

Host plant variation in plant-mediated indirect effects: moth boring-induced susceptibility of willows to a specialist leaf beetle

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Abstract. 1. We examined the plant-mediated indirect effects of the stem-boring moth *Endoclyta excrescens* (Lepidoptera: Hepialidae) on the leaf beetle *Plagioderia versicolora* (Coleoptera: Chrysomelidae) in three willow species, *Salix gilgiana*, *S. eriocarpa*, and *S. serissaefolia*.

2. When the stem-boring moth larvae damaged stems in the previous year, willows were stimulated to produce vigorously growing lateral shoots on these stems. These new lateral shoots were significantly longer and the upper leaves had significantly higher nitrogen and water content than current-year shoots on unbored stems, although the carbon content and leaf dry mass were not different between lateral and current-year shoots.

3. In the field, leaf beetle larvae and adults had significantly greater densities on lateral shoots of bored stems than on current-year shoots of unbored stems. A laboratory experiment showed that female beetles had significantly greater mass and fecundity when fed on leaves of newly-emerged lateral shoots. Thus, the stem-boring moth had a positive effect on the temporally and spatially separated leaf beetle by increasing resource availability by inducing compensatory regrowth.

4. The strength of the indirect effects on the density and performance of the leaf beetle differed among willow species, because there was interspecific variation in host quality and herbivore-induced changes in plant traits. In particular, we suggest that the differences in magnitude of the changes among willow species in shoot length and leaf nitrogen content greatly affected the strength of the plant-regrowth mediated indirect effect, coupled with host-plant preference of the leaf beetle.

Key words. Boring insect, compensatory regrowth, *Endoclyta excrescens*, induced response, interaction strength, *Plagioderia versicolora*, plant-mediated indirect effect.

Introduction

The prevalence of interspecific interactions among herbivorous insects has long been discounted in insect community ecology, because of the traditional view that food limitation for herbivores rarely occurs, and that therefore interspecific competition is unlikely to be important (Hairston *et al.*, 1960; Lawton & Strong, 1981). Recently, however, there has been increasing evidence that herbivorous insects sharing a host plant can affect one another by altering the quality and/or quantity of the host plant (Faeth, 1986; Damman, 1993; Denno *et al.*, 1995; Ohgushi,

2005, 2007; Kaplan & Denno 2007). Herbivory by one species often induces morphological, phenological, and chemical changes in a host plant (Karban & Baldwin, 1997), which, in turn, alters the resource availability to other herbivorous insects (Harrison & Karban, 1986; Moran & Whitham, 1990; Strauss, 1991; Nakamura *et al.*, 2003). Because herbivore-induced changes in plants are ubiquitous in terrestrial systems (Karban & Baldwin, 1997; Ohgushi, 2005), interactions among herbivore species that are separated in time and/or space are common (Ohgushi, 2005). Herbivore-induced changes in plant quality, such as decreases in nutritional status and biomass, and/or increase in secondary substances, leaf toughness, and density of thorns, spines, and trichomes (Masters & Brown, 1992; Inbar *et al.*, 1995; Denno *et al.*, 2000; Tindall & Stout, 2001; Wise & Weinberg, 2002; Denno & Kaplan, 2007), often have a negative

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impact on the survival and reproduction of insect herbivores. Herbivory can also induce compensatory regrowth (Whitham *et al.*, 1991) that often has a positive effect on other herbivorous insects by increasing the quality or quantity of food available (Damman, 1989; Martinsen *et al.*, 1998; Nozawa & Ohgushi, 2002; Nakamura *et al.*, 2003). Thus, insect herbivory that stimulates re-growth in host plants may increase their susceptibility to insect herbivores that emerge at a later time.

Winter browsing by herbivorous mammals often induces regrowth responses in many deciduous trees and shrubs, which result in longer and more vigorous shoots from browsed stumps or stems (Bryant, 1981; Danell & Huss-Danell, 1985; Bergström & Danell, 1987; Roininen *et al.*, 1997). Herbivorous insects, such as sucking, chewing, mining, and galling species, often greatly prefer the previously browsed branches (Danell & Huss-Danell, 1985; Hjältén & Price, 1996; Roininen *et al.*, 1997; Martinsen *et al.*, 1998; Olofsson & Strengbom, 2000), because young plant tissues often have improved nutritional status (Danell & Huss-Danell, 1985; Martinsen *et al.*, 1998). Insect herbivory can also have positive effects on other insect herbivores by inducing changes in plant traits (Craig *et al.*, 1986; Damman, 1989; Nakamura *et al.*, 2003). For example, early-season bud damage by the leaf beetle *Blepharida rhois* induces the production of basal vegetative shoots in the smooth sumac *Rhus glabra*, and these basal shoots are preferred as oviposition sites by cerambycid stem-boring larvae (Strauss, 1991). These studies have indicated that different feeding guilds of herbivorous insects that are separated in time and space can be linked in positive interactions through plant compensatory regrowth (Ohgushi, 2007).

Because plants have substantial interspecific variation in morphological and physiological traits that influence resistance and susceptibility to herbivores (Fritz, 1992; Fritz & Simms, 1992; Kennedy & Barbour, 1992), this variation may affect the strength of plant-mediated indirect effects. Moreover, plants also have interspecific variation in the induction of chemical, physical, morphological, and nutritional responses to herbivores (Fritz, 1992; Strauss & Agrawal, 1999). For example, differences in the availability of root-stored resources, which are determined by the species-specific shoot/root ratio, results in the different strength of compensatory regrowth among plant species (van der Meijden *et al.*, 1988; Schierenbeck *et al.*, 1994). The magnitude of changes in these plant traits after herbivory may determine the strength of plant-mediated indirect effects because the degree of induced plant susceptibility may be determined by the increases in leaf size, leaf nitrogen, and shoot length produced as compensatory responses to herbivory (Danell & Huss-Danell, 1985; Roininen *et al.*, 1997). Although understanding the strength of indirect effects is critical to develop predictions about the impacts of indirect effects in complex ecological communities (Wootton, 1997, 2002; Wootton & Emmerson, 2005), little is known about the causes of among-species variation in the strength of plant-mediated indirect effects.

Early summer stem-boring by the swift moth *Endoclita excrescens* (Butler) (Lepidoptera: Hepialidae) induces subsequent lateral shoot regrowth in three willow species, *Salix gilgiana*, *S. eriocarpa*, and *S. serissaefolia*. The newly-emerged lateral shoots grow more vigorously in response to the moth boring than current-year shoots on unbored stems, and moreover, the growth

rate and length of the newly-emerged lateral shoots differs among the three willow species (Utsumi & Ohgushi, 2007). Therefore, we predicted that swift moth boring will affect the feeding preference and performance of other insect herbivores by initiating plant compensatory regrowth, and that the strength of the plant-mediated indirect effects between herbivorous insects will depend on changes in plant traits as a result of herbivory.

We examined whether moth boring indirectly affects food availability for the leaf beetle *Plagioderia versicolora* (Laicharting) (Coleoptera: Chrysomelidae) that is a specialist on salicaceous plants. Specifically, we addressed the following questions: (i) does moth boring in the previous year induce a willow regrowth response? (ii) if so, how does the regrowth response alter the leaf nutrition of *S. gilgiana*, *S. eriocarpa*, and *S. serissaefolia*? (iii) how does the regrowth response affect the abundance and performance of the leaf beetle? and (iv) how does the strength of indirect effects on the leaf beetle, mediated by plant regrowth response, differ among willow species?

Materials and methods

Study area and organisms

A study plot 1 km × 300 m in area was located in a floodplain along the Yasu River (35°N, 136°E) in Shiga Prefecture, central Japan. In this study area, there is a patchy distribution of seven willow species: *Salix serissaefolia* Kimura, *Salix eriocarpa* Franch. et Savat., *Salix subfragilis* Andersson, *Salix integra* Thunb., *Salix gilgiana* Seemen, *Salix caenomeloides* Kimura, and *Salix gracilistyla* Miq. Understorey vegetation is dominated by *Solidago altissima* (Compositae) and *Miscanthus sacchariflorus* (Gramineae). Entrance tunnels bored by swift moth larvae were observed on all willow species. For this study, we chose three willow species, *S. gilgiana*, *S. eriocarpa*, and *S. serissaefolia*, which had high frequency of moth attacks.

The swift moth *E. excrescens* is a common hepialid moth in Japan. Hepialidae is a primitive group of Lepidoptera (Schulz *et al.*, 1990), called *ghost moths* or *swift moths*, which has a worldwide distribution (Kan *et al.*, 2002). They attack various herbaceous and woody plants (Enda, 1971; Igarashi, 1994). Females oviposit from September to October, and eggs hatch in the following spring. Newly-hatched larvae immediately bore into herbaceous plants and live there until the fourth instar when the larvae leave and bore into woody plants where they live from June until August. In general, willow stems that are ≥3 years old and ≥2.5 cm diameter are attacked, and larvae make cylindrical tunnels about 1.5 cm in diameter where they grow until adult eclosion (S. Utsumi and T. Ohgushi, unpubl. data). Larvae pass through 9–11 instars before pupation in the tunnels in September, and they usually eclose about 4 weeks later. However, some individuals overwinter as larvae and go through 12–15 instars before pupating in the following September (Enda, 1971; Igarashi, 1994). We could easily distinguish swift moth holes from those made by other borers because the larval tunnel entrance is made of frass and bound with silk and it has an easily identified architecture.

The leaf beetle *P. versicolora* is a specialist herbivore that feeds on leaves of *Salix* species (Kimoto & Takizawa, 1994).

Adult females lay 10–20 eggs in a cluster. Larvae pass through three instars, feed gregariously in the first and second instars, and then disperse within a plant as they develop (Kagata *et al.*, 2005). *Plagiodera versicolora* is distributed widely over Asia, Europe and North Africa (Kimoto & Takizawa, 1994). In our study area, it is one of the most abundant herbivorous insects on willows.

Effects of moth boring on willow regrowth and quality

We carried out a field survey to investigate how willow trees responded to larval feeding by the swift moth in the previous year. In mid-May 2001, five trees of each willow species were randomly selected, and we marked all moth entrances found on stems within 2.5 m of the ground. Afterwards, we checked monthly for new moth entrances until the end of 2001. In mid-May 2002, we recorded the number of lateral shoots that had emerged from the stems with moth entrances constructed in 2001. The lateral shoots produced in response to moth boring grew proximal to the entrance tunnel, and the upper part of the stem was rarely killed (Utsumi & Ohgushi, 2007). In each tree, we also counted the number of lateral shoots on three randomly selected unbored stems that were 3–5 cm in diameter to serve as controls. We calculated the lateral shoot density as the mean number of lateral shoots per 100 cm stem length. Mann–Whitney *U*-tests were used to compare the number and length of lateral shoots on bored stems with those on unbored stems.

To examine whether swift moth boring affects host plant quality through shoot regrowth, we compared the shoot length, dry mass, and the nitrogen, carbon, and water content of the upper leaves of newly-emerged lateral shoots of bored stems and current-year shoots of unbored stems. In mid-April 2002, five bored trees that had 12–15 cm basal trunk diameters were randomly selected in each willow species. In each tree, we randomly sampled five pairs of lateral shoots from bored stems and of current-year shoots from unbored stems, and brought them to the laboratory. A replicated pair consisted of a bored and an unbored stem branching from one stem. To determine leaf water content, we measured the fresh mass of the upper five leaves and the dry mass after they had been oven dried at 60 °C for 48 h. Percentage of water content was calculated as (fresh mass – dry mass)/fresh mass × 100. After the dried leaves were ground, nitrogen and carbon content were determined using an elemental analyser (NC-ANALYZER SUMIGRAPH NC-900, Sumika Chemical Analysis Service Ltd., Osaka, Japan). A Wilcoxon signed-rank test was used to compare shoot length, leaf dry mass, and the nitrogen, carbon, and water content in the leaves.

Effects of regrowth shoots on leaf beetle density

We conducted field surveys from May to September 2002, to investigate whether the foliage that sprouted in response to swift moth boring affected leaf beetle density. In mid-April, from each of the three willow species, we randomly selected five trees, with trunks of 12–15 cm basal diameter, in each of two herbivory classes: heavily bored by moths and lightly bored by moths (i.e. 10 trees per species total). Lightly bored trees were

defined as trees in which bored stems were ≤20% of all stems, and heavily bored were >20% of all stems. On each heavily bored tree, we selected five pairs of stems: one that was unbored and one that was bored by swift moth larvae in 2001. A replicated pair consisted of a bored and an unbored stem branching from one stem. As controls, we selected five unbored stems from the lightly bored trees of each willow species. All stems were 3–5 cm in diameter. On 3 May, we marked all newly-emerged lateral shoots on selected bored stems, and we also marked 5–20 randomly selected current-year shoots randomly on each of the unbored and control stems. Each month we recorded the numbers of leaf beetle larvae and adults on the marked shoots of three shoot types (on bored trees, newly-emerged lateral shoots of a bored stem and current-year shoots of unbored stems, and on less bored trees, current-year shoots of control stems). We defined a current-year shoot as a shoot growing from a 1-year-old shoot on selected stems, and a newly-emerged lateral shoot as a shoot growing proximal to the boring entrance of a bored stem (Utsumi & Ohgushi, 2007). We calculated the mean numbers of the leaf beetles on each shoot of the three shoot types from May to August, and each stem was treated as a replicate ($n = 25$). To examine the effects of shoot length on leaf beetle density, in early June we also measured the length of the marked shoots on each stem. We performed an ANCOVA test with shoot types and willow species as main effects on beetle density and shoot length as a covariate. A least significant difference (LSD) method multiple comparison was performed as a *post hoc* test. For these analyses, we used log ($n + 1$)-transformed numbers because the assumption of normality was not met.

Effects of regrowth shoots on performance of the leaf beetle

We conducted a laboratory experiment to examine whether changes in leaf quality through shoot regrowth affected survival from hatch until eclosion, adult mass, and reproduction of the leaf beetle. Twenty egg masses of *P. versicolora* were collected from the study site in mid-May 2002. Each egg mass was placed in a plastic container (10 × 14 × 2.5 cm) in the laboratory. Larvae were used in an experiment within 24 h after hatching. Ten to 20 larvae hatched from a single egg mass and they were randomly divided into two groups to assign to a bioassay of either leaves from newly-emerged lateral shoots on bored stems, or of leaves from current-year shoots on unbored stems. The groups of beetle larvae were provided with one to two intact mature leaves taken from the upper reaches of shoots in a plastic container lined on the bottom with moist filter paper and they were reared until adult eclosion in an environmental chamber at 23 °C, LD 16:8 h. These leaves were collected from newly-emerged lateral shoots from bored stems and from current-year shoots of unbored stems of five trees in each of three willow species in the field site. Although *P. versicolora* adults prefer young leaves, larvae feed on mature leaves in the field (Raupp & Denno, 1983). To estimate how the quality of food fed on by the larvae in the field affected larval growth and survival, mature leaves were used as food for beetle larvae in the rearing experiment. To obtain mature leaves, we chose dark green leaves from the 8th–15th nodes from the top of a shoot with newly flushing

leaves. We did not use light green leaves at 1st–5th nodes because they were young aged <1 week after bud break. Leaves were replaced every other day until pupation. Adults were weighed within 24 h after eclosion individually, and their sex was determined by morphology and size. The survival rate from larva hatched to adult eclosion was also determined. Afterwards, we randomly selected 10 pairs of male and female adults from reared beetles in each willow species. Each pair was provided with five to six leaves taken from the upper reaches of shoots, which were collected and prepared for the bioassay in the same way as they were for the larvae. We recorded the oviposition schedule for 3 weeks. A two-way ANOVA test was performed to determine effects of shoot types (new lateral shoots of bored stems and current-year shoots of unbored stems) and willow species on larval survival rate, body mass, and number of total eggs. Before analyses, the data on survival rates were arcsine square-root transformed, and numbers of total eggs were square-root transformed because the assumptions of normality and equal variances were not met.

Strength of plant-mediated indirect effects in three willow species

We compared the relative changes in larval and adult densities among three willow species, to examine how interspecific variation among host plants affected the strength of plant-mediated indirect effects of moth boring on the leaf beetle. For these analyses, we used the field survey data and applied the log response ratio, which is widely used to compare interaction strength (Paine, 1992; Borer *et al.*, 2005). Changes in leaf beetle density were expressed as log response ratio, using $\ln[(LSi)/(CSi)]$. LS and CS are values for the newly-emerged lateral shoots on bored stems, and the current-year shoots on unbored stems, respectively. *i* denotes a replicate of a pair of LS and CS. We also calculated the log response ratio of female body mass, and total number of eggs laid. Density and fecundity were $(n + 1)$ transformed before calculation. An ANOVA test was performed to examine the effects of willow species on the log response ratio of the leaf beetle density and performance. When the species effect was significant, a LSD multiple comparison was then conducted as a *post hoc* test. We also compared the changes in shoot length and leaf quality in response to moth boring to examine how the trait modification of host plants affected the strength of the plant-mediated indirect effects. The log response ratios of shoot length, leaf dry mass, water, nitrogen, and carbon content were calculated and these values were analysed using a MANOVA test to examine the effects of willow species on the magnitude of trait changes.

Results

Effects of moth boring on willow regrowth and quality

Moth boring in the previous year stimulated the production of lateral shoots in the spring (Fig. 1). The density of new lateral shoots on bored stems in spring 2002 was 3–42 times higher than that on unbored stems (Mann–Whitney *U*-test: *S. gilgiana*,

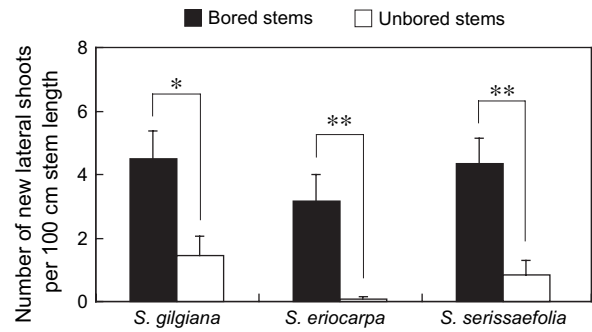


Fig. 1. Mean density of new lateral shoots on stems bored by swift moth larva (*S. gilgiana*: $n = 37$, *S. eriocarpa*: $n = 33$, *S. serissaefolia*: $n = 67$) and unbored stems ($n = 15$ for each species). Vertical bars indicate SE. * $P < 0.05$, ** $P < 0.01$.

$U = 160$, $P = 0.015$; *S. eriocarpa*, $U = 123$, $P < 0.01$; *S. serissaefolia*, $U = 276.5$, $P < 0.01$). The shoot characteristics of new lateral shoots of bored stems were significantly different from those of current-year shoots of unbored stems (Table 1). The new lateral shoots of bored stems were three to five times longer than the current-year shoots of unbored stems. Upper leaves of lateral shoots had 1.1–1.3 times greater nitrogen and 1.03–1.09 times higher water content than those of current-year shoots. On the other hand, there were no significant differences in carbon content and leaf dry mass between leaves from bored and unbored stems except on *S. eriocarpa*.

Effects of regrowth shoots on leaf beetle density

The field survey showed that swift moth boring, willow species, and their interaction significantly affect the number of larvae and adults of *P. versicolora* (Table 2, Fig. 2). Results of the ANCOVA suggest that the increase in leaf beetle density resulted from not only the increase in shoot length of lateral shoots but also other differences among shoot types. Larval density was 8–45 times higher on the new lateral shoots compared with the density on the current-year shoots of control stems in each willow species (LSD test: $P < 0.05$), and adult density increased by 5–10 times on the new lateral shoots except for *S. serissaefolia* (LSD test: $P < 0.05$). We found no significant differences in larval and adult densities between current-year shoots of unbored stems and controls among three willow species (LSD test: $P > 0.05$). In contrast, larval and adult densities on the new lateral shoots were significantly higher in *S. gilgiana* than those in the other two species (LSD test: $P < 0.05$). Also, there were no significant differences in densities of adults and larvae between current-year shoots of unbored stems and controls in each willow species (LSD test: $P > 0.05$).

Effects of regrowth shoots on performance of the leaf beetle

The laboratory experiment showed that feeding on leaves of the lateral shoots of bored stems improved the performance of

Table 1. Characteristics of newly-emerged lateral shoots of bored stems and current-year shoots of unbored stems in three willow species.

Characteristics	Willow species	Newly-emerged lateral shoot, Mean (SE)	Current-year shoot, Mean (SE)	Wilcoxon signed-rank test	
				Z	P
Shoot length (cm)	<i>S. gilgiana</i>	34.88 (3.66)	6.43 (0.64)	-3.407	<0.001
	<i>S. eriocarpa</i>	19.17 (1.92)	6.11 (0.74)	-3.621	<0.001
	<i>S. serissaefolia</i>	14.93 (1.54)	4.36 (0.39)	-3.407	<0.001
Leaf dry mass (mg)	<i>S. gilgiana</i>	34.19 (4.26)	43.84 (5.15)	-1.682	0.093
	<i>S. eriocarpa</i>	45.66 (6.71)	63.67 (7.65)	-2.435	0.015
	<i>S. serissaefolia</i>	8.32 (0.74)	8.63 (0.58)	-0.349	0.726
Nitrogen content (% dry mass)	<i>S. gilgiana</i>	3.63 (0.10)	3.43 (0.09)	-2.127	0.033
	<i>S. eriocarpa</i>	3.61 (0.01)	2.77 (0.09)	-4.608	<0.01
	<i>S. serissaefolia</i>	3.75 (0.10)	3.40 (0.09)	-2.533	0.011
Carbon content (% dry mass)	<i>S. gilgiana</i>	46.22 (0.24)	46.08 (0.28)	0.530	0.530
	<i>S. eriocarpa</i>	45.95 (0.30)	45.21 (0.19)	-2.274	0.023
	<i>S. serissaefolia</i>	46.11 (0.42)	44.91 (0.36)	-1.717	0.086
Water content (% fresh mass)	<i>S. gilgiana</i>	77.70 (0.48)	71.07 (0.90)	-4.023	<0.01
	<i>S. eriocarpa</i>	74.23 (0.51)	72.07 (0.68)	-2.005	0.045
	<i>S. serissaefolia</i>	76.68 (0.27)	74.22 (0.66)	-3.242	<0.01

Mean and SE are presented ($n = 25$).

the leaf beetle (Table 3). Female larvae fed on leaves of the new lateral shoots were 1.1–1.2 times heavier than those fed on leaves of current-year shoots in each willow species (LSD test: $P < 0.05$), although in males a significant difference was found only in *S. eriocarpa* (Fig. 3). The total egg production of females that fed on leaves of the new lateral shoots was 1.4–7.2 times greater than those that fed on leaves of current-year shoots in three willow species (LSD test: $P < 0.05$). Shoot types did not significantly affect larval survival rates (Table 3).

Significant effects of willow species were detected on female body mass and total egg production (Table 3). Although the body mass of females fed on leaves of current-year shoots of unbored stems did not differ among the three willow species, females fed on leaves of the new lateral shoots of *S. eriocarpa* were significantly heavier than those of other two species (LSD test: $P < 0.05$, Fig. 3). However, it should be noted that total egg production of the adult beetles fed on leaves of new lateral and current-year shoots was significantly greater in *S. gilgiana* than those in the other willow species, (LSD test: $P < 0.05$). Also, no significant difference was detected in male body mass of the larvae fed on leaves of current-year shoots among three willow

species (LSD test: $P > 0.05$), and willow species did not significantly affect larval survival rates.

Strength of plant-mediated indirect effects in three willow species

The willow-species effect was significant in the MANOVA test of log response ratios of plant trait changes (Wilk's lambda = 0.428, $F_{10,136} = 7.190$, $P < 0.0001$). The log response ratios of shoot length and leaf nitrogen content were significantly different among the three willow species (shoot length: $F_{2,72} = 16.053$, $P < 0.0001$, nitrogen content: $F_{2,72} = 11.590$, $P < 0.0001$, Fig. 4). Moth boring had a 1.6–1.7 times greater response effect on shoot length in *S. gilgiana* relative to the other species (LSD test: $P < 0.05$) and 2.7–4.7 times greater response effect on the upper leaf nitrogen content of the lateral shoots in *S. eriocarpa* relative to other species (LSD test: $P < 0.05$). No significant differences were detected in the response ratio of carbon content, water content, and leaf dry mass (carbon content: $F_{2,72} = 2.286$, $P = 0.109$, water content: $F_{2,72} = 0.0346$, $P = 0.966$, leaf dry mass: $F_{2,72} = 1.242$, $P = 0.295$).

Table 2. ANCOVA for the effects of three shoot types (new lateral shoots of bored stems, current-year shoots of unbored stems, and current-year shoots of controls) and willow species on densities of larvae and adults of the leaf beetle, *Plagioderma versicolora*. Because tests for differences in regression slopes (shoot type \times covariate and willow species \times covariate interactions) and the interaction term type \times species \times covariate were not significantly different ($P > 0.05$), these were omitted from the models.

Source of variation	Larva			Adult		
	d.f.	F	P	d.f.	F	P
Shoot type	2, 215	23.28	<0.001	2, 215	15.12	<0.001
Willow species	2, 215	17.25	<0.001	2, 215	6.92	0.001
Type \times Species	4, 215	16.66	<0.001	4, 215	5.91	<0.001
Shoot length (covariate)	1, 215	6.39	0.012	1, 215	0.05	0.821

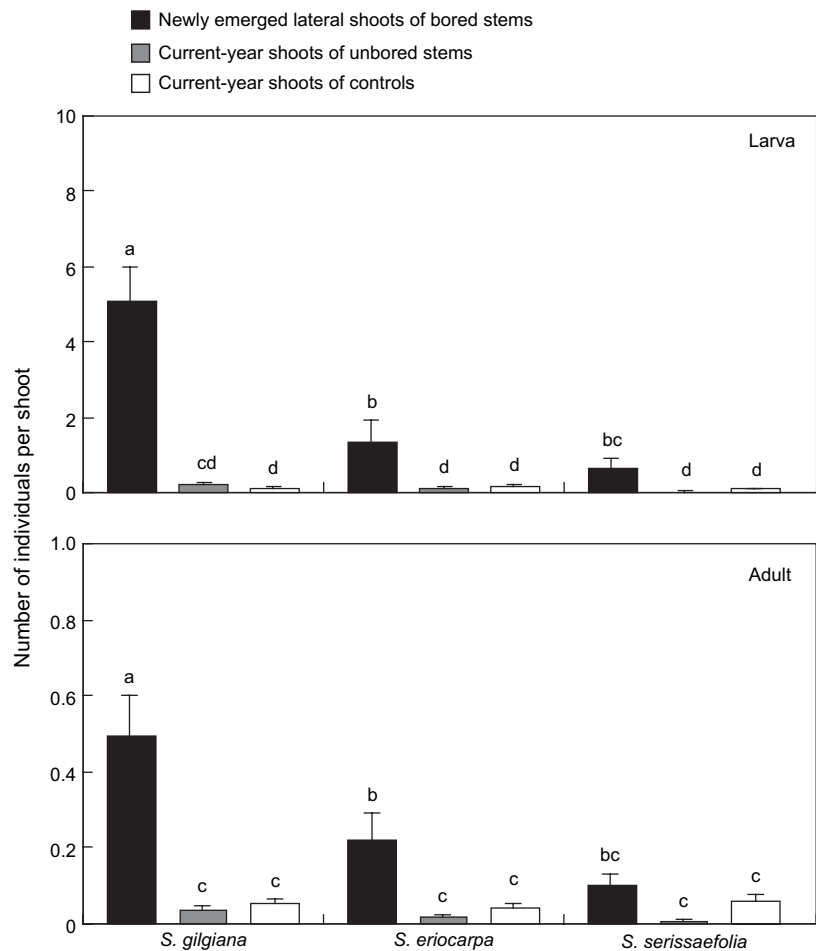


Fig. 2. Mean density of the leaf beetle larvae and adults on three types of shoots ($n = 25$). Vertical bars indicate SE. Different letters show significant difference with $P < 0.05$.

Response effects in larval and adult densities of the leaf beetle were 2.5–4.2 times greater in *S. gilgiana* (LSD test: $P < 0.05$, Fig. 4). Moth boring increased the response effects on both female body mass by 1.9–3.1 times and total egg production by 1.2–5.6 times in *S. eriocarpa* relative to other species (LSD test: $P < 0.05$, Fig. 4).

Discussion

This study clearly demonstrates that swift moth boring in the previous year stimulates the production of long and vigorous lateral

shoots with high quality leaves. Because moth boring improves the resource availability both in quantity and quality as the result of the willow regrowth response, moth boring increases the leaf beetle density. Leaf beetle performance, in terms of body mass and egg production, was improved when fed on leaves of the newly-emerged lateral shoots. These results support the plant vigor hypothesis (Price, 1991) that insect herbivores are more abundant on more vigorous plant tissues. The interaction between moth boring and willow species affected the density and performance of the leaf beetle. The magnitude of changes in host plant traits varied among willow species, and as a result the increases in leaf beetle density and performance differed among willow species.

Table 3. Two-way ANOVA for the effects of food resource of two shoot types (new lateral shoots of bored stems, current-year shoots of unbored stems) and willow species on performance parameters of the leaf beetle in the laboratory experiment.

Performance	Shoot type			Willow species			Type × species		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Survival rate	1,53	0.12	0.726	2,53	0.56	0.573	2,53	0.02	0.982
Male body mass	1,47	7.67	0.008	2,47	1.55	0.224	2,47	1.20	0.311
Female body mass	1,48	22.08	<0.001	2,48	5.07	0.010	2,48	1.01	0.373
Total egg production	1,48	20.11	<0.001	2,48	58.74	<0.001	2,48	0.72	0.491

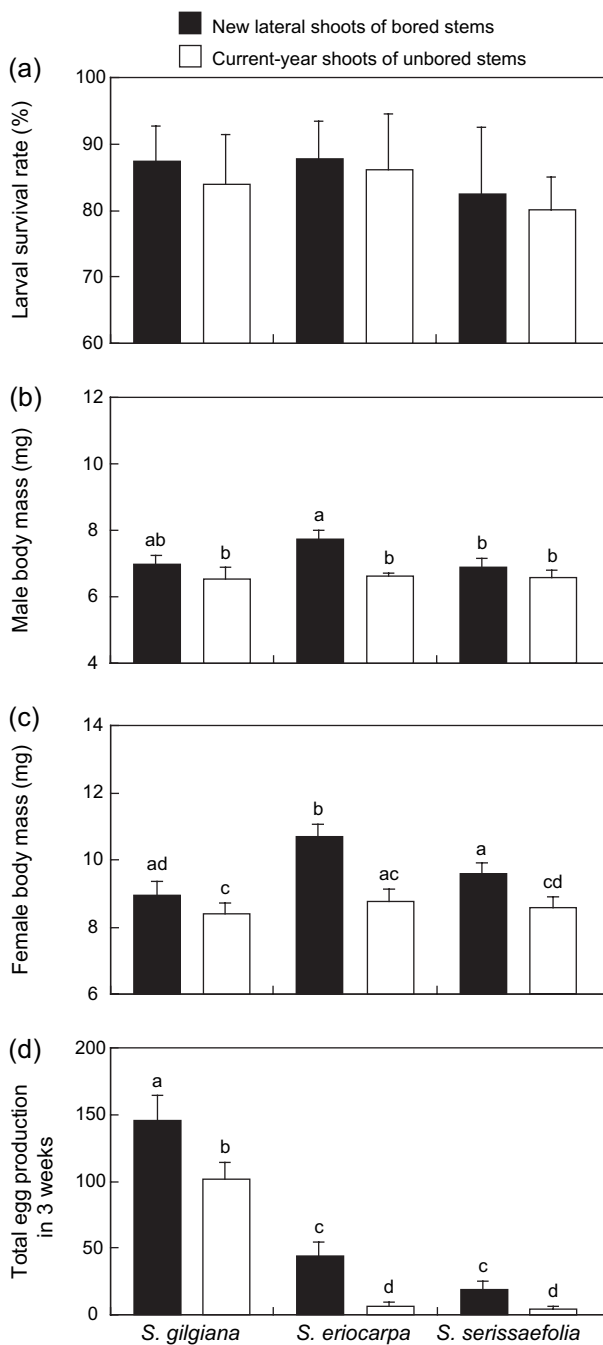


Fig. 3. Performance of the leaf beetle fed on leaves of newly-emerged lateral shoots on bored stems and current-year shoots on unbored stems. (a) Survival rate of larvae, (b) male adult mass, (c) female adult mass, and (d) total number of eggs laid per female in 3 weeks. Vertical bars indicate SE. Different letters show significant difference with $P < 0.05$.

Willow regrowth in response to stem boring

The lateral shoot production was initiated within a month after moth boring in these willows (S. Utsumi and T. Ohgushi, unpubl. data), and this study revealed that the regrowth response

of damaged trees carried over into the following year. Several studies have shown such long-term responses to damage over years in willows (Nozawa & Ohgushi, 2002; Nakamura *et al.*, 2005). It is widely accepted that herbivory that destroys plant apical meristems can release dormant buds from apical dominance, resulting in enhanced lateral branching (Whitham & Mopper, 1985; Strauss, 1991; Whitham *et al.*, 1991; Pilson, 1992; Nakamura *et al.*, 2003). Although swift moths do not kill apical meristems, they may alter sink-source relationships within a tree and subsequently induce compensatory regrowth (Utsumi & Ohgushi, 2007). Furthermore, regrowth shoots produced new leaves with higher concentrations of nitrogen and water in all three willow species. Several other studies have also shown that compensatory regrowth of woody plants not only increases shoot biomass but also improves leaf and shoot nutritional status (Danell & Huss-Danell, 1985; Martinsen *et al.*, 1998; Nakamura *et al.*, 2003). These nutritional changes are as a result of the induction of the new vigorous plant tissue growth in response to herbivory (Bryant *et al.*, 1983).

We found that *S. gilgiana* responded most strongly in increasing shoot growth, and *S. eriocarpa* in increasing nitrogen content after herbivory. However, the response ratios of water and carbon content were not significantly different among willow species. Plant compensatory responses to herbivory often vary, depending on extrinsic (herbivory type, timing of attack, severity of damage, and resource availability) and intrinsic (plant species and genotype) factors (Rosenthal & Kontanen, 1994). Artificial boring that caused the same level of damage resulted in the same trend of increasing shoot growth among these three willow species (Utsumi & Ohgushi, 2007) as did moth boring. Therefore we concluded that variation among willow species in trait changes induced by moth boring in this study are likely to be mainly as a result of willow species. Species-specific factors that influence plant regrowth include growth rate, storage capacity, flexibility of photosynthetic rates, allocation patterns, and nutrient uptake (Rosenthal & Kontanen, 1994; Strauss & Agrawal, 1999). Several studies have demonstrated that lateral shoot elongation differs among plant species because of species-specific resource reallocation within a plant after herbivory (Maschinski & Whitham, 1989; Schierenbeck *et al.*, 1994). There is also interspecific variation in the capacity for resource reallocation among willow species (Ceulemans *et al.*, 1996), and *S. gilgiana* may have a greater capacity of resource reallocation than other willow species. The relative nitrogen increase was greater in *S. eriocarpa* than in the other two species, but the underlying mechanism is unclear.

Indirect effects mediated by plant regrowth

Insect herbivores living on a shared host plant have the potential to influence each other by modifying the architecture, physiology, or biochemistry of the plant (Crawley, 1997; Ohgushi, 2005, 2007). Herbivory often induces compensatory regrowth, which subsequently increases density of other herbivorous insects (Danell & Huss-Danell, 1985; Hjältén & Price, 1996; Roininen *et al.*, 1997; Martinsen *et al.*, 1998; Olofsson & Strengbom, 2000; Nakamura *et al.*, 2003). This is because

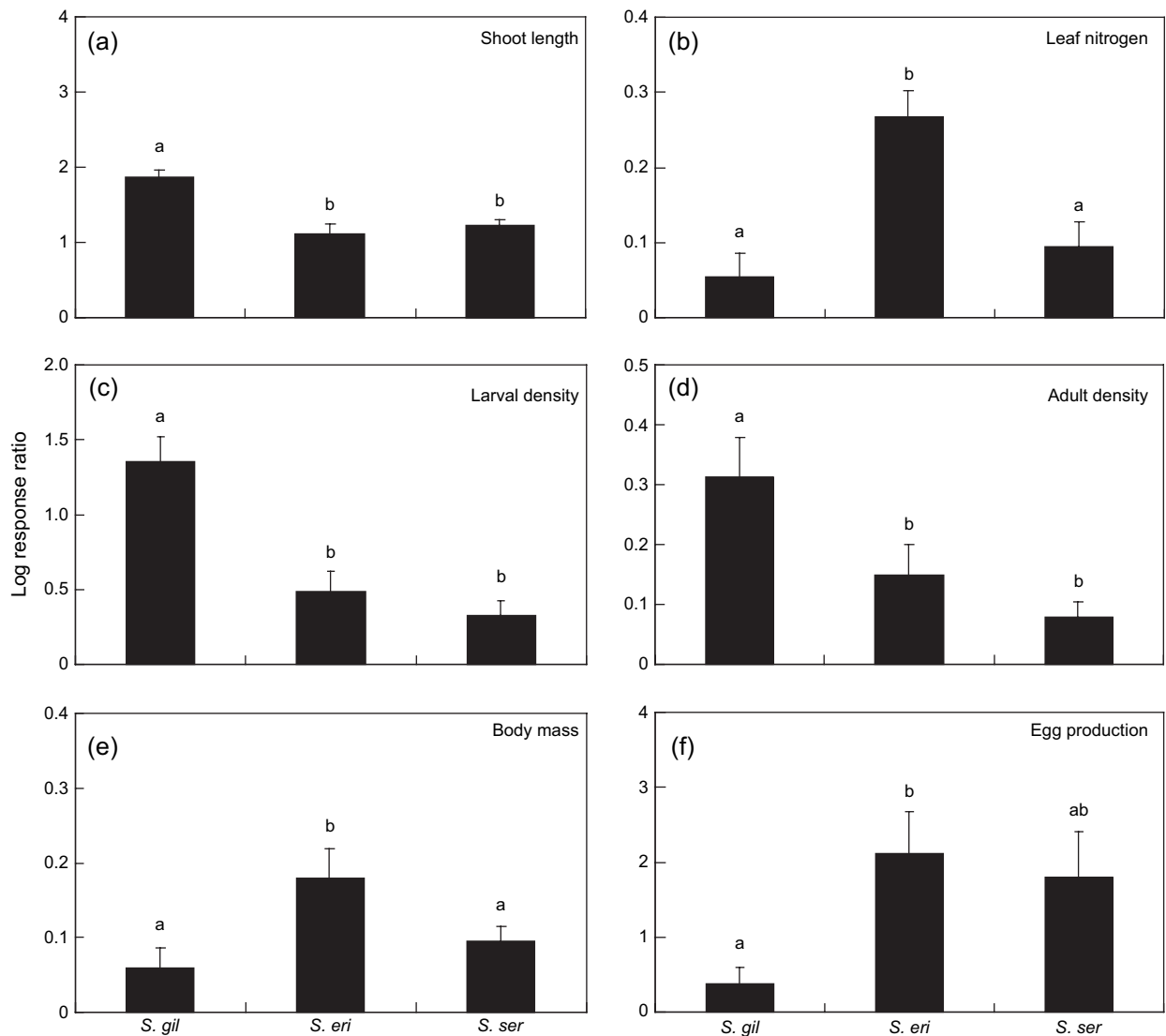


Fig. 4. Log response ratio calculated as $\ln[(LS)/(CS)]$. LS is a measure of the leaf beetle and shoot traits on newly-emerged lateral shoots in response to boring. CS is a measure of those on current year shoots on unbored stems (see Materials and methods). Relative changes in (a) shoot length and (b) foliar nitrogen content of host plants, relative density increase in (c) leaf beetle larvae and (d) adults in the field, and relative increase in (e) female body mass of the leaf beetle adults and (f) egg production per female adult were shown. *S. gil*: *S. gilgiana*, *S. eri*: *S. eriocarpa*, *S. ser*: *S. serissaefolia*. Vertical bars indicate SE. Different letters show significant difference with $P < 0.05$.

regrowth shoots produced in response to damage often provide increased food resources with high nutritional quality for herbivores (Danell & Huss-Danell, 1985; Roininen *et al.*, 1997; Bryant, 2003; Nakamura *et al.*, 2003), and the enhanced plant quality increases herbivorous insect performance as indicated by such factors as increases in body mass in herbivorous insects (Martinsen *et al.*, 1998; Kagata *et al.*, 2005). We know little about whether plant regrowth after herbivory can affect the egg production of herbivorous insects that subsequently attack the plant (but see Brown & Weis, 1995). Previous studies have reported that the fecundity of herbivore species increases because foliage nitrogen increases when plants are fertilized (Jauset *et al.*, 1998; Awmack & Leather, 2002; Wang *et al.*,

2006). Hence, swift moth boring is likely to increase egg production of the leaf beetle as a result of increased leaf nitrogen content. Moreover, enhanced shoot elongation, which is often correlated with faster leaf initiation rates, can provide more preferred food resources for adult beetles (Raupp & Denno, 1983; Price, 1991; Wait *et al.*, 2002). Therefore, the increase in leaf beetle density in response to the compensatory regrowth is likely to have resulted both from enhanced colonization by the adult beetles, and increased reproductive output as a result of the high food quality of the new lateral shoots. Consequently, moth boring positively influenced not only the density and body mass, but also the reproductive performance of the leaf beetle through plant-mediated indirect effects.

Variable strength of the plant-mediated indirect effects among willow species

This study revealed that the strength of the positive indirect effects varied among willow species. There are two factors responsible for causing the among-species variation in the strength of the plant-mediated indirect effect: (i) the difference in the preference among host plant species by a focal herbivore, and (ii) the difference in the intensity of changes in host plant traits among host species in response to herbivory. First, most herbivorous insects show difference in feeding and/or oviposition preference among host plants (e.g. Waddell & Mousseau, 1996; Yamaga & Ohgushi, 1999; Craig & Ohgushi, 2002). However, biotic and abiotic factors, such as host plant abundance, existence of non-host plants, apparency of host plants, soil nutrition, and shading, often alter the host preference in the field (Courtney & Kibota, 1990; Thompson & Pellmyr, 1991; Waddell & Mousseau, 1996). Thus, herbivore density on different host plants is often inconsistent with the expectation by its host plant preference (Courtney & Kibota, 1990; Rousi *et al.*, 1996; Forkner & Hunter, 2000). For example, Forkner and Hunter (2000) demonstrated that 1.4-fold variation in leaf-chewer density between two oak species increased to 2.4-fold variation when plant sizes of both species increased similarly by fertilization. In the laboratory experiment, *S. gilgiana* originally provided more suitable food for the leaf beetle than the other two species as indicated by the 16 times greater egg production of the leaf beetle fed on *S. gilgiana* leaves compared with that fed on other willow species. However, beetle density on non-regrowth *S. gilgiana* did not differ from that on other willow species in the field. This is because young leaves, for which adult beetles have a strong preference, may often be lacking as a result of seasonal decline in leaf production and concentration of feeding on young leaves. When moth boring induced secondary regrowth and resulted in subsequent leaf flushing in *S. gilgiana*, adult and larval densities significantly increased compared with those on other willow species. Second, there is also an interspecific variation in the intensity of the compensatory response to herbivore, which can affect subsequent attack by herbivores (van der Meijden, 1988; Schierenbeck *et al.*, 1994; Rosenthal & Welter, 1995). Positive indirect effects mediated by plant compensatory regrowth are mostly caused by an increase in plant vigor, such as increases in leaf size, leaf nitrogen, and shoot length (Danell & Huss-Danell, 1985; Price, 1991; Roininen *et al.*, 1997). In contrast, a few studies demonstrated that browsing of willows and aspens often reduced the densities of galling and leaf-feeding insects because of the reduction in leaf size and shoot length as a result of undercompensation after browsing (Bailey & Whitham, 2003; den Herder *et al.*, 2004). These findings suggest that the sign and the strength of indirect effects mediated by the plant compensatory response largely depend on the extent of the compensation. We suggest that these two factors are not mutually exclusive, so the variation among the three willow species in the strength of the indirect effects could result from the combined effects of them. After moth boring, the regrowth response of *S. gilgiana* provides both more abundant resource with rich quality and more preferable resource. Therefore, plant-mediated indirect effects

produced larger, increases in leaf beetle density on *S. gilgiana* than on the other two willows. On the other hand, the relative increase in foliar nitrogen content was greater in *S. eriocarpa* than in the other two species, and this produced the larger increases in female body mass and egg production on this species compared with that on the other two species. Moth boring did not affect the adult beetle density in *S. serissaefolia* because neither shoot length nor nitrogen content increased significantly. Thus, the strength of the plant-mediated indirect effect is likely to be determined by the interaction between host preference of the focal herbivore and the relative changes in plant traits, such as shoot length and leaf nitrogen content.

Our study clearly illustrates the indirect effects mediated by changes in plant traits caused by moth boring; swift moth boring stimulates the lateral shoot production of *S. gilgiana*, *S. eriocarpa*, and *S. serissaefolia* in the following year. This secondary lateral shoot production enhances the abundance and reproduction of the leaf beetle through increased resource availability. Herbivore preference among host plant species and the intensity of herbivore-induced trait changes that vary in a species-specific manner interact to affect the variation in the strength of the plant-mediated indirect effects on the leaf beetle density among willow species. In particular, the magnitude of increases in shoot length and leaf nitrogen content is likely to be a key factor in determining the strength of the plant-regrowth mediated indirect effects. To understand the consequences of plant-mediated indirect effects in herbivore insect assemblages, we should pay more attention to how variation in herbivore-induced plant trait changes alters the strength of the plant-mediated indirect effects. Future studies need to explore how plant characteristics including taxa, life histories, life forms, and trade-offs between different traits, produce a variation of herbivore-induced trait modifications. Such studies would provide a valuable insight to understand a mechanistic basis for variable plant-mediated indirect interactions among herbivorous insects.

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