

Chapter 9

Arthropod Community



Junichi Yukawa

Abstract The arthropod community centered upon gall midges and their host plants including various additional organisms that rely on the existence of galls is treated in this chapter. First, a new food web connecting two communities centered upon *Pseudasphondylia neolitseae* on *Neolitsea sericea* and *Daphnephila machilicola* on *Machilus thunbergii* is demonstrated. Effects of predators and herbivores on the community members are explained. In particular, direct and indirect effects of a stem borer, *Oberea hebescens*, on *N. sericea* and its associated insects are highlighted. Parasitoids are excluded from the explanation because they are mentioned in Chap. 11. Then, examples of inquiline, successor, and cecidophagy are reviewed. Cynipid inquilines are briefly introduced for comparison with cecidomyiid inquilines. Detailed explanation is given for ecological traits of a successor, *Lasioptera yadokariae*, based on a long-term field survey. The last section elaborates on various types of cecidophagy including gall-sucking behavior.

Keywords Food web · Community · Predator · Herbivore · Inquiline · Successor · Cecidophagy

9.1 Food Web

9.1.1 Introduction

Galls provide extremely favorable breeding conditions to a great variety of organism with its localized concentration of highly nutritive substances and its marked succulence (Mani 1964). The arthropod community centered upon gall midges and their host plants includes various additional organisms that rely on the existence of galls, such as inquilines, successors, and cecidophagous species, hence it is much

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more complex than common communities of external herbivores and their host plants. Interactions among tritrophic levels have been studied from various aspects, such as population ecology, chemical ecology, biological control, etc. (e.g. Price et al. 1980; Price 1986; Turlings and Erb 2018). Thus, the survey of arthropod community is fundamentally necessary for better understanding the inter-relations of these diverse organisms and for promoting further studies of the gall-inducing arthropods and their associated inhabitants (Yukawa 1983). In addition, we need to note that community ecology has been facilitating studies of a geographic mosaic of coevolution among members belonging to tritrophic levels (e.g. Craig et al. 2020; see Sect. 2.2).

9.1.2 A Food Web Consisting of Two Jointed Arthropod Communities

Previously Yukawa (1983) demonstrated a food web of the arthropod community centered upon *Pseudasphondylia neolitseae* Yukawa on *Neolitsea sericea* (Blume) Koidzumi. In this chapter, a new food web is provided in Fig. 9.1 by joining another community centered upon *Daphnephila machilicola* Yukawa on *Machilus thunbergii* Siebold & Zuccarini to the previous one. These two communities are associated with lauraceous host plants and co-existing in the same evergreen broad-leaved forest in southern Kyushu, Japan. Some minor members of the communities are excluded from the food web because their densities are very low, or they do not

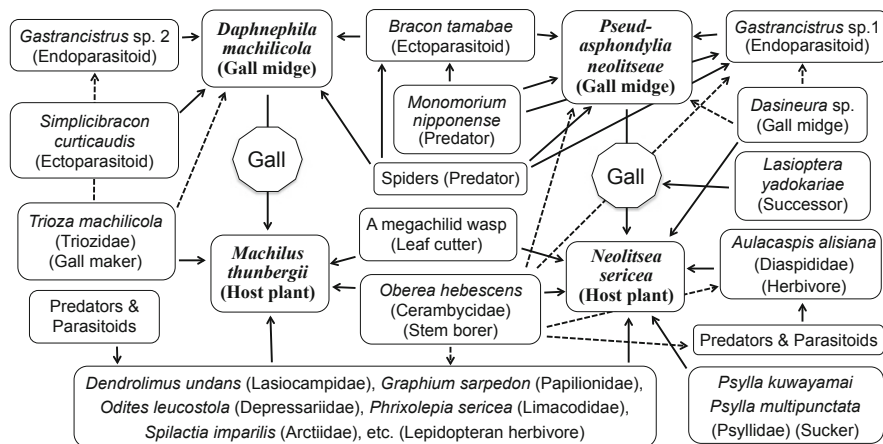


Fig. 9.1 A food web of two jointed arthropod communities centered upon *Pseudasphondylia neolitseae* on *Neolitsea sericea* and *Daphnephila machilicola* on *Machilus thunbergii*. The two communities are associated with lauraceous host plants and co-existing in the same evergreen broad-leaved forest in southern Kyushu, Japan. Allows point toward food resources. Dashed lines indicate indirect effects on organisms pointed

always appear in the communities. Naturally, the new food web becomes more complex than the web of single community, and some community members are related to both communities.

9.1.3 Parasitoids and Predators

Among parasitoids, the two species of *Gastrancistrus* (Pteromalidae) (endoparasitic early attacker) (Fig. 9.2c) are naturally monophagous, while *Bracon tamabae* Maeto (Braconidae) (ectoparasitic late attacker) (Fig. 9.2d) attacks both *P. neolitseae* and *D. machilicola* (Maetô 1991) (see Chapter 11 for details of the parasitoids). No further information on host range is available as to *Simplicibracon curticaudis* Maetô (Braconidae).

In March and April, workers of the ant, *Monomorium intrudens* Smith (= *nipponense*) (Formicidae) were observed to remove mature larvae and pupae of *P. neolitseae* and its parasitoids from the galls by opening the operculum on the hypophyllous surface of the galls (Yukawa 1983). Evidences of the predation were observed almost every year on a few restricted host trees, where the local gall midge populations were largely and concentratedly destroyed.

The ant can easily open the operculum because the mature larva prepares an exit before pupation by making layers beneath the exit very thin. Pupae push open the operculum with their apical spines and stretch themselves halfway out of galls for emergence (Yukawa et al. 1976). In contrast, such predation by ants has never been observed until today for the galls of *D. machilicola* on *M. thunbergii* possibly because the larval cavity is plugged with a thick subglobular lid, which falls off when adult emerges (Yukawa 1974).

At least 11 species of spiders were observed to feed on adults of *P. neolitseae* at the time of emergence or of oviposition (Yukawa 1983). Under the high population density of *P. neolitseae*, heavily galled leaves of *N. sericea* increase and are frequently folded outward, providing favorable webbing conditions to the spiders. The adults of *P. neolitseae* are not only killed by direct predation but also caught in the webs and then attacked by the spiders.

Unlike the leaves of *N. sericea*, those of *M. thunbergii* are thick and tough, and heavily galled leaves are not folded outward but rather inward. In addition, the barrel-shaped galls on the lower leaf surface are about 7 mm tall. Thus, the galled leaves of *M. thunbergii* do not provide favorable conditions to the spiders for webbing between or over the galls, resulted in the low mortality of *D. machilicola* at the time of emergence.

The spiders are sometimes observed to catch females of *P. neolitseae* or *D. machilicola* after their arrival at newly extending host buds for oviposition. Even if the spiders fail to catch the females, their oviposition action is disturbed and they must fly off the host buds to find the others, which occasionally promotes mistaken oviposition (see Sect. 2.1).

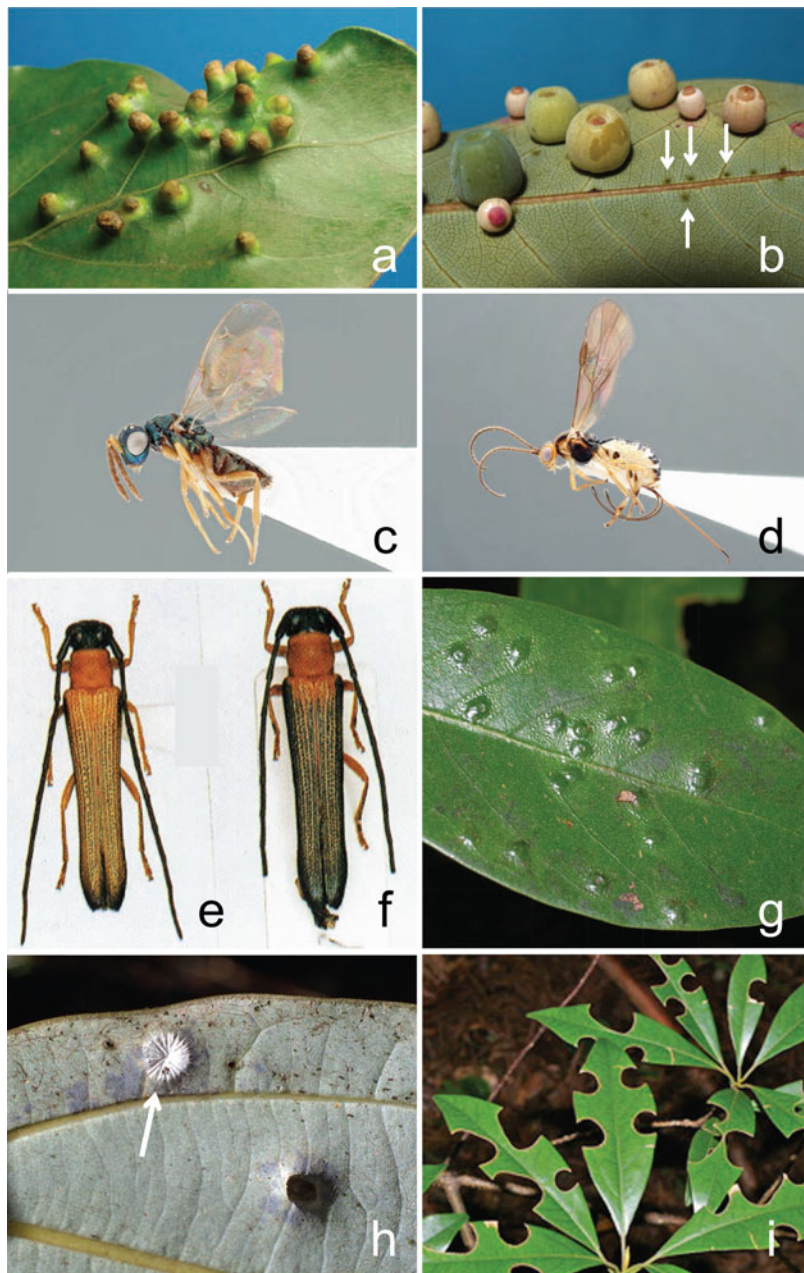


Fig. 9.2 Galls and some of community members in the food web shown in Fig. 9.1. (a), leaf galls induced by *Pseudasphondylia neolitseae* on *Neolitsea sericea*; (b), leaf galls induced by *Daphnephila machilicola* on *Machilus thunbergii* (arrows point toward scars made by the larvae that hatched and sank into the leaf tissue but did not induce galls in the first year, postponed to the second year due to long-term diapause: see Sect. 6.3); (c), *Gastrancistrus* sp. 1; (d), *Bracon tamabae*; (e), *Oberea hebescens* ♂; (f), *ibid.* ♀; (g), pit galls induced by *Trioza machilicola* on a leaf of *Machilus thunbergii*; (h), leaf galls induced by *P. neolitseae* on *N. sericea* (showing lower

9.1.4 A Longicorn Beetle, *Oberea hebescens*

Oberea hebescens Bates (Coleoptera: Cerambycidae) (Fig. 9.2e, f) is a stem borer of trees of Lauraceae, such as *N. sericea*, *Cinnamomum tenuifolium* (Makino) Sugimoto ex Hara and *Lindera praecox* (Siebold & Zuccarini) Blume (Ohbayashi and Niisato 2007). In May, females of *O. hebescens* lay their eggs one by one in the distal portion of newly extended shoots. Through mid-May to October, hatched larvae bore tunnels downward in the shoot toward the basal end of current twig and subsequently toward the 1-year old twigs. Current leaves attached to the infested shoot dry out because of the original infestation. When the cerambycid larvae reach the 1-year old twig, leaves attached to non-oviposited current shoots extending from the same 1-year old shoot dry out (Yukawa 1977). At the same time, galls on the current leaves of *N. sericea* dry out and the larvae of *P. neolitseae* and *Gastrancistrus* sp. (Pteromalidae) inhabiting the galls die (Yukawa and Akimoto 2006). Herbivores feeding on these leaves also lose their food resources.

Larvae of the cerambycid have never been observed boring the shoots and twigs of *M. thunbergii* that grows nearby *N. sericea*. The main shoot of *M. thunbergii*, as well as *Machilus japonica* Siebold & Zuccarini ex Blume, is quite short and the side shoots are not thick enough for the cerambycid larvae to bore (Yukawa et al. 2018). Adults of *O. hebescens* feed on the midribs of lauraceous plants, but this infestation was negligible in contrast to the prominent damage of shoots and twigs by larvae.

9.1.5 Herbivores

There are various species of herbivores associated with *N. sericea* or *M. thunbergii*. A few of them are monophagous, some are oligophagous on Lauraceae, and the others are polyphagous. Some of them feed on galls facultatively or rarely obligatorily. Cecidophagy will be mentioned in Sect. 9.4.

Dasineura sp. (Cecidomyiidae) is a monophagous and univoltine species. According to Yukawa (1983), in April, the females lay their eggs inside the leaf buds, which remain closed and wither gradually. Later, the leaf buds containing the mature larvae fall to the ground, where they spend summer, autumn and winter. At the same time, the eggs or the first instars of *P. neolitseae*, if any, are killed by the fall and the successive decay of the infested leaf buds.

Auracaspis alisiana Takagi (Hemiptera: Diaspididae) is an invasive pest, being host-specific to *N. sericea*, and has three overlapped generations in Fukuoka, Japan. The nymphs settle on the lower surface of *N. sericea* leaves, but they do not attack

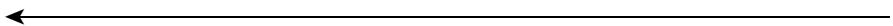


Fig. 9.2 (continued) surface of the leaf, arrows point towards vacated galls plugged with fungal mycelium in which a larva of successor *Lasioptera yadokariae* lives); (i), scars of *Machilus thunbergii* leaves cut by an unidentified megachilid wasp

newly emerged leaves although they generally prefer younger leaves (Mediga and Takasu 2018). Therefore, the larvae of *P. neolitseae* in the galls on the current leaves would not suffer bad influence by the scale insect.

Two species of Psyllidae (Heteroptera), *Psylla kuwayamaii* (Grawford) and *Psylla multipunctata* Miyatake are frequently found on the current leaves of *N. sericea*. They do not induce galls, but cause fading on the affected parts by sucking, resulted in yellowish flecks on the leaves. There is, however, no evidence that the galls or the gall midge larvae are ill influences by the psyllids on such leaves (Yukawa 1983). *Trioza machilicola* Miyatake (Trioziidae) is oligophagous and univoltine, and many nymphs settle on the lower surface of current leaves of *M. thunbergii* or *M. japonica* (Fig. 9.2g) (Yukawa and Masuda 1996). They induce as many as 500 pit-hole galls on upper surface of the leaves. No barrel-shaped galls of *D. machilicola* can appear on the lower surface of current leaves under such highly dense conditions of the psyllid galls.

Several herbivorous species of Lepidoptera can be seen occasionally on the leaves of lauraceous plants including *N. sericea* and *M. thunbergii* (Fig. 9.1). Since all these species are oligo- or polyphagous species, they are not tightly associated with *N. sericea* and *M. thunbergii*. In addition, larvae of most herbivorous species, such as *Graphium sarpedon* Linnaeus (Papilionidae), avoid galled parts when they feed on the host leaf blade. Therefore, these herbivores do not cause damages to both the host trees and the gall midge populations.

Adults of an unidentified megachilid (Hymenoptera) sometimes cut off a part of *N. sericea* leaves in summer (Fig. 9.2i), but they always avoid collecting the galled portion of the leaves.

Each of these herbivorous species is attacked by a wide variety of parasitoids or predators, hence the number of community members increase accordingly. Of course, every member cannot play the lead in community ecology. However, unlike the study of population dynamics, multiple members should be regarded as leading characters in the study of “community dynamics” to clarify long-term interrelations between members of the community.

9.2 Inquiline

9.2.1 Introduction

An inquiline is an animal that lives commensally in the nest, gall, burrow, or dwelling place of an animal of another species. Unlike parasitoids or predators, inquilines do not have a deleterious effect on the host species. Among insects, the most commonly known inquilines are found in the nests of social insects, especially ants and termites. Arthropods other than ants and termites inhabit their nest are called myrmecophiles and termitophiles, respectively.

Inquilines inhabiting arthropod galls are known among cecidomyiids (e.g. Yukawa and Rohfritsch 2005), cynipids (Askew 1984; Ronquist 1994), aphids

(Akimoto 1988; Miller and Crespi 2003), thrips (Raman and Ananthkrishnan 1984), tanaostigmatids (LaSalle 1997), and psyllids (Yang et al. 2001). Among them, both cecidomyiids and cynipids are distinctly abundant in the Holarctic Region, while Maia et al. (2014) reported that cecidomyiids are the most frequent gall-inhabiting inquilines in the Brazilian coastal vegetation.

Gall-inhabiting inquilines are treated in this section separated from other arthropods associated with gall inducers because they are important members constituting arthropod communities centered upon gall-inducing species and their host plants.

9.2.2 *Cynipid Inquilines*

The family Cynipidae includes about 1400 species belonging to 12 tribes (Ronquist et al. 2015), many of which are gall-inducing herbivores (e.g. Stone et al. 2002; Abe et al. 2007). Most cynipid inquilines belong to Synergini, which comprise about 180 species of seven genera including *Synergus* (Ide et al. 2018). *Synergus* is the most species-rich genus including at least 110 species in the world (Schwéger et al. 2015). Cynipid inquilines usually live in cynipid galls, but rarely in galls of other arthropods. For example, *Synergus yukawai* (Wachi et al. 2011) inhabits cecidomyiid stem galls on *Quercus acutissima* Blume (Fagaceae) (Wachi et al. 2011) and *Rhoophilus loewi* Mayr is an inquiline in galls induced by species of *Cecidoses* and *Eucecidoses* (Lepidoptera: Cecidosidae) on *Searsia* (previously identified as *Rhus*) and *Schinus* species (Anacardiaceae) (Van Noort et al. 2007).

Until recently, all species of Synergini were thought to be inquilines and not to be able to initiate gall formation although they can modify the galls of other species. However, Abe et al. (2011) showed that *Synergus itoensis* Abe, Ide & Wachi induces galls by itself inside the acorns of *Quercus glauca* Thunberg (Fagaceae). Then, Abe et al. (2011) speculated that an ability of gall induction might have evolved within Synergini. Subsequently, *Saphonecrus hupingshanensis* Liu, Yang & Zhu and *Synergus castaneus* Pujade-Villar, Bernardo & Viggiani were reported as possible gall inducers in Synergini (Liu et al. 2012; Bernardo et al. 2013). Based on a comprehensive phylogenetic analysis of Synergini, Ide et al. (2018) concluded that *S. itoensis* together with its two unidentified congeners evolved from inquilines and recently acquired their ability to induce galls independently from other cynipid gall inducers. If the two species mentioned by Liu et al. (2012) and Bernardo et al. (2013) are gall inducers, gall-inducing ability is considered to have evolved from inquilines independently at least three times in Synergini (Ide et al. 2018).

9.2.3 *Tanaostigmatid Inquilines Inhabiting Cecidomyiid Galls*

Tanaostigmatidae are predominantly phytophagous. According to LaSalle (1997), they are mainly associated with galls on fabaceous plants and, in general, have been presumed to be the gall formers although detailed biological information is very few for members. Many records of tanaostigmatids as gall-formers are undoubtedly correct, but inquilinism may be more common than previously suspected.

Protanaostigma kyushuana Masi (Hymenoptera: Tanaostigmatidae) was described, without any biological information, based on a single female collected in 1938 from Kyushu, Japan (Masi 1940). Later, Kamiyo (2000) confirmed that it is an inquiline wasp inhabiting lenticular cecidomyiid galls on the leaves of *Pueraria lobata* (Willdenow) Ohwi (Fabaceae) (Fig. 2.10a, b). Thereafter, Yukawa et al. (2012) described a new species *Ptydiplosis puerariae* Yukawa, Ikenaga & Sato that is responsible for the lenticular leaf galls on *P. lobata* and *Pueraria montana* (Loureiro) Merrill in Japan, mainland China, Taiwan, and South Korea. Until today, many larvae, pupae and adults of the inquiline species have been obtained both from the galls of *P. puerariae* and from subglobular galls induced by an unidentified gall midge species on the under-leaf surface of *P. lobata* and *P. montana*. Therefore, redescription and an exact identification of *P. kyushuana* are needed based on these specimens in addition to the single female type specimen.

Tanaostigmodes puerariae Yang & Pitts (Hymenoptera: Tanaostigmatidae) was described from mainland China as an inducer of the lenticular gall on *Pueraria* (Yang et al. 2004). However, Yukawa et al. (2012) pointed out that it is apparently not a gall-inducing species but an inquiline wasp inhabiting the cecidomyiid galls.

From Brazil, Fernandes et al. (1987) reported one inquiline species in a gall of *Anadiplosis* sp. on *Machaerium aculeatum* Raddi (Fabaceae). LaSalle (1987) subsequently described this species as *Tanaostigmodes ferbandesi* LaSalle (Hymenoptera: Tanaostigmatidae). The galls containing the inquiline were larger than normal cecidomyiid galls, and gall shape was different between them. Because the cecidomyiid larvae were never found in the galls inhabited by *T. ferbandesi*, they were possibly killed and/or consumed by the inquiline larvae. This information suggests that the same thing may also happen in *P. puerariae* galls inhabited by inquilines, *P. kyushuana* and *T. puerariae*.

9.2.4 *Cecidomyiid Inquilines*

According to Gagné and Jaschhof (2017), at least 110 species of Cecidomyiinae have been regarded as inquilines or possibly inquilines inhabiting galls induced by other cecidomyiid species. (Table 9.1). They are known from three genera of Cecidomyiidi and four of Lasiopteridi. This means that the inquiline habit has evolved more than once in the subfamily Cecidomyiinae.

Table 9.1 The number of cecidomyiid inquiline species, their supertribal position, distribution and host cecidomyiids (picked up from Gagné and Jaschhof 2017, based on a key word “inquiline”)

Supertribe	Genus of inquilines	Distribution and the number of species	Larval habit	Host cecidomyiids
Cecidomyiidi	<i>Anabremia</i>	Palaearctic; 6 spp.	All inquilines or possibly inquilines	<i>Dasineura</i> spp. on Fabaceae
Cecidomyiidi	<i>Tricholaba</i>	Palaearctic; 5 spp.	Inquilines or possibly inquilines	<i>Dasineura</i> spp. on Fabaceae
Cecidomyiidi	<i>Youngomyia</i>	Nearctic, neotropical, oriental; 6 spp.	Inquilines or possibly predaceous	Other cecidomyiines
Lasiopteridi	<i>Camptoneuromyia</i>	Neotropical, nearctic; 15 spp.	Mostly inquilines	Other Cecidomyiinae
Lasiopteridi	<i>Domolasioptera</i>	Neotropical; 7 spp.	All inquilines	Other Cecidomyiinae
Lasiopteridi	<i>Macrolabis</i>	Palaearctic; 61 spp., nearctic 1sp.	Most species are inquilines	Other cecidomyiids
Lasiopteridi	<i>Trotteria</i>	Cosmopolitan; 23 spp.	All inquilines	Chiefly Asphondyliini

Among the seven genera listed in Table 9.1, the genus *Macrolabis* contains the most abundant inquilinous species, 61 from the Palaearctic Region and one from the Nearctic Region. For example, the larvae of *Macrolabis mali* Anfora were found to live as inquilines in leaf galls of the apple leaf curling gall midge *Dasineura mali* (Kieffer) on *Malus domestica* Borkhausen (Rosaceae) in Italy (Anfora et al. 2005). Each gall usually contains 20–50 larvae of *D. mali* and 20–40 larvae of *M. mali*. The larvae quit the galls to drop to the ground, where they pupate. Both species are multivoltine, five to six generations per year. At the end of the season, the number of *M. mali* larvae in a gall becomes larger than that of *D. mali*, resulted in the death of host larvae (Anfora et al. 2005).

Dorchin et al. (2006) newly discovered an inquilinous gall midge of the genus *Macrolabis* in the Nearctic Region. The larvae of *Macrolabis americana* Dorchin inhabit galls induced by *Dasineura folliculi* Felt on *Solidago rugosa* Miller and *Solidago gigantea* Aiton (Asteraceae). Unlike known *Macrolabis* species in the Palaearctic Region, *M. americana* is multivoltine and is found in the galls successively through the generations. The larvae of both species leave the galls to pupate in the soil. Emergence occurred between dusk and dawn and adults lived 1–2 days. Sex ratio was female biased, 1:2 to 1:4 (Dorchin et al. 2006).

In addition to the seven genera in Table 9.1, the genus *Dasineura* also contains some inquilinous species. For example, the larvae of *Dasineura balsamicola* (Lintner) inhabit bud galls induced by the balsam gall midge *Paradiplosis tumifex* Gagné on balsam fir *Abies balsamea* (Linnaeus) Miller (Pinaceae) in Canada and USA. Of 376 incipient galls of *P. tumifex* examined, 75 contained one, 20 contained two, and seven contained more than two larvae of *D. balsamicola* (Akar and Osgood 1987). Carleton et al. (2015) observed daily activities of both *P. tumifex* and *D.*

balsamicola. Both species were most active during 17:00–22:00 h. Male gall inducer activity was largely confined to the space below the crown. Calling and mating by the gall inducer occurred at ground level and were followed by dispersal of females to the vegetative crown. Peak oviposition occurred between 20:00 and 21:00 h. Female inquilines displayed similar activity patterns, although no calling or mating behavior was observed. Inquiline flight and search for oviposition sites were more active than the gall inducer, with shorter rest periods and more buds visited than the gall inducer.

Because *P. tumifex* is a major pest for the Christmas tree industry and the inquiline *D. balsamicola* is involved in the population dynamics of the balsam gall midge, Guay et al. (2016) surveyed their spring phenology in the field, as well as their survival during winter diapause under simulated climatic scenarios in the laboratory. They observed that spring asynchrony between fir host trees and *P. tumifex* in the first year of study had no impact on summer abundance, but they clarified that overwintering habitats and strategies differ between the galler and its inquiline. Experimental overwintering data suggested that diapausing conditions affect these species differentially.

Dasineura hybanthi Kolesik & Skuhrová was found from galls caused by an unknown gall midge on *Hybanthus floribundus* (Lindley) F. Mueller (Violaceae) in Australia but its detailed life history traits have never been studied (Kolesik and Skuhrová 1997).

Although most inquiline species inhabit galls induced by other cecidomyiid species, they are rarely found living in the galls induced by arthropods other than gall midges. For example, the larvae of *Resseliella* (= *Profeltiella*) *dizygomyzae* (Barnes) live gregariously as inquilines in mines of *Dizygomyza barnesi* Hendel (Diptera: Agromyzidae) on *Salix* spp. (Salicaceae) (Barnes 1933).

Thus, inquilines often affect their host populations by crowding or other forms of competition. Therefore, the existence of inquilines in arthropod communities cannot be ignored, but intensive and long-term population dynamics of inquilines have not yet been studied.

9.3 A Successor, *Lasioptera yadokariae*, Using Vacated Galls

9.3.1 Introduction

Successors inhabit galls after the gall-inducing organisms and their associates, parasitoids, predators, and inquilines, have departed (Mani 1964). As the galls usually do not decay sometime after the departure of these organisms, the vacated galls provide shelters to a variety of arthropods and breeding ground for fungi. Some of the successors utilize galls as occasional shelters or nests, but others are associated with particular sorts of galls and have become wholly specialized for living in

vacated galls. Many species of arthropods, such as ants, aphids, thrips, psocids, and mites, are known to inhabit empty galls (e.g. Walsh 1864/1866; Ping 1920; Mani 1964, Yukawa 1983; Patton 1987; Yukawa and Rohfritsch 2005).

In the subfamily Cecidomyiinae, *Lasioptera cerasiphera* Stelter, *Lasioptera querciflorae* Felt, *Lasioptera tibialis* Felt, and *Lasioptera yadokariae* Yukawa & Haitsuka have been known as successor species that live in vacated galls (Gagné 1989; Yukawa and Haitsuka 1994; Gagné and Jaschhof 2017). Among these species, *L. yadokariae* has been most intensively studied by Yukawa and Haitsuka (1994).

9.3.2 Galls Utilized by *Lasioptera yadokariae* and Associated Fungus

Lasioptera yadokariae utilizes the following three sorts of gall (Yukawa and Haitsuka 1994): brownish swellings induced by *P. neolitseae* on the leaves of *N. sericea*; angular, pear- or club-shaped galls of *Daphnephila* sp. on the under leaf surface of *M. japonica*; and thick type suboval leaf blisters (see Sect. 2.3) induced by *Masakimyia pustulae* Yukawa & Sunose on *Euonymus japonicus* Thunberg (Celastraceae). *Daphnephila machilicola* also produces barrel-shape galls on the under surface of the leaves of a related host plant, *M. thunbergii*, but *L. yadokariae* has never been found on this plant, possibly because the larval cavity and the exit hole are too large for the successors to inhabit.

Galls inhabited by larvae of *L. yadokariae* contain fungal mycelium on which the larvae feed. During the first larval stadium, mycelium of the host fungus is not distinct in the gall. When the larvae become the second instars, the exit hole of the gall is plugged with a thick growth of the mycelium (Fig. 9.2h). After mature larvae quit the galls to drop to the ground, the mycelium is weakened and disappears. The fungus obtained from the vacated gall on *N. sericea* was identified as *Pestalotia* sp. (Fungi Imperfecti: Melanconiales: Melanconiaceae) (Yukawa and Haitsuka 1994).

9.3.3 Life History

In southern Kyushu, Japan, the aforementioned three gall-inducing host midges are normally univoltine, and adults emerge in April and May (Yukawa 1974, 1983; Yukawa and Sunose 1976; Yukawa and Haitsuka 1994). Therefore, vacated galls are available for *L. yadokariae* in this season. Exit holes of the gall midge and its parasitoids are made under leaf side of the galls. The emergence of *L. yadokariae* from the ground usually begins in early April and continues until early May.

The duration of the egg stage is not precisely known. According to Yukawa and Haitsuka (1994), 84% of the larvae found in the vacated galls on *N. sericea* were first

instars in mid-April. The dissection of galls indicated that two or three first instars inhabited a gall more frequently than what expected from random distribution. The first instars rapidly developed into second, and then 48% of the larvae became third instars in early May. At this time, there was no case where two or more third instars coexist in a gall. This suggests that there was an intraspecific competition among the first or second instars. There was no sign of attack by any parasitoid species. All third instars quitted the galls to drop to the ground by mid-May. Thereafter, neither successor larvae nor fungus mycelia were found in the empty galls in the field.

The larvae possibly spin cocoons on the ground and pass through the summer, autumn, and winter, and pupate in the following spring. In addition, 33 out of the 129 larvae collected in April 1987 became adults after being exposed for one cycle of the four artificial seasons in an incubator for a relatively short period of time (see Table 1 in Yukawa and Haitsuka 1994). These results suggest that the successor is univoltine.

It should be remarked here that two of the 129 larvae became adults after being exposed for two cycles of the four artificial seasons. This result indicates the possibility that some individuals of *L. yadokariae* have a 2-year life cycle as has been noted for other gall midge species such as *Sitodiplosis mosellana* Géhin and *Contarinia tritici* Kirby, some of whose larvae diapause in the ground for more than 1 year (e.g. Barnes 1952, 1958; see Sect. 6.3). No adult successor emerged after three cycles of the four artificial seasons, which means that the remainder of the 129 larvae died during the incubation (Yukawa and Haitsuka 1994).

9.3.4 Emergence, Sex Ratio, Life Span, and Oviposition

Laboratory experiments indicated that the emergence of both males and females occurred mostly in the morning between 5:00 and 12:00. A few adults emerged in the afternoon. Sex ratio at the time of emergence was nearly 1:1. The average life span of unmated males and females was 6.67 ± 2.16 h ($n = 6$) and 6.67 ± 2.74 h ($n = 12$), respectively (Yukawa and Haitsuka 1994).

After mating, the females start to fly actively under the host leaves in search of vacated galls and lay their eggs inside the vacated galls one by one. The average time required for one egg laying was 14.2 ± 6.9 s ($n = 21$). The females of *L. yadokariae* did not show any preference between the galls vacated by the gall midge or its parasitoids, *Gastrancistrus* sp. and *B. tamabae*. In addition, the females did not distinguish unused empty galls from those already utilized by themselves or other conspecific females. We observed sometimes in the field that a female came back to the gall where she had oviposited before several minutes. There was a case where two females oviposited in a gall at the same time.

9.3.5 Population Fluctuation

The density of gall-inducing species and their parasitoids, which fluctuates independently of the density of the successor, is considered to influence the abundance and survival of *L. yadokariae*. In addition, synchronization of the emergence season of *L. yadokariae* adults with that of gall-inducing cecidomyiids and their parasitoids is an important factor in determining the abundance of the successor because its adult life span is very short and the females choose fresh vacant galls for oviposition (Yukawa and Haitsuka 1994; Yukawa et al. 2006).

Figure 9.3 shows the annual changes in the number of vacated galls that were unused and used by *L. yadokariae*. The vacated galls include those made by *P. neolitseae* and its parasitoids, *Gastrancistrus* sp. and *B. tamabae*. The vacated galls used by *L. yadokariae* fluctuated from 9 in 1979 up to 108 in 1989. The proportion of vacated galls utilized by *L. yadokariae* fluctuated from year to year between 3.1% in 1985 and 36.0% in 1987 (Yukawa et al. 2006). The vacated galls of *B. tamabae* were most frequently used by *L. yadokariae*, followed by those of *P. neolitseae*, while those of *Gastrancistrus* sp. were less frequently used.

Yukawa et al. (2006) concluded that when the density of *P. neolitseae* or *B. tamabae* is high, *L. yadokariae* increases its population number by utilizing the abundant vacated galls made by their emergence prior to the emergence of *L. yadokariae*, whereas the high density of *Gastrancistrus* sp. does not fully contribute to an increase of the successor because its emergence season occur a little after the emergence of *L. yadokariae*. The high density of *B. tamabae*, however, would decrease the number of *L. yadokariae* in the following generation, because the high percentage parasitism will reduce the density of *P. neolitseae*, resulting in a shortage of vacated galls.

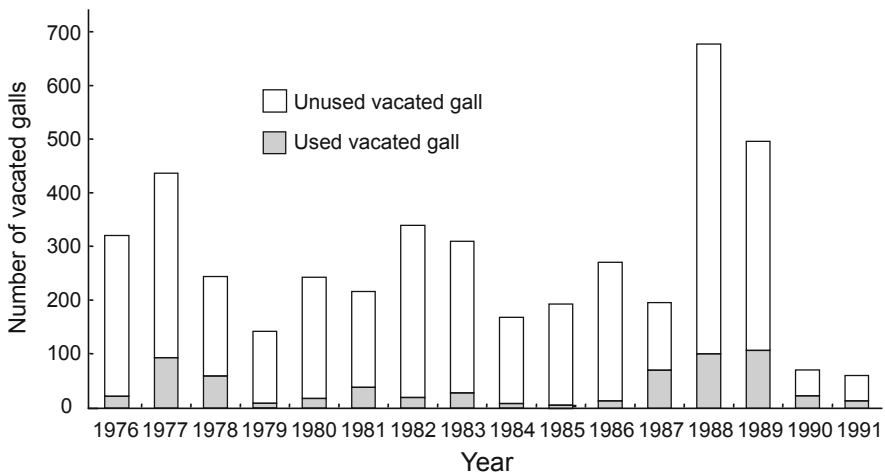


Fig. 9.3 Annual changes in the number of vacated galls that were unused and used by *Lasioptera yadokariae* (modified from Fig. 4 in Yukawa et al. 2006)

9.4 Cecidophagy

9.4.1 Introduction

Cecidophagy is a habit of feeding on the inside and outside of galls either obligatorily or facultatively, and frequently causes the death of gall inducers by destroying galls and leaving feces. In comparison with accidental feeding on galls, facultative cecidophagy is considered to be rather common in various cecidophagous species, although examples of obligatory cecidophagy are relatively rare. Some of facultative cecidophagous species prefer galled tissues or organs to ungalled parts.

9.4.2 Cecidomyiid Galls Fed by Dipteran, Lepidopteran and Coleopteran Insects

Miyatake et al. (2000) found *Bactrocera scutellata* (Hendel) (Diptera: Tephritidae) emerging from stem galls induced by a gall midge, *Lasioptera* sp., on wild gourds, *Diplocyclos palmatus* (Linnaeus) C. Jeffrey, *Trichosanthes cucumeroides* (Seringe) Maximowicz, and *Melothria liukiuensis* Nakai (Cucurbitaceae), on Okinawa Island, Japan. Because *B. scutellata* preferably feeds on the stem galls to ungalled parts of the gourds, it is regarded as a cecidophagous fruit fly.

Sugiura and Yamazaki (2006) observed larvae of *Chyliza splendida* Iwasa (Diptera: Psilidae) feeding on leaf bud galls induced by *Asphondylia baca* Monzen on its winter host, *Weigela floribunda* (Siebold & Zuccarini) K. Koch (Caprifoliaceae) (Fig. 6.4e). The mortality rate of *A. baca* was extremely high, 98.0% ($n = 51$) and 98.2% ($n = 58$), in the galls with and without *C. splendida* larvae, respectively, but there was no significant difference between the rates. Therefore, the effect of *C. splendida* larvae on the survivorship of *A. baca* was considered to be minimal.

Yamazaki and Sugiura (2003a) observed larvae of *Amaya stellate* Butler (Lepidoptera: Noctuidae) feeding on the epidermis of stem galls induced by *Lasioptera achyranthii* Shinji on *Achyranthes bidentata* Blume (Amaranthaceae) and larvae of *Nippopectilia vitis* (Sasaki) (Lepidoptera: Pterophoridae) feeding inside fruit galls induced by *A. baca* on its summer host, *Ampelopsis glandulosa* var. *heterophylla* (Thunberg) Momiyama (Vitaceae). *Amaya stellate* little affected *A. baca* larvae, while *N. vitis* frequently caused the death of the gall midge larvae by destructing the fruit galls.

Two tortricid moth species emerged from axillary bud galls of *Schizomyia sasakii* (Monzen) on *Ilex crenata* Thunberg (Fig. 2.10c) (Aquifoliaceae), and from those of *Schizomyia soyogo* Kikuti on *Ilex chinensis* Sims, *Ilex integra* (Thunberg) (Fig. 2.10d) and *Ilex pedunculosa* Miquel (Sugiura et al. 2006) (see Elsayed et al. 2018 and Sect. 2.7 for taxonomic treatments and host ranges of the two *Schizomyia* species). Larvae of *Rhopobota ustomaculana* (Curtis) (Lepidoptera: Tortricidae) bored into

the galls of *S. sasakii* on *I. crenata*, and *S. soyogo* on *I. pedunculosa*, respectively. *Rhopobota ustomaculana* (Curtis) larvae fed on leaves as well as gall tissues of *I. pedunculosa*, suggesting that it is a facultative cecidophage. Comparison of chemical properties between the gall and normal plant tissues of *I. pedunculosa* indicated that the axillary bud galls seem to be relatively favorable food resources for *R. ustomaculana* larvae because of higher water content and lower carbon and polyphenol contents in spite of poorer nitrogen content.

The infestation of young fruit of *Ligustrum japonicum* Thunberg (Oleaceae) by larvae of *Lemyra imparilis* (Butler) (Arctiidae) caused the death of first instars of *Asphondylia sphaera* Monzen by desiccation of internal tissues of the fruit, but Key-factor and key-stage analysis indicated that this infestation less contributed than bottom up mortality factors to the annual changes of total survival rate of the gall midge (Yukawa et al. 2016).

Fujii et al. (2012) obtained adults of *Darumazo distinctus* Morimoto & Miyakawa (Coleoptera: Curculionidae) from axillary bud galls induced by *S. sasakii* on *Ilex crenata* Thunberg var. *hachijoensis* Nakai (Aquifoliaceae). Later, Kojima (2013) found larvae of *D. distinctus* in the galls of *S. soyogo* (as *S. sasakii*, misidentification) on *I. integra* and regarded it as a cecidophagous insect. Further investigations are needed to confirm if its feeding habit is facultative or obligatory.

9.4.3 Cecidophagy on the Galls Other Than Those of Cecidomyiids

9.4.3.1 By Lepidopteran Species

Larvae of *Nola innocua* Butler (Lepidoptera: Nolidae) are obligatorily cecidophagous, feeding on the internal tissue of aphid galls on the leaves of *Distylium racemosum* Siebold & Zuccarini (Hamamelidaceae) (Itô and Hattori 1982, 1983). *Batrachedra striolata* Zeller (Lepidoptera: Batrachedridae) larvae fed on gall tissue within the gall of *Euura lasiolepis* Smith (Hymenoptera: Tenthredinidae) but killed only 1% of the sawfly larvae (Price and Craig 1984).

Yamazaki and Sugiura (2003a) reared four lepidopteran species, *Anatrachyntis japonica* Kuroko (Cosmopterygidae), *Hypatima* sp. (Gelechiidae), *Andrioplecta pulverula* Meyrick (Tortricidae), and *Characoma ruficirra* Hampson (Noctuidae) from twig galls of *Trichagalma serratae* (Ashmead) (Hymenoptera: Cynipidae) on *Q. acutissima*. Larvae of *A. japonica* fed on the lignified gall tissues and destroyed the larval cells, while cecidophagy by the larvae of *Hypatima* sp. could not be confirmed (Yamazaki and Sugiura 2003a). Both *A. pulverula* and *C. ruficirra* are facultatively cecidophagous species and their larvae fed more on unisexual galls of *T. serratae* than on leaves of *Q. acutissima* (Abe 1995).

The larvae of *Stathmopoda auriferella* (Walker) (Lepidoptera: Stathmopodidae) were observed feeding on the stem galls induced by *Eucosma metzneriana*

(Treitschke) (Lepidoptera: Tortricidae) on *Artemisia indica* Willdenow var. *maximowiczii* (Nakai) H. Hara (Asteraceae) (Yamazaki and Sugiura 2003b).

9.4.3.2 By Coleopteran Species

Larvae of *Orchestes hustachei* (Klima) (Coleoptera: Curculionidae) were known to feed on the inner wall of leaf galls induced by *Paracolopha morrisoni* (Baker) (Hemiptera: Aphididae) on *Zelkova serrata* (Thunberg) Makino (Ulmaceae) (Yamazaki and Sugiura 2001) but it is now regarded as an aphidophagous rather than a cecidophagous species (Tomisawa and Akimoto 2004). Females of *Demotina fasciculata* Baly (Coleoptera: Chrysomelidae) feed on tissues of bisexual generation galls induced by *Andricus moriokae* Monzen (Hymenoptera: Cynipidae) on the leaves of *Quercus serrata* Thunberg ex Murray (Fagaceae) (Katsuda and Yukawa 2010).

9.4.4 Gall-Sucking Behavior

There are various observations of gall-sucking behavior by hemipteran species (e.g. Pepper and Tissot 1973; Wachi 2010; Yang et al. 2001; Miller and Crespi 2003). Yamazaki and Sugiura (2005) observed in Osaka and Kyoto Prefectures, Japan seven hemipteran species sucking on six sorts of gall induced by six species of insects on six plant species belonging to six families (see Table 1 in Yamazaki and Sugiura 2005). Among them, there was only one example in which cecidomyiid galls were sucked by a pentatomid. Adults of *Carbula humerigera* (Uhler) (Hemiptera: Pentatomidae) were found sucking on oval or subglobose stem galls induced by *L. achyranthii* on *A. bidentata*. Because *C. humerigera* is known to suck from stems and flowers of various asteraceous herbs and rosaceous shrubs, it is regarded as a facultative gall-sucking species.

9.4.5 Gall Wall Thickness

Generally, parasitoids are restricted to attacking larvae inhabiting galls within reach of their ovipositor. Therefore, a thick gall-wall is considered to serve in defense of galls from natural enemy attacks (e.g. Abrahamson and Weis 1997; Craig et al. 1990; Jones 1983; Stone et al. 2002; Katsuda and Yukawa 2010). In contrast, thick-walled galls may attract cecidophagous insects because many works have demonstrated a high concentration of potentially nutritive compounds in galls (e.g. McNeill and Southwood 1977; Rohfritsch and Shorthouse 1982; Price et al. 1987). However, there are some examples in which nutrient concentrations are lower in galls than in ungalled tissues (e.g. Hartley 1998; St. John and Shorthouse 2000) and some chemicals that could be deleterious to herbivores accumulate in galls (Cornell

1983; Rohfritsch and Shorthouse 1982; Price et al. 1987). Nevertheless, various insects have overcome some of such difficulties, if any, and evolved to be able to feed on gall tissues either obligatorily or facultatively, as shown in this section.

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