

Bottom-up cascade in a tri-trophic system: different impacts of host-plant regeneration on performance of a willow leaf beetle and its natural enemy

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Abstract. 1. Plant quality can directly and indirectly affect the third trophic level. However, little attention has been paid to how changes in plant quality affect the performance of predators through trophic levels, and which herbivores or predators are affected more strongly by host-plant quality. The present study examined the effects of artificial cutting of willows on the performance of a willow leaf beetle (*Plagioderia versicolora* Laicharting) and its predatory ladybird beetle (*Aiolocaria hexaspilota* Hope).

2. Laboratory experiments showed that performance (survival rate, developmental time, and adult mass) of the willow leaf beetle was higher when fed with leaves of cut willows than when fed with leaves of uncut willows. Performance (developmental time and adult mass) of the predatory ladybird was also improved when it was fed on the leaf beetle larvae that had been fed on leaves of cut willows, compared with those that had been fed on leaves of uncut willows. This indicates that a bottom-up cascade occurs in the tri-trophic system.

3. In a comparison of improved performance parameters between the leaf beetle and the ladybird, regenerated willows shortened the developmental time of the willow leaf beetle more than that of the ladybird. This indicates that the impacts of willow cutting on insect performance differ between the second and third trophic levels.

Key words. Food chain, indirect interaction, leaf beetle, predatory ladybird, willow.

Introduction

Interactions between herbivorous insects and their natural enemies are directly and indirectly influenced by the herbivores' host plants (Price *et al.*, 1980). The direct effects of plant volatiles and architecture on the searching efficiency of natural enemies of prey herbivores have been well demonstrated (Clark & Messina, 1998; Legrand & Barbosa, 2003). Also, non-volatile chemicals in plant tissues can indirectly affect natural enemies via herbivores as defensive chemicals against natural enemies (Nishida & Fukami,

1989; Pasteels *et al.*, 1989), and as stimulants to specialist predators (Rank & Smiley, 1994; Köpf *et al.*, 1997). Therefore, herbivores on different host plants often differ in their susceptibility to natural enemies (Rank & Smiley, 1994; Lill *et al.*, 2002; Zvereva & Rank, 2003). In addition, plant quality may indirectly affect performance of natural enemies, because plant quality affects herbivore performance (Cole, 1997; Zvereva & Rank, 2003) and changes in prey availability (e.g. nutrient quality) for natural enemies, which in turn affects performance of natural enemies (Harvey, 2000; Omkar & Srivastava, 2003). This bottom-up cascade in insect performance has been detected in systems involving plants, caterpillars, and parasitic wasps (Barbosa *et al.*, 1991; Havill & Raffa, 2000; Teder & Tammaru, 2002), and plants, aphids, and predatory ladybirds (Francis *et al.*, 2000; Francis *et al.*, 2001).

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The aim of the present study is to detect such bottom-up effects of host plant on a leaf beetle and its natural enemy. These effects originate in changes in leaf quality due to the artificial cutting of plants. Several tree species are known to regenerate following damage due to cutting, fire, flooding, and herbivory (Stein *et al.*, 1992; Romme *et al.*, 1995; Karlsson & Weih, 2003). It has also been shown that the regeneration or regrowth induced by this damage alters the quality of nutrient conditions for herbivores (Martinsen *et al.*, 1998; Havill & Raffa, 2000; Nakamura *et al.*, 2003). The effects of regrowth would be transmitted to the third trophic level (predators and parasitoids) through food chains. However, little attention has been paid to how changes in plant quality after damage affect performance of natural enemies, and which herbivores or natural enemies are affected more strongly by host-plant quality.

The present study focused on the direct effects of willow regeneration on performance of the leaf beetle *Plagioderia versicolora* Laicharting, and indirect effects on performance of the predatory ladybird *Aiolocaria hexaspilota* Hope through the leaf beetle. Two laboratory experiments were conducted to determine whether performance of the willow leaf beetle is affected by feeding on leaves produced by compensatory regrowth of cut willows, and whether performance of the predatory ladybird is affected by feeding on the leaf beetle larvae that fed on these leaves.

Materials and methods

Study site

This study was conducted in 2003 on a flood plain of the Yasu River in Shiga Prefecture, central Japan. Willows are the predominant woody plants in the study area, where at least seven species of willows occur sympatrically: *Salix chaenomeloides* Kimura, *S. eriocarpa* Franchet et Savatier, *S. gilgiana* Seemen, *S. gracilistyla* Miquel, *S. integra* Thunberg, *S. serissaefolia* Kimura, and *S. subfragilis* Andersson. Of these willows, *S. eriocarpa* and *S. serissaefolia* occur most frequently in this area. Willow trees were cut down by randomly selective logging in mid-March 2003. This cutting was conducted for flood control by the River Bureau of the Japanese Ministry of Land, Infrastructure, and Transport. In the study area, more than 100 trees of several willow species were cut 50 cm above the ground. On average, the cut trees were 17.3 cm in diameter 50 cm above the ground, and 8.0 m in height. The cut logs were immediately removed from the study area. Bud break on both cut and uncut willows occurred in early April.

Willow, leaf beetle, and predatory ladybird

Salix eriocarpa is a common riparian willow species in western and central Japan (Kimura, 1989), which reaches 5–10 m in height. After cutting, the willows regenerated vigorously and 10–40 shoots sprouted from a single

stump. Newly emerged leaves on the sprouting shoots of cut willows were less tough and had higher water and nitrogen contents than those on shoots of uncut willows (M. Nakamura, H. Kagata & T. Ohgushi, unpublished data).

The willow leaf beetle *P. versicolora* (Coleoptera: Chrysomelidae) is multivoltine and feeds on several willow species (Kimoto & Takizawa, 1994). The leaf beetle was more abundant on *S. eriocarpa* and *S. serissaefolia* in the study area (Inui *et al.*, 2003), although the relationship between host preference of the leaf beetle and chemical composition of willow leaves is unknown. Adult beetles lay 10–20 eggs in a cluster. Larvae pass through three instars, feed gregariously during first and second instars, and disperse as they develop.

One of the major natural enemies of the leaf beetle in the study area is the predatory ladybird *Aiolocaria hexaspilota* (Coleoptera: Coccinellidae), which is univoltine and a specialist predator of leaf beetles, including willow leaf beetles *Chrysomela vigintipunctata* and *P. versicolora*, and the walnut beetle *Gastrolina depressa* (Matsura, 1976). Larvae and adults of the ladybird feed on eggs and larvae of *P. versicolora*, but not on the pupae and adults. Adult ladybirds lay eggs in clusters of 30–40 eggs on the leaf surface of the prey's host plants, and the larvae pass through four instars.

Performance of the leaf beetle and ladybird

Egg masses of *P. versicolora* and *A. hexaspilota* were collected on *S. gilgiana* in the field in mid-May 2003. They were placed separately in plastic cases (70 × 120 × 30 mm) in the laboratory. Larvae were used for the experiment within 24 h after hatching. Larvae hatched from a single egg mass were divided into two groups and assigned to cut and uncut treatments respectively. Ten larvae of the leaf beetle were put together in a plastic case lined on the bottom with wet paper and reared until adult eclosion in an environmental chamber at 23 °C, LD 16:8 h. The larvae were provided with one or two undamaged mature leaves taken from the upper reaches of the shoots. These were collected at the field site in the morning from three cut and uncut *S. eriocarpa* trees. While *P. versicolora* adults prefer young leaves, larvae usually feed on mature leaves in the field (Raupp & Denno, 1983). Hence, mature leaves were used as food for the leaf beetles in the experiment. The leaves from the three cut and three uncut trees were mixed respectively, and provided to each larval group to decrease the effects of tree individuals. Leaves were replaced every other day, and were removed from the cases after pupation. Survival rate and developmental time until adult eclosion were examined. Adults within 24 h after eclosion were dried in an oven at 60 °C for 72 h, and weighed individually. Additionally, five larvae of the ladybird were put together in a plastic case and reared until adult eclosion. Each ladybird larva was provided with 10–20 leaf beetle eggs for the first two days of the experiment, and 20–100 leaf beetle larvae

every day thereafter. The leaf beetle larvae which were used for prey were collected at the field site in the morning from five cut and uncut *S. eriocarpa* trees. During the experiment, only one incidence of cannibalism among ladybird larvae occurred. Other procedures in the experiment were the same as those for the leaf beetle. Twelve and six replicates were conducted for each treatment for the leaf beetle and the ladybird respectively.

Statistics

Differences in survival rate, developmental time, and dry mass of the leaf beetle and the ladybird between treatments were tested by randomised block analysis of variance (randomised block ANOVA). In the analyses, the main factor was the treatment (cut or uncut willows), and the effect of egg mass was treated as a block. Survival rate was arcsine-square-root-transformed prior to the analysis. Mean values in developmental time and dry mass in each case were used in the analysis. To determine the relative impacts of willow cutting on performance of second and third trophic levels, the ratios of each performance parameter in cut and uncut treatments were compared between the leaf beetle and the ladybird. The ratios for each performance parameter, i.e. survival rate, developmental time, and adult body mass, were obtained by dividing the parameters from the cut treatment by those from the uncut treatment. Differences in the relative impact of willow cutting on performance between the leaf beetle and ladybird were tested using ANOVA.

Results and discussion

The laboratory experiment clearly demonstrated that leaves of cut willows improved performance of the leaf beetle, resulting in higher survival rate ($F_{1,11} = 5.40$, $P = 0.04$; Fig. 1a), shorter developmental time ($F_{1,11} = 247.65$, $P < 0.0001$; Fig. 1b), and greater body mass ($F_{1,11} = 33.55$, $P < 0.0001$; Fig. 1c). This improved performance would be due to the high quality of the leaves from the cut willows. In fact, leaves of cut willows had 1.5 times and 1.2 times greater nitrogen and water contents respectively, and were 2.2 times less tough than those of uncut willows (M. Nakamura, H. Kagata & T. Ohgushi, unpublished data). Previous studies have shown that plants that regrew following damage have a higher nutrient quality for herbivores (Danell & Huss-Danell, 1985; Nakamura *et al.*, 2003; Spiller & Agrawal, 2003), and therefore such damaged plants result in faster development and larger body size in herbivorous insects than undamaged plants (Martinsen *et al.*, 1998).

The present study also demonstrated that cut willows improved the performance of the predatory ladybird, with shorter development time ($F_{1,5} = 18.83$, $P = 0.007$; Fig. 1e) and greater body mass ($F_{1,5} = 21.79$, $P = 0.005$; Fig. 1f), but did not affect survival rate ($F_{1,5} = 0.003$, $P = 0.96$; Fig. 1d). These findings are consistent with other studies, which

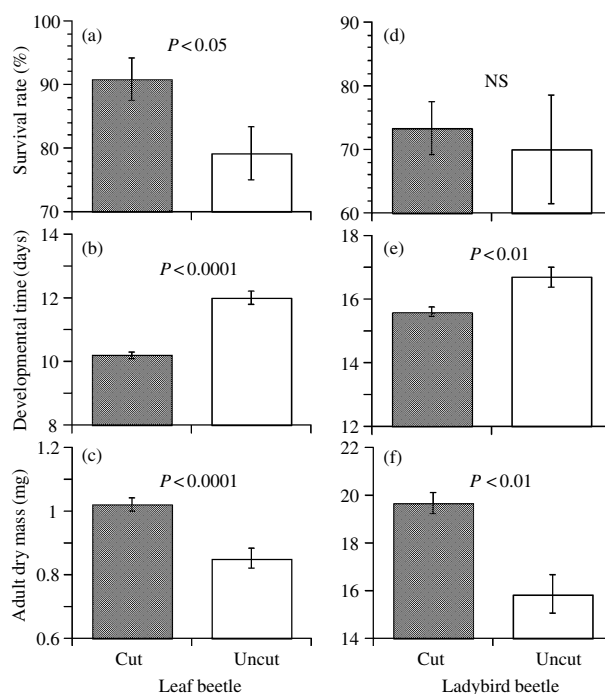


Fig. 1. Performance of the leaf beetle (left side) and the ladybird beetle (right side) in cut and uncut treatments. (a) and (d) survival rate, (b) and (e) developmental time, and (c) and (f) adult dry mass. Horizontal bars show SE.

demonstrated that the body size of predators and parasitoids was affected by quality of the herbivore's food (Barbosa *et al.*, 1991; English-Loeb *et al.*, 1993; Mayntz & Toft, 2001; Teder & Tammaru, 2002; Zvereva & Rank, 2003). There are three possible explanations, which are not mutually exclusive, for the improved performance of the ladybird. Firstly, the large body size in the leaf beetle larvae that fed on cut willows would enhance foraging efficiency of the ladybird. It is well known that foraging efficiency of arthropod predators increases with increasing prey size (e.g. Hirvonen & Ranta, 1996). Secondly, the higher nutrient status of the leaves of cut willows may have improved performance of the ladybird via the high nutrient quality of leaf beetle larvae. For example, Slansky and Feeny (1977) demonstrated that nitrogen content of *Pieris* larvae was increased by feeding on leaves of crucifer plants with a high nitrogen content. High nutrient conditions of prey herbivores would increase the growth of predators (Mayntz & Toft, 2001). Thirdly, the changes in defensive secretion of the leaf beetle due to willow cutting may affect the performance of the ladybird. This is because several leaf beetles use plant-derived chemicals to defend themselves against their natural enemies (Pasteels *et al.*, 1989; Pasteels *et al.*, 1990), and hence their defence ability would largely depend on chemical compounds of the host plants (Denno *et al.*, 1990). For example, larvae of the leaf beetle *Chrysomela confluenta* fed on cottonwood that regrew following beaver browsing were better protected from their predators than

those fed on undamaged plants (Martinsen *et al.*, 1998). This indicates that the leaf beetle used plant chemicals from regrown plant tissues for their own defence. *Plagioderia versicolora* also has a defensive secretion (Meinwald *et al.*, 1977; Sugeno & Matsuda, 2002), but it is independent of plant chemical status, because the secretion of *P. versicolora* does not originate from the host plant (Pasteels *et al.*, 1984). However, the amount of the defensive secretion may depend on quality of the host plant, and thus it could affect the performance of the ladybird.

Consequently, willow cutting positively and directly affected performance of the leaf beetle and indirectly affected performance of the predatory ladybird via its prey. However, it should be noted that the impacts of willow cutting differed between the two trophic levels. Relative impact of willow cutting on developmental time was significantly greater in the leaf beetle than that of the ladybird ($F_{1,16} = 11.1$, $P = 0.004$). The developmental time of the leaf beetle was $14.7 \pm 1.6\%$ (mean \pm SE) shorter in cut treatment than control, but it was $6.3 \pm 1.4\%$ shorter for the ladybird. On the other hand, the impacts on survival rate and adult dry mass did not differ between the leaf beetle and the ladybird ($F_{1,16} = 0.06$, $P = 0.80$ for survival rate; $F_{1,16} = 0.75$, $P = 0.40$ for adult dry mass). Thus, the impact of willow cutting was greater on the leaf beetle than on the ladybird. One possible explanation for the different impact is that the accumulation rate of nutritional elements differed between plants and herbivores (Fagan *et al.*, 2002). Slansky and Feeny (1977) demonstrated that leaf nitrogen of a crucifer plant was increased 4.1 times by fertilisation. On the other hand, nitrogen content in *Pieris* larvae that fed on the fertilised plants also increased, but only 1.1 times. This is because herbivorous insects enhance nitrogen accumulation rate on poor quality host plants to maintain homeostasis in their body elemental composition (Slansky & Feeny, 1977), even though nitrogen content of plants varies greatly (Mattson, 1980). In the present study, nitrogen content in willow leaves increased 1.5 times due to cutting (M. Nakamura, H. Kagata & T. Ohgushi, unpublished data). However, the increased nitrogen content in the leaf beetle could be lower than the increased level found in the willow. If so, the ladybird performance would be less improved by willow cutting than that of the leaf beetle. Another explanation for the differential impact of willow cutting between the two trophic levels concerns difference in nitrogen limitation between herbivores and predators. It is known that the nitrogen content in herbivorous insects is 10–20 times higher than that in plants (Mattson, 1980; Elser *et al.*, 2000), while the nitrogen content in predatory insects is only 1.15 times higher than that in herbivorous insects (Fagan *et al.*, 2002). This indicates that predatory insects may be less nitrogen limited than herbivorous insects (Fagan *et al.*, 2002), and this may reduce the impacts of improved plant quality on the ladybird performance, compared with the leaf beetle.

Mayntz and Toft (2001) pointed out that previous studies on the detection of bottom-up cascade effects have mainly focused on numerical changes of the third trophic level in

response to changes in prey abundance depending on host-plant conditions. In addition, the past studies have overlooked the strength of the bottom-up impacts of plants on second and third trophic levels (Teder & Tammaru, 2002). In this context, the present study demonstrated that plant quality affected performance of both the leaf beetle and the predatory ladybird, but the impacts differed between the two trophic levels. Further research is needed to reveal mechanisms responsible for the different impacts of plants on different trophic levels, which will then provide more understanding of bottom-up effects in multi-trophic systems.

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