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## Carbon–nitrogen stoichiometry in the tritrophic food chain willow, leaf beetle, and predatory ladybird beetle

Received: 24 April 2006 / Accepted: 16 October 2006 / Published online: 22 December 2006  
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**Abstract** Although plant quality can indirectly increase the performance of the third trophic level by bottom-up cascading effects, the mechanisms of this indirect effect are still unclear. In this study the carbon–nitrogen stoichiometry in a tri-trophic system consisting of the willow, a leaf beetle, and a predatory ladybird beetle were examined to determine the mechanisms of the bottom-up cascading effect. The bottom-up cascade is initiated by increasing leaf nitrogen, because of artificial cutting of willow trees. The relative growth rate (RGR) of the leaf beetle increased when fed on cut willow leaves, because of the high leaf nitrogen in the cut willows. Ladybird beetle RGR also increased when fed on leaf beetles fed on cut willow leaves. The increased RGR of the ladybirds cannot be explained by the quality of the prey, however, because leaf beetle nitrogen was not affected by host plant quality. Thus, the carbon–nitrogen stoichiometry could not be a mechanism of the bottom-up cascade through multiple trophic levels.

**Keywords** Bottom-up cascade · C:N ratio · Ecological stoichiometry · Terrestrial food chain · Tri-trophic interaction

### Introduction

The concentration of nitrogen in host plants is an important factor affecting the survival, growth, and reproduction of herbivorous insects (Mattson 1980; White 1993). The discrepancy in nitrogen concentration between host plants and herbivorous insects has been well recognized (Mattson 1980), and the nitrogen concentration in herbivores (mean  $\pm$  SE =  $9.6 \pm 0.2\%$  in dry mass) is usually higher than that in plants (Fagan

et al. 2002). Herbivorous insects have therefore evolved behavioral, morphological, and physiological adaptations to efficiently utilize available nitrogen (Mattson 1980). Similarly, survival and growth of predatory arthropods are also limited by the nutritional quality of their prey (Toft and Wise 1999; Mayntz and Toft 2001). Fagan et al. (2002) argued that the concentration of nitrogen in predatory insects ( $11.0 \pm 0.2\%$ ) is 15% higher than that in herbivorous insects, indicating a possibility of nitrogen-limited growth of predatory insects (Denno and Fagan 2003).

The foliar nitrogen concentration in plants varies greatly with season and ontogeny (Feeny 1970; Mattson and Scriber 1987; Kudo 2003), environmental conditions, for example light, soil nutrients, and CO<sub>2</sub> concentration (Cotrufo et al. 1998; Crone and Jones 1999; Lower and Orians 2003), and herbivory (Faeth 1986; Martinsen et al. 1998). Changes in the concentration of nitrogen in host plants may affect not only herbivorous insects, but also higher trophic levels, including predatory and parasitic insects, through bottom-up cascading effects (Price et al. 1980; Teder and Tammaru 2002; Hunter 2003). Plants of better quality may result in an increase in the population density of predators in response to the increased density of prey herbivores (Hunter and Price 1992). In addition, plants of better quality may result in higher performance of individual predators (Mayntz and Toft 2001). A few studies have revealed that plant quality indirectly affected the performance of insects in the third or fourth trophic levels (Teder and Tammaru 2002; Harvey et al. 2003). One hypothetical mechanism of this indirect effect is that better plant quality may improve the quality of herbivorous insects as prey, which may subsequently increase the performance of predatory insects (Mayntz and Toft 2001). This hypothesis has not been tested by measuring the quality of herbivorous insects, however. Kagata et al. (2005) have also demonstrated the bottom-up cascading effect in a tri-trophic system consisting of the riparian willow *Salix eriocarpa* Franchet et Savatier (Salicaceae), the willow leaf beetle *Plagiodera versicolora*

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Laicharting (Coleoptera: Chrysomelidae), and the predatory ladybird beetle *Aiolocaria hexaspilota* Hope (Coleoptera: Coccinellidae). The bottom-up cascading effect arose as a result of changes in leaf quality in response to artificial cutting of willows for flood control. After the cutting the willow trees regrew vigorously, which resulted in greater adult size and shorter development time not only of the willow leaf beetle, but also of the predatory ladybird beetle. The nutritional status of each trophic level was not examined by Kagata et al (2005), however, and so the mechanism of the increased performance of the predatory ladybird remains unclear.

In this study the carbon–nitrogen stoichiometry in a bottom-up cascading effect in the above tri-trophic system, one year after willow cutting, was examined to determine the mechanism of the cascading effect. First, the cascading effect reported in Kagata et al. (2005) was examined again with increased experimental replication, to confirm the trophic cascade continues for one year after willow cutting. Laboratory experiments were also conducted to determine whether percentage survival and relative growth rate (RGR) of the leaf beetle are affected by feeding on leaves which resprouted from cut willows, and whether those of the ladybird beetle are affected by feeding on the leaf beetle larvae that fed on these leaves. In addition, carbon and nitrogen concentrations in the willow leaves, leaf beetles, and predatory ladybirds were measured to determine the mechanism of bottom-up cascading effects.

## Materials and methods

### Study site

This study was conducted on the flood plain of the Yasu River in Shiga Prefecture, central Japan. Willows are the predominant woody plants in the study area, and seven species of willow occur sympatrically. Willow trunks were cut at a height of 50 cm above the ground by randomly selective logging in mid-March 2003. This was conducted for flood control by the River Bureau of the Japan Ministry of Land, Infrastructure, and Transport. On average, the cut trees were 17.3 cm in diameter at height of 50 cm above the ground, and 8.0 m in height. After the cutting, the willows regenerated vigorously, with 10–40 shoots sprouting from a single stump.

### Willow, leaf beetle, and predatory ladybird

*Salix eriocarpa*, a common riparian willow species in western and central Japan (Kimura 1989), reaches 5–10 m in height. The willow leaf beetle *P. versicolora* is multivoltine and feeds on several willow species (Kimoto and Takizawa 1994). Adult beetles lay clusters of 10–20 eggs on the surface of the host plant leaves. Larvae pass through three instars, feeding gregariously during the

first and second instars, and disperse as they develop. The predatory ladybird *A. hexaspilota* is one of the major natural enemies of *P. versicolora*. The ladybird is univoltine and a specialist predator of several leaf beetles, including *P. versicolora*, *Chrysomela vigintipunctata* (Marseul), and *Gastrolina depressa* Baly (Matsura 1976). At the study site, *P. versicolora* is the dominant leaf beetle on the willows and the other two leaf beetles were rarely observed. Ladybirds at the study site are, therefore, likely to feed on *P. versicolora* exclusively. Adult ladybirds lay clusters of 30–40 eggs on surface of leaves of host plants of the prey leaf beetles, and larvae pass through four instars.

### Insect performance

Egg clusters of *P. versicolora* and *A. hexaspilota* were collected from the field in mid-May 2004. They were placed individually in plastic cases (70 mm × 120 mm × 30 mm) in the laboratory. Larvae were used for the experiment within 24 h of hatching. Larvae hatched from a single egg cluster were divided into two groups which were assigned to cut and uncut treatments. Ten leaf beetle larvae were put together in a plastic case lined at the bottom with wet paper and reared for six days, almost the whole larval period, in an environmental chamber at 23°C, 70% r.h., and LD 16:8 h. This is because the predatory ladybirds feed preferentially on leaf beetle larvae, but not pupae and adults. The larvae were provided with one or two undamaged mature leaves taken from the upper reaches of the shoots of cut and uncut willows. Because larvae of *P. versicolora* usually feed on mature leaves (Raupp and Denno 1983), mature leaves were used as food for the leaf beetles in the experiment. Leaves were replaced every other day, and these were collected from the field site in the morning. Leaves from the ten cut and ten uncut trees were mixed, separately, and provided randomly to each larval group to reduce the effect of individual trees. On the sixth day of the experiment, surviving larvae were counted, and their fresh mass was measured. Ladybird larvae also were placed individually in plastic cases and reared for six days. They were provided with 10–20 leaf beetle eggs on the first day of the experiment and 20–100 leaf beetles, depending on larval development of the ladybirds, every day thereafter. The prey provided was sufficient and no food shortage occurred during the experiment. The leaf beetle larvae were collected in the morning from cut and uncut *S. eriocarpa* trees. Other procedures in the experiment were the same as those for the leaf beetle. Twenty and twenty-two replicates were conducted for each treatment of the leaf beetle and the ladybird, respectively. One uncut treatment of the leaf beetle was excluded from the analysis, however, because leaves became moldy and all the larvae died. Percentage survival and RGR of the leaf beetle and predatory ladybird were examined. RGR was calculated using the equation:

$$\text{RGR} = \frac{\ln(\text{final mass}) - \ln(\text{initial mass})}{\text{duration}}$$

initial larval mass was measured within 24 h of hatching and averages were calculated by weighing several larvae (leaf beetle  $0.17 \pm 0.004$  mg (mean  $\pm$  SE),  $n = 13$ ; ladybird beetle  $0.73 \pm 0.05$  mg,  $n = 12$ ).

### Qualitative traits of willow and insects

In late May 2004, one year after willow cutting, six mature leaves from each of the ten cut and ten uncut trees were collected and immediately brought to the laboratory in a cool box. The toughness of three leaves from each tree was measured using a penetrometer (Model 9500, Aiko, Yokohama, Japan) by recording the force necessary for a rod (2 mm in diameter) to penetrate the leaf tissues. The remaining three leaves from each tree were weighed to determine fresh mass, dried in an oven at  $60^\circ\text{C}$  for 72 h, and weighed again. The dried leaves were then ground, and the carbon and nitrogen concentration was measured using an elemental analyzer (JM 1000CN, J-Science, Kyoto, Japan).

The water, carbon, and nitrogen concentrations of the leaf beetle and the predatory ladybird reared in the above experiments were also measured. After the experiments finished, the larvae were dried in an oven at  $60^\circ\text{C}$  for 72 h and then weighed. The dried larvae were ground, and the carbon and nitrogen concentrations were measured by use of the elemental analyzer.

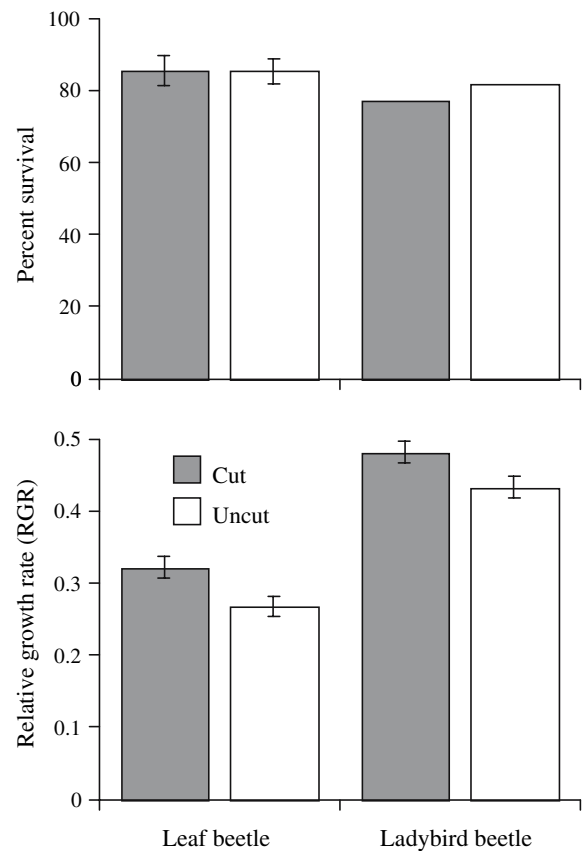
### Statistical analysis

All data except percentage survival of the ladybird beetle, RGR of both insects, and C:N ratios were tested by use of one-way ANOVA. Percentage survival of the leaf beetle was arcsine-square-root-transformed before the analysis. Tree means or experimental group means were used in analysis of the traits of the willow, the leaf beetle, and the ladybird beetle. Percentage survival of the ladybirds was tested using the Fisher exact test because it was reared individually. The RGR of both insects was tested by two-way ANOVA. To compare C:N ratios, two-way ANOVA with the Tukey–Kramer test ( $P < 0.05$ ) was performed after log-transformation of the data.

## Results

### Insect performance

Percentage survival over six days of both the leaf beetle and ladybird beetle did not differ significantly between the cut and uncut treatments ( $F_{1,17} = 0.15$ ,  $P = 0.70$ , for the leaf beetle;  $P = 0.99$ , for the ladybird; Fig. 1). Relative growth rates of the two insects were signifi-



**Fig. 1** Percentage survival (*top*) and relative growth rate (*bottom*) of the willow leaf beetle and the predatory ladybird beetle. Means  $\pm$  SE are presented except for percentage survival of the ladybird beetle (see [Materials and methods](#))

**Table 1** ANOVA table for the relative growth rate of the leaf beetle and the ladybird beetle

	df	ss	F value	P value
Treatment (cut or uncut)	1	0.05	11.97	0.0009
Insect (leaf beetle or ladybird)	1	0.48	122.12	< 0.0001
Treatment $\times$ insect	1	< 0.01	0.04	0.84
Residual	70	0.28		

**Table 2** Qualitative traits of cut and uncut willow leaves

	Cut	Uncut (control)	F value	P value
Leaf toughness (N)	$1.54 \pm 0.04$	$1.54 \pm 0.04$	< 0.001	0.90
% Water (FM)	$63.82 \pm 0.51$	$62.12 \pm 0.62$	2.05	0.20
% Carbon (DM)	$44.90 \pm 0.75$	$45.23 \pm 0.59$	0.12	0.73
% Nitrogen (DM)	$2.64 \pm 0.11$	$2.31 \pm 0.06$	7.61	0.0193

FM, fresh mass; DM, dry mass

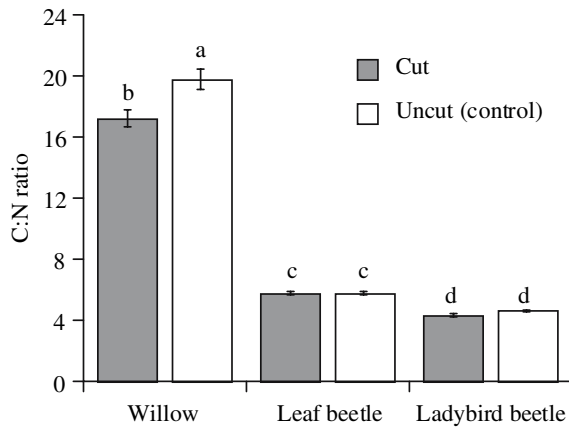
Means  $\pm$  SE are presented. Degrees of freedom for F value = 1.18

cantly higher for the cut treatment than for the uncut treatment (Table 1). The RGR of the leaf beetle and the ladybird were, respectively, 23.1 and 11.0% higher in the cut treatment (Fig. 1).

**Table 3** Larval traits of the willow leaf beetle and predatory ladybird beetle in the cut and uncut treatments

	Cut	Uncut (control)	<i>F</i> value	<i>P</i> value
<b>Leaf beetle</b>				
Larval mass (mg FM)	5.20 ± 0.33	3.71 ± 0.19	14.70	0.0005
% Water (FM)	76.29 ± 0.57	76.52 ± 0.42	0.10	0.75
% Carbon (DM)	48.73 ± 1.52	48.65 ± 1.31	0.001	0.97
% Nitrogen (DM)	8.43 ± 0.20	8.48 ± 0.16	0.04	0.85
<b>Ladybird beetle</b>				
Larval mass (mg FM)	64.70 ± 4.10	50.81 ± 4.54	5.10	0.0307
% Water (FM)	78.80 ± 0.51	78.93 ± 0.58	0.03	0.87
% Carbon (DM)	45.75 ± 1.96	42.47 ± 1.23	2.06	0.16
% Nitrogen (DM)	10.68 ± 0.50	9.23 ± 0.28	6.50	0.0156

Means ± SE are presented. Degrees of freedom for *F* value for leaf beetle and ladybird beetle = 1.37 and 1.33, respectively. FM, fresh mass; DM, dry mass

**Fig. 2** Carbon:nitrogen ratio of the willow, willow leaf beetle, and predatory ladybird beetle. Means ± SE are presented. Different letters show significant difference**Table 4** ANOVA table for the CN ratio of the willow, willow leaf beetle, and predatory ladybird beetle

	<i>df</i>	<i>ss</i>	<i>F</i> value	<i>P</i> value
Treatment	1	0.02	11.70	0.001
Trophic level	2	5.12	1636.09	< 0.0001
Treatment × trophic level	2	0.01	4.48	0.014
Residual	88	0.14		

#### Qualitative traits of willow and insects

Toughness, water, and carbon concentration of the willow leaves did not differ between cut and uncut trees (Table 2). leaf-nitrogen concentration was affected by willow cutting, however; it was 14.3% higher for cut than for uncut willows. Larval mass of the leaf beetle for the cut treatment was significantly greater than for the uncut treatment (Table 3). Water, carbon, and nitrogen concentrations did not differ between treatments, however. Similarly, larval mass of the predatory ladybird beetle for the cut treatment was significantly greater than for the uncut treatment. Nitrogen concentration was also significantly higher for the cut treatment than for uncut treatment, although water and carbon

concentrations in the ladybirds did not differ between treatments (Table 3).

Note that the C:N ratio for the cut tree leaves was significantly lower than for the uncut trees (Fig. 2). No differences were found between the treatments for the leaf beetle and ladybird beetle, however. In addition, the C:N ratio varied among trophic levels (Table 4; Fig. 2). The willow leaves had the highest C:N ratio, followed by the leaf beetle, then the predatory ladybird beetle. The C:N ratio for willow leaves was 3.0–3.4 times higher than for the leaf beetle, and that for the leaf beetle was 1.3 times higher than that for the ladybird.

#### Discussion

This study found a bottom-up cascade effect on insect growth in a tri-trophic system consisting of the willow, a leaf beetle, and a predatory ladybird beetle, one year after cutting of the willow. Kagata et al. (2005) suggested three possible mechanisms causing this cascading effect:

1. larger leaf beetle larvae on cut willows may increase the foraging efficiency of the ladybird;
2. higher quality of cut willow leaves may improve ladybird performance by increasing nutrient quality of the leaf beetle larvae; and
3. decreasing defensive chemicals of the leaf beetle larvae because of changes in willow leaf quality may improve ladybird performance.

Here, we focus discussion on nutritional quality, especially on carbon and nitrogen, as a mechanism of the cascading effect in the tritrophic system.

Matsumura et al. (2004) showed that the C:N ratio decreased (or nitrogen concentration increased) from lower to higher trophic levels in salt marsh plants and associated arthropods, and that there was a large difference between the C:N ratios of plants and herbivores, but not between those of herbivores and predators, i.e.  $C:N_{\text{plants}} \gg C:N_{\text{herbivores}} > C:N_{\text{predators}}$ . Results in this study were in agreement, giving the pattern:  $C:N_{\text{willow}} \gg C:N_{\text{leaf beetle}} > C:N_{\text{ladybird beetle}}$ . According to the stoichiometric theory, these differences in C:N

ratio among trophic levels indicate that development of herbivores may be strongly limited by host plant nitrogen (Mattson 1980), and that the development of predators may be also limited by nitrogen in their prey, although less so than for herbivores (Fagan et al. 2002; Denno and Fagan 2003).

This study showed that the RGR of the leaf beetle increased as a result of feeding on leaves of the cut willows, which had a higher nitrogen concentration and lower C:N ratio than the uncut willows. The RGR would be independent of the number of available leaves, because enough leaves were supplied to avoid food shortage throughout the experiment. In addition, the toughness, water concentration, and carbon concentration of the leaves could not affect the RGR because these did not differ between the cut and uncut trees. Defensive chemicals, for example tannins, can reduce insect performance by reducing nitrogen intake or efficiency of nitrogen use (Simpson and Raubenheimer 2001; Nomura and Itioka 2002). In general, concentrations of these defensive chemicals were negatively correlated with leaf nitrogen (Haukioja et al. 1985; Hikosaka et al. 2005). The increased RGR of the leaf beetle is, therefore, likely to result from the increased nitrogen intake, and/or nitrogen use efficiency, because of the presence of smaller amounts of the defensive chemicals in the leaves of the cut willows, although the defensive chemicals were not measured in this study.

Several authors have shown that the development of arthropod predators, for example spiders, is limited by prey nitrogen concentration (Toft and Wise 1999; Mayntz and Toft 2001). In this study the ladybird RGR increased as a result of feeding on leaf beetle larvae that fed on leaves from cut willows. Likewise the leaf beetle, the RGR of the ladybird was independent of the amount of available prey, because enough leaf beetles were supplied to the ladybird to avoid food shortage throughout the experiment. However, the mechanism causing the increased RGR may be different for the leaf beetle, because leaf beetle nitrogen and C:N ratio were not affected by willow leaf quality. Therefore, increased performance of the ladybird would not be because of prey nitrogen, and it did not support the hypothesis by Mayntz and Toft (2001) that predator performance may increase because of increased nutritional quality of prey which fed on a higher quality diet, at least for nitrogen. The constant nitrogen concentration and C:N ratio of the leaf beetle are likely to result from homeostasis which maintains constant elemental composition in the body. Homeostasis in body nitrogen concentration or C:N ratio has been widely recognized in several taxa, including bacteria, fungi, zooplankton, and insects (Slansky and Feeny 1977; Anderson and Hessen 1991; Sterner and Elser 2002; Makino and Cotner 2004). For example, Slansky and Feeny (1977) demonstrated that while leaf-nitrogen concentration of a crucifer plant was increased greatly by fertilization, nitrogen concentration in cabbage butterfly larvae that fed on the fertilized plants hardly changed. Similarly, Kagata and Ohgushi

(2006) demonstrated that nitrogen concentration in the willow leaf beetle, *P. versicolora*, hardly changed through generations, even though leaf nitrogen of the host willows varied seasonally by large amounts. This is because herbivorous insects deal with nitrogen-poor diets by prolonging feeding period, increasing nitrogen use efficiency, and reducing body size. They also deal with nitrogen-rich diets by excretion of excess nitrogen, to maintain their body element composition (Slansky and Feeny 1977; Obermaier and Zwölfer 1999; Raubenheimer and Simpson 2004). Our experiment showed, however, that nitrogen concentration in the predatory ladybird differed between the treatments. This could be because of the different larval stage of the predatory ladybird. Nitrogen concentration in insects varies depending on the larval stage (Kagata and Katayama 2006). The experimental period of six days was in approximate agreement with the molting period from third to fourth instar of the ladybird larvae. Because larval growth of the ladybird differed between treatments, different instars were used to measure nitrogen concentration. A longer experimental period is needed to confirm the result obtained for nitrogen concentration in ladybird larvae.

Thus, this study reveals that the mechanism increasing the performance of insects may be different in plant-herbivore and herbivore-predator interactions, and, therefore, that carbon-nitrogen stoichiometry cannot be a mechanism causing the bottom-up cascade through the multitrophic levels. Other mechanisms suggested by Kagata et al. (2005), i.e. enhancing foraging efficiency and reducing defensive chemicals, should be tested to answer the question why ladybird performance increased when fed on leaf beetle larvae that were reared on leaves of the cut willows. We must carefully interpret our data, however, because we did not evaluate the quality of the leaf beetle as prey for the ladybird beetle in a strict sense. Although carbon and nitrogen concentrations were measured for the leaf beetles from the rearing experiment, the ladybird beetles were reared on the leaf beetles from a field population. Hence, it remains a possibility that the quality of the leaf beetles in the field population differs from those in the rearing experiment, although, in general, insect elemental composition would not be affected by environmental conditions (Fagan et al. 2002; Kagata and Ohgushi 2006). In addition, although the bottom-up cascade detected in the present study was in a laboratory experiment, we did not examine it in the field. Because not only resource quality but also quantity may interactively affect insect performance, we do not conclude the cascading effect is always true in the field.

This stoichiometric approach provides a valuable contribution to understanding the bottom-up regulation of multitrophic levels in terrestrial food webs. Carbon-nitrogen stoichiometry in this study attracted attention to a large difference between C:N ratios in plants and herbivores but a small difference between that in herbivores and predators (Fig. 2). Sterner and Elser (2002)

predicted that consumers' productivity would be limited by resource carbon or energy in stoichiometrically balanced systems, i.e. the supply of nutrient composition by a resource matches the demand by the consumer but would be limited by resource nutrients in stoichiometrically unbalanced systems. Focusing the resource–consumer relationship on carbon–nitrogen stoichiometry, the plant–herbivore relationship would be an unbalanced system but the herbivore–predator relationship would be a relatively balanced system. This indicates that herbivore performance may be strongly influenced by nutrients in host plants, because there is a large nutrient gap between plant and herbivore whereas the nutrients may be less important to predator performance, because of small nutrient gap between herbivore and predator. Thus, a different stoichiometric balance between resource and consumer would result in different mechanisms determining the different performance of the herbivorous leaf beetle and the predatory ladybird beetle.

**Acknowledgments** We thank the River Bureau of the Ministry of Land, Infrastructure, and Transport for allowing us to conduct research at the Yasu River. We also thank A. Davis for valuable discussion. This study was supported by the Ministry of Education, Culture, Sports, Science, and Technology Grant-in-Aid for scientific research (A-15207003) to T. Ohgushi, the 21st Century COE Program (A14), and the River Environment Fund in charge of the Foundation of River and Watershed Environmental Management, Japan.

## References

- Anderson T, Hessen DO (1991) Carbon, nitrogen, and phosphorus concentration of freshwater zooplankton. *Limnol Oceanogr* 36:807–814
- Cotrufo MF, Ineson P, Scott A (1998) Elevated CO<sub>2</sub> reduces the nitrogen concentration of plant tissues. *Glob Change Biol* 4:43–54
- Crone EE, Jones CG (1999) The dynamics of carbon–nutrient balance: effects of cottonwood acclimation to short-and long-term shade on beetle feeding preferences. *J Chem Ecol* 25:635–656
- Denno RF, Fagan WF (2003) Might nitrogen limitation promote omnivory among carnivorous arthropods. *Ecology* 84:2522–2531
- Faeth SH (1986) Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* 67:479–494
- Fagan WF, Siemann E, Mitter C, Denno RF, Huberty AF, Woods HA, Elser JJ (2002) Nitrogen in insects: implications for trophic complexity and species diversification. *Am Nat* 160:784–802
- Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51:555–581
- Harvey JA, Van Dam NM, Gols R (2003) Interactions over four trophic levels: foodplant quality affects development of a hyperparasitoid as mediated through a herbivore and its primary parasitoid. *J Anim Ecol* 72:520–531
- Haukioja E, Niemelä P, Sirén S (1985) Foliage phenols and nitrogen in relation to growth, insect damage, and ability to recover after defoliation, in the mountain birch *Betula pubescens* ssp. *tortuosa*. *Oecologia* 65:214–222
- Hikosaka K, Takashima T, Kabeya D, Hirose T, Kamata N (2005) Biomass allocation and leaf chemical defense in defoliated seedlings of *Quercus serrata* with respect to carbon–nitrogen balance. *Ann Bot* 95:1025–1032
- Hunter MD (2003) Effects of plant quality on the population ecology of parasitoids. *Agric For Entomol* 5:1–8
- Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural community. *Ecology* 73:724–732
- Kagata H, Katayama N (2006) Does nitrogen limitation promote intraguild predation in an aphidophagous ladybird? *Entomol Exp Appl* 119:239–246
- Kagata H, Ohgushi T (2006) Nitrogen homeostasis in a willow leaf beetle, *Plagioderma versicolora*, independence of host plant quality. *Entomol Exp Appl* 118:105–110
- Kagata H, Nakamura M, Ohgushi T (2005) 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. *Ecol Entomol* 30:58–62
- Kimoto S, Takizawa H (1994) Leaf beetles (Chrysomelidae) of Japan. Tokai University Press, Tokyo
- Kimura Y (1989) Salicaceae. In: Satake Y, Hara H, Watari S, Tominari T (eds) Wild flowers of Japan. Woody plants Heibonsha, Tokyo, pp 31–51
- Kudo G (2003) Variations in leaf traits and susceptibility to insect herbivory within a *Salix miyabeana* population under field conditions. *Plant Ecol* 169:61–69
- Lower SS, Orians CM (2003) Soil nutrients and water availability interact to influence willow growth and chemistry but not leaf beetle performance. *Entomol Exp Appl* 107:69–79
- Makino W, Cotner JB (2004) Elemental stoichiometry of a heterotrophic bacterial community in a freshwater lake: implications for growth-and resource-dependent variations. *Aquat Microb Ecol* 34:33–41
- Martinsen GD, Driebe EM, Whitham TG (1998) Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. *Ecology* 79:192–200
- Matsumura M, Trafelet-Smith GM, Gratton C, Finke DL, Fagan WE, Denno RF (2004) Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology* 85:2601–2615
- Matsura T (1976) Ecological studies of a coccinellid, *Aiolocaria hexaspilota* Hope. I. Interaction between field populations of *A. hexaspilota* and its prey, the walnut leaf beetle (*Gastrolina depressa* Baly). *Jpn J Ecol* 26:147–156 (in Japanese)
- Mattson WJ (1980) Herbivory in relation to plant nitrogen concentration. *Ann Rev Ecol Syst* 11:119–161
- Mattson WJ, Scriber JM (1987) Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. In: Slansky F, Rodrigues JG (eds) Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York, pp 105–146
- Mayntz D, Toft S (2001) Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia* 127:207–213
- Nomura M, Itioka T (2002) Effects of synthesized tannin on the growth and survival of a generalist herbivorous insect, the common cutworm, *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae). *Appl Entomol Zool* 37:285–289
- Obermaier E, Zwölfer H (1999) Plant quality or quantity? Host exploitation strategies in three Chrysomelidae species associated with Asteraceae host plants. *Entomol Exp Appl* 92:165–177
- Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Ann Rev Ecol Syst* 11:41–65
- Raubenheimer D, Simpson SJ (2004) Organismal stoichiometry: quantifying non-independence among food components. *Ecology* 85:1203–1216
- Raupp MJ, Denno RF (1983) Leaf age as a predictor of herbivore distribution and abundance. In: Denno RF, McClure MS (eds) Variable plants and herbivores in natural and managed systems. Academic, New York, pp 91–124
- Simpson SJ, Raubenheimer D (2001) The geometric analysis of nutrient–allelochemical interactions: a case study using locusts. *Ecology* 82:422–439

- Slansky F, Feeny P (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecol Monogr* 47:209–228
- Sterner RW, Elser JJ (2002) *Ecological stoichiometry*. Princeton University Press, Princeton
- Teder T, Tammaru T (2002) Cascading effects of variation in plant vigour on the relative performance of insect herbivores and their parasitoids. *Ecol Entomol* 27:94–104
- Toft S, Wise DH (1999) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* 119:191–197
- White TCR (1993) *The inadequate environment*. Springer, Berlin Heidelberg New York