論文の内容の要旨

森林科学専攻

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氏名　パニサラ　ピンカンタヨン

指導教員名　　鎌田直人教授

論文題目　Studies on population dynamics of the larch sawfly, *Pristiphora erichsonii*(Hartig)during an outbreak in the University of Tokyo Hokkaido Forest, central　Hokkaido

（北海道中央部に位置する東京大学北海道演習林の大発生期におけるカラマツハラアカハバチの個体群動態に関する研究）

The larch sawfly, *Pristiphora erichsonii* (Hartig), is known to be cosmopolitan species. Outbreaks of this insect were reported in Eurasia and North American continents, and Japan. Its population outbreaks are known to persist over long periods. In Hokkaido, larch trees are non-native species that were artificially introduced from the mainland of Japan and Krill Island, Sakhalin and the Eurasia Continent. Outbreak records of *P. erichsonii* in Hokkaido updated in 1977. In this dissertation, population dynamics of *P. erichsonii* and mortality factors were investigated to clarify reasons why *P. erichsonii* outbreaks continue so long compared to other forest defoliators. The study was conducted at eight stands of larch plantation, seven *Larix kaempferi* stands and one stand of *L. gmelinii* var. *japonica* and a hybrid (*L. gmelinii* var. *japonica* x *L. kaempferi*) in the University of Tokyo Hokkaido

Forests (22,717 ha), located in central Hokkaido Island, Japan from 2009 to 2012. Both field and laboratory studies were carried out for investigating population density, natural enemies, and host tree response against herbivory.

Two types of canopy photos, normal color and infrared red, were taken in June and October to determine defoliation intensity. Five litter traps, 1 m x 1 m each, were deployed on forest floor to collect fallen insect frass drops as an indicator of defoliation. Severe insect defoliation was found at two sites in 2009 and at all stands of *L. kaempferi* in 2010 and 2011. In 2012, severe defoliation was found only at one stand among the eight. One stand, where conspicuous defoliation was observed in all the four years, seemed like an epicenter. Although, population outbreaks of *P. erichsonii* were believed to continue for many years in each area at a landscape level, this study first revealed that, at a stand level, the high density with conspicuous defoliation do not continue throughout the outbreak period.

Because the current generation's cocoons are indistinguishable from previous generations' cocoons and small mammal predation had started before the sampling, it was difficult to estimate the number of newly spun cocoons and predation by small mammals with high precision. Therefore, in this study, a hierarchical Bayesian model was developed to estimate these values by one-time sampling of soil every year. Ten 0.04-m^2 soil samples were annually collected from each site in mid-October. The abundance of unopened cocoons (I), cocoons emptied by small mammal predation (M), and empty cocoons caused by something other than small mammal predation (H) was determined. This study estimated the abundance of newly spun cocoons, the predation rate by small mammals before and after the cocoon sampling, and the annual remaining rate of empty cocoons in the soil using the hierarchical Bayesian model. The model had acceptable fit: a posterior predictive check yielded a Bayesian *P*-

values of 0.54, 0.48 and 0.07 for *I*, *M*, and *H*, respectively. The *I* value were found peaked in 2010 or 2011 depending on a site and decreased in 2012 with one exception, whereas the *M* and *H* tended to increase year after year.

Abundance of small mammals was determined by snap traps. The abundance declined in winter until 2009. However, after 2009 when the recent *P. erichsonii* outbreak started, small mammal abundance did not decrease in winter, most likely because the high density of cocoons acted as a supplemental diet during the winter and improved winter survivorship of the small mammals. As a result, a significant numerical response to the cocoons was found in *Apodemus argenteus, A. speciosus* and *Myodes rufocanus bedfordiae*. The predation rates by small mammals were also significantly influenced by abundance of these small mammals and year but not by cocoon density itself. On the other hand, overall, the percentage of cocoon killed by parasitoids and entomophatogenic fungi was low. Neither any significant spatial density dependence was found for parasitic wasps, parasitic flies, nor entomophatogenic fungi.

Responses of the Japanese larch (*Larix kaempferi*) to defoliation by *P. erichsonii* were examined from a perspective of a carbon/nutrient balance hypothesis (CNBH). This study was conducted in seven stands with Japanese larch. The chemical and physical properties of the foliage were determined from 2010 to 2012. A decrease in foliar nitrogen and increases in phenolics, tannins, and the CN ratio were found in the years following severe defoliation and were significantly influenced by the 2009 defoliation intensity. The influence of defoliation in 2010 and 2011 was weaker probably due to strong defoliation in almost all sample trees. These results indicated that the past defoliation history additively affected the foliage properties even in the two years following insect defoliation. In addition to the 2009 defoliation effects, site effects were found on phenolics, sugars, and the CN ratio. The CN ratio was high at both sites where severe defoliation was found in 2009. Phenolics and sugars did not increase linearly with the CN ratio, indicating some limitations other than available carbon resource in their synthesis. These results suggest that the induced changes in *L. kaempferi* properties are partially up-regulated under nitrogen limitation but that secondary compound synthesis was, most likely, influenced by external site-dependent factors other than nitrogen limitation.

Previous insect defoliation may alter foliage quality, which in turn affects the performance of insect in either the current or subsequent generations. After severe defoliation, not only decreased in foliar nitrogen and related increase of defensive secondary compounds but also food shortage were found, which were likely causes of body size reduction of *P. erichsonii.* Forewing length of *P. erichsonii* females was also measured as a parameter of body size in this study. Adult body size decreased greatly from generation 2009 to generation 2012. In generations 2010 and 2011, the reduction of body size was influenced by both food deterioration and food shortage. On the contrary, generation 2012, the body size reduced greatly without food shortage.

In conclusion, only in a small epicenter, *P. erichsonii* population densities exhibited sustained type of eruption. From the epicenter to peripherals, an outbreak type gradually changed from sustained type to pulse type. A hierarchical model provided reasonable approximations to observed values for number of newly spun cocoons and the number of cocoons preyed on by small mammals. The percentage of *P. erichsonii* emergence decreased year by year. Small-mammal predation increased year by year and attributed to the reduction, however, it could not depress *P. erichsonii* outbreaks at high density. Some other natural enemies sometimes acted as density dependence way, but not strong enough to regulate population outbreaks of this species. Changes in food quality induced by previous defoliation by *P. erichsonii* may have a substantial effect on the population cycle of it. Also, the past defoliation history additively affected the foliage properties. Reduction of the adult body size, caused by food deterioration, was likely to reduce fecundity and initial density of the next generation. However, the interaction proceeded slowly. These are likely causes of sustained type of outbreaks at a landscape level.