Effects of Gall Formation by Neothoracaphis yanonis (Hemiptera : Aphididae) on Shoot,Fruit,and Seed Production of Its Host Plant,Distylium racemsum (Hamamelidaceae)

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Effects of Gall Formation by *Neothoracaphis yanonis* (Hemiptera: Aphididae) on Shoot, Fruit, and Seed Production of Its Host Plant, *Distylium racemosum* (Hamamelidaceae)[1]

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Abstract. Effects of leaf gall formation by *Neothoracaphis yanonis* (Hemiptera: Aphididae) on the growth and reproduction of its host plant, *Distylium racemosum* (Hamamelidaceae), were studied in a viewpoint of sink-source relationship. Gall formation on the leaves of current-year spring shoots did not affect the production of lammas shoots in later seasons of the current year and of spring shoots in the following year. Many galled leaves abscised in late May and early June after the gall dehisced and alates left the galls, but the abscission of galled leaves appeared unrelated to the production of lammas and spring shoots. The leaf gall formation reduced significantly the production of fruit and seeds. In particular, the abscission of galled leaves affected the seed production more severely than the fruit production.

Key words: gall aphid, *Distylium racemosum*, fruit production, seed production, shoot production.

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Introduction

Plants are always at a disadvantage in the inter-relation between gallers and host plants, and galls reduce growth and reproduction of plants (Price *et al.*, 1987). Many examples of deleterious effects on host plants have been demonstrated in various studies. For example, heavy galling on the branch of *Salix lasiolepis* Bentham (Salicaceae) by *Euura lasiolepis* (Smith) (Hymenoptera: Tenthredinidae) stunts or kills growth distal to the gall, stimulating sprouting by indefinitely dormant buds located near branch bases (Craig *et al.*, 1986). The presence of shoot galls of *E. lasiolepis* led to a significant reduction in reproductive buds and, thus, inflorescences on individual shoots on both male and female plants (Sacchi *et al.*, 1988). *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) is one of the most important pests of chestnut tree, *Castanea crenata* Siebold et Zuccarini (Fagaceae), in Japan. The bud gall formation by *D. kuriphilus* reduced the leaf area, biomass ratio of leaf per shoot, and the number of winter buds on galled shoots, resulted in the retardation of development of photosynthetic organ and biomass reduction of host trees in the following year (Kato & Hijii, 1997). In some cases, stem galls may significantly reduce the seed production of host plants (e.g., Denill, 1985; Sacchi *et al.*, 1988; Fernandes *et al.*, 1993). Silva *et al.* (1996) demonstrated that gall formation by *Tomoplagia rudolphi* Lutz et Costa Lima (Diptera: Tephritidae) on the stem of *Vernonia polyanthes* Less (Asteraceae) caused a significant reduction in seed viability but did not affect flower head production and seed germination velocity.

Galls act as strong sinks and compete for assimilates with plant sinks. Fay *et al.* (1996) tested for functional interaction between galls and adjacent ungalled shoots in *Adelges cooley* (Gillette) (Hemiptera: Adelgidae) on *Picea engelmanni* Parry ex Engelmann (Pinaceae) and obtained results suggesting that surrounding shoots constitute an extended and flexibly utilized resource base for adelgid galls. Larson & Whitham (1997) demonstrated that the genotypes of resistant cottonwood tree, *Populus* (Salicaceae) have more natural sinks (i.e., buds) relative to sources (i.e., stem volume) than susceptible trees, and intraplant sink competition was greater on resistant trees. Based on these observations, Larson & Whitham (1997) proposed the ‘sink competition hypothesis’ to account for the performance of gallers on their host plants. As predicted, reduction of competing sinks (bud removal) significantly increased the survival of *Pemphigus betae* Doane (Hemiptera: Pemphigidae) on resistant trees of cottonwood. From these results, they suggested that a sink competition model is needed to explain the distribution of the diverse group of herbivores that act as phloem parasites.

Although effects of leaf gall formation on reproductive organs have seldom been studied in a viewpoint of sink-source relationship, there is an example in which gall formation by *Hayhurstia atriplicis* (Linnaeus) (Hemiptera: Aphididae) on the leaves of *Chenopodium album* Linnaeus (Chenopodiaceae) reduces overall host mass and seed set (Moran & Whitham, 1990).

During our field survey, in Kagoshima, Japan, of gall aphids associated with their host plant, *Distylium racemosum* Siebold et Zuccarini (Hamamelidaceae) (Ngakan & Yukawa, 1996; Ngakan & Yukawa, 1997), stem mothers of *Neothoracaphis yanonis* (Matsumura) (Hemiptera: Aphididae) were observed to develop much faster, produce galls more quickly, and produce more offspring than those of another leaf gall aphid, *Dinipponaphis autumna* (Monzen) (Hemiptera: Aphididae), on the same host. Leaf gall formation by *N. yanonis* was also observed to cause earlier abscission of galled host leaves in late May and early June. From these observations, we suspected that *N. yanonis* could be a relatively strong sink and considered that gall formation, associated with imbibition of phloem sap, might reduce growth and reproduction of *D. racemosum*. The objective of this study is to investigate this possible reduction.

Materials and Methods

Field surveys were conducted from 1995 to 1996 on two census trees, T1 (6 m high) and T2 (3.5 m high) in the arboretum of Kagoshima University, Kagoshima City, Japan.

In order to confirm effects of gall formation on shoot production, 125 newly extended spring shoots of T1 were numbered with plastic tapes in March 1995. On these shoots, the number of leaves per shoot and the number of galls of *N. yanonis* on each leaf were recorded. Thereafter, the number of surviving or fallen leaves and the number of newly emerged lammas shoots were monitored monthly until April 1996. Then, the number of newly extended spring shoots of the year 1996 (produced from those of 1995) was recorded. A linear regression test was used to confirm the effects of gall formation on shoot production. Spring shoots extended in 1996 successively from lammas shoots were not included in the test to avoid influence of those lammas.

Fifty flower-bearing spring shoots of the year 1995 were labeled on T2 in April 1995 in order to survey the effects of gall formation by *N. yanonis* on fruit and seed production. The number of flowers per shoot, the number of leaves per shoot, and the number of galls per leaf were recorded. Thereafter, the numbers of surviving or fallen leaves and fruit were monitored monthly until late November 1995. Then, all (136) of mature fruit were collected from the 50-labeled shoots on T2 and dissected to examine the number of seeds fertile inside. Seed production was expressed by the total number of fertile seeds per shoot, because a mature fruit of *D. racemosum* contained two fertile seeds optimally, but occasionally only one or none. Linear regression was used to detect the effects of gall formation.

Results

Effect of gall formation on shoot production

Lammas shoot production in later seasons of the current year (Table 1) and spring shoot production in the following year (Table 2) were not affected, significantly, by the presence of galls caused by *N. yanonis* on the leaves of current-year spring shoots. The abscission of galled leaves after the dehiscence of the galls appeared unrelated to the production of lammas and spring shoot.

Effects of gall formation on fruit and seed production

Flowers that grow from axillary bud associated with leaves galled by *N. yanonis* could not develop normally and contained infertile or instead no seed (Fig. 1). Fruit production (the number of fruit per shoot) was affected positively by the initial number of flowers, but negatively by the presence of leaf galls (Table 3). There was no significant relation between fruit production and the number of leaves abscised.

As well as fruit production, seed production (the total number of fertile seeds per shoot) was correlated positively with the initial number of flowers but negatively with the presence of leaf galls (Table 4). The seed production was also affected negatively by the number of abscised galled leaves (Table 4). Thus, the leaf gall formation by *N. yanonis* reduced both fruit and seed production, whilst the abscission of galled leaves affected seed production alone. The p value for the relation between galls and seed production was < 0.0041 (Table 4), i.e., much smaller than that between galls and fruit production, < 0.0405 (Table 3). This suggests that some of fruit remain on the tree until maturity but do not contain seeds.

Discussion

Many examples are available to suggest that leaf gall formation causes earlier abscission of galled leaves. For example, mean longevity of heavily galled leaves of *Euonymus japonicus* Thunberg (Celastraceae) induced by *Masakimyia pustulae* Yukawa et Sunose (Diptera: Cecidomyiidae) was considerably shortened, whereas ungalled and lightly galled leaves were seldom shed (Sunose & Yukawa, 1979). Gall induction by *Contarinia* sp. along the midrib of an evergreen oak, *Quercus glauca* Thunberg (Fagaceae), also caused earlier drop of galled leaves in April-May, whereas ungalled leaves survived more than 26 months on an average (Yukawa & Tsuda, 1986). However, evidences indicating the effects of leaf gall formation on shoot production have been limited.

Table 1. Coefficient correlation (r), regression equation, and probability (p) indicating the level of effect of gall formation by *Neothoracaphis yanonis* and the abscission of galled leaves on the production of lammas shoots.

	Lammas shoot (x_{ls})		
	r	x_{ls}	p
Number of galls ($y1$)	- 0.0146	0.0092 - 0.0006 $y1$	< 0.8715
Number of leaves abscised ($y2$)	- 0.0035	0.0083 - 0.0004 $y2$	< 0.9687

Table 2. Coefficient correlation (r), regression equation, and probability (p) indicating the level of effect of gall formation by *Neothoracaphis yanonis* and the abscission of galled leaves on the production of spring shoots.

	Spring shoot (x_{ss})		
	r	x_{ss}	p
Number of galls ($y1$)	- 0.0726	1.2106 - 0.0439 $y1$	< 0.3917
Number of leaves abscised ($y2$)	- 0.0812	1.2293 - 0.1206 $y2$	< 0.3680

Table 3. Coefficient correlation (r), regression equation, and probability (p) indicating the level of effects of gall formation by *Neothoracaphis yanonis* and the abscission of galled leaves on the production of fruit.

	Number of fruits (x_f)		
	r	x_f	p
Number of galls ($y1$)	- 0.2908	3.4129 - 0.3394 $y1$	< 0.0405
Number of leaves abscised ($y2$)	- 0.0968	3.1638 - 0.2359 $y2$	< 0.5039
Number of flower ($y6$)	- 0.3613	1.1729 - 0.3547 $y6$	< 0.0099

Table 4. Coefficient correlation (r), regression equation, and probability (p) indicating the level of effect of gall formation by *Neothoracaphis yanonis* and the abscission of galled leaves on the production of seeds.

	Number of seeds (x_S)		
	r	x_S	p
Number of galls ($y1$)	- 0.3988	5.0105 - 0.6833 $y1$	< 0.0041
Number of leaves abscised ($y2$)	- 0.2380	4.6747 - 0.8516 $y2$	< 0.0960
Number of flowers ($y6$)	- 0.3331	1.7456 - 0.4802 $y6$	< 0.0181

According to J. Yukawa (unpublished data), leaf gall formation by *Pseudasphondylia neolitseae* Yukawa (Diptera: Cecidomyiidae) reduced shoot production on *Neolitsea sericea* (Blume) Koidzumi (Lauraceae) in the following spring, whilst, that by *Daphnephila machilicola* Yukawa (Diptera: Cecidomyiidae) did not so on *Machilus thunbergii* Siebold et Zuccarini (Lauraceae). Like the *Daphnephila-Machilus* inter-relation, gall formation by *N. yanonis* and abscission of galled leaves did not reduce, significantly, the production of spring shoots. Thus, the effects of leaf gall formation on shoot production vary with different inter-relations between gallers and host plants. Because shoot production is influenced by various factors, such as the amount of stored nutrients, water stress, and compensatory reactions to herbivore infestation, the effects of gall formation cannot be evaluated clearly.

Fig. 1. Mature fruit of *Distylium racemosum* on a shoot, of which some leaves bear galls of *Neothoracaphis yanonis*. Fruit on the axil of leaves that bear gall(s) did not develop normally.

There are many gallers that are directly responsible for the reduction of fruit and seed production by inducing galls on these organs (e.g., Yukawa & Masuda, 1996; Redfern *et al.*, 2002), but there are only limited examples indicating that the existence of galls on vegetative organs affects reproductive organs. In particular for leaf gall aphids, as mentioned in the introduction, only one example was available for *H. atriplicis* on *C. album* (Moran & Whitham, 1990). Larson & Whitham (1991) suggested a possibility that aphid induced galls may compete for assimilates with plant sinks such as fruit and seeds. As reviewed by Stephenson (1981), it has been known that carbohydrates and recycled nutrients from vegetative organ enter fruit from the phloem, and there is a strong tendency for resources to flow into fruit from the nearest leaves, although fruit has the potential for attracting resources from leaves that are a meter or more away. These suggestions and evidences support the finding in the present study that leaf gall formation by *N. yanonis* reduced the fruit and seed production of *D. racemosum*, because the aphid imbibes nutrients from the phloem and leaf abscission causes the shortage of resources for fruit.

However, the abscission of galled leaves did not influence significantly on fruit production, although it reduced seed production. This can be explained by the fact that the current shoots bore young fruit before the galled leaves begin to abscise in late May. In this season, the seeds inside the fruit are still in the process of development, and fruit matures in late November (Satake *et al.*, 1989).

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