

Akiko Fukui

Indirect interactions mediated by leaf shelters in animal–plant communities

Received: July 24, 2000 / Accepted: February 15, 2001

Abstract Leaf shelters indirectly mediate interactions in animal–plant communities by providing the occupants with several kinds of benefits, as physical ecosystem engineering. The occupants benefit from favorable microhabitat, reduction in antiherbivore defense, and protection from natural enemies. The primary shelter maker has to spend energy and time and producing silk, but shelter users have great advantages without incurring costs. Shelter users consist of a wide range of arthropod taxa and can be divided into two groups: coexisting organisms that live with a primary shelter maker in the same shelter, and secondary users, which inhabit a leaf shelter after it is utilized by a shelter maker. Leaf shelters mediate interactions between (1) primary shelter makers and coexisting organisms or (2) primary shelter makers and secondary users, (3) secondary users, (4) shelter users and their natural enemies, and (5) primary shelter makers, secondary users, and their host plants. Most interactions between primary shelter makers and coexisting organisms constitute a direct trophic linkage rather than indirect ones. There are actually unidirectional beneficial effects from a primary shelter maker to secondary shelter users, whereas leaf shelters mediate competition and predation among shelter users. By providing a leaf shelter, a shelter maker leads to increased diversity of interactions. Leaf shelters modify the distribution of organisms on the host plant and influence herbivory on the host plant. In tritrophic interactions, leaf shelters act as cues for natural enemies that search for a shelter user as prey. Furthermore, by enhancing habitat heterogeneity, leaf shelters affect the abundance and species richness of arthropods on host plants.

Key words Diversity of interactions · Habitat heterogeneity · Shelter maker · Manipulation · Physical ecosystem engineer · Secondary user

Introduction

Forest ecosystems provide habitat and food resources for animals. Many herbivores alter microenvironments on a host plant by favorably modifying plant parts such as leaves. Through architectural modifications, some herbivores have advantageous or disadvantageous impacts on plant survival, growth, and reproduction, also impacting other arthropods associated with the plant (Mopper et al. 1991). Here, such advantageous impact on other species is called positive and disadvantageous impact is called negative. This article reviews indirect interactions mediated by leaf shelters, including any types of transformation of leaves by herbivores, such as leaf-folds, -galls, -rolls, -sandwiches, and -ties.

Shelter-mediated interactions constitute three categories of indirect interactions among herbivores together with food resource- and enemy-mediated interactions (Damman 1993). Shelter-mediated interactions involve the provision of a shelter by one herbivore species to another (shelter user), thereby altering the availability of plant physical structures. In food resource-mediated interactions, feeding by one herbivore species leads to changes in the quality of the plant as food for other species. In enemy-mediated interactions, herbivores interact indirectly by affecting the population dynamics or foraging behavior of shared natural enemies.

Making leaf shelters is common and widespread in herbivorous arthropods. Herbivores are exposed to mortality agents including abiotic factors and bottom-up and top-down effects (Gaston et al. 1991). Leaf shelters enable the occupants to reduce these negative effects. It is important to point out that not only shelter makers but also other organisms frequently use leaf shelters. Here, an organism is called a shelter user when it occupies a leaf shelter made by another species.

A. Fukui
Laboratory of Wildlife Biology, School of Agriculture and Life Sciences, The University of Tokyo, Tokyo, Japan

Present address: Center for Ecological Research, Kyoto University, Kamitanakami, Hirano-cho, Otsu 520-2113, Japan
Tel. +81-77-549-8262; Fax +81-77-549-8201
e-mail: aki@fieldnote.com

Shelter makers have a great positive influence on shelter users. Shelter users have the advantages, without the cost of making a shelter (Carroll and Kearby 1987; Lewis 1979; Cappuccino 1993; Kudo 1994; Larsson et al. 1997). The making of a leaf shelter needs much time and energy (Ford 1977; Ruggiero and Merchant 1986; Otto 1987; Berenbaum et al. 1993). The time spent on the leaf surface increases vulnerability to enemies (Marston et al. 1978; Bergelson and Lawton 1988; Loader and Damman 1991; Loeffler 1996). Shelter-making behavior prevents a shelter maker from foraging, resulting in slower growth and prolonged developmental rates (Damman 1987; Ruehlmann et al. 1988; Hunter and Willmer 1989; Loeffler 1996).

Thus, shelter makers can be considered as “physical ecosystem engineers” that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials (Jones et al. 1994). Jones et al. (1997) pointed out that physical ecosystem engineers could play important roles as keystone species in ecosystems. However, fewer studies have focused on shelter-mediated interactions than on interactions based on trophic linkages, such as food resource- and enemy-mediated interactions (Cappuccino 1993; Damman 1993).

This article attempts to demonstrate the significance of leaf shelters as resources on host plants. First, the benefits for occupants of leaf shelters are emphasized. Second, evidence for shelter utilization by other organisms (shelter users) and for unidirectional beneficial interactions between shelter makers and users is shown. Then, I demonstrate that leaf shelters act as a mediator of indirect interactions in an animal–plant community, focusing on (1) the modified distributions of herbivory, (2) tritrophic interactions, and (3) abundance and species richness on host plants.

Benefits for occupants of leaf shelters

Evading abiotic environmental factors

Abiotic factors, such as humidity, radiation, temperature, and wind, directly affect reproductive capacity and longevity of insects (Willmer 1982). Insects usually suffer high mortality in young immature instars, and mortality is critical to population dynamics (Cornell and Hawkins 1995). Desiccation is a major environmental hurdle for immature insects, especially during molting (Willmer 1982). Relative humidity inside shelters is significantly higher than that of the leaf surface (Henson 1958a; Willmer 1980; Hunter and Willmer 1989; Larsson et al. 1997). Because insect larvae survive and grow better at high humidity than at low humidity (Hunter and Willmer 1989; Larsson et al. 1997), shelters provide a favorable microclimate for shelter occupants.

Radiation (including sunrays and radiant heat) affects herbivores directly and indirectly by changing plant quality (see next section). Radiation and wind are factors changing air temperature (Porter and Gates 1969). The temperature

within various types of leaf shelters differs from ambient temperature, and thus it might affect growth rates of the larvae inside (Henson 1958b). Many factors determine temperature in microhabitats: the shape of structure, air circulation at its surface or inside, surface-volume ratio, color, or orientation to the sunrays (Henson 1958b).

Reduction in bottom-up effects

Sagers (1992) showed that leaf-rolls reduced physical and chemical defenses on the host plants without altering the nutritional status. In the neotropical shrub *Psychotri horizontalis*, shading by rolled leaves decreased the toughness of the expanding leaves by 31% and tannin concentration by 15% while having no effect on nitrogen and water content; this is similar to the differences between shaded plants and plants growing under high light levels. Sun leaves are thicker, containing more fibers (Givnish 1988) and higher levels of defense chemicals than shade leaves at both inter- and intraindividual scales (Boardman 1977; Mole et al. 1988).

Concentrations of antiherbivore defense compounds are reduced in leaf shelters compared to normal leaves (Berenbaum 1978; Sandberg and Berenbaum 1989). The presence of hypericin in *Hypericum perforatum* (Guttiferae) reduces survivorship and prolongs the development of tortricid larvae (*Heliothis zea* and *Platynota flavedana*) that feed on leaves in the light. When wavelengths photoactivating the toxin hypericin are excluded by filters, larval survival is enhanced. In the wild, *Platynota flavedana* successfully survives on the plant by tying together leaves and feeding inside the ties. Thus, the larvae are protected from phototoxic compounds by their mode of feeding (Sandberg and Berenbaum 1989).

Reduction in top-down effects

Leaf shelters also protect the occupants from general predators, such as ants, birds, and spiders (Table 1). Fowler and MacGarvin (1985) found that aphid-attending ants reduced the density of free-living leaf-chewers (Lepidoptera) more than the density of leaf-tiers (Lepidoptera) and nomadic leafminers (Lepidoptera) on *Betula pubescens*. These results show that ants can change the guild structure of herbivorous insect communities.

Shelter users

Shelter users can be divided into coexisting organisms and secondary users (Table 2). Coexisting organisms live with a shelter maker in the same shelter. Most of them are conspecifics of the shelter maker (caterpillars: Werner 1977; Carroll and Kearby 1978; Carroll et al. 1979; Cappuccino 1993; aphids: Akimoto 1988; Fukui, unpublished) and potential natural enemies of shelter makers (Cappuccino 1993; Dickson and Whitham 1996; Fukui, unpublished).

Table 1. Positive effects of leaf shelters for shelter users

Protection from	Shelter form	Shelter user	Host plant	Reference
Effects from abiotic environmental factors:				
Desiccation	Leaf roll	Caterpillar, <i>Compsolechia niveopulvella</i> (Tortricidae)	<i>Populus tremuloides</i>	Henson (1958a)
Temperature	Leaf gall, leaf roll, leaf tie	Caterpillars	<i>Populus tremuloides</i>	Henson (1958b)
Desiccation	Leaf roll	Caterpillar, <i>Toetrix viridana</i> (Tortricidae)	<i>Quercus fagella</i>	Willmer (1980)
Desiccation	Leaf roll	Caterpillar, <i>Toetrix viridana</i> (Tortricidae)	Pedunculate oak, <i>Quercus rober</i>	Hunter and Willmer 1989
Desiccation	Leaf roll	Leaf beetle, <i>Galerucella lineola</i> ^a	<i>Salix viminalis</i>	Larsson et al. (1997)
Bottom-up effects	Leaf roll	Armyworm, <i>Spodoptera eridania</i> (Noctuidae)	Parsnip <i>Pasitacna sativa</i> (Umbelliferae)	Berenbaum (1978)
Furanocoumarin	Leaf roll	Grasshopper, <i>Melanoplus differentialis</i> (Orthoptera: Acrididae)	Sunflower, <i>Helianthus annuus</i>	Lewis (1979)
Leaf toughness	Tied leaf	Caterpillar, <i>Platynota flavedata</i> (Tortricidae)	<i>Hypericum perforatum</i> (Guttiferae)	Sandberg and Berenbaum (1989)
Antitherbivore chemical hypericin	Leaf roll	Caterpillar, Pyralidae and Ctenuchidae	<i>Psychotria horizontalis</i>	Sagers (1992)
Tannin, leaf toughness	Leaf roll	Caterpillar, <i>Metricostola betulae</i> (Pyralidae)	<i>Betula pubescens</i>	Fowler and McGarvin (1985)
Top-down effects	Tied leaf	Caterpillar, sawfly	Bracken fern, <i>Pteridium aquilinum</i>	Heads and Lawton (1985)
Ant, <i>Formica lugubris</i>	Leaf roll	Pyralid moth, caterpillar <i>Omphalocera munroei</i>	<i>Asimina</i> spp.	Damman (1987)
Ants, <i>Formica lemami</i> , <i>Myrmica</i> sp.	Leaf spin, together	Caterpillar, <i>Diurnea fagella</i> (Oecophoridae)	<i>Quercus rubus</i>	Hunter (1987a,b)
Ants, spiders, wasps	Leaf glove	Caterpillar, <i>Herocotogramma aeglealis</i>	Christmas fern, <i>Polystichum acrostichoides</i>	Ruehlmann et al. (1988)
Natural enemies of arthropods (e.g., spider)	Spin together	Geometris, tortricids (Geometridae, Tortricidae)	Bilberry <i>Vaccinium myrtillus</i>	Atlegim (1989)
Predators and parasites	Leaf roll, leaf sandwich	Sawfly (Hymenoptera: Symphyta), caterpillar, <i>Tortrix sinapina</i> , <i>Kawabeia nigricolor</i> , <i>Pyralidae</i> sp.; three species of Gelechiidae; <i>Zenitaphera fulvomixtana</i>	<i>Quercus dentata</i>	Ito and Higashi (1991)
Birds: great tit, <i>Parus major</i> ; hazel hen chicks, <i>Tetrastes bonasia</i> ; pied flycatcher, <i>Ficedula hypoleuca</i>	Ant-proof leaf tunnel	Caterpillar, <i>Stenomoma charitara</i> (Oecophoridae)	<i>Myrmecophytic melastome</i> , <i>Maieta guianensis</i>	Vasconcelos (1991)
Ant, <i>Formica yessensis</i>	Leaf sandwich	Pyralid caterpillar, <i>Acrospila gastralis</i>	Bettula papyrifera	Cappuccino (1993)
Ant, <i>Phoidola minula</i>	Silking together	Birch tube-maker, <i>Acrobasis betuella</i>	Ant-defended acacia, <i>Acacia cornigera</i>	Eubanks et al. (1997)
Ant, <i>Pseudomyrmex ferrugina</i> (Formicidae)	Leaf-tie, roll, fold	Caterpillar <i>Polyhymno</i> sp. (Gelechiidae)	Mulberry, <i>Morus bombycis</i>	Kudo (1994)
Provide molting sites		Stink bug, <i>Elasmucha putoni</i> ^a		

^aSecondary users

Table 2. List of interactions between shelter maker and secondary users mediated by leaf shelters

Shelter maker	Shelter type	Secondary user	Host plant	References
Larvae of spear-marked moth, <i>Rheumaptera hastata</i>	Leaf sandwich	Conspecific individuals of the shelter maker	Paper birch, <i>Betula papyrifera</i>	Werner (1977)
Caterpillar (Gelechiidae, Oecophoridae, Stenomidae)	Leaf tie	Shelter makers (Lepidoptera: Gelechiidae, Oecophoridae, Stenomidae); other species of Oecophoridae; <i>Erymnis juvenalis</i> (Lepidoptera); <i>Salebriaria engeli</i> (Lepidoptera); <i>Nephoteryx</i> (Lepidoptera); Asiatic oak weevil, <i>Cryptostomus castaneus</i> (Coleoptera); caterid (Coleoptera); staphylinid (Coleoptera); chrysomelid (Coleoptera); coccinellid adults, <i>Scymnus rubicaudus</i> ; leafhopper, <i>Aphrodes</i> sp. (Hemiptera: Cicadellidae); aphid (Hemiptera)	Oak, <i>Quercus</i> spp.	Carroll and Kearby (1978)
Caterpillar	Leaf roll	Grasshopper, <i>Melanolpus differentialis</i> (Orthoptera: Acrididae)	Sunflower, <i>Helianthus annuus</i>	Lewis (1979)
<i>Psilocoris reflexella</i> (Lepidoptera; 1st generation)	Leaf tie	Second generation, conspecific species	Oak, <i>Quercus</i> spp.	Carroll et al. (1979)
<i>Psilocoris quercicella</i> (Lepidoptera; 1st generation)	Leaf tie	Second generation conspecific species		
<i>Psilocoris reflexella</i> (2nd generation)	Leaf tie	<i>Antaeotricha schlaegeri</i> (Lepidoptera: Stenomidae)		
<i>Psilocoris quercicella</i> (1st and 2nd generation)	Leaf tie	<i>Psilocoris cryptotelechiella</i> (2nd generation), <i>Chionodes</i> sp.; (Lepidoptera: Gelechiidae), <i>Arogalea cristifasciella</i> (Gelechiidae)		
<i>Psilocoris reflexella</i> , <i>Psilocoris quercicella</i> , <i>Psilocoris cryptotelechiella</i>	Leaf tie	<i>Chionodes macimarginella</i> (Gelechiidae); <i>Chionodes fuscomacilla</i> (Gelechiidae); <i>Telphusa latifaciella</i> (Lepidoptera); <i>Antaeotricha humilis</i> (Stenomidae); <i>A. osseella</i> ; <i>Setiosoma xanthobasis</i>		
Caterpillar	Leaf tie	<i>Teratophia aspertella</i> (Lepidoptera: Pyralidae); <i>Salebriaria engeli</i> ; <i>Nephoteryx subcaesilla</i>		
Spider or caterpillar	Leaves spun together	Aphid, <i>Callipterinella calliptera</i>	Birch, <i>Betula pendula</i>	Hajek and Dahlsten (1986)
<i>Eriosoma japonicum</i> (Hemiptera: Pemphigidae)	Leaf roll gall	Conspecific species, <i>Eriosoma auratum</i> , <i>E. yangi</i>	Japanese elm, <i>Ulmus davidiana</i>	Akimoto (1981, & 1988)
<i>Eriosoma auratum</i>	Leaf roll gall	Conspecific species, <i>Eriosoma japonicum</i> , <i>E. yangi</i>		
<i>Eriosoma harunire</i>	Leaf roll gall	<i>Eriosoma japonicum</i> , <i>E. auratum</i> , <i>E. yangi</i>		
<i>Acrobasis betulella</i> (Lepidoptera)	Leaf sandwich	Second generation of the shelter maker, Tenthredinae (Hymenoptera), spider	Paper birch, <i>Betula papyrifera</i>	Cappuccino (1993)

Artificial shelter	Leaf sandwich	<i>Acrobasis betuella</i> (Lepidoptera: Pyralidae); <i>Psilocorsis reflexella</i> (Lepidoptera: Oecophoridae); <i>Psilocorsis quercicella</i> (Oecophoridae); <i>Coleopteritechnites</i> spp. (Lepidoptera: Gelechiidae); <i>Teletodes</i> sp. (Gelechiidae); <i>Pseudotelphusa belangerella</i> (Gelechiidae); <i>Antaeotricha schlaegeri</i> (Lepidoptera: Stenomitidae); <i>Caloptila betulivora</i> (Lepidoptera: Gracillamidae); <i>Rheumaptera hastata</i> (Geometridae); Tenthredinae (Hymenoptera)	Mulberry <i>Morus bombycis</i>	Kudo (1994)
<i>Olwthreutes morivorum</i> (Lepidoptera: Tortricidae)	leafroll, leaf tie, leaf fold	Stinkbug, <i>Elasmucha putoni</i> (Hemiptera: Acanthosomatidae)		
<i>Pseudasphondylia neoliseae</i> (Diptera: Cecidomyiinae)	Leaf gall	<i>Lasioptera yadokariae</i> (Diptera: Cecidomyiinae)	<i>Neolisea sericea</i> (Lauraceae)	Yukawa and Hattusuka (1994)
<i>Daphnephila machilicola</i> (Diptera: Cecidomyiinae)	Leaf gall	<i>Lasioptera yadokariae</i> (Diptera: Cecidomyiinae)	<i>Machilus japonica</i> (Lauraceae)	
<i>Masakimya pustula</i> (Diptera: Cecidomyiinae)	Leaf gall	<i>Lasioptera yadokariae</i> (Diptera: Cecidomyiinae)	<i>Euonymus japonicus</i> (Celastraceae)	
<i>Pemphigus betae</i> (Hemiptera)	Aphid-leaf-gall	Seven orders of arthropods, free-feeding aphid (Hemiptera: Aphididae)	Hybrid cottonwoods, <i>Populus angustifolia</i> × <i>P. fremontii</i>	Dickson and Whitham (1996)
Artificial shelter and <i>Dasineura marginetorquens</i> (Diptera: Cecidomyiinae)	Leaf roll	Leaf beetle, <i>Galerucella lineola</i> (Coleoptera: Chrysomelidae)	Willow, <i>Salix viminalis</i>	Larsson et al. (1997)
<i>Anacamptis niveopulvella</i>	Leaf roll	Trombiculidae sp. (Acarina); Araneidae 4 spp.; Salticidae 3 spp. (Araneae); Forficulidae 1 sp. (Dermaptera); <i>Apateticus</i> sp. (Hemiptera: Pentatomidae); <i>Anthocoris</i> sp. (Hemiptera: Anthocoridae); Miridae 1 sp. (Hemiptera); Cicadellinae 2 spp.; Idiocerinae sp.; Cixiidae, sp.; Chaitophorinae sp.; Diaspididae sp. (Hemiptera); <i>Chaitophorus populocola</i> (Hemiptera: Aphididae); <i>Chrysopa</i> sp. (Neuroptera: Chrysopidae); <i>Adalia bipunctata</i> ; Otiorthynchinae sp. (Coleoptera: Curculionidae); Tortricidae sp. (Lepidoptera); <i>Alsophila pomataria</i> (Lepidoptera: Geometridae); Dolichoderinae sp.; <i>Formica propinqua</i> (Hymenoptera: Formicidae)	Hybrid cottonwoods, <i>Populus angustifolia</i> × <i>Populus fremontii</i>	Martinsen et al. (2000)
Aphid, <i>Sorbaphis chaertosiophon</i> (Hemiptera)	Leaf-rolling gall	Ant, lady beetle, caterpillar, Diptera, earwig, aphid, weevil, <i>Orchestes</i> sp.	Mountain ash, <i>Sorbus commixta</i>	Fukui (unpublished)
Caterpillar	Leaf roll	Aphid, <i>Chaitophorus salmiger</i> , earwig, spider, stinkbug, weevil	willow, <i>Salix miyabeana</i>	Nakamura (unpublished)
Caterpillar, <i>Homonopsis fodenratana</i>	Leaf roll	Ant, caterpillar, Diptera, earwig, aphid <i>Acyrtosiphon syringae</i> , spider, stinkbug, weevil, snail, Collembola	Japanese lilac, <i>Syringa reticulata</i>	Fukui (unpublished)

Additionally when shelter makers are aphids, aphid-attending ants may often accompany them (Fukui, unpublished).

Secondary users inhabit a leaf shelter after it has been utilized by a shelter maker. Some secondary users spend most of their larval stages in leaf shelters (Table 2: caterpillars, grasshopper, leaf beetles, and weevils), and others stay temporarily in leaf shelters (Table 2: adult moths, earwigs, spiders, stinkbugs, and insects during molting). Furthermore, secondary users of leaf shelters are divided into potential shelter makers and free-living species that do not construct their own shelters (Table 2).

Potential shelter makers are organisms that use a shelter made by other species, even though they can make their own shelters. Potential shelter makers may be conspecific or heterospecific to the shelter makers. The first category includes late-generation caterpillars that use leaf shelters made by the first generation of their own species (Carroll and Kearby 1978; Carroll et al. 1979; Cappuccino 1993; Cappuccino and Martin 1994). The second category is represented by caterpillars and spiders (see Table 2). Fully expanded mature leaves are tougher than young leaves (Feeny 1970; Schultz et al. 1982; Coley et al. 1985). Because tougher leaves should obligate shelter makers to spend more energy and time in making a shelter, the cost of making a shelter may be higher for larvae late in the season than for larvae early in the season. Thus, if larvae have a chance to occupy a shelter without the cost of making it, larvae late in the season would elect to use an existing leaf shelter secondarily.

Free-living species of secondary users include a wide range of taxa including Coleoptera, Dermaptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Orthoptera, spiders, and terrestrial isopods (Table 2). Some of them are herbivorous (caterpillars, grasshopper, herbivorous stinkbugs, leaf beetles, and weevils) and others are predaceous (larvae of predaceous flower flies, earwigs, lacewings, predaceous stinkbugs, spiders, and staphylinids).

Interactions between shelter makers and users

Most interactions between shelter makers and coexisting organisms are direct trophic linkages rather than indirect ones mediated by shelters. If shelters are made by the cooperation of several conspecific individuals, each individual may benefit from reduced costs of making a shelter (arrows A1 and A2 in Fig. 1). Some of them, however, might be cheaters that do not cooperate in a shelter construction (arrows A1 and A3 in Fig. 1). Akimoto (1981) demonstrated that *Eriosoma yangi parasiticum*, which does not make its own gall, is actually a parasite of galls made by other *Eriosoma* species. *Eriosoma yangi parasiticum* are sometimes observed to kill the gall-maker. Taking over galls by a different species suggests that galls can be used physiologically by a species allied to the shelter maker. Conspecific individuals can more easily become shelter parasites because their demands are in common with those of the shelter maker.

The secondary users interact with a shelter maker via a leaf shelter because they are temporally separated. There are asymmetrical positive effects from a shelter maker to secondary users (arrow B in Fig. 1). The neonate larvae of the leaf beetle *Galerucella lineola* inhabit and grow up in an artificially rolled shelter or a leaf-gall made by the cecidomyiid *Dasineura marginemtorquens* to escape from desiccation (Larsson et al. 1997). Leaf-rolls made by caterpillars reduced leaf toughness and provided food more easily consumed by grasshoppers (Lewis 1979). Kudo (1994) reported that the nymphs and newly molted adults of the acanthosomatid bug *Elasmucha putoni* are found more often in leaf shelters than on leaves, suggesting that this behavior might protect molting bugs from predators and adverse weather conditions.

The indirect interaction among secondary users mediated by leaf shelters deserves to be mentioned (arrows C in

Fig. 1. Interactions among organisms mediated by leaf shelters. Note that the interactions are not always positive. Though shelter makers give positive effects on the coexisting organisms A1, other effects are sometime negative A2, A3. There are asymmetrical positive effects from shelter makers to secondary users that include both predacious and herbivorous organisms B. The interactions among secondary users are competitive C1 or predatory C2. The leaf shelters could control herbivory on a host plant. If the secondary user is predacious, herbivory may increase D. If the secondary user is herbivorous, herbivory may decrease due to increased predation pressure on the herbivore E

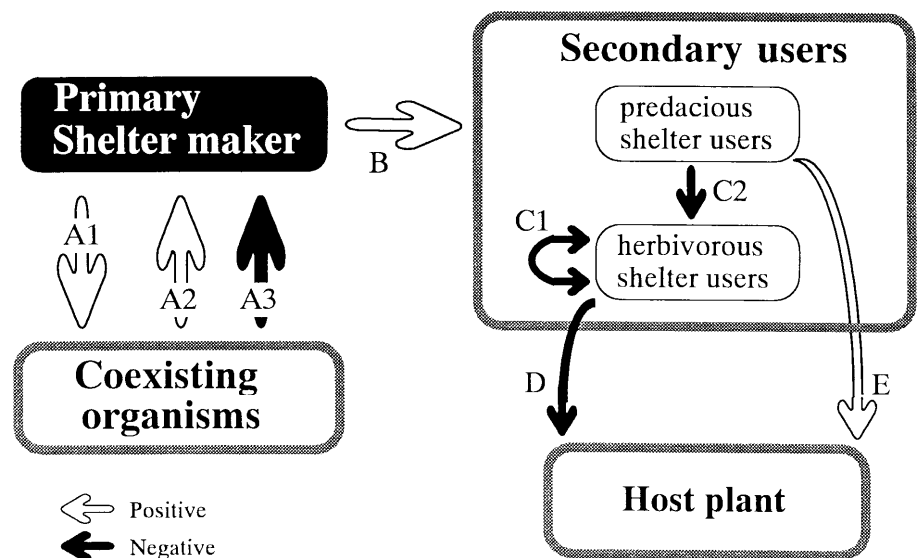


Fig. 1). A leaf shelter sometimes contains more than one species or several individuals (Werner 1977; Carroll and Kearby 1978; Carroll et al. 1979; Cappuccino 1993). It is unclear whether the interaction among them is mutually beneficial. Cappuccino (1993) suggested that disadvantages are involved in the cohabitation of leaf shelters. Changes in leaf quality with the accumulation of damage and frass may lead to a decline in the developmental rate of the shelter occupants (arrow C1 in Fig. 1). A leaf shelter may mediate predation because both herbivores and their predators are secondary users of a leaf shelter on the same host plant (see Table 2). There is evidence that some arthropod predators (spiders, staphylinids, clerid larvae, and lacewings) and parasitoids attack insect herbivores within leaf shelters (arrow C2 in Fig. 1) (Carroll and Kearby 1978; McNeil et al. 1978; Danthanarayana 1983).

The modified distributions of herbivory

Distributions of some herbivores on a plant reflect their microclimatic requirements and difference in the quality of host tissues (Casey 1976; Willmer 1980; Hunter and Willmer 1989; Cappuccino 1993; Larsson et al. 1997). The distribution of the shelter-making caterpillar *Omphalocera munroei* depends on the distribution of microhabitats suitable for making leaf ties, regardless of nutritional levels (Damman 1987).

Several species of insects disperse to seek shelter sites (Willmer 1980; Akimoto 1981; Hajek and Dahlsten 1986; Damman 1987; Larsson et al. 1997). Neonate larvae of *Galerucella lineola* move up along the shoot and initiate feeding in rolled young leaves, which are naturally located only at the top of *Salix viminalis* (Larsson et al. 1997). When larvae found rolled artificial shelters close to their hatching site, they accepted mature leaves for feeding and stopped moving to the top of shoots. This is another example in

which the preference for habitats depends on leaf structure rather than nutritional value.

The presence of a leaf shelter may promote oviposition of occupant species (Cappuccino 1993). However, plant quality in shelters may be responsible for the attraction to females, instead of a female response to the shelter itself. To test this hypothesis, Cappuccino (1993) constructed artificial shelters randomly on a paper birch. Females of *Acrobasis betulella* responded not to leaf quality but to the presence of leaf shelters that protect their larvae from natural enemies. Thus, the distributions of leaf shelters affect distributions of secondary users, resulting in the modified distribution of the latter (Fig. 2).

Leaf shelters mediate feedback effects involving shelter occupants and host plants. When a leaf shelter protects herbivorous secondary users, shelters may increase herbivory of plant tissue (arrows B and D in Fig. 1). The presence of predaceous organisms sometimes controls herbivory on host plants (Atlegrim 1989; Gastreich 1999; Ruhren and Handel 1999). In contrast, when a leaf shelter protects predaceous secondary users, shelters may decrease herbivory (arrows B and E in Fig. 1). Thus, the leaf shelter might indirectly increase or decrease total damage by herbivory on the host plants through increased preference of shelter users (Fig. 2). Furthermore, such feedback effects may enhance the heterogeneity of herbivory within a plant owing to uneven distribution of shelters.

Tritrophic level interaction

It is necessary to discern trophic interactions mediated by leaf shelters. Induced chemical compounds and the structural damage by herbivory act as cues for natural enemies searching for prey (Hassell 1968; Greenberg and Gradwohl 1980; Odell and Godwin 1984; Roland et al. 1986; Faeth

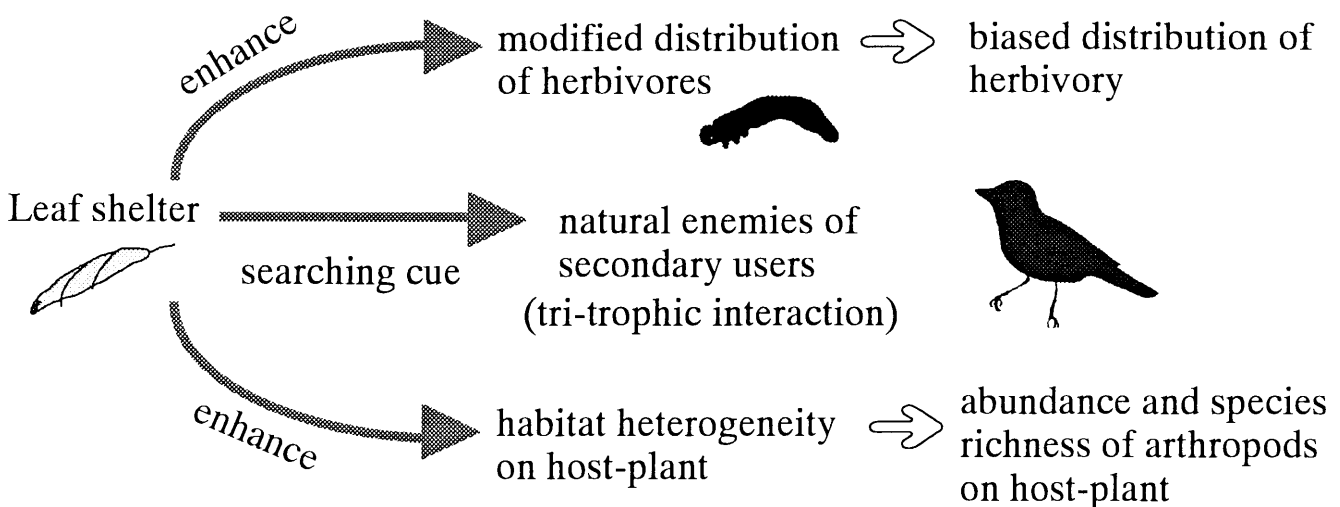


Fig. 2. Three pathways mediated by leaf shelters. Leaf shelters have effects on a) the modified distributions of herbivory, b) tri-trophic interaction, and c) abundance and species richness on a host-plant

1990). Thus, leaf shelters act as mediator of tritrophic interactions.

Structures on the leaf surface also act as the mediator of tritrophic interactions. Tufts of hairs and other minute structures in the vein axils are called leaf domatia. A leaf domatia is a kind of leaf shelter that is provided by the plant for mites. Predaceous mites benefit from leaf domatia by securing a safe place for oviposition and molting (Walter and Dennis 1992; Walter 1996). Plants benefit from having leaf domatia because predatory mites could inhabit them before attack by plant parasites (herbivorous mites).

Do leaf shelters mediate tritrophic interactions among host plants, shelter occupants, and their natural enemies? Although leaf shelters protect caterpillars from birds, some birds can learn that leaf-rolls contain larvae, thus using them as cues for searching larvae. Birds that have learned search for rolled leaves, open them, and feed on the occupants (Heinrich and Collins 1983; Greenberg 1987; Murakami 1999). Therefore, the changed structure of the plant by shelter makers mediates mutualistic interactions between host plant and natural enemies (see Fig. 2). In addition, attracting natural enemies might increase predation pressures on free-living herbivores, thus controlling plant damage by herbivory.

Abundance and species richness on host plant

In general, greater habitat heterogeneity supports greater species richness (Moran and Hamilton 1980; Lawton 1983; Dennis et al. 1998; Bell et al. 1991). Leaf shelters provide new physical architecture that increase habitat diversity (heterogeneity) in the ecosystem. There is evidence that leaf shelters have clearly positive effects on arthropod diversity (see Fig. 2) (Cappuccino and Martin 1994; Waltz and Whitham 1997; Martinsen et al. 2000; Fukui, unpublished). On mountain ash (*Sorbus commixta*), some species of weevils (*Orchestes* sp.) were found within an aphid leaf-gall but they were never found outside the gall (Fukui, unpublished). Removal of galls of the aphid *Pemphigus betae* on hybrid cottonwoods decreased richness and relative abundance of species because the aphid galls provided shelters for other species (Waltz and Whitham 1997). When shoots of hybrid cottonwoods have leaf rolls made by larvae of *Anacamptis niveopulvella*, the species richness and species abundance of associated herbivores were four and seven times, respectively, as high as those on adjacent shoots without leaf rolls (Martinsen et al. 2000). On paper birch, removal of early season shelter makers, *Acrobasis betulella*, reduced the abundance of species appearing later in the season, and this indirect effect remained in the following year (Cappuccino and Martin 1994).

Conclusions

Leaf shelters increase the diversity of interactions in an animal-plant community. A shelter maker usually produces

positive effects on secondary users. However, a leaf shelter sometimes mediates negative indirect interactions. Shelter users sometimes act as a shelter parasite when they coexist in a shelter and there is no alternative shelter. Leaf shelters sometimes promote the activities of predators when the leaf shelter includes predaceous secondary users or when natural enemies use the leaf shelter as a searching cue. Furthermore, shelter makers influence the distribution of herbivores and the degree of herbivory on a plant. Thus, current evidence shows that leaf shelters act as an important mediator of indirect interactions. More attention should be paid to leaf shelters and shelter makers acting as physical ecosystem engineers.

Recently, experiments have become part of the standard protocol in field studies, including removal or additions of some major natural factors artificially (Connell 1983; Shi et al. 1985; Wootton 1994). Previous studies have indicated the effectiveness of artificial leaf shelters to evaluate the effects of leaf shelters as physical structure resources (Cappuccino 1993; Larsson et al. 1997). Manipulation could help us to know the impact of the leaf shelters as physical structure resources on animal-plant communities (Cappuccino and Martin 1994; Dickson and Whitham 1996; Waltz and Whitham 1997; Martinsen et al. 2000).

Acknowledgments I am grateful to N. Ohsaki for inviting me to the symposium of the Society of Population Ecology held in Shiga. I thank S. Larsson, T. Ohgushi, and M. Yasuda for valuable comments on an earlier draft of this paper. Financial support was provided by the Japanese Ministry of Education, Science, Sports, and Culture Grant-in-Aid for Creative Basic Research (#09NP1501).

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