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Bottom-up trophic cascades and material transfer in terrestrial food webs

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Abstract In contrast to top-down trophic cascades, few reviews have appeared of bottom-up trophic cascades. We review the recent development of research on bottom-up cascades in terrestrial food webs, focusing on tritrophic systems consisting of plants, herbivorous insects, and natural enemies, and attempt to integrate bottom-up cascade and material transfer among trophic levels. Bottom-up cascades are frequently reported in various tritrophic systems, and are important to determine community structure, population dynamics, and individual performance of higher trophic levels. In addition, we highlight several features of bottom-up cascades. Accumulation or dilution of plant nutritional and defensive materials by herbivorous insects provides a mechanistic base for several bottom-up cascades. Such a stoichiometric approach has the potential to improve our understanding of bottom-up cascading effects in terrestrial food webs. We suggest a future direction for research by integration of bottom-up cascades and material transfer among trophic levels.

Keywords Ecological stoichiometry · Grazing food chain · Herbivorous insects · Indirect interaction · Tritrophic levels

Introduction

Trophic cascades, defined as reciprocal consumer-resource effects that alter the abundance, biomass or productivity of a population, community or trophic level across more than one link in a food web (Pace et al.

1999), generally represent indirect effects of a higher trophic level on nonadjacent lower trophic levels, i.e. top-down cascade. While the top-down cascade has been well documented in aquatic systems (Strong 1992), it is thought to occur rarely in terrestrial systems because of high diversity in food webs and strong antiherbivore defense of plants, under which trophic cascades are unlikely to occur (Strong 1992; Polis 1999; Halaj and Wise 2001). However, recent studies have revealed that the top-down cascade commonly occurs in a wide variety of terrestrial systems (Schmitz et al. 2000), and focus has shifted to a cross-ecosystem comparison of the strength of trophic cascades (Pace et al. 1999; Schmitz et al. 2000; Shurin et al. 2002; Borer et al. 2005).

While such a top-down concept in which a higher trophic level dominates populations and/or communities of lower trophic levels has been widely accepted, lower trophic levels can also propagate upward to nonadjacent higher trophic levels (Hunter and Price 1992; Price 2002); this is called “bottom-up cascade”, or “cascading upward” (Hunter and Price 1992). Hunter and Price (1992) proposed a model that synthesizes the top-down and bottom-up concepts for terrestrial food webs. They suggested that species at any trophic levels can dominate other trophic levels due to feedback loops of top-down and bottom-up cascading effects (Hunter and Price 1992). There is increasing evidence of bottom-up cascading effects in various terrestrial systems (e.g. Siemann 1998; Forkner and Hunter 2000; Teder and Tammaru 2002; Gratton and Denno 2003). Although the top-down cascade has been repeatedly reviewed (Pace et al. 1999; Schmitz et al. 2000; Haraj and Wise 2001; Shurin et al. 2002; Borer et al. 2005), few systematic reviews have appeared for the bottom-up cascade, although it has been partially documented by Andow (1991), Hare (2002), and Lövei and Arpaia (2004).

We review the recent development of research on the bottom-up cascades in terrestrial food webs, focusing on tritrophic systems consisting of plants, herbivorous insects, and natural enemies, and show how quantitative and qualitative traits of plants indirectly affect natural

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enemies via herbivorous insects at the community, population, and individual levels. We do not include another important bottom-up effect: the direct effect of plants on natural enemies via plant architecture or leaf volatile compounds (see Turlings et al. 2002; Langellotto and Denno 2004). Moreover, the relative importance of top-down and bottom-up forces in tritrophic systems is not considered here, because it has been repeatedly discussed by many researchers (e.g. Power 1992; Walker and Jones 2000; Dyer and Coley 2002; Stregbom et al. 2005). Instead, we attempt to integrate bottom-up cascading and material transfer in terrestrial food webs. Since nutrient or other materials, such as defensive chemicals, which are fixed or produced by plants are transmitted upward to higher trophic levels through food chains, the material flow is in the same direction as the effects of bottom-up cascades (Fig. 1). Such nutrient or defensive materials of plants would be important materials to determine survival and growth of predators as well as herbivores (Mattson 1980; Hagen 1987; White 1993). Hence, an integration of bottom-up cascades and material transfer among trophic levels may lead to a new aspect for mechanisms and consequences of the bottom-up cascades in terrestrial food webs.

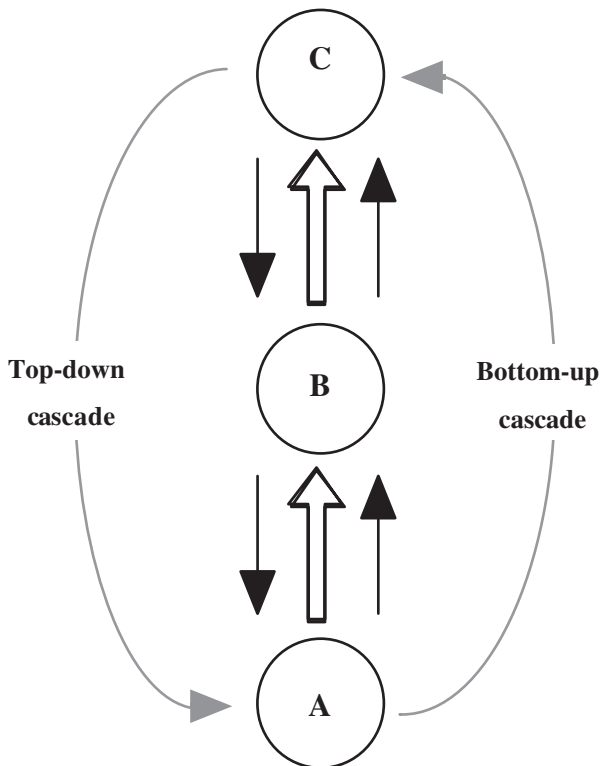


Fig. 1 Top-down and bottom-up cascades and material flow in the tritrophic system. *Black, gray, and white* arrows show the directions of direct effects, indirect effects, and material flow, respectively. *A, B, C* represent plants (lower trophic level), herbivores (mediating trophic level), and predators (higher trophic level), respectively

Bottom-up trophic cascades at various levels

While top-down cascades have been generally examined by experiments removing top predators in food webs (Schmitz et al. 2000), bottom-up cascades have been detected as indirect effects of heterogeneity of plants on third trophic levels through herbivorous insects. Plant heterogeneity represents differences in species richness, abundance, productivity, and quality (Table 1). Bottom-up cascades are categorized as community-, population-, and individual-level cascades, depending on the properties of the third trophic level (Table 1).

Community-level cascades

Effects of plant diversity on communities of higher trophic levels have been focused on agroecosystems as an issue in pest and natural enemy management, i.e. monoculture vs. polyculture (Andow 1991). Plant diversity may affect herbivore diversity, and subsequently predator diversity (Hunter and Price 1992). Siemann (1998) was the first to study experimentally this community-level cascade, demonstrating that plant diversity cascaded up to the natural enemy community through the herbivore community. Since then, several studies have detected community-level cascades which were initiated by manipulation of species richness or biomass of the plant community using fertilization or planting (Table 1). For example, Knops et al. (1999) showed that increasing plant species richness results in increased species richness of herbivores and predators. Similarly, Hawes et al. (2003) detected the same pattern in terms of abundance of each trophic level. Note that most of these studies showed that changes in species richness and abundance of herbivores and predators are in the same direction as changes in their resources, i.e. high diversity (abundance) of plants can support high diversity (abundance) of herbivores, which can support high diversity (abundance) of predators (Hunter and Price 1992). However, Koricheva et al. (2000) showed that the responses of each arthropod to plant diversity were different depending on taxa.

On the other hand, changes in plant diversity and abundance generally involve changes in vegetation structure and in abundance of alternative food, such as flower nectar. These changes may directly affect diversity and abundance of predators and parasitoids (Langellotto and Denno 2004). For example, Brose (2003) found that increasing plant diversity increased species richness in a carabid beetle community, and concluded that the increased diversity of the carabid beetles would result from direct effects of vegetation structure which depends on plant diversity. Therefore, the community-level cascades detected in several studies may include not only cascading effects through herbivores, but also direct effects of plant structure or alternative food on predators and parasitoids.

Table 1 Bottom-up trophic cascades in terrestrial systems, consisting of plants, herbivorous insects, and natural enemies, at the community, population, and individual levels. Community-level cascades do not focus on certain species of herbivores and natural enemies

Level/study type ^a	Plant	Herbivore	Natural enemy	Heterogeneity of plants	Variable of natural enemies	Reference
Presence of bottom-up cascades						
Community level						
Field experiment	Grasses, forbs	–	–	Productivity	Species richness, abundance	Siemann (1998)
Field experiment	Grasses, forbs	–	–	Species richness	Species richness	Siemann et al. (1998)
Field experiment	Grasses, forbs	–	–	Species richness	Species richness	Knops et al. (1999)
Field experiment	Grasses, forbs	–	–	Species richness	Species richness	Haddad et al. (2000)
Field experiment	Trees	–	–	Quality	Density	Forkner and Hunter (2000)
Field experiment	Grasses, forbs	–	–	Biomass	Abundance	Hawes et al. (2003)
Field sampling	Grasses etc.	–	–	Species richness	Species richness, abundance	Perner et al. (2003)
Field experiment	Forbs	–	–	Abundance	Abundance	Fonseca et al. (2005)
Population level						
Field experiment	Tree	Mite	Mites	Quality	Density	Walde (1995)
Field experiment	Forb	Tephritid fly	Parasitic wasps	Biomass, quality	Density	Masters et al. (2001)
Field experiment	Grass	Planthopper etc.	Spider etc.	Biomass, quality	Population dynamics	Gratton and Denno (2003)
Field experiment	Tree	Leaf beetle	Mirid bugs	Growth	Population dynamics	Bjökman et al. (2004)
Field experiment	Tree	Leaf beetle	Ladybird, spider	Growth	Density	Nakamura et al. (2005)
Individual level						
Laboratory assay	Forbs	Moth	Parasitic wasp	Quality	Survivorship, body size, developmental time	Barbosa et al. (1991)
Laboratory assay	Forbs	Butterfly	Parasitic wasp	Quality ^b	Survivorship, developmental time, longevity	Karowe and Schoonhoven (1992)
Laboratory assay	Tree	Moth	Parasitic wasp	Quality	Survivorship, body size	Roth et al. (1997)
Laboratory assay	Forb	Moth	Stinkbug	Quality	Body size, developmental time	Stamp et al. (1997)
Laboratory assay	Forb	Moth	Stinkbug	Quality	Body size, developmental time	Traugott and Stamp (1997)
Laboratory assay	Grass	Aphid	Parasitic wasp	Quality	Survivorship, body size	Fuentes-Contreras et al. (1998)
Laboratory assay	Tree	Moth	Parasitic wasp	Quality	Survivorship	Havill and Raffa (2000)
Field sampling	Forb	Mealybug	Ladybird	Quality ^b	Survivorship, developmental time, fecundity	Le Rü and Mitsipa (2000)
Laboratory assay	Forbs	Aphids	Ladybird	Quality	Survivorship	Francis et al. (2001)
Field sampling	Grass	Moth	Parasitic wasp	Growth	Body size	Teder and Tamaru (2002)
Field sampling	Forbs	Leaf miner	Parasitic wasps	Quality ^b	Body size	Salvo and Valladares (2002)
Laboratory assay	Forbs	Moth	Parasitic wasps	Quality	Developmental time, longevity	Baur and Boethel (2003)
Field experiment	Tree	Moth	Parasitic fly	Quality	Survivorship	Holton et al. (2003)
Laboratory assay	Forbs	Moth	Parasitic wasps	Quality	Body size	Harvey et al. (2003)
Field sampling	Tree	Leaf beetles	Parasitic flies	Quality	Body size	Zvereva and Rank (2003)
Laboratory assay	Grass	Weevil	Parasitic wasp	Quality	Survivorship	Bultman et al. (2003)
Laboratory assay	Forbs	Moths	Parasitic wasps	Quality	Survivorship, developmental time, body size	Sznajder and Harvey (2003)
Field sampling	Forbs	Moth	Parasitic wasp	Quality	Survivorship	Ode et al. (2004)
Laboratory assay	Artificial diet	Aphid	Parasitic wasp	Quality	Survivorship, developmental time	Azzouz et al. (2005)
Laboratory assay	Tree	Leaf beetle	Ladybird	Quality ^b	Body size, developmental time	Kagata et al. (2005)

Absence of bottom-up cascades									
Community level									
Field experiment	Forbs	–							Dyer and Stireman (2003)
Field experiment	Tree	–							Gruner (2004)
Population level									
Field experiment	Shrub	Stem borer	Ant						Dyer et al. (1999)
Laboratory experiment	Forb	Moth	Parasitic wasp						Karimzadeh et al. (2004)
Individual level									
Laboratory assay	Forb	Leaf beetle	Stinkbug						Bouchard et al. (2003)
Greenhouse experiment	Forb	Aphid	Ladybird						Down et al. (2000)
Field experiment	Forb	Aphid	Parasitic wasps						Cowgill et al. (2004)

^aStudy type categorized in terms of methodology: *experiment* insect sampling from, or rearing on, plants with artificial manipulations, such as fertilization; *sampling* insect sampling from plants without artificial manipulation; *assay* insect rearing on leaves collected from plants or artificial diet mixed with leaf materials

^bSuggested but not measured

Population-level cascades

The population-level cascade (cf. species-level cascade, Polis 1999) is determined by changes in individual numbers of predators and/or parasitoids corresponding to changes in plant biomass, growth, and quality, through herbivorous insects (Table 1). Although there are a number of studies showing that host plants affect the attack or parasitism rates on herbivorous insects by natural enemies (e.g. Gross and Price 1988; Rank and Smiley 1994; Martinsen et al. 1998; Barbosa et al. 2001; Lill and Marquis 2001), the present review includes only studies that directly examined the density of natural enemies. Like the community-level cascades, changes in plant traits generally result in responses in the same direction of both herbivorous insects and their natural enemies in population-level cascades (e.g. Masters et al. 2001; Nakamura et al. 2005). In other words, when the direct effects of plants on herbivorous insects are positive, the indirect effects on natural enemies are also positive. Nakamura et al. (2005) showed that regrowth of riparian willows after damage due to flooding results in a higher density not only of a leaf beetle, but also of its natural enemies. In addition, population-level cascades are initiated by changes in plant quality induced by other herbivorous insects. Masters et al. (2001) found that root herbivory by coleopteran and dipteran larvae resulted in a greater number of both a seed predator and its parasitic wasps. This is because root herbivory was likely to increase resource allocation to reproductive organ of plants, which resulted in high quality of seeds. Then, such high quality seeds were attacked by greater number of seed predators, which attracted parasitic wasps (Masters et al. 2001). However, there is another possibility that changes in plant architecture or flower size may directly affect natural enemies.

While most studies have examined the cascading effects at a point in time, a few studies have detected temporal changes in bottom-up cascades (Gratton and Denno 2003; Bjökman et al. 2004). These studies have shown that the bottom-up cascade was maintained for several years after plant manipulation in the experiment (Gratton and Denno 2003), but the response each year differed between herbivorous insects and their natural enemies (Bjökman et al. 2004). For example, high quality in the resprouting willows after harvesting resulted in high densities of the leaf beetles and their natural enemies, but the leaf beetle density peaked 2 years after the harvesting, whereas the natural enemies consistently increased after 4 years (Bjökman et al. 2004). This result indicates that the leaf beetle density would be increased by high plant quality for the first 2 years after harvesting, but thereafter may be decreased by the top-down force of increased predators due to a delayed cascading effect of harvesting, as a feedback in the bottom-up cascade.

Individual-level cascades

Compared to the community- and population-level cascades, individual-level cascades have been studied more frequently (Table 1). Note that there are many studies which are not listed in Table 1 (e.g. see Groot and Dicke 2002; Lövei and Arpaia 2004). An important question arising from these studies is whether plant nutritional conditions and defensive chemicals affect performance of natural enemies via herbivorous insects. Hence, the variables measured in the individual-level cascades include various performance parameters, such as survivorship, developmental time, body size, and fecundity, while the heterogeneity of host plants almost represents plant quality (Table 1). Barbosa et al. (1991) examined the indirect effects of three defensive chemicals of plants, including nicotine, rutin, and hordenine, on performance of the parasitoid *Cotesia congregata* via tobacco hornworm *Manduca sexta*. Although the influences of these chemicals differed, in general they decreased the performance of both the hornworm and its parasitoid. Teder and Tammaru (2002) have demonstrated that plants with more vigorous growth are associated with a larger body size of the lepidopteran larvae, which subsequently leads to an increase in the body size of their parasitoids. Furthermore, effects of the plant quality can cascade up to the fourth trophic level, i.e. hyperparasitoid, via herbivorous insect and its primary parasitoid (Harvey et al. 2003). A more recent consideration is whether improving plant quality by increasing atmospheric CO₂ or by using transgenic plants affects performance of natural enemies via herbivorous insects (Groot and Dicke 2002; Holton et al. 2003; Lövei and Arpaia 2004). For example, transgenic cotton expressing a toxin for herbivorous insects prolonged larval developmental time and shortened adult longevity of parasitoid, as a result of slow growth and reduced pupal size of the host lepidopteran larvae (Baur and Boethel 2003, but see Groot and Dicke 2002).

Thus, most studies of the individual-level cascades, as well as community- and population-level cascades, have shown that plant quality results in responses in the same direction of both herbivorous insects and their natural enemies (e.g. Barbosa et al. 1991; Teder and Tammaru 2002; Zvereva and Rank 2003), i.e. high nutritional (defensive) plants increase (decrease) the performance of herbivorous insects, and subsequently increase (decrease) that of their natural enemies. In addition, Teder and Tammaru (2002) and Kagata et al. (2005) demonstrated that plant quality affects more strongly the performance of herbivorous insects than that of their natural enemies, while the responses of herbivorous insects and natural enemies to plant quality are in the same direction. For example, in high quality leaves of willows the developmental time of a leaf beetle was 14.7% shorter than in low quality leaves, but the developmental time of its predatory ladybird was only 6.3% shorter (Kagata et al. 2005).

These studies indicate that effects of plant quality on insect performance may be weakened through trophic levels in the bottom-up cascades. On the other hand, a few studies have shown opposite responses of a herbivorous insect and its natural enemy to plant quality (Karowe and Schoonhoven 1992; Holton et al. 2003). Karowe and Schoonhoven (1992) examined the effects of four different plants, including Brussels sprouts, nasturtium, rape, and Swedish turnip, on the performance of the cabbage butterfly *Pieris brassicae* and its parasitoid *Cotesia glomerata*. They found that cabbage butterfly larvae on nasturtium showed the lowest performance (in terms of survivorship, growth rates, and body size), but the performance of the parasitoids developed in the host larvae on nasturtium was the highest (in terms of developmental time and longevity) among the four plants. Although the reason why there are different responses of the butterfly and its parasitoid to host quality remains unclear, the authors pointed out that a difference in sensitivity to plant chemicals between the herbivore and parasitoid could explain the different responses (Karowe and Schoonhoven 1992).

Absence of bottom-up cascades

Although many studies have investigated bottom-up cascades at various levels, several studies did not detect cascading effects from plants to natural enemies at the community, population, or individual level (Table 1). For example, Dyer and Letourneau (1999) found no evidence of effects of plant biomass on predator density through herbivores. The following reasons for the absence of bottom-up cascading effects have been suggested: strong top-down control (Dyer and Letourneau 1999; Karimzadeh et al. 2004), competition among herbivores (Karimzadeh et al. 2004), dilution of plant chemicals in the body of herbivores (Cowgill et al. 2004), and diet range of natural enemies (Koricheva et al. 2000).

Material transfer in bottom-up cascades

Previous studies on nutritional ecology (cf. Slansky and Rodrigues 1987) have focused on the fate of plant defensive chemicals and nutritional materials ingested by herbivorous insects (e.g. Mattson 1980; Lindroth 1991). They have provided an insight into the integration of material transfer among trophic levels and bottom-up trophic cascades in multitrophic systems.

Several herbivorous insects, especially specialists, can rapidly excrete or detoxify plant defensive or toxic chemicals (Tabashnik and Slansky 1987; Lindroth 1991; Glendinning 2002), which may weaken or interrupt the cascading effects of plant chemicals on natural enemies. Recently, this detoxification ability of herbivorous insects has been often examined in agro-

ecosystems as a factor in the effects of plant chemicals produced by transgenic crops on multitrophic levels (Groot and Dicke 2002; Lövei and Arpaia 2004). For example, snowdrop lectin expressed by a transgenic potato that reduces aphid fecundity was absent or in negligible amounts within the aphids, and was not detected in their predatory ladybird (Down et al. 2000). Therefore, there are no cascading effects from transgenic plants on the performance of natural enemies (Down et al. 2000). However, oryzacystatin I, a protease inhibitor, in transgenic plants accumulates in aphid tissue, which decreases its parasitoid performance in terms of developmental time and body size (Azzouz et al. 2005). This negative effect may have resulted from the low ability of the aphid to excrete or invalidate the harmful transgenic products. On the other hand, several herbivorous insects can voluntarily accumulate plant defensive chemicals within their body to protect themselves from natural enemies (Pasteels et al. 1989; Martinsen et al. 1998; Francis et al. 2001). Francis et al. (2001) demonstrated that the aphid *Brevicoryne brassicae* accumulates glucosinolates derived from host plants, which results in 100% mortality of the predatory ladybird feeding on these aphids. This indicates that the effects of plant defensive chemicals cascade up to a natural enemy through accumulation of the chemicals by herbivorous insects.

In addition to plant defensive chemicals, nutritional materials in host plants, such as nitrogen and phosphorus, also accumulate in insects through trophic levels (Fagan et al. 2002; Woods et al. 2002). The nitrogen content increases (or the C:N ratio decreases) from lower to higher trophic levels in tritrophic systems (i.e. $N_{\text{plants}} \ll N_{\text{herbivores}} < N_{\text{predators}}$; Fagan et al. 2002; Matsumura et al. 2004). This difference in the nitrogen content among trophic levels indicates that consumer development would be limited by the amount of nitrogen in the resources (White 1993). Indeed, it is known that the amount of nitrogen in the resources is an important factor limiting survival and growth of several herbivores and predators (Mattson 1980; Denno and Fagan 2003). Therefore, the amount of nitrogen in host plants and its accumulation by herbivorous insects may influence the performance of natural enemies. One hypothesis for explaining individual-level cascades is that a higher nitrogen level in host plants leads to an increase in the nitrogen content of herbivorous insects, which in turn leads to an increase in predator performance (Mayntz and Toft 2001). H. Kagata and T. Ohgushi (unpublished) tested this hypothesis using a willow-leaf beetle-predatory ladybird system, but their findings did not support it. Although a higher nitrogen content of the willows was associated with better growth rates of both the leaf beetle and the predatory ladybird, the leaf beetle nitrogen content was not affected by the nitrogen content of the willow leaves, because of the nitrogen homeostasis in herbivorous insects (Slansky and Feeny 1977).

Conclusion and perspectives

Bottom-up trophic cascades in terrestrial food webs

This review clearly illustrated several features of bottom-up cascades in terrestrial systems. First, the responses of herbivores and natural enemies to plant heterogeneity are in the same direction, i.e. when the plant positively affects herbivores, the indirect effect on natural enemies is also positive. This contrasts to top-down cascading effects, in which the direction of the effects between adjacent trophic levels is generally opposite: an increase in the abundance of predators results in a decrease in herbivores and subsequently an increase in plant biomass (Pace et al. 1999). Second, a few studies have suggested that the impact of bottom-up cascades weakens through trophic levels, and that there is a time lag in the appearance of the bottom-up cascades between herbivores and natural enemies. These two features may make detecting feedback loops in the top-down and bottom-up cascading effects difficult (cf. Hunter and Price 1992; Bjökman et al. 2004). Third, several studies have shown that investigating bottom-up cascades is important to elucidate the effects of increasing CO₂ and transgenic crops on the dynamics of multitrophic levels. In this context, we would like to emphasize that the concept of the bottom-up cascade can predict the ecosystem risk due to such environmental issues in the future. However, note that several studies of bottom-up cascades have shown direct effects of plant architecture and leaf volatiles on natural enemies, without mediation of herbivorous insects. Hence, the effects of plant heterogeneity due to experimental manipulation should be carefully interpreted, especially for community- and population-level cascades where it would be difficult to discriminate the direct effects of plants from the cascading effects on natural enemies.

Integrating bottom-up cascades and material transfer

This review also highlights the relationship between bottom-up cascades and material transfer in tritrophic systems, and argues that accumulation or dilution of materials that are fixed or produced by plants through trophic interactions provides a mechanistic base for individual-level cascades. Ecological stoichiometry links trophic interactions and changes in content of several materials between resources and consumers, and it is a useful idea to explore population and community dynamics in aquatic systems (Sterner and Elser 2002; Moe et al. 2005). However, in terrestrial systems most studies on stoichiometry have concerned soil-plant interactions, such as the relationship between the decomposition process and plant productivity (e.g. Vitousek 2004). This is probably because materials fixed or produced by plants almost flow into the decomposition system directly, but only small

amounts into grazing food chains (Cebrian 1999; Polis 1999). However, many heterotrophs are supported by nutritional materials from plants through grazing food chains. Moreover, as we showed, the effects of plant materials cascade up to, and the materials themselves are transmitted to, higher trophic levels in several systems. Hence, the stoichiometric approach has the potential to improve our understanding of bottom-up cascading effects in terrestrial systems, as well as aquatic systems (Moe et al. 2005). In this context, although a few recent studies have shown a relationship between material transfer among trophic levels and individual-level cascades (Down et al. 2000), material transfer in population- and community-level cascades remains unclear, but this approach will provide a useful insight into the mechanisms or consequences of bottom-up cascades on population dynamics and community structure. For example, Schade et al. (2003) demonstrated that soil phosphorus availability links population dynamics of a herbivorous insect through changes in the carbon:phosphorus ratio (C:P ratio) of the host plants and in the phosphorus content of the herbivorous insect. Although their study was not expanded to multitrophic system, it indicates that a population-level cascade may occur with changes in the C:P ratio of each trophic level. Recent studies have revealed an important effect of phosphorus on insect growth (Frost and Elser 2002; Perkins et al. 2004) as well as on plant growth (Vitousek 2004). In addition, whether material transfer among trophic levels changes in community-level cascades which involve changes in species diversity is a challenging question. This could bridge the gap between species diversity of heterotrophs and its ecosystem functioning in terrestrial systems.

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