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Population dynamics of the beech caterpillar, *Syntypistis punctatella*, and biotic and abiotic factors

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Abstract The beech caterpillar, *Syntypistis punctatella* (Motschulsky) (Lepidoptera: Notodontidae), often causes extensive defoliation of beech forests in Japan. Outbreaks have often occurred synchronously among different areas at intervals of 8–11 years. Synchrony of outbreaks was considered to be caused by synchrony of weather. Populations of this insect exhibit periodical dynamics in both outbreak and nonoutbreak areas. Factors that might influence the population dynamics of the beech caterpillar were classified from the point of view of the natural bioregulation complex, which includes a coleopteran predator, *Calosoma maximowiczii*, avian predators, parasitoids, entomopathogenic fungi, and delayed induced defensive response (DIR) of beech trees. Because such periodic population dynamics are believed to be caused by one or more delayed density-dependent factors, delayed density-dependent mortality has been identified as a likely source of population cycles. The DIR and pathogenic diseases showed a high order of density dependence. An infectious pathogen, *Cordyceps militaris*, was considered to be the most plausible agent responsible for periodic dynamics of the beech caterpillar population because insect diseases were effective in cases in which the *S. punctatella* population started to decrease without reaching outbreak densities, but DIR was not. Conspicuous defoliation caused by this insect tends to occur at certain elevations, where forests are composed of pure stands of beech trees. I propose three different hypotheses to explain this phenomenon: the diversity–stability hypothesis, the resource concentration hypothesis, and the altitudinal soil nutrient hypothesis.

Key words Quasi-periodic outbreaks · Time delay · Density dependence · Insect disease · Delayed induced response · Site dependence

Biology, outbreaks, and density fluctuation

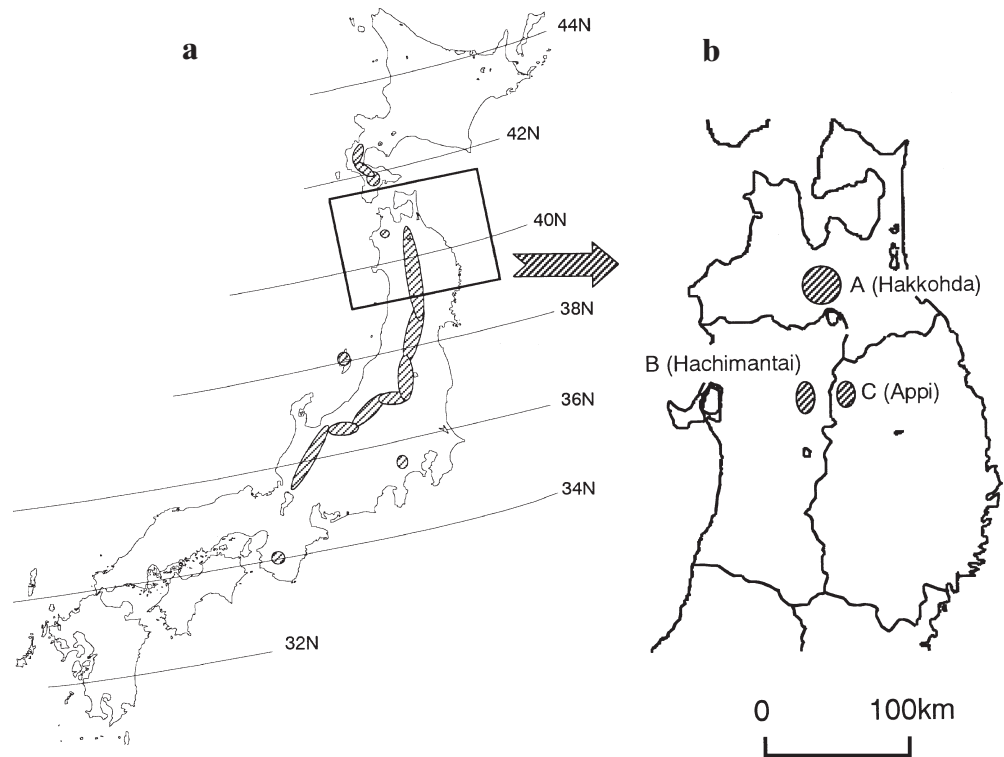
The beech caterpillar *Syntypistis* (= *Quadricalcarifera*) *punctatella* (Motschulsky) (Lepidoptera: Notodontidae), is a foliage-feeding insect species that is associated with beech (*Fagus crenata* Blume and *F. japonica* Maxim.) in Japan. *Syntypistis punctatella* is a univoltine species (Igarashi 1975), overwintering as pupae in the forest floor and emerging as adults from late May to late July. Fecundity typically ranges from 300 to 400 eggs (Kamata and Igarashi 1995a), which are laid in masses of 20–100 eggs on the backs of beech leaves. Larvae undergo three to four molts, which requires 30–60 days under typical field conditions. Final development is usually completed around early to mid-August.

Outbreaks of this species are known to occur in the Honshu and Hokkaido islands of Japan (Yanbe and Igarashi 1983) and to occur synchronously among different areas at intervals of 8–11 years (Liebhold et al. 1996). The moth populations exhibit 8- to 11-year periodicity and are widely synchronized in both outbreak and nonoutbreak areas (Kamata and Igarashi 1995c; Liebhold et al. 1996).

The final instar larval densities were investigated in three disjunct beech forests in northern Japan (areas A, B, and C; Fig. 1) during 1985–1994 (Fig. 2) (Kamata and Igarashi 1995c; Kamata 1998). In some plots of area A (Hakkohda), populations reached outbreak levels and beech trees were severely defoliated in 1989 and 1990. In area B (Hachimantai), there were records of past outbreaks but an outbreak did not occur during the research period. In area C (Appi), no outbreaks have been recorded. Although the outbreak characteristics of the three areas are different, the insect densities in these areas changed in similar ways (Fig. 2): populations in the three areas continued to increase synchronously during 1986–1990. In 1989 and 1990, populations reached outbreak levels ($>80\text{m}^{-2}$ in the final instar larvae), causing the complete defoliation of beech trees in several plots (A-1, A-2, A-3, and A-4) of area A. This type of outbreak is categorized as a typical gradation.

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Fig. 1. Approximate locations of historical incidence of defoliation caused by *Syntypistis punctatella* outbreaks since 1910 **a** and those of the research area **b**. Seven study sites were established in area A (Hakkohda), four in area B (Hachimantai), and three in C (Appi). Study sites within an area were located 2–20 km apart



The insect densities then decreased in 1991 in all the plots at all three areas, and those in area A have thereafter remained latent. However, the populations in areas B and C started to increase again in 1992. The population in area B reached a peak in 1993, and the population in area C continued to increase until 1994. During the period of complete defoliation, the final instar larval densities estimated by fallen frass ranged from 80 to 160 m⁻². The final instar larval densities were apparently limited by the biomass of the foliage in the canopy. The lowest density was recorded as 0.017 m⁻² at plot B-2 in 1986. Based on our observations, the population density of the final instar of *S. punctatella* varied by a factor of more than 10000.

Larval density increased from 1986 to 1990 in all areas and reached the outbreak level in some plots of area A in 1989 and 1990. A synchronous population decrease was observed in 1991. At a regional level among three study areas, a strong spatial density dependence was observed in the rate of increase of 1990–1991 (Fig. 3). At local levels within each area, however, spatial density dependence was recognized in area A but not in areas B and C (Fig. 3). Because the insect populations in area A of 1990 were in the outbreak phase, density-dependent mortality factors were effective. However, in areas B and C, the density of 1990 was not high enough for density-dependent mortality agents to operate effectively. A long and intense rainy season in the summer of 1991 is speculated to have been a cause of the concurrent population decrease that year (Kamata and Igarashi 1994; Kamata and Igarashi 1995c).

Population dynamics were simulated under a simple assumption that the density increased with a constant rate of increase (R) throughout the research period but decreased

only in 1991 with the coefficient of decrease (a); i.e., the rate of increase of 1990–1991 was aR . The result of the simulation was not shown for site A-1, where the density of *S. punctatella* started to decrease in 1989. During the increasing periods, the rate of increase (R) differed greatly among study sites (see Fig. 2). Because outbreak populations tended to have a larger R value (>4.4) than nonoutbreak populations, the factors determining this the rate of increase are likely to be related to site dependence in population outbreaks (see later section). However, the coefficient of decrease (a) in 1991 was similar at a local level within each area, about 0.115 in all the plots of area B and 0.040 in area C (Fig. 2), indicating that within these areas density-independent mortality factors were prevalent during the period of 1990–1991. A bad weather anomaly is speculated to be a major cause of similar population decrease at a local scale (= within area) and is discussed later in “Influence of weather.” In area A, however, where density-dependent mortality factors were effective, the value a varied greatly among study sites, and the insect densities after 1991 were kept lower than those expected from the R value (Fig. 2), indicating that the density-dependent mortality had time lags.

Periodicity of population outbreaks

Liebholt et al. (1996) characterized the periodicity of outbreaks by using historical records of the incidence of defoliation caused by the beech caterpillar, *S. punctatella*, in northern Japanese prefectures from 1910 to 1993.

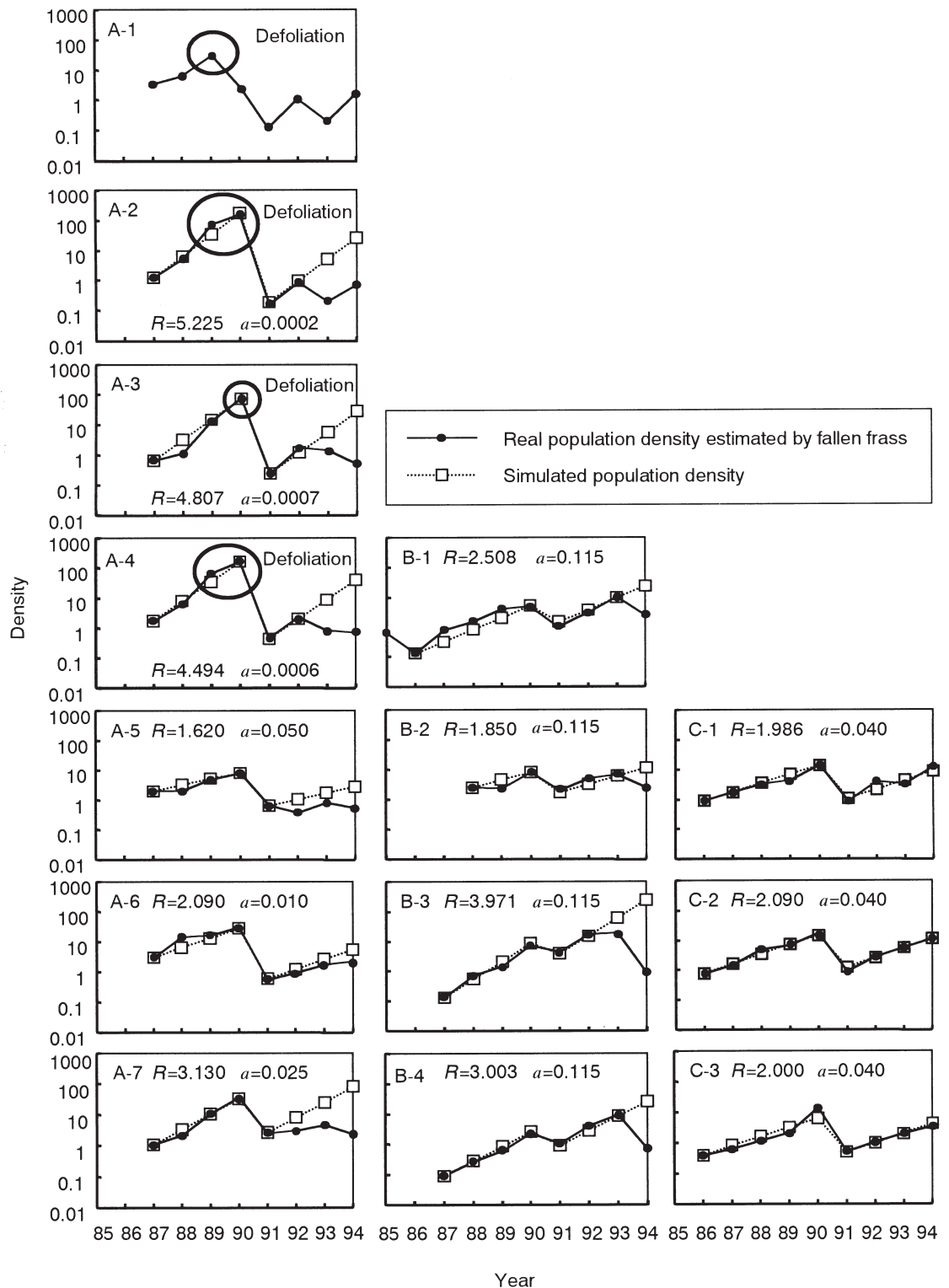


Fig. 2. Annual changes in the final instar larvae of *Syntypistis punctatella* in three disjunct beech forests in northern Japan. Area A, Hakkohda; area B, Hachimantai; area C, Appi. There are historical records of the incidence of defoliation caused by this insect in areas A and B but not in area C. In 1989–1990, insect defoliation was observed in the four plots of area A (A-1, A-2, A-3, and A-4). During 1986–1990, the population density increased synchronously in all the plots of these three locations. Concurrent population decrease was observed in 1991. Except for site A-1, the population dynamics was simulated under a simple assumption that the density increased with a constant rate of increase (R) throughout the research period but decreased only in 1991 with the coefficient of decrease (a)

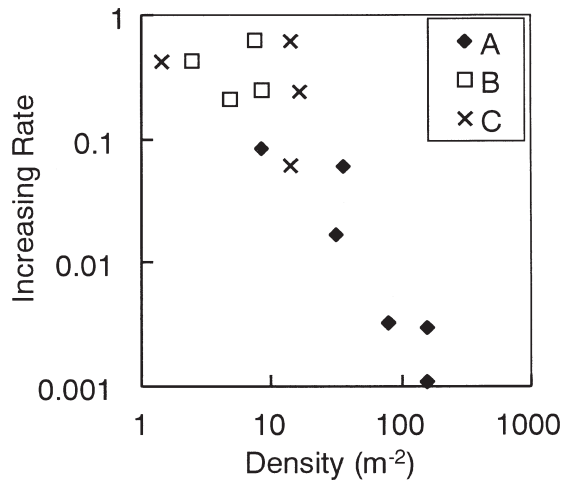


Fig. 3. Spatial density dependence during the period between the final instars of 1990–1991. At a regional scale, strong spatial density dependence was observed. At a local level within each area, spatial density dependence was not observed in areas B and C but was in area A. A dataset of site A-1 was eliminated because the population started to decrease in 1990

The periodicity was quantified using standard Box–Jenkins time series methods (Box and Jenkins 1976) as well as spectral analysis and simple Markov models. Statistical analysis of these records indicated the presence of periodic behavior with 8–11 years between outbreaks. This pattern can be observed in the actual series: every 8–11 years, an outbreak of *S. punctatella* occurred somewhere in Japan.

Two alternatives can be considered as a model to explain such a periodicity of population outbreaks. One possible model is that this insect population fluctuates with an 8- to 11-year cycle and the periodicity of outbreaks is the result of the population cycle. Theoretical studies have shown that 8–11 generation cycles may be caused by one or more mortality factors that are time delayed and density dependent (Varley 1947; May et al. 1974; Berryman 1987). “Time lags” or the order of density dependence may be closely related to the population cycles (Royama 1992; Bjornstad et al. 1995). Although second-order density dependence, which acts with a time lag of one generation and is effective for only one generation, can generate long-term cycles with 8–11 generations, the probability that a long-term population cycle is generated becomes greater when the order of density dependence becomes higher (Bjornstad et al. 1995). Another possible model is that there is never density-dependent mortality, except at very high densities, in which severe defoliation causes populations to crash. After that, the population could be on a “random walk” and this still might result in the appearance of quasi-periodicity. In this model, the time delay in density dependence is not essential to cause quasi-periodicity of outbreaks.

At this moment, I do not have enough real population data to judge which model is more plausible for *S. punctatella*. However, delayed density-dependent mortality has been identified as a likely source of population cycles both in theoretical systems and in many other species.

Factors influencing insect populations: order of density dependence

Overview of mortality factors during outbreak periods

Several natural enemies of *Syntypistis punctatella* have been reported. *Calosoma maximowiczii* Morawitz, a coleopteran predator, greatly increases in numbers during outbreaks and feeds on larvae and pupae of *S. punctatella* (Igarashi 1975; Igarashi and Suzuki 1980). Birds such as the long tailed tit, *Angithalos caudatus*, the jungle crow, *Corvus macrorhynchos*, and others were observed to feed intensively on *S. punctatella* larvae (Togashi 1984; Kamata and Igarashi 1990; Kamata et al. 1994). An entomopathogenic fungus, *Cordyceps militaris* Link, was speculated to be an important mortality factor that terminates outbreaks because great numbers of fruiting bodies of this fungus appeared in summers following outbreaks (Igarashi 1975; Igarashi and Suzuki 1980; Yanbe and Igarashi 1983). During and after outbreaks, many insect cadavers were observed scattered on the forest floor (Igarashi and Suzuki 1980; Yanbe and Igarashi 1983). Some of the insects were thought to have died of starvation, but most had been killed by entomopathogenic fungi or insect parasitoids (Kamata 1998). Many cocoons of tachinid flies were found in the soil in the year following *S. punctatella* outbreaks (Igarashi 1975, 1982; Igarashi and Suzuki 1980). Two tachinid flies, *Pales pavida* and *Eutachina japonica*, have been identified (Kamata 1998).

An insect predator, *Calosoma maximowiczii*: first-order density dependence

Calosoma maximowiczii Morawitz (Coleoptera: Carabidae) is a generalist predator that feeds on a wide range of lepidopteran larvae and pupae. This predator increased greatly during outbreak periods of *S. punctatella* although the density of this beetle was usually low (Igarashi 1975; Igarashi and Suzuki 1980). This situation is similar to the relationship between *Calosoma sycophanta* L. and the gypsy moth, *Lymantria dispar* L., in Europe and the United States (Weseloh 1990). Furthermore, *C. maximowiczii* is distributed throughout Siberia, China, the Korean Peninsula, the Japanese Archipelago, and Taiwan (Yamaya 1989). In places where *S. punctatella* does not occur, this beetle increases during outbreak periods of other lepidopterous species, such as the gypsy moth in Hokkaido (P.W. Schaefer, personal communication) and *Lymantria xyliina* in Taiwan (P.W. Schaefer, personal communication). Because *C. maximowiczii* merely increases greatly when the density of any lepidoptera increases during their “active seasons,” and because *S. punctatella* is the only lepidopterous species whose density becomes high in the summer in the beech forests in Japan (Kamata and Igarashi 1996), in the beech forests of North Japan, this beetle predator traced the density oscillation of *S. punctatella*. Thus, *C. maximowiczii* is thought to be one of the important natural enemies that impacts *S. punctatella* outbreaks. Adults of this beetle feed on larvae

of *S. punctatella* on beech trees and on the ground, and the larvae of this predator also feed on larvae and pupae of *S. punctatella* on the ground and in the litter layer.

The life history of *C. maximowiczii*, according to Kamata and Igarashi (1995b), indicates that adults can live for several years, feed and reproduce during the short period from July to August, and then reenter the soil in September and stay there until the next summer. From late July to early August, females lay eggs in the soil and the larvae live on the ground surface. The full-grown carabid larvae pupate in the soil and become adults in late September. The new adults undergo overwintering in the soil until the following summer. The larvae develop very quickly: the period to maturation was 17.6 days at 20°C and 10.0 days at 25°C (Katsuyuki Kohno, personal communication). This predator can complete larval development by utilizing large larvae of *S. punctatella*, which is the dominant lepidopteran species in beech forests but emerges for very short periods in summer (Kamata and Igarashi 1995b). Females lay more than 100 eggs (Katsuyuki Kohno, personal communication), and this fecundity is greater than that of most other carabid species that have been reported (Sota 1984). Kamata and Igarashi (1995b) showed that *C. maximowiczii* acted as a density-dependent mortality factor in both time and space. The beetles were caught by pitfall traps only in plots where the density of the final instar of *S. punctatella* was greater than 10m⁻². The numbers of both trapped adults and larvae of this beetle were strongly related to the caterpillar density. The agile flying capability and high reproductive potential of this hunter enabled it to respond to the caterpillar increase: i.e., by an aggregative response and a numerical response. The adults consumed more nutritious food and laid more eggs than usual, like some carabid beetles (Sota 1985).

Larvae completed their development by utilizing the abundant food. This mechanism can generate a 1-year time lag in the *S. punctatella*–*C. maximowiczii* system because a greater number of *C. maximowiczii* finished larval development at the year of peak density of *S. punctatella* and were thought to emerge the following year (Kamata and Igarashi 1995b). However, the beetle also decreased greatly in the following year when the beech caterpillar decreased. Although the reasons are not clear, the possible causes include adult dispersal from outbreak areas to nonoutbreak areas and outbreaks of natural enemies of *C. maximowiczii*. This predator–prey interaction alone cannot generate 8- to 11-year periodic dynamics of *S. punctatella* because its density dependence has no time delay; *C. maximowiczii* are likely to have merely tracked the density oscillation of *S. punctatella*. Furthermore, a numerical response was not observed in places where caterpillar density did not reach outbreak level.

Avian predators: Holling's type III functional response

Kamata et al. (1994) conducted bird censuses in four plots of area A (A-1, A-2, A-4, and A-7). The bird community was surprisingly stable despite great changes in caterpillar

density. In all plots from 1989 to 1994, the three predominant species were the narcissus flycatcher *Ficedula narcissina*, the coal tit *Parus ater*, and the great tit *P. major*. In breeding seasons, the number of species and the estimated number of individuals ranged from 13 to 22 per 15 ha and from 42.5 to 61.3 per 15 ha, respectively. These results indicate that little numerical response was recognized in the bird populations, even in outbreak periods of *S. punctatella*. The percentage of the beech caterpillar population preyed on by birds decreased when the caterpillar density became high (Holling's type III), although *S. punctatella* accounted for 75% of the diet of predatory birds during outbreaks. The decrease in predation at these caterpillar densities suggests that caterpillar densities could continue to increase once they exceeded a certain density threshold. According to preliminary experiments, the threshold seemed to exist at density levels of 1–10m⁻² for the final instar larvae of *S. punctatella* (Kamata, unpublished data).

Parasitoids

During outbreaks, percentage parasitism of insect parasitoids on the *S. punctatella* larvae was high (Kamata 1998). Insect parasitoids included two tachinid flies, *Pales pavidus* and *Eutachina japonica*, and one hymenopterous parasitoid, *Europhus larvarum* (Kamata and Igarashi 1994). The tachinid parasitoids caused higher mortality in places nearer the epicenter, indicating that these parasitoids operated as spatially density-dependent mortality factors. During *S. punctatella* outbreaks, in fact, the parasitoids showed stronger spatial density dependence than did entomopathogenic fungi. Ovipositional behavior of these two parasitoids differs greatly: *E. japonica* lay their eggs on the surface of *S. punctatella* larvae and hatched larvae penetrate into the host; *P. pavidus* lay microtype eggs on beech leaves, and parasitism is successful only when *S. punctatella* feed these eggs with beech foliage. Although parasitism of the two tachinid flies occurs during the larval stage, the moth is killed in the larval to pupal stages (Kamata and Igarashi 1994). There have been several reports that many puparia of tachinid flies were found in the soil in the year after *S. punctatella* outbreaks (Igarashi 1975, 1982; Igarashi and Suzuki 1980), so these flies also play important roles in terminating beech caterpillar outbreaks. However, a time delay in density dependence of these tachinid flies is not yet clear, because there are no reports on these parasitoids in decreasing phase and endemics of *S. punctatella*.

Several species of hymenopterous parasitoids have emerged from eggs of *S. punctatella* (Kamata, personal observation), but they have not been identified.

Insect diseases: high-order density dependence

There have been several reports that fruiting bodies of *C. militaris* appeared the year following *S. punctatella* outbreaks (Igarashi 1975, 1982; Igarashi and Suzuki 1980; Yanbe and Igarashi 1983), so it has been speculated that *C. militaris* is an important factor in terminating outbreaks

(Igarashi 1982; Yanbe and Igarashi 1983). Most of the *S. punctatella* collected in the field during outbreaks had been parasitized by entomopathogenic fungi or insect parasitoids (Kamata 1998). *Cordyceps militaris*, *Paecilomyces farinosus*, and *Beauveria bassiana* were the main species of entomopathogenic fungi. Mortality of old larvae ranged from 96.0% to 100%, suggesting important roles of these parasites in terminating *S. punctatella* outbreaks (Kamata 1998).

Because very high mortality (>99%) was caused by fungal diseases when lab-reared insect pupae were artificially introduced to the soils of severely defoliated beech forests (Kamata 1998), fungal disease could have given the outbreaks a finishing blow. Five entomopathogenic fungi (*Cordyceps militaris*, *Beauveria bassiana*, *Metarhizium anisopliae*, *Paecilomyces fumosoroseus*, and *P. farinosus*) were found to be mortality agents of pupae of *S. punctatella* in the soil, with *C. militaris* being the most prevalent (Kamata et al. 1997). In the year preceding the peak generation (1992 in area B), the survival rate was high (i.e., more than 75% of individuals survived) (Kamata 1998). *Cordyceps militaris* was found only in one plot where the field population density of *S. punctatella* was highest among the four study plots in area B, but the percentage mortality caused by the fungus was low.

In the year of maximum density (1993), the survival rate decreased greatly: the percentage survival was highest where the *S. punctatella* density was lowest and lowest where the field density was highest. This result shows that these pathogens caused high mortality in nonoutbreak areas as well as in outbreak areas. More than 70% of the artificially introduced pupae were infected with *C. militaris* in this plot. As for the field population of *S. punctatella*, many fruiting bodies of *C. militaris* were found on dead pupae there, and the density of *S. punctatella* pupae killed by *C. militaris* in that year was estimated at 2.5/m². Infection by *C. militaris* occurred in all the study plots. *Paecilomyces farinosus* caused the second largest mortality during that peak year. In 1994, when the density of *S. punctatella* decreased greatly, these entomopathogenic fungi still caused high mortality: mortality of introduced pupae caused by *C. militaris* was almost the same as that in the peak year. The mortality of artificially introduced pupae caused by *C. militaris* in the soil decreased gradually year by year; it was about 70% in the second year after the peak (1995), and about 40% in the third year after the peak (1996).

From the point of view of temporal density dependence, these fungal diseases acted as delayed density-dependent mortality factors (greater than second-order), and *C. militaris* was the most effective among them. The mortality caused by *C. militaris* also showed spatial density dependence: the mortality was highest where the population density was highest and lowest in the plot with the lowest caterpillar density.

The next question is why these entomopathogenic fungi can create a feedback time delay longer than one generation (= year) (greater than second-order density dependence). The time lag depends mainly on the fruiting bodies

or coremia of the fungi because these organs scatter their spores to the air in the summer following the infection of the insects by the fungi. *Cordyceps militaris* scatters ascospores from its fruiting bodies in July–August, and *P. farinosus* and *P. fumosoroseus* scatter their conidia from their coremia in June–September. These spores directly infect *S. punctatella* larvae on trees (Sato et al. 1998) and also increase the density of fungi in the soil (Kamata et al. 1997). This mechanism causes a 1-year time delay (i.e., second-order) in the insect–disease system. Another important feature relating to the higher-order density dependence of these entomopathogenic fungi is that they can live in the ground as soil fungi without infecting insect hosts (Watanabe 1994). Although the fungi increase less intensively in the soil than within the insects, fungal populations probably persist for several years in the soil.

At present, this entomopathogenic fungal complex appears to be the most plausible cause of periodic population dynamics of *S. punctatella*. Among them, *C. militaris* is the most important.

Delayed-induced response of host plant

As reported in a large number of insect–plant systems, a delayed induced defensive response was observed in the *S. punctatella*–*F. crenata* system. In the year following severe defoliation, the chemical and physical characteristics of the foliage changed greatly (Kamata et al. 1996a,b). Survival rate and body size of *S. punctatella* were low on foliage on trees defoliated in the preceding year(s). Reduced foliar nitrogen and increased tannin content were probably the main causes of the low insect performance. Leaves were less tough on defoliated trees than on controls. Leaf toughness reduces leaf consumption by some insects (Karban and Baldwin 1997). However, in this case, chemical deterioration masked the effects of this physical change. Two successive years of manual defoliation caused a stronger induced defensive response than did 1 year of defoliation. In the field, heavily defoliated beech trees did not recover their foliar nitrogen concentration even 3 years after defoliation (Kamata et al. 1996b); this is probably related to the fact that beech forests in Japan are ecosystems with low nitrogen availability (Kamata 1999). Although 84%–90% of total nitrogen is in the soil of beech forests, most of it exists in the organic form unavailable to plants (Katagiri and Tsutsumi 1978). The annual mineralization rate of organic nitrogen to the inorganic form in the soils of this ecosystem was estimated to be equal to only 1.8%–5.0% of total nitrogen in the ecosystem per year (Katagiri and Tsutsumi 1978; Ito 1991). Thus, inorganic nitrogen in the soil is only 1.2–1.3 times that needed for trees every year (Ito 1991).

The quantity, as well as the quality, of the foliage decreased in the year following manual defoliation; the total weight of leaves on a tree was less than one-half of that before treatment. Severe defoliation may cause a decrease of leaves the following year, and starvation may limit populations. According to the results of a manual defoliation experiment by Kamata et al. (1996a), following 1 year of

defoliation leaf biomass decreased to less than half the biomass before treatment. This finding indicates that canopy biomass may not be constant but instead may change in response to herbivore densities. During one outbreak, *S. punctatella* defoliated about 60% of the total canopy, and about 20% of beech trees were completely defoliated in the year before the peak density (Kamata and Igarashi 1996). Starvation was apparently an important mortality factor during the peak generation (Igarashi and Suzuki 1980). Defoliation reduced foliar biomass, and it may act as a negative feedback in this insect–plant relationship.

Delayed induced defensive response of beech trees could be a driving force in the cyclic population dynamics of *S. punctatella* because it introduces time lags into the negative feedback loops that regulate *S. punctatella* populations (greater than second-order density dependence). However, it is not likely to be an essential one, because effective delayed induced defense was not demonstrated in beeches from nonoutbreak areas although *S. punctatella* populations in these areas also showed a similar cycle as outbreak populations. Effective delayed induced defense was recognized in only the trees that had been more than 50% defoliated in the previous year when the density of the final instar of *S. punctatella* was greater than 70m^{-2} .

Changes in fecundity and quality of the fluctuating insect population

Variation in fecundity is an important factor that determines changes in population density. When population density increases, reduced body size and low fecundity can cause a decrease in the population growth rate, and this is one of the most important mechanisms of population regulation in some insect species (Klomp 1966; Dempster 1975). Body size changes are associated with many insect outbreaks. During a period when population density is increasing, body size and fecundity also increase, and when population density is declining, body size and fecundity decrease. This phenomenon is not restricted to outbreak populations. These changes in fecundity are considered to be important factors causing cyclic dynamics in some insect populations (Fischlin and Baltensweiler 1977; Myers 1990), and the negative effect of population density is maternally transferred (Ginzburg and Taneyhill 1994). In the years following outbreaks, *S. punctatella* females laid a high percentage of unfertilized eggs. Moths that had experienced outbreaks in their larval stages decreased 80% in size, which is thought to have been mainly caused by the food deficit during outbreak.

Because fecundity had a strong positive relationship with adult size (Kamata and Igarashi 1995a), it is estimated that fecundity decreased by about 30% in the outbreak population. In the generations following the outbreak, adult size gradually increased year by year. However, even in the 3 years after outbreaks, the adult size was still smaller than that before outbreaks. These results suggest that not only the food deficit but also other factors caused body size to decrease, because the moths would have regained their

former size in the next generation of the outbreak if only food deficit had caused the decrease in body size. Possible causes include the maternal effects hypothesis (Ginzburg and Taneyhill 1994) and a hypothesis in which delayed induced response of plants has a relaxation time of several years. *Syntypistis punctatella* eggs were collected from the three areas (areas A, B, and C) in 1994, 4 years after the outbreak in area A, and the insects were reared on beech trees in the three areas (two-dimensional 3×3 experiment) to examine the effect of location of foliage and insect populations (Kamata et al. 1996b). The pupal weight was significantly influenced by location of both foliage and insects, but their interaction was not significant, indicating that both deterioration of food and the locations of insects were responsible for the small adult size in the years following the population outbreaks.

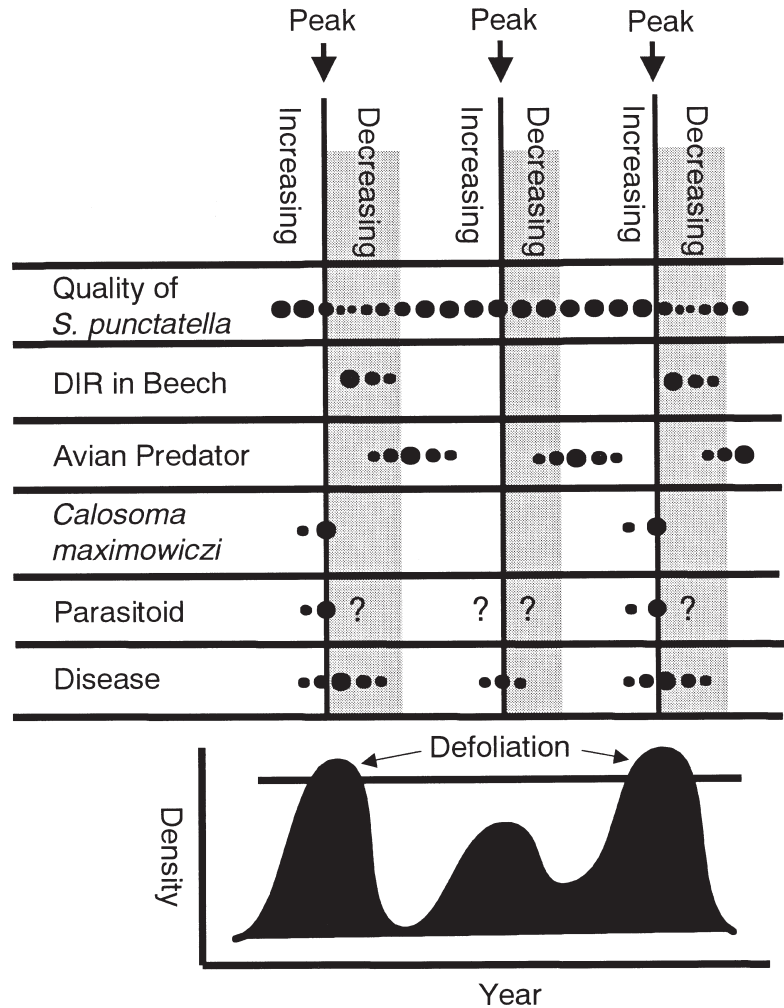
The sex ratio of light-trapped adults changed with the population density. A few females were caught during the endemic phase (% female, 0%–5%) (Kamata et al., unpublished data). The percentage of females increased gradually in the increasing phase. The percentage of females was 25% in 1990 (the outbreak year) and 20% in 1991 (outbreak generation). It is not clear whether the changes in sex ratio of light-trapped adults were caused by the changes in real sex ratio according to the population density or were merely caused by behavioral changes in the adults.

Natural bioregulation complex

The population dynamics of this insect showed periodicity in both outbreak and nonoutbreak areas. The infectious diseases, mainly *C. militaris*, were considered to be the most plausible factor for generating periodic dynamics of the beech caterpillar population because this acted as a high-order density-dependent mortality factor both in outbreak and in nonoutbreak areas.

Factors that might influence the population dynamics of the beech caterpillar were classified from the point of view of a natural bioregulation complex (Fig. 4). During outbreaks, a coleopteran predator, *C. maximowiczi*, and many parasitoids as well as entomopathogenic fungi were effective factors in terminating the population outbreaks of *S. punctatella*. In the years following outbreaks, entomopathogenic fungi and delayed induced defense of beech trees played an important role in depressing the population. These two factors had been effective for several years following outbreaks. Avian predators are also effective during such low-density periods. However, once these diseases and plant defenses became weak, the *S. punctatella* population started to increase. Although the population density in nonoutbreak areas increased synchronously with those in outbreak areas, the only mortality factor that effectively decreased the density was entomopathogenic fungi. As a result, the rates of population decrease in nonoutbreak areas were smaller than those in outbreak areas when the population started to decrease. The magnitudes of the population fluctuation in nonoutbreak areas (10^2 – 10^3) were also smaller than those in outbreak areas (10^3 – 10^4).

Fig. 4. A scheme for natural bioregulation of the population dynamics of *Syntypistis punctatella*. Delayed induced defensive response (DIR) of beech trees and insect diseases showed a high order of density dependence. Insect diseases were effective when the *S. punctatella* population started to decrease without reaching the outbreak density level, but DIR was not effective. Insect diseases seemed to be the most plausible factor responsible for *S. punctatella* cycles



Influence of weather and synchrony of outbreaks

Liebhold et al. (1996) also characterized the synchrony of quasi-periodic outbreaks by using historical records of the incidence of defoliation caused by the beech caterpillar in northern Japanese prefectures from 1910 to 1993. The periodicity was quantified using standard time series methods (Box and Jenkins 1976). Kamata and Takagi (1991) theorized that most populations of *S. punctatella* exhibit periodic dynamics but individual populations may only occasionally reach outbreak levels, which may explain why defoliation was not detected in every prefecture during each 8- to 11-year cycle. The onset of outbreaks typically varied by 1 or 2 years among different prefectures, but because this was small in comparison to the length of the cycle (8–11 years), the outbreaks were essentially synchronous. Although the presence or absence data analyzed by Liebhold et al. (1996) provided a very crude approximation of actual population densities, the hypothesis that disjunct populations of *S. punctatella* are synchronous is supported by the data in Fig. 2, which show that measurements of outbreak and suboutbreak population densities were highly synchronous among three disjunct locations sampled in

Aomori, Akita, and Iwate Prefectures during a 10-year period.

Determination of the effects of weather on insect population dynamics can be a complex task because much care is needed to avoid spurious correlations (Martinat 1987). The most common approach to investigating the effects of weather on insect dynamics is based upon the assumption that weather is directly associated with the release of populations to outbreak densities. The values of various climatic variables during years of increasing population levels are compared with values during other years. These studies often use climatic measurements in previous years to test the hypothesis that conditions in years preceding outbreaks are causally linked with population increases. This approach has been widely used to investigate relationships between weather and forest insect dynamics in species including the fall webworm *Hyphantria cunea* (Morris 1964), the western spruce budworm *Choristoneura occidentalis* (Thompson et al. 1984; Swetnam and Lynch 1993), the forest tent caterpillar *Malacosoma disstria* (Ives 1973), and the pine caterpillar *Dendrolimus superans* (Maeto 1991). Kamata and Takagi (1991) analyzed *S. punctatella* outbreak time series from Hakkohda Mountans, Aomori Prefecture, and concluded that June temperature and July precipitation

in the preceding 3 years were associated with the onset of outbreaks, although they did not conduct any statistical tests. Liebhold and Kamata (unpublished data) also found that July precipitation tended to be lower during the 3 years preceding outbreaks but that the difference was not statistically significant ($0.05 < P < 0.1$).

In Japan, the climate is typical oceanic and June and July are the rainy season (*Tsuyu* in Japanese). For example, the monthly precipitation of July averaged 140.8mm (max, 302mm; min, 34mm) in 1976–1996 at Sukayu (920m a.s.l.), the AMeDAS (Automatic Meteorological Data Acquisition System) station nearest plot A-7. *Syntypistis punctatella* spends July in the adult, egg, and young larval stages. Three different ways in which successive years of dry summers could trigger a gradual increase in the moth population have been hypothesized: (1) abundant rainfall directly curtails feeding behavior of the larvae and has several influences on larval growth and mortality (Kamata and Igarashi 1994); (2) low rainfall indirectly reduces the mortality caused by fungal diseases in the soil because soil moisture is an important determinant of growth of fungi, which are important mortality factors of *S. punctatella* pupae (Kamata 1998); and (3) the resultant increase in food quality caused by water stress lowers mortality rates, enhances development, and increases body size (Mattson and Haack 1987; Rhoades 1985; White 1974). Kamata and Tanabe (1999) investigated the foliage quality and insect performance on water-stressed beech trees. In water-stressed beech trees, foliar nitrogen was high but the rapid induced response was weak; the increase of tannins was relatively small, even after the beech caterpillar consumed the foliage. Insect performance (i.e., survivorship and pupal weight) on water-stressed beeches was high. However, the delayed induced response was completely different from the rapid induced response; it tended to be strong in highly water-stressed plants. In the year following defoliation, insect performance tended to be low because foliar nitrogen was low and tannins were high in highly water-stressed plants.

The preceding results can explain the relationship between *S. punctatella* population cycles and host plant properties in relation to the weather. Successive years of dry summers make beech foliage properties more suitable to *S. punctatella*: the foliage has a higher nitrogen concentration and a relatively low rate of increase of tannins, and these two changes trigger a gradual increase in the moth population. However, when the population reaches the outbreak level and beech trees are heavily defoliated, the delayed induced defensive response appears prominently in the following year. The moth population is depressed greatly by this “stronger” defensive response of beech trees, although other factors, notably natural enemies such as infectious diseases, parasitoids, and predators, are also involved (Kamata and Igarashi 1995b; Kamata et al. 1997; Kamata 1998).

Early workers assumed that the cause of population cycles would also be the cause of the synchrony. However, Moran (1953a,b) dismissed the need for a single causation hypothesis and pointed out that, if two populations had the same density-dependent structure, then correlated density-

independent factors (usually weather induced) would bring the population fluctuations into synchrony (Hudson and Cattadori 1999). It is impossible to investigate the presence of the “Moran effect” in historical records of the incidence of defoliation. Data on actual population densities are not sufficient to test the hypothesis. However, we found the opposite example, namely, that weather anomalies disturbed population synchrony. The caterpillar density (in terms of final instar density) in all three areas (A–C) changed in a similar manner (see Fig. 2). Larval density increased from 1986 to 1990 in all areas and reached the outbreak level in some plots of area A in 1989 and 1990. A synchronous population decrease was observed in 1991. A bad weather anomaly is speculated to have caused the concurrent population decrease that year (see earlier). However, in areas B and C, the density began to increase again in 1992. The density peak occurred in 1993 in area B and in 1994 in area C.

I speculate that the peak of population density would have been earlier than 1993–1994 if there had not been a bad weather anomaly in 1991 (Fig. 5b). In this case, a bad weather anomaly in 1991 delayed the population peak and disturbed the population synchrony. The population phase in which bad weather anomalies occurred and the intensity of bad weather anomalies are likely to influence the result. Recently, Ranta et al. (1999) demonstrated the results of 25 computer-simulated subpopulations of Moran–Ricker second-order nonlinear process with 9- to 10-year periodicity linked with global and local noise and dispersal, which yields a substantially long period of “phase-locking,” drift out of phase, and disappearance and reappearance of synchrony.

Site dependence in population outbreaks

Syntypistis punctatella outbreaks tend to occur more frequently in beech forests in northern Japan than in southern Japan (Yanabe and Igarashi 1983; Liebhold et al. 1996). Similar geographic variation in outbreak characteristics has been reported for voles in Hokkaido (Saitoh et al. 1998) and rodents in Europe (Hanski et al. 1991). Real population data to test the ecological basis of this phenomenon in *S. punctatella* are not available at present. At a smaller scale, another site-dependent characteristic of *S. punctatella* outbreaks is that the insect defoliation tends to occur at certain elevations. The elevation range depends on the region, but the outbreak zone tended to be lower at higher latitudes; e.g., 300–500m in southern Hokkaido (42°N) (Kazuo Tachi, personal communication), 600–800m in Hakkohda (area A; 40°40'N) (Kamata and Igarashi 1990), 900–1100m in Hachimantai (area B; 40°N) (Yanabe and Igarashi 1983), and 1100–1300m in Hakusan (36°15'N) (Togashi 1984). The defoliated area spread horizontally like an altitudinal belt, which is closely related to the vertical distribution of the vegetation. For example, in Hakkohda (area A), beech trees are distributed in the range 400–1100m (Yoshioka 1943). *Quercus cripisula* is a predominant tree species at the

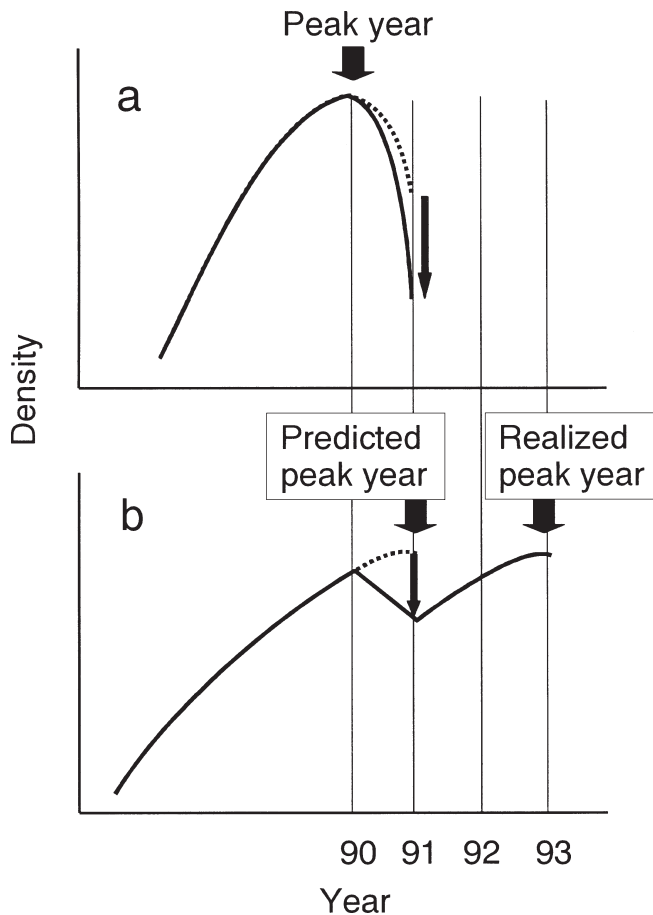


Fig. 5. Bad weather anomalies disturb population synchrony. A synchronous population decrease was caused by a bad weather anomaly in 1991. In the population that had already reached the outbreak level in 1990, the population decreased greatly in 1991 and the density has remained low thereafter because higher-order density-dependent mortality factors had been effective after 1991 **a**. The density began to increase again in 1992 and peaked in 1993 because no density-dependent mortality factor was effective against the increasing population **b**. The peak was predicted to have occurred in 1991 if there had not been a bad weather anomaly in 1991

lower edge of the distribution of the beech, and subalpine coniferous species are mixed with beech trees at the upper edge. The predominant species gradually changes from *Q. crispula* to from *F. crenata* and *F. crenata* to subalpine coniferous species according to the altitude.

Syntypistis punctatella outbreaks tended to occur in pure beech stands (Kamata et al., unpublished data). Because outbreak populations tended to have a larger value of the rate of increase R (>4.4) than nonoutbreak populations, the factors determining this rate of increase are likely to be related to site dependence in population outbreaks (Fig. 2). At present, I have three different hypotheses that can explain the site-dependent characteristics 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 (Voute 1946; Elton 1958): Complex ecosystems are more stable

than simple ones. Outbreaks tend to occur in simple ecosystems.

2. The resource concentration hypothesis (Root 1973; Redfearn and Pimm 1987): 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 elevational range where beech occurs in pure stands versus mixed with other species. Old instar (i.e., 3rd–5th) larvae of *S. punctatella* often fall on the ground accidentally or intentionally to escape from its natural enemies. They climb up on the tree trunk to reach their food. However, they cannot distinguish the tree species until they reach the foliage. When they have gone up on trees other than beech, they crawl down the trunk then climb up another tree. In the pure beech stands, the probability to select their food plant is higher than in the mixed stands, which makes the mortality low.

3. The altitudinal soil nutrient hypothesis (Kamata 1999): Outbreaks of *S. punctatella* tend to occur in places where both foliar nitrogen concentration and nitrogen use efficiency are high; soil nitrogen availability is low and the nitrogen absorption rate of trees before natural abscission is high. Foliage with a high nitrogen concentration enhances the rate of increase of herbivore density. However, under such nitrogen-poor conditions, foliar nitrogen decreases greatly when beech trees suffer severe insect defoliation, which increases the fluctuation of herbivore density.

Conclusions and future studies

My studies on the population dynamics of *S. punctatella* have continued for 15 years. This span seems a long time to one person but is too short to fully understand the population dynamics of this fascinating insect. Most of my time in Forestry and Forest Products Research Institute, Morioka, was devoted to studying the population dynamics of northern *S. punctatella* populations. In northern populations, both outbreak and nonoutbreak populations changed synchronously with 8- to 11-year quasi-periodicity of the population outbreak. Many factors were involved in the dynamics, but an entomopathogenic fungus, *C. militaris*, seemed to be the dominant factor responsible for population dynamics of this insect. In contrast, few population density data are available for southern populations, which rarely reach the outbreak level. I relocated to Kanazawa in December 1997, and started sampling southern populations in the Hakusan area beginning in the summer of 1998 to evaluate the population dynamics and contrast the population processes with northern populations. Fortunately, almost 90 years of historical records of the incidence of defoliation caused by *S. punctatella* are available from this area. However, only one outbreak was recorded, in 1982–1983 in Hakusan. The important questions for future studies are as follows:

1. Do southern populations also exhibit 8- to 11-year quasi-periodicity of the population peaks?

2. If so, is *Cordyceps militaris* also responsible for the population dynamics? Are there any other important factors that influence the insect population dynamics?
3. Why do southern populations seldom reach the outbreak level?

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References

- Berryman AA (1987) Theory and classification of outbreaks. In: Barbosa P, Schultz JC (eds) Insect outbreaks. Academic Press, San Diego, pp 3–30
- Bjornstad ON, Falck W, Stenseth NC (1995) A geographic gradient in small rodent density fluctuations: a statistical modeling approach. *Proc R Soc Lond B* 262:127–133
- Box GEP, Jenkins GM (1976) Time series analysis: forecasting and control (revised edn). Holden-Day, San Francisco
- Dempster JP (1975) Animal population ecology. Academic Press, New York
- Elton C (1958) The ecology of invasion by animals and plants. Methuen, London
- Fischlin A, Baltensweiler W (1977) Systems analysis of the larch bud moth system. Part 1: The larch-larch bud moth relationship. *Mitt Schweiz Entomol Ges* 52:273–289
- Ginzburg LR, Taneyhill DE (1994) Population cycles of forest Lepidoptera: a maternal effect hypothesis. *J Anim Ecol* 63:79–92
- Hanski I, Hansson L, Henttonen H (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *J Anim Ecol* 60:353–367
- Hudson PJ, Cattadori IM (1999) The Moran effect: a cause of population synchrony. *Trends Ecol Evol* 14:1–2
- Igarashi M (1975) The beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep., Notodontidae), as an important defoliator of beech, *Fagus crenata* Blume. Monthly report of Tohoku Research Center (in Japanese). *For For Prod Res Inst* 162:1–4
- Igarashi M (1982) Ecology of the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep., Notodontidae) (in Japanese). *Trans Annu Meet Tohoku Br Jpn For Soc* 34:122–124
- Igarashi M, Suzuki M (1980) Outbreaks of the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep., Notodontidae) in Mt. Iwaki (in Japanese). *Mon Rep Aomori For Bur* 175:4–9
- Ito T (1991) Nutrient dynamics in the beech forests and forest management. In: Murai H, Yamaya K, Kataoka H, Yui M (eds) Natural environment and its conservation on buna (*Fagus crenata*) forest (in Japanese). Soft Science, Tokyo, pp 182–189
- Ives WGH (1973) Heat units and outbreaks of the forest tent caterpillar, *Malacosoma dissiria* (Lepidoptera: Lasiocampidae). *Can Entomol* 105:529–543
- Kamata N (1998) Periodic outbreaks of the beech caterpillar, *Syntypistis punctatella*, and its population dynamics: the role of insect pathogens. In: McManus ML, Liebhold AM (eds) Population dynamics, impacts, and integrated management of forest defoliating insects. Gen Tech Rep NE-247, USDA Forestry Service, Washington, DC, pp 34–46
- Kamata N (1999) Ecological characteristics of a beech, *Fagus crenata* Blume, and plant-herbivore system (in Japanese). *Bull Soc Popul Ecol* 56:29–46
- Kamata N, Igarashi Y (1990) Outbreaks of *Syntypistis punctatella* in Hakkohda mountains: principles in forecasting the insect outbreaks (in Japanese). Monthly report of Tohoku Research Center. *For For Prod Res Inst* 347:1–3
- Kamata N, Igarashi Y (1994) Influence of rainfall on feeding behavior, growth, and mortality of larvae of the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep. Notodontidae). *J Appl Entomol* 118:347–353
- Kamata N, Igarashi M (1995a) Relationship between temperature, number of larval instars, larval growth, body size, and adult fecundity of the beech caterpillar, *Quadricalcarifera punctatella* (Lep., Notodontidae): interpretation as a cost-benefit trade-off. *Environ Entomol* 24:648–656
- Kamata N, Igarashi Y (1995b) An example of numerical response of the carabid beetle, *Calosoma maximowiczii* Morawitz (Col., Carabidae), to the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep., Notodontidae). *J Appl Entomol* 119:139–142
- Kamata N, Igarashi Y (1995c) Synchronous population dynamics of the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky): rainfall is the key. In: Haine F, Salom SM, Ravlin WF, Payne T, Raffa KF (eds) Behavior, population dynamics and control of forest insects. Ohio State University, Wooster, pp 452–473
- Kamata N, Igarashi Y (1996) Seasonal and annual change of a folivorous insect guild in the Siebold's beech forests associated with outbreaks of the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) (Lep., Notodontidae). *J Appl Entomol* 120:213–220
- Kamata N, Takagi Y (1991) Factors influencing long term population dynamics of a beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky). I. Comparison with fluctuating pattern of temperature and precipitation (in Japanese). *Trans Annu Meet Tohoku Br Jpn For Soc* 43:136–138
- Kamata N, Tanabe H (1999) Performance of beech caterpillar (*Syntypistis punctatella* (Motschulsky)) on water-stressed beech. In: Lieutier F, Mattson WJ, Wagner MR (eds) Physiology and genetics of tree-phytophage interactions. INRA, Paris, pp 313–322
- Kamata N, Suzuki Y, Igarashi Y, Nakamura M (1994) Annual and seasonal changes of food menu of breeding birds in relation to biomass of folivorous insects in the natural beech forests in N Japan (in Japanese). *Trans Annu Meet Tohoku Br Jpn For Soc* 46:37–38
- Kamata N, Igarashi Y, Ohara S (1996a) Induced response of the Siebold's beech (*Fagus crenata* Blume) to manual defoliation. *J For Res* 1:1–7
- Kamata N, Igarashi Y, Ohara S (1996b) Defoliation of *Fagus crenata* affects the population dynamics of the beech caterpillar, *Quadricalcarifera punctatella*. In: Mattson WJ, Niemela P, Rousi M (eds) Dynamics of forest herbivory: quest for pattern and principle. Gen Tech Rept NC-183, USDA Forestry Service, Washington, DC, pp 68–85
- Kamata N, Sato H, Shimazu M (1997) Seasonal changes in the infection of pupae of the beech caterpillar, *Quadricalcarifera punctatella* (Motsch.) (Lep., Notodontidae), by *Cordyceps militaris* Link (Clavicipitales, Clavicipitaceae) in the soil of the Siebold's beech forest. *J Appl Entomol* 121:17–21
- Karban R, Baldwin IT (1997) Induced responses to herbivory. University of Chicago Press, Chicago
- Katagiri S, Tsutsumi T (1978) The relationship between site condition and circulation of nutrients in forest ecosystem. V. The difference in nutrient circulation between stands located on upper part of slope and lower part of slope (in Japanese). *J Jpn For Soc* 60:195–202
- Klomp H (1966) The dynamics of a field population of the pine looper (Lepidoptera, Geometridae). *Adv Ecol Res* 3:207–303
- Liebhold AM, Kamata N, Jacob T (1996) Cyclicity and synchrony of historical outbreaks of the beech caterpillar, *Quadricalcarifera punctatella* (Motschulsky) in Japan. *Res Popul Ecol* 38:87–94
- Maeto K (1991) Outbreaks of *Dendrolimus superans* (Butler) (Lepidoptera: Lasiocampidae) related to weather in Hokkaido. *Appl Entomol Zool* 26:275–277
- Martinat PJ (1987) The role of climatic variation and weather in forest insect outbreaks. In: Barbosa P, Schultz JC (eds) Insect outbreaks. Academic Press, San Diego, pp 241–268
- Mattson WJ, Haack RA (1987) The role of drought in outbreaks of plant-eating insects. *Bioscience* 37:110–118
- May RM, Conway GR, Hassel MP, Southwood TRE (1974) Time delays, density dependence and single species oscillations. *J Anim Ecol* 43:747–770
- Moran PAP (1953a) The statistical analysis of the Canadian lynx cycle. I. Structure and prediction. *Aust J Ecol* 1:163–173

- Moran PAP (1953b) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Aust J Ecol* 1:291–298
- Morris RF (1964) The value of historical data in population research with particular reference to *Hyphantria cunea* Drury. *Can Entomol* 96:356–368
- Myers JH (1990) Population cycles of western tent caterpillars: experimental introductions and synchrony of fluctuations. *Ecology* 71:986–995
- Ranta E, Kaitala V, Lundberg P (1999) Synchrony in population systems: cause and consequences mixed. *Trends Ecol Evol* 14:400–401
- Redfearn A, Pimm SL (1987) Insect outbreaks and community structure. In: Barbosa P, Schultz JC (eds) *Insect outbreaks*. Academic Press, San Diego, pp 99–133
- Rhoades DF (1985) Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *Am Nat* 125:205–238
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol Monogr* 43:95–124
- Royama T (1992) *Analytical population dynamics*. Chapman and Hall, London
- Saitoh T, Stenseth NR, Bjornstad ON (1998) The population dynamics of the vole *Clethrionomys rufocanus* in Hokkaido, Japan. *Res Popul Ecol* 40:61–76
- Sato H, Kamata N, Shimazu M (1998) Aerial infection of *Cordyceps militaris* Link (Clavicipitales: Clavicipitaceae) against larvae of *Quadricalcarifera punctatella* (Motschlsky) (Lepidoptera: Notodontidae). *Appl Entomol Zool* 32:249–252
- Sota T (1984) Long adult life span and polyphagy of a carabid beetle, *Leptocarabus kumagaii* in relation to reproduction and survival. *Res Popul Ecol* 26:389–400
- Sota T (1985) Limitation of reproduction by feeding condition in a carabid beetle, *Carabus yaconinus*. *Res Popul Ecol* 27:171–184
- Swetnam TW, Lynch AM (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol Monogr* 63:399–424
- Thompson AJ, Sheoherd RF, Harris JWE, Silversides RH (1984) Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia. *Can Entomol* 116:375–381
- Togashi I (1984) Moths feeding on leaves of beech, *Fagus crenata* Blume (in Japanese). *Jpn Heterocycl J* 129:59–62
- Varley GC (1947) The natural control of population balance in the knapweed gall-fly (*Urophora jaceana*). *J Anim Ecol* 16:139–187
- Voite AD (1946) Regulation of the density of the insect population in virgin forest and cultivated woods. *Arch Neerl Zool* 7:435–470
- Watanabe T (1994) *Pictorial atlas of soil and seed fungi: morphologies of cultured fungi and key to species*. Lewis, Boca Raton
- Weseloh RM (1990) Gypsy moth predators: an example of generalist and specialist natural enemies. In: Watt AD, Leather SR, Hunter MD, Kidd NAC (eds) *Population dynamics of forest insects*. Intercept, Andover, pp 233–243
- White TCR (1974) A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia (Berl)* 16:279–301
- Yamaya B (1989) *Calosoma maximowiczii* Morawitz. In: East Japan Research Group of Carabid Beetles (ed) *Carabid beetles in the east Japan* (in Japanese). Bunanoki Shuppan, Yonezawa, Yamagata, pp 42–45
- Yanbe T, Igarashi M (1983) Outbreaks of beech caterpillar and its parasite *Cordyceps militaris* Link (in Japanese). *For Pests (Jpn)* 32:115–119
- Yoshioka K (1943) Vertical distribution of predominant tree species in Hakkohda mountains (in Japanese). *Ecol Rev* 9:187–198