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Nitrogen Cycling and Arthropod Population Outbreaks in Forest Ecosystems

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Abstract – Arthropod outbreaks have positive and negative effects on forest ecosystems through multiple pathways: Decomposition rate, nitrogen mineralization rate, proportion of the incident irradiation reaches forest floor, proportion of direct rainfall, mycorrhiza, tree response (defense and growth). In this project, litter fall supply, nutrient cycling, growth and defense of trees will be investigated in three systems: a larch-millipede (decomposer) system, a larch-defoliator system, and a beech-defoliator system. Adding to these field observations, artificial defoliation and insect defoliation experiments will be also carried out.

I. Arthropod Outbreaks and Site Dependence

Insect population outbreak is fascinating phenomena and has been studied by many researchers. Population cycles and spatial synchrony have been widely recognized in many forest insect species for some time [1, 2]. Another characteristics of insect outbreaks are the site-dependence. Kamata [3] introduced site-dependent insect population outbreaks on a beech, *Fagus crenata* Blume in Japan. There is a relationship between outbreaks of some defoliators and both altitudes and latitudes. In beech forests in Japan, four insect species often reach outbreak levels and cause severe defoliation. These are the beech caterpillar, *S. punctatella*, a beech sawfly, *Fagineura crenativora* Vikberg & Zinovjevthe (Hymenoptera: Tenthredinidae), a gall midge, *Oligotrophus faggalli* Monzen (Diptera: Cecidomyiidae), and the chrysomelid beetle, *Chujoa uetsukii* Chujo (Coleoptera: Chrysomelidae). These defoliations tend to occur at certain sites (fig. 1). The elevation range depends on the region, but the outbreak zone tends to be lower at higher latitudes because microclimate (temperature regime) is similar. Defoliation by *S. punctatella* occurs at the highest elevations and the most northern regions followed by *F. crenativora*. The gall midge, *O. faggalli*, and the chrysomelid beetle, *C. uetsukii*, cause severe defoliation at lower elevations. Population outbreaks of *C. uetsukii* occur in the most southern regions. Environmental factors relating to elevation, which include stand structure, natural enemies, competitors, host plant quality, and climate, are the likely cause of site-dependent outbreaks of these insects [3]. The causal factor generating site-dependent outbreaks probably depends on insect species because the outbreak area differs each other.

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 [4, 5]. Spectacular adult emergences, or "broods", occur at predictable (8-year) intervals. The situation is similar to periodical cicadas, *Magicalicada* spp. (Homoptera: Cicadidae) [6]. It is supposed that long life cycles and synchronized emergences of periodical millipedes allow them to escape natural control by predators. In emergence years, millipede numbers are so high that predators apparently can eat all they want without significantly reducing the population. Consequently, predators cannot build up in response because these millipedes are available as food only once every 8 years. It has been reported that there were several millipede broods in the central Japan [7, 8, 9]. Spatial synchrony of outbreaks between disjunct populations of the train millipede is also known. Population outbreaks of the train centipede also show strong site dependence because each outbreak derives from one brood. Outbreaks of each brood tend occur in the same area at every 8-yr interval.

II. Tree Damage by Insect Defoliation

Population outbreaks of forest defoliating insects often cause serious damage to host trees.

The impact insect defoliation will have on a particular forest stand depends on (1) how much defoliation occurs in the stand, and (2) how well the trees in the stand can tolerate that level of defoliation. The amount of defoliation a stand experiences depends on the population level of the defoliators in the area, the tree species composition. Stands that contain a high proportion of preferred food species are more likely to be defoliated than those with more species variability. Individual tree response to defoliation will be affected by the amount of defoliation and the tree's condition. The amount of defoliation depends on the size of the insect population in the stand and on the tree species. Light defoliation will weaken but usually not kill a tree. Heavy (more than 50/60 percent) defoliation of broadleaf deciduous trees will often cause them to lose their remaining leaves and develop a second set of smaller, less efficient leaves. Weakened, less vigorous trees are more susceptible to secondary pests such as bark beetles or root diseases. Repeated annual defoliation of broadleaf deciduous trees will ultimately result in the death of the tree. In contrast, conifers often die as a direct result of the initial heavy defoliation because they are unable to produce a second set of leaves. Stands containing low vigor trees and/or trees that have been stressed during the previous two or three years by such things as prior defoliation, drought, extensive timber

harvesting, or other site disturbances will not tolerate defoliation as well as unstressed stands, and will usually sustain some mortality.

III. Dendroecology: A Tool For Evaluating The Past

A variety of dendroecological techniques have been used to distinguish the effect of insect outbreaks and to reconstruct historic patterns of outbreaks [10]. Such analyses could be useful in determining periodicity of outbreaks, radial growth losses, and changes in stand structure.

This technique was based on the assumption that, if nonhost and host trees responded in a similar manner to climatic variations, then the differences between standardized ring-width chronologies of nonhost and host trees will primarily reflect nonclimatic environmental variations, such as effects of defoliating insects. In practice, this technique has been highly effective in reconstruction long histories, but imperfect because nonhost and host tree species do not have exactly the same response to climatic variations. Despite this limitation, outbreak histories of western spruce budworm (*Choristoneura occidentalis* Freeman) [e.g. 11], Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) [e.g. 12], larch sawfly (*Pristiphora erichsonii* (Htg.)) [e.g. 13] have been well defined.

A particular advantage of tree-ring reconstructions is that they provide the necessary temporal length for evaluating dynamical properties of insect populations characterized by long intervals between outbreaks. Robust statistical assessments of cyclical or more complex behaviors require time series with many iterations of outbreak and endemic phases. Adequate tests of association between population numbers and environmental factors, such as climate, may also depend on availability of time series with sufficient temporal length and spatial coverage.

V. Induced Response to Herbivory

A. Constitutive Defense VS Induced Defensive Response

Until recently, plant defenses were generally assumed to be constitutive, that is, always expressed in the plant. Constitutive defense change over evolutionary time and even during the normal maturation of an individual plant, but they function independently of damage. Recently, it has been recognized that many of the traits and processes that defend plants against herbivores change following attack.

B. Plant Defence: the dilemma... To grow or to defend?

All plants face a dilemma, which constrains their defensive strategies, their growth patterns, and their responses to herbivory: defence costs. "They must grow fast enough to compete, yet maintain the defenses necessary to

survive in the presence of pathogens and herbivores [14]." In this symposium, Koike [15] summarized effects of defoliation on the defense responses of deciduous broadleaf trees from a viewpoint of forest ecosystem stability: foliage of late-successional tree species is more defensive than those of early-successional species. Tree species that live under nitrogen-rich environments compensate insect damage by growth. On contrary, those living under nitrogen-poor conditions respond to herbivory by defense.

C. The Carbon-Nutrient Balance Hypothesis

The CNB hypothesis is really a variant of the much older 'overflow metabolism' hypothesis that supposes that secondary metabolites are produced to reduce abnormal concentrations of cellular constituents [16, 17]. When nitrogen limits plant growth, the CNB hypothesis predicts that carbohydrates will accumulate in plant tissues. This increased concentration of carbohydrates will lead, by simple mass-action, to an increased synthesis of carbon-based secondary metabolites such as phenolics and terpenes. Conversely, when light limits photosynthesis, all available carbohydrates will be shunted to growth, reducing the concentration of carbohydrates in plant tissues and lowering the carbon/nitrogen (C/N) ratio in plant tissues. This change in C/N ratio will lead to decreased synthesis of carbon-based secondary metabolites and, because of increased availability of nitrogen, to increased synthesis of nitrogen-containing secondary compounds such as alkaloids and cyanogenic glycosides.

An appealing aspect of the CNB hypothesis is that it makes specific predictions about patterns of allocation to plant secondary metabolite production. Nitrogen fertilization and shading are both expected to lower C/N ratios and lead to a decrease in carbon-based defenses. Although many experiments have yielded results that are consistent with this prediction, there are many others with results that are not consistent [e.g. 14, 18, 19]. With more than 200 studies having direct bearing on the hypothesis, it is now clear that CNB fails to correctly predict outcomes in a substantial proportion of cases [20, 21]. They concluded that CNB cannot predict the quantity of any single carbon-based secondary compound (CBSC) but 'can only make valid predictions concerning the total amount of carbon that can be allocated to CBSCs'. However, the appeal of the CNB hypothesis lay in its intended ability to predict concentrations of individual compounds [18, 22]. Despite the wide-ranging shortcomings of CNB, the hypothesis continues to be invoked in the design and interpretation of experiments.

D. A New Theory is Needed

Kamata et al. [23] found that, in an outbreak area, understory beech foliage became less defensive in the year following manual defoliation. Hikosaka et al. [24] also

found in pot experiment using current-year and 3rd-year-old seedlings that Plant nitrogen concentration significantly decreased just after defoliation but recovered to similar or higher levels than that of untreated plants at 3 or 6 weeks after following the defoliation. Foliar nitrogen concentration was also significantly higher in defoliated plants. Although these trends were different from previous observations for woody species, in which defoliation generally reduces both leaf and plant nitrogen concentrations, they were similar to responses to defoliation in herbaceous species. Leaf mass per total mass was positively correlated with plant nitrogen concentration but the relationship was significantly different between defoliated and untreated plants. When compared at the same plant nitrogen concentrations, defoliated plants had lower leaf mass per total mass. When focused on leaf and root that were newly produced after defoliation, however, the relationship between the leaf to root ratio and plant nitrogen concentration did not differ between defoliated and untreated plants. Concentrations of total phenolics and condensed tannins were significantly lower in defoliated plants, which are contradictory to previous studies. However, as in the previous studies, tannin concentration of foliage was negatively correlated with leaf foliar nitrogen concentration, suggesting that the amount of defensive compounds was controlled by carbon-nutrient balance at a leaf level. It is concluded that the carbon-nutrient balance is an important factor for biomass allocation and chemical defense. However, the effect of defoliation on carbon-nutrient balance in at an individual a plant level is not simple, probably leading to various responses of chemical defense to defoliation between species and between studies. A new theory is needed.

VI. Arthropods As Ecosystem Engineers

Arthropods are among the most abundant and diverse forms of life on Earth. They inhabit nearly every ecosystem and play a variety of ecological roles. In agroecosystems, pest and beneficial arthropods occur in soil, in water, in and on plants, and in the air. Arthropods are vital in decomposition processes and nutrient cycling. Herbivores may initiate the process of plant decomposition by removing or otherwise damaging plant tissue or creating routes of entry for plant pathogens. Senescing or dead plant material in or on soil is further fragmented by the feeding of detritivores such as springtails and mites, some of which are also sometimes classified as pests. These microarthropods reduce particle size and increase the surface area of decaying plant material making it accessible to soil microorganisms to further decompose it and return nutrients to soil. Herbivore activity may increase nutrient turnover rate, by making plant nutrients available directly to soil microbes via excretion of readily decomposable frass (insect feces) (Price, 1997).

VII. Arthropod Outbreaks and Nutrient Cycling

A. Impact of Decomposer Outbreaks on Ecosystem

As shown in Kaneko [5], millipede outbreaks induced change in soil matter flow and nutrient cycling. Both 7th instar juveniles and adults (8th instar) feed on both organic matter and soil. 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. This is a function of an ecosystem engineer that is well known to an earthworm. The microcosm experiment revealed that soil carbon storage increased in the high-density treatment of the millipedes. Kaneko [5] speculated that the millipede feeding behavior was 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-linear effects on soil carbon dynamics with increasing density. On the other hand, it is recognized that 6th–8th (adult) stages of the millipede enhanced soil nitrate release. Tree radial growth was compared in an outbreak site and a non-outbreak site [25]. In the outbreak site, radial growth rate was high in years of outbreak (year of adult stage) and the precedent year (year of 8th juvenile). In the same years, however, this tendency was not recognized in the non-outbreak area. Kaneko [25] concluded that periodical adult emergences, or "broods", enhanced tree growth by accelerating nutrient cycling.

However, under the assumption that the system is in equilibrium, temporal and rapid increase in decomposition rate does not seem to enhance a long-term average of plant growth because it does not seem that plants can efficiently utilize all parts of mobilized minerals and nitrogen increased temporally by the "eruption".

Negative effects of millipede eruption on forest ecosystems are pointed out [5]. The millipede may give destructive effects on habitat for the microarthropods. The ectomycorrhiza may also be harmed by the feeding and moving activity of the millipede. Food resource (organic matter) change and destruction of mycelial network may reduce host plant growth [5].

B. Impact of Defoliator Outbreaks on Ecosystem

Defoliations have been thought to have the following effects [26]:

1. They change the host's physiological status.
2. They cause increased litter fall, including leaves, twigs, and branches, as well as frass and insect carcasses.
3. More nutrient reach the soil litter system through leaching from trees.
4. Some trees die in the classes of weakened, old, or suppressed trees, and this changes the distribution of light, heat, nutrients, and other abiotic factors for the survivors, enhancing their growth.
5. Activity of soil microorganisms is stimulated and numbers increase, accelerating nutrient cycling in the system. The defoliating insects therefore play an important role in maintaining relatively high primary

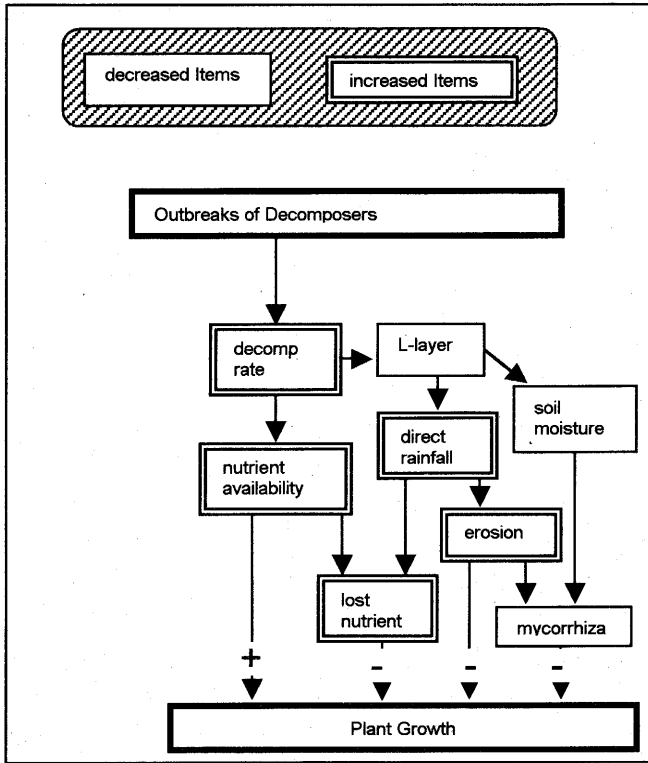


Fig. 1. Possible pathways of influence of decomposer outbreaks on plant growth and defense.

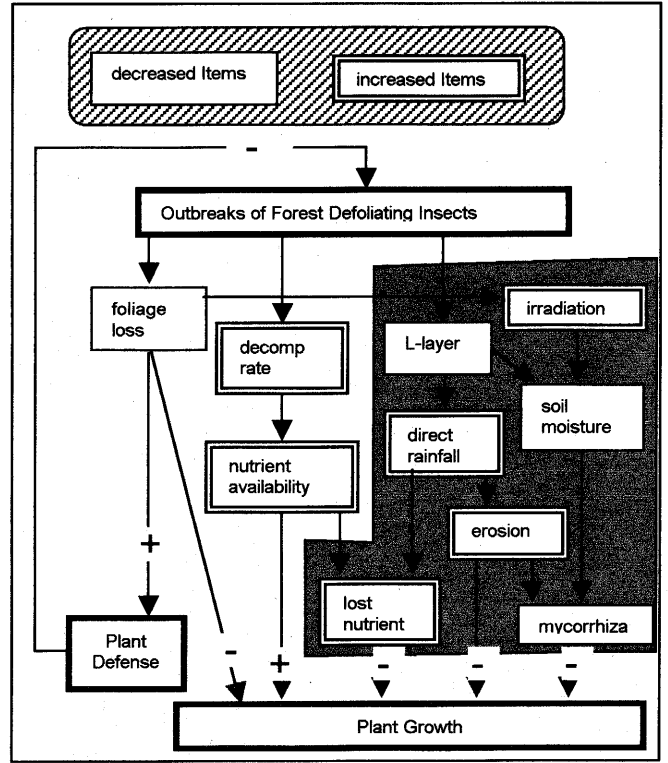


Fig. 2. Possible pathways of insect-defoliation influence on plant growth and defense. Factors in a gray polygon are not conspicuous during the period of intermittent level of insect grazing.

production and nutrient cycling.

However, during population outbreaks of defoliators, stories are more complex. Nutrient cycling is also accelerated during outbreaks of defoliators as well as decomposer. Not only forest canopy but also most of litter and humus layer disappear lost because of this accelerated rate of decomposition in successive years [27]. A greater proportion of the incident irradiation reaches forest floor because forest canopy coverage have decreased. The soil surface becomes dry, which may have negative effects on activity of soil microorganisms. Disappearance of forest canopy and litter and humus layer increases a proportion of direct rainfall, which may cause soil erosion. Here, it can be easily recognized that the response of plant growth to a degree of insect defoliation is non-linear. Moderate defoliation has a positive effect on plant growth by enhancing nutrient cycling and activity of soil microorganisms, in which factors enclosed in the right-side polygon are not prevailing. However, severe defoliation has a negative effect on plant growth through decreased activity of Mycorrhiza, enhanced soil erosion, and enhanced nutrient loss from the system such as leaching and runoff.

C. Insect VS Artificial Defoliation

Some obvious differences exist between artificial defoliation used in the numerous experiments and defoliation by insects. One of the great differences is that artificial defoliation by clipping foliage or shoots does not include possible effects of nutrient cycling from insect frass [26, 28-31], and saliva [15].

VIII. Where Do We Go From Here?

The title of our project is "nitrogen cycling and arthropod population outbreaks in forest ecosystems." Where do we go from here?

TABLE I
Locations of Field Experiment

| Site | Plant | Arthropod | Place |
|------|-------|------------|--------------------------|
| A | Larch | Decomposer | Yatsugateke Yamanashi |
| B | Larch | Defoliator | Mt. Iwate Iwate |
| C | Beech | Defoliator | Hachimantai Akita |

Three different systems were selected as study sites (TABLE I). In site A, interaction between plants and

decomposers will be investigated using a larch-millipede system. Nobuhiro Kaneko and his colleagues (Yokohama National University) have collected long-term data of millipedes. In site B, effects of insect defoliation will be determined by a larch-defoliator system. Masatoshi Yui's group (Iwate Prefectural University) has controlled bird density by providing artificial nest boxes for > 10 years. Quantity of foliage consumed by insect defoliators has been less in plots where the number of birds increased by artificial nest boxes. In site C, located in natural beech forests, the tree-defoliator relationship will be studied using a beech-beech caterpillar system. Naoto Kamata (Kanazawa University) has been studying population dynamics of *S. punctatella* for 18 years. 18-yr data of the moth abundance and that of larval density is available. The insect density strongly depends on altitude.

In the three systems, common basic-research protocols will be conducted and compared:

1. Estimation of insect frass and leaf-litter supplied to forest floor.
2. Foliage properties, such as concentration of nitrogen, carbom, tannins, pehnolics, water contents, Rubisco, and so on.
3. Chemical characteristics of insect frass.
4. Analysis of tree radial growth.
5. Nutrient cycling (nitrogen mineralization rate, nitrification rate, nitrogen leaching).

These features will be compared between outbreak plot and non-outbreak plot (site A), between bird-introduced plot and a control plot (site B), and among plots allocated along with altitudinal gradient (site C).

In addition to these field researches, we will conduct several kinds of experiments:

1. Artificial defoliation experiments to test C/N balance hypothesis. Light intensity and nutrient availability will be controlled in these experiments.
2. Microcosm experiments to study effects of insect defoliation on plants. Levels of insect defoliation will be controlled by changing the number of caterpillars added to each of test trees. Trees growth and defense will be compared among, insect defoliation, artificial defoliation and control.
3. Microcosm experiment, in which the density of millipede will be controlled at several levels.

The final goal of our project is to promote a better understanding of possible pathways of arthropod outbreak influence on forest ecosystems.

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