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Population dynamics of leafminers on a deciduous oak *Quercus dentata*

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ABSTRACT

Population dynamics of leafminers on a deciduous oak *Quercus dentata*, were studied for 9 years in northern Japan. Most leafminers in the study site were bivoltine, while a gregarious *Stigmella* species was univoltine. Many leafminers showed species-specific patterns of population fluctuations. In the major bivoltine leafminers (*Phyllonorycter*, solitary *Stigmella* and *Caloptilia* species), the densities of autumn generation mines were highly correlated with those of summer generation mines when analysed on the basis of the densities at the early developmental stage. Thus, their mortality and egg productivity in this phase (i.e., from late June to early September) varied only a little from year to year. In *Phyllonorycter*, however, correlation of densities between these two generations became lower when analysed on the basis of the densities at the tissue-feeding stage, suggesting that their mortality from the early developmental stage to the tissue-feeding stage in the autumn generation varied from year to year. Regression analyses suggest that yearly variation in precipitation in July and August was responsible for this variation. Correlations of densities between the autumn generation and the summer generation of the next year in the major leafminers were not high. Thus, their mortality and/or egg productivity in this phase (i.e., from September to June of the next year) varied from year to year. Regression analyses suggest that climatic factors that affected the population dynamics in this phase varied among the leafminers, except some factors have been suggested to be commonly effective in the two *Phyllonorycter* species. Density-dependent effects were not explicit in the population dynamics of the present leafminers.

1. Introduction

The abundance of a species is dependent on various factors that are categorized into biotic (e.g. resource quality and quantity, competition and predation) and abiotic ones (e.g. climatic conditions), and the relative importance of these factors varies from species to species, population to population and time to time. In the population dynamics of endophytic insects such as leafminers and gall-makers, the importance of biotic factors has often been stressed. Leafminers and gall-makers are restricted to islands of individual leaves or shoots, and therefore competition for resources has

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been expected to act as a density-dependent factor (Quiring and McNeil, 1984; Stiling et al., 1984; Bultman and Faeth, 1986; Auerbach and Simberloff, 1989; Auerbach et al., 1995; Eber, 2004). In addition, leafminers and gall-makers are often associated with diverse parasitoid species (Askew and Shaw, 1986; Hawkins and Lawton, 1987; Hochberg and Hawkins, 1992; Sato et al., 2002), and they are sometimes subjected to the top-down population regulation by these enemies (Faeth and Simberloff, 1981; Kato, 1994). Furthermore, enemy-mediated apparent competition is suggested to affect their population regulation (Rott and Godfray, 2000; Morris et al., 2004). Climatic factors such as temperature or precipitation could also have effects in their population dynamics (Price and Clancy, 1986; Price, 1991; Scheirs and De Bruyn, 2005), but the importance of climatic factors is seldom documented. This is partly attributable to the scarceness of long-term studies which are indispensable to detect the effects of climatic factors. Here, we studied the population fluctuations of leafminers on a deciduous oak *Quercus dentata* Thunberg for 9 years in northern Japan to understand how their population densities were determined.

2. Methods

2.1. *Study site and trees*

The present study was carried out in a *Q. dentata* forest on the Ishikari Coast (43°12′ N, 141°19′ E) in Hokkaido, northern Japan. In this area, nearly pure forests of *Q. dentata* develop along the seashore (Ishida et al., 2004). Trees in this area, especially near the forest edge at the seashore, are dwarfed, perhaps because of winds from the sea.

We set a 10 m × 50 m quadrat in which 66 individuals of *Q. dentata* grew. Among them, 30 individuals were arbitrarily selected for monitoring of leafminers. However, five individuals died during the study, and therefore data were obtained from 25 individuals. For these individuals, bud-burst timing, i.e., the day when half of 100 randomly chosen leaf-buds opened, was monitored from 1997 to 2005.

2.2. *Leafminers*

Leafminers on this oak in the study area were mainly Lepidoptera; two species of *Phyllonorycter* (Gracillariidae: *P. leucocorona* (Kumata) and *P. persimilis* Fujihara, Sato and Kumata), *Caloptilia sapporella* (Matsumura) (Gracillariidae), three species of *Stigmella* (Nepticulidae: *S. kumatai* Kemperman and Wilkinson, *S. pulla* Kemperman and Wilkinson and an undetermined species), and two species of *Tischeria* (Tischeriidae: *T. quercifolia* Kuroko and *T. decidua* Wock) (Sato, 1990; Shibata et al., 2001; Ishida et al., 2003, 2004; Kitamura et al. 2007). In addition to the above species, some undetermined leafminer species of the family Tenthredinidae (Hymenoptera) were also observed (Sato, 1991; Shibata et al., 2001), but they were not analysed in this study since their species status was not settled.

The larval stage of *Phyllonorycter* species is divided into two in terms of feeding type: sap-feeding and tissue-feeding stages. Mines of the two *Phyllonorycter* species cannot be discriminated at the sap-feeding stage, but are easily discriminated at the tissue-feeding stage; mines of *P. persimilis* are 3–4 times larger than those of *P. leucocorona*, and the former lacks an oval-shaped frass cocoon which is present in the latter (Sato, 1986). *Caloptilia sapporella* larvae are also initially sap feeders, and become tissue feeders in later developmental stages. Mines of the two species of *Tischeria* are discriminated by the colour; *T. quercifolia* forms whitish mines, while *T. decidua* forms brownish ones. On the other hand, mines of *Stigmella kumatai* and *S. pulla* could not be discriminated from each other, and therefore they were treated together in this study. The above leafminers form solitary mines (those made by single individuals). On the other hand, an undetermined *Stigmella* species forms gregarious mines and therefore can be easily distinguished from the others.

The species of *Phyllonorycter*, *Caloptilia*, solitary *Stigmella* and *Tischeria* produce two (summer and autumn) generations in a year, but the gregarious *Stigmella* species produces only one (autumn) generation (Sato, 1990; Shibata et al., 2001). In the bivoltine species, summer generation larvae (mines) appear in mid June, pupate in late July, and emerge as adults in August. Autumn generation larvae appear in late August and pupate from late September to late October. In *Phyllonorycter* species, larvae of the summer generation grow to the tissue-feeding stage in late June to mid July, and those of the autumn generation do in September. *Phyllonorycter, Caloptilia* and *Stigmella* species overwinter as pupae and *Tischeria* species overwinter as larvae, and all species emerge as adults in early June of the next year. In autumn when the present sampling was performed, summer and autumn generation mines could be discriminated by the colour and conditions; summer generation mines were much darker and were often torn.

2.3. *Densities of leafminers*

The present oak flushes leaves in mid to late May in the study area, and retains them until late autumn unless serious damage occurs. Secondary flush of leaves sometimes occurs in summer, but the frequency of secondary leaves is very low.

In this study, 50 ‘‘sun’’ leaves were randomly collected from the canopy area (2–5 m above the ground) of each tree in early October for 9 years (1997–2005). Collected leaves were examined for area: leaf outline was scanned using an image scanner (CanoScan LiDE 60, Canon Co., Tokyo, Japan), and area was measured using an image processor (Image J program developed by the US National Institutes of Health). Mines on collected leaves were identified to species or genus, and further discriminated into the summer and autumn generations according to the colour and conditions. For all leafminers, the mine density was determined at the early developmental stage. In *Phyllonorycter*, the mine density was also determined at the tissue-feeding stage separately for the two species, *P. persimilis* and *P. leucocorona*, since they could be discriminated at this stage. The density of mines was given as the number of mines per unit leaf area (100 cm^2).

2.4. *Analyses*

To clarify factors that affected the population dynamics of major bivoltine leafminers (*Phyllonorycter*, solitary *Stigmella* and *Caloptilia* species), multiple regression analysis was conducted (stepwise procedure; independent variables entered the analysis if $P < 0.25$). The analysis was performed independently for two phases; i.e., from the summer generation to the autumn generation of the same year (phase 1) and from the autumn generation to the summer generation of the next year (phase 2). In this analysis, the dependent variable was the rate of population increase from one generation to the next generation. Independent variables were the density of conspecific mines (congeneric mines in the case of solitary *Stigmella*), bud-burst timing and weather variables (i.e. monthly mean temperature and precipitation during the inter-generation period). The inter-generation period differed whether the analysis was performed on the basis of the density at the early developmental stage or at the tissue-feeding stage. When the analysis was performed on the basis of the density at the early developmental stage, phase 1 corresponded to a period from late June to early September, and phase 2 to a period from mid September to mid June of the next year. When the analysis was performed on the basis of the density at the tissue-feeding stage (in *Phyllonorycter* species), phase 1 corresponded to a period from late July to late September, and phase 2 to a period from early October to mid July of the next year. In addition to multiple regression analysis, simple regression analysis was carried out using single independent variables, since multiple regression analysis did not always detect important relations. In this analysis, the density of mines and the rate of population increase were log-transformed. All statistical analyses were performed with JMP 6.0 (SAS Institute, Cary, NC, USA).

3. Results

Fig. 1 shows fluctuations of leafminer densities at the early developmental stage (closed symbols) and those of *P. persimilis* and *P. leucocorona* densities at the tissue-feeding stage (open symbols) in the study area (data on 25 trees were pooled). The density of tissue-feeding *Phyllonorycter* mines (data on the two species were pooled) was significantly correlated ($r = 0.817$, $P < 0.001$) with the density of their early-stage mines. The pattern of population fluctuations varied among the leafminers, although similar patterns were observed between *P. leucocorona* and *P. persimilis* ($r = 0.645$, $P = 0.004$), between *P. leucocorona* and *C. sapporella* ($r = 0.753$, $P < 0.001$) and between solitary *Stigmella* species and *T. quercifolia* ($r = 0.605$, $P = 0.008$).

Figs. 2 and 3 show correlations of mine densities between the summer generation and the autumn generation (left panels) and between the autumn generation and the summer generation of the next year (right panels) in the major bivoltine leafminers, *Phyllonorycter*, *Caloptilia* and solitary *Stigmella*. When analysed on the basis of the densities at the early developmental stage, the densities of autumn generation mines were significantly and positively correlated with those of mines in the previous generation (i.e., the summer generation of the same year), whereas the densities of summer generation mines were not significantly correlated with those of mines in the previous generation (i.e., the autumn generation of the previous year) (Fig. 2, first panels; Fig. 3). In *Phyllonorycter*, the analysis was also performed on the basis of density at the tissue-feeding stage (Fig. 2, second panels): correlation of densities between these two generations became lower. Similar results were obtained when the analysis was performed separately for the two species, *P. persimilis* and *P. leucocorona* (Fig. 2, lower two panels).

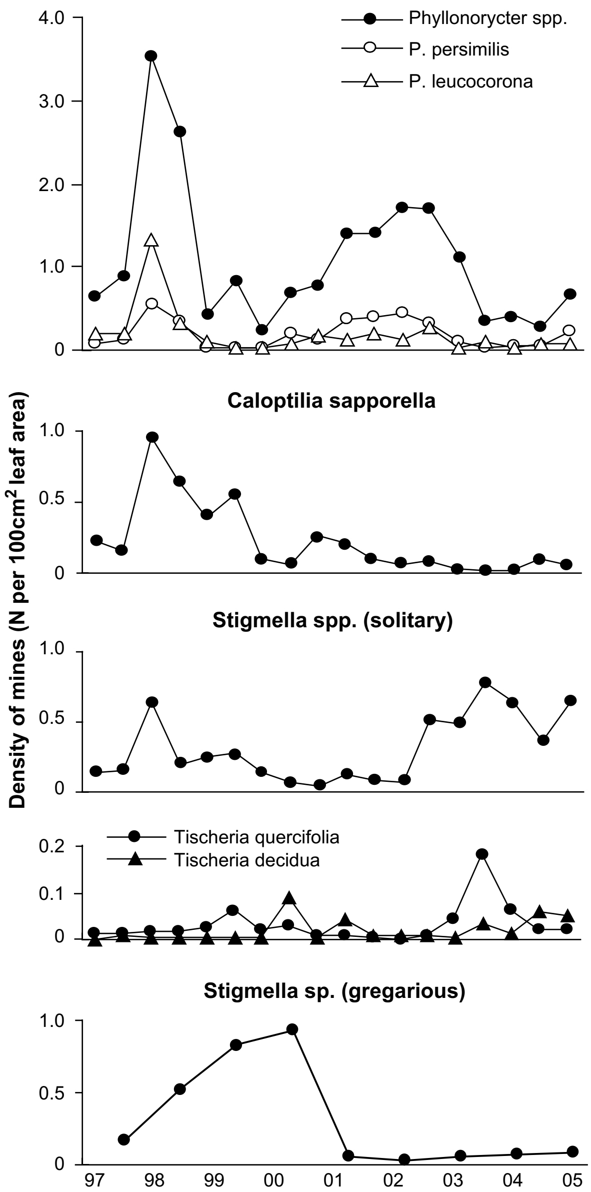

Fig. 1 – Population fluctuations of leafminers from 1997 to 2005. A gregarious *Stigmella* species was univoltine, while others were bivoltine. Closed symbols, densities of mines at the early developmental stage; open symbols, densities of mines at the tissue-feeding stage.

Table 1 shows the results of regression analyses. In phase 1 (a period from the summer generation to the autumn generation), precipitation in July and August showed significant positive effects in both of *P. persimilis* and *P. leucocorona* in multiple regression analysis (MRA), and precipitation in July showed a significant effect in *P. persimilis* in simple regression analysis (SRA). The density of conspecific mines showed a significant positive effect in *C. sapporella* in MRA and SRA, but

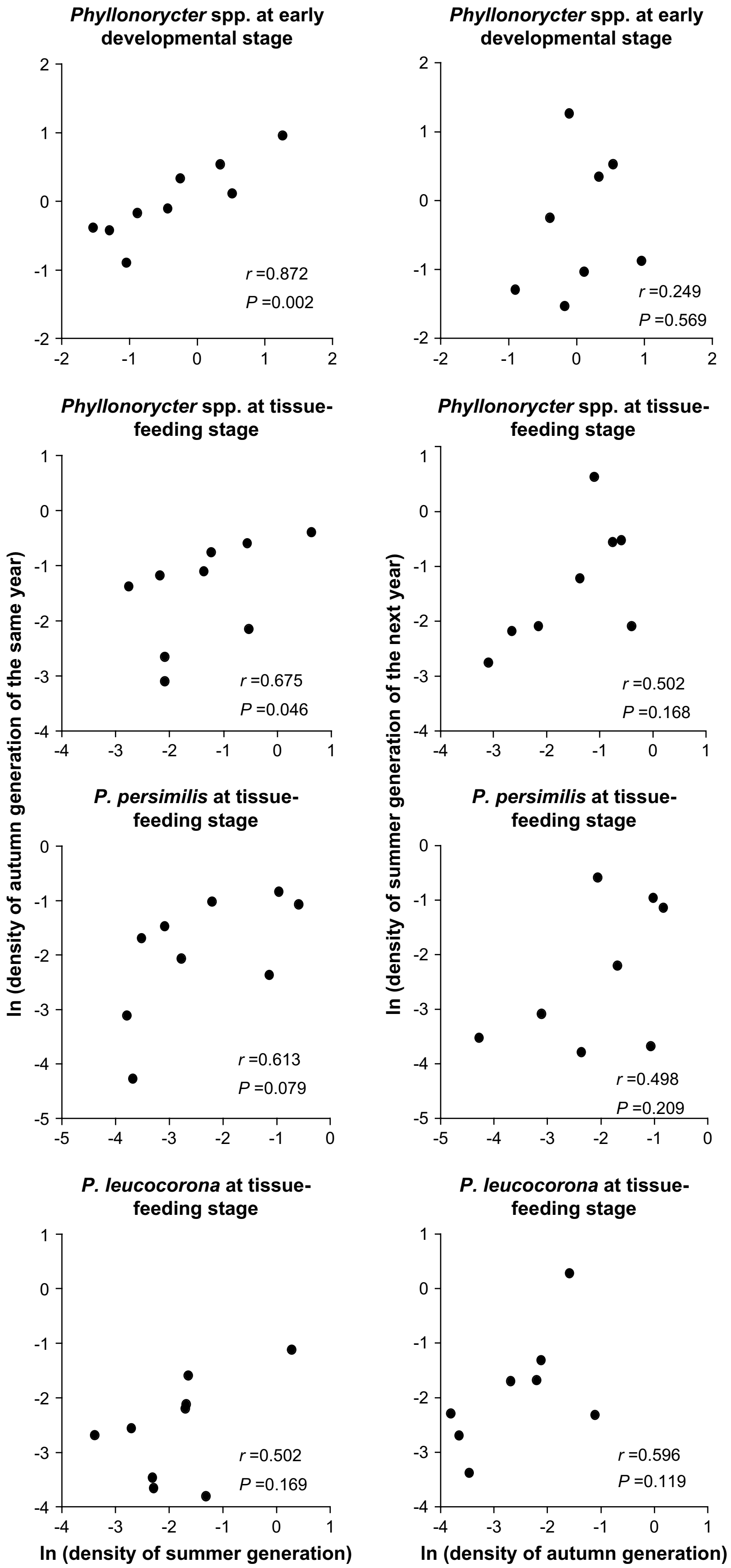

Fig. 2 – Correlations between the densities of autumn generation mines and those of summer generation mines of the same year (left panels) and between the densities of summer generation mines and those of autumn generation mines of the previous year (right panels) in *Phyllonorycter*. Densities were determined at the early developmental or the tissue-feeding stage together for the two species (upper two panels) or separately for *P. persimilis* and *P. leucocorona*. The axes of graphs show the log-transformed density.

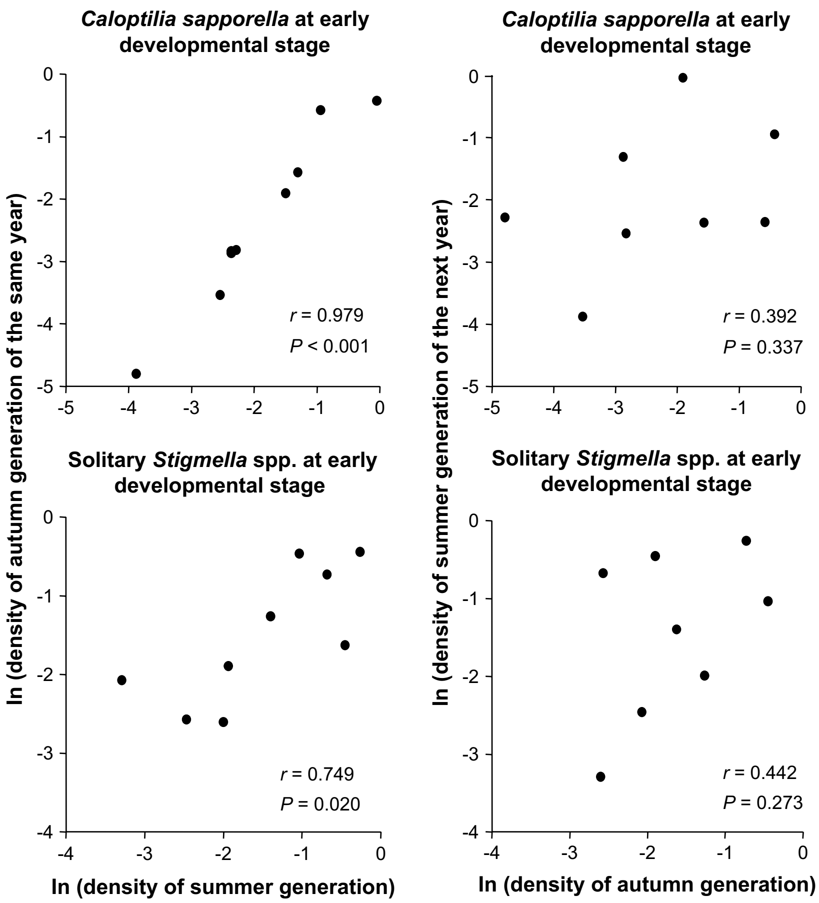

Fig. 3 – Correlations between the densities of autumn generation mines and those of summer generation mines of the same year (left panels) and between the densities of summer generation mines and those of autumn generation mines of the previous year (right panels) in *Caloptilia sapporella* and solitary *Stigmella* species. Densities were determined at the early developmental stage. The axes of graphs show the log-transformed density.

a significant negative effect in solitary *Stigmella* species in MRA.

In phase 2 (a period from the autumn generation to the summer generation of the next year), various variables showed significant effects in MRA, and variables showing significant effects varied among the leafminers, except that precipitation in May showed significant negative effects commonly in *P. persimilis* and *P. leucocorona*. In SRA, however, temperature in October showed significant negative effects in both *Phyllonorycter* species. In SRA, precipitation in June and temperature in September also showed significant effects in *P. persimilis* and *P. leucocorona*, respectively. On the other hand, precipitation in December and temperature in August showed significant effects in *C. sapporella* and solitary *Stigmella* species, respectively.

4. Discussion

In the major bivoltine leafminers, *Phyllonorycter*, solitary *Stigmella* and *Caloptilia*, the densities of autumn generation mines were highly correlated with those of summer generation mines when analysed on the basis of the densities at the early developmental stage. Thus, their mortality and egg productivity in this phase varied only a little from year to year. In *Phyllonorycter*, however, the correlation of densities between these two generations became lower when analysed on the basis of the densities at the tissue-feeding stage. Similar results were obtained when the analyses were performed independently for the two species or with pooled data. These results suggest that mortality of *Phyllonorycter* larvae in September (i.e., a period for the development from the early developmental stage to the tissue-feeding stage in the autumn generation) varied from year to year. Regression analyses suggest that yearly variation in precipitation in July and August was responsible for this variation. High precipitation in this period may lower mortality of *Phyllonorycter* larvae in September by modifying leaf quality. This notion is consistent with the plant vigour hypothesis that herbivores prefer and perform better on vigorously growing plants, i.e., those under lower water stress (Price, 1991; Huberty and Denno, 2004; Scheirs and de Bruyn, 2005), but inconsistent with the plant stress hypothesis that environmental stress such as drought increases the suitability of leaves as food for herbivores (White, 1969; Mattson and Haack, 1987).

Table 1 – Results of multiple regression analysis (stepwise procedure; independent variables entered analysis if $P < 0.25$). Variables that show significant contribution was shown with coefficients in parentheses. Variables that also show significant contribution in single regression analysis (SRA) was suggested by underlines. Den, density of conspecific or congeneric individuals; T, temperature; P, precipitation. *$P < 0.05$, **$P < 0.01$

Leafminers	Variables that show significant contribution in MRA					
Rate of population increase						
From summer generation to autumn generation (phase 1)						
Phyllonorycter persimilis[a]	JunT (0.440*)	JulP (0.020*)	AugP (0.022*)			
P. leucocorona[a]	JunT (−0.202**)	JulT (0.106**)	AugT (0.071**)	JulP (0.017**)	AugP (0.020**)	SepP (−0.00004*)
Caloptilia sapporella[b]	JunP (−0.002*)	Den (0.310**)				
Solitary *Stigmella* spp.[b]	JunT (0.973**)	JulP (−0.010**)	Den (−0.887**)			
From autumn generation to summer generation of the next year (phase 2)						
P. persimilis[a,c]	JanT (−0.147**)	AprT (0.127*)	JanP (−0.002*)	MayP (−0.005**)	JunP (0.054**)	Den (−0.688**)
P. leucocorona[a,d]	OctT (−1.642**)	JunT (0.691**)	SepP (0.001**)	JanP (0.004**)	AprP (−0.007**)	MayP (−0.012**)
C. sapporella[b]	Jan T (−10.776*)	OctP (0.014**)	DecP (0.050**)	FebP (−0.008*)	MayP (0.015**)	
Solitary *Stigmella* spp.[b]	AugT (−0.606**)	DecT (0.380*)	MarT (−0.264*)	AprP (0.022**)	Den (−0.732*)	

a The density was determined at the tissue-feeding stage.
b The density was determined at an early developmental stage.
c Temperature in October shows a significant effect in SRA ($P < 0.05$).
d Temperature in September shows a significant effect in SRA ($P < 0.05$).

Correlations of densities between the autumn generation and the summer generation of the next year were not high in the major bivoltine leafminers. Thus, their mortality and/or egg productivity in this phase varied from year to year. In multiple regression analysis, various factors were suggested to have significant effects on the rate of population increase in this phase (Table 1). In addition, effective factors varied among the leafminers. For example, the factors that were suggested to have significant effects in both multiple and single regression analyses were precipitation in June in *P. persimilis*, temperature in October in *P. leucocorona*, precipitation in December in *C. sapporella*, and temperature in August in solitary *Stigmella* species. Different species would have responded to weather in different ways.

However, there may be common effective factors in the two *Phyllonorycter* species, since the patterns of their population fluctuations coincided to some extent. Precipitation in May was suggested to have significant negative effects commonly in the two *Phyllonorycter* species in multiple regression analysis, and temperature in October was suggested to have significant negative effects in both species in simple regression analysis. However, it was not explicit how these factors affected mortality and/or egg productivity. In multiple and simple regression analyses, precipitation in June also showed a significant positive effect in *P. persimilis* and a positive but insignificant (simple regression analysis, $P = 0.205$) effect in *P. leucocorona*. As has been suggested for high precipitation in July and August, high precipitation in June may also has lowered larval mortality or enhanced female egg productivity.

In multiple regression analysis, the density of conspecific mines was suggested to have significant effects in *C. sapporella* and solitary *Stigmella* species, but the effects were opposite between them. In simple regression analysis, the density effect was significant only in *C. sapporella*. Thus, the density-dependent process was not explicit in the present leafminers. In contrast, previous studies suggested that resource shortage often occurs in leafminers and acts as a density-dependent mortality factor (Quiring and McNeil, 1984; Stiling et al., 1984; Bultman and Faeth, 1986; Auerbach and Simberloff, 1989; Auerbach et al., 1995; Eber, 2004). In the present oak, leaves are much larger than the size of mines; for example, *Phyllonorycter* mines of tissue-feeding stage do not exceed 5 cm^2, whereas average leaf size is 88 cm^2. Therefore, resource shortage seems to be unlikely for the present leafminers. In fact, even in 1998 when the density of *Phyllonorycter* species was very high, mean areas occupied by their mines would not exceed 15% of the leaf area.

5. Conclusion

The present study suggests that climatic factors played important roles in the population dynamics of leafminers on an oak, *Quercus dentata*, in northern Japan. Especially, high precipitation seemed to lower larval mortality of *Phyllonorycter* species, possibly by modifying leaf quality. Different leafminer species usually showed different patterns in their population dynamics, but two *Phyllonorycter* species showed similar patterns, indicating that they responded to climatic factors in similar manners. Density dependent effects were not explicit in the present leafminers.

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