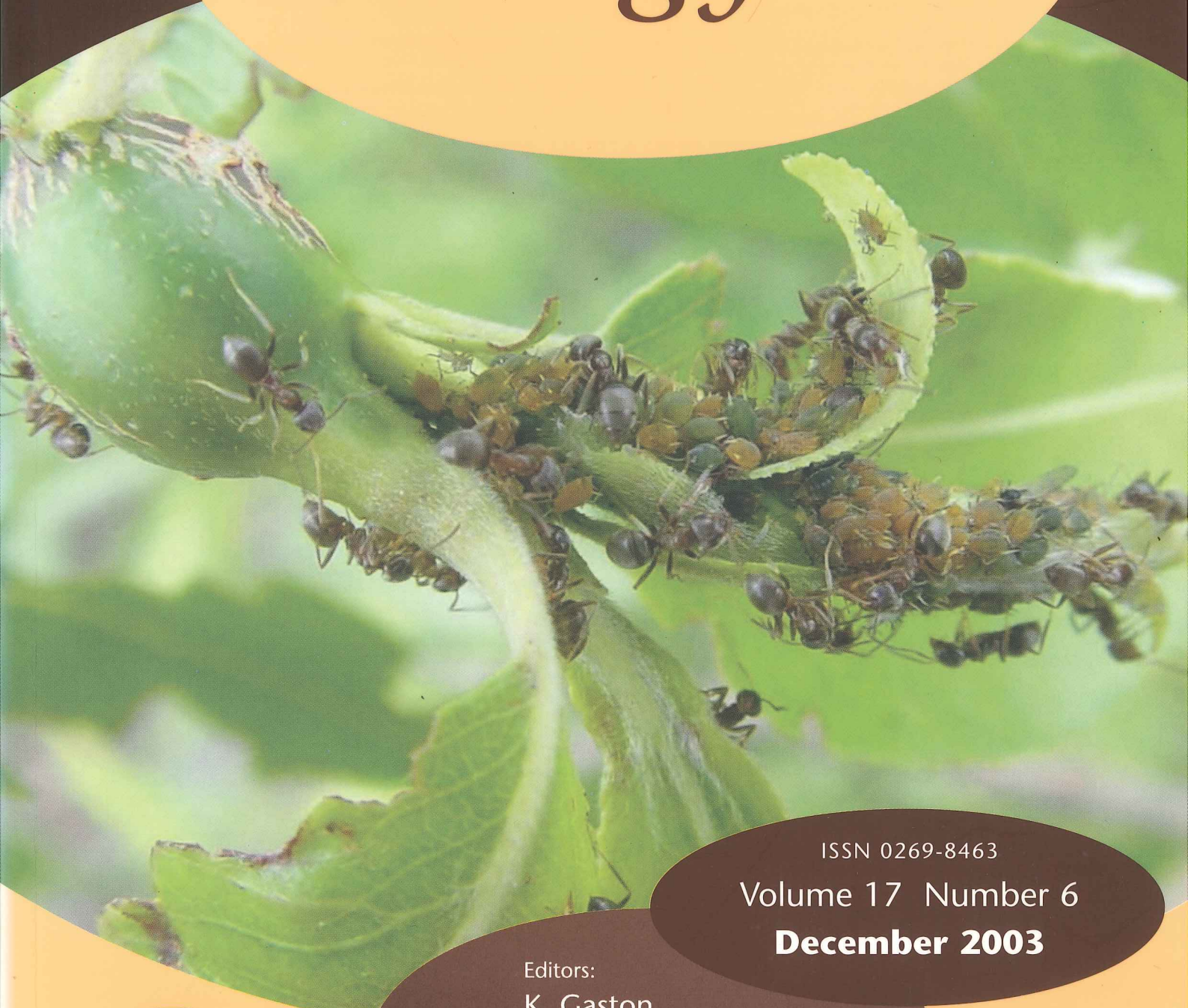


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Gall initiation enhances the availability of food resources for herbivorous insects

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Summary

1. Insect herbivory may have not only negative but also positive plant-mediated effects on other insect herbivores. We investigated plant-mediated effects of the stem gall midge *Rabdophaga rigidae* on other insect herbivores through regrowth response of the willow *Salix eriocarpa*.

2. Gall initiation on current-year shoots stimulated the development of lateral shoots, followed by a secondary leaf flush. Lateral shoots and upper leaves on galled shoots were less tough and had a higher water and nitrogen content.

3. Colonization rates by the aphid *Aphis farinosa* were significantly higher on galled shoots than on ungalled shoots, because this aphid frequently colonized lateral shoots.

4. Adults of two leaf beetles, *Plagioderma versicolora* and *Smaragdina semiaurantiaca*, were more abundant on galled than on ungalled shoots; they preferentially fed on young leaves produced during the secondary leaf flush.

5. Gall initiation positively affected aphids and leaf beetles by enhancing the availability of food resources as a result of the regrowth responses of *S. eriocarpa*. This indicates that the regrowth responses of plants to insect herbivory provide an important mechanism responsible for positive effects on other insect herbivores.

Key-words: Increase in nutritional quality, indirect interactions, lateral shoots, positive plant-mediated interactions, regrowth responses, secondary leaf flush

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Introduction

Insect herbivory can influence the performance of other herbivorous insects either positively or negatively (Faeth 1991; Damman 1993; Denno, McClure & Ott 1995; Ohgushi 1997). Several authors have illustrated that herbivorous insects can induce increases in secondary chemicals and/or decreases in the nutritional status of many plants (Schultz & Baldwin 1982; Karban & Myers 1989). These changes can negatively affect the survival and growth of other insect herbivores that appear later in the season (Faeth 1986; Faeth 1987; Haukioja & Neuvonen 1987; Faeth 1988; Karban & Myers 1989; Denno *et al.* 2000; Thaler *et al.* 2001). On the other hand, several authors have illustrated that insect herbivory often induces regrowth responses that partially or fully compensate for lost tissues in woody and herbaceous plants (Mopper *et al.* 1991; Whitham *et al.* 1991). These regrowth responses produce young

plant tissues, which are a preferred food resource for many herbivores (Feeny 1970; Hough & Pimentel 1978; Rausher 1981; Coley 1983; Damman 1989). Therefore if herbivory by insects stimulates regrowth responses in host plants, it may have great potential for positive plant-mediated effects on other herbivores by enhancing the availability of food resources.

Winter browsing by herbivorous mammals often induces regrowth responses in many deciduous trees and shrubs, which result in longer and more vigorous shoots that grow from browsed stumps or stems (Bryant 1981; Danell & Huss-Danell 1985; Bergström & Danell 1987; Bryant *et al.* 1991; Roininen, Price & Tahvanainen 1994; Roininen, Price & Bryant 1997). Herbivorous insects, including sucking, chewing, mining and galling species, prefer such previously browsed branches (Danell & Huss-Danell 1985; Roininen, Price & Tahvanainen 1994; Hjältén & Price 1996; Roininen, Price & Bryant 1997; Martinsen, Dreibe & Whitham 1998; Olofsson & Strengbom 2000). This preference is likely because young plant tissues contain reduced concentrations of secondary compounds (Danell & Huss-Danell 1985) and/or have increased nutritional status (Danell & Huss-Danell 1985; Martinsen, Dreibe & Whitham 1998).

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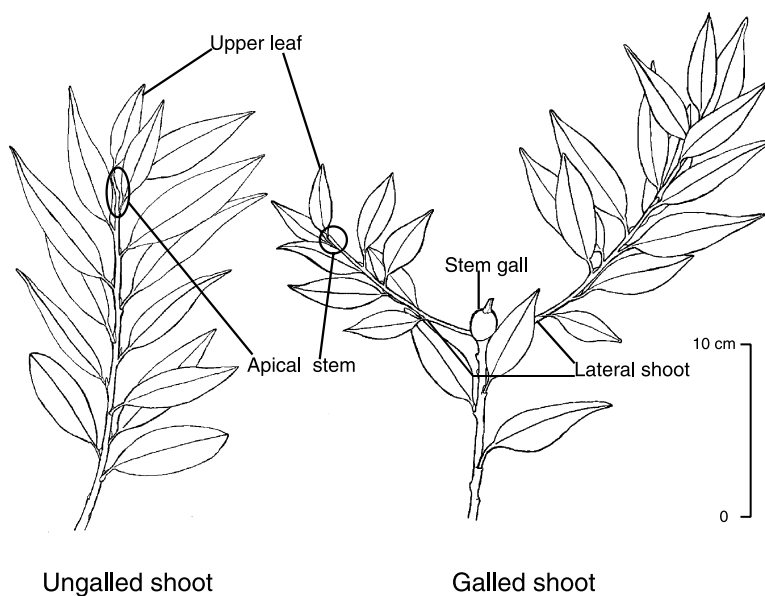


Fig. 1. Ungallo and gallo shoots of *Salix eriocarpa*.

Not only browsing by mammals, but also herbivory by insects has positive plant-mediated effects on other insect herbivores (Craig, Price & Itami 1986; Damman 1989; Pilson 1992). Herbivorous insects often induce regrowth responses in host plants by destroying the apical meristems of shoots (Mopper *et al.* 1991; Whitham *et al.* 1991), which enhances the availability of food resources to other insect herbivores. For example, Pilson (1992) demonstrated that herbivory by stem and rosette gallers, moth caterpillars and beetles stimulated lateral branching in the goldenrod *Solidago altissima* L., and that aphids and spittlebugs were more abundant on these branched goldenrods. However, little attention has been paid to positive plant-mediated interactions among insect herbivores, because many authors have assumed that herbivory by insects induces defensive responses in host plants, thereby limiting further herbivory (Faeth 1991).

In central Japan, the willow *Salix eriocarpa* Franch. et Savat is commonly attacked by the gall midge *Rabdophaga rigidae* Shinji, which initiates stem galls on the apical regions of current-year shoots (Fig. 1). After gall initiation in mid-May, lateral shoots develop vigorously from the leaf axils below the stem galls. As a result, young leaves are produced in a secondary leaf flush on the lateral shoots. The aphid *Aphis farinosa* Gmelin then colonizes the apical stems of the lateral shoots. Adults of two leaf beetles, *Plagioderma versicolora* Laicharting and *Smaragdina semiaurantiaca* Fairmaire, are frequently observed feeding gregariously on young leaves. Therefore we predicted that gall initiation has positive plant-mediated effects on the feeding preferences of these three insect species.

In this paper, we examined if gall initiation affects the availability of food resources to these three herbivorous insects. In particular, we addressed the

following questions: (1) Does gall initiation induce regrowth responses in the willow? (2) If so, how do these regrowth responses affect the nutritional and physical properties of the willow? (3) How do the regrowth responses affect the feeding preferences of other insect herbivores?

Materials and methods

STUDY SITE AND HOST PLANT

This study was performed on a floodplain along the Yasu River (35° N, 136° E) in Shiga Prefecture, central Japan in 2000 and 2001. In and around the study site, six willow species (*Salix chaenomeloides* Kimura, *Salix eriocarpa* Franch. et Savat, *Salix gilgiana* Seemen, *Salix integra* Thunb, *Salix serissaefolia* Kimura and *Salix subfragilis* Andersson) grow naturally, together with the herbs *Artemisia*, *Solidago* and *Miscanthus*. Field observations were conducted on *Salix eriocarpa*, one of the dominant willow species in the study area. *Salix eriocarpa* is a deciduous woody plant, and shoot elongation and leaf flush occur rapidly from early April to late May. Thereafter, this species grows gradually until late September.

GALL MIDGE

The gall midge *Rabdophaga rigidae* (Diptera: Cecidomyiidae) is a common insect herbivore on *S. eriocarpa* and initiates stem galls on the apical regions of current-year shoots (Fig. 1). Adults emerge in April, and females lay eggs on the surface of leaves and stems of growing current-year shoots (Yukawa & Masuda 1997). Newly hatched larvae crawl to the apical region of current-year shoots and initiate swollen stem galls in mid-May. Larval development is completed within the galls in the year of gall induction, they overwinter in the larval stage, and then adult exit from the galls in the following spring.

APHID AND LEAF BEETLES

Aphis farinosa (Hemiptera: Aphidinae) is a common sap-feeding insect on *S. eriocarpa*, and in the study area this aphid is found on willows from June to August. Aphid colonies form on apical stems of lateral shoots.

Adults of the two leaf beetles *Plagioderma versicolora* (Coleoptera: Chrysomelidae) and *Smaragdina semiaurantiaca* (Coleoptera: Chrysomelidae) occur on *S. eriocarpa* throughout the growing season, although their abundance varies greatly among years. They have been observed to feed gregariously on young willow leaves. *Plagioderma versicolora* is a specialist that feeds exclusively on the leaves of *Salix* spp. (Kimoto & Takizawa 1994), whereas *S. semiaurantiaca* is more of a generalist, feeding on the leaves of *Salix* spp. as well as *Artemisia capillaris* Thunb. ex Murray, a species that is associated with *Salix* spp. in the study area.

EFFECTS OF GALL INITIATION ON SHOOT
DEVELOPMENT

To determine if gall initiation affected the development of lateral shoots in *S. eriocarpa*, we conducted field surveys in 2000 and 2001. On 14 July 2000, we randomly selected six *S. eriocarpa* trees and 10 1-year-old shoots on each tree. We then counted the number of lateral shoots on ungallo and galloed shoots. In 2001, the same survey was conducted from 16–17 July on 22 randomly selected trees, on each of which 10–20 1-year-old shoots were randomly selected.

EFFECTS OF GALL INITIATION ON LEAF FLUSH

We examined temporal changes in leaf flush in 2001 to determine if gall initiation affected the pattern of leaf flush in *S. eriocarpa*. We randomly selected five willow trees and tagged seven 1-year-old shoots on each tree. After 16 May, when gall initiation was first observed, we counted the number of newly expanded leaves on ungallo and galloed shoots every week until 24 July, when secondary leaf flush was almost complete. The newly expanded leaves were individually marked with indelible oil marker to avoid double counting.

EFFECTS OF REGROWTH RESPONSES ON
PLANT QUALITY

To examine if the regrowth responses affected the nutritional and physical properties of *S. eriocarpa*, we measured nitrogen and water content, as well as the toughness of plant tissues, on galloed and ungalloed shoots. Aphids were observed colonizing apical stems of shoots, and adults of the two leaf beetles fed on leaves on the upper parts of shoots. We therefore measured N and water content, and the toughness of apical stems and upper leaves (Fig. 1). On 4 July 2001 we randomly selected 10 trees. On each tree, we randomly sampled a pair of ungalloed shoots and lateral shoots growing from galloed shoots (Fig. 1). Afterwards, we took these sampled shoots to the laboratory. To determine the toughness of apical stems and upper leaves, we used a penetrometer (Aikoh, Inc., Yokohama, Japan) to record the weight necessary to force a rod 0.6 or 2 mm in diameter through the apical stems and upper leaves, respectively. To determine the percentage water content, we measured the fresh weight of apical stems and upper leaves, and the weight after they had been oven-dried at 60 °C for 48 h. Percentage water content was calculated as (fresh weight – dry weight)/fresh weight. After the dried stems and leaves had been ground, we measured the percentage N content using an elemental analyser (CHN Corder MT-3, Yanaco, Kyoto, Japan).

EFFECTS OF REGROWTH RESPONSES ON
OTHER INSECT HERBIVORES

We conducted field surveys in 2000 and 2001 to determine if regrowth responses affected the feeding prefer-

ences of leaf beetles and aphids. On 14 July 2000, we randomly selected 10 1-year-old shoots from each of six randomly selected trees. We counted the number of adult *P. versicolora* on galloed and ungalloed shoots. We also counted the number of shoots with aphid colonies to estimate the colonization rate by aphids. The aphid colonization rate was defined as the number of shoots with aphids divided by the total number of observed shoots. In 2001, the same survey was conducted from 16–17 July on 22 randomly selected trees, on each of which 10–20 1-year-old shoots were randomly selected. Moreover, we counted the number of *S. semiaurantiaca* adults on ungalloed and galloed shoots, as *S. semiaurantiaca* adults were frequently observed feeding on young leaves in 2001.

STATISTICAL ANALYSES

Wilcoxon paired rank tests were used to compare the numbers of adult beetles, lateral shoots, and newly expanded leaves in mid-July between ungalloed and galloed shoots, where individual trees were replicates in the analysis. Fisher's exact test was used to compare aphid colonization rates between ungalloed and galloed shoots. A Mann–Whitney *U*-test was used to compare N and water content, as well as toughness of apical stems and upper leaves between ungalloed and lateral shoots.

Results

EFFECT OF GALL INITIATION ON WILLOW
REGROWTH

Gall midges stimulated the development of lateral shoots in *S. eriocarpa*. Galloed shoots produced five and six times as many lateral shoots as ungalloed shoots in 2000 and 2001, respectively (Wilcoxon paired rank test: $n = 6$, $Z = -2.201$, $P = 0.03$ for 2000; $n = 22$, $Z = -4.015$, $P < 0.01$ for 2001; Fig. 2). Moreover, gall midges affected temporal patterns of leaf flush in *S. eriocarpa* (Fig. 3). In mid-June, a secondary leaf flush occurred rapidly on galloed shoots and continued until late July. In contrast to the rapid leaf flush on galloed shoots, the cumulative number of leaves produced on ungalloed shoots increased gradually until late July. Consequently, galloed shoots produced seven times more newly expanded leaves per week in mid-July than did ungalloed shoots ($n = 5$, $Z = -2.023$, $P = 0.04$).

EFFECTS OF REGROWTH RESPONSES ON
PLANT QUALITY

We found large differences in nutritional and physical properties between apical stems of lateral shoots and those of ungalloed shoots. Apical stems of lateral shoots had a greater N and water content than those of ungalloed shoots (Mann–Whitney *U*-test: N content, $n = 10$, $U = 7$, $P < 0.01$; water content, $n = 10$, $U = 0$,

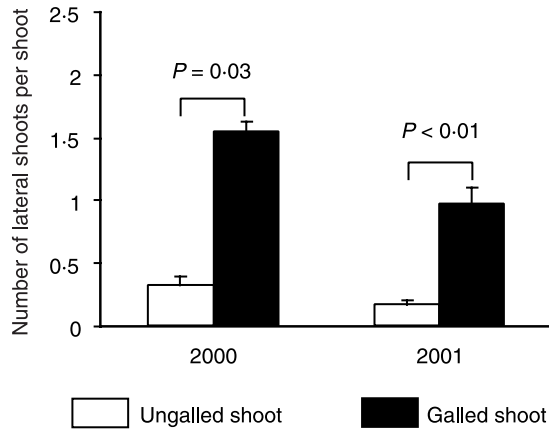


Fig. 2. Number of lateral shoots on ungalled and galled shoots (mean ± SE).

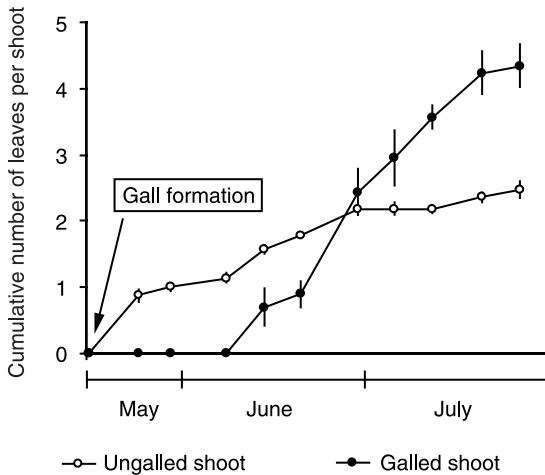


Fig. 3. Cumulative number of leaves produced on ungalled and galled shoots (mean ± SE).

$P < 0.01$; Table 1). Furthermore, apical stems of lateral shoots were softer than those of ungalled shoots ($n = 10$, $U = 0$, $P < 0.01$). Large differences in plant quality were also detected between upper leaves on lateral shoots and those on ungalled shoots. Upper leaves on lateral shoots had a greater N and water content than those on ungalled shoots (N content, $n = 10$, $U = 11$, $P < 0.01$; water content, $n = 10$, $U = 0$, $P < 0.01$; Table 1), and they were more tender than those on ungalled shoots ($n = 10$, $U = 0$, $P < 0.01$).

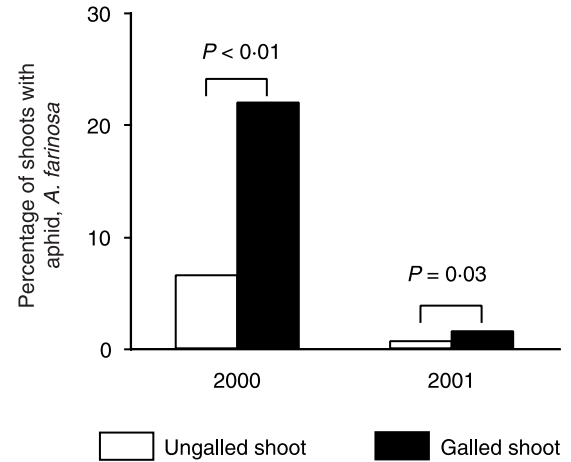


Fig. 4. Percentage of ungalled and galled shoots colonized by the aphid *Aphis farinosa* in mid-July. The total numbers of ungalled and galled shoots were 384 and 259 in 2000, and 461 and 200 in 2001, respectively.

EFFECTS OF REGROWTH RESPONSES ON OTHER INSECT HERBIVORES

It was clear that galled shoots were highly attractive to aphids and leaf beetles. Although there were variations among individual trees, the aphid colonization rate was significantly higher on galled than on ungalled shoots in both 2000 and 2001 (Fisher's exact test: $df = 1$, $\chi^2 = 28.316$, $P < 0.01$ for 2000; $df = 1$, $\chi^2 = 5.017$, $P = 0.03$ for 2001; Fig. 4). Aphids preferentially colonized apical stems of lateral shoots. The difference in the number of adult *P. versicolora* between ungalled and galled shoots was marginally significant in 2000 (Wilcoxon paired rank test: $n = 6$, $Z = -1.753$, $P = 0.08$; Fig. 5), although no difference was detected in 2001 ($n = 22$, $Z = -1.289$, $P = 0.20$). On the other hand, the number of *S. semiaurantiaca* adults was 10 times greater on galled shoots than on ungalled shoots in 2001 ($n = 22$, $Z = -3.479$, $P < 0.01$) (Fig. 5). Adults of both beetle species aggregated and fed on young leaves that were produced during the secondary leaf flush on galled shoots.

Discussion

This study clearly illustrated that gall initiation on current-year shoots stimulated the development of lateral

Table 1. Nitrogen and water contents, and toughness of apical stems and upper leaves of lateral and ungalled shoots

Characteristics	Shoot	Lateral shoots Mean ± SE	Ungalled shoots Mean ± SE
Nitrogen content (% DW)	Apical stems	1.61 ± 0.13 ^a	1.05 ± 0.08 ^b
	Upper leaves	2.55 ± 0.14 ^a	1.95 ± 0.07 ^b
Water content (% FW)	Apical stems	70.0 ± 1.3 ^a	59.9 ± 0.5 ^b
	Upper leaves	73.6 ± 0.7 ^a	61.5 ± 0.7 ^b
Toughness (N)	Apical stems	0.60 ± 0.05 ^a	2.22 ± 0.22 ^b
	Upper leaves	0.58 ± 0.18 ^a	1.92 ± 0.06 ^b

Different superscript letters show significant differences ($P < 0.01$).

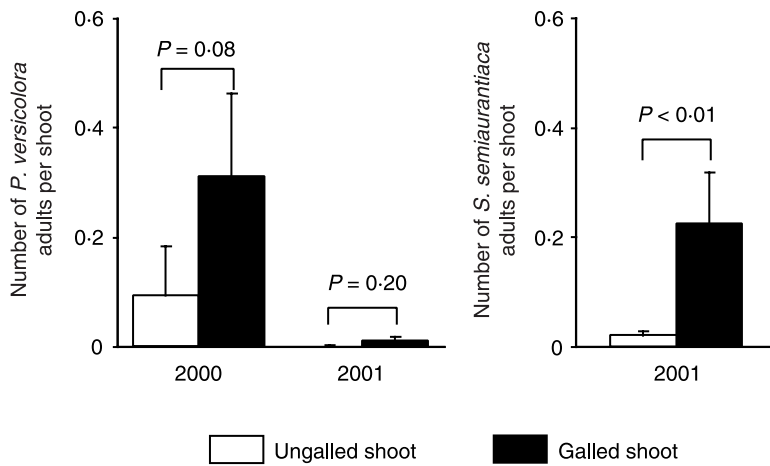


Fig. 5. Number of adult *Plagioder a versicolora* and *Smaragdina semiaurantiaca* on ungallo and gallo shoots in mid-July (mean \pm SE).

shoots, followed by a secondary leaf flush in *S. eriocarpa*. In addition, lateral shoots and upper leaves of gallo shoots were less tough and contained more water and N. Because the gall midge improved the availability of food resources in both quality and quantity through the regrowth responses of the willow, numbers of the aphid *A. farinosa* and the two leaf beetles *P. versicolora* and *S. semiaurantiaca* significantly or marginally increased on gallo shoots.

REGROWTH RESPONSES OF *SALIX ERIOCARPA*

The destruction of the apical meristem can release lateral shoots from apical dominance (Moorby & Wareing 1963). Apical dominance is defined as the control exerted by the shoot apex over the outgrowth of lateral buds, and is controlled by the ratio of cytokinin to auxin (Cline, Wessel & Iwamura 1997). Many studies have reported that the release of apical dominance stimulates lateral branching (Whitham & Mopper 1985; Mopper *et al.* 1991; Whitham *et al.* 1991; Pilson 1992). Our study also showed that gall initiation in the top regions of current-year shoots stimulated lateral branching in *S. eriocarpa*. This result strongly supports the apical dominance mechanism. Similarly, Nozawa & Ohgushi (2002) demonstrated that oviposition by the spittlebug *Aphrophora pectoralis* Matsumura into the upper parts of 1-year-old shoots in the previous autumn greatly enhanced the growth of current-year shoots in the following spring in two willow species of *Salix miyabeana* and *S. sachalinensis*.

IMPROVED NUTRITIONAL STATUS OF GALLO SHOOT

Herbivory often induces nutritional and/or physical changes in host plants (Schultz & Baldwin 1982; Danell & Huss-Danell 1985; Faeth 1986; Faeth 1987; Faeth 1988; Karban & Myers 1989; Bryant *et al.* 1991).

Most previous studies have demonstrated that insect herbivory decreases the nutritional status of damaged parts in host plants (Faeth 1986; Faeth 1987; Faeth 1988). For example, Schultz & Baldwin (1982) reported that leaves of red oak that had flushed after defoliation by the gypsy moth contained less water and N, and were tougher. In contrast, gallo shoots had lateral shoots and young leaves that were less tough, and had higher water and N content. These nutritional and physical changes were the result of the newly developing plant tissues during the regrowth responses of *S. eriocarpa*. This strongly indicates that gall initiation improved the host-plant quality of the willows. Similarly, Danell & Huss-Danell (1985) reported that after browsing by moose, birch trees produced larger leaves with more N as a result of compensatory regrowth.

POSITIVE PLANT-MEDIATED INTERACTIONS

Different insect herbivores living on a shared host plant have the potential to influence one another by modifying the architecture, physiology or biochemistry of the host plant (Crawley 1997). Our results showed that aphid and leaf beetle densities significantly or marginally increased on gallo shoots. These increases were due to the newly developing plant tissues resulting from the regrowth responses of *S. eriocarpa*. In this case, the regrowth responses not only increased plant biomass, but also improved the nutritional status of the gallo shoots. Thus the gall midge had positive plant-mediated effects on the feeding preferences of the aphid and the leaf beetles. Similarly, several studies have demonstrated that browsing by mammals induces compensatory regrowth in the browsed host plants, which increases or maintains the availability of food resources for many herbivorous insects (Danell & Huss-Danell 1985; Roininen, Price & Tahvanainen 1994; Hjäältén & Price 1996; Roininen, Price & Bryant 1997; Martinsen, Dreibe & Whitham 1998; Olofsson & Strengbom 2000). We emphasize that not only mammalian browsing, but also insect herbivory, has great potential to enhance the availability of food resources for other insect herbivores, when herbivory stimulates regrowth responses in host plants.

Previous studies have focused mainly on the increases in secondary chemicals and/or decreases in the nutritional status of host plants, both of which can negatively affect other insect herbivores (Faeth 1986; Faeth 1987; Haukioja & Neuvonen 1987; Faeth 1988; Karban & Myers 1989; Damman 1993; Denno, McClure & Ott 1995; Ohgushi 1997). This trend is probably due to the prevailing assumption that herbivory induces defensive responses in host plants which limit further herbivory (Faeth 1991). Therefore, regrowth responses of host plants following herbivory by insects have often been overlooked in studies of plant-mediated interactions (but see Craig, Price & Itami 1986; Damman 1989; Pilson 1992). In contrast, our study clearly illustrated that the gall midge stimulated regrowth

responses in *S. eriocarpa* which, in turn, positively affected the aphid and leaf beetles. This implies that the plant-mediated effects of insect herbivory can range from negative to positive for other insect herbivores (Faeth 1991; Damman 1993; Denno, McClure & Ott 1995; Ohgushi 1997). To understand the exact role of positive plant-mediated interactions, future studies are needed to seek for more evidence and underlying mechanisms of positive plant-mediated interactions on terrestrial plants, which have long been overlooked in plant–insect interactions.

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