Research

Community-wide impacts of herbivore-induced plant regrowth on arthropods in a multi-willow species system

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It has been widely accepted that herbivory induces morphological, phenological, and chemical changes in a wide variety of terrestrial plants. There is an increasing appreciation that herbivore-induced plant responses affect the performance and abundance of other arthropods. However, we still have a poor understanding of the effects of induced plant responses on community structures of arthropods. We examined the community-level effects of willow regrowth in response to damage by larvae of swift moth *Endoclita excrescence* (Lepidoptera: Hepialidae) on herbivorous and predaceous arthropods on three willow species, *Salix gilgiana*, *S. eriocarpa* and *S. serissaefolia*. The leaves of sprouting lateral shoots induced by moth-boring had a low C:N ratio. The overall abundance and species richness of herbivorous insects on the lateral shoots were increased on all three willow species. Densities of specialist chewers and sap-feeders, and leaf miners increased on the newly emerged lateral shoots. In contrast, the densities of generalist chewers and sap-feeders, and gall makers did not increase. Furthermore, ant and spider densities, and the overall abundance and species richness of predaceous arthropods increased on the lateral shoots on *S. gilgiana* and *S. eriocarpa*, but not *S. serissaefolia*. In addition to finding that effects of moth-boring on arthropod abundance and species richness varied among willow species, we also found that moth-boring, willow species, and their interaction differentially affected community composition. Our findings suggest that moth-boring has community-wide impacts on arthropod assemblages across three trophic levels via induced shoot regrowth and increase arthropod species diversity in this three willow species system.

Understanding the mechanisms of the maintenance of local species diversity is a central theme in ecology (Abrams 1995, Chesson 2000, Gallet et al. 2007). The diversity of organisms comprising biological communities is influenced by interactions among species. Previous studies on these biotic interactions have mainly focused on competition, predation, parasitism, and mutualism (Paine 1966, Lawton and Strong 1981). Recently, several authors have argued that community structure and species diversity of arthropods on terrestrial plants are affected by plant-mediated indirect interactions among insect species (Waltz and Whitham 1997, Martinsen et al. 2000, Ohgushi 2005, Ohgushi et al. 2007).

It is widely accepted that herbivory induces morphological, phenological and chemical changes in most terrestrial plants (Karban and Baldwin 1997, Ohgushi 2005). Herbivore-induced modification of plant quality often has negative impacts on the survival and reproduction of insect herbivores, because of decreases in nutritional status, and/or increased defense in terms of secondary chemicals, leaf toughness, density of thorns, spines and trichomes (Masters and Brown 1992, Denno et al. 2000, Tindall and Stout 2001, Denno and Kaplan 2007). Herbivory also induces plant responses that can compensate partially or fully for damaged tissues in many woody and herbaceous plants

(Whitham et al. 1991, Rosenthal and Kontanen 1994). These compensatory regrowth responses often have positive effects on the abundance and performance of herbivorous insects via increases in food quality or quantity (Danell and Huss-Danell 1985, Strauss 1991, Martinsen et al. 1998, Nakamura et al. 2003).

Only a few studies have demonstrated that herbivore-induced plant responses have impacts on community structures and species diversity of arthropods (Waltz and Whitham 1997, Agrawal 2000, Bailey and Whitham 2002, Van Zandt and Agrawal 2004). There are three features of a community-wide impact of herbivore-induced plant responses. First, the induced plant response to a particular herbivore can cause either positive or negative effects on the preference and performance of other herbivores, depending on the feeding habits, diet specialization, and life histories of the focal herbivores (i.e. specificity of effects) (Agrawal 2000, Van Zandt and Agrawal 2004, Viswanathan et al. 2005). Van Zandt and Agrawal (2004) demonstrated that monarch butterflies avoided plants damaged by weevils, although weevils were attracted to plants previously damaged by weevils. In some cases, specialist and generalist herbivores respond differently to a plant damaged by a particular insect (Agrawal and Karban 1999). Second, induced plant responses can influence overall abundance,

species richness, and species composition of arthropod communities (Bailey and Whitham 2002, Van Zandt and Agrawal 2004). The overall abundance and species richness of herbivorous insects can be altered by induced plant responses such as changes in resistance, nutritional status, and biomass that alter plant susceptibility and availability (Price 1991, Bailey and Whitham 2002, Van Zandt and Agrawal 2004). Finally, plant-mediated indirect effects between herbivorous insects can propagate to the community of organisms, initiating cascades of other interactions including trophic, antagonistic and mutualistic interactions (Ohgushi et al. 2007). For example, herbivore-induced plant responses can indirectly affect predator abundance and/or predation pressure through bottom–up trophic cascades (Masters et al. 2001, Bailey and Whitham 2003). Several authors have argued that increased abundance or species richness of herbivores may result in increased abundance or species richness at higher trophic levels (Hunter and Price 1992, Siemann 1998).

In the present study, we focused on the herbivore-induced regrowth response in salicaceous woody plants. Salicaceous plants show enhanced lateral shoot production in response to damage by various herbivores, such as mammals (Roininen et al. 1997, Martinsen et al. 1998, Bailey and Whitham 2002), gall makers (Craig et al. 1986, Nakamura et al. 2003), and a stem-borer (Utsumi and Ohgushi 2007). Stem-boring by *Endoclita excrescence* (Lepidoptera: Hepialidae) induces lateral shoot sprouting of willow trees as a regrowth response (Utsumi and Ohgushi 2007). The herbivore-induced regrowth response in salicaceous trees often not only increases shoot biomass but also changes foliage quality in terms of chemical compounds and nutritional status (Martinsen et al. 1998, Nakamura et al. 2003, Utsumi and Ohgushi 2008). Therefore, willow regrowth in response to moth-boring may cause different impacts on the densities of various herbivores depending on their species identity and may alter the community structures of herbivorous insects. Furthermore, induced regrowth would also influence the community structures of predaceous arthropods through bottom-up trophic cascades. Although there is increasing appreciation of herbivore-induced community-wide impacts, we still have a poor understanding of the community effects of plant regrowth induced by herbivorous insects. In addition, we used the three willow species to examine interspecific variation and the interactive effects between moth-boring and the plant species diversity on the arthropod communities. To our knowledge, there are no reported studies examining how induced plant responses and plant species interactively affect arthropod community structures.

Our aim in this study is to examine the impacts of moth-boring-induced willow regrowth on arthropod communities in a three willow species system. Specifically, we address three questions: (1) how does moth-boring affect overall abundance and species richness of herbivorous insects on willow shoots? (2) How does induced willow regrowth change abundance and species richness of predaceous arthropods? (3) How does induced willow regrowth affect arthropod community composition? (4) How do moth attack and the three willow species interactively affect arthropod community structure?

Material and methods

Study organisms

A field study was performed in 2002 on a floodplain along the Yasu River (35°N, 136°E) in Shiga Prefecture, central Japan. The study plot consisted of a 1 km × 300 m area. In this study site, there is a patchy distribution of seven willow species (*Salix serissaefolia*, *S. eriocarpa*, *S. subfragilis*, *S. integra*, *S. gilgiana*, *S. caenomeloides* and *S. gracilistyla*). The understory vegetation is dominated by *Solidago altissima* (Compositae) and *Miscanthus sacchariflorus* (Gramineae). The entrances of tunnels bored by swift moth *E. excrescens* larvae were observed on all willow species. We chose three willow species, *S. gilgiana*, *S. eriocarpa* and *S. serissaefolia*, for this study because they were dominant in this site, and because moth attacks were frequently observed on these species.

The swift moth *Endoclita excrescens* is a common hepialid moth in Japan. The swift moth larvae attack various herbaceous and woody plants. Female adults oviposit from September to October, and eggs hatch in the following spring. Newly hatched larvae immediately bore into herbaceous plants and grow there until they reach fourth instar. From June to August, the larvae leave and bore into woody plants. In general, willow stems that are ≥ three years old and ≥ 2.5 cm diameter are attacked, and larvae make cylindrical tunnels about 1.5 cm in diameter and grow until adult eclosion. Larvae pass through 9–11 instars before pupating in these tunnels in September and then most pupae eclose about four weeks later. However, some larvae overwinter and reach 12–15 instars before pupating in the following September. Because the larval tunnel entrance forms a specific architecture that is made of frass and bound with silk, we could easily distinguish its holes from those made by other borers. Although the damage caused by moth larvae usually induces lateral shoot production by the willow trees about three weeks later, lateral shoot sprouting can carry over into the following spring (Utsumi and Ohgushi 2008). Vigorously growing lateral shoots rarely sprout from woody stems of willows that do not suffer from a large-scale disturbance, such as fire or flooding.

Leaf trait change in response to moth-boring

To determine whether quality of foliage of the newly emerged lateral shoots differs from that of other shoots, we measured C:N ratio of upper leaves of newly emerged lateral shoots of bored stems and current-year shoots of unbored stems in the field. In mid-April 2002, five bored trees with basal trunk diameter of 12–15 cm were randomly selected in each willow species, *S. gilgiana*, *S. eriocarpa* and *S. serissaefolia*. From each tree, we randomly took two lateral shoots from each of five bored stems. As control shoots, we randomly took five current-year shoots from each of five unbored stems. These shoots were brought to the laboratory immediately, and the uppermost five leaves of each shoot were oven-dried at 60°C for 48 h. After they were dried, these five leaves of each shoot were ground together, and nitrogen and carbon contents were determined using a CN

analyzer, and mean C:N ratio of lateral and control shoots from each stem was calculated. We performed two-way ANOVA with effects of shoot type (newly emerged lateral and control shoots) and willow species on C:N ratio. Also, for each willow species, a randomized block ANOVA was used to compare the foliage C:N ratio between the lateral and control shoots. The main factor was the shoot type (newly emerged lateral and control shoots), and the effect of individual tree was treated as a block. Each stem was treated as a replicate.

Arthropod responses to willow regrowth

To determine how shoot regrowth affects arthropod community on a willow shoot, we conducted a field survey monthly from May to August 2002. In mid-April, we randomly selected five trees bored by moths with trunks of 12–15 cm basal diameter for three willow species. In these trees, about 20% of all stems had been bored by moths. From each tree, we selected five unbored stems and five stems bored by swift moth larvae and selected two newly emerged lateral shoots from each of the five bored stems (i.e. total 10 shoots per tree) and five current-year shoots from each of the five unbored stems (i.e. total 25 shoots per tree). All selected stems were woody and 3–5 cm in diameter. We then recorded the number of species and the abundance of each species present on the two shoot types (newly emerged lateral shoots of a bored stem and current-year shoots of unbored stems) in every census. Current-year shoots of unbored stems were designated as controls. We identified all arthropods to species or morphspecies within known genera or families. To determine the effects of the regrowth response on herbivores and predators, we analyzed data from herbivorous and predaceous arthropods separately.

We used the data from our field survey to examine the effects of willow regrowth on the overall abundance and species richness of herbivorous and predaceous arthropods on a shoot. To prevent common species from swamping the overall abundance of less common species, we calculated the relative abundance of herbivorous and predaceous arthropods as follows. We calculated the mean number of each species in every census. Afterwards, the relative abundance value of each species was expressed as log $(n+1)$-transformed number per 10 shoots, which was then standardized so that the number of each taxon had standard deviation of 1 and mean of 0.5, to weight all species equally (Whitham et al. 1994). The standardized values were summed separately for herbivorous insects and predaceous arthropods. All census data throughout the season were combined to estimate species richness. Both relative abundance and species richness met the assumption of normality. We performed two-way ANOVA with effects of shoot types and willow species. Afterward, for each willow species, a randomized block ANOVA was used to compare species richness and relative abundance of herbivorous and predaceous arthropods between the newly emerged lateral and control shoots. The main factor was the shoot type, and the effect of individual tree was treated as a block. Each stem was treated as a replicate. Moreover, for analyses of herbivore abundance and

richness, we also added shoot length as a covariate in the models to examine the effect of shoot size. To examine the effect of herbivore abundance on the overall abundance and richness of predaceous arthropods, we also added the relative abundance of herbivores as a covariate in analyses of abundance and species richness of predaceous arthropods. Finally, to examine whether differences in overall arthropod species richness were caused by differences in arthropod abundance, we constructed rarefaction curves for each shoot type in each willow species, using cumulative species abundances (EcoSim 7.72, 10 000 iterations; Gotelli and Entsminger 2005, Rudgers and Clay 2008).

To examine changes of densities of arthropod organisms on regrowth shoots, we classified species by their feeding modes or taxa. Herbivorous insects were classified into seven feeding groups: specialist chewers, specialist sap-feeders, generalist chewers, generalist sap-feeders, gall makers, leaf miners and leaf folders. We defined 'specialist' as a monophagous insect found only on salicaceous plants and 'generalist' as an insect that can utilize both salicaceous and other plant families. The predaceous arthropods were classified into four groups: ants, spiders, lady beetles and other predators. Because lady beetles and other predators were rarely observed in the field survey, we excluded them from this analysis. We calculated the mean number of each group per shoot in every census. To examine the effects of shoot size on each density, we measured the length of the marked shoots on each stem in early June. The data of arthropod densities and shoot length were log-transformed because the assumption of normality was not met. A randomized block ANOVA was used to compare densities between the newly emerged lateral and control shoots in each willow species. The main factor was the shoot type, and the effect of individual tree was treated as a block. We also used shoot length as a covariate in the models, but only included this effect when it was significant at $p < 0.1$ (Van Zandt and Agrawal 2004). Each stem was treated as a replicate.

Principal components analysis (PCA), an eigenanalysis ordination technique that maximizes the variance explained by each successive orthogonal axis, was used to examine the response of community composition to the willow regrowth. PCA was based on the data of the mean densities of herbivore feeding groups and of predator taxa on the new lateral and control shoots in each tree. Each individual tree was treated as a replicate in the analysis. Detrended correspondence analysis allows the calculation of the gradient length of variables comprising all samples and PCA is the successful ordination method with the short gradient (<3 SD units) abundance data (Van Wijngaarden et al. 1995, Hirst and Jackson 2007). In our case, gradient lengths of the first, second, third axes were <1.9 (SD units). We used the software R (R Development Core Team 2008) and the vegan package (Oksanen et al. 2008) in the analyses to estimate gradient lengths and extract axes that summarize the composition of each representative arthropod community. The first three PCA axes were assessed using ANOVA to determine how willow species and moth-boring interact to explain the resulting arthropod community composition.

Results

Leaf trait change in response to moth-boring

The newly emerged lateral shoots induced by moth-boring produced leaves with higher nutritional value than control shoots (Fig. 1). There were significant effects of the shoot type and willow species on C:N ratio (shoot, $F_{1,143} = 47.27$, $p < 0.001$; species, $F_{2,143} = 40.66$, $p < 0.001$). We also detected a significant shoot type x species interaction ($F_{2,143} = 11.64$, $p < 0.001$). In separate analyses for each willow species, C:N ratio of lateral shoots was significantly reduced by 5%, 17% and 5% relative to the controls in *S. gilgiana* ($F_{1,44} = 7.97$, $p = 0.007$), *S. eriocarpa* ($F_{1,44} = 59.35$, $p < 0.001$), and *S. serissaefolia* ($F_{1,43} = 4.81$, $p = 0.034$), respectively.

Arthropod responses to willow regrowth

As a consequence of inducing shoot regrowth, moth-boring altered the herbivorous insect community structure. Regrowth shoots supported a significantly higher relative abundance of herbivores (shoot type, $F_{1,144} = 58.83$, $p < 0.001$; willow species, $F_{2,144} = 2.73$, $p = 0.069$), and the magnitude of this effect differed among the willow species (shoot × species, $F_{2,144} = 5.76$, $p = 0.004$). Separate analyses for each species revealed that the relative abundance of herbivorous insects was 3.4-fold, 2.0-fold, and 1.6-fold greater on the newly emerged lateral shoots than on controls in *S. gilgiana*, *S. eriocarpa* and *S. serissaefolia*, respectively (*S. gilgiana*, $F_{1,44} = 39.37$, $p < 0.001$; *S. eriocarpa*, $F_{1,44} = 16.54$, $p < 0.001$; *S. serissaefolia*, $F_{1,44} = 8.60$, $p = 0.005$, Fig. 2).

We identified 40 taxa from 22 families of four orders of herbivorous insects in the field survey (Appendix 1). Regrowth shoots supported significantly greater species richness of herbivores ($F_{1,144} = 35.39$, $p < 0.001$). Herbivore species richness was significantly different among willow species ($F_{2,144} = 15.56$, $p < 0.001$), but we did not detect a significant shoot × species interaction effect on the species richness ($F_{2,144} = 1.95$, $p = 0.146$). For each willow species, the species richness of herbivorous insects
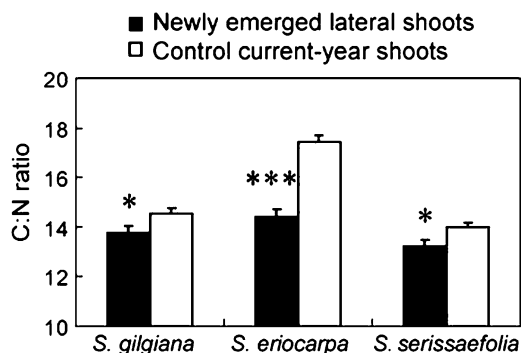
was 1.4–1.9 times greater on the newly emerged lateral shoots than on control shoots (*S. gilgiana*, $F_{1,44} = 18.30$, $p < 0.001$; *S. eriocarpa*, $F_{1,44} = 15.94$, $p < 0.001$; *S. serissaefolia*, $F_{1,44} = 5.10$, $p = 0.029$, Fig. 2). When shoot length was included as a covariate, the effect of shoot type on overall abundance and species richness of herbivores was also significant in *S. gilgiana* and *S. eriocarpa*, but not in *S. serissaefolia* (Table 1).

There were significant effects of regrowth and willow species on the relative abundance of predators (shoot type, $F_{1,144} = 9.51$, $p = 0.002$; willow species, $F_{2,144} = 4.27$, $p = 0.016$; shoot × species, $F_{2,144} = 2.68$, $p = 0.072$). In separate analyses for each species, the relative abundance of predators was 2.9-fold and 1.9-fold greater on the newly emerged lateral shoots than on controls in *S. gilgiana* and *S. eriocarpa*, respectively (*S. gilgiana*, $F_{1,44} = 15.04$, $p < 0.001$; *S. eriocarpa*, $F_{1,44} = 5.51$, $p = 0.023$; Fig. 2), but no significant difference was found in *S. serissaefolia* ($F_{1,44} = 0.01$, $p = 0.907$).

We identified 17 taxa from eight families of four orders of predaceous arthropods in the field survey (Appendix 1). We found significant effects of regrowth and willow species on the species richness of predaceous arthropods (shoot, $F_{1,144} = 10.44$, $p = 0.002$; species, $F_{2,144} = 5.29$, $p = 0.006$; shoot × species, $F_{2,144} = 1.97$, $p = 0.143$). In each willow species, predator species richness was 2.0–6.5 times greater on the lateral shoots than on controls (*S. gilgiana*, $F_{1,44} = 10.78$, $p = 0.002$; *S. eriocarpa*: $F_{1,44} = 6.46$, $P = 0.015$; Fig. 2), although there was no significant difference for *S. serissaefolia* ($F_{1,44} = 0.53$, $p = 0.819$). When herbivore abundance was included as a covariate, in *S. gilgiana* and *S. serissaefolia* neither the relative abundance nor the species richness of predators was significantly influenced by a direct effect of shoot type, but both of them were significantly affected by herbivore abundance (Table 1). In contrast, we found a significant effect of shoot type on the abundance and species richness of predaceous arthropods in *S. eriocarpa* (Table 1).

Arthropod species richness on the new lateral shoots lied significantly above that of controls when the samples were rarefied to similar number of individuals, except for *S. serissaefolia* (Fig. 3). The rarefaction curves showed that observed differences in species richness in *S. gilgiana* and *S. eriocarpa* were not only due to differences in the abundance.

Shoot regrowth had different effects on the densities of different feeding groups of herbivorous insects (Table 2, Fig. 4). Specialist chewers and sap-feeders had significantly higher densities on the new lateral shoots than on controls, except for sap-feeders on *S. eriocarpa*. Similarly, the density of leaf miners was significantly increased on the lateral shoots, except in *S. serissaefolia*. The effect of shoot length on these increases was not significant (Table 2). Although the density of leaf folders increased only on *S. eriocarpa*, this correlated significantly with shoot length (Table 2). In contrast, the number of gall makers was significantly decreased on the new lateral shoots relative to controls for *S. eriocarpa*. In contrast, no significant differences in the densities of generalist chewers and sap-feeders were found in the three willow species.

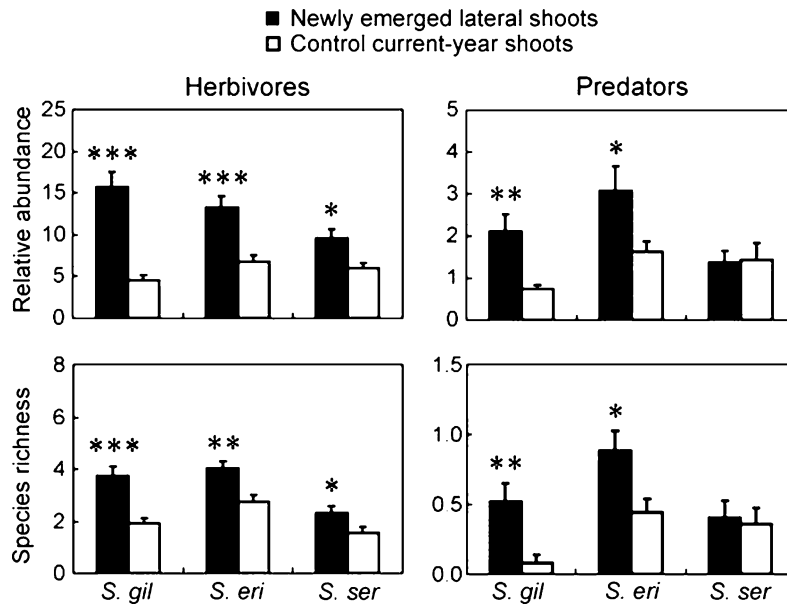Furthermore, the induced regrowth response significantly affected the densities of predaceous arthropods

Figure 1. Foliage C:N ratios of the newly emerged lateral shoots in response to moth-boring and control shoots. Means and SE are presented. Asterisks indicate significant differences between the lateral and current-year shoots for each willow species (***$p < 0.001$, **$p < 0.05$, *$p < 0.05$).

■ Newly emerged lateral shoots
□ Control current-year shoots

Figure 2. The relative abundance and species richness of herbivorous insects and predaceous arthropods per shoot. *S. gil*: *S. gilgiana*, *S. eri*: *S. eriocarpa*, *S. ser*: *S. serissaefolia*. Means and SE are presented. Asterisks indicate significant differences between newly emerged lateral shoots and controls (***p <0.001, **p <0.01, *p <0.05).

(Table 2, Fig. 4). The responses of predator taxa differed among willow species. In *S. gilgiana* ant density was significantly greater on the lateral shoots than on controls, but no significant difference in spider density was found. However, in *S. eriocarpa*, spider density was significantly increased on the lateral shoots relative to controls, but no significant difference in ant density was found. In *S. serissaefolia*, there were no significant differences in ant or spider densities between the new lateral shoots and controls.

The arthropod community composition varied among trees in response to the effects of willow species and regrowth induced by moth-boring. In a PCA ordination of among trees, axis 1, 2 and 3 explained 35.6%, 23.4% and 13.8% of the total variation in community composition, respectively, a total of 72.8% of the total variation in arthropod assembly among trees. PCA scores among trees for each combination of the shoot type and willow species for each of the first three PCA axes are presented in Fig. 5. Differences in the average PCA scores along each axis indicated the degree to which arthropod community composition shifted in response to shoot regrowth and willow species. We detected significant effects of the shoot type and the shoot × species interaction on the community composition for PCA axis 1 (shoot type, $F_{1,24} = 10.75$, p =0.003; willow species $F_{1,24} = 2.25$, p =0.127; shoot × species, $F_{2,24} = 3.56$, p =0.044). Willow species effects were observed for axis 2 (shoot type, $F_{1,24} = 1.75$, p =0.198; willow species $F_{1,24} = 4.19$, p =0.016; shoot × species, $F_{2,24} = 2.30$, p =0.122) and axis 3 (shoot type, $F_{1,24} = 0.14$, p =0.710; willow species $F_{1,24} = 3.55$, p =0.044; shoot × species, $F_{2,24} = 1.66$, p =0.211).

Discussion

This study demonstrated that moth-boring had community-wide impacts on arthropods on the three willow species

via the enhanced production of lateral shoots. Moth-boring not only increased shoot biomass but also decreased the foliage C:N ratio of the sprouting shoots. We found that moth-boring was associated with increases in the overall abundance and species richness of herbivorous insects and predaceous arthropods. However, the effects of moth-boring varied among willow species. Furthermore, induced regrowth, willow species, and their interaction differentially affected the arthropod community composition. In this study, we used willow trees that had been already attacked by the moth caterpillars instead of applying them to randomly-chosen trees. Although we did not provide trees without moth herbivory to experimentally remove effects of the moth herbivory in advance, moth-boring induced the sprout of lateral shoots from woody stems for randomly-chosen trees of *S. serissaefolia* in a moth-manipulated experiment (Utsumi and Ohgushi 2007). Thus, the present study strongly supports the community-wide impacts of the moth-induced plant response.

Willow regrowth in response to moth-boring

Herbivory can stimulate the production of rapidly growing shoots in willows (Craig et al. 1986, Nakamura et al. 2003). In our previous studies willows produced vigorously growing lateral shoots in response to moth-boring (Utsumi and Ohgushi 2007, 2008). As a result, willows can partially compensate for biomass loss resulting from the stem-boring (Utsumi and Ohgushi 2007). It is widely accepted that alteration of the relationships between sink and source organs of plants, which regulate the flow of assimilates in response to herbivory, results in lateral shoot production (Whitham et al. 1991). Reallocation of resources from root tissues may allow salicaceous trees to compensate for the loss of aboveground tissues (Bailey and Whitham 2002).

Table 1. Results of ANOVA for the effects of shoot type and a covariate (shoot length) on the overall abundance and species richness of herbivores, and for the effects of shoot type and a covariate (overall abundance of herbivores) on the overall abundance and species richness of predators. Bold F-values indicate significant effects (p <0.05).

(a) Herbivores	S. gilgiana		S. eriocarpa		S. serissaefolia	
	Abundance	Richness	Abundance	Richness	Abundance	Richness
Source of variation	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$
Shoot type	**27.31**	**14.41**	**5.16**	**6.04**	1.92	1.28
Shoot length (covariate)	2.69	2.07	0.19	0.01	0.09	0.02
(b) Predators	S. gilgiana		S. eriocarpa		S. serissaefolia	
	Abundance	Richness	Abundance	Richness	Abundance	Richness
Source of variation	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$	$F_{1,43}$
Shoot type	0.43	1.53	**5.66**	**6.44**	11.18	0.51
Herbivore (covariate)	**13.64**	3.08	0.55	0.54	**5.77**	**5.30**

Regrowth shoots caused by moth-boring produced new leaves with low C:N ratio in the three willow species. This was brought about by increased foliage nitrogen concentration (Utsumi and Ohgushi 2008). Likewise, compensatory regrowth of woody plants can improve leaf and shoot nutritional status (Danell and Huss-Danell 1985, Martinsen et al. 1998, Nakamura et al. 2003). Such a nutritional improvement is due to the presence of newly developed plant tissues produced by the regrowth response (Bryant et al. 1983). The reduction in C:N ratio is likely to be one of trait changes in the regrowth response because concentrations of phenolic compounds often increase in the regrowth foliage of salicaceous plants (Martinsen et al. 1998). Willow regrowth, and the resulting increase in foliage nitrogen, are often local responses of shoots and stems that have undergone herbivory rather than a systemic response of an individual tree (Nakamura et al. 2003, Utsumi and Ohgushi 2007).

Note that the changes in C:N ratio differed among the willow species. Not only the nitrogen status but also other plant traits such as shoot growth and length of induced lateral shoots following moth-boring differed among these willow species (Utsumi and Ohgushi 2007, 2008). Plant compensatory responses to herbivory often vary, depending on extrinsic (herbivory type, timing of attack, severity of damage, and resource availability) and intrinsic (species and genotypes of plants) factors (Rosenthal and Kontanen 1994). Artificial boring that caused the same level of damage resulted in the same trend of different shoot regrowth among these three willow species as did moth-boring (Utsumi and Ohgushi 2007, 2008). Therefore, in the present study, the among-species variation in willow trait changes may be due to intrinsic plant factors.

Effects of shoot regrowth on herbivores

A few studies have demonstrated that plant regrowth induced by large-scale damage such as browsing, fire, and trunk-cutting increased both overall abundance and species richness of herbivorous insects (Bailey and Whitham 2002, Nakamura et al. 2006). In our study, moth-boring increased the overall abundance of herbivorous insects on the newly emerged lateral shoots in three willow species. In addition, moth-boring also increased the herbivore species

richness. Nine herbivorous species (26% of the total number of herbivore species) were newly emerged on the lateral shoots, while five species (14%) were found only on current-year shoots (Appendix 1).

Increases in the overall abundance and species richness of herbivorous insects via plant regrowth may in general result from increases in the quality and quantity of food resources
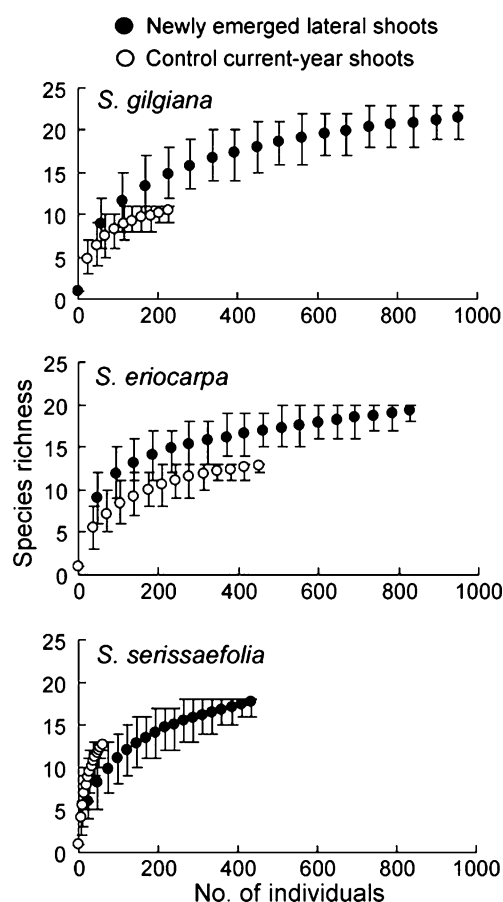

Figure 3. Rarefaction curves plotting the number of species against the number of individuals sampled in response to moth-induced plant regrowth. Bars represent 95% CI obtained from 10 000 re-sampling iterations. Bars that do not overlap the mean for the alternate indicate significant difference (p <0.05).

Table 2. Results of ANOVA to test for the effects of shoot type on the densities of feeding groups of herbivorous insects and predaceous taxa. Models included shoot length as a covariate where its effect was significant at $p < 0.1$. Bold F-values indicate significant effects (shoot type: $p < 0.05$, shoot length: $p < 0.1$).

| Feeding group/taxa | S. gilgiana | | | | S. eriocarpa | | | | S. serissaefolia | | | |
| | Shoot type | | Shoot length | | Shoot type | | Shoot length | | Shoot type | | Shoot length | |
	DF	F	DF	F	DF	F	DF	F	DF	F	DF	F
Specialist chewer	1,44	**107.23**	1,43	0.37	1,44	**19.78**	1,43	0.92	1,44	**5.29**	1,43	0.69
Specialist sap-feeder	1,43	**13.45**	1,43	**3.83**	1,44	1.57	1,43	0.96	1,44	**13.03**	1,43	0.87
Leaf miner	1,43	**17.62**	1,43	**4.18**	1,44	**7.47**	1,43	0.53	1,44	1.22	1,43	0.01
Leaf folder	1,44	1.60	1,43	0.58	1,43	0.35	1,43	**2.96**	1,44	0.02	1,43	1.85
Gall maker	–	–	–	–	1,44	**7.07**	1,43	0.08	1,44	0.28	1,43	0.01
Generalist chewer	1,44	2.66	1,43	0.58	1,44	0.66	1,43	0.23	1,44	0.11	1,43	2.41
Generalist sap-feeder	1,44	0.32	1,43	0.47	1,44	1.43	1,43	1.83	1,44	0.86	1,43	1.81
Ant	1,43	**8.51**	1,43	**8.39**	1,44	0.66	1,43	0.01	1,44	0.01	1,43	0.90
Spider	1,44	0.20	1,43	0.77	1,44	**4.38**	1,43	1.99	1,44	0.04	1,43	0.01

on the lateral shoots (Bailey and Whitham 2002, Nakamura et al. 2006). It has suggested that a greater number of herbivorous species can be supported as a result of increases in biomass and quality of food resources (Price 1991, Srivastava and Lawton 1998, Nakamura et al. 2006). Because plant size (i.e. shoot length) did not have significant effects on the overall abundance of herbivores in this study, changes in plant quality, such as the reduction of C:N ratio, are likely to be responsible for the increase in the overall abundance. In fact, the body size and egg production of the leaf beetle *Plagiodera versicolora* increased when the beetles fed on the leaves of new lateral shoots induced by moth-boring, indicating high foliage quality (Utsumi and Ohgushi 2008). Many authors have argued that herbivorous insects increase on regrowth plants because of greater colonization and performance following the improvement of resource quality (Danell and Huss-Danell 1985, Roininen et al. 1997, Martinsen et al. 1998, Utsumi and Ohgushi 2008).

Three explanations have been proposed for the increase in herbivore species richness with increasing resource availability: 1) increases in the colonization and persistence of rare species, 2) increases in rare resources, and 3) decrease in interspecific competition (Price 1991, Abrams 1995, Siemann 1998). It should be noted that increase in species richness was not due to plant size, and effects of moth attack on species richness persisted even when the samples were rarefied to similar numbers of individuals, except in *S. serissaefolia*. Furthermore, the impact of plant regrowth on herbivore density differed among the feeding groups. These findings suggest that increase in species richness may reflect not only enhanced colonization of rare species but also more resource variation within new lateral shoots. The contrasting responses of the feeding groups would be primarily due to species-specific feeding or oviposition preferences for morphologically and/or chemically different types of resources within a tree (Ruusila et al. 2005, Roslin et al. 2006). Specialist herbivores often have stronger ability to discriminate differences in food quality within host plants than generalists (Bernays and Funk 1999) and more abundant on induced plants (Poelman et al. 2008). Some specialists, such as the aphid *Cavariella salicicola,* the spittle bug *Aphrophora pectoralis,* and the leaf miner *Phyllonorycter* sp., were observed only on the new lateral shoots in this study (Appendix 1). In contrast, there were no specialists within species, which were only found on current-year shoots. The foliage of regrowth shoots in salicaceous plants often contains more abundant phenolic compounds and has larger leaves (Martinsen et al. 1998). Specialists can utilize them as feeding and oviposition stimulants, while generalists may avoid or fail to respond to the induced plant responses (Karban and Baldwin 1997, Agrawal 2000). Moreover, not only mean values but also variation in resource quality may be greater on the regrowth shoots because the traits of all leaves on a shoot, such as morphology, nitrogen and phenolic content, can vary more markedly, depending on leaf age (Utsumi unpubl.). Therefore, alterations of resource conditions resulting from the plant regrowth induced by moth-boring, which corresponds to the second explanation, may expand niches for herbivore species.
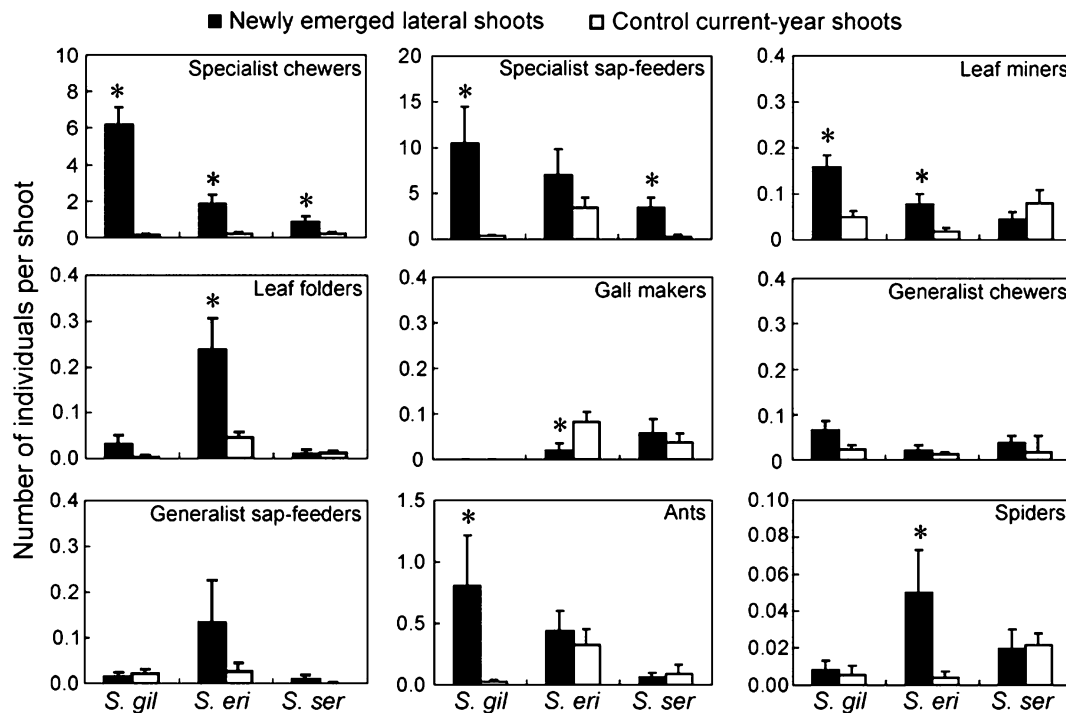
Figure 4. The densities of feeding groups of herbivorous insects and predaceous arthropod taxa per shoot. Means and SE are presented. *S. gil*: *S. gilgiana*, *S. eri*: *S. eriocarpa*, *S. ser*: *S. serissaefolia*. Asterisks indicate significant differences between the lateral and current-year shoots for each willow species ($p < 0.05$).

Bottom–up cascade effects on predaceous arthropods

Ohgushi (2005) emphasized that herbivore-induced plant responses not only affect herbivores but also propagate to predators through a bottom–up cascade effect. In this study, the overall abundance and species richness of predaceous arthropods increased on the lateral shoots in response to moth-boring in *S. gilgiana* and *S. eriocarpa*. Abundance of predaceous arthropods can increase as a result of the numerical and spatial tracking of prey (Hassell 1978, Ives et al. 1993). Also, increased herbivore abundance and species richness can result in increased predator species richness (Hunter and Price 1992, Abrams 1995, Cardinale et al. 2006). In addition, in *S. serissaefolia* predator abundance and species richness were correlated with the overall herbivore abundance, while moth-boring did not significantly affect the community properties of predators.

The increases in the overall abundance and species richness of predators were mainly due to enhanced aggregation of ants and spiders. The increase in ants may have been due to the increased abundance of prey herbivores or due to increased honeydew production resulting from the increased specialist sap-feeders such as the aphids *Chaitophorous saliniger* and *Pterocomma pilosum*. In support of the honeydew hypothesis, ant density did not increase on *S. eriocarpa* and *S. serissaefolia*, on which there was only a slight increase in specialist sap-feeders. For spiders, plant architectural complexity may be an important trait (Halaj et al. 2000, Langellotto and Denno 2004, de Souza and Martins 2005). An induced shoot regrowth response may increase plant architectural complexity, such as foliage density, spatial foliage distribution, and lateral branching (Cooper et al. 2003). In the present study, web-lacking

spiders including Salticidae, Thomisidae and Clubionidae predominately contributed to the increase in overall spider density on the lateral shoots. Web-lacking spiders often prefer complexly structured habitats on plants, because these provide more suitable sites for constructing retreats for protection, molting or egg laying (Halaj et al. 2000, de Souza and Martins 2006). The significant direct effect of shoot type on predator abundance and species richness in *S. eriocarpa* suggests that changes in plant characteristics, such as the architectural complexity, also contributed to the increases in spider abundance and species richness (Halaj et al. 2000, de Souza and Martins 2006).

Overall, we conclude that moth-boring induced bottom–up cascade effects across three trophic levels, resulting in increased predator abundance and species richness. The strength and relative contribution of indirect interactions through herbivores and direct interactions between a plant and predators depended on the species identity of willows and appeared to be driven by differences in the composition of supporting herbivore species and plant architecture.

How do plant species diversity and herbivore attack interactively affect arthropod diversity?

Previous studies have demonstrated that the diversity of plant species (Siemann 1998, Haddad et al. 2001) and/or genotypes (Wimp et al. 2005, Crutsinger et al. 2006) positively affect arthropod species diversity. Moreover, herbivore attack often increases arthropod species diversity through induced plant responses (Bailey and Whitham 2002, Van Zandt and Agrawal 2004) and the function
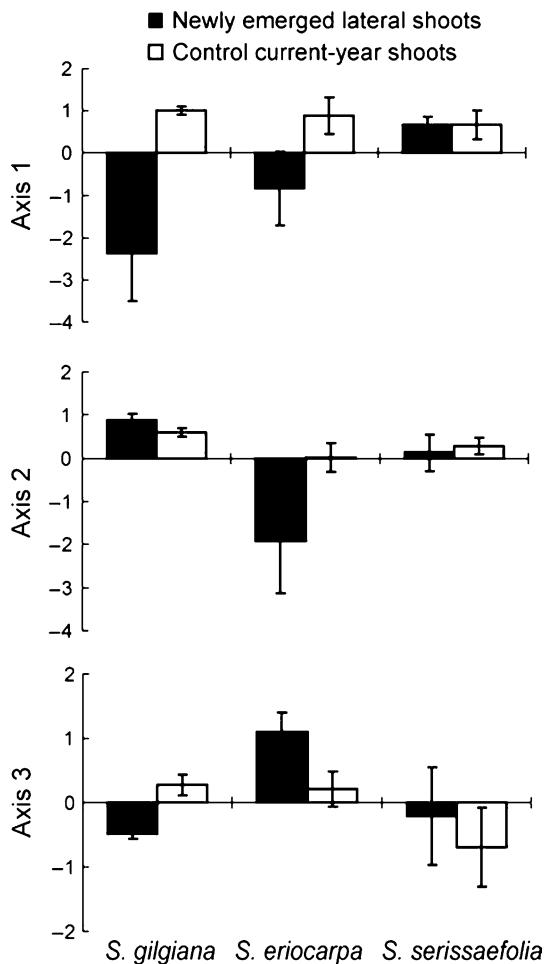
Figure 5. Principal components analysis of arthropod community composition. The x-axis indicates the willow species categories. The PCA was based on the average abundances of herbivore feeding groups and predator taxa per shoot in each tree. Values presented are the means and SE of community scores.

of herbivore ecosystem engineers (Lill and Marquis 2003). However, there are no studies that address how plant diversity and herbivore-induced plant responses interactively affect arthropod species diversity. We showed that moth-induced willow regrowth increased arthropod abundance and species richness, suggesting that moth-induced regrowth may increase alpha diversity of arthropod species on each willow species. Moreover, the effects of willow species on arthropod abundance and species richness varied depending on whether moth attack occurred or not, and willow species, moth-boring, and the species × moth attack interaction differentially affected the community composition of arthropods. This suggests that willow species diversity and moth attack may interactively increase beta diversity of arthropods. Thus, the niche expansion for herbivorous species through induced regrowth following herbivory may be enhanced by plant species diversity.

This study clearly demonstrated that herbivore-induced willow regrowth influenced the structure of both herbivore and predator communities. The overall abundance and species richness of herbivores increased on the regrowth shoots, which was likely to have an influence on predators

through bottom–up cascade effects. There is increasing appreciation that induced defenses can affect the structure of arthropod communities (Van Zandt and Agrawal 2004, Viswanathan et al. 2005, Poelman et al. 2008). However, few studies tested for community-wide consequences of induced plant regrowth following damage by herbivorous insects (but see Tscharntke 1999). Plant regrowth following herbivory is a widespread response in terrestrial ecosystems, and can mediate indirect interactions between herbivores. To gain a comprehensive understanding of the effects of induced plant responses and plant diversity on arthropod community structure, future studies should pay more attention to the nature of community-wide impacts of the plant regrowth response to herbivory.

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Appendix 1. Arthropod species found on willow trees.

Order	Family	Species	Group	L shoot	C shoot
Araneae	Clubionidae	*Chiracanthium japonicum*	S	Y	
	Salticidae	*Myrmarachne japonica*	S	Y	Y
	Tetragnathidae	*Tetragnatha praedonia*	S	Y	Y
		Tetragnatha squamata	S	Y	Y
	Thomisidae	*Misumenops tricuspidatus*	S	Y	Y
		Misumenops japonicus	S	Y	
		Thomisus labefactus	S	Y	
Coleoptera	Buprestidae	*Trachys minuta salicis*	LM	Y	Y
	Chrysomelidae	*Plagiodera versicolora*	SCh	Y	Y
		Cryptocephalus approximatus	GCh	Y	Y
		Smaragdina semiaurantiaca	GCh	Y	Y
		Fleutiauxia armata	GCh	Y	Y
		Crepidodera japonica	SCh	Y	
		sp. 1	GCh		Y
	Curculionidae	sp. 1	GCh	Y	
	Elateridae	*Agrypnus binodulus*	GCh	Y	Y
	Scarabaeidae	*Adoretus tenuimaculatus*	GCh		Y
		Rhomborrhina japonica	GCh	Y	
	Cantharidae	*Athemus suturellus*	OP		Y
	Coccinellidae	*Aiolocaria hexaspilota*	B	Y	Y
		Propylea japonica	B	Y	
		Harmonia axyridis	B	Y	Y
		Coccinella septempunctata	B	Y	Y
Diptera	Cecidomyiidae	*Rabdophaga rigidae*	GM	Y	Y
	Tachinidae	*Anthomyiopsis plagioderae*	OP	Y	
	Delphacidae	sp. 1	GSp	Y	
	Diaspididae	*Comstockaspis perniciosa*	GSp	Y	Y
	Dictyopharidae	*Dictyophara patruelis*	GSp		Y
	Plataspidae	*Megacopta punctatissima*	GSp		Y
	Tropiduchidae	*Metasalis populi*	SSp	Y	Y
	Reduviidae	sp. 1	OP	Y	
	Aphididae	*Chaitophorous saliniger*	SSp	Y	Y
		Aphis farinosa	SSp	Y	Y
		Pterocomma pilosum	SSp	Y	Y
		Cavariella salicicola	SSp	Y	
	Aphrophoridae	*Aphrophora pectoralis*	SSp	Y	
Hymenoptera	Tenthredinidae	*Phyllocolpa* sp. 1	GM	Y	Y
		Stauronematus compressicornis	SCh	Y	Y
		Pontania sp. 1	GM	Y	Y
		sp. 1	GCh	Y	Y
	Formicidae	*Pristomyrmex pungens*	A	Y	Y
		Lasius sakagamii	A	Y	Y
		Lasius japonicus	A	Y	
Lepidoptera	Geometridae	sp. 1	GCh	Y	Y
		sp. 2	GCh	Y	
	Gracillariidae	*Phyllonorycter pastorella*	LM	Y	Y
Lepidoptera	Gracillariidae	*Phyllonorycter* sp. 1	LM	Y	
		Phyllocnistis sp. 1	LM	Y	
		Phyllocnistis sp. 2	LM	Y	Y
		Caloptilia stigmatella	LM	Y	
	Limacodidae	*Monema flavescens*	GCh		Y
	Notodontidae	*Furcula furcula sangaica*	SCh	Y	Y
		Clostera anastomosis	SCh	Y	Y
	Psychidae	*Cryptothelea minuscula*	GCh	Y	Y
	Sphingidae	*Smerinthus planus planus*	GCh	Y	Y
	Tortricidae	sp. 1	LF	Y	Y
		sp. 2	LF	Y	Y

Notes: herbivore species are classified into 11 feeding groups: specialist chewers (SCh), leaf miners (LM), leaf folders (LF), gall makers (GM), specialist sap-feeders (SSp), generalist chewers (GCh), and generalist sap-feeders (GSp). Predator species are classified into four groups: spiders (S), ants (A), lady beetles (B), and others (OP). Y indicates that individuals of the species were found on each shoot. L shoots and C shoots mean the newly emerged lateral shoots in response to moth-boring and control shoots, respectively.