

Yponomeuta evonymellus outbreaks in southern Finland: spatial synchrony but different local magnitudes

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Defoliations of *Prunus padus* by *Yponomeuta evonymellus* were monitored in two areas in southern Finland. During a long-term study (1980–1995) in the area with high peak defoliations, *P. padus* trees recorded two defoliation peaks, leading to complete defoliation of many trees. The negative relationship between pupal mass and current year tree defoliation during the peak years suggested shortage of food affected reproductive potential of *Y. evonymellus*. Furthermore, no delayed induced resistance was observed in these populations. Interannual correlations in degrees of defoliation experienced by individual trees were low, i.e. high defoliation in one year did not predict the degree of defoliation the following year. We also detected a sharp increase in parasitism rates with defoliation between years. In the other study area located about 150 km NW, only 4% of more than 200 study trees experienced defoliations higher than 50%. In this population, high defoliation of tree individuals in one year predicted low defoliation in the following year. In addition, rates of parasitism were less variable and intermediate compared to those in the high peak area. Altogether, the relatively rapidly operating negative feedback in the low peak — compared with the high peak area — was consistent with the difference between both areas in the levels of peak densities.

1. Introduction

We need to understand both temporal and spatial aspects of variation in population densities in order to explain the eruptive or “outbreak” nature of insect populations. Natural enemies, plant quality, and weather conditions, along with intra- and inter-specific competition, have been proposed as factors related to drastic temporal variation in populations of different insect species (*see* Barbosa & Schultz 1987 for an extensive review). Studies of different eruptive species have indicated that: (1) since weather patterns usually do not occur at regular intervals, causal explanations for cyclicity (i.e., peak densities at regular intervals) are usually linked to biotic interactions or intrinsic changes in population quality (Baltensweiler 1964, Baltensweiler *et al.* 1977, Haukioja *et al.* 1983, but *see* Hunter & Price 1998, Myers 1998); (2) when population declines begin before the shortage of food, the effect of natural enemies seems to be relevant for the population dynamics (Berryman 1996), although fluctuations in food quality can seldom be ruled out (Haukioja & Neuvonen 1987). Additionally, factors leading to the initiation of the eruptive phase have been less studied, but they may be not the same as those which cause the decline and contribute to the low density periods (Ruohomäki *et al.* 2000).

It has been observed for spatial variation that (1) the same insect species can show drastic variation in density in some areas but not in others (Tenow 1972, Baltensweiler *et al.* 1977), (2) all host-plant populations in the same region do not receive the same level of damage (Kaitaniemi 1996, Harrison 1997, Ruohomäki *et al.* 1997), and (3) all individual plants in a population do not support the same densities of defoliators or become equally defoliated even during the peak defoliation phase (e.g., Kaitaniemi 1996, Hunter *et al.* 1997). Weather variation among sites (Martinat 1987) and differences in plant quality following defoliation (Haukioja 1980) have been proposed as explanations for the observed patterns at a larger scale. Differences between outbreak and non-outbreak populations in herbivore or plant features have not received much attention. Moreover, since herbivore densities may result from different mechanisms at different spatial scales (Ruohomäki *et al.* 2000), studying both temporal

and spatial variation contributes to a better understanding of the processes of natural regulation of herbivorous insects populations, and thus to explain observed outbreak and non-outbreak patterns. Additionally, interannual consistency in the defoliation experienced by individual trees is essential to evaluate the hypotheses implying physiological changes in plants (Haukioja & Honkanen 1997), and the potential for herbivores to cause evolutionary changes in plants (but *see* Karban 1992).

This study focuses on the interaction between the bird cherry, *Prunus padus* L. (Rosaceae), and the small ermine moth, *Yponomeuta evonymellus* L. (Lepidoptera: Yponomeutidae) in southern Finland. *Yponomeuta* populations have been reported to display regular cycles in Finland (Junnikkala 1960, Leather & Lehti 1982), although outbreaks do not occur in all sites, and may be even restricted only to a few trees within a site (within tens of meters apart) (Junnikkala 1960). In the present study, defoliation levels, parasitism rates, and pupal masses as a measure of insect fecundity, were studied between 1980 and 1995, during and after two population peaks, in two closely situated *Y. evonymellus* populations in southern Finland. The same variables were studied for a shorter period in another population where high population densities were not recorded. The aims of the study were to (1) determine the relationship between defoliation levels and parasitism rates in populations of *Y. evonymellus* during outbreak periods, and (2) study the interannual consistency in levels of defoliation in individual trees in high and low peak populations.

2. Material and methods

2.1. Study species

Prunus padus is a deciduous tree which often grows in clumps of a few trees. The species is widely distributed in Europe, and it is by far the most abundant *Prunus* species in Finland (Leather 1991). *Prunus padus* has a remarkable ability to recover after insect defoliation, being able to produce new leaves later in the season after defoliation by *Yponomeuta evonymellus* (*see also* Leather 1996 and references therein).

Yponomeuta evonymellus is, in Finland, the most common lepidopteran species feeding on *P. padus* leaves (Junnikkala 1960, Leather & Lehti 1982). Eggs are laid in late summer and individuals overwinter as first instar larvae. In spring, *Y. evonymellus* larvae emerge from larval shields at the same time than *P. padus* trees are flushing leaves, and larval groups build web-like structures ("tents") that connect adjacent leaves (Junnikkala 1960, Leather 1986). *Yponomeuta evonymellus* larvae are monophagous on *P. padus* and feed within the tents to the 5th instar. Some of the most delayed larvae can complete their development in the new leaves produced after heavy defoliations. Afterwards, several feeding groups may join together and form large bunches of cocoons either on tree branches or at the tree base; the pupal stage lasts one to two weeks (Junnikkala 1960, Leather 1986).

2.2. Methods

Two different areas were monitored in this study. In a long-term study, levels of defoliation by *Y. evonymellus* were monitored between 1980 and 1995 in two *P. padus* populations (distance: ~ 8 km) located in southwestern Finland (60°N, 23°E), near the villages of Paimio (Ankka site) and Suksela. Trees were labelled at the beginning of the study. The only criterion used to select trees was that they were easily distinguishable individuals, thus, widespread bushes were excluded from the sample. In 1990, a new group of trees was included because several of the previously sampled trees had been cut (see Fig. 1 for sample sizes). Degrees of defoliation were visually estimated at 10% accuracy after completion of the larval stage in 10 years during the study period (Fig. 1). Defoliation between 1984 and 1989 was negligible in the area.

In 1981, 1982 and 1983, *Y. evonymellus* pupae were haphazardly collected from the pupal bunches of the sampled trees. Some of them were frozen, kept in cold, and afterwards defrosted and immediately weighed to estimate pupal masses. In 1980, pupal masses were estimated from size measurements by using the linear regression between (length × width) and mass obtained from an independent sample ($N = 42$, $R^2 = 0.56$, $P <$

0.0001). The rest of collected pupae were enclosed in plastic vials to obtain an estimate of parasitism rates. Numbers of cocoons producing parasitoids and moths were counted, and parasitism rates were then calculated as $100 \times [(\text{cocoons producing parasitoids})/(\text{total number of cocoons})]$. The most common parasitoid species were the Hymenoptera *Diadegma armillata* Gravenhorst and *Ageniaspis fuscicollis* Dalm, and the Dipteran *Agria mamillata* Pandelle. Distribution of pupal body masses and parasitism rates did not differ significantly from a normal distribution at $P = 0.05$ level.

We tested the existence of cyclicity in defoliations with repeated-measures ANOVA (proc GLM with REPEATED statement, SAS Institute 1996) using polynomial contrasts on defoliation rates in 6 individual trees from the Suksela population that had been sampled during nine years along the study period (data from 1994 could not be included).

Annual variation in pupal masses during the period 1980–1982 was analysed with ANOVA to determine if insect performance varied with defoliation. Multiple regressions with current and previous years' defoliation intensities were also used to test whether delayed effects occurred. Parasitism rates were analysed with repeated measures ANOVA.

A short-term study (1993–1994) was conducted in another *P. padus* population located in Reposaari, Pori (61°N, 22°E), where *Y. evonymellus* outbreaks have not been recorded. This population occupies a larger area and more individuals were available. Therefore, defoliation levels of the trees, and parasitism rates, and pupal masses of *Y. evonymellus* were determined for 228 *P. padus* individuals in this second study area.

3. Results

3.1. Long-term study

Defoliation levels caused by *Y. evonymellus* varied among years in Suksela and Ankka populations (Fig. 1). Although both populations reached the highest defoliation levels in the same study years, profiles were not exactly the same, and differences in mean defoliation level were statisti-

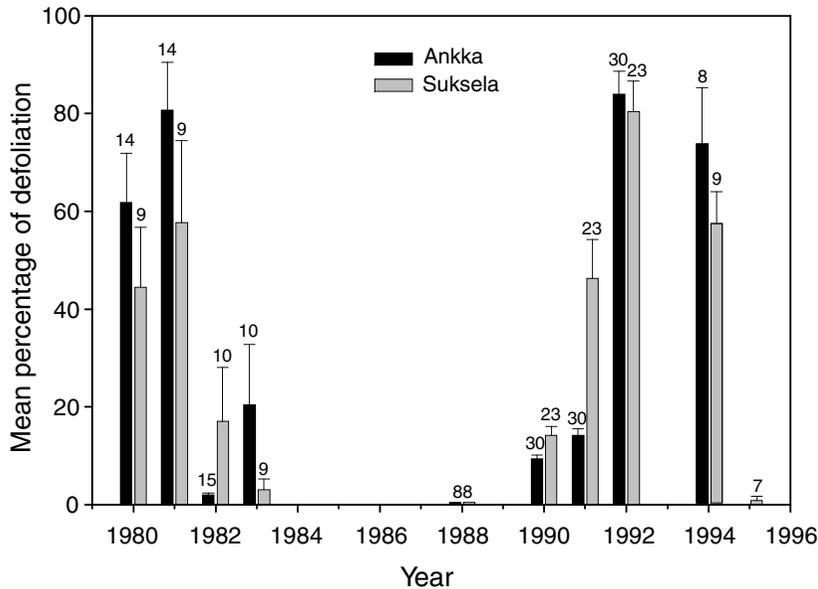


Fig. 1. Mean defoliation level (+SE) of *Prunus padus* trees located in the two long-term study sites monitored from 1980 to 1995. Sample sizes are indicated above histograms.

cally significant in 1991 ($\chi^2 = 11.5$, d.f. = 1, $P < 0.001$; Fig. 1). The more powerful repeated analysis could be conducted on the six trees in Suksela site that were monitored during nine study years between 1980 and 1995 (Fig. 2). Defoliation levels of these six trees followed a 3rd order polynomial series (repeated measures analysis, $F = 14.59$, d.f. = 1,5, $P = 0.012$; Fig. 2), indicating the existence of two peaks with an 11-year span between both peaks, the first of which had begun before the onset of this study.

During the years of highest defoliation (1981 and 1992), variation in the levels of defoliation among individual trees was considerable as indicated by the high coefficients of variation recorded during both the first peak (45.4 and 87.3, in Ankka and Suksela respectively), and the second one (30.4 and 37.4). The correlations between defoliation levels of individual trees during the two peak phases varied from null to significantly positive (Table 1). Scatter plots (figure not shown) revealed that the statistically significant correlations were due to the existence of a few trees with low defoliation level in both years. Instead, no obvious patterns appeared among the trees with

high defoliation during the peak years. Among-peak comparisons were possible only for six trees (Fig. 2), making it hard to detect any general pattern in repeatability of degree of defoliation among individual trees. At any case, individual variation was large. For instance, the S2 tree registered 100% defoliation in consecutive years during the first peak and then recorded only a 30% as maximum defoliation during the second peak, alternatively the S6 tree reached 100% in both outbreak phases, and the S10 tree recorded low defoliations in all the nine study years. When ranks of defoliation in 1981 and 1992 were compared, the correlation was not statistically significant ($r = 0.49$, $N = 6$, $P = 0.32$).

Mean pupal masses of *Y. evonymellus* did not differ between sites in any of the study years (Table 2). However, pupae were significantly heavier during the population increase, in 1980, than in 1981 or 1982 in both study sites (Table 2).

The relationships between pupal masses and tree defoliation during the period 1980–1982 were analysed to evaluate the effects of current and previous year's defoliation on potential fecundity of the herbivore. We observed a negative rela-

Fig. 2. Defoliation level experienced by the six study trees monitored during nine study years between 1980–1995 in Suksela site.

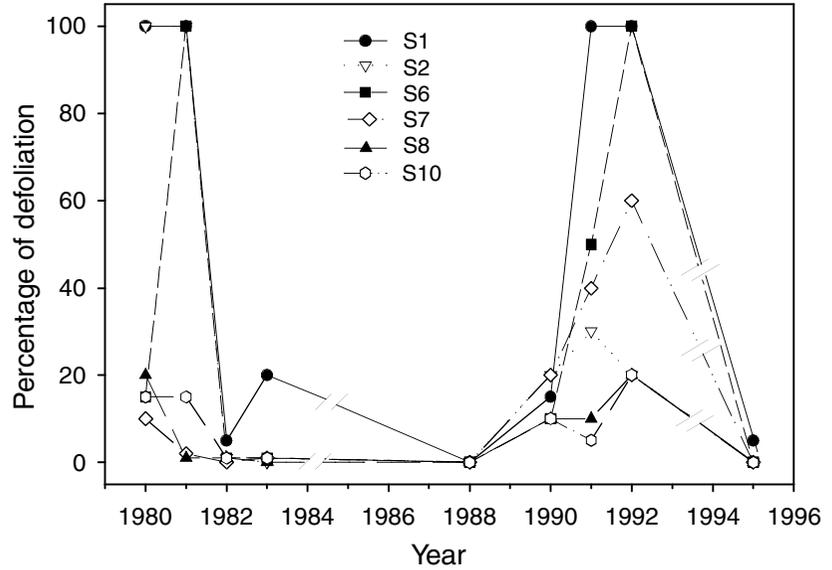


Table 1. Spearman correlation coefficients for defoliation levels recorded in individual trees during the two study population peaks. ** = $P < 0.001$, * = $P < 0.05$, ns = $P \geq 0.05$.

	1981	1982	1983	1991	1992
Ankka					
1980	0.81 ** ($N = 14$)	0.54 * ($N = 14$)	0.23 ns ($N = 9$)	1990	0.04 ns ($N = 30$)
1981		0.32 ns ($N = 14$)	0.29 ns ($N = 9$)	1991	-0.10 ns ($N = 30$)
1982			0.40 ns ($N = 10$)		
Suksela					
1980	0.54 ns ($N = 9$)	0.66 ns ($N = 9$)	-0.01 ns ($N = 9$)	1990	0.67 ** ($N = 23$)
1981		0.50 ns ($N = 9$)	0.40 ns ($N = 9$)	1991	0.47 * ($N = 23$)
1982			0.51 ns ($N = 9$)		

Table 2. Tree-specific mean *Yponomeuta evonymellus* pupal masses (mg fresh weight) recorded during the first outbreak period 1980–1982. Mean pupal masses did not differ between sites for any study year. Different letters in the same row indicate statistically significant differences between years ($P < 0.05$, Student–Newman–Keuls test).

Site	Sex	1980			1981			1982		
		<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE
Ankka	Males	13	29.85 ^a	1.3	15	21.67 ^b	1.1	12	19.98 ^b	0.5
	Females	11	39.55 ^a	2.2	15	26.90 ^b	2.0	10	28.21 ^b	0.9
Suksela	Males	9	32.45 ^a	1.2	9	19.96 ^b	1.9	6	21.47 ^b	1.3
	Females	9	41.02 ^a	1.6	9	24.56 ^b	3.1	5	28.66 ^b	1.8

tionship between mean pupal mass and defoliation levels of the tree from which they were collected. This relationship was statistically significant in 1981, when pupae collected from trees with a defoliation level lower than 20% were significantly heavier than those collected from trees with a defoliation level over 80% (Fig. 3) in both study sites. When a stepwise regression model was applied to the *Y. evonymellus* pupal masses recorded in 1981, having the current and the previous year defoliation of the tree as the independent variables, only the current year defoliation entered into the models explaining a high percentage of variance ($0.62 < R^2 < 0.99$) in all cases (Ankka: $F_{[\text{females}]} = 38.63$, $F_{[\text{males}]} = 19.65$, d.f. = 1,12, $P < 0.001$; Suksela: $F_{[\text{females}]} = 679.1$, $F_{[\text{males}]} = 92.2$, d.f. = 1,6, $P < 0.0001$). The higher importance of the current instead of previous year rate of defoliation on pupal masses was similar in 1982, too, but remained non-significant in the small data set. This suggested that starvation was probably related to population decrease, but delayed induced detrimental changes in leaf quality were not.

Parasitism rates were relatively low during 1980 (Fig. 4), with a statistically significant increase from 1980 to 1983 (time effect, $F = 60.5$, d.f. = 2,12, $P < 0.0001$; repeated measures ANOVA on 15 trees sampled in all years), and a significant interaction time \times site ($F = 4.7$, d.f. = 2,12, $P = 0.03$) due to the faster increase of parasitism in Ankka site than in Suksela in 1981 (Fig. 4). Parasitism rates were not significantly related to the current or previous year defoliation level of the tree in which the larvae had grown ($P > 0.05$ for both sites and all study years).

3.2. Short-term study

Although detailed data were not collected in 1992, occasional observations indicated that Reposaari population had its defoliation peak in 1993. Mean defoliation levels recorded at Reposaari site varied from 23% in 1993 to 16% in 1994, these levels being similar to those observed in the high peak populations during the increasing and decreasing phases of the outbreaks, and lower than defoliation levels reached during the peak years (Fig. 1). Defoliation levels of individual trees ranged from 0% to 90% in both study years. Con-

sistency in defoliation levels experienced by individual trees during the two consecutive study years was very weak ($R^2 = 0.04$, $F = 9.7$, d.f. = 1,226, $P = 0.002$). The scatter plot (Fig. 5a) revealed, however, some trends. When only the trees with defoliation levels below 50% in both study years were considered, defoliations in the latter year were positively related to previous year defoliation ($F = 12.4$, d.f. = 1,209, $P = 0.0005$), although the regression only explained 5.6% of variance. There were no trees showing defoliation levels higher than 50% in both the study years (Fig. 5a): trees that recorded defoliations higher than 50% in 1993 showed a very low defoliation level in 1994, and those recording levels higher than 50% of defoliation the second year had recorded between 20 and 40% in the previous year. When only trees with (at least) one recording of high (>50%) degree of defoliation were analysed, the relationship was negative and explained 66.6% of variance ($F = 29.8$, d.f. = 1,15, $P < 0.0001$; Fig. 5a). In fact, the probability of recording a lower defoliation the second year increased with the level of defoliation recorded in the previous season (Fig. 5b), being more evident when defoliation was higher than 50%. This suggested that defoliated trees become less suitable or preferred for *Y. evonymellus* in the low peak population. This result clearly differed from the high peak populations where null or positive relationships were found between defoliations in consecutive years.

Mean pupal masses of *Y. evonymellus* recorded in 1994 were not related to intensities of current year or previous year defoliations.

The rate of parasitism varied between the study years, with parasitism rates increasing slightly between 1993 (mean \pm SE: $27.5 \pm 1.4\%$) and 1994 ($34.4 \pm 1.1\%$). Furthermore, parasitism rates in 1994 were positively related to tree defoliation in the same year ($F = 20.8$, d.f. = 1, 159, $P < 0.0001$), while the relationship with the previous year defoliation was not statistically significant ($F = 0.2$, d.f. = 1, 159, $P = 0.66$).

4. Discussion

Yponomeuta spp. are not usually included within the classic eruptive species, although they share typical characteristics with several outbreak spe-

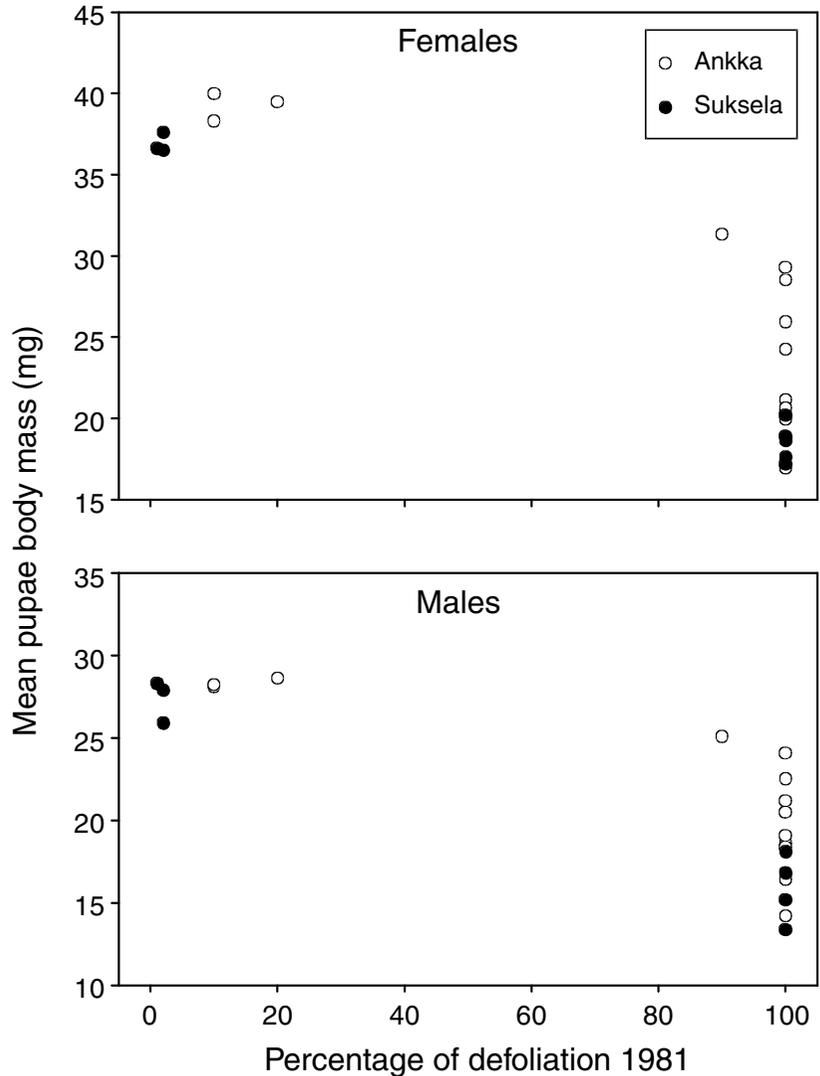


Fig. 3. Relationship between mean *Y. evonymellus* pupal masses (males in panel a, females in panel b) and the defoliation level of the *P. padus* individual in which they grew. Data from Ankka and Suksela site are represented by different symbols.

cies (Nothnagle & Schultz 1987): they are univoltine, lay eggs in masses, and larvae feed on young growing leaves of deciduous trees. Here we demonstrated the existence of two peaks of defoliation by *Y. evonymellus* between 1980 and 1995, leading to complete defoliation of many *P. padus* trees in two populations in Southern Finland (Fig. 1). An increment of defoliation was also observed during the same years in Reposaari population located 150 km NW from the others, illustrating that synchrony in abundance variation of *Y. evonymellus* populations remained at short and intermediate distances (Hanski & Woiwod 1993). However, the magnitude of peak defoliations re-

corded differed from place to place, and Reposaari population, with a maximum average defoliation lower than 25%, might be even not considered as eruptive. Thus, although there is a spatial synchrony in the fluctuation of *Y. evonymellus* populations, the magnitude of their variations is not the same (see also Leather & Lehti 1982). This suggested the existence of differences among sites in some factor(s) related to *Y. evonymellus* population dynamics, and in this study we examined some potential factors related to insect population fluctuations (Haukioja *et al.* 1983) such as food availability, delayed induced resistance, and parasitism.

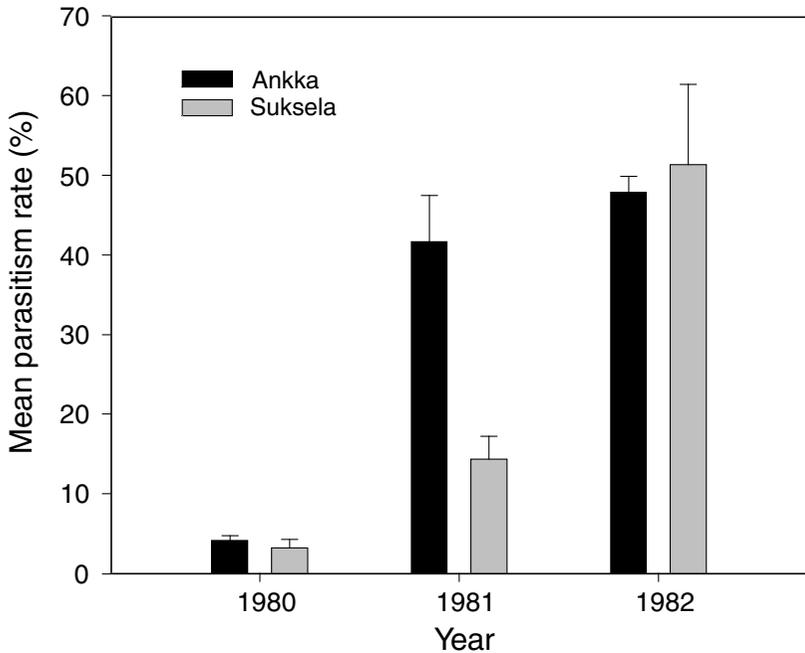


Fig. 4. Parasitism rates during the first outbreak period (1980–1982) in the two long-term study sites.

Previous year defoliation did not explain *Y. evonymellus* performance (measured as pupal mass) or parasitism in individual trees at any of the studied sites. This indicated absence of delayed induced resistance in *P. padus*, and thus, one of the possible causes of multiannual cycles of herbivores population densities (Haukioja & Honkanen 1997) was excluded. The negative relationship between pupal mass and current year tree defoliation suggests that shortage of food resources affected reproductive potential of *Y. evonymellus* during the high peak defoliation years, while this was not obvious in the low peak area where no relationship was found. Thus, the decrease in *Y. evonymellus* densities may be partially attributable to lower reproductive potential of adults (and probably lower larval survivorship) caused by starvation during the high peaks of defoliation.

Another important difference between the high and low peak populations studied was related to parasitism. In the low peak population parasitism rates were higher in trees with higher defoliation levels, something that was not observed in the other populations. This inverse density-dependent mechanism acting without delay might explain the absence of high peak defoliations in Reposaari population. Furthermore, in the high peak area the average parasitism rate varied with degree of de-

foliation during the peak years (Fig. 4), but they were more stable and of intermediate level in the low peak area. More stable parasitism could prevent herbivore population to vary drastically, and supports the idea that parasitoids are important in controlling those populations that do not deplete their food resources (Berryman 1996).

In addition, defoliation patterns of individual trees could also contribute to explain the difference in the magnitude of peak defoliations between areas. Defoliations of individual trees in the low peak area displayed negative feedback after extensive foliar damages, while severely defoliated trees in the high peak populations did not. None of the trees in Reposaari population recorded defoliations higher than 50% in the two consecutive study years (Fig. 5a), and there was a negative relationship indicating that high defoliation in one year predicted low defoliation the following year. Instead, in the high peak area, a much smaller sample of trees displayed individual trees having even total defoliations during consecutive years (Fig. 2), and even during both peaks. The causes of this difference between areas are uncertain but variation in parasitoids behaviour, as discussed above, and other factors such as changes in phenology or behaviour of ovipositing females could be related.

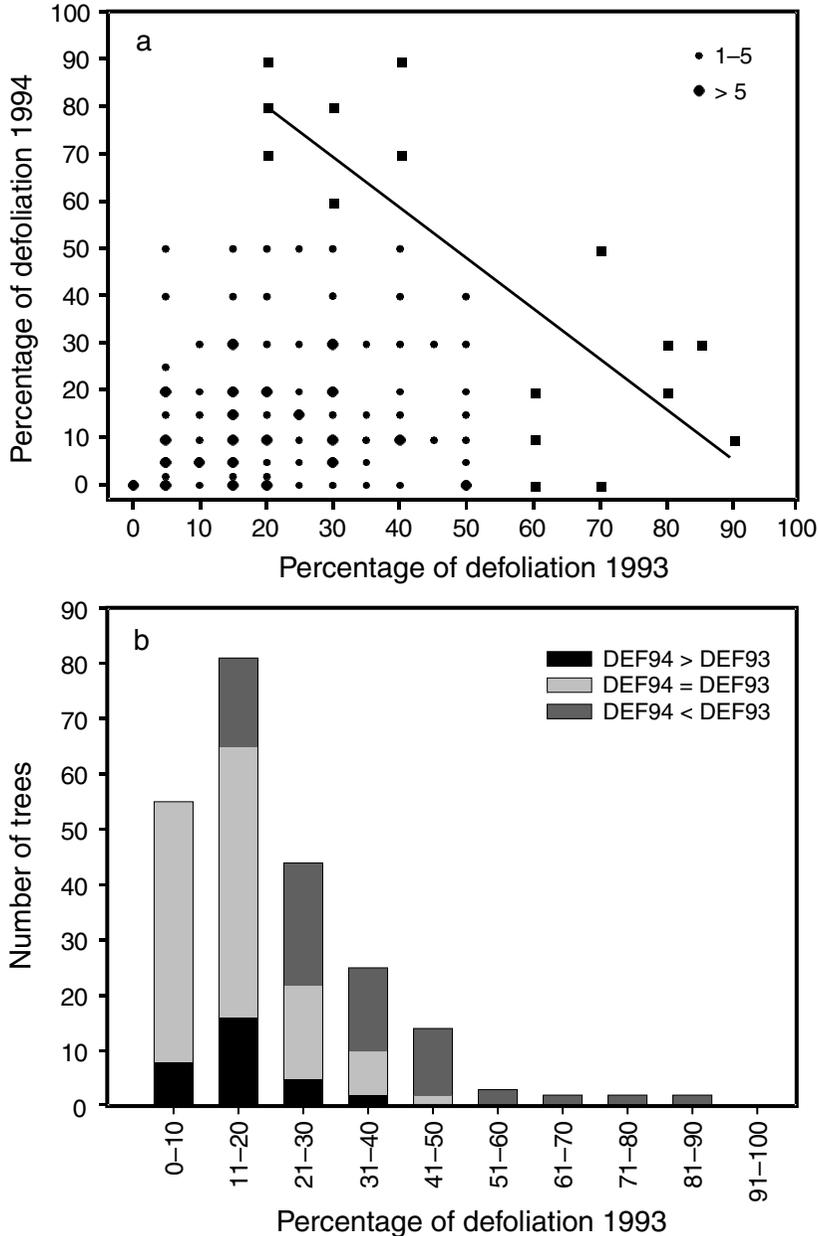


Fig. 5. Defoliation levels experienced in two consecutive years by the $N = 228$ study trees in the low peak defoliation site of Reposaari. — a: Scatter plot and regression line for trees with defoliation level higher than 50% in one study year (represented by squares, with one square = one observation). Due to high number of ties in the data set small dots were used to symbolize points with 1 to 5 observations, and big dots represent more than 5 observations. — b: Probability that tree defoliation level increases, decreases or remains stable with respect to defoliation recorded the previous year. Defoliation was considered similar when the difference between both study years was not higher than 10%.

Further studies are still needed to determine the causes giving rise to *Y. evonymellus* cycles. We suggest here that comparison of biotic and

abiotic factors affecting population dynamics in sites differing in their maximum defoliations will put insight into this plant-herbivore interaction.

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