivory in the Neotropical ant–plant association between *Azteca* ants and *Cecropia* trees: response of ants to potential inducing cues.** *Behav Ecol Sociobiol* 1999, **45**:47-54.

23. Wackers FL, Wunderlin R: **Induction of cotton extrafloral nectar production in response to herbivory does not require a herbivore-specific elicitor.** *Entomologia Experimentalis Applicata* 1999, **91**:149-154.

24. Brouwer YM, Clifford HT: **An annotated list of domatia-bearing species.** *Notes from the Jodrell Laboratory* 1990, **12**:1-33.

25. Walter DE: **Living on leaves: mites, tomenta, and leaf domatia.** *Annu Rev Entomol* 1996, **41**:101-114.

26. Agrawal A, Karban R, Colfer R: **How leaf domatia and induced resistance affect herbivores, natural enemies and plant performance.** *Oikos* 2000, **89**:70-80.

27. Fryxell PA: *The Natural History of the Cotton Tribe*. College Station, Texas: Texas A&M University Press; 1978.

28. Wright RJ, Thaxton PM, El-Zik KM, Paterson AH: **Molecular mapping**
•   **of genes affecting pubescence of cotton.** *J Hered* 1999, **90**:215-219.
An example of the use of quantitative trait loci mapping to identify the genetic basis of traits, in this case the pubescence of cotton, that influence interactions with herbivores and natural enemies of herbivores.

29. English-Loeb G, Norton AP, Gadoury DM, Seem RC, Wilcox WF: **Control of powdery mildew in wild and cultivated grapes by a tydeid mite.** *Biol Control* 1999, **14**:97-103.

30. Norton AP, English-Loeb G, Gadoury DG, Seem RC: **Mycophagous**
••  **mites and foliar pathogens: leaf domatia mediate tritrophic interactions in grapes.** *Ecology* 2000, **81**:490-499.
The authors employ natural genetic variation and manipulation of leaf domatia to show that these foliar structures influence populations of fungus-eating mites; plants with larger domatia have more mites and a reduced incidence of powdery mildew disease. Although little studied, leaf domatia and mites show promise as tools for biological disease control.

31. Krips OE, Willems PEL, Dicke M: **Compatibility of host plant resistance and biological control of the two-spotted spider mite *Tetranychus urticae* in the ornamental crop gerbera.** *Biol Control* 1999, **16**:155-163.

32. Eigenbrode SD, Kabalo NN: **Effects of *Brassica oleracea* waxblooms on predation and attachment by *Hippodamia convergens*.** *Entomologia Experimentalis Applicata* 1999, **91**:125-130.

33. Coll M: **Living and feeding on plants in predatory heteroptera.** In *Predatory Heteroptera: Their Ecology and Use in Biological Control*. Edited by Coll M, Ruberson JR. Lanham, Maryland: Entomological Society of America; 1998:89-129.

34. Eubanks MD, Denno RF: **The ecological consequences of variation**
•   **in plants and prey for an omnivorous insect.** *Ecology* 1999, **80**:1253-1266.
Omnivores eat both plants and animals; non-harmful feeding on the plant by insects that are mostly predaceous may increase their retention and the effectiveness of these insects as biological control agents.

35. Agrawal AA, Kobayashi C, Thaler JS: **Influence of prey availability**
•   **and induced host plant resistance on omnivory by western flower thrips.** *Ecology* 1999, **80**:518-523.
The authors describe an example of how induced plant resistance can be synergistic by reducing herbivory by herbivores, reducing herbivory by omnivores, and increasing predation on herbivores by omnivores.

36. Agrawal A, Klein C: **What omnivores eat: direct effects of induced plant resistance on herbivores and indirect consequences for diet selection by omnivores.** *J Animal Ecol* 2000, **69**:525-535.

37. Eubanks M, Denno R: **Plants mediate omnivore–herbivore interactions and influence prey suppression.** *Ecology* 2000, **81**:in press.

38. Venzon M, Janssen A, Pallini A, Sabelis M: **Diet of a polyphagous predator affects refuge-seeking of its prey.** *Animal Behav* 2000, in press.

39. Hail RS: **Genetically modified plants — the debate continues.** *Trends Ecol Evol* 2000, **15**:14-18.

40. Chilcutt CF, Tabashnik BE: **Effects of *Bacillus thuringiensis* on adults of *Cotesia plutellae* (Hymenoptera : braconidae), a parasitoid of the diamondback moth, *Plutella xylostella* (Lepidoptera : plutellidae).** *Biocontrol Sci Tech* 1999, **9**:435-440.

41. Schuler TH, Potting RPJ, Denholm I, Poppy GM: **Parasitoid**
•   **behaviour and *Bt* plants.** *Nature* 1999, **400**:825-826.
This work illustrates the importance of behavior in tri-trophic interactions and how communication between the trophic levels may influence the evolution of resistance to pesticides in herbivorous insects.

42. Hilbeck A, Moar WJ, Pusztai-Carey M, Filippini A, Bigler F:
•   **Prey-mediated effects of Cry1Ab toxin and protoxin and Cry2A protoxin on the predator *Chrysoperla carnea*.** *Entomologia Experimentalis Applicata* 1999, **91**:305-316.
The authors demonstrate that Cry1Ab and Cry2b *Bt* toxins have direct negative effects on predators of herbivores and indirect negative effects through hosts (i.e. caterpillars) that are largely resistant to the effects of *Bts*.

43. Ali MI, Bi JL, Young SY, Felton GW: **Do foliar phenolics provide protection to *Heliothis virescens* from a baculovirus?** *J Chem Ecol* 1999, **25**:2193-2204.

44. Birch ANE, Geoghegan IE, Majerus MEN, McNicol JW, Hackett CA, Gatehouse AMR, Gatehouse JA: **Tri-trophic interactions involving pest aphids, predatory 2-spot ladybirds and transgenic potatoes expressing snowdrop lectin for aphid resistance.** *Mol Breed* 1999, **5**:75-83.

45. Nevitt GA, Veit RR, Kareiva P: **Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds.** *Nature* 1995, **376**:680-682.

46. Stachowicz JJ, Hay ME: **Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense.** *Ecology* 1999, **80**:2085-2101.

47. Stachowicz JJ, Hay ME: **Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores.** *Ecology* 1999, **80**:495-509.

48. Landolt P, Tumlinson J, Alborn D: **Attraction of colorado potato**
•    **beetle (Coleoptera: Chrysomelidae) to damaged and chemically induced potato plants.** *Environ Entomol* 1999, **28**:973-978.
The authors show that herbivore damage and the application of jasmonates and volicitin, but not artificial damage, induce plant volatiles that

are attractive to herbivores. The use of volatiles by herbivores potentially represents an ecological cost in tritrophic interactions.

49. Rosenheim JA, Kaya H, Ehler LE, Marois JJ, Jaffee BA: **Intraguild predation among biological-control agents: theory and evidence.** *Biol Control* 1995, **5**:303-335.

50. Fuentes-Contreras E, Pell JK, Niemeyer HM: **Influence of plant resistance at the third trophic level: interactions between parasitoids and entomopathogenic fungi of cereal aphids.** *Oecologia* 1998, **117**:426-432.