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The Periodical Millipede Determines Nutrient Cycling in a Larch Forest

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Abstract - The periodical millipede (*Parafontaria laminata*; Xystodesmidae) has been known its exact 8 years periodical swarming of adult high density populations in foothills of Mt. Yatsugatake, central Japan. Nutrient cycling, soil carbon and nitrogen pool, soil structure, bacteria and fungal biomass, and soil fauna were surveyed. Cumulative soil change and periodical plant growth change were suggested.

I. Introduction

Soil is fundamental to primary production, since it provides water and nutrient for plants. The soil functions; such as water holding capacity, nutrient reserve and source for plants in natural soil are maintained by soil organisms. Soil animals have been ignored for their soil function, instead, soil microorganisms (bacteria and fungi) were believed to be responsible for decomposition of soil organic matter. Soil microorganisms are able to produce enzymes which assimilate dead organic matter, however soil animals are not able to produce such enzymes [12]. However, soil animals enhance decomposition via interaction with soil microorganisms. They enhance fragmentation of dead organic matter, and help dispersal of microorganisms, thus encourage microbial activity [4, 15]. The animals change species competition of microorganisms by their selective feeding [6, 7]. Adding soil animals to soil with soil microorganisms increase microbial activity, hence nutrient cycling in soil. Many studies have been done with manipulating soil food web in a mini-ecosystem (a pot with plant) (e.g. [9, 10]).

Contrasting to the clear results obtained by those pot experiments, there are few results which showed the relationship between soil animal community structure and plant growth in a field condition [16]. According to studies of a wide range of ecosystems, soil invertebrates mediate about 15% of the carbon and 30% of the nitrogen turnover [14]. Nevertheless, the importance of the activity of soil animals in the forest ecosystem has been underestimated, because the spatio-temporal scale of soil animals and trees is quite different; trees have longer life spans and their living unit sizes are far larger than those of soil animals. Therefore, due to their small scale, linking the species activity of soil animals to ecosystem processes is very difficult in forest ecosystems [1].

The periodical millipede (the train millipede) (*Parafontaria laminata*; Diplopoda, Xystodesmidae) has been known its exact 8 years periodical swarming of adult high density populations in foothills of Mt. Yatsugatake, central Japan. The periodical occurrence of a high density of the adult population of the train millipede provides us a good opportunity to observe an effect of animal activity on nutrient cycling, since millipedes play an important role in the decomposition of forest soils [2]. Nevertheless, it is difficult to clarify contributions of soil macrofauna under field conditions, because the density and distribution of these animals are highly heterogeneous. The microcosm method has been successfully used to observe the interactions between soil animals and microflora and the faunal effects on various soil processes [13]. Generally, macrofauna affect microorganisms biomass [17]. Therefore, the train millipede will not only change soil quality, litter and soil organic matter considerably, but also microbial activity.

Linking population/community ecology and ecosystem ecology is very important and urgent research theme, because 1) relation between biodiversity and ecosystem function should be understood for conservation of natural system [11], 2) biological interaction is probably responsible for global nutrient cycling [5]. Thus before we lose biological diversity by the human activity which is now influential to global nutrient cycling of carbon and nitrogen, the relationship between biodiversity and ecosystem function should be studied for various kind of ecosystem.

To link species activity to ecosystem consequence, we applied both population, community approach to soil animals, and at the same time, in a same place, we measured nutrient cycling together with plant response. Our hypothesis was that the periodical appearance of the train millipede in rather simple larix plantation will gave nutrient pulse at the time of adult emergence, thus 8 years cyclic system change will be observed.

II. Study sites and methods

A. *Study sites*

The study sites are located at Mt. Tennyo (35 ° 55'N, 135°23'E, 1400 m a.s.l) and Kannondaira (35°55'N, 135°20'E, 1360 m a.s.l), foothills of Mt. Yatsugatake, Yamanashi Prefecture, central Japan. According to our preliminary study, the train millipedes showed a very high density at Mt. Tennyo; however, at Kannondaira, the millipedes were hardly observed. Two replicate plots of 20 m x 20 m were established at each site for a total of four study sites named TA, TB (Mt. Tennyo), KA and KB (Kannondaira). The study sites were plantation forests of Japanese larch, *Larix kaempferi* (Lamb.) Carrière. Tree height was about 15m and 18m at Mt. Tennyo and Kannondaira, respectively. Dwarf bamboo, *Sasa nipponica* Makino et Shibata, dominated the shrub layer. Soil type was Andosol (FAO-UNESCO 1990) and the organic layer horizon (L and F layers) was 4 cm thick.

Fig.1. Swarming population of the train millipede (*Parafontaria laminate*) in a larch forest at Yanamashi Prefecture, September 28, 2000. Milliped body length is about 35 mm.

B. Ecosystem properties

Five 50 cm x 50 cm litter traps were put in each study site and litters in the traps were collected monthly from May through November in each year. The accumulated organic layer at each site was measured for 3 years from 1999 to 2001. The organic layer of each site was collected in August 1999, 2000 and 2001. The reason to collect in August was to avoid the influence of the increase in the organic layer by autumn litter fall. Four 50 cm x 50 cm quadrants were chosen randomly in each plot at each study site.

Tree growth of the larch at each four site was monitored using dendrometer. Diameter changes of 20 trees were measured every month during from April to November of 1998 through 2001.

C. Field population and density

P. laminata around Mt. Yatsugatake area moulted in August 1999 and became 7th instar larvae. After over wintering, they became adults in August 2000. The adults swarmed in autumn after the moulting (fig. 1). Swarming was observed during the night and during rainy or cloudy days. They started reproduction in the early summer of the next year and died after oviposition by August 2001. The adult lives about one year after the last ecdysis in a field condition.

Field population density of millipedes was surveyed using hand-sorting methods on October 1999 and 2000, respectively and on June 2001. Biomass of each stage was estimated by measuring the weight of about 100 individuals collected in the study site. Body weights were measured after they were forced to starvation for 5-6 hours to make their guts empty in the laboratory.

Fig. 2. Soil microcosm set at TB site.

D. Field manipulation – a linker of species to ecosystem

Soil microcosms composed of PVC pipe cylinders with an inner diameters of 15.5cm and a height of 30cm for a content volume of 2.9 L, and containing litter and soil with and without millipedes were incubated in the forest floor from May 17 to November 5, 1999 (174 days) and from April 24 to October15, 2000 (174 days). Litter and soil were separately taken from the study site of the accumulated larch litter layer and surface soil (depth 0-30cm). Stones, roots (>2mm), and macrofauna were removed by hand. After all larch litter and soil were homogenized separately, they were placed into the microcosm separately. Oi (5.59g dry) and Oe (8.36g dry) litters were introduced at the weight measured at the study site. The Oi and Oe layers were separately introduced in 2000; however, those layers were homogenized before introduction in 1999. After the homogenization of soil and litter, sub-samples were taken for analysis of soil moisture, carbon and nitrogen contents.

Millipede density was artificially manipulated into four levels each with six replications. The density of 6th instar larvae of sampled ranged from 160- 1088 m^{-2} in the study site on October 1998, 106- 2156 m^{-2} near the study site on June 1999 (Toyota unpublished data). In 1999, the four levels of densities were zero (control), 530 (Low density treatment), 1060 (Middle), and 2121 (High) m^{-2} corresponded the field density ranged of high and low levels. The number of individual of seventh instar larvae was 469± 240 individuals m^{-2} (Mean±SD), therefore the four levels were zero (control), half (Low), average (Middle, about 469 m^{-2}), and twice (High) of the study site density of 7th instar larvae on April 2000. In order to imitate the environmental conditions of the field including temperature, moisture, and rainfall, the microcosms were set in a forest floor, in a randomized block design of six replications. The upper end of each microcosm was covered with a mesh lid to allow the effects of free rainfall and gas exchange.

III. Millipede induced change in soil matter flow and nutrient cycling

The densities of the millipede were shown in Table I. Biomass obtained in TA and TB was extremely high. The density decreased during the study period, however there were increase in biomass because of individual body growth. Therefore, the biomass of the millipede showed a maximum in September 2000. Because juveniles are very small, and the millipede dominated in the soil fauna at each study site, there seems to be a sudden decrease of biomass on August 2001.

TABLE I

Average and SE Of Density and Biomass of The Juvenile and Adult Train Millipedes in The Study Sites (N=5).

	1999 Oct. (last instar larvae)		2000 Oct. (adults)		2001 Jun. (adults)	
	density (m^{-2})	biomass (g dry m^{-2})	density (m^{-2})	biomass (g dry m^{-2})	density (m^{-2})	biomass (g dry m^{-2})
TA	349	12.2	165	15.1	53±	5.3±
	±157	±5.5	±79	±7.2	29	2.9
TB	448	15.7	311	28.6	6±	0.6
	±174	±6.1	±178	±16.4	8	±0.8
KA	29	1.0	11	1.0		
	±17	±0.5	±10	±0.9	n.d.	n.d.
KB	109	3.8	17	1.6		
	±56	±1.9	±10	±0.9	n.d.	n.d.

*: Data from Hashimoto et al. (submitted)

Hashimoto *et al.* (submitted) showed that consumption of soil organic layer by the millipede happened in both 1999 and 2000, however they could not observe clear reduction of accumulated organic matter of forest floor. Both 7th instar juveniles and adults (8th instar) feed on both organic matter and soil. Matsuda (unpublished Master Thesis, 2003) showed that feces of adult millipede had intermediate carbon and nitrogen stable isotopic signature of litter and soil, hence the adults mixed litter and soil at feeding. Juveniles younger than 6th instar stay in mineral layer, thus they seem to be geophagous. Dioplopoda geophagy is very rare [3], however *P. tonominea,* a congeneric species to *P. laminata* was also reported to be geophagous. Both species distribute wide range in central to western Japan, therefore their effect on soil should not be ignored.

Soil carbon storage increased in the high density treatment of the microcosm experiment in 2000 (Toyota *et al.* submitted), and the millipede feeding behavior seems to be responsible for preserving carbon in their feces. Since carbon loss from the soil was observed at the control without millipede and the low density treatment, the millipede gave non-liner effects on soil carbon dynamics with increasing density.

Soil nitrate release was enhanced by the millipede both 6th and 7th juveniles (1999), and also by the 7th and adults (2000) (Toyota unpublished data).

IV. Scaling up the species activity to ecosystem consequence

The train millipede in the study area seems to be a key stone species which determines nutrient cycling between plants and soil. Fig 3 illustrates a hypothetical interaction between the millipede, larch, ectomycorrhiza associated with the larch and soil microarthropods. The soil microarthropods always dominate and are most important soil animals in boreal forest soils [8]. In this forest, the biomass of the millipede was extremely high especially at the time of adult appearance, therefore the millipede will exploit organic matter and gave destructive effect on habitat for the microarthropods (Kaneko unpublished data). At the adult appearance, the ectomycorrhiza will also be harmed by the feeding and moving activity of the millipede (Koide unpblished data). Food resource (organic matter) change and destruction of mycelial network may reduce host plant (larch) growth. Soil bacterial to fungal biomass was also affected by the millipede, and bacterial activity was enhanced by the high density of the millipede (Toyota unpublished data).

Carbon and nitrogen dynamics reflected the millipede activity. Probably the changes in nutrient cycling rate seems to be more than 30% increase in the year of 7th instar juveniles and adult appearance, plant will respond to the favorable soil condition. However the damage to the mycorrhiza and soil microarthropod will be strongest at the adult appearance, plant growth will be retarded for some years since the adult appearance.

During the years of juveniles from 1st to 6th instars, the millipede population may enhance nutrient cycling. These juveniles are geophagous and living in the soil down to ca. 20 to 30cm depth, thus soil aggregate formation and enhancement of microbial activity will be expected.

All these interactions caused by the high density train millipede population, which is composed of single age and synchronized occurrence in a wide area around Mt. Yatsugatake, will bring periodical larch tree growth.

According to our preliminary data, the larch growth peaked one year before the adult emergence and declined for four years before recovery. The high density of single species of soil macrofauna in a cool temperate forest is not normal [8], and it seems that the phenomena is in the state of outbreak. However, the analysis of the soil subsystem with the train millipede gives us an idea when considering species impact on ecosystem level.

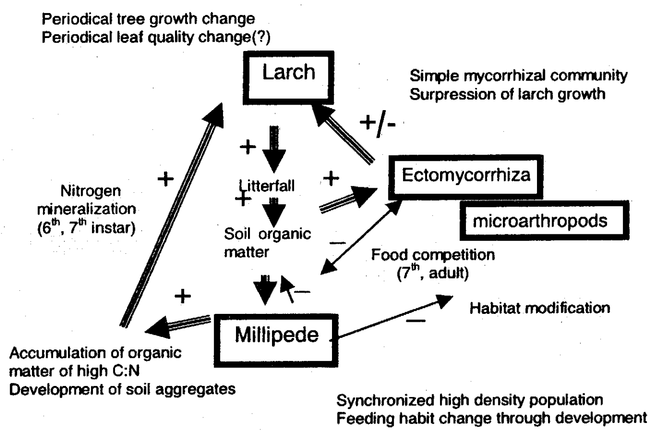

Fig. 3. Hypothetical interaction between the train millipede, larch, ectomycorrhiza and soil microarthropods, via direct and indirect ecological interacation.

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