INDIRECT INTERACTION WEBS:
Herbivore-Induced Effects Through Trait Change in Plants

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■ **Abstract**   Although predation has a lethal effect on prey, mature terrestrial plants
are rarely killed by herbivores, but herbivory can change plant allelochemistry, cell
structure and growth, physiology, morphology, and phenology. This review explores
the herbivore-induced indirect effects mediated by such plant responses following her-
bivory in terrestrial systems. Herbivore-induced indirect effects are ubiquitous in many
plant–herbivore systems, and indirect interactions occur among temporally separated,
spatially separated, and taxonomically distinct herbivore species. Unlike interspecific
competition, herbivores can benefit each other through plant-mediated indirect ef-
fects. Herbivore-induced changes in plants occur at low levels of herbivory, which in-
creases the likelihood of plant-mediated indirect interactions between herbivores. The
herbivore-induced indirect effects result in interaction linkages, which alter species
richness and abundance in arthropod communities. Such interaction linkages should
be depicted using indirect interaction webs, which incorporate nontrophic, indirect
links. The idea of interaction linkages by herbivore-induced indirect effects that shape
community organization and biodiversity is an important revision of the traditional
view of plant-based terrestrial food webs.

INTRODUCTION

A central issue in ecology is understanding how trophic interactions make up
food webs in various ecosystems (Berlow et al. 2004, Hunter & Price 1992, Paine
1980, Polis & Winemiller 1996). Recent studies of interactions between plants
and herbivores reveal that plants respond to herbivore damage by changes in al-
lelochemistry, cell structure and growth, physiology, morphology, and phenology
(Karban & Baldwin 1997). Because herbivory is common and usually nonlethal
on terrestrial plants, this ensures in many ecosystems that most plants have traits
altered by herbivory. In the past, studies of trophic interactions at the ecosys-
tem level have concentrated on how the relative abundance of biomass or energy

produced by one trophic level is transferred to another (Leibold et al. 1997, Oksanen et al. 1981, Polis 1999). In contrast, the consequences of ubiquitous nonlethal indirect links in plant–herbivore interactions in terrestrial systems have long been overlooked.

In this review, I argue for the prevalence of herbivore-induced plant responses in generating interaction linkages, which in turn affect herbivore community structure across trophic levels. I suggest that herbivore-induced interaction linkages have the potential to contribute greatly to the maintenance of species richness and interaction diversity in terrestrial systems. My arguments are largely restricted to herbivorous insects because they are among the richest contributors to biodiversity on the Earth, and they exhibit diverse feeding relationships with plants that produce many well-understood induced plant responses.

INTERACTION LINKAGE ON TERRESTRIAL PLANTS

In terrestrial systems, individual plant species with their associated herbivores form plant-based food chains that are interconnected with each other, producing a network of interacting species. Many studies focus on single interactions, although indirect effects can link multiple interactions in a community (Jones et al. 1998, Strauss 1997), and such interaction linkages are common in multitrophic systems (Dicke & Vet 1999, Gange & Brown 1997, Price et al. 1980). Both above- and belowground interactions are frequently influenced by indirect effects (Masters & Brown 1997, Van der Putten et al. 2001). Nevertheless, few studies have integrated the impacts of multiple indirect interactions in structuring ecological communities.

As an example of the important indirect interaction linkages, I illustrate how multiple plant–insect interactions are connected with each other on the willow *Salix miyabeana* (Figure 1). The spittlebug *Aphrophora pectoralis* is a specialist insect herbivore on the willow. In autumn, females lay eggs in the distal part of current shoots, which die within one week because of mechanical damage. This damage induces a compensatory shoot growth in the next year, producing longer shoots with a greater number of leaves (Nozawa & Ohgushi 2002). This enhanced shoot growth resulted in the increased density of 23 species of leafrolling caterpillars in early spring. After leafrolling caterpillars eclosed and left their leaf shelters, most leaf shelters were colonized by other insects, in particular, the aphid *Chaitophorus saliniger*, which is highly specialized for utilizing leafrolls (Nakamura & Ohgushi 2003). These aphids were tended by three species of ant that harvested aphid honeydew. The increased number of ants, in turn, reduced the larval survival of the leaf beetle *Plagiodera versicolora*. Direct interspecific competition is unlikely to have significant impacts on these herbivorous insects. The willow had a low level of leaf herbivory (less than 20% leaf consumption), suggesting that interspecific competition between leaf chewers is rare. Indeed, we detected a positive correlation between sap-sucking spittlebugs and aphids. Moreover, spittlebug nymphs and leaf beetle larvae are mobile so that they can avoid damaged plant tissues, even
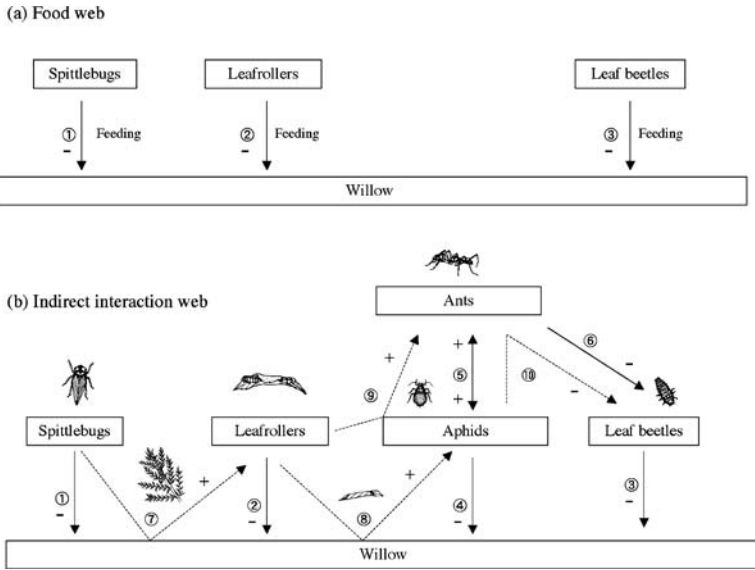
Figure 1 Comparison between a food web (*top*) and its indirect interaction web (*bottom*) of herbivorous insects on the willow *Salix miyabeana*. *Solid* and *broken lines* show direct and indirect effects, respectively. *Plus* and *minus signs* indicate positive and negative effects from an initiator to a receiver species, respectively.

if interspecific competition occurs. In contrast, spittlebug oviposition led to major indirect effects on other species. This unexpected linkage in the chain of indirect interactions indicates that such indirect effects provide an underlying mechanism responsible for a network of interactions in ecological communities.

INDIRECT EFFECTS OF HERBIVORE-INDUCED CHANGES IN PLANTS

In this section, I explore herbivore-induced indirect effects in terrestrial systems, focusing on how herbivores sharing the same host-plant have indirect interactions mediated by changes in plant characteristics. I compiled a representative set of examples of plant-mediated indirect interactions between herbivores covering a broad spectrum of plant–herbivore systems. The database was compiled by key-word searches using "indirect effects/interactions" or related concepts in articles published between 1985 and 2004 in major ecological journals including *Ecology*, *Oikos, Oecologia*, *Journal of Animal Ecology*, *Journal of Ecology*, *Functional Ecology*, *Ecological Entomology*, and *American Naturalist*. I also surveyed the reference sections of the papers obtained and of reviews on the topic in the *Annual Review of Ecology, Evolution, and Systematics*; the *Annual Review of Entomology*,

and *Trends in Ecology and Evolution*. I included studies on indirect interactions between herbivores, including insects, mammals, fungi, and pathogens, through herbivore-induced changes in plants. I refer to the "initiator" as an herbivore that causes induced plant responses, the "receiver" as an impacted herbivore, and the "transmitter" as a plant fed upon by the initiator. Herbivore-induced indirect interactions produced by changes in plants are a type of trait-mediated indirect interaction (Abrams et al. 1996); they occur when an initiator species causes changes in traits of a transmitter species that, in turn, affects a receiver species. The cited studies meet the following criteria: (*a*) induced plant responses to initiators were directly or indirectly demonstrated, and (*b*) effects of trait changes in plants on receivers were measured by performance and/or population parameters. The final database consists of 83 pairwise interactions, which are summarized in Table 1. Detailed information on each reference is shown in Supplemental Appendix 1 (follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org/).

Interactions among Temporally Separated Herbivore Species

Herbivore damage on plants often changes their nutrient status, production of defensive chemicals and volatile substances, physical defense structures of thorns, spines, and trichomes, plant architecture by compensatory regrowth, and phenology of plants including bud burst, leaf flush, and flowering onset (Karban & Baldwin 1997). These changes in plant traits following herbivory are important in determining food and habitat suitability for herbivores that subsequently utilize the same plant. These alterations in the plant are the mechanistic basis for indirect interactions between temporally separated herbivore species (Table 1).

Larvae of the ranchman's tiger moth *Platyprepia virginalis* and the western tussock moth *Orgyia vetusta* both feed on leaves of the bush lupine *Lupinus arboreus*. The former appears from February–April and the latter from May–July. Harrison & Karban (1986) demonstrated that feeding by the tiger moth larvae in early spring negatively affected the suitability of the host plant to the tussock moth larvae late in the season. Spring feeding by the tiger moth significantly reduced larval growth, pupal weight, and thus fecundity of the tussock moth. Also, it was suggested that early herbivory by the tiger moth decreased nitrogen levels in subsequently emerged leaves, which may have reduced performance of the tussock moth. Denno et al. (2000) found indirect interactions between the salt marsh-inhabiting planthoppers. Previous feeding by one planthopper species had detrimental effects on the subsequent performance and survival of the other. Prior feeding by *Prokelisia dolus* resulted in prolonged development and reduced body size in *P. marginata*, whereas development was protracted in *P. dolus* when plants were previously exposed to *P. marginata*. The mechanism of the delayed competitive effects between the two planthoppers is most likely diminished plant nutrition, because feeding by *P. dolus* significantly reduced the concentration of essential amino acids.

TABLE 1 Herbivore-induced indirect interactions between herbivorous species through changes in plant traits (see Supplemental Appendix 1, for details; follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org/)

Type of interaction	Effect of initiator on receiver	Initiator→Receiver	Plant traits changed[a]	Effect on receiver[a]	Reference
Nonseparated	Negative	Caterpillar → spittlebug; aphid → aphid; planthopper → planthopper	Quality (−), leaf production (−), early senescence	Survival (−), growth (−), reproductive success (−)	Inbar et al. (1995), Karban (1986), Matsumura & Suzuki (2003)
Temporally separated	Negative	Aphid → aphid; caterpillar → caterpillar, aphid, sawfly, weevil, planthopper, leaf beetle; planthopper → planthopper; leaf beetle → leaf beetle; thrips → bumblebee; sap beetle → bumblebee	Quality (−), growth (−), defense chemicals (−), trichome (+), nectar and pollen production (−)	Survival (−), growth (−), oviposition preference (−), visitation rate (−), density (−), species richness (−)	Denno et al. (2000), Harrison & Karban (1986), Petersen & Sandström (2001), studies 5, 7–8, 10, 16–17, 20–22, 24–25, and 27–29 in Supplemental Material, Appendix 1
	Positive	Aphid → caterpillar; caterpillar → caterpillar, gall midge; flea beetle → cerambycid beetle; caterpillar, gall midge → aphid, spittlebug	Quality (+), regrowth (+)	Growth (+), density (+), species richness (+)	Damman (1989), Strauss (1991a), Williams & Myers (1984), studies 9, 12, 14–15, and 18–19 in Supplemental Material, Appendix 1

(*Continued*)

TABLE 1 (*Continued*)

Type of interaction	Effect of initiator on receiver	Initiator → Receiver	Plant traits changed[a]	Effect on receiver[a]	Reference
Spatially separated	Negative	Aphid → aphid; agromyzid fly → bracken chafer; click beetle → caterpillar	Quality (−), defense chemicals (+), biomass (−), seed set (−)	Growth (−), leaf consumption (−), density (−)	Bezemer et al. (2003), Masters & Brown (1992), Moran & Whitham (1990), Salt et al. (1996)
	Positive	Bracken chafer → aphid, agromyzid fly, tephritid fly; weevil, cranefly → tephritid fly	Quality (+), early flowering	Growth (+), fecundity (+), adult longevity (+)	Gange & Brown (1989), Masters & Brown (1992), Masters et al. (2001)
Temporally and spatially separated	Negative	Caterpillar → aphid, bee, syrphid fly; scarab, leaf beetle, grasshopper → caterpillar	Pollen production (−), flower number (−), flower size (−), floral tube (−), delayed flowering, phloem hydraulic pressure (−)	Visitation rate (−), time spent per flower (−), survival (−)	Johnson et al. (2002), Lehtilä & Strauss (1997), Strauss et al. (1996), study 39 in Supplemental Appendix 1
	Positive	Gall midge → leaf beetle, aphid; wireworm → honeybee, hover fly, bumblebee	Quality (+), regrowth (+), nectar production (+)	Visitation rate (+), density (+)	Nakamura et al. (2003), Poveda et al. (2003)
Temporally and taxonomically separated (pathogen–insect)	Negative	Spider mite → wilt fungus; leaf beetle → rust fungus; wilt fungus → spider mite; rust fungus → leaf beetle	Leaf quantity (−), defense chemicals (+)	Survival (−), growth (−), fecundity (−), density (−), infection (−)	Hatcher et al. (1994), Karban et al. (1987), Simon & Hilker (2003)
	Positive	Leaf beetle → rust fungus	—	Infection (+)	Simon & Hilker (2003)

Temporally and taxonomically separated (mammal–insect)	Negative	Sheep, ibex → leaf beetle; elk → sawfly	Flower number (−), fruit abundance (−), leaf quality for oviposition (−)	Density (−)	Bailey & Whitham (2003), Gómez & Gonzáles-Megías (2002)
	Positive	Moose → aphid, psyllid, leaf-miner, leaf-galler; eastern cottontail, snowshoe hare, moose, reindeer, elk → galling sawfly; beaver → leaf beetle	Vigor shoot (+), regrowth (+), defense chemicals (+), quality (+)	Defense ability (+), growth (+), density (+), species richness (+)	Danell & Huss-Danell (1985), Martinsen et al. (1998), Roininen et al. (1997), studies 50 and 54–55 in Supplemental Appendix 1
Spatially and taxonomically separated (mycorrhiza–insect)	Negative	Stem- and cone-boring caterpillar, scale → ectomycorrhizal fungus; arbuscular mycorrhizal fungus → caterpillar, tephritid fly	C/N ratio (+), defense chemicals (+)	Survival (−), growth (−), leaf consumption (−), colonization rate (−), gall size (−)	Gange & West (1994), Gehring et al. (1997), Vicari et al. (2002), studies 60 and 64 in Supplemental Appendix 1
	Positive	Arbuscular mycorrhizal fungus → caterpillar, bean beetle, aphid	Quality (+), defense chemicals (−), biomass (+)	Survival (+), growth (+), fecundity (+), pupation rate (+)	Borowicz (1997), Gange et al. (1999), Goverde et al. (2000)

(*Continued*)

TABLE 1   (*Continued*)

Type of interaction	Effect of initiator on receiver	Initiator → Receiver	Plant traits changed[a]	Effect on receiver[a]	Reference
Spatially and taxonomically separated (endophyte–insect)	Negative	Endophyte → aphid, caterpillar	Quality (−), defense chemicals (+), phytosterol metabolism (−)	Survival (−), growth (−), density (−), population growth rate (−)	Bultman et al. (2004), Omacini et al. (2001), Raps & Vidal (1998)
	Positive	Endophyte → aphid, grasshopper	Quality (+)	Growth (+), fecundity (+), density (+)	Gange (1996), Saikkonen et al. (1999)
Spatially and taxonomically separated (pathogen–insect)	Negative	Fungal pathogen → leaf beetle	Stem diameter (−), leaf production (−)	Survival (−), growth (−), oviposition preference (−)	Kruess (2002)
	Positive	Fungal pathogen → aphid	Quality (+), defense chemicals (+)	Growth (+), embryo development (+), density (+), population growth rate (+)	Johnson et al. (2003)
Ecosystem engineer mediated	Positive	Caterpillar → caterpillar, aphid, springtail; galling sawfly → aphid; eriophyid mite → spider mite	Leaf shelter (+)	Density (+), species richness (+)	Martinsen et al. (2000), Lill & Marquis (2003), Nakamura & Ohgushi (2003), studies 75–76 and 80–83 in Supplemental Appendix 1

[a](+), increase; (−), decrease.

In contrast, positive effects of early-attacking insects on later-emerging insects have been documented (Table 1). For instance, the fall webworm *Hyphantria cunea* feeding on leaves of the red alder from August–September, had larger pupal size and higher pupation rate on trees that were previously damaged by the western tent caterpillar *Malacosoma californicum pluviale* (Williams & Myers 1984). The heavier pupae on damaged trees resulted in a 12.5% increase in fecundity over pupae on undamaged trees.

Herbivore-induced architectural responses also generate indirect interactions between temporally separated species (Table 1). Strauss (1991a) showed that early-season bud damage by the leaf beetle *Blepharida rhois* caused subsequent production of basal vegetative shoots in the smooth sumac *Rhus glabra*. These basal shoots are the preferred oviposition site for the cerambycid stem borer *Oberea ocellata*, and stem-borer attack increased significantly after leaf beetle attack. Gall initiation by the stem gall midge *Rabdophaga rigidae* stimulates the development of lateral shoots of the willow *Salix eriocarpa* followed by a secondary leaf flush. Nakamura et al. (2003) found that lateral shoots and upper leaves on galled shoots were less tough and had a higher water and nitrogen content. As a result, density of the aphid *Aphis farinosa* was significantly higher on galled shoots than on ungalled shoots, because the aphid frequently colonized lateral shoots. Also, adults of the leaf beetles *Plagiodera versicolora* and *Smaragdina semiaurantiaca* were more abundant on galled shoots than on ungalled shoots, because they preferentially fed on young leaves produced by the secondary leaf flush.

Interactions among Spatially Separated Herbivore Species

Interactions between spatially separated insects, which share one plant but utilize different parts of it, have revealed that insects often interact significantly with each other, although the species never encounter one another directly (Table 1). These spatially separated indirect interactions could occur because tissues of an individual plant depend on a common resource budget.

Moran & Whitham (1990) described a plant-mediated interaction between two aphid species that feed on different parts of the lamb's-quarters *Chenopodium album*. One aphid *Hayhurstia atriplicis* makes leaf galls, whereas the other aphid *Pemphigus betae* feeds underground on roots. The root feeder had no significant effects on its host, but the leaf feeder severely reduced root biomass. As a result, the number of the root feeder significantly decreased, with *Pemphigus* often being eliminated entirely. Conversely, the garden chafer *Phyllopertha horticola* feeding on roots of the shepherd's purse *Capsella bursa-pastoris* improved performance of the sap-sucking aphid *Aphis fabae* (Gange & Brown 1989). The root feeder induced water stress to the host plant by a large reduction in vegetative tissue, resulting in an increase in soluble nitrogen. The enhanced host-plant quality increased growth rate and longevity, and thus fecundity of the aphid. On the other hand, the aphid affected neither the host plant nor the garden chafer. However, the garden chafer interacted with a dipteran leaf miner *Chromatomyia syngenesiae* in quite a different

way on the common sow thistle *Sonchus oleraceus* (Masters & Brown 1992). Root herbivory increased pupal mass of the leaf miner and thus its fecundity, probably because of changes in host quality initiated by root feeding. In contrast, leaf herbivory reduced the growth rate of the root feeder, because leaf miner herbivory reduced root biomass considerably.

Interactions among Herbivores and Pollinators

Leaf herbivory by insects often changes considerably the quantity and/or quality of floral traits, which are of crucial importance in pollinator service (Bronstein et al. 2006, Strauss 1997). Foliar leaf damage early in the season decreases flower number, flower size, pollen production, pollen performance, and nectar production, which can affect plant relationships with pollinators (Table 1).

Strauss et al. (1996) and Lehtilä & Strauss (1997) experimentally studied how leaf damage affects plant attractiveness to pollinators in the wild radish *Raphanus raphanistrum*. Leaf damage by larvae of the white butterfly *Pieris rapae* significantly decreased the number and size of flowers. Pollinators discriminated against damaged plants by visiting such plants less frequently and by spending less time on them. Damaged plants received fewer visits by native bees than undamaged plants, probably because flower number was the main cue attracting native bees to plants. Also, syrphid flies, which were abundant pollinators, spent less time per flower on the damaged than on undamaged plants. These studies emphasize how pollination service is largely influenced by previous herbivory, which has long been ignored in pollination ecology.

Interactions among Distantly Related Herbivore Species

Hochberg & Lawton (1990) argued that organisms in different phyla or even kingdoms may compete for the same resources, and that such interactions may be one of the most pervasive forms of interspecific competition in nature, yet still be one of the most poorly understood. As induced plant responses can influence a variety of different herbivores, the initiator and the receiver species may be related taxonomically only distantly.

INTERACTIONS AMONG HERBIVOROUS MAMMALS AND INSECTS   Mammalian browsing often affects indirectly herbivorous insects in negative or positive ways (Table 1). Danell & Huss-Danell (1985) found that herbivorous insects including aphids, psyllids, leaf miners, and leaf gallers were more abundant on birch trees of *Betula pendula* and *B. pubescence* previously browsed upon by the moose *Alces alces* than on unbrowsed trees. Browsed trees subsequently produced larger leaves with more nitrogen and chlorophyll, and this improved leaf quality resulted in higher densities of the herbivorous insects. Natural browsing by hares and moose had strongly positive effects on densities of galling insects on two host plants, *Populus balsamifera* and *Salix novaeangliae* (Roininen et al. 1997). When the mammalian browsers attacked these plants, numbers of newly developed vigorous

shoots on ramets increased significantly. As a result, leaf-edge galling sawfly density increased significantly because of the improved plant quality.

The beaver *Castor canadensis* often cuts down cottonwoods *Populus* sp., removing nearly all aboveground biomass. Resprout growth from the stumps and roots of beaver-cut trees contains more phenolic glycosides and total nitrogen than normal juvenile growth. The specialist leaf beetle *Chrysomela conuens* is attracted to the resprouted growth. Martinsen et al. (1998) experimentally demonstrated the positive effects of the beaver on the leaf beetle. Beetle larvae that had fed on resprout growth were better defended against ants than those that fed on nonresprout growth, because the increased defensive chemicals in the resprout growth were sequestered and used by the beetles for their own defenses. Beetle larval development on resprout growth was also significantly faster and larval weight higher at maturity because of the increased total leaf nitrogen. Regrowth of plants following herbivory often changes plant architecture by increasing the biomass of vegetative and reproductive parts or by inducing rapid branching. When browsed heavily by mule deer and/or elk in spring, the number of inflorescences on the scarlet gilia *Ipomopsis arizonica* increased. The increased number of inflorescences, in turn, increased the density of a fruit-feeding noctuid caterpillar (Mopper et al. 1991).

INTERACTIONS AMONG MICROORGANISMS AND HERBIVOROUS INSECTS Indirect interactions between highly unrelated organisms can also include microorganisms—such as pathogens, endophytes, and mycorrhizae—sharing a host plant (Table 1). The fungal pathogen *Verticillium dahliae* was less likely to cause symptoms of verticillium wilt on cotton seedlings previously attacked by *Tetranychus* spider mites (Karban et al. 1987). Conversely, spider mite densities decreased on seedlings infected with fungal disease, probably because of the reduced leaf tissue by fungal infection. In contrast, Johnson et al. (2003) found positive indirect effects of the fungal pathogen *Marssonina betulae* of silver birch on preference, performance, and population growth of the aphid *Euceraphis betulae*. Aphids reared on infested leaves were heavier, possessed longer hind tibiae, and displayed enhanced embryo development, compared to aphids on intact leaves. Population growth rate of aphids was also positively correlated with fungal infection. Fungal-infected leaves contained higher concentrations of free amino acids, resulting in the positive interaction between the fungus and aphids.

Systemic endophytes are well known for increasing host-plant defenses against insect herbivores and pathogenic microorganisms by producing mycotoxins (Clay 1997). Thus, insect herbivores exhibit reduced performance and/or population density on endophyte-infected plants (Table 1). However, infection by fungal endophytes may have positive effects on herbivorous insects. The sycamore aphids *Drepanosiphum platanoidis* and *Periphyllus acericola* had significantly higher densities, heavier weight, and more fecundity on infected than uninfected trees of the sycamore maple *Acer pseudoplatanus* (Gange 1996). The infected leaves had higher soluble nitrogen, which may have increased aphid performance and density.

Effects of arbuscular mycorrhizal fungi on herbivorous insects vary from negative to positive (Table 1) depending on diet breadth of insects or soil nutrients (Gange 2006). Arbuscular mycorrhizal fungi decreased herbivory by chewing and leaf-mining insects on *Plantago lanceolata* by increasing the level of the carbon-based feeding deterrents aucubin and catalpol (Gange & West 1994). In contrast, they improved performance of the aphids *Myzus ascalonicus* and *M. persicae*; adults gained greater weight and fecundity (Gange et al. 1999). On the other hand, ectomycorrhizal fungi are negatively affected by herbivorous insects (Gehring & Whitham 1994), because herbivore-induced reductions in aboveground biomass reduce the carbon-source capacity of plants to such a degree that there is insufficient carbon to meet the demands of mycorrhizal fungi.

Interactions Mediated by Insect Ecosystem Engineers

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994). Insect ecosystem engineers manipulate plants to create structural alterations that influence interactions among species. This contrasts with the trait mediation by insects discussed in previous sections where herbivory altered plant responses without causing structural changes.

Ecosystem engineering is ubiquitous on terrestrial plants. Obvious candidates include gall makers, leafrollers, case bearers, and stem borers, all of which are common insect herbivore guilds, and which provide new habitats to other herbivores and/or their natural enemies. In particular, shelter building is a very common lifestyle among the microlepidoptera and in some weevils, sawflies, and even grasshoppers. Insects that are secondary occupants of shelters can gain several benefits, including avoidance of natural enemies (Damman 1987), protection from adverse microclimates (Hunter & Willmer 1989, Larsson et al. 1997), and access to more easily eaten food (Sagers 1992) and highly nutritious food (Fukui et al. 2002).

Lawton & Jones (1995) argued that ecologists fail to recognize the role of ecosystem engineers as keystone species that exert a great influence on community organization. As we can see in the function of leafrolling caterpillars as ecosystem engineers on the willow (Figure 1), recent studies have shown that insect ecosystem engineers have the potential to greatly affect other arthropods (Marquis & Lill 2006, Table 1).

Features of Herbivore-Induced Indirect Interactions

The literature survey clearly demonstrates that herbivore-induced indirect effects through trait change in plants are widespread in many plant–herbivore systems (Supplemental Appendix 1; follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org/). Although the potential importance of trait-mediated indirect effects in ecological communities has been widely accepted (Abrams et al. 1996, Strauss 1991b, Wootton 1994), they have been studied much less frequently than density-mediated indirect effects such

as keystone predation, trophic cascades, and apparent competition (Holt & Lawton 1994, Menge 1995, Pace et al. 1999, Polis et al. 2000). More recently, some authors have stressed the community consequences of trait-mediated indirect interactions in herbivore–predator systems (Werner & Peacor 2003, Bolker et al. 2003). Werner & Peacor (2003) argued that ecological communities are replete with trait-mediated indirect effects that arise from phenotypic plasticity, and that these effects are quantitatively important to community dynamics. Nevertheless, trait-mediated indirect interactions have received little attention in plant–herbivore systems (but see Callaway et al. 2003).

Table 2 summarizes features of indirect effects in plant–herbivore interactions by comparing them with those found in herbivore–predator interactions. This review reveals that substantial indirect interactions caused by herbivore-induced changes in terrestrial plants frequently occur among temporally separated, spatially separated, and distantly related herbivore species. These interactions have been poorly explored for two reasons. First, the traditional view on within-trophic-level interactions has emphasized that interactions should be most prevalent among closely related species within guilds or among species that utilize the same part of a resource at the same time. Second, unlike interspecific competition, these plant-mediated indirect interactions commonly occur at low levels of herbivory resulting in underestimation of the ubiquitous indirect interactions among herbivores.

Note that herbivores sharing the same host-plant can benefit each other (47% of 83 pairwise interactions in Supplemental Appendix 1; follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews. org/), because herbivory often enhances resource availability through improved nutritional quality and/or increased biomass of plants because of compensatory regrowth. In addition, ecosystem engineers benefit secondary users that colonize newly constructed domiciles later in the season. Despite the fact that positive interactions are ubiquitous in many ecological communities (Bruno et al. 2003, Hay et al. 2004), the beneficial interactions within the same trophic level have been largely ignored. This is because the traditional view of community ecology has largely emphasized interspecific competition as the interaction of primary importance between organisms at the same trophic level.

In terrestrial systems, trait-mediated indirect effects should predominate in plant–herbivore interactions, whereas density-mediated indirect effects should be most common in herbivore–predator interactions. This is because predators kill individuals of the lower trophic level, whereas herbivores only alter their traits. Thus, indirect effects through changes in density because of mortality by consumers occur infrequently in plant–herbivore systems. For example, Müller & Godfray (1999) suggested that indirect effects by trait mediation are less frequent than indirect effects by density mediation in aphid–parasitoid systems. There is increasing appreciation of trait-mediated indirect effects resulting from changes in prey behavior to avoid predation risk, i.e., the nonlethal effects of predators (Losey & Denno 1998, Schmitz 1998, Schmitz et al. 2004). However, there is a large difference in trait-mediated indirect effects between herbivore–predator and

TABLE 2 Comparison of features of indirect effects in plant–herbivore and herbivore–predator interactions in terrestrial systems

Type of interaction	Effect of feeding	Response of herbivore/ plant after feeding	Indirect effects involved predominantly	Within-trophic interactions at a consumer level		
				Indirect interactions among separated species	Ecosystem engineering	Positive interactions
Plant–Herbivore	Nonlethal	Trait change	Trait-mediation	Common	Common	Common
Herbivore–Predator	Lethal	Mortality	Density-mediation	Less frequent	Less frequent	Less frequent

plant–herbivore systems in terms of when herbivores or plants respond to attack by their enemies. The indirect effects mediated by changes in behavior of an herbivore prey result from the presence of a predator before feeding, whereas the plant-mediated indirect effects occur after feeding by herbivores. In other words, the trait-mediated indirect effects in plant–herbivore interactions emerge in the postfeeding process, whereas those in herbivore–predator interactions appear in the prefeeding process. In consequence, indirect interactions between herbivores via changes in plants should occur more frequently than those between predators via changes in behavior of a shared herbivore prey.

WHY ARE HERBIVORE-INDUCED INDIRECT INTERACTIONS SO COMMON IN TERRESTRIAL SYSTEMS?

The importance of interspecific interactions between herbivorous insects has long been discounted, because empirical studies often show lack of competition in nature (Lawton & Strong 1981, Seifert 1984, Strong 1984). In addition, the concentration on direct interactions has caused us to overlook the importance of widespread herbivore-induced indirect interactions on terrestrial plants. Direct interspecific competition for limited resources requires high levels of herbivory, whereas plant-mediated indirect interactions can occur at low levels of herbivory. One reason for this is that plant defenses that mediate herbivore indirect interactions are often rapidly induced at low levels of herbivory before it causes plant mortality. Conversely, heavy defoliation can actually decrease indirect interactions. Plants that are heavily exploited during outbreaks of forest defoliators, for example, cannot compensate for lost tissue. Also, habitats previously created by ecosystem engineers are hardly maintained under heavy herbivory. A lack of visible depletion of green plants, therefore, does not mean that interspecific interactions between herbivores rarely occur. Instead, limited herbivory greatly increases the likelihood of indirect interactions between herbivores mediated by changes in plant characteristics. Thus, it is inferred that plant-mediated indirect interactions between herbivores predominate at low levels of herbivory, whereas the relative importance of direct interspecific competition is apparent at high levels of herbivory.

In this context, plant-mediated indirect effects should be more common in terrestrial than in aquatic systems. In terrestrial systems, the average consumption rate by herbivores varies from 4% to 18% of aboveground plant biomass (Polis 1999), whereas in aquatic systems herbivore consumption often exceeds 50% of primary production. Indeed, primary production in aquatic systems is mainly by phytoplankton, which are killed by predation leaving an absence of organisms that can retain induced responses. The low level of herbivory in terrestrial plants therefore produces a predominance of plant-mediated indirect effects in terrestrial systems, whereas the high level of herbivory in aquatic systems produces more direct effects of grazing. Recent reviews strongly support this view that the

majority of interactions between terrestrial herbivorous insects are likely to be indirect, mediated by changes in plants following herbivory (Damman 1993, Denno & Kaplan 2006, Denno et al. 1995, Masters & Brown 1997). For example, Denno et al. (1995) stressed that over half of the 145 documented cases of interspecific competition among insect herbivores involved delayed, plant-mediated competition in which previous feeding by one species induced either nutritional or allelochemical changes in the plant that adversely affected the performance of another species feeding on it later in the season.

INTEGRATING MULTIPLE INTERACTIONS INTO INDIRECT INTERACTION WEBS

In this section, I emphasize the important role of herbivore-induced indirect effects through plant traits in forming indirect interaction webs. I also illustrate that the indirect interaction web provides a conceptual tool to efficiently explore the structure and biodiversity of ecological communities by comparing the traditional food web approach.

How Does Interaction Linkage Affect Biodiversity?

Most of the Earth's biodiversity is in its interaction diversity: the tremendous variety of ways in which species are linked together into constantly interacting networks. Thus, ecologists have recognized diversity of species interactions as one of the most important components of biodiversity (Price 2002, Thompson 1996). For example, many of the adaptations and counter-adaptations of plants and their insect herbivores indicate that much of the biodiversity of the Earth results from the arms race between herbivores and their host plants (Strauss & Zangerl 2002). Temporal and spatial resource heterogeneity can increase species richness and interaction diversity in terrestrial systems (Hunter et al. 1992). Specifically, temporal and spatial heterogeneity in the food and habitat provided by terrestrial plants is greatly promoted by the feedbacks resulting from changes in plant quality and architecture in response to herbivory and the creation of physical structures by ecosystem engineers.

An understanding of interaction linkages propagated by herbivore-induced indirect effects can provide valuable insight into how a network structure of species interactions affects biodiversity in ecological communities. We are starting to examine indirect effects on biodiversity components in plant–herbivore systems (Bailey & Whitham 2002, Martinsen et al. 2000, Ohgushi 2006, Ohgushi et al. 2006, Omacini et al. 2001, Van Zandt & Agrawal 2004, Waltz & Whitham 1997). Herbivore-induced changes in terrestrial plants can generate changes that cascade upward to higher trophic levels and, thus, influence biodiversity. These bottom-up cascading effects can have repercussions through entire herbivorous insect communities and alter species richness and abundance of each species. For example, larvae of leafrollers on cottonwoods construct leaf shelters, which are later

colonized by other arthropods. Martinsen et al. (2000) found four times greater species richness and seven times greater abundance of arthropods on shoots with a rolled leaf compared to adjacent shoots without leafrolls. Likewise, Lill & Marquis (2003) found that the presence of a leaf-tying caterpillar *Pseudotelphusa* sp. had a great impact on species composition of herbivorous insects on white oak *Quercus alba*. In their removal experiments, a decrease in shelter availability significantly decreased by 14–38% species richness of leaf-chewing insects. This is because positive effects of the ecosystem engineers on other arthropods that secondarily use leaf shelters later caused the increased arthropod biodiversity. Another example is the leaf-galling aphid *Pemphigus betae* and the leaf beetle *Chrysomela conuens*, which had positive and negative effects on other arthropod species on cottonwoods, respectively (Waltz & Whitham 1997). Aphid removal decreased species richness by 32% and relative abundance by 55%, respectively, because the aphids attracted various predators and parasitoids and herbivorous insects because of changes in plant quality. In contrast, the leaf beetle decreased species richness of other herbivorous insects because the leaf beetles negatively affected plants by reducing terminal shoot growth. These studies indicate that indirect interaction linkages have a significant impact on arthropod biodiversity on terrestrial plants.

Indirect Interaction Webs

Indirect effects have the potential to strongly influence biodiversity components in ecological communities by shaping a network structure of interacting species. The most complete ecological network descriptions available are food webs, a basic tool to analyze community structure (Polis & Winemiller 1996). Because food webs focus on direct trophic interactions, nontrophic interactions are not included. As I stressed, the nontrophic, herbivore-induced indirect interactions can connect herbivore species indirectly mediated by trait change in plants. Thus, plant-based terrestrial food webs that ignore nontrophic indirect links are an inadequate tool for understanding the structural organization of arthropod communities. Furthermore, the principles of trophic interactions in food webs are not of much value in understanding ecosystem engineering. To understand how multiple interactions are connected, we can use "indirect interaction webs" that include nontrophic, indirect links. The indirect interaction webs can efficiently illustrate the linkage of multiple interactions, thereby providing a tool to explore the interaction diversity in a community. Food webs alone can clarify only feeding interactions, which are a part of indirect interaction webs. In this context, Berlow et al. (2004) pointed out that the future challenge to develop the theory of food web dynamics is to incorporate nontrophic links into food web structure. Menge & Sutherland (1987) originally termed "interaction web" as a trophic structure of strong interactions. It is always a subset of the species in a food web, deriving from Paine's functional web (Paine 1980). Although recent arguments include nontrophic or indirect interactions only if they are detected as strong interactions (Menge & Branch 2001), the interaction webs are principally based on the traditional food web concept. The indirect interaction webs are an alternative that explicitly incorporate

nontrophic and indirect interactions into components of traditional food webs. Food webs consist of direct trophic interactions with energy transfer, whereas indirect interaction webs include nontrophic effects without energy transfer as mediators to connect multiple interactions.

Again, let us look at an indirect interaction web illustrating the interaction linkage of herbivorous insects on the willow. A food web approach detected three independent trophic interactions (Figure 1*a*) consisting of spittlebugs, leafrollers, and leaf beetles that feed on plants (interactions 1, 2, and 3), each of which is temporally or spatially separated from the others. The aphids were not included in the food web because they did not directly colonize the willow in the absence of leaf shelters constructed by leafrollers. In the indirect interaction web, the following indirect interactions were added (Figure 1*b*): the interaction between spittlebugs and leafrollers through compensatory shoot growth (interaction 7), the interaction between leafrollers and aphids through leaf shelters (interaction 8), the interaction between leafrollers and three ant species through aphid colonies (interaction 9), and the interaction between aphids and leaf beetles through increased tending by ants (interaction 10). Because the aphids were included in this web when leaf shelters were available, three direct interactions were newly established: the interaction between aphids and willow (interaction 4), the interaction between aphids and three species of ants (interaction 5), and the interaction between ants and leaf beetles (interaction 6). Thus, the indirect interaction web revealed six direct and four indirect interactions including four positive interactions, whereas the food web approach encompassed only three negative, direct interactions. Will we find in general that direct plus indirect interaction webs increase the detection of species' influences on each other by over three times, as in the case above? The indirect interaction webs will differ greatly and depict the interaction network and diversity in ecological communities more realistically than do the traditional food webs.

FUTURE DIRECTIONS

The study of indirect effects is an increasingly rich subfield of community ecology (Wootton 2002). Indeed, there is rapidly expanding evidence to suggest the importance of herbivore-induced indirect effects as mediators of interaction linkages shaping indirect interaction webs. This subject is of great importance in understanding not only community organization but also in identifying the underlying mechanisms of maintenance of biodiversity. Thus, the study of herbivore-induced indirect effects is at a very challenging stage (Ohgushi et al. 2006). Here, I emphasize several promising directions for future research.

1. We need further evidence to determine how common and widespread herbivore-induced indirect effects are, not only in terrestrial but also in aquatic systems. As herbivore-induced indirect interactions occur at low levels of herbivory, I predict that they will be much more frequent in terrestrial systems than in pelagic systems. Note that in marine systems, seaweeds may provide

plant-mediated indirect effects because they can induce chemical defenses following herbivory (Cronin & Hay 1996, Pavia & Toth 2000).

2. We should seek out plant characteristics that provide favorable conditions for herbivore-induced indirect effects by comparing plant responses following herbivory among taxa, life histories, and life forms.

3. We need to explore herbivore-initiated interaction linkages as the important community consequences of trait-mediated indirect effects. Also, a comparison of trait-mediated indirect effects in plant–herbivore and herbivore–predator systems will contrast the two different forms of indirect effects through trait mediation.

4. Long-term studies are crucial to clarify temporal variation in herbivore-induced indirect effects. In particular, we need multigenerational studies of the population dynamics of key species that initiate indirect effects to understand how the temporal changes in indirect effects alter the structure of indirect interaction webs in ecological communities.

5. We need to know how the interaction linkages caused by nontrophic indirect effects determine community organization and biodiversity. Specifically, we should pay much attention to the positive effects of ecosystem engineering and plant compensatory growth on species richness and interaction diversity.

6. Ecologists should recognize that indirect interaction webs are a valuable tool for understanding the importance of nontrophic indirect links and interaction diversity in nature. This is because traditional food webs can rarely predict underlying mechanisms of community organization that are frequently shaped by nontrophic indirect effects.

7. We need to compare multitrophic interactions in terrestrial and aquatic systems in the context of the presence or absence of nonlethal effects that produce trait-mediated indirect effects. Because the nonlethal effects of herbivores on terrestrial plants provide a mechanistic basis for feedbacks cascading upward through trophic levels via plant-mediated indirect effects, I predict that they would be of secondary importance in pelagic systems because zooplankton has primarily lethal effects on phytoplankton.

8. Plant-mediated interactions between leaf-feeding and root-feeding insects and those between leaf- or sap-feeding insects and mycorrhizae can link above- and belowground communities (Van der Putten et al. 2001). There is increasing evidence that aboveground herbivory can change root carbon allocation, root exudation, root biomass, and morphology (Bardgett et al. 1998). Thus, the quantity and quality of organic matter input from plants damaged by herbivores have the potential to greatly influence abundance, species composition, and activity of the soil organisms in the rhizosphere by altering interactions in soil food webs.

9. Because plant responses to herbivores provide a mechanistic basis for indirect interaction linkages shaping nontrophic indirect interaction webs, an

essential question is, How do plant responses to herbivores evolve in communities that consist of diverse assemblages that interact directly and indirectly? In this context, selection pressures caused by one species can change in the presence of other species and, thus, variation in the community composition can alter the coevolutionary outcomes of interactions (Siepielski & Benkman 2004, Thompson 1994). Furthermore, we should explore the evolutionary consequences of plant-mediated indirect effects (Agrawal & Van Zandt 2003, Craig 2006). Specifically, I predict that trait-mediated indirect effects limit the potential for pairwise coevolution, and that this limitation can be seen in the diffused evolutionary arms race between plant resistance and its herbivores because multiple herbivores attack the same host-plant. On the other hand, plant-mediated indirect effects will provide valuable insights to understanding how evolutionary alterations of plant traits, in turn, affect community organization of higher trophic levels by reforming interaction linkages.

If simple systems, such as willow and its herbivorous insects discussed here, can reveal three times more interactions when both direct and indirect interactions are examined, we have a lot more ecology to study. There is also much to evaluate in terms of relative strengths of direct and indirect effects, and density- and trait-mediated effects. In addition, we have more mechanisms to understand in relation to the maintenance and increase of biodiversity. Emphasis on nontrophic and indirect effects offers great promise for enriching ecological investigations and the understanding of nature.

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