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# Flood initiates bottom-up cascades in a tri-trophic system: host plant regrowth increases densities of a leaf beetle and its predators

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## Summary

**1.** Following the passing of a typhoon over central Japan in late August 2001, a large-scale flood occurred owing to the heavy precipitation. Willow trees on the banks of the Yasu River were badly damaged. In the following year, we examined the effects of the flood on the regrowth response of a willow, *Salix eriocarpa* (Franch), and its subsequent effects on the densities of a leaf beetle, *Plagiodera versicolora* (Laicharting), and its predators.
**2.** We used 10 randomly selected pairs of heavily and lightly damaged trees. Field observations showed that the number of sprouting shoots was significantly greater on heavily damaged trees than on lightly damaged trees. The sprouts continued to grow until August, producing lateral shoots and leaves.
**3.** The numbers of leaf beetles at all developmental stages (egg, larva, pupa and adult) significantly increased on heavily damaged trees as compared to numbers on lightly damaged trees. Adults of the leaf beetle aggregated predominantly on sprouting shoots throughout the growing season.
**4.** As a result of the increase in the number of leaf beetles, leaf herbivory on heavily damaged trees was significantly greater than on lightly damaged trees.
**5.** Two arthropod predators, the larvae of the ladybird *Aiolocaria hexaspilota* (Hope) and the web-building spider *Agelena opulenta* (L. Koch), also increased significantly on heavily damaged trees. These findings indicate that the flood caused by the typhoon initiated bottom-up cascading effects from the willow to arthropod predators through herbivorous insects by increased foliage sprouting.

*Key-words*: abiotic disturbances, compensation, riparian habitat, sprouting shoots, typhoon.

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## Introduction

It has been widely accepted that large-scale destruction by biotic (e.g. herbivory) and abiotic factors (e.g. fires and hurricanes) has the potential to stimulate compensatory regrowth of many trees and shrubs (Bryant *et al.* 1991; Whitham *et al.* 1991; Romme *et al.* 1995; Cooper-Ellis *et al.* 1999; Bellingham & Sparrow 2000; Bond & Midgley 2001; Del Tredici 2001). For example, browsing by mammals often induces foliage sprouting (reviewed by Bryant *et al.* 1991; Whitham *et al.* 1991). The resprout foliage can vary in secondary compounds and nutritional quality (Danell & Huss-Danell 1985; Martinsen, Dreibe & Whitham 1998). Thus herbivorous insects that emerge later in the season prefer such browsed trees and shrubs (Danell & Huss-Danell 1985; Roininen, Price & Tahvanainen 1994; Hjältén & Price 1996; Roininen, Price & Bryant 1997; Martinsen *et al.* 1998; Olofsson & Strengbom 2000). Furthermore, recent studies have reported that abiotic factors such as fires and hurricanes initiate regeneration via the sprouting

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of woody plants. This subsequently increases plant susceptibility to insect herbivores (e.g. Stein *et al*. 1992; Vieira, Andrade & Price 1996; Hunter & Forkner 1999; Radho-Toly, Majer & Yates 2001; Bailey & Whitham 2002, 2003; Spiller & Agrawal 2003).

In addition to the effects on insect herbivores, large-scale destruction may affect the abundance and/or distribution of arthropod predators indirectly. As arthropod predators tend to numerically track prey densities (Solomon 1949; Hassell 1978), an increase in insect herbivores following large-scale destruction would be expected to result in an increase in predator densities. This implies that large-scale destruction followed by regrowth of terrestrial plants may have the potential to initiate bottom-up cascading effects through three trophic levels. There is an increasing appreciation of the effects of biotic factors on community organization in a three trophic-level context (Faeth 1986; Havill & Raffa 2000; Masters, Jones & Rogers 2001; Bailey & Whitham 2003). For example, Masters *et al*. (2001) demonstrated that root herbivory caused increased densities of not only a seed predator, *Terellia ruficauda*, but also its parasitoids, *Pteromalus elevatus* and *Torymus chloromerus*, on thistle plants. This probably occurred because root herbivory enhanced the nutritional quality of the thistle plant via physiological changes within the host plant. However, we still understand poorly how abiotic disturbances affect bottom-up cascades in terrestrial food webs (see Hunter & Price 1992), although abiotic disturbances physically damage terrestrial plants as herbivory does.

In this study, we focused on the food webs based on willow trees. Most *Salix* trees are pioneer woody plants that commonly grow on floodplains (Ishii *et al*. 2000) in which flooding is a major abiotic disturbance (Nilsson 1987; Niiyama 1990; Newsholme 1992). Flooding often knocks down *Salix* trees and partly removes their branches above the ground. The majority of *Salix* trees are well adapted to the physical damage of floods. One such adaptation may be a rapid regrowth response following disturbance that enables *Salix* trees to compensate for lost tissues (Craig *et al*. 1988).

In Japan, seasonal floods frequently occur during the rainy season from June to July and during the typhoon season from August to September. In late August 2001, a typhoon passed directly over Shiga Prefecture in central Japan. As a result of the heavy rainfall, a large-scale flood occurred, and willow trees were heavily damaged on the banks of the Yasu River. Consequently, we expected that rapid sprouting would occur on heavily damaged trees and that this increase in foliage would cause an increase in the density of the common leaf beetle, *Plagiodera versicolora* (Laicharting), and its arthropod predators. In addition, we predicted that the flood would increase leaf herbivory as a result of an increased number of leaf beetles.

This study tested the hypothesis that flooding initiates bottom-up cascading effects from willow to herbivorous insects and their arthropod predators by causing increased foliage sprouting. In particular, we addressed the following four questions: (1) does flooding stimulate rapid regrowth of the willow, (2) does foliage sprouting influence the density of the leaf beetle; (3) does flooding indirectly influence leaf herbivory; and (4) does flooding indirectly influence the densities of arthropod predators of the leaf beetle?

## Materials and methods

### STUDY SITE

This study was performed in 2002 on the floodplain of the Yasu River (35°N, 136°E) in Shiga Prefecture, central Japan. Seven willow species (*Salix eriocarpa* Franch et Savatier, *S. gracilistyla* Miquel, *S. gilgiana* Seemen, *S. serissaefolia* Kimura, *S. subfragilis* Andersson, *S. chaenomeloides* Kimur, and *S. integra* Thunb) were distributed sympatrically at the study site. On 22 August 2001, a typhoon passed over Shiga Prefecture followed by a large flood owing to its heavy rain. Approximately one-fourth of the willow trees were knocked down at the study site, and their branches were partly removed.

### SELECTION OF STUDY TREES

For the field survey of plant regrowth and arthropod densities following the typhoon, on 13 April 2002, we selected randomly 10 pairs of heavily and lightly damaged trees of *Salix eriocarpa*, one of the dominant willow species in the study area. We measured the angle that line from proximal to distal points of each tree trunk made with the ground (Fig. 1). Heavily damaged trees were defined as those with trunks making angles of less than 40° with the ground, while lightly damaged trees were defined as those with trunks making angles of greater than 60° with the ground (Wilcoxon signed-rank test, $Z = -2{\cdot}829$, $P < 0{\cdot}01$; Table 1). To remove the size effects of trees, heavily and lightly damaged

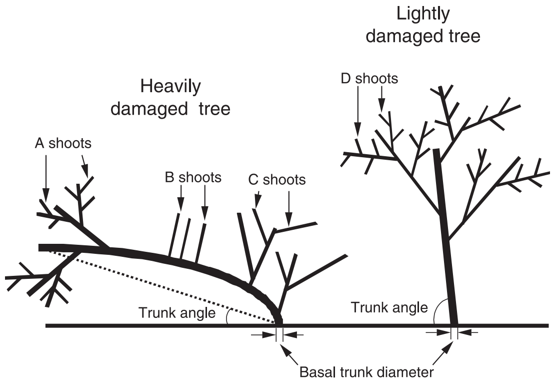

**Fig. 1.** Illustrations of heavily and lightly damaged trees of *Salix eriocarpa*. Current-year shoots in 2002 on heavily damaged trees were classified into three types: (1) shoots from 1-year shoots (A shoots); (2) 2002 sprouting shoots from trunks (B shoots) and (3) shoots from 2001 sprouting shoots (C shoots). Most of the current-year shoots on lightly damaged trees were growing from 1-year shoots (D shoots).

**Table 1.** Characteristics of heavily and lightly damaged trees of *S. eriocarpa*. Mean and SE are presented. Different letters show significant difference (Wilcoxon's signed-rank test: $P < 0{\cdot}05$)

| Characteristics ($n = 10$) | Heavily damaged tree | Lightly damaged tree |
|---|---|---|
| Trunk angle (°) | $32{\cdot}0 \pm 2{\cdot}9^a$ | $81{\cdot}0 \pm 3{\cdot}1^b$ |
| Basal trunk diameter (mm) | $133 \pm 20^a$ | $136 \pm 19^a$ |
| No. of 2001 sprouting shoots (1 m above ground) | $19{\cdot}1 \pm 3{\cdot}4^a$ | $0{\cdot}4 \pm 0{\cdot}3^b$ |
| No. of 2002 sprouting shoots (1 m above ground) | $19{\cdot}2 \pm 3{\cdot}2^a$ | $0{\cdot}1 \pm 0{\cdot}1^b$ |

trees of similar basal trunk diameter were paired (Wilcoxon's signed-rank test, $Z = -0{\cdot}204$, $P = 0{\cdot}84$; Table 1). Furthermore, the numbers of sprouting shoots which grew in both 2001 and 2002 were significantly greater on heavily damaged trees than on lightly damaged trees (Wilcoxon's signed-rank test, 2001: $Z = -2{\cdot}810$, $P < 0{\cdot}005$; 2002: $Z = -2{\cdot}807$, $P < 0{\cdot}01$; Table 1). Therefore we classified current-year shoots in 2002 on heavily damaged trees into three types (Fig. 1): (1) shoots from 1-year shoots (A shoots); (2) 2002 sprouting shoots from trunks (B shoots); and (3) shoots from 2001 sprouting shoots (C shoots). On the other hand, most current-year shoots on lightly damaged trees had grown from 1-year shoots; these shoots were considered to be a fourth type (D shoots). Although both A and D shoots grew from 1-year shoots, we distinguished them because they grew from trees with different levels of damage.

### EFFECT OF FLOOD ON WILLOW GROWTH

To determine whether the flood influenced the growth pattern of *S. eriocarpa* in the following year, we conducted monthly field surveys of plant growth, from April to August. We randomly selected five each of A, B and C shoots of each heavily damaged tree and 10 D shoots of each lightly damaged tree. Then we counted the numbers of lateral shoots and leaves per shoot and measured the total shoot length of each shoot type. For each month the data were analysed using a non-parametric Dunnett-type test to compare D shoots (control) with each of the other shoot types, as a *post hoc* test (Zar 1999). Data were $\log_{(n+1)}$-transformed and analysed using a repeated-measure ANOVA to test for the effects of shoot type, season and their interaction. Individual willow trees were replicates in the analysis.

### EFFECT OF FLOOD ON LEAF BEETLE DENSITY

The leaf beetle *Plagiodera versicolora* (Laicharting) is a specialist herbivore that feeds on *Salix* species (Kimoto & Takizawa 1994). In the study area it is a dominant herbivore species, and adults exclusively feed on young leaves of *S. eriocarpa* (Nakamura, Miyamoto, & Ohgushi 2003). Larvae of the leaf beetle do not acquire defensive chemicals from the host plant to avoid predators (Sugawara *et al*. 1979; Pasteels *et al*. 1984). To examine how the sprouting of foliage after the flood affected the density of the leaf beetle, we conducted a monthly field census for the leaf beetle, from April to August. We randomly selected 15 each of A, B and C shoots of each heavily damaged tree and 30 D shoots of each lightly damaged tree. Then we counted the numbers of egg clutches, larvae, pupae and adults of the leaf beetle on each shoot type. A Kruskal–Wallis test was conducted to detect differences in beetle densities among the four shoot types for each month. A non-parametric Dunnett-type test was performed to compare D shoots (control) with each of the other shoot types, as a *post hoc* test (Zar 1999). Individual willow trees were replicates in the analysis.

### INDIRECT EFFECT OF FLOOD ON LEAF HERBIVORY

To examine how the flood indirectly influenced leaf herbivory through an increase in the leaf beetle, a visual survey was conducted on 17 July 2002. We selected randomly five each of A, B and C shoots of each heavily damaged tree and 10 D shoots of each lightly damaged tree. Then we visually scored the percentage of consumed leaf area of individual leaves: 0% = 0, 1–20% = 1, 21–40% = 2, 41–60% = 3, 61–80% = 4 and 81–100% = 5. The index of each rank was used for the statistical analysis of leaf herbivory. A Kruskal–Wallis test was conducted to detect differences in index of leaf herbivory among the four shoot types. A non-parametric Dunnett-type test was performed to compare D shoots (control) with each of the other shoot types, as a *post hoc* test (Zar 1999). Individual willow trees were replicates in the analysis.

### INDIRECT EFFECT OF FLOOD ON ARTHROPOD PREDATORS

To examine how the flood indirectly influenced the densities of arthropod predators, we conducted a monthly field census for arthropod predators, from May to August. The larvae of a ladybird, *Aiolocaria hexaspilota* (Hope), are one of the major predators and feed mainly on eggs, larvae and pupae of the leaf beetle. In addition, there was a number of webs of the spider *Agelena opulenta* (L. Koch), and adults of *P. versicolora* were frequently found on the webs in the study area. Therefore, we counted the numbers of ladybird larvae and spider webs over a span of 2 min for each of the heavily and lightly damaged trees. The ladybird census was conducted monthly from May to August; spider webs were counted from June to August. A Wilcoxon signed-rank test was used to examine the differences in predator densities between heavily and lightly damaged trees. Individual willow trees were replicates in the analysis.

To determine the prey composition of the web-building spider, we identified the species of prey remaining on each spider web and counted their numbers monthly from June to August. We conducted this survey on as many spider webs as we could find (June: heavily = 178 webs, lightly = 20 webs; July: heavily = 153 webs, lightly = 18 webs; Aug: heavily = 110 webs, lightly = 10 webs). Mainly elytra and adult bodies of the leaf beetle remained on the spider webs of both heavily and lightly damaged trees; thus we compared the numbers of elytra and adult bodies per web between heavily and lightly damaged trees using a Mann–Whitney *U*-test. Individual webs were replicates in the analysis.

## Results

### EFFECT OF FLOOD ON WILLOW GROWTH

There were significant differences in the numbers of lateral shoots and leaves and in the total shoot length among the four shoot types (ANOVA, $P < 0{\cdot}01$, Table 2). After June, B and C shoots (sprouting shoot types) on heavily damaged trees produced more lateral shoots than did D shoots (control) on lightly damaged trees (Dunnet test, $P < 0{\cdot}05$, Fig. 2a). Similarly, the numbers of leaves and the total shoot lengths of B and C shoots were significantly greater than those of D shoots throughout the growing season (Dunnet test, $P < 0{\cdot}05$, Fig. 2b,c). However, A shoots and D shoots did not differ with regard to these plant characteristics. On the other hand, there was a significant interactive effect of shoot type and season on the numbers of lateral shoots and leaves and on the total shoot length (ANOVA, $P < 0{\cdot}01$, Table 2). This implies that the differences in plant growth among the four shoot types differed by season, but all shoot types consistently increased until August.

### EFFECT OF FLOOD ON LEAF BEETLE DENSITY

The densities of all developmental stages of the leaf beetle *P. versicolora* differed significantly among the four shoot types (Kruskal–Wallis test, $P < 0{\cdot}05$, Fig. 3). Throughout the growing season, adult densities on B and C shoots (sprouting shoot types) were significantly higher than on D shoots (control) (Dunnet test, $P < 0{\cdot}05$,

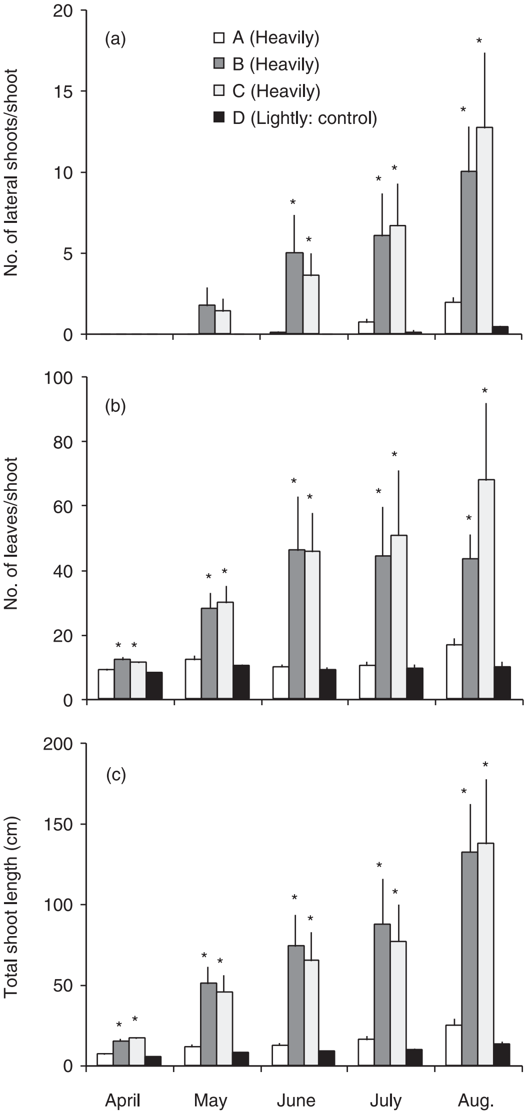

**Fig. 2.** Number of lateral shoots (a), number of leaves per shoot (b), and total shoot length (a) among the four shoot types from April to August 2002. Mean and SE are presented. Asterisk shows significant difference (Dunnet test for comparing D shoots to each of the other shoot types, $P < 0{\cdot}05$).

**Table 2.** Analysis of variance for the effects of shoot type, season and their interaction on numbers of lateral shoots and leaves and total shoot length ($n = 10$)

| Characteristics | Source of variation | d.f. | *F* | *P* |
|---|---|---|---|---|
| No. lateral shoots | Shoot type | 3 | 14·357 | < 0·01 |
| | Season | 4 | 98·65 | < 0·01 |
| | Shoot type × season | 12 | 12·19 | < 0·01 |
| No. leaves | Shoot type | 3 | 29·45 | < 0·01 |
| | Season | 4 | 119·547 | < 0·01 |
| | Shoot type × season | 12 | 16·595 | < 0·01 |
| Total shoot length | Shoot type | 3 | 32·996 | < 0·01 |
| | Season | 4 | 119·205 | < 0·01 |
| | Shoot type × season | 12 | 7·287 | < 0·01 |

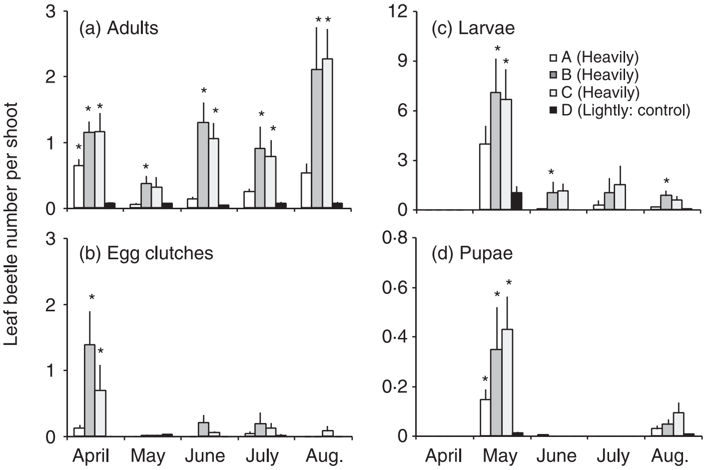

**Fig. 3.** Densities (number per shoot) of adults (a), egg clutches (b), larvae (c) and pupae (d) of the leaf beetle *P. versicolora* among the four shoot types from April to August 2002. Mean and SE are presented. Asterisk shows significant difference (Dunnet test for comparing D shoots to each of the other shoot types, $P < 0{\cdot}05$).

Fig. 3a). In April, significantly more egg clutches were found on B and C shoots than on D shoots (Dunnet test, $P < 0{\cdot}05$, Fig. 3b), and subsequently the larval density in May was significantly higher on B and C shoots than on D shoots (Dunnet test, $P < 0{\cdot}05$, Fig. 3c). In June and August, B shoots had significantly more larvae than did D shoots. Throughout the growing season, however, there were no significant differences in the densities of adults, egg clutches, or larvae between A and D shoots, yet the pupal density was significantly higher on A, B, and C shoots than on D shoots in May (Dunnet test, $P < 0{\cdot}05$, Fig. 3d).

### INDIRECT EFFECT OF FLOOD ON LEAF HERBIVORY

Leaf herbivory also differed significantly among the four shoot types (Kruskal–Wallis test, $P < 0{\cdot}05$, Fig. 4). The mean index of consumed leaf area was significantly greater on A, B and C shoots than that on D shoots (control) (Dunnet test, $P < 0{\cdot}05$, Fig. 4).

### INDIRECT EFFECT OF FLOOD ON ARTHROPOD PREDATORS

The densities of arthropod predators were significantly higher on heavily damaged trees than on lightly damaged trees (Fig. 5). In May, the larval density of the ladybird *A. hexaspilota* was significantly higher on heavily damaged trees than on lightly damaged trees (Wilcoxon's signed-rank test, $P < 0{\cdot}05$, Fig. 5a), although no larvae were found after June. The web density of the spider *A. opulenta* was significantly higher on heavily damaged trees than on lightly damaged trees from June to August (Wilcoxon's signed-rank test, $P < 0{\cdot}05$, Fig. 5b).

We found insect species belonging to four orders as well as snails on spider webs (Table 3). Approximately 80% of the prey found on webs was composed of elytra (59·2%) and adult bodies (18·7%) of the leaf beetle (Table 3). In July and August, the number of the beetle elytra per web was significantly greater on heavily damaged trees than on lightly damaged trees (Mann–Whitney *U*-test, $P < 0{\cdot}05$, Fig. 6a). Similarly, a greater number of adult bodies were found per web on heavily damaged trees than on lightly damaged trees in July and August, although the difference was not significant (Mann–Whitney *U*-test, $P > 0{\cdot}05$, Fig. 6b).

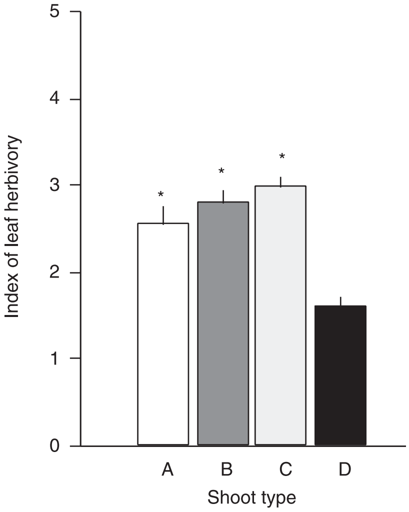

**Fig. 4.** Index of leaf herbivory among the four shoot types in mid-June 2002. Mean and SE are presented. Asterisk shows significant difference (Dunnet test for comparing D shoots to each of the other shoot types, $P < 0{\cdot}05$).

## Discussion

This study illustrates clearly that the large-scale flood caused by a typhoon stimulated the development of sprouting shoots which vigorously produced a greater number of lateral shoots and leaves throughout the growing season. The sprouted foliage resulted in an increase in the densities of all stages of the leaf beetle,

**Table 3.** Number and proportion of prey items remained on spider webs ($n = 467$)

| Order | Species/taxa | Stage | Number | Proportion (%) |
|---|---|---|---|---|
| Coleoptera | *Plagiodera versicola* | Adult (elytron) | 187 | 59·2 |
| | | Adult (body) | 59 | 18·7 |
| | | Pupa | 4 | 1·3 |
| | | Larva | 2 | 0·6 |
| | *Smaradina semiaurantiaca* | Adult | 5 | 1·6 |
| | Other beetles | Adult | 8 | 2·5 |
| Lepidoptera | Moth | Adult (wing) | 18 | 5·7 |
| | | Larva | 1 | 0·3 |
| Homoptera | Stinkbug | Adult | 2 | 0·6 |
| | Aphid | Adult | 9 | 2·8 |
| Hymenoptera | Ant | Adult | 11 | 3·5 |
| Stylommatophora | Snail | Adult | 10 | 3·2 |

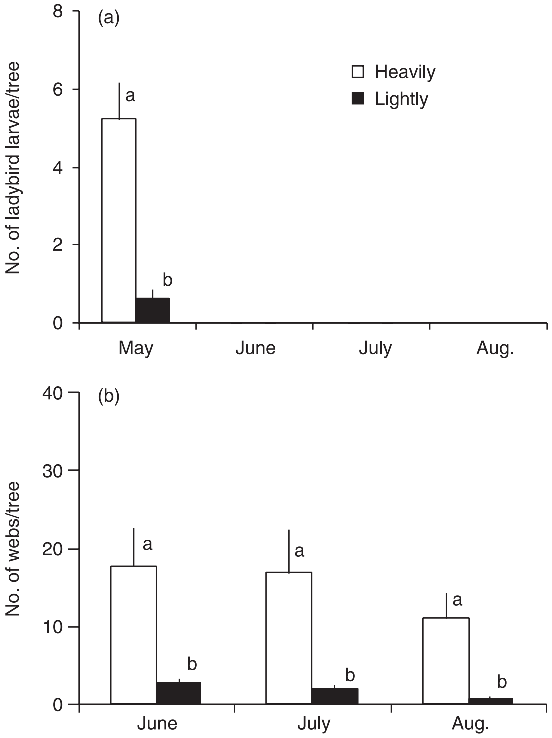

**Fig. 5.** Number of larvae (a) of the ladybird *A. hexaspilota* per tree observed within 2 min, from May to August, and number of webs (b) of the spider *A. opulenta* per tree observed within 2 min, from June to August 2002, on heavily and lightly damaged trees. Mean and SE are presented. Different letters show significant differences (Wilcoxon's signed-rank test, $P < 0·05$).

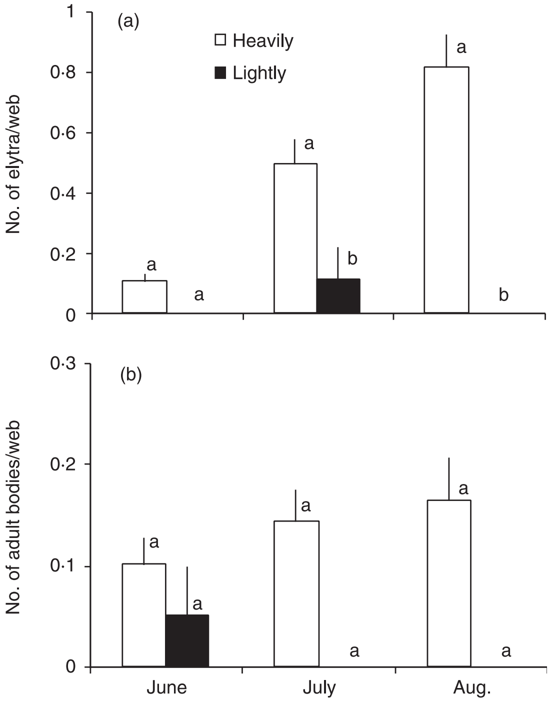

**Fig. 6.** Number of elytra (a) and adult body (b) remains of the leaf beetle *P. versicolora* per spider web on heavily and lightly damaged trees from June to August 2002. Mean and SE are presented. Different letters show significant differences (Mann-Whitney *u* test, $P < 0·05$).

and the greater number of leaf beetles, in turn, caused an increase in leaf herbivory. Furthermore, the increase in leaf beetles resulted in an increase in the densities of their arthropod predators, ladybird larvae and web-building spiders.

### RAPID WILLOW GROWTH IN RESPONSE TO FLOOD

The flood apparently changed the plant growth patterns of *S. eriocarpa*. Our results showed that heavily damaged trees produced more sprouting shoots and that these shoots grew continuously throughout the growing season. In contrast, such rapid growth of sprouting shoots was hardly observed on lightly damaged trees. These differences in plant growth patterns may be caused by a release of the apical dominance which controls the outgrowth of shoots from dormant buds (Cline, Wessel & Iwamura 1997) and regulates the allocation of resources throughout the plant (Haukioja *et al.* 1990). In the study area, the flood knocked down trunks and partly removed above-ground branches of willow trees. Such heavy physical damage may release the apical dominance of *Salix* trees. On the other hand, the effect of the flood on the lightly damaged trees may not have been sufficient to release apical dominance.

Furthermore, because much of the mass of *Salix* trees is underground (Craig *et al*. 1988), the re-allocation of resources from the remaining underground tissues may have allowed *Salix* trees to compensate for the losses of above-ground tissues (Stein *et al*. 1992; Bailey & Whitham 2002). However, there was no difference in plant growth patterns between A and D shoots, suggesting that the release of apical dominance may have different impacts among shoot types.

In Japan, seasonal floods occur frequently in riparian habitats during the rainy season from June to July and during the typhoon season from August to September. As a result of adaptation to the physical damage caused by such floods, *S. eriocarpa* is likely to have the ability to resprout, which would be advantageous in competing for space and light after floods (Craig, Price, & Itami 1986; Craig *et al*. 1988). This implies that, under environmental conditions that include frequent abiotic disturbances such as floods, not only herbivory (e.g. mammal browsing) but also abiotic disturbances may be important selective forces for the compensatory growth of plants (Craig *et al*. 1986, 1988; Price 1991; Roininen *et al*. 1994; Rosenthal & Kotanen 1994).

### RESPONSE OF LEAF BEETLES TO FOLIAGE SPROUTING

Rapid plant growth often provides high quality resources for insect herbivores (Price 1991). We found that overwintering adults of the leaf beetle *P. versicolora* rapidly aggregated on the sprouting shoots of heavily damaged trees in April, because adults have a strong preference for the young, soft leaves which contain high water and nitrogen levels (Nakamura *et al*. 2003). As the foliage sprouting continued until August, a high adult density was maintained on sprouting shoots throughout the growing season. Subsequently, the greater number of adult females laid more egg clutches, thus increasing the larval and pupal densities per shoot on heavily damaged trees. This process suggests that the increases in the numbers of leaf beetles at all developmental stages were caused by the greater availability of sprouted foliage for reproductive adults. Recent studies have similarly reported that abiotic disturbances (e.g. fires and hurricanes) positively influence the preference and performance of insect herbivores (Stein *et al*. 1992; Hunter & Forkner 1999; Bailey & Whitham 2002, 2003) because rapid plant regrowth after these disturbances provides high quality resources (Vieira *et al*. 1996; Radho-Toly *et al*. 2001; Spiller & Agrawal 2003).

Moreover, herbivory on young leaves increased on heavily damaged trees because the increased number of adults fed exclusively upon the young leaves produced by sprouting (Nakamura *et al*. 2003). As larvae tend to feed on mature leaves (Raupp & Denno 1983), a higher level of herbivory was also found on mature leaves on heavily damaged trees. Therefore, enhanced leaf herbivory was found not only on B and C shoots but also on A shoots of heavily damaged trees as a result of the greater cumulative numbers of adults and larvae on A, B and C shoots than on D shoots. These results suggest that flooding may have negative effects on the performance of the willow by leading to increased leaf herbivory.

### BOTTOM-UP CASCADING EFFECTS ON HIGHER TROPHIC LEVELS

In general, arthropod predators will track numerically the densities of prey insects (Solomon 1949; Hassell 1978). Thus flooding may positively affect the density of arthropod predators by increasing the insect herbivore. In the study area, larvae of the predatory ladybird *A. hexaspilota* and webs of the spider *A. opulenta* significantly increased on heavily damaged trees. Larvae of the ladybird are specialist predators, feeding mainly on eggs, larvae and pupae of leaf beetles (Hidaka 1998). Meanwhile, the primary food of the spiders is adult leaf beetles, and the amount of the beetle remains was greater in spider webs on heavily damaged trees. These findings indicate that the increase in the leaf beetle resulted in an increase in the densities of their arthropod predators. Thus flooding initiated bottom-up cascading effects from the willow, to the leaf beetle, to arthropod predators. Furthermore, because lateral branching by compensatory regrowth of the willow is likely to increase web attachment points, the complex architecture of the branching may be related to the increase in spider abundance (Uetz 1991; McNett & Rypstra 2000; Langellotto & Denno 2004).

In conclusion, our study illustrates clearly that a large-scale flood stimulated the compensatory responses of *S. eriocarpa*, which subsequently initiated cascading effects at higher trophic levels. Previous studies have demonstrated that abiotic disturbances can change plant growth patterns and consequently influence the abundance and/or distribution of herbivorous insects (Stein *et al*. 1992; Viera *et al*. 1996; Hunter & Forkner 1999; Radho-Toly *et al*. 2001; Bailey & Whitham 2002, 2003; Spiller & Agrawal 2003). In addition, we suggest that the influence of flooding can reach predators at the third trophic level. Besides floods, other abiotic disturbances also may have the potential to initiate bottom-up cascading effects through three trophic levels caused by plant compensatory regrowth (Romme *et al*. 1995; Cooper-Ellis *et al*. 1999; Bellingham & Sparrow 2000; Bond & Midgley 2001; Del Tredici 2001). Further research on both herbivorous insects and their predators following abiotic disturbances would reveal the importance of bottom-up cascading effects on insect community organization on terrestrial plants.

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