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Altitudinal Variation in Beech Foliage Properties: With Special Reference to Insect Outbreaks and Nitrogen Cycling

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Abstract - The beech caterpillar, *Syntypistis punctatella* (Motschulsky) (Lepidoptera: Notodontidae), often causes serious defoliation in beech forests in Japan. Outbreaks of this species are typically restricted to a narrow range of altitude. Thus defoliated areas typically appear as horizontal altitudinal belts. This paper examines alteration of foliage quality following manual defoliation in relation to altitude. Foliage quality was highest at a plot where beech caterpillar populations reached outbreak levels both on manually defoliated trees and control trees. In the year following manual defoliation, foliage was more defensive on manually defoliated trees than on the control trees in four plots out of five. The only exception was a plot where *S. punctatella* reached outbreak levels. In this plot, foliage quality was highest on trees that had been manually defoliated in the previous year than on the control trees. Our results suggest that the foliage quality is one of the possible causes of site-dependent outbreaks of *S. punctatella*: During an increasing period, high quality food at outbreak sites promotes population growth of this insect. When beech trees suffer heavy defoliation in the non-outbreak areas, foliage quality deteriorates, which slows down *S. punctatella* population growth. In contrast, in outbreak areas, quality increases in the year following heavy defoliation, and this may promote population growth and outbreaks. A positive feedback process thus may operate among nutrient cycling, foliage quality and insect population growth. A fertilizing effect from herbivory was a proximate factor causing higher soil nitrogen availability in the outbreak area. A carbon-nutrient balance hypothesis or growth-differentiation balance hypothesis can explain this phenomenon. Carbon gain also appeared to be an important factor determining foliar nitrogen concentration.

I. Introduction

A. Population Outbreaks of *Syntypistis punctatella*

The beech caterpillar, *Syntypistis* (= *Quadricalcarifera*) *punctatella* (Motschulsky) (Lepidoptera: Notodontidae) is a foliage-feeding insect species that is associated with beech, *Fagus crenata* Blume and *F. japonica* Maxim., in Japan.

Outbreaks of this species are known to occur in the Honshu and Hokkaido islands of Japan [1] and to occur synchronously among different areas at intervals of 8 – 11 years [2]. The moth populations exhibit 8 – 11 year periodicity and are widely synchronized both in outbreak and non-outbreak areas [2, 3]. Based on our observations, the population density of the final instar of *S. punctatella* varied by a factor or more than 10,000.

B. Altitudinal Dependence of the population outbreaks

Syntypistis punctatella outbreaks tend to occur more frequently in beech forests in northern Japan than in southern Japan [1, 2]. Similar geographical variation in outbreak characteristics has been reported for voles in Hokkaido [4] and rodents in Europe [5]. Extensive population data to test the ecological basis of this phenomenon in *S. punctatella* are not available at present. At smaller scales, another site-dependent characteristic of *S. punctatella* outbreaks is that the insect defoliation tends to be restricted to a specific range of elevations [6]. These elevation ranges vary among regions, but the outbreak zone tends to be lower at higher latitudes; e.g. 300 – 500 m in southern Hokkaido (42°00'N) (Kazuo Tachi, personal communication), 600 – 800 m in Hakkohda (40°40'N) [7], 900 – 1100 m in Hachimantai (40°00'N) [1], and 1100 – 1300m in Hakusan (36°15'N) [8]. Defoliated areas are typically distributed horizontally in an altitudinal belt. This is closely related to the vertical distribution of the vegetation. For example, in Hakkohda (area A), beech trees are distributed in the range 400 – 1100 m [9]. A deciduous oak, *Quercus crispula*, is a predominant tree species at the low elevation limit of the distribution of beech, and subalpine coniferous species, such as *Abies* spp., are mixed with beech trees at the high elevation limit. The predominant species gradually changes from *Q. crispula* to *F. crenata* and from *F. crenata* to *Abies* spp. according to the altitude. *Syntypistis punctatella* outbreaks tend to occur in pure beech stands. Because population growth tends to be larger ($R > 4.4$) in outbreak populations than in non-outbreak populations [10], the factors determining the rate of growth are likely to be related to site dependence in population outbreaks. We explore here three hypotheses that could explain this site-dependent character of *S. punctatella* outbreaks. These three hypotheses are not mutually exclusive, which makes it difficult to test which one is the most plausible.

1. The diversity-stability hypothesis [11, 12]: Complex ecosystems are more stable than simple ones. Outbreaks tend to occur in simple ecosystems.

2. The resource concentration hypothesis [13, 14]: Insect outbreaks tend to occur in a monoculture because herbivores can reach their host easily and successfully in such an environment. Outbreaks of *S. punctatella* tend to occur in the altitudinal range where beech occurs in pure stands vs.

mixed with other species. Late-instar (i.e. 3rd – 5th) larvae of *S. punctatella* often fall on the ground accidentally or intentionally to escape from natural enemies and then climb up tree trunks to return to foliage for feeding. However, larvae apparently cannot distinguish among tree species until they reach foliage. When they climb non-hosts, they crawl back down on trunks, then climb up another tree. In pure beech stands, the probability of successfully locating food plants is higher than in the mixed stands, which makes the mortality lower.

3. Soil nutrient hypothesis [10]: We will explore this new hypothesis in the following section.

II. Soil Nutrient Hypothesis

Perennial plants resorb some parts of foliar nitrogen before natural abscission and so that it may be used in the following season. This nitrogen resorption rate tends to be higher in under conditions of low nitrogen availability [15, 16, 17, 18, 19]. Nitrogen concentration in leaf litter tends to be low in plants with high nitrogen resorption rates [20]. The rate of leaf litter decomposition tends to be low in nutrient-poor leaf litter [21], and this results in poor soil nutrient conditions. It can easily be understood that there is a positive-feedback loop among nitrogen availability in the soil, the nitrogen resorption rate before natural abscission, and the decomposition rate of leaf litter [22]. It is anticipated that the quality of foliage in plants with high rates of nitrogen resorption deteriorates greatly in years following severe insect defoliation; nitrogen concentration decreases greatly in the following years and it takes a long time to recover to ordinary levels because of high rates of nitrogen resorption of plants and low soil nitrogen availability. This great change in foliage quality could result in large fluctuations in herbivore density.

Because most of foliar nitrogen is used for Rubisco in protoplasts, foliage with a high nitrogen concentration can achieve a higher maximum photosynthetic rate. Foliar carbon is the main constituent of both physical and chemical defensive substances, i.e., cellulose, lignin, phenolics *etc.* Foliage with high carbon concentrations tends to be defensive against herbivores. In an environment with high nitrogen availability, plants tend to allocate more resource to growth than to defense.

We will consider the response of foliage characteristics to altitude. Temperature tends to be low at high elevations. At higher altitudes, low temperatures cause low rates of nitrogen mineralization and of nitrification. Therefore, soil nitrogen availability tends to be low at high elevations. Predicted characteristics of foliage are more defensive with a high C/N ratio. In contrast, foliage with high nitrogen concentrations can be expected to enhance photosynthetic ability in high elevations because the growing-season length for deciduous trees becomes short [23]. The realized relationship between elevation and foliar nitrogen was convex: i.e. foliar nitrogen concentration tends to increase with elevation, eventually reaching a peak and finally

decreasing higher elevations [24]. From low elevations to the peak, nitrogen use efficiency of plants increases with altitude because the foliar nitrogen concentration becomes high and because soil nitrogen availability becomes low. It is speculated that the peak is a limit at which plants cannot enhance their nitrogen use efficiency any further. Foliar nitrogen concentration tended to decrease above the threshold because of the limitation of nitrogen use efficiency.

III. Experiment to Test SN Hypothesis

A. SN Hypothesis and Outbreaks of *S. punctatella*

Kamata [10] found that the relationship between altitude and the foliar nitrogen concentration in beech showed a convex curve. Defoliation by *S. punctatella* occurred at elevations higher than the point where the foliar nitrogen showed a peak. The peak was the point that the soil transitioned from acid brown forest soil to dark brown forest soil. Conspicuous defoliations by *S. punctatella* were found in beech forests where the soil type was dark brown forest soil. Dark brown forest soil has characteristics of stronger acidity, lower levels of exchangeable base, and a slower rate of nitrogen mineralization than acid brown forest soil [25].

According to this hypothesis, population outbreaks of *S. punctatella* tend to occur in places where both foliar nitrogen concentration and nitrogen use efficiency are high. Because nitrogen availability in the dark brown forest soil is low and because beech has foliage with relatively high nitrogen concentration, nitrogen must be used efficiently by enhancing the nitrogen resorption rate before natural abscission. In the year following severe insect defoliation, nitrogen the deficit would be more severe and delayed induced defense would be stronger on plants that live on such an environment because insect defoliation deplete foliar nitrogen that would have to be reused in that year. Kamata [10] predicted that, in places where *S. punctatella* causes severe defoliation, the combination of better foliar quality during a period of population growth and stronger delayed induced defense following the outbreak would cause a greater amplitude of population fluctuation.

Kamata et al. [26] reported that most shade leaves were defoliated in the previous year of the peak population density of *S. punctatella* although many sun leaves were left. Because *S. punctatella* larvae prefer shade leaves to sun leaves, several features of shade leaves of beech trees were evaluated with respect to altitude before and after manual defoliation.

B. Materials and Methods

To test SN hypothesis, we conducted manual defoliation experiment on beech saplings in natural forests in Hachimantai, in which most recent severe defoliation by *S. punctatella* was recorded in 1981 and 1982 [1]. In 1993 and

2000 insect density reached a peak (Kamata unpublished). Peak densities were not sufficiently high to cause conspicuous defoliation.

Five plots were established in July 2000: No. 1 (600 m ASL), No. 2 (750 m ASL), No. 3 (890 m ASL), No. 4 (1050 m ASL), and No. 5 (1260 m ASL). Ten young understory trees (3–4 m at height) were selected in July 2000. Five trees among the ten test trees of each of the plots were manually defoliated on July 28 2000. In the following year, we sampled ten leaves that had not been fed on by any folivores from each of the test trees. The following properties of the foliage samples were determined: nitrogen concentration, water content, concentration of total phenolics [27], concentration of condensed tannins [28], and LMA (leaf mass per area). These properties were compared between manually defoliated trees and untreated test trees and among the plots. In 2001, the year following manual defoliation, all leaves on the test trees were photographed using a digital camera. Proportions of leaf area loss by insects were determined by analyzing the photos.

Five soil samples, each consisting of five sub-samples (ca. 200 ml), were sampled in May 2002. Soil nitrogen availability was determined by measuring NO_3^- , NO_2^- , and NH_4^+ using automatic ion analyzer (Bran+Luebbe Autoanalyzer 2).

Dry mass of fallen insect frass was measured with the use of frass traps. Five rectangular traps (1mX1m) made of cloth were spread out near the forest floor in four plots from mid-July to late August, when the final instar of *S. punctatella* appeared. The trap contents were periodically returned to the laboratory and dried in an electric drier at 60°C. Frass was separated from other debris, then weighed to the nearest 0.001g.

C. Results

On untreated trees, foliage quality was highest in plot No. 4, located in an outbreak area. The relationship of foliage quality with respect to altitude was convex. In the year following manual defoliation, delayed induced defense response was observed and foliage quality was deteriorated in plots except for the No. 4 plot. In plot 4 foliage quality improved in the following year.

Folivorous insects responded to the difference in foliage quality. Leaf area loss by defoliating insects was greater on trees with better foliage quality: in plot 4, where foliage quality improved in a year following manual defoliation, leaf area loss was greater on treated trees ($28.0 \pm 9.2\%$, $n=5$) than on untreated trees ($14.5 \pm 5.5\%$, $n=5$), but in plot 1 where foliage quality deteriorated following manual defoliation, the loss was greater on untreated trees.

NO_3^- tended to decrease in high elevation plots. However, NH_4^+ was convex with respect to altitude. Therefore soil nitrogen availability ($\text{NO}_3^- + \text{NH}_4^+$) was also convex with respect to altitude with a peak in plot 4.

The mass of insect frass falling to the forest floor was also convex with respect to altitude.

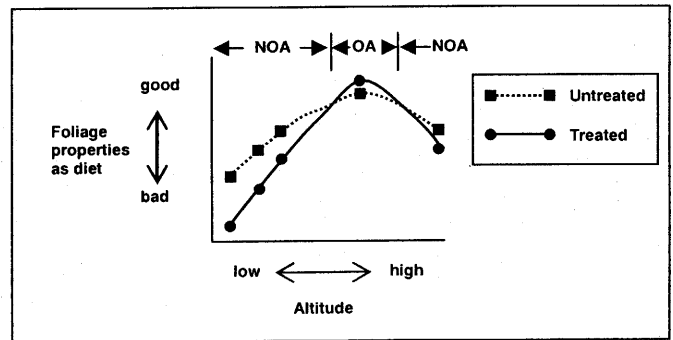


Fig. 1. Summary schema of a manual-defoliation experiment to test soil nutrient hypothesis. Foliage properties in the year following manual defoliation are shown for manually defoliated trees (treated) and control (untreated). NOA: Non-outbreak area, OA: Outbreak area.

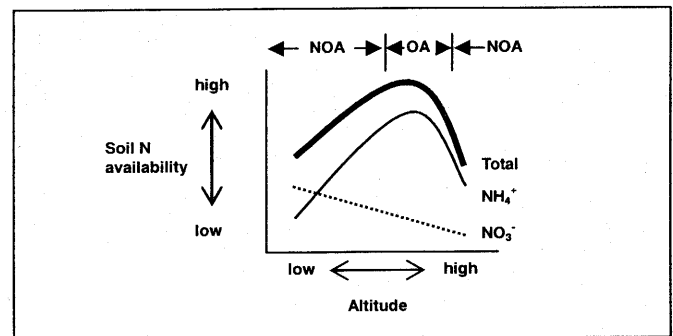


Fig. 2. Summary schema of relationship between soil nitrogen availability and altitude. Soil nitrogen availability was determined by NO_3^- , NH_4^+ , and $\text{NO}_3^- + \text{NH}_4^+$. NOA: Non-outbreak area, OA: Outbreak area.

D. Discussion

Contrary to our expectations from the SN hypothesis, foliage properties of beech trees in the outbreak area improved in the year following manual defoliation. In non-outbreak areas, foliage quality was lower than that in outbreak areas, and this can be expected to slow the rate of *S. punctatella* population increase. Foliage quality deteriorates by delayed induced defense of plants when population density of this insect increases, which will depress the insect population. However, in outbreak areas, higher foliage quality results in higher rates of insect population growth. Foliage quality improved in the year following severe defoliation, resulting in population growth.

Contrary to our expectations, soil nitrogen availability was positively correlated to foliage quality, i.e. both showed a peak in outbreak area. This was probably related to the fact that a large amount of insect frass was generated in the outbreak area. The rate of insect frass (fecal materials) decomposition is known to be greater than that of leaf litter,

and this enhances nutrient cycling and soil nitrogen availability [29]. It is likely that another positive feedback process than expected in the section II operated among nutrient cycling-foliage quality-insect population growth (Fig.3). Previous reports indicate that cattle grazing has a positive effect on both biomass production and species richness and is responsible for a substantial fraction of nutrient cycling in systems [30].

Thus, our working hypothesis (SN hypothesis) could not explain the observed altitudinal dependent outbreaks of *S. punctatella*. We must therefore seek factors causing altitude dependent outbreaks of *S. punctatella* outside the feedback loop.

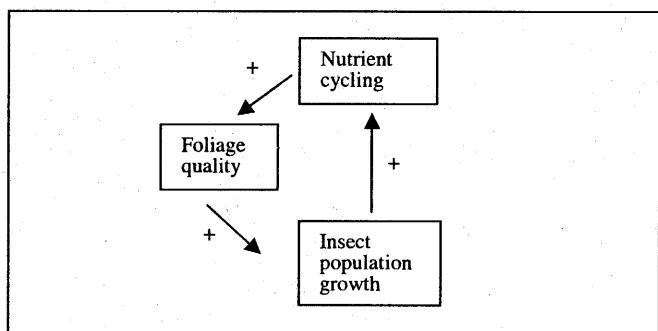


Fig. 3. A positive feedback loop recognized in a beech forest system by manual defoliation experiment.

Körner [30] proposed a theory of plant response to altitude: Alpine plants (in essence forbs) of polar mountains exhibit much higher leaf N concentrations than alpine plants in equatorial mountains, but are proportionally thinner [23, 31]. Consequently, N per unit leaf area changes little with latitude. This global "natural experiment" hints at some possible causes for the observed patterns in N concentration in alpine plants. Tropical-alpine species are not restricted by a short season and invest/accumulate more C per unit area (in fact, they contain on average 2.4 times as much carbon per area as arctic-alpine forbs). Accounting for day-length differences, their potential carbon gain per year (at equal photosynthetic capacity) would be ca. 2.9 times greater than in the arctic. This comparison suggests that the product % N in leaves and effective season length is maintained fairly constant latitudes. It appears that carbon rather than nitrogen per leaf area varies in response to seasonal length under such marginal life conditions. Greater carbon (and thus diluted N) concentration in leaves of tropical-alpine plants is associated with leaf life (C amortization), greater mechanical rigidity and reduced attractiveness for herbivores. Whatever limits mountain plants at even higher elevations, it does not seem to be a general limitation of metabolic capacity per unit leaf area by low levels of leaf nitrogen. There are no indications of any unusual mineral nutrient shortages in tissues of alpine plants. Concentrations in alpine forbs compare well with those in plants from fertile agricultural land at low altitudes. This may be related to the fact that in cold, infertile habitats

plants tend to grow slowly and build up higher concentrations of nitrogen by "luxurious consumption" [23, 32]. Direct growth limitation due to low temperatures, particularly during nights, may further restrict nutrient "dilution".

Comparing beech trees living in 600m ASL and those in 1250 m ASL, the difference in growing season length is > 1 month because the timing of both leaf flush and natural leaf abscission differ 2-3 weeks. Because of the limitation in the length of growing season and in temperature, carbon gain per year would be lower at high elevations. As Körner [30] pointed out, direct growth limitation due to low temperatures, may have further restricted nutrient "dilution" in high elevations.

In plot 4, carbon deficit was probably more severe than nitrogen deficit in the year following severe insect defoliation. C/N ratio of new leaves decreased. As a consequence, these leaves will be less defensive than those before manual defoliation. This can be expected both by carbon/nutrient balance hypothesis [34] and by growth/differentiation balance hypothesis [35].

The next question is why carbon deficit was more severe in trees in plot 4 (1050 m ASL) than plot 5 (1260 m ASL). Vegetation changes with altitude as follows: the predominant species changes from oak to beech, and beech to subalpine conifer. Beech is highly shade-tolerant and creates dense shade. In contrast, canopies of beech-conifer stands are sparse. Understories of beech-conifer stands are more light than those of pure beech stands. Light intensity in relation to stand structure probably caused the "reversion" in carbon gain between plots 4 and 5.

Another possible hypothesis to explain higher foliar nitrogen in high elevations is an atmospheric deposition hypothesis [36]. It has been reported that high-elevation forests receive high annual inputs of nitrogen via atmospheric deposition [37, 38, 39, 40]. Because nitrogen is deposited in forms readily available to plants NO_3^- and NH_4^+ , atmospheric deposition could produce phenotypic changes in tree allocation patterns like those typically associated with fertilization [23, 35, 41]

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