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# Plant Productivity is Temporally Enhanced by Soil Fauna Depending on the Life Stage and Abundance of Animals

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## 1. Introduction

In terrestrial ecosystems, nutrient recycling is driven by the belowground decomposition process because it supplies most of the production to the soil system (Swift *et al.* 1979; Cebrian 1999). Soil links the aboveground plants and the belowground community (Wardle, 2002). Soil nutrient cycling is controlled by interactions among living soil organisms, plant litter quality, soil physical and chemical status, temperature, and water condition. In soil-organism processes, large soil animals rapidly change microbial activity (Hanlon and Anderson 1980) and the litter decomposition rate (Bonkowski *et al.* 1998) and modify soil structure (Barois *et al.* 1993). Consequently, primary decomposition and plant growth are affected not only by microbes but also by soil animals (Wall and Moore 1999; Wardle 2002). The overall faunal contribution to nitrogen (N) mobilization has been estimated as approximately 30% in forest ecosystems (Verhoef and Brussaard 1990). Schröter *et al.* (2003) calculated that the total amount of N mineralized by fauna in European coniferous forests ranged from 11 kg N ha<sup>-1</sup> a<sup>-1</sup> in northern Sweden to 73 kg N ha<sup>-1</sup> a<sup>-1</sup> in Germany.

The presence of keystone species strongly affects decomposition and nutrient dynamics. In particular, the train millipede *Parafontaria laminata* is widely dominant in soil invertebrate communities of central Japan, with its late-stage (from the 6<sup>th</sup> to final instar) larvae enhancing N availability by 69% (Toyota *et al.* in press). The enhancement of soil N availability in forest soils by late-stage larvae of this millipede can lead to changes in aboveground plant productivity. Earthworm casts stimulate the growth of most plant species in grassland soil (Zaller and Arnone 1999), but whether soil animals alter plant productivity under natural conditions in forest soils remains poorly understood.

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Previous studies on the effects of soil fauna on plant production have mainly been laboratory microcosm experiments, and they have produced mixed conclusions (Brown *et al.* 1999; Scheu 2003). Some studies found that soil animals increase plant production and nutrient utilization (*e.g.*, Setälä and Huhta 1991; Bardgett and Chan 1999), while others reported redundant or negative impacts of soil animals. One possible reason for this discrepancy is that soil animals have different effects on soil nutrient dynamics depend on their feeding type (Lavelle *et al.* 1997). Another possible reason is that differences in soil chemical composition and organic matter input to soil lead to changes in soil animal effects (Tiunov and Scheu 2004).

The rates of nutrient cycling are usually not constant, even in a mature forest ecosystem, due to the effects of processes such as seed masting (Selås *et al.* 2002) and periodic insect outbreaks. The 17-year periodic appearance of cicadas in North America provides a nutrient pulse to the forest soil resulting from the mass of carcasses, in turn increasing foliage N content and seed mass (Yang 2004). Despite these temporal differences in nutrient dynamics, many studies assume links between plant growth and decomposition processes on a forest floor in the short-term.

Populations of *P. laminata* have a synchronized life cycle and undergo simultaneous molts at particular stages according to seasonal temperature rhythms (Fujiyama 1996). The larvae live in the soil for 7 years (Fig. 1a, b) before they reach the adult stage (Fig. 1c). Their population consists of only a single age cohort, so adult swarming is observed at 8-year intervals (Niiijima and Shinohara 1988). The huge abundance and synchronized cohort of *P. laminata* provide a good opportunity to investigate the soil-animal contributions to nutrient dynamics at the forest floor (Hashimoto *et al.* 2004; Toyota *et al.* 2006). Due to their heterogeneous abundance within the same region in forest soil, the effects of *P. laminata* on plants can be distinguished, even under field conditions.

The train millipede *P. laminata* can enhance plant production in two major ways. First, changes in soil N availability through millipede activity affect plant production. Late-stage larvae enhance N mineralization in soil when millipede abundance is high (Toyota *et al.* in press). By contrast, adults contribute to transforming plant litter into soil, but do not increase N availability in the adult phase. Due to differences in soil N dynamics with developmental stage, the larvae and adults may affect plant productivity differently. Second, carcasses of adults contain higher concentrations of available phosphorus (P) for plant (Toyota, unpublished data). Since forest production is usually limited by P availability in soil (*e.g.*, Crews *et al.* 1995; Vitousek and Farrington 1997), the P supplied from their carcasses to the forest floor after the death of adults will result in increased plant production and changes in leaf quality.

Here, we studied how aboveground production can be affected by soil animal abundance and developmental stage. Effects of the train millipede were estimated to compare production between natural low-abundance and high-abundance millipede plots in the field. To test whether they temporally have different effects from late stage larvae to after the death of adults, the periods examined for estimating plant productivity were the 2 years before and after the adult active year, over a total of 5 years. Annual herbaceous plants should detect such temporal effects easily. In this paper, we tested the following two predictions: late stage larvae enhance leaf N content and production in the herb layer, and

after adult death, the millipede decomposition increases herbaceous annual plant production and leaf P content. Specifically, we examined the effects of the millipedes on the productivity of annual dwarf bamboo, which dominates the undergrowth of temperate forests in Japan.



Fig. 1. The train millipede, *P. laminata*, in the soil as (a) a 6<sup>th</sup>-instar larva, (b) 7<sup>th</sup>-instar larvae, and (c) on the forest floor as an adult.

## 2. Materials and methods

### 2.1 Study site

We established research plots at four different field sites in larch forests of Mt. Yatsugatake in Yamanashi Prefecture, central Japan (1350–1400 m above sea level, 35°54'12–46"N, 138°20'32"–24'03"E). The plots comparing low- (reference) and high-abundance areas of the train millipede were carefully chosen to avoid differences in soils, vegetation, and topography among plots. This region is characterized by a cool-temperate climate with mean annual precipitation of 1100 mm and mean air temperature of 10.6°C (Japan Weather Association 1998). The vegetation is a plantation forest of Japanese larch [*Larix kaempferi* (Lamb.) Sargent]. The sizes and ages of the larch in each plot are shown in Table 1. The shrub layer was sparse and was dominated by *Quercus crispula* Blume, *Prunus incisa* Thumb., *Ligustrum tschonoskii* Decaisne, *Symplocos coreana* Ohwi, and *Rhododendron obtusum* Planch. Dwarf bamboo (*Sasa nipponica* Makino) dominates the herb layer with *Osmunda japonica* at 50–70 cm height.

Plots	Latitude and longitude	Altitude (m a.s.l.)	Aspect and slope	Japanese larch			
				Planted in	Canopy density (ind./ha)	Average height (m)	Average DBH (cm)
L1	35° 54' N, 138° 20' E	1350	S16E, 13°	1952	950	17.5	20.4
L2	35° 54' N, 138° 21' E	1360	S42W, 18°	1951	1100	19.4	21.5
H1	35° 54' N, 138° 23' E	1400	S52E, 20°	1961	800	14.6	19.4
H2	35° 54' N, 138° 24' E	1390	N72E, 24°	1961	750	15.6	21.8

Table 1. Location of the study plots and abundance of the larch trees.

The organic layer on the forest floor is mainly composed of larch foliage mixed with larch twigs and bamboo stalks and leaves. The soil type is a well-developed aggregate structure of Andosols (FAO *et al.* 1998). About 50% of the total soil C at 0–100-cm depth was stored in the surface 10 cm, and about 75% was in the upper 0–30 cm (Morisada *et al.* 2002). Volcanic material was deposited after eruptions of Mt. Yatsugatake from 1,300,000 to 10,000 years before present. After that, forests had expanded. In the region around the study plots, natural larch forests remain, and natural larch regeneration at the early stage follows wildfires. The vegetation was fired artificially in around 1900 (Suka, 2008). In another disturbance, an extraordinarily strong typhoon passed through this region in 1959.

In October 1998, the population of *P. laminata* at this site consisted of only 6<sup>th</sup> instar larvae (Fig. 1a), which subsequently molted and became 7<sup>th</sup> instar larvae (Fig. 1b) in August 1999. Adults emerged in late August 2000, and swarming on the forest floor was observed from September (Fig. 1c); the adults died after egg deposition in July 2001 in the foothills of Mt. Yatsugatake (Toyota personal observations). The density of 6<sup>th</sup> instars ranged from 160 to 1088 m<sup>-2</sup> (mean ± SD, 485 ± 302 m<sup>-2</sup>; n = 3) in October 1998 (Toyota personal observation) and from 106 to 2156 m<sup>-2</sup> (619 ± 208 m<sup>-2</sup>; n = 10) in June 1999, in the high-abundance area. The density of 7<sup>th</sup> instar larvae in the high-abundance area ranged from 144 to 720 m<sup>-2</sup> (469 ± 240 m<sup>-2</sup>; n = 6) in April 2000 (Toyota *et al.* 2006). The average dry biomass of 7<sup>th</sup> instar larvae in the high-abundance areas (plots H1 and H2) was 15.7 g m<sup>-2</sup> and 12.2 g m<sup>-2</sup>, respectively, in October 1999, and the average dry biomass of adults reached 28.6 g m<sup>-2</sup> and 15.1 g m<sup>-2</sup>, respectively, in October 2000 (Hashimoto *et al.* 2004). By contrast, the average dry biomass of

7<sup>th</sup> instar larvae in the low-abundance areas (plots L1 and L2) was 3.8 g m<sup>-2</sup> and 1.0 g m<sup>-2</sup>, respectively, in October 1999, and average dry biomass of adults was 1.0 g m<sup>-2</sup> and 1.6 g m<sup>-2</sup>, respectively, in October 2000 (Hashimoto *et al.*, 2004).

## 2.2 Measurements

Four quadrats (1 × 1 m) were harvested in each plot to estimate the aboveground dwarf bamboo biomass in the period of maximal development of the dwarf bamboo vegetation (from late August to early September 1999, 2000, 2001, 2002, and 2003). The aboveground herb samples were dried at 40°C for 4 days and weighed. After removing the bamboo stalks, samples were homogenized. The 20-g subsamples of dwarf bamboo leaves were ground in a blender and used for N and P analysis. The N content was analyzed using a gas chromatograph (Sumigraph NC-95A; Shimadzu, Kyoto, Japan). The P content was analyzed using a Futura autoanalyzer (Actack, Alliance Instruments, Frépillon, France) for continuous flow analysis.

## 2.3 Statistical analysis

To test for differences in aboveground biomass, leaf N and P content through the sampling years, multiple comparisons among sampling years within a treatment were performed using the Tukey–Kramer test. Linear regression was used for correlation analysis between millipede biomass and leaf N and P content. All statistical analyses were performed using R 2.8.0 (R Development Core Team 2008).

## 3. Results

### 3.1 Temporal changes in aboveground production and leaf quality

The aboveground biomass in high-density train millipede plots varied significantly among years (H1:  $P = 0.037$ ; H2:  $P = 0.001$ ; Fig. 2). No significant differences among years were observed in low-density millipede plots (L1:  $P = 0.187$ ; L2:  $P = 0.09$ ). The observed pattern of the aboveground biomass in high-density plots tended to be high in 1999 (6<sup>th</sup> instar larvae). In plot H1, aboveground biomass in 1999 (6<sup>th</sup> instar larvae) was significantly higher than that in 2003 (2 years after adult death). In plot H2, the aboveground biomass in 1999 (6<sup>th</sup> instar larvae) and 2002 (1 year after adult death) was significantly higher than in 2000 (7<sup>th</sup> instar larvae) and 2001 (adult) (Tukey–Kramer,  $P < 0.05$ ).

The N content in leaves varied significantly among years in all plots. Temporal dynamics of the N content differed between high- and low-density plots. Similar to the aboveground biomass in high-density plots, the N content tended to be high in 1999 (6<sup>th</sup> instar larvae). By contrast, in low-density plots, the N content tended to be low in 1999 (6<sup>th</sup> instar larvae).

The P content in high-density plots varied significantly among years ( $P < 0.001$ ), but not in the low-density plots (L1,  $P = 0.45$ ; L2,  $P = 0.08$ ). The P contents in 2000 (7<sup>th</sup> instar larvae), 2001 (adult) and 2002 (1 year after adult death) were significantly lower than that in 1999 (6<sup>th</sup> instar larvae) and 2003 (2 years after adult death) in both plots H1 and H2 (Tukey–Kramer,  $P < 0.05$ ).

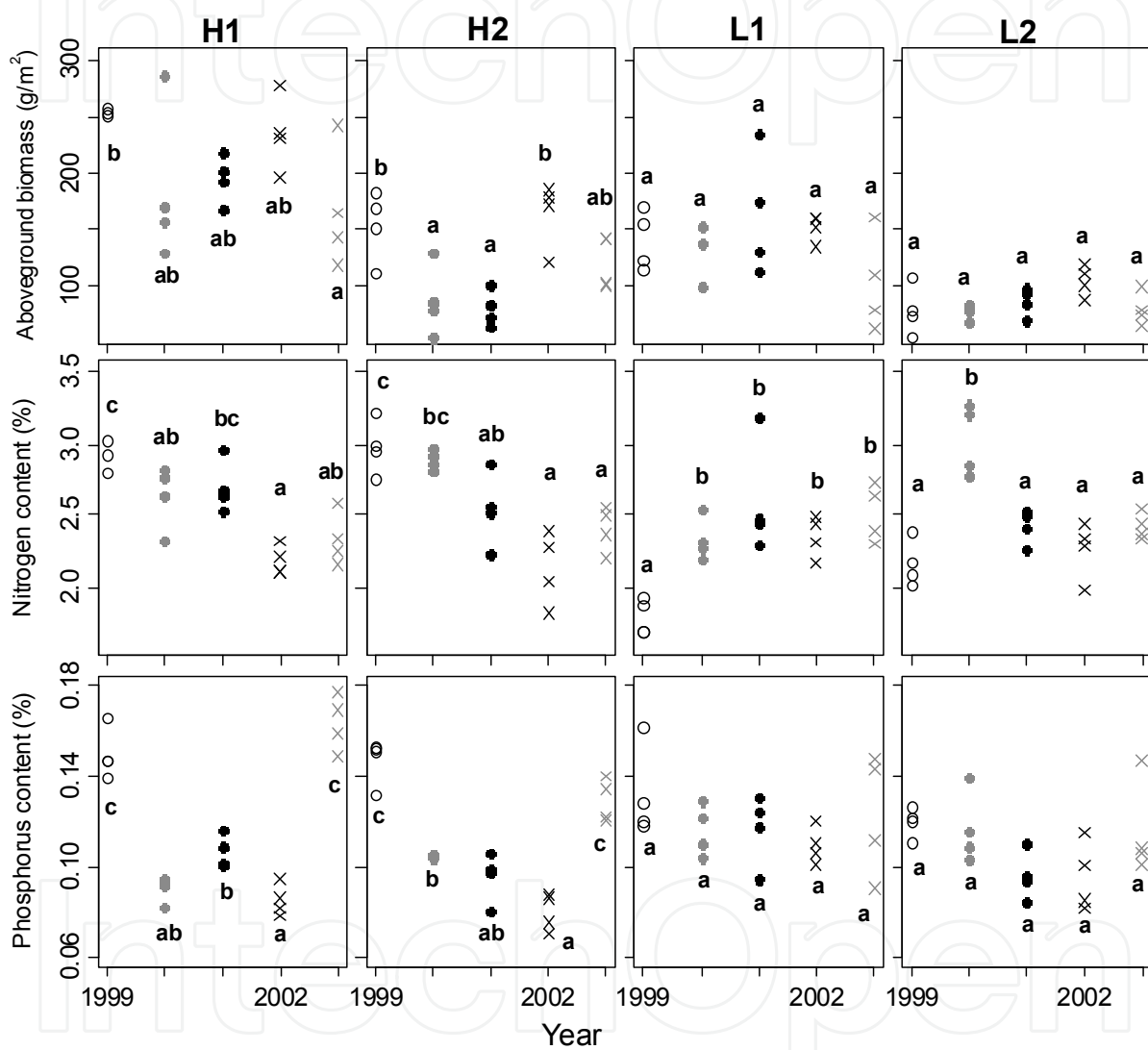


Fig. 2. Temporal variation in the aboveground biomass, nitrogen content, and phosphorus content with developmental stage: open circles, 6<sup>th</sup>-instar larvae; grey circles, 7<sup>th</sup>-instar larvae; black circles, adults; and crosses, after the adult period. The same letter indicates no significant difference among years based on the Tukey-Kramer test ( $P < 0.05$ ).

### 3.2 Effects of the train millipede on leaf quality

The N content of leaves was closely positively correlated with 6<sup>th</sup> instar larval biomass in 1999 (Fig. 3), but not in other years (Figs. 3, 4). The P content was positively correlated with 6<sup>th</sup> instar larvae biomass in 1999 (6<sup>th</sup> instar larvae) and adult biomass in 2003 (2 years after adult death). By contrast, it was negatively correlated with the final instar larvae biomass in 2000 (7<sup>th</sup> instar larvae) and adult biomass in 2002 (1 year after adult death).

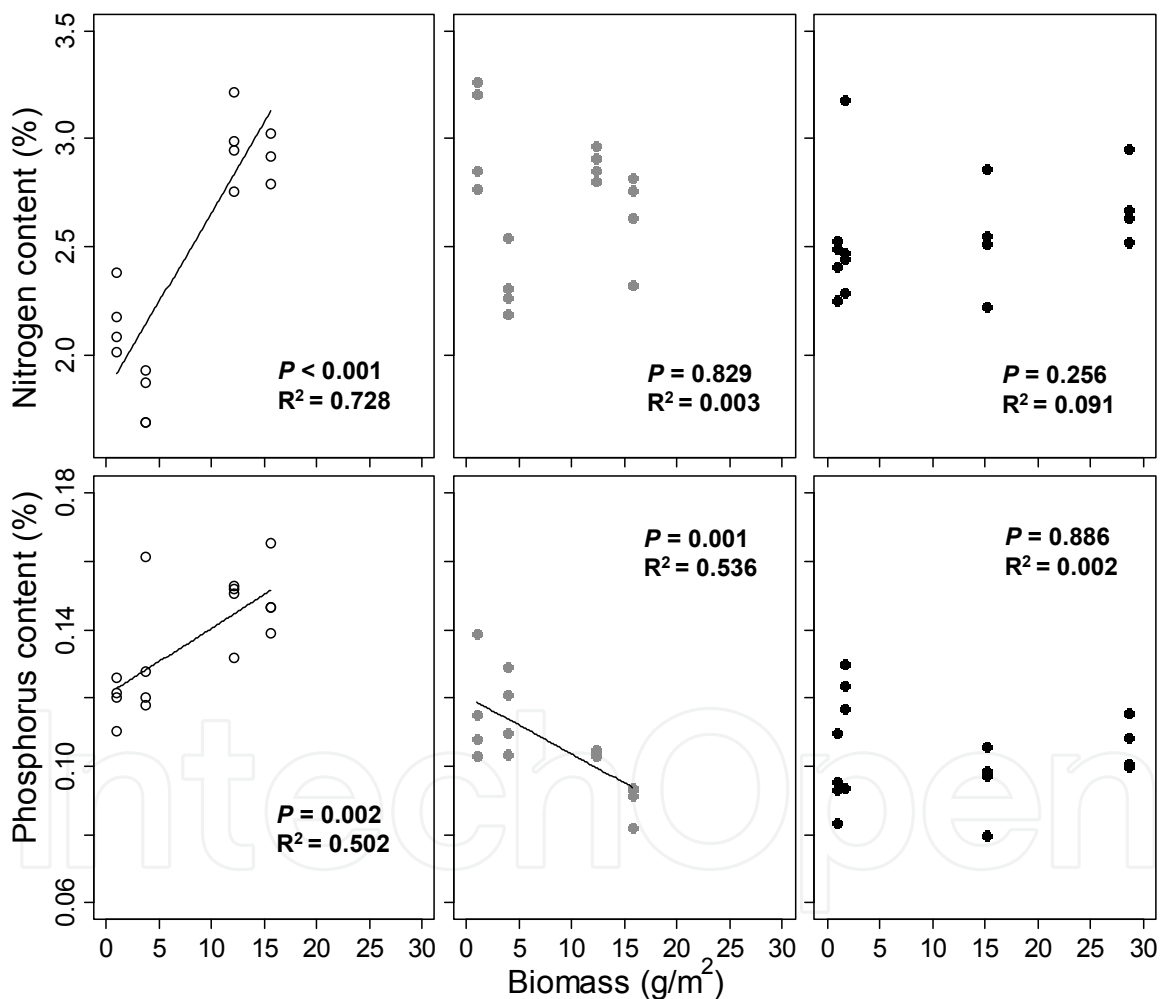


Fig. 3. Developmental stage-dependent effects of the millipede on leaf nitrogen and phosphorus contents: open circles, 6<sup>th</sup>-instar larvae; grey circles, 7<sup>th</sup>-instar larvae; and black circles, adults. Solid lines are significant linear regressions.



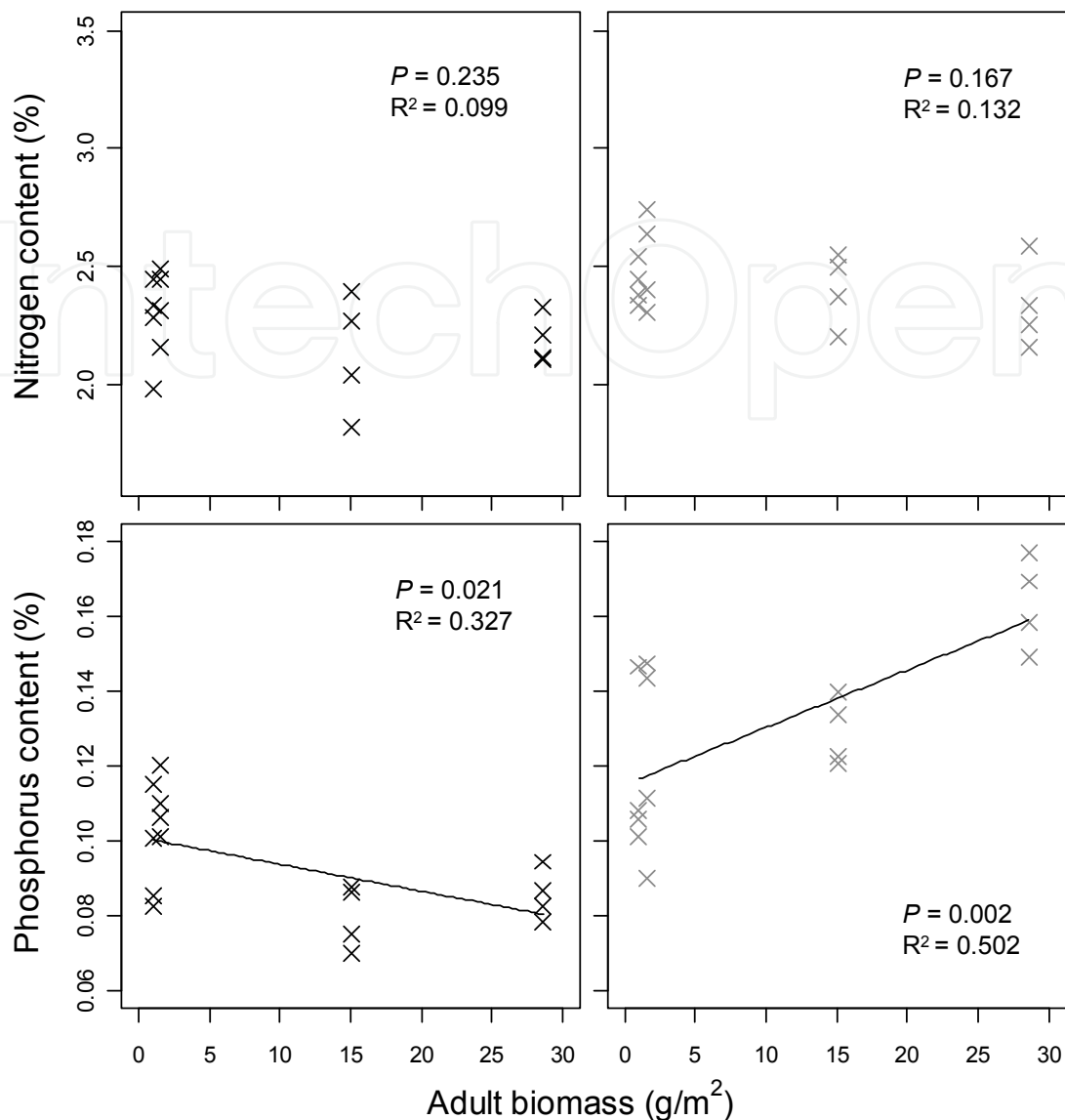


Fig. 4. Effects of adult biomass after adults died on the leaf nitrogen and phosphorus contents. The black crosses indicate 1 year after the adult period. The grey crosses indicate the 2 years after the adult period. Solid lines are significant linear regressions.

#### 4. Discussion

Our results show that temporal changes in dwarf bamboo production and leaf P content occur in plots with high densities of the train millipede, but not in low-density millipede plots. We found that the effects of the millipede on plant leaf N and P content differed with millipede development stage. In agreement with our hypothesis, 6<sup>th</sup> instar larvae had positive effects on plant production, N and P contents in leaves. In contrast to our hypothesis, the millipede had no effect on dwarf bamboo production and leaf quality during the adult phase, negative effects on the P content for 7<sup>th</sup> instar larvae and 1 year after the adult phase, and positive effects on the P content in 2 years after the adult phase. The contribution of the millipede to plant growth is therefore twofold. Here, we discuss factors promoting the close relationship between plants and millipedes.

#### 4.1 Temporal differences in production and nitrogen

Observed temporal patterns in production and N content of dwarf bamboo leaves were related to soil N availability in this forest. Increases in soil N availability for plants by 6<sup>th</sup> instar larval activity (Toyota *et al.* in press) immediately resulted in stimulation of plant biomass and N content in leaves. Under low N availability conditions during the adult phase, plant growth and N content did not increase. These patterns suggest that N limitation may occur in these forests and that millipede larvae can alleviate N limitation in the forest soil system.

#### 4.2 Changes in phosphorus content

Leaf P content increased with the incremental increase in the millipede biomass of 6<sup>th</sup> instar larvae (Fig. 3). Consequently, the larvae would provide not only available N but also P. However, during the 7<sup>th</sup> instar, the millipede reduced the leaf P content (Fig. 3). Arbuscular mycorrhizal fungi (AMF), which have a critical role in P uptake by plants, are suppressed by N fertilization (Bradley *et al.* 2006). Similarly, the increase in soil N availability with 6<sup>th</sup> instar larvae would reduce AMF in the next year, so plants would utilize less P with the incremental increase in millipede biomass. Furthermore, 7<sup>th</sup> instar larvae may alter soil chemical and physical conditions for the following reasons: (1) excess P consumption by 7<sup>th</sup> instar larvae might occur to create the adult body, which might result in a reduction of soil P availability, and (2) molting chambers of 7<sup>th</sup> instar larvae could physically hold P in the soil, lead to a substantial reduction in uptake of P by plants. The train millipedes make molting chambers from their own fecal pellets during summer, for several years the compact structure of the molting chamber of last instar (7<sup>th</sup> instar) larvae remains in the field at soil depths between 5 and 15 cm (Toyota, unpublished data). Nijjima (1984) suggested that the physical structure of soil is greatly altered by 7<sup>th</sup> instar larvae millipedes due to their large molting chamber (ca. 15 mm in diameter).

After 1 year of the adult phase, the previous adult biomass was negatively correlated with the leaf P content. These decreases in leaf P content can be attributed to the following three reasons. First, P absorption ability in the soil could be high in our forests because of soil engineering by adults (so the P uptake by plants would be low). Second, adult activity might reduce P utilization ability of plants. Adult millipedes were observed in soil to a depth of around 12 cm, near dwarf bamboo roots during the winter (Nijjima 1984). This adult activity in soil may damage ectomycorrhizal fungal growth and fine roots of plants due to soil disturbance, which could result in reduced P uptake by plants. Third, there would be fewer adult carcasses on forest floor in high-density millipede plots than adult abundance in the previous year (Hashimoto *et al.* 2004); consequently, phosphate from carcasses would be insufficient to increase the leaf P content.

After 2 years of the adult phase, however, the previous adult biomass was positively correlated with leaf P content. In the previous year, P was probably limited for plants. A lack of P availability leads to the preferential allocation of more resources to root biomass than to aboveground biomass as a plant response (Lynch 1995). Theory predicts a negative correlation between root allocation and aboveground growth rate. Observed low aboveground production in high-density millipede plots after 2 years of the adult phase is consistent with this prediction. Ryan *et al.* (2001) showed that organic acid was supplied

from plant roots under low P conditions, and found that roots dissolved iron- or aluminium-bound phosphates by organic acid. Consequently, available P may increase in soil by the activity of plant roots with high-density the millipede. Since plants would allocate carbon to the root system, damaged ectomycorrhizal fungi may recover. Eventually, incremental increases in available P will lead to increases in leaf P content. Further study is required to examine whether P forms and their availability for plants in soil differ according to the developmental stage of train millipedes.

## 5. Conclusions

By comparing plant production over time between areas with high and low train millipede abundance, we showed that plant growth and leaf quality were differently affected by millipede developmental stage. The plant aboveground biomass and leaf P content varied temporally when millipedes were very abundant but not when their abundance was low. Only 6<sup>th</sup> instar larvae have a significant role in enhancing both the leaf N and P content with increment in soil mineral N. Last (7<sup>th</sup>) instar larvae act in the opposite direction; they have a negative effect on the leaf P content. Adults have negative and positive effects after the adult phase probably due to their large impact on rhizosphere and the effects of their carcasses. The roles of the train millipede involve different types of feedback from soil to plant. This different response may lead to changes in competitive ability and in the species composition of the plant community. Although the interactions among plants, microbes, and animals in soil are quite complex, our results indicate that soil animals regulate plant productivity, even in mature forest ecosystems. This insight would be useful for understanding the aboveground-belowground feedback mechanism in the soil community.

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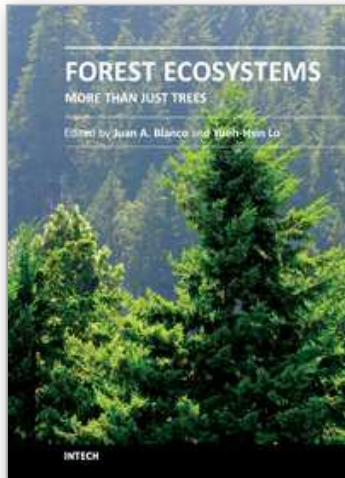
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## **Forest Ecosystems - More than Just Trees**

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The common idea for many people is that forests are just a collection of trees. However, they are much more than that. They are a complex, functional system of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself. This complexity produces combinations of climate, soils, trees and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component for the research in forest ecosystems, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, should also be the focal point in ecological studies and management plans to be carried out in forest ecosystems. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The research described here is not just on trees and is focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but are equally important to maintain the diversity, function and services provided by forests. The first section of this book explores the structure and biodiversity of forest ecosystems, whereas the second section reviews the research done on ecosystem structure and functioning. The third and last section explores the issues related to forest management as an ecosystem-level activity, all of them from the perspective of the other parts of a forest.

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