

Community consequences of herbivore-induced bottom–up trophic cascades: the importance of resource heterogeneity

Shunsuke Utsumi^{1*}, Masahiro Nakamura² and Takayuki Ohgushi¹

¹Center for Ecological Research, Kyoto University, Japan; and ²Tomakomai Experimental Forest, Hokkaido University, Japan

Summary

1. Herbivory often changes resource quality for herbivorous insects through induced plant responses depending on the intensity of damage. We hypothesized that the willow's response following herbivory affects the entire arthropod community structure on the tree due to changes in plant quality. To examine this hypothesis, we investigated arthropod communities on three willow species, *Salix gilgiana*, *Salix eriocarpa* and *Salix serissaefolia*.

2. In our common garden, cuttings were established in 2003 and experimental treatments were applied in 2005. Damage by a boring caterpillar of a swift moth (*Endoclita excrescens*) and artificial cutting of 25% stems were applied as partial herbivory within individual trees, and 100% cutting of stems was applied to represent severe herbivory to whole individual trees. These treatments stimulated lateral shoot production depending on damage intensity, resulting in full compensation for biomass loss.

3. Positive relationships were detected between within-tree variation in foliar nitrogen content and overall abundance/species richness of herbivores. Moth boring and 25% cutting increased herbivore abundance and species richness relative to controls. However, we found no significant differences in herbivore abundance and species richness between 100% cut and control trees. Community composition of herbivore species was significantly different between the following three groups: (i) bored and 25% cut; (ii) 100% cut; and (iii) control trees. Changes in community structure of herbivores were likely due to changes in plant quality depending on the intensity of damage.

4. Although total predator abundance and species richness were not significantly different among treatments, community composition of predator species was significantly different among treatments.

5. These results indicate that herbivore-induced willow responses can largely determine the entire arthropod community structure of multitrophic levels due to changes in plant quality. We suggest that heterogeneous resource conditions induced by herbivory within and among plant individuals increase the species diversity of arthropods.

Key-words: community structure, compensatory regrowth, herbivory, induced plant response, species diversity

Introduction

Recently, several authors have argued that arthropod communities on plants are structurally organized by plant-mediated indirect effects (Denno, McClure & Ott 1995; Waltz & Whitham 1997; Martinsen *et al.* 2000; Agrawal 2005; Denno & Kaplan 2007; Ohgushi, Craig & Price 2007). In this con-

text, herbivore-induced changes in terrestrial plants can generate bottom–up trophic cascades from plants to higher trophic levels and can thus influence biodiversity within a community (Ohgushi 2005).

There is increasing evidence that herbivory induces morphological, phenological and chemical changes in a wide variety of terrestrial plants (Karban & Baldwin 1997; Ohgushi 2005). Herbivore-induced modifications in plant quality often have negative impacts on the survival and

*Correspondence author. E-mail: shun@ecology.kyoto-u.ac.jp

reproduction of insect herbivores because of decreased nutrition and biomass, and/or increased chemical and morphological resistance (Masters & Brown 1992; Inbar, Eshel & Wool 1995; Denno *et al.* 2000; Tindall & Stout 2001; Wise & Weinberg 2002; Denno & Kaplan 2007). It should be noted that herbivory also induces another type of plant response that can compensate for damaged tissues in many woody and herbaceous plants (Whitham *et al.* 1991; Strauss & Agrawal 1999). The compensatory regrowth response can have positive effects on abundance and performance of herbivorous insects via increasing food quality and/or quantity (Danell & Huss-Danell 1985; Damman 1989; Strauss 1991; Martinsen, Driebe & Whitham 1998; Nakamura, Miyamoto & Ohgushi 2003). There are a growing number of studies reporting that damage-induced plant responses can affect arthropod community structure (Bailey & Whitham 2002; Van Zandt & Agrawal 2004; Rodriguez-Saona & Thaler 2005; Viswanathan, Narwani & Thaler 2005; Nakamura, Kagata & Ohgushi 2006). For example, trunk cutting increased species richness and abundance of insect herbivores on willow trees by sprouting regrowth shoots (Nakamura *et al.* 2006). Increased resource quality and quantity, such as nutritional status and shoot biomass, due to the induced regrowth response are likely to facilitate herbivores (Price 1991; Nakamura *et al.* 2006).

Note that induced plant response can play another important role in influencing species richness of herbivorous insects through increased resource heterogeneity. Induced plant responses commonly increase resource heterogeneity within damaged plants (Orians & Jones 2001). Herbivory is generally distributed locally and varies in intensity within individual plants (Raupp & Denno 1983; Whitham, Williams & Robinson 1984; Barker, Wratten & Edwards 1995). Subsequent changes in morphology, chemistry and growth patterns in response to local herbivory may cause resource quality to be more heterogeneous for herbivorous insects within a plant (Hunter & Price 1992; Orians & Jones 2001). Also, differences in damage intensity among conspecific plants may cause heterogeneous conditions among plant individuals because plant phenotypes often change depending on damage intensity (Karban & Baldwin 1997; Guillet & Bergström 2006). Severe damage, such as overall defoliation by herbivorous insect outbreaks and browsing by large mammals, may provide a distinct type of resource for herbivores compared with plants with a low level of herbivory. On the other hand, severe damage may cause homogenous resource conditions within plant individuals. For example, when severe herbivory induces host plant regrowth, plant tissues are mostly replaced with rapidly growing regrowth tissues. Although several authors have suggested that increased resource heterogeneity can increase species richness of herbivorous insects (Lawton 1983; Strong, Lawton & Southwood 1984; Hunter & Price 1992), no studies have addressed whether resource heterogeneity induced by herbivory can affect species richness and abundance of herbivore communities.

Herbivore-induced plant responses also indirectly affect predator abundance and/or predation pressure through bottom-up trophic cascades (Masters, Jones & Rogers 2001; Bailey & Whitham 2003; Nakamura *et al.* 2005, 2006). Several authors have argued that increased abundance or species richness at lower trophic levels may result in increased abundance or species richness at higher trophic levels (Hunter & Price 1992; Abrams 1995; Siemann 1998). Hence, the plant regrowth response following herbivory may have a subsequent influence on abundance and species richness of predaceous arthropods by altering both species composition and abundance of prey herbivores.

Salicaceous woody plants enhance lateral shoot production in response to damage by various herbivores, such as mammals (Roininen, Price & Bryant 1997; Martinsen *et al.* 1998; Bailey & Whitham 2002), gall-makers (Craig, Price & Itami 1986; Nakamura *et al.* 2003) and a stem-borer (Utsumi & Ohgushi 2007, 2008). The induced regrowth response in salicaceous trees can positively affect the abundance of herbivorous insects (Martinsen *et al.* 1998; Nakamura *et al.* 2003). Likewise, lateral shoot regrowth of willows in response to damage by caterpillars of a stem-boring insect, *Endoclyta excrescence* (Butler; Lepidoptera: Hepialidae), increased density, body mass and egg production of a leaf beetle *Plagioderia versicolora* (Laicharting) that feeds on the leaves of newly emerged lateral shoots (Utsumi & Ohgushi 2008). Because shoot regrowth following moth boring is likely to be a local response within a tree rather than a systemic response (Utsumi & Ohgushi 2007), moth boring may increase within-tree resource heterogeneity for herbivorous insects.

We hypothesized that herbivore-induced plant regrowth alters the entire arthropod community structure on an individual willow tree, depending on damage intensity. To test this hypothesis, we address the following three questions: (i) How does partial (moth boring and 25% artificial cutting) and severe (100% artificial cutting) herbivory induce willow regrowth and affect resource nutritional status? (ii) How does prior herbivory affect overall abundance, species richness and composition of herbivorous insects on a whole tree? and (iii) How does prior herbivory influence overall abundance, species richness and composition of predaceous arthropods? Finally, we discuss the importance of resource heterogeneity induced by herbivory within and among individual plants.

Materials and methods

STUDY ORGANISMS

Three willow species, *Salix gilgiana* Seemen, *Salix eriocarpha* Franch. et Savat. and *Salix serissaefolia* Kimura, occurred in a floodplain along the Yasu River (35°N, 136°E) in Shiga Prefecture, central Japan. Understorey vegetation was dominated by *Solidago altissima* (Compositae) and *Miscanthus sacchariflorus* (Gramineae). The entrances of tunnels bored by the caterpillars of the swift moth, *Endoclyta excrescens*, were observed in the three willow species. The swift moth is a common hepialid moth in Japan, and its caterpillars attack various herbaceous and woody plants (Enda 1971; Igarashi 1994). In general, willow stems of ≥ 3 year old and

≥ 2 cm in diameter are attacked between *c.* June and August, and caterpillars make cylindrical tunnels with 1.5 cm in diameter. Caterpillars stay in the tunnels until pupation in September and adults eclose about four weeks later, although some overwinter and pupate the following September.

EXPERIMENTAL DESIGN

To examine whether induced plant responses to herbivory affect the entire community structure of arthropods, we conducted a field experiment in a common garden in the Center for Ecological Research, Kyoto University, in Shiga prefecture, central Japan. In mid-June 2003, we cut off 10 willow stems (1 cm \times 50 cm) from eight clones each for the willow species, *S. gilgiana*, *S. eriocarpa* and *S. serissaefolia*, on the floodplain along the Yasu River (10.6 km north of the common garden). These cuttings were individually transplanted into 10-L pots containing compost. The pots were placed in the common garden with a daily water supply. In the spring of 2004, we randomly selected four plants from each clone of the three willow species, and the selected plants were randomly transplanted to the common garden (680 m²) in 6 \times 16 rows. The plants were watered daily and were separated by 2 m both within each row and between rows to prevent them from touching each other. In 2005, four plants of each clone were assigned randomly to one of following four treatments: (i) bored trees where one stem that grew in 2003 received inoculation of a swift moth caterpillar; (ii) 25% cut trees where a quarter of the stems, which grew in 2003, was randomly cut; (iii) 100% cut tree, in which all stems were cut; and (iv) control trees that did not receive any treatment. We applied 25% cutting to simulate a willow response to moth damage because the same level of regrowth is likely to occur in response to natural damage (S. Utsumi, personal observation). A cutting of 100% simulates severe damage to salicaceous saplings by several herbivores including large mammals (e.g. Guillet & Bergström 2006) and/or aggregative macrolepidopteran caterpillars (S. Utsumi, personal observation) in natural systems, although the swift moth caterpillars are unlikely to cause such damage. In the field, less than 5% of the willows have severe damage by insect herbivores are exceptionally low level. As for the swift moth, boring was observed in *c.* 20% of the stems (> 2 cm in diameter). On 9 June 2005, we collected 24 sections (20 cm in length) of *Miscanthus sacchariflorus* stems containing one swift moth caterpillar from the floodplain. The grass section was tightly bound to a stem of each tree for the boring treatment, and we confirmed that the caterpillar had emerged from the grass section and bored into the bound stems within a few days. When we observed caterpillars boring into the trees, we cut stems for trees of the 100% and 25% cutting treatments on 12 June 2005. All trees were 90–110 cm tall just before the boring and cutting treatments. Experimental trees did not receive natural moth borings during the experimental period. Both moth boring and artificial cutting stimulated the production of rapidly growing lateral shoots from the dormant buds in the damaged stems.

WILLOW REGROWTH IN RESPONSE TO NATURAL AND ARTIFICIAL HERBIVORY

To determine whether boring and cutting treatments influenced lateral shoot production, we counted numbers of newly emerged lateral shoots and measured their shoot length in late July 2005. We calculated the mean number, length and overall length of the lateral shoots. Also, to examine the effects of boring and cutting treatments on plant growth, we measured tree height in late June 2006. Overall above-ground biomass was measured in early November 2006. For

biomass measurements, all above-ground plant tissues were harvested on 30 and 31 October and oven-dried at 60 °C for 72 h. Normality and equal variance were met, and thus the data were analysed using an ANOVA to detect effects of boring and cutting treatments on these plant traits, followed by a Tukey post hoc test.

To examine whether swift moth boring affected the host plant's nutritional status through shoot regrowth, we measured foliar nitrogen content. In particular, leaves on regrowth shoots often have significantly greater nitrogen content (Martinsen *et al.* 1998; Utsumi & Ohgushi 2008). In late August 2005, we randomly selected three newly emerged lateral shoots each from damaged stems and current-year shoots from undamaged stems in both bored and 25% cut trees. Also, six shoots were randomly selected for both 100% cut and control trees. We defined a current-year shoot as a shoot that grew from a 1-year stem. We took the upper five leaves of each selected shoot and oven-dried them at 60 °C for 48 h. After the dried leaves were ground, nitrogen content was determined using an elemental analyser (JM 1000CN; J-Science, Kyoto, Japan). We calculated foliar nitrogen content of each shoot and the mean foliar nitrogen content for each tree. To estimate within-tree spatial variability of nitrogen content, we calculated the coefficient of variation (CV). The data of mean nitrogen content were square-arc-sine-transformed, while CV were not transformed. We used an ANOVA to detect effects of treatments, followed by a Tukey post hoc test. Each individual tree was a replicate.

ARTHROPOD COMMUNITIES IN RESPONSE TO WILLOW REGROWTH

After the regrowth shoots emerged in boring and cutting treatments in July 2005, we monitored arthropod abundance and species richness four times: in August and September 2005 and May and July in 2006. During the censuses, we recorded the number of species and abundance of each of the species present on each tree. We sorted all arthropods by species using field guides (Ito, Okutani & Hiura 1977; Inoue *et al.* 1982; Kawai 1982; Hayashi, Morimoto & Kimoto 1984; Kurosawa, Hisamatsu & Sasaji 1985; Ueno, Kurosawa & Sato 1985; Morimoto & Hayashi 1986). To determine the effects of the regrowth response on herbivores and predators separately, we analysed data of herbivorous and predaceous arthropods, respectively. To prevent common species from swamping the abundance of less common species, we calculated relative abundance of herbivorous and predaceous arthropods as follows. We calculated the mean number of each species throughout the season. Afterwards, the relative abundance value of each species was expressed by $\log(n + 1)$ -transformed number per plant, which was then standardized so that the number of each taxon had an SD of 1 and a mean of 0.5, to equally weight all species (Whitham, Morrow & Potts 1994). The standardized values were then summed to calculate relative abundance per tree for herbivorous insects and predaceous arthropods, respectively. Also, all census data throughout the season for species richness were combined for each experimental tree. Because normality and equal variance were met, the data were analysed using a linear regression to examine the relationship between CV of foliar nitrogen and relative abundance/species richness. An ANOVA was also used to detect effects of treatments, followed by a Dunnett test as a post hoc. Each individual tree was treated as a replicate.

To determine whether there were differences in herbivore and predator community composition among treatments, we conducted an analysis of similarity (ANOSIM) using Bray–Curtis dissimilarity coefficient (Faith, Minchin & Belbin 1987; Bailey & Whitham 2002). The significance of the results was determined using Monte Carlo

permutations (1000) and reported as the ANOSIM *R*-statistics, which varies between 0 and 1; 0 indicates complete randomness, and 1 indicates that all replicates within a treatment are more similar to one another than any replicates from other treatments. Furthermore, Canonical Correspondence Analysis (CCA; ter Braak 1986) was performed to visually summarize differences in arthropod composition. Our treatments were entered as an environmental factor and the significance of the results was determined using Monte Carlo permutations (1000). The representative point for a class of a nominal environmental factor is located at the centroid (weighted average) of the experimental trees belonging to that class (ter Braak 1986). With abundance data, CCA was the successful ordination method with the long gradient (> 3 SD units; Van Wijngaarden *et al.* 1995; Hirst & Jackson 2007). In our case, gradient lengths of axes were > 3.0 (SD units). In each willow species, ANOSIM and CCA were performed for herbivore and predator communities, based on the log(*n* + 1)-transformed number of individuals of each species. Arthropod species with a low occurrence (those that emerged on six trees or fewer for each willow species) were removed from the data set prior to analyses. We used R software (R Development Core Team 2008) and the Vegan package (Oksanen *et al.* 2008).

Results

WILLOW REGROWTH IN RESPONSE TO NATURAL AND ARTIFICIAL HERBIVORY

Moth boring and cutting induced sprouting of new lateral shoots in contrast to control trees, where no lateral shoots

emerged. One month after the treatments were applied, the number and overall length of lateral shoots per tree differed significantly among bored, 25% cut and 100% cut trees, although no significant difference in the mean length of lateral shoots was found (Table 1). In each willow species, the number of lateral shoots on 100% cut trees was 4.2–12 times greater than that of bored and 25% cut trees (Tukey test: $P < 0.05$; Table 1), but we found no significant difference between bored and 25% cut trees. Similarly, in each willow species, the overall length of lateral shoots of 100% cut trees was 4.4–10.5 times longer than bored and 25% cut trees ($P < 0.05$), although no significant difference was found between bored and 25% cut trees. Note that all shoots in 100% cut trees were regrowth shoots.

Tree height did not significantly differ among bored, 25% cut, 100% cut and control trees in *S. eriocarpa* and *S. serissaefolia*, except for *S. gilgiana*. In *S. gilgiana*, bored trees were significantly taller than 100% cut trees. Also, a significant difference in above-ground biomass was not detected among treatments in any of the willow species. Thus, shoot regrowth of willows compensated for biomass loss by boring and cutting (Table 1).

The CV and means of nitrogen content of upper leaves within individual trees changed due to shoot regrowth in response to boring and cutting treatments, except for mean nitrogen content in *S. serissaefolia* (Table 1). Within-tree mean nitrogen contents of upper leaves were the smallest in

Table 1. Plant characteristics of the experimental trees of three willow species. Means (SE) are presented. Different letters show significant difference (Tukey test, $P < 0.05$)

Plant characteristics	Bored	25% cut	100% cut	Control	<i>F</i>	<i>P</i>
No. of newly emerged lateral shoots						
<i>Salix gilgiana</i>	2.63 (0.78) ^a	3.13 (0.67) ^a	32.13 (5.75) ^b	0.00 ^c	25.42	< 0.001
<i>Salix eriocarpa</i>	1.63 (0.42) ^a	4.86 (0.94) ^a	20.63 (4.58) ^b	0.00 ^c	22.09	< 0.001
<i>Salix serissaefolia</i>	3.22 (1.68) ^a	5.29 (2.29) ^a	24.14 (3.74) ^b	0.00 ^c	23.17	< 0.001
Lateral shoot length (cm)						
<i>S. gilgiana</i>	10.05 (3.14)	6.75 (2.23)	6.51 (1.50)	–	0.69	0.514
<i>S. eriocarpa</i>	12.63 (5.02)	7.39 (2.21)	7.68 (2.89)	–	0.65	0.534
<i>S. serissaefolia</i>	9.32 (4.02)	4.26 (1.54)	5.15 (1.72)	–	0.18	0.83
Overall length of lateral shoots (cm)						
<i>S. gilgiana</i>	33.94 (15.21) ^a	22.38 (6.71) ^a	235.01 (54.33) ^b	–	13.28	< 0.001
<i>S. eriocarpa</i>	32.24 (19.15) ^a	31.97 (7.74) ^a	163.83 (50.81) ^b	–	5.40	0.013
<i>S. serissaefolia</i>	28.80 (14.75) ^a	20.34 (7.10) ^a	126.03 (42.95) ^b	–	5.08	0.017
Height (cm)						
<i>S. gilgiana</i>	194.25 (7.40) ^a	185.81 (8.63) ^{ab}	153.50 (13.44) ^b	184.69 (8.54) ^{ab}	3.34	0.033
<i>S. eriocarpa</i>	171.11 (10.67)	172.50 (10.34)	144.00 (11.68)	185.71 (12.08)	2.39	0.206
<i>S. serissaefolia</i>	172.67 (23.68)	191.79 (14.67)	131.86 (17.83)	162.00 (12.53)	2.19	0.116
Above-ground biomass (g)						
<i>S. gilgiana</i>	624.86 (67.30)	525.21 (102.17)	333.39 (54.26)	555.56 (80.71)	2.53	0.077
<i>S. eriocarpa</i>	482.28 (83.76)	523.01 (96.84)	293.01 (50.11)	472.60 (63.64)	1.62	0.205
<i>S. serissaefolia</i>	370.22 (57.18)	405.15 (73.81)	293.19 (84.89)	343.61 (63.74)	0.42	0.739
Mean nitrogen content (% dry weight)						
<i>S. gilgiana</i>	2.55 (0.16)	2.35 (0.05) ^{bc}	2.81 (0.11) ^a	2.11 (0.05) ^c	8.07	< 0.001
<i>S. eriocarpa</i>	2.17 (0.08)	2.11 (0.06)	2.36 (0.10) ^a	1.81 (0.05) ^b	9.28	< 0.001
<i>S. serissaefolia</i>	2.05 (0.08)	2.14 (0.13)	2.22 (0.09)	2.01 (0.15)	0.57	0.636
Coefficient of variation of nitrogen content						
<i>S. gilgiana</i>	13.60 (1.76) ^a	11.61 (1.76) ^{ab}	4.24 (0.67) ^C	6.75 (0.99) ^{bc}	9.62	< 0.001
<i>S. eriocarpa</i>	11.69 (1.34) ^{ab}	12.09 (1.63) ^a	4.70 (1.43) ^C	6.14 (1.51) ^{bc}	6.50	0.001
<i>S. serissaefolia</i>	9.84 (2.12) ^a	8.22 (1.36)	2.27 (0.34) ^C	3.37 (0.82) ^{bc}	7.58	0.001

control trees among treatments and were the highest in 100% cut trees. On the other hand, CV of foliar nitrogen were smallest in 100% cut trees and were highest in bored and 25% cut trees.

ARTHROPOD COMMUNITIES IN RESPONSE TO WILLOW REGROWTH

We identified 106 taxa in 46 families of 8 orders of arthropods on the experimental willow trees (Appendix S1). In each willow species, herbivore relative abundance and species richness significantly increased with the CV of foliar nitrogen (abundance: *S. gilgiana*, $r^2 = 0.31$, $P < 0.0001$; *S. eriocarpa*, $r^2 = 0.42$, $P < 0.0001$; *S. serissaefolia*, $r^2 = 0.42$, $P < 0.0001$; richness: *S. gilgiana*, $r^2 = 0.40$, $P < 0.0001$; *S. eriocarpa*, $r^2 = 0.36$, $P < 0.0001$; *S. serissaefolia*, $r^2 = 0.37$, $P < 0.0001$; Fig. 1). However, no significant relationships between these community properties and mean nitrogen contents were found ($P > 0.05$; Fig. 1). We found significant differences in species richness of herbivorous insects among treatments (*S. gilgiana*, $F_{3,28} = 8.46$, $P < 0.001$; *S. eriocarpa*, $F_{3,28} = 3.53$, $P = 0.027$; *S. serissaefolia*, $F_{3,28} = 3.72$, $P = 0.023$; Fig. 2). Moth boring and 25% cutting significantly increased herbivorous species richness by 1.3–1.6 times greater than the controls (Dunnnett test: $P < 0.05$). However, species richness did not differ between 100% cut and control trees. There was a marginally significant difference in species richness of predaceous arthropods among treatments in *S. gilgiana*

($F_{3,28} = 2.95$, $P = 0.050$), and there was no significant difference for *S. eriocarpa* ($F_{3,28} = 1.44$, $P = 0.253$) or *S. serissaefolia* ($F_{3,28} = 1.73$, $P = 0.183$; Fig. 2). We found significant differences in relative abundance of herbivorous insects among treatments (*S. gilgiana*, $F_{3,28} = 5.97$, $P = 0.003$; *S. eriocarpa*, $F_{3,28} = 4.71$, $P = 0.009$; *S. serissaefolia*, $F_{3,28} = 4.06$, $P = 0.017$; Fig. 2). Relative abundance of herbivorous insects in bored and 25% cut trees was 1.4–1.7 times greater than in controls in all three willow species (Dunnnett test, $P < 0.05$), but no significant difference was found between 100% cut and control trees. Although a significant effect of herbivory treatments on relative abundance of predaceous arthropods was detected in *S. gilgiana* (*S. gilgiana*, $F_{3,28} = 4.58$, $P = 0.010$; *S. eriocarpa*, $F_{3,28} = 0.584$, $P = 0.630$; *S. serissaefolia*, $F_{3,28} = 1.46$, $P = 0.249$), moth boring and 25% and 100% cut treatments did not significantly alter predator abundance compared with the control trees (Dunnnett test, $P > 0.05$; Fig. 2).

ANOSIM and CCA ordination indicated that the moth boring and artificial cutting treatments altered community composition of herbivorous species (Table 2 and Fig. 3). The ANOSIM indicated that herbivore communities were separated into three groups. In *S. gilgiana* and *S. eriocarpa*, herbivore community composition of moth boring and 25% cut, 100% cut and control trees differed significantly from each other (Table 2). In *S. serissaefolia*, herbivore communities of moth boring and 25% cut trees differed significantly from control trees, but those of the 100% cut trees did not differ

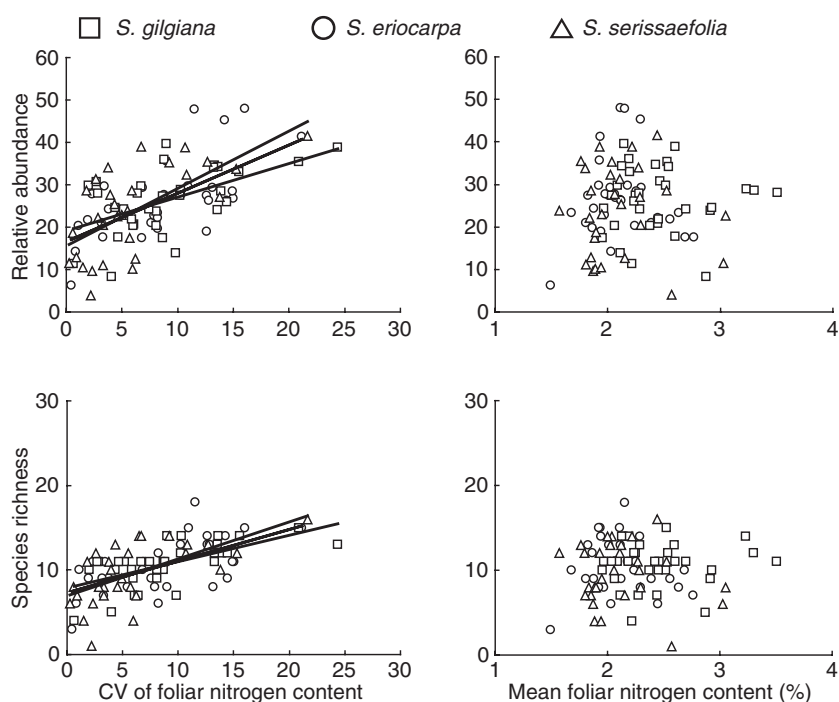


Fig. 1. Effects of mean and variation of foliar nitrogen content on relative abundance and species richness of herbivores on an individual tree significantly increased with coefficient of variations of foliar nitrogen content in each willow species (abundance: *Salix gilgiana*, $y = 0.80x + 19.14$; *Salix eriocarpa*, $y = 1.14x + 16.60$; *Salix serissaefolia*, $y = 1.35x + 15.67$; richness: *S. gilgiana*, $y = 0.31x + 7.89$; *S. eriocarpa*, $y = 0.38x + 7.26$; *S. serissaefolia*, $y = 0.44x + 6.98$), but not with mean foliar nitrogen content. Each symbol represents a single experimental tree.

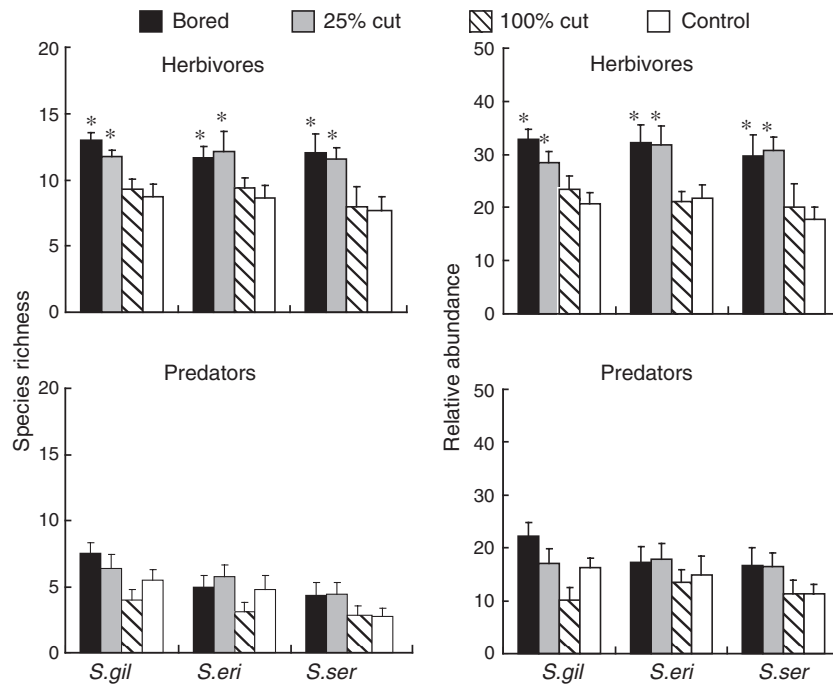


Fig. 2. Effects of herbivory treatments on species richness and relative abundance of herbivorous insects and predaceous arthropods on a willow tree. Relative abundance is overall abundance values calculated by making all species equally weighted (see Methods). Means and SE are presented. Asterisk shows significant difference from controls in each willow species (Dunnett test: $P < 0.05$). *S. gil*, *Salix gilgiana*; *S. eri*, *Salix eriocarpa*; *S. ser*, *Salix serissaefolia*.

Table 2. Results of ANOSIM for the similarity between four groups of arthropod communities associated with bored, 25% cut, 100% cut and control trees. *R* is a statistic value indicating how far groups are separated from each other, ranging from 0 (indistinguishable) to 1 (all similarities within groups are less than any similarity between groups). Significant values ($P < 0.05$) are indicated by bold letters

Species	Treatment	Bored		25% cut		100% cut		Global	
		<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Herbivore community									
<i>Salix gilgiana</i>	25% cut	-0.078	0.794						
	100% cut	0.149	0.045	0.195	0.020			0.285	< 0.001
	Control	0.359	0.003	0.294	0.008	0.725	0.001		
<i>Salix eriocarpa</i>	25% cut	-0.072	0.813						
	100% cut	0.179	0.048	0.423	0.002			0.230	0.001
	Control	0.181	0.029	0.214	0.008	0.488	0.002		
<i>Salix serissaefolia</i>	25% cut	0.114	0.116						
	100% cut	0.452	0.001	0.163	0.046			0.264	< 0.001
	Control	0.497	0.001	0.388	0.002	0.011	0.384		
Predator community									
<i>S. gilgiana</i>	25% cut	0.063	0.138						
	100% cut	0.044	0.177	0.002	0.418			0.091	0.014
	Control	0.256	0.011	0.182	0.017	0.044	0.246		
<i>S. eriocarpa</i>	25% cut	-0.038	0.684						
	100% cut	0.342	0.002	0.287	0.004			0.163	0.020
	Control	0.137	0.049	0.137	0.037	0.091	0.158		
<i>S. serissaefolia</i>	25% cut	0.094	0.160						
	100% cut	-0.027	0.556	0.000	0.443			0.057	0.181
	Control	0.051	0.312	0.147	0.081	-0.022	0.522		

ANOSIM, analysis of similarity.

significantly from the controls. Likewise, CCA indicated that herbivore species composition was related to herbivory treatments ($P < 0.001$; Fig. 3). The centroids of bored and 25%

cut trees were placed between those of 100% cut and control trees except for *S. serissaefolia*. Similarly, predator community composition significantly differed among treatments

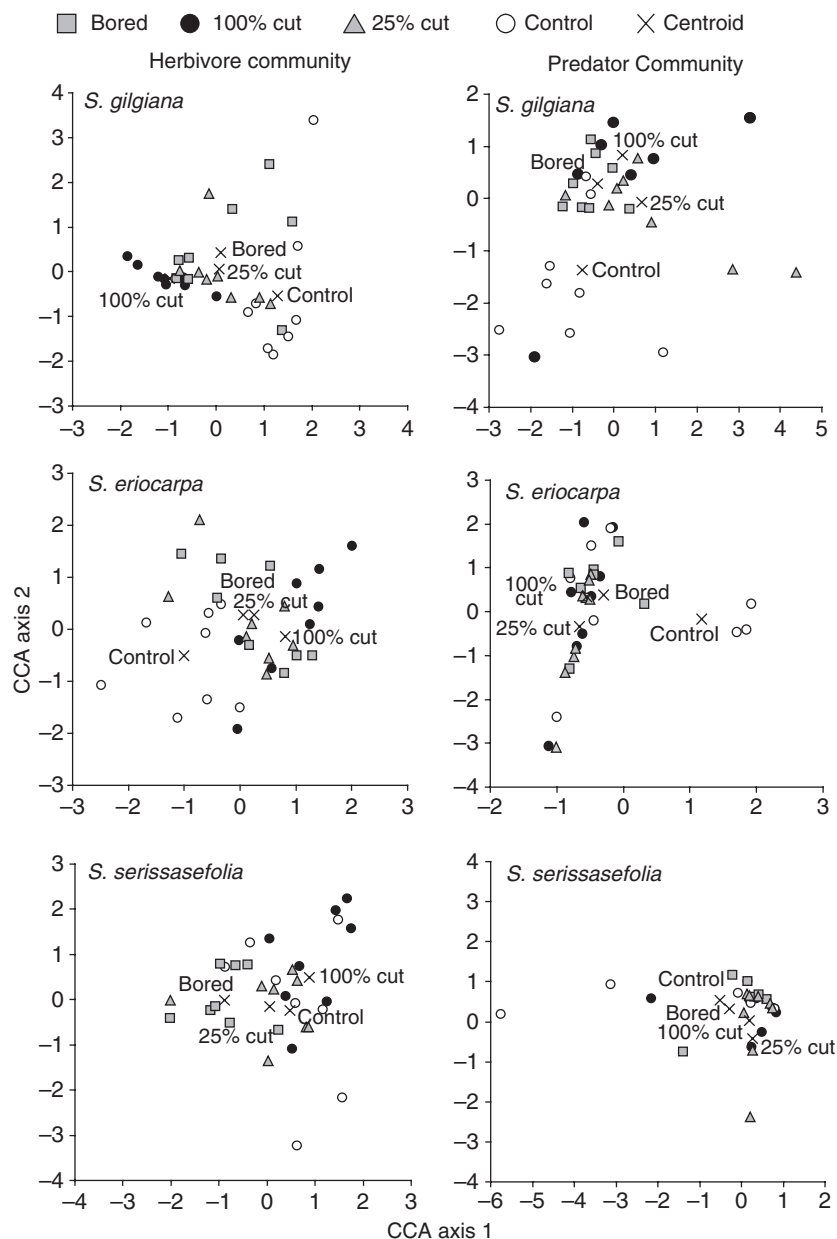


Fig. 3. Canonical Correspondence Analysis ordination plot, first two axes, for herbivore species on the left panel and for predator species on the right panel. The data set with individual numbers of each species was analysed. \times represents a centroid for each treatment and each symbol represents the community on a single experimental tree.

except for *S. serissaeifolia* (Table 2), and this was also supported by CCA ($P < 0.05$; Fig. 3). In ANOSIM, we detected significant differences between regrowth trees (moth boring, 25% cut and 100% cut trees) and controls in *S. gilgiana*. In *S. eriocarpa*, moth boring and 25% cut trees differed significantly from the controls, but those of the 100% cut trees did not differ significantly from the controls.

Discussion

This study clearly illustrated that moth boring and artificial herbivory had a significant, indirect impact on community structure of herbivorous and predaceous arthropods of the

three willow species. Our field experiment revealed that these effects were due to changes in plant quality but not plant biomass. It should be noted that community responses were different between bored/25% cut trees and 100% cut trees, despite that these herbivory treatments induced shoot regrowth of the willows.

WILLOW REGROWTH IN RESPONSE TO NATURAL AND ARTIFICIAL HERBIVORY

Previous studies have demonstrated that natural herbivory and stem cutting can stimulate production of rapidly growing shoots in willows (Craig *et al.* 1986; Hjältén & Price 1996;

Nakamura *et al.* 2003, 2006; Guillet & Bergström 2006; Utsumi & Ohgushi 2007). In our experiment, willows produced newly emerged lateral shoots in response to moth boring, 25% cutting and 100% cutting. As a result, willows fully compensated for the biomass loss due to these herbivory treatments (Table 1). Moth boring and 25% cutting had similar effects on the intensity of shoot regrowth in terms of the number and overall length of newly emerged lateral shoots. It is widely accepted that altering the sink–source relationship in response to herbivory, which regulates the flow of assimilates, results in lateral shoot production (Whitham *et al.* 1991).

Regrowth shoots in response to boring and cutting produced leaves with greater nitrogen content relative to current-year shoots (Nakamura *et al.* 2006; Utsumi & Ohgushi 2008). Likewise, several studies have reported that compensatory regrowth of woody plants improves the nutritional status of leaf and shoot (Danell & Huss-Danell 1985; Martinsen *et al.* 1998; Nakamura *et al.* 2003). As a result, in 100% cut trees, mean nitrogen content generally increased, but within-tree variation decreased because all above-ground growth consisted of regrowth shoots. On the other hand, bored and 25% cut trees had intermediate nitrogen content and showed the greatest within-tree variation in nutritional status because regrowth shoots and current-year shoots were mixed. As most vascular plants have a modular and sectorial architecture, plant responses to local herbivory are often localized in partially independent plant parts (Watson & Casper 1984; Orians & Jones 2001; Orians, Ardón & Mohammad 2002). In the regrowth response of salicaceous trees, foliar nutritious status is often positively correlated with the concentration of secondary metabolites such as phenolics (Bryant *et al.* 1991; Martinsen *et al.* 1998). Thus, the presence of moth herbivory or differences in damage intensity would increase phenotypic variation of plants within and among individual trees. Also, note that the lateral shoot regrowth varied among willow species. In *S. serissaefolia*, trait changes in response to moth boring were significant but small in comparison with *S. gilgiana* and *S. eriocarpa* (Utsumi & Ohgushi 2008). As a result, the increase in within-tree means of nitrogen content would be cancelled out by among-tree variation, even if within-tree variation would differ significantly among treatments.

EFFECTS OF SHOOT REGROWTH ON HERBIVORE COMMUNITY

Several authors have argued that species richness and overall abundance of herbivorous insects increase with increasing resource quantity and quality (Mattson 1980; Price 1991; Siemann 1998; Srivastava & Lawton 1998; Nakamura *et al.* 2006). Because biomass and quality of food resources often increase on regrowth shoots, more herbivore species can colonize there (Nakamura *et al.* 2006). In most cases, however, it is difficult to determine whether quantity or quality is responsible for the increase in species richness and abundance of herbivores because both biomass and quality of

plant tissues often change correlatively. We emphasized that community-level effects were due to induced changes in plant quality but not to changes in plant biomass in our experiment. Thus, differences in plant quality among plant individuals depending on the intensity of herbivory are more likely to determine species richness and overall abundance of herbivore communities. However, it remains unclear which components of changed plant quality involved in regrowth response, such as primary and secondary metabolites, physical status and/or architectural complexity, were responsible for the patterns of community structure.

Mean foliar nitrogen content did not explain changes in overall abundance of herbivorous insects. On the other hand, the positive correlation between overall abundance and CV of nitrogen content may be explained by changes in other plant traits in addition to foliar nitrogen and species-specific preference of insects. For example, leaves produced by shoot regrowth often contain more phenolics as well as rich nitrogen (Bryant *et al.* 1991; Martinsen *et al.* 1998). Phenolic compounds often deter herbivores, while specialist herbivorous insects often adapt to use such compounds as feeding stimulants (Kolehmainen *et al.* 1995; Ikonen 2002). Herbivorous insects often show species-specific preference for morphologically and chemically distinct resources within and among individual plants (Whitham *et al.* 1984; Suomela 1996; Martinsen *et al.* 1998) and specific response to induced plant responses (Van Zandt & Agrawal 2004; Agrawal 2005; Viswanathan *et al.* 2005). For example, in our study, the specialist willow leaf beetle *P. versicolora* and the specialist aphid *Chaitophorous saliniger* preferentially colonize on rapidly regrowing shoots within plant individuals (Nakamura *et al.* 2003; Utsumi & Ohgushi 2008). In contrast, generalist herbivores often forage more preferentially on mature leaves of current-year shoots on willows (Cates 1980). Our previous study found that specialist chewers, specialist sap-feeders and leaf miners increased on the regrowth shoots, although generalist chewers and sap-feeders did not increase (S. Utsumi & T. Ohgushi, unpublished data). Thus, partial regrowth response within individual plants would increase the overall abundance of herbivores due to increase in the abundance of species that prefer regrowth shoots. On the other hand, whole tree regrowth in response to severe herbivory would increase the abundance of some herbivores but would deter other herbivores, resulting in no change in overall abundance.

Likewise, the increase in species richness on bored and 25% cut trees and the positive correlation with CV of nitrogen content could also be explained by the species-specific response of herbivores to shoot regrowth. The total number of herbivore species increased throughout the survey by 27% on bored and 25% cut trees relative to the control trees. Some herbivore species, such as the leaf beetle *Chrysomela populi*, the spittlebug *Aphrophora pectoralis* and the leaf miner *Phyllocnistis* sp. were observed only on regrowth shoots. In contrast, the total number of herbivore species decreased by 13% on 100% cut trees relative to the controls. For example,

several generalist species, such as the click beetle *Agrypnus binodulus*, the lygaeid bug *Drymus marginatus* and the bean bug *Riptortus clavatus* were never observed on 100% cut trees. Induced changes in plant quality can affect not only abundance but also species richness of herbivore communities due to the species-specific response of herbivores (Van Zandt & Agrawal 2004).

CCA and ANOSIM results strongly supported our interpretation on herbivore community response. Compositional structures on individual trees were separated into three groups: (i) bored and 25% cut trees; (ii) 100% cut trees; and (iii) control trees. The centroids of communities on bored and 25% cut trees were located between those of 100% cut and control trees in the ordination plots, except for *S. serissaefolia*. These results suggest that herbivore species that prefer either 100% cut or control trees would assemble together on individual plants in which regrowth and non-regrowth shoots were mixed. This is consistent with the results obtained by Bailey & Whitham (2002). Fire of intermediate severity and moderate levels of elk browsing resulted in the greatest increase in species richness and abundance of arthropod communities. In contrast, high-severity fire and severe browsing reduced species richness and abundance. Also, the interaction of fire intensity and elk browsing resulted in distinct arthropod composition. Similarly, Hunter (1992) illustrated that abundances of leaf miners, leaf chewers and sap feeders in late season on *Quercus robur* were affected by early season defoliation in a different way. This is because of different performance and preference of three herbivore guilds to regrowth leaves, and he suggested that the guild-specific responses to different levels of early defoliation would result in different patterns of late-season community structure. Thus, heterogeneous conditions in which individual trees have both regrowth and non-regrowth shoots within willow individuals may increase species diversity of herbivores on plants. Moreover, compositional differences among treatments suggest that heterogeneous conditions among plant individuals with different levels of herbivory increases species diversity of herbivores at the plant population level by increasing the phenotypic diversity of host plants.

There has been a great deal of recent research on the effects of plant genotype and plant genetic diversity on arthropod communities (Whitham *et al.* 2006; Hughes *et al.* 2008; for reviews). These community genetics studies indicate that phenotypic diversity caused by multiple plant genotypes increases species diversity of arthropods on plants. However, much less is known about the community-level effects of phenotypic plasticity including induced plant responses (but see Van Zandt & Agrawal 2004; Rodriguez-Saona & Thaler 2005). Our study emphasizes that intraspecific variation due to herbivore-induced differences within and among plant individuals can have significant effects on arthropod communities (Ohgushi 2005) as well as plant genetics. Future studies should examine how plant genotypes and induced plant responses interact to cause community-level effects on arthropods (McGuire & Johnson 2006).

EFFECTS OF SHOOT REGROWTH ON PREDATOR COMMUNITY

The increase in species richness and abundance at lower trophic levels could enhance species richness and abundance at higher trophic levels because of increases in prey abundance, alternative prey species and prey species available to specialist predators (Hassell 1978; Hunter & Price 1992; Abrams 1995; Siemann 1998; Cardinale *et al.* 2006). The regrowth response can increase abundance and species richness of arthropod predators by increasing species richness and abundance of insect herbivores (Nakamura *et al.* 2006). In this study, although species richness and overall abundance of predators were unaffected by herbivory treatments, community composition of predators differed significantly among treatments. This change in community composition was likely responsible for changes in densities of ant and spider species. In *S. gilgiana*, ant density increased by 6- to 9-fold on regrowth plants, which may be caused by increased abundance of prey herbivores or honeydew production by 2.8- to 6-fold increase in densities of specialist sap-feeders such as the aphids *C. saliniger* and *Pterocomma pilosum* (e.g. Johnson 2008). On the other hand, plant architectural complexity may encourage aggregation of spiders, because of increase in refuges, web attachment points for web-spiders or habitats with favourable microclimates (McNett & Rypstra 2000; Langelotto & Denno 2004). Species richness and abundance of spiders can increase due to increase in complexity of shoot structure, expressed by foliage density and lateral branching (Halaj, Ross & Moldenke 2000; de Souza & Martins 2005). We observed that spider density increased 2.3-fold and species richness of webless spiders (Salticidae, Thomisidae, Oxyopidae and Clubionidae) increased 1.4-fold on bored and 25% cut trees relative to the control trees in *S. eriocarpa*. These spiders often emerged preferentially on the lateral shoots (S. Utsumi & T. Ohgushi, unpublished data). In addition, abundance and species richness of orb-weavers (Araneidae and Nephilidae) were unaffected. This is probably because lateral shoot production may not contribute to increase in web attachment points for orb-weavers.

These predators often prevent increases in species richness and abundance of other predators (Polis & Holt 1992; Wimp & Whitham 2001; Johnson 2008). For example, Wimp & Whitham (2001) demonstrated that aphid-attending ants decreased species richness of spiders on aspens through removal effects. Also, intraguild predation often occurs between webless spiders and other predaceous arthropods (Finke & Denno 2003; Denno *et al.* 2004). Thus, predator effects, in addition to bottom-up effects, may result in compositional changes in predator communities (Johnson 2008). We should pay more attention to ecological consequences of induced plant responses of third trophic communities.

Several authors have argued that an individual tree is a mosaic of heterogeneous resources rather than an island of uniform quality (Whitham *et al.* 1984; Orians & Jones 2001; Roslin *et al.* 2006). Herbivores are some of the most important agents to induce changes in plant traits, and they subse-

quently create a mosaic of heterogeneous resources within and among plant individuals (Orians & Jones 2001; Viswanathan & Thaler 2004; Rodriguez-Saona & Thaler 2005; Viswanathan, McNickle & Thaler 2008). This study clearly illustrated that changes in resource quality induced by herbivory can affect the local diversity of arthropod communities. In particular, induced resource heterogeneity may be important in determining community structure. Further evidence on the role of induced resource heterogeneity in structuring arthropod communities is needed to understand community consequences of herbivore-induced responses in terrestrial plants. Future studies should pay more attention to the nature of plant-mediated indirect interactions that can promote diversity of arthropod communities.

Acknowledgements

The authors thank A.A. Agrawal, H. Roininen, P.W. Price and anonymous reviewers for helpful comments on earlier drafts of the manuscript. They also thank I. Kojima, A. Matsumoto and Y. Ando for their assistance in establishment of. In addition, they thank the River Bureau of Ministry of Land, Infrastructure and Transport for allowing to conduct research at the Yasu River. This study was partly supported by the 21st Century COE Program (A14), and the Global COE Program (A06).

References

- Abrams, P.A. (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? *Ecology*, **76**, 2019–2027.
- Agrawal, A.A. (2005) Future directions in the study of induced plant responses to herbivory. *Entomologia Experimentalis et Applicata*, **115**, 97–105.
- Bailey, J.K. & Whitham, T.G. (2002) Interactions among fire, aspen, and elk affect insect diversity: reversal of a community response. *Ecology*, **83**, 1701–1712.
- Bailey, J.K. & Whitham, T.G. (2003) Interactions among elk, aspen, galling sawflies and insectivorous birds. *Oikos*, **101**, 127–134.
- Barker, A.M., Wratten, S.D. & Edwards, P.J. (1995) Wound-induced changes in tomato leaves and their effects on the feeding patterns of larval lepidopteran. *Oecologia*, **101**, 251–257.
- ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.
- Bryant, J.P., Danell, K., Provenza, F., Reichardt, P.B., Clausen, T.A. & Werner, R.A. (1991) Effects of mammal browsing on the chemistry of deciduous woody plants. *Phytochemical Induction by Herbivores* (eds D.W. Tallamy & M.J. Raupp), pp. 135–155. John Wiley, New York.
- Cardinale, B.J., Weis, J.J., Forbes, A.E., Tilmon, K.J. & Ives, A.R. (2006) Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator–prey system. *Journal of Animal Ecology*, **75**, 497–505.
- Cates, R.G. (1980) Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. *Oecologia*, **46**, 22–31.
- Craig, T.P., Price, P.W. & Itami, J.K. (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology*, **67**, 419–425.
- Damman, H. (1989) Facilitative interactions between two lepidopteran herbivores of *Asimina*. *Oecologia*, **78**, 214–219.
- Danell, K. & Huss-Danell, K. (1985) Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos*, **44**, 75–81.
- Denno, R.F. & Kaplan, I. (2007) Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past. *Ecological Communities: Plant Mediation in Indirect Interaction Webs* (eds T. Ohgushi, T.P. Craig & P.W. Price), pp. 10–50. Cambridge University Press, Cambridge.
- Denno, R.F., McClure, M.S. & Ott, J.R. (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology*, **40**, 297–331.
- Denno, R.F., Peterson, M.A., Gratton, C., Cheng, J., Langellotto, G.A., Huberty, A.F. & Finke, D.L. (2000) Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology*, **81**, 1814–1827.
- Denno, R.F., Mitter, M.S., Langellotto, G.A., Gratton, C. & Finke, D.L. (2004) Interaction between a hunting spider and web-builder: consequences of intraguild predation and cannibalism for prey suppression. *Ecological Entomology*, **29**, 566–577.
- Enda, N. (1971) *Ecology of Important Pests on Fast Grower Trees*. Ringyo Kagaku Shinkojo, Tokyo.
- Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, **69**, 57–68.
- Finke, D.L. & Denno, R.F. (2003) Intra-guild predation relaxes natural enemy impacts on herbivore populations. *Ecological Entomology*, **28**, 67–73.
- Guillet, C. & Bergström, R. (2006) Compensatory growth of fast-growing coppice willow (*Salix*) in response to simulated large herbivore browsing. *Oikos*, **113**, 33–42.
- Halaj, J., Ross, D.W. & Moldenke, A.R. (2000) Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos*, **90**, 139–152.
- Hassell, M.P. (1978) *The Dynamics of Arthropod Predator–Prey Systems*. Princeton University Press, New Jersey.
- Hayashi, M., Morimoto, K. & Kimoto, S. (1984) *The Coleoptera of Japan in Color, Vol. 4*. Hoikusha publishing Co., Ltd., Osaka (in Japanese).
- Hirst, C.N. & Jackson, D.A. (2007) Reconstructing community relationships: the impact of sampling error, ordination approach, and gradient length. *Diversity and Distributions*, **13**, 361–371.
- Hjältén, J. & Price, P.W. (1996) The effect of pruning on willow growth and sawfly population densities. *Oikos*, **77**, 549–555.
- Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008) Ecological consequences of genetic diversity. *Ecology Letters*, **11**, 609–623.
- Hunter, M.D. (1992) Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. *The Effects of Resource Distribution on Animal–Plant Interactions* (eds M.D. Hunter, T. Ohgushi & P.W. Price), pp. 287–325. Academic Press, San Diego.
- Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom–up and top–down forces in natural communities. *Ecology*, **73**, 724–732.
- Igarashi, M. (1994) Boring insects of lepidoptera. *Forest Insects* (eds F. Kobayashi & A. Takeya), pp. 239–241. Yokendo, Tokyo (in Japanese).
- Ikonen, A. (2002) Preferences of six leaf beetle species among qualitatively different leaf age classes of three Salicaceous host species. *Chemoecology*, **12**, 23–28.
- Inbar, M., Eshel, A. & Wool, D. (1995) Interspecific competition among phloem-feeding insects mediated by induced host-plant sinks. *Ecology*, **76**, 1506–1515.
- Inoue, H., Sugi, S., Kuroko, H., Moriuchi, S., Kawanabe, A. & Owada, M. (1982) *Moths of Japan*. Kodansha Co., Ltd, Tokyo (in Japanese).
- Ito, S., Okutani, T. & Hiura, I. (1977) *Colored Illustrations of the Insects of Japan, Vol. 2*. Hoikusha publishing Co., Ltd., Osaka (in Japanese).
- Johnson, M.T. (2008) Bottom–up effects of plant genotype on aphids, ants, and predators. *Ecology*, **89**, 145–154.
- Karban, R. & Baldwin, I.T. (1997) *Induced Responses to Herbivory*. University of Chicago Press, Chicago.
- Kawai, S. (1982) *Scale Insects of Japan in Colors*. Zenkoku Nōson Kyōiku Kyōkai, Tokyo (in Japanese).
- Kolehmainen, J., Julkunen-Tiitto, R., Roininen, H. & Tahvanainen, J. (1995) Phenolic glucosides as feeding cues for willow-feeding leaf beetles. *Entomologia Experimentalis et Applicata*, **74**, 235–243.
- Kurosawa, Y., Hisamatsu, S. & Sasaji, H. (1985) *The Coleoptera of Japan in Color, Vol. 3*. Hoikusha publishing Co., Ltd., Osaka (in Japanese).
- Langellotto, G.A. & Denno, R.F. (2004) Response of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.
- Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23–29.
- Martinsen, G.D., Driebe, E.M. & Whitham, T.G. (1998) Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology*, **79**, 192–200.
- Martinsen, G.D., Floate, K.D., Waltz, A.M., Wimp, G.M. & Whitham, T.G. (2000) Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. *Oecologia*, **123**, 82–89.
- Masters, G.J. & Brown, V.K. (1992) Plant-mediated interactions between two spatially separated insects. *Functional Ecology*, **6**, 175–179.

- Masters, G.J., Jones, T.H. & Rogers, M. (2001) Host-plant mediated effects of root herbivory on insect seed predators and their parasitoids. *Oecologia*, **127**, 246–250.
- Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.
- McGuire, R.J. & Johnson, M.T. (2006) Plant genotype and induced responses affect resistance to herbivores on evening primrose (*Oenothera biennis*). *Ecological Entomology*, **31**, 20–31.
- McNett, B.J. & Rypstra, A.L. (2000) Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. *Ecological Entomology*, **25**, 423–432.
- Morimoto, K. & Hayashi, N. (1986) *The Coleoptera of Japan in Color, Vol. 1*. Hoikusha Publishing Co., Ltd., Osaka (in Japanese).
- Nakamura, M., Miyamoto, Y. & Ohgushi, T. (2003) Gall-initiation enhances the availability of food resources for herbivorous insects. *Functional Ecology*, **17**, 851–857.
- Nakamura, M., Utsumi, S., Miki, T. & Ohgushi, T. (2005) Flood initiates bottom-up cascades in a tri-trophic system: host plant regrowth increases densities of a leaf beetle and its predators. *Journal of Animal Ecology*, **74**, 683–691.
- Nakamura, M., Kagata, H. & Ohgushi, T. (2006) Trunk cutting initiates bottom-up cascades in a tri-trophic system: sprouting increases biodiversity of herbivorous and predaceous arthropods on willows. *Oikos*, **113**, 259–268.
- Ohgushi, T. (2005) Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 81–105.
- Ohgushi, T., Craig, T.P. & Price, P.W. (2007) *Ecological Communities: Plant Mediation in Indirect Interaction Webs*. Cambridge University Press, Cambridge.
- Oksanen, J., Kindt, R., Legendre, P., O'hara, B., Simpson, G.L., Stevens, H.H. & Wagner, H. (2008) Vegan: Community Ecology Package. R package version 1.13-12, <http://vegan.r-forge.r-project.org/>
- Orians, C.M. & Jones, C.G. (2001) Plants as resource mosaics: a functional model for predicting patterns of within-plant resource heterogeneity to consumers based on vascular architecture and local environmental variability. *Oikos*, **94**, 493–504.
- Orians, C.M., Ardón, M. & Mohammad, B.A. (2002) Vascular architecture and patchy nutrient availability generate within-plant heterogeneity in plant traits important to herbivores. *American Journal of Botany*, **89**, 270–278.
- Polis, G.A. & Holt, D.A. (1992) Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution*, **7**, 151–154.
- Price, P.W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos*, **62**, 244–251.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Raupp, M.J. & Denno, R.F. (1983) Leaf age as a predictor of herbivore distribution and abundance. *Variable Plants and Herbivores in Natural and Managed Systems* (eds R.F. Denno & M.S. McClure), pp. 91–124. Academic Press, New York.
- Rodriguez-Saona, C. & Thaler, J.S. (2005) Herbivore-induced responses and patch heterogeneity affect abundance of arthropods on plants. *Ecological Entomology*, **30**, 156–163.
- Roininen, H., Price, P.W. & Bryant, J.P. (1997) Response of galling insects to natural browsing by mammals in Alaska. *Oikos*, **80**, 481–486.
- Roslin, T., Gripenberg, S., Salminen, J.-P., Karonen, M., O'Hara, R.B., Pihlaja, K. & Pulkkinen, P. (2006) Seeing the trees for the leaves – oaks as mosaics for a host-specific moth. *Oikos*, **113**, 106–120.
- Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, **79**, 2057–2070.
- de Souza, A.L.T. & Martins, R.P. (2005) Foliage density of branches and distribution of plant-dwelling spiders. *Biotropica*, **37**, 416–420.
- Srivastava, D.S. & Lawton, J.H. (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist*, **152**, 510–529.
- Strauss, S.Y. (1991) Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology*, **72**, 543–558.
- Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*, **14**, 179–185.
- Strong, D.R., Lawton, J.H. & Southwood, R. (1984) *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific Publications, Oxford.
- Suomela, J. (1996) Within-tree variability of mountain birch leaves causes variation in performance for *Epirrita autumnata* larvae. *Vegetatio*, **127**, 77–83.
- Tindall, K.V. & Stout, M.J. (2001) Plant-mediated interactions between the rice water weevil and fall armyworm in rice. *Entomologia Experimentalis et Applicata*, **101**, 9–17.
- Ueno, S., Kurosawa, Y. & Sato, M. (1985) *The Coleoptera of Japan in Color, Vol. 2*. Hoikusha Publishing Co., Ltd., Osaka (in Japanese).
- Utsumi, S. & Ohgushi, T. (2007) Plant regrowth response to a stem-boring insect: a swift moth-willow system. *Population Ecology*, **49**, 241–248.
- Utsumi, S. & Ohgushi, T. (2008) Host plant variation in plant-mediated indirect effects: moth boring-induced susceptibility of willows to a specialist leaf beetle. *Ecological Entomology*, **33**, 250–260.
- Van Wijngaarden, R.P.A., Van den Brink, P.J., Oude Voshaar, J.H. & Leeuwangh, P. (1995) Ordination techniques for analyzing response of biological communities to toxic stress in experimental ecosystems. *Ecotoxicology*, **4**, 61–77.
- Van Zandt, P.A. & Agrawal, A.A. (2004) Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). *Ecology*, **85**, 2616–2629.
- Viswanathan, D.V. & Thaler, J.S. (2004) Plant vascular architecture and within-plant spatial patterns in resource quality following herbivory. *Journal of Chemical Ecology*, **30**, 531–543.
- Viswanathan, D.V., Narwani, A.J.T. & Thaler, J.S. (2005) Specificity in induced plant responses shapes patterns of herbivore occurrence on *Solanum dulcamara*. *Ecology*, **86**, 886–896.
- Viswanathan, D.V., McNickle, G. & Thaler, J.S. (2008) Heterogeneity of plant phenotypes caused by herbivore-specific induced responses influences the spatial distribution of herbivores. *Ecological Entomology*, **33**, 86–94.
- Waltz, A.M. & Whitham, T.G. (1997) Plant development affects arthropod communities: opposing impacts of species removal. *Ecology*, **78**, 2133–2144.
- Watson, M.A. & Casper, B.B. (1984) Morphogenetic constraints on patterns of carbon distribution in plants. *Annual Review of Ecology and Systematics*, **15**, 233–258.
- Whitham, T.G., Williams, A.G. & Robinson, A.M. (1984) The variation principle: individual plants as temporal and spatial mosaics of resistance to rapidly evolving pests. *A New Ecology: Novel Approaches to Interactive System* (eds P.W. Price, C.N. Slobodkinoff & W.S. Gaud), pp. 15–51. John Wiley and Sons, New York.
- Whitham, T.G., Maschinski, J., Larson, K.C. & Paige, K.N. (1991) Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (eds P.W. Price, T.M. Lewinsohn, W.W. Benson & G.W. Fernandez), pp. 227–256. John Wiley, New York.
- Whitham, T.G., Morrow, P.A. & Potts, B.M. (1994) Plant hybrid zones as centers of biodiversity: the herbivore community of two endemic Tasmanian eucalypts. *Oecologia*, **97**, 481–490.
- Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., Leroy, C.J., Lonsdorf, E.V., Allan, G.J., Difazio, S.P., Potts, B.M., Fischer, D.G., Gehring, C.A., Lindroth, R.L., Marks, J.C., Hart, S.C., Wimp, G.M. & Wooley, S.C. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**, 510–523.
- Wimp, G.M. & Whitham, T.G. (2001) Biodiversity consequences of predation and host plant hybridization on an aphid-ant mutualism. *Ecology*, **82**, 440–452.
- Wise, M.J. & Weinberg, A.M. (2002) Prior flea beetle herbivory affects oviposition preference and larval performance of a potato beetle on their shared host plant. *Ecological Entomology*, **27**, 115–122.

Received 11 April 2008; accepted 22 April 2009
Handling Editor: Simon Leather

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Arthropod species found on observational and experimental willow trees.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.