

Consequences of defoliation on phenological interaction between *Epirrita autumnata* and its host plant, Mountain Birch

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Summary

1. Defoliation-induced changes in the budbreak phenology of Mountain Birches (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman), and their effects on herbivore performance, were investigated during an outbreak of the spring-feeding geometrid, *Epirrita autumnata* (Bkh.).
2. Total defoliation (followed by refoilation) by *E. autumnata* larvae was required to achieve significant delaying of budbreak of Mountain Birch one year after damage.
3. Delayed budbreak has potentially deleterious effects on herbivore performance. However, *E. autumnata* larvae show phenotypic responses that increase the synchrony between larvae and leaves: high larval density, a prerequisite for severe defoliation, delays egg hatch in the following year.
4. Late hatching larvae performed as well on birches with delayed budbreak due to the previous year's total defoliation as did early hatching larvae on birches with earlier budbreak.

Key-words: *Betula*, inducible responses, insect–plant interactions, larval crowding, outbreak

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Introduction

Natural variation in timing of budbreak may occur at many levels: among plant species (Mitter *et al.* 1979; Lechowicz 1984; Jordano & Gomariz 1994; Stoyenoff, Witter & Montgomery 1994), among individuals within a species (Crawley & Akhteruzzaman 1988; Hunter 1992; Senn, Hanhimäki & Haukioja 1992; Quiring 1994), among branches within individual plants (Tuomi *et al.* 1989; Carroll & Quiring 1994) and among buds within a branch (Isaev, Baranchikov & Malutina 1988; Quiring 1993). In addition, after budbreak, the rate at which leaf characteristics change varies among species (Raupp, Werren & Sadof 1988; Hunter & Lechowicz 1992).

There are at least two possible consequences of this phenological variation to herbivores. First, if herbivores have a poor ability to disperse, or cannot resist starvation, they face an increased risk of mortality and reduced growth in the case of their asynchrony with host phenology (Feeny 1970; Raupp *et al.* 1988; Aide & Londoño 1989; Hunter 1990; Hunter & Lechowicz 1992; Quiring 1992; Stoyenoff *et al.* 1994). This is especially relevant for larvae of species that feed on young expanding leaves, when the larvae may not survive at all on mature foliage of their natural food

plants (Feeny 1970; Raupp *et al.* 1988; Quiring 1992; Jordano & Gomariz 1994). Second, if herbivores have a good dispersal ability, or can resist starvation, they may have better chances of finding a suitable host among phenologically variable host individuals (e.g. Floate, Kearsley & Whitham 1993).

Accordingly, host plant phenology partially determines the realized degree of herbivory (e.g. Crawley & Akhteruzzaman 1988; Hunter 1992; Floate *et al.* 1993; Connor *et al.* 1994; Quiring 1994; Mopper & Simberloff 1995), but the converse may also be true: defoliation by herbivores may modify plant phenology (Benz 1974; Heichel & Turner 1976; Haukioja *et al.* 1988b; Tuomi *et al.* 1989). This second possibility has potential repercussions for herbivore populations.

In this paper, we investigated herbivore-induced changes in the phenology of Mountain Birches (*Betula pubescens* ssp. *tortuosa*) and assessed their importance in the performance of an eruptive geometrid (*Epirrita autumnata*) at different population sizes and phases of its cycle. We also examined the importance of delayed inducible resistance (DIR) of birches as a possible factor that modifies the consequences of phenological asynchrony between larvae and foliage.

Materials and methods

STUDY ORGANISMS

Epirrita autumnata is a spring feeder whose northern populations fluctuate in 9–10-year intervals, resulting in severe defoliation of Mountain Birch forests during population peaks (Tenow 1972; Haukioja *et al.* 1988a; Bylund 1995). Its larvae are polyphagous, but Mountain Birch is the most important food plant in northern Europe, owing to its relative abundance. *E. autumnata* overwinters as an egg, and its larvae hatch at the time of birch budbreak and feed for 4–6 weeks. Pupal period lasts for 6–9 weeks, after which females lay eggs (usually singly) among the lichen cover of trees (Tenow & Bylund 1989; Tammaru, Kaitaniemi & Ruohomäki 1995).

Previous studies have identified the importance of synchrony between egg hatch and budbreak of Mountain Birches for *E. autumnata* larvae. Even a slight delay in larval development may result in considerably lowered growth rates, which is associated with rapid declines in nutrient and water content in birch leaves, and a rapid increase in leaf toughness (Ayres & MacLean 1987).

Manual defoliation of Mountain Birch induces both delayed budbreak (Haukioja *et al.* 1988b; Tuomi *et al.* 1989) and DIR (reviewed in Neuvonen & Haukioja 1991), which have both been suggested to play a role in the population dynamics of *E. autumnata*. On the other hand, high larval density, which is a precondition of extensive defoliation, also induces a phenotypic crowding effect in larvae, and this may alleviate the effects of defoliation-induced responses in the host (Haukioja *et al.* 1988b). Compared with solitary larvae, crowded larvae perform relatively better on poor quality diets, and may be better able to compensate for the effects of DIR than solitary larvae. In addition, high larval density prolongs the pupal period, which results in late emergence of adults, later egg-laying in the autumn and delayed egg hatch in the following spring (Haukioja *et al.* 1988b).

MOUNTAIN BIRCH PHENOLOGY AND LEAF QUALITY AFTER AN *EPIRRITA AUTUMNATA* OUTBREAK

On 29 May 1993, at the time of *E. autumnata* egg hatch, four experimental sites, 5–25-km apart, were chosen from an area of an outbreak near Lake Porttipahta in northern Finland. The sites at Kunasenvaara (67°59'N, 26°40'E), Mäntypää (67°57'N, 26°50'E), Mustaselkä (68°01'N, 26°36'E) and Tenniövaara (67°51'N, 26°24'E) were located at the perimeter of the area where high larval densities had been observed at the beginning of the outbreak in 1992. From each site, 30 mature trees with a manageable height for larval rearings (1.5–3 m, see below) were selected. No differences could be observed in larval densities between trees with different size and height. Half of the trees at each site were randomly

assigned to pyrethroid spraying to prevent defoliation (5 ml *Folition* (Bayer, Germany), containing fenitrothion as a killing agent, in 10 l water), and the other half were sprayed with water. To ensure uniform distribution of trees with different sprayings within the sites, randomizations were made for groups of two to four nearby trees. After the larval feeding period, defoliation degrees were visually estimated as the percentage of the canopy consumed. Pre-experiment defoliation degrees at the study sites had been low before 1992, and in 1992 they were half from those observed in this study (see Results). Our unpublished data show that previous defoliation had not induced any changes in leaf quality, except at Mustaselkä, where DIR probably was present already in 1993 (P. Kaitaniemi, K. Ruohomäki & E. Haukioja, unpublished observations). Therefore, we do not discuss on the effects of DIR as regards Mustaselkä.

In 1994, larval performance was measured on individuals whose hatching was synchronized in relation to the budbreak of trees that had remained undefoliated in the previous year owing to pyrethroid spraying, and on individuals with delayed hatching in relation to the budbreak. Growth trials with synchronized larvae were started on 21 May 1994, which was at the beginning of the natural egg-hatching period (single wild first instar larvae were observed in some trees). Eggs were enclosed in a mesh bag in the top 60 cm of each experimental tree. Within each bag, there were 20 eggs (belonging to 20 different broods), which had been preadjusted to hatch within a few hours (Haukioja & Neuvonen 1985a).

On the same day, when the accumulated thermal sum above 5 °C (dd5 hereafter) was 25 (based on temperature recordings of a weather station located 60 km south of the sites), budbreak phenology of trees was classified by estimating the length of unfurling leaves in relation to the length of bud scales (see Sulkioja & Valanne 1987). Six categories, ranging from 0 (bud still closed) to 1 (with tips of the outcoming leaves as long as bud scales) were used, which was a slightly more precise scale than that presented in Sulkioja & Valanne (1987).

In order to test for effects of delayed hatching, 2 weeks later (dd5 was 54) an extra bag was put on all control trees and trees defoliated in the previous year that had enough leaves in a suitable branch. This was done at two experimental sites where wild larvae were still observed hatching from the eggs. Because smaller bags were used this time, only 10 eggs were enclosed per bag. The density of delayed larvae per amount of foliage was somewhat higher, but they still had an excess of foliage. Use of bags has not been found to affect leaf quality as food for *E. autumnata* larvae (Hanhimäki & Senn 1992; Kaitaniemi, Ruohomäki & Haukioja 1997). This suggests that, for example, temperatures inside the bags are not different from outside temperatures to the extent of biasing the results of rearing experiments.

To estimate the rate of leaf expansion between the dates when synchronized and delayed larval rearings began, the phenological state of buds was classified with a scale comprising five categories ranging from 1 (see above) to 3 (leaves fully emerged), again modified from the classification of Sulkinoja & Valanne (1987). The leaf expansion rate was described as the difference between the phenological states of the buds (i.e. difference in leaf lengths) on the two dates.

At the end of the larval period, the bags in both phenology groups were checked daily for pupating larvae, which were then removed and allowed to pupate in 48-ml plastic vials (one larva per vial) with *Sphagnum* moss. Pupae were weighed 2 weeks later. Pupal mass was used as an index of larval performance, because it strongly correlates with *E. autumnata* reproductive capacity (Haukioja & Neuvonen 1985b; Tammaru, Ruohomäki & Saikkonen 1996).

EFFECTS OF THE INSECTICIDE

Possible effects of the pyrethroid on tree phenology were checked in a separate experiment at the Kevo Subarctic Research Station (69°45'N, 27°01'E). This site was located outside the current outbreak area and had low larval density. Thirty trees were chosen and randomly assigned to insecticide- or water-spraying treatments on 4 June 1993, which corresponded phenologically to sprayings in the outbreak area.

The insecticide did not affect the timing of bud-break the following year: at the start of budbreak (on 24 May 1994; when dd5 was 3.4, based on the temperature readings of a local weather station in Kevo), the mean phenological state of buds was 0.2 both in the pyrethroid-sprayed and in the water-sprayed trees and all the trees belonged to two successive phenology classes.

The insecticide spraying may have led to a slight increase in leaf quality in the following year (Kaitaniemi *et al.* 1997), but no leaf quality comparisons were made between insecticide- and water-sprayed trees, except for differences between them for synchronized and delayed larvae. This comparison was also repeated without the use of an insecticide in the experiment below.

RESPONSES OF CROWDED AND SOLITARILY REARED LARVAE TO CHANGES IN LEAF QUALITY

In spring 1994, 30 mature, low stature (1–2-m tall) Mountain Birches were selected near the Kevo Research Station. To induce DIR, 15 trees were subjected to experimental *E. autumnata* defoliation, and the nearest 15 similar neighbouring trees of each of the defoliated trees were left as intact controls, so that the trees formed distinctive pairs sharing a common microsite (mean distance \pm SD of trees in pairs was 5.4 ± 2.8 m). Larval defoliation was induced by attaching wooden sticks with large numbers of *E.*

autumnata eggs into the trees. The larvae hatching from the eggs were allowed to defoliate the trees freely until pupation. Owing to high rates of parasitism by the hymenopteran *Cotesia jucunda* (Marshall), defoliation almost ceased when most larvae were in their third to fourth instar. Therefore, the defoliation degree of trees (5–25%) was mostly below that of trees in the natural outbreak in the Lake Porttipahta area.

In the following year, the performance of larvae reared in the laboratory both alone and in groups was tested on the foliage of these trees. The performance test was replicated at different phenologies: hatching of half of the test larvae was synchronized with birch leaf flush and hatching of the other half was delayed by 13 dd5. All the larvae belonging to given phenology treatments were reared in 48-ml plastic vials either as singletons or in groups of three. They were fed every third day with an excess of birch leaves, initially from non-experimental trees, but subsequently on foliage from the experimental trees (see below). The rearing temperature was alternated between 10 and 20 °C to track the temperature outdoors, until the larvae reached the fourth instar. Because rearing of synchronized larvae was initiated earlier, the larvae received phenologically younger leaves in relation to their developmental stage throughout the rearing period than did the delayed larvae (leaves were taken from different trees on each feeding date). Finally, the development of larvae was adjusted with temperature chambers so that first the synchronized larvae moulted to the fifth instar on the same morning, and 30 dd5 (outdoor temperature) later the delayed larvae did the same. Thereafter, the fifth instar larvae were fed with foliage excised from the petioles of experimental (control or defoliated in the previous year) trees until pupation. Six singly grown and three crowded larvae were used to test the quality of each experimental tree. To avoid possible effects of leaf excision on leaf quality experienced by the delayed larvae, five trees, which did not have enough untouched short shoots, were excluded for the delayed rearings and two trees were omitted for the group rearings. This was done even though excising the leaves by scissors from petioles has not been found to induce changes in the quality of the remaining foliage (K. Ruohomäki & S. Hanhimäki, unpublished data).

STATISTICAL ANALYSIS

Relationships between the degree of defoliation, bud-break phenology and larval performance were analysed with Spearman rank correlations calculated separately for each of the four outbreak sites. Only the defoliated trees and the synchronized larvae were used in these correlations, because these data were available from all sites.

Comparisons of larval performance between synchronized and delayed larval phenology treatments at

the outbreak area, and between control trees and trees defoliated in the previous year, were conducted with one-way ANOVAS. The two sites where these experiments were conducted (Kunnasenvaara and Mustaselkä) had different defoliation histories, and the analyses were therefore conducted separately. Defoliation degrees had been high at Mustaselkä before 1993, when the experiments started (unpublished data), and Mustaselkä was the only site where larvae totally defoliated some of the experimental trees. Refoliation occurred in totally defoliated trees and in some branches of two moderately defoliated trees during the summer of 1993. The trees of Mustaselkä were therefore classified into the following three groups: control, moderate defoliation and total defoliation. Two trees with 85% and 90% defoliation were included in the group of totally defoliated trees, because the remaining foliage suffered from severe desiccation and consequent necrosis. Dunnett's test was used for comparing moderately and totally defoliated trees with control trees after the ANOVA (Winer 1971).

The analyses were also conducted separately for the bags with delayed and synchronized larvae, because lack of suitable branches prevented use of all trees for both groups, and because larval densities in these groups were different.

In the experiment with experimentally generated larval defoliation at Kevo, the control trees were paired with the nearest defoliated trees to account for possible pair-specific differences in microsites, or in defoliation degrees. These pairs were then used as a block term in a multivariate ANOVA (MANOVA) with repeated measures (larvae in synchrony or delayed in relation to birches) in addition to treatment (defoliation or not) and larval density (single or crowded). Roy's greatest root was used as a test statistic

(Scheiner 1993). Assumptions of normality and homoscedasticity were tested for the dependent variables (pupal masses of delayed and synchronized larvae) individually (Lindman 1992, p. 330; Scheiner 1993, p. 110) with Shapiro-Wilk's tests (Proc Univariate, SAS Institute Inc. 1990) and Cochran's tests (Winer 1971), respectively.

Before the analyses of larval performance were conducted, the differences between male and female pupal masses were removed by calculating the ramet-specific LSMEANS values (Proc GLM, SAS Institute Inc. 1990) such that the pupal masses were adjusted for differences between sexes.

Results

BUDBREAK OF MOUNTAIN BIRCHES AFTER AN
EPIRRITA AUTUMNATA OUTBREAK

There was no overall difference in timing of budbreak or in leaf expansion rates between control and defoliated trees (Table 1). Totally defoliated trees at Mustaselkä were an exception: their leaves flushed later and expanded more slowly than those of other trees (Table 1).

Despite the lack of overall differences, there were relationships between the degree of previous year defoliation and the current year budbreak phenology at each site: timing of budbreak and leaf expansion rate correlated mostly negatively, and in many cases significantly, with the degree of defoliation (Fig. 1). Defoliation did not cause a significant overall delay in bud development, and this suggests that the natural defoliation degrees experienced by the trees were not sufficient to induce responses that would have outweighed the normal phenological variation of undefoliated (insecticide-sprayed) trees.

Table 1. Effects of previous year larval defoliation on the budbreak phenology of mountain birches in 1994. Phenological state indicates the length of outcoming leaves in relation to the length of bud scales at the start of synchronized *E. autumnata* rearings on the same trees. The leaf expansion rate is the mean difference between the given phenological state, and the phenological state on 5 June when rearings of delayed *E. autumnata* larvae were started (see text).

Location	Treatment	Phenological state of buds on 21 May	Kruskal-Wallis test result	Leaf expansion rate	Kruskal-Wallis test result
Kunnasenvaara	Control	0.4	$P = 0.6968$	1.4	$P = 0.9100$
	Defoliation	0.4		1.5	
Mäntypää	Control	0.5	$P = 0.9358$	1.5	$P = 0.3075$
	Defoliation	0.5		1.5	
Tenniövaara	Control	0.4	$P = 0.7036$	1.6	$P = 0.2407$
	Defoliation	0.3		1.5	
Mustaselkä	Control	0.6	$P = 0.0251$	1.5	$P = 0.0312$
	Moderate defoliation	0.4		1.4	
	Total defoliation	0.1		0.9	

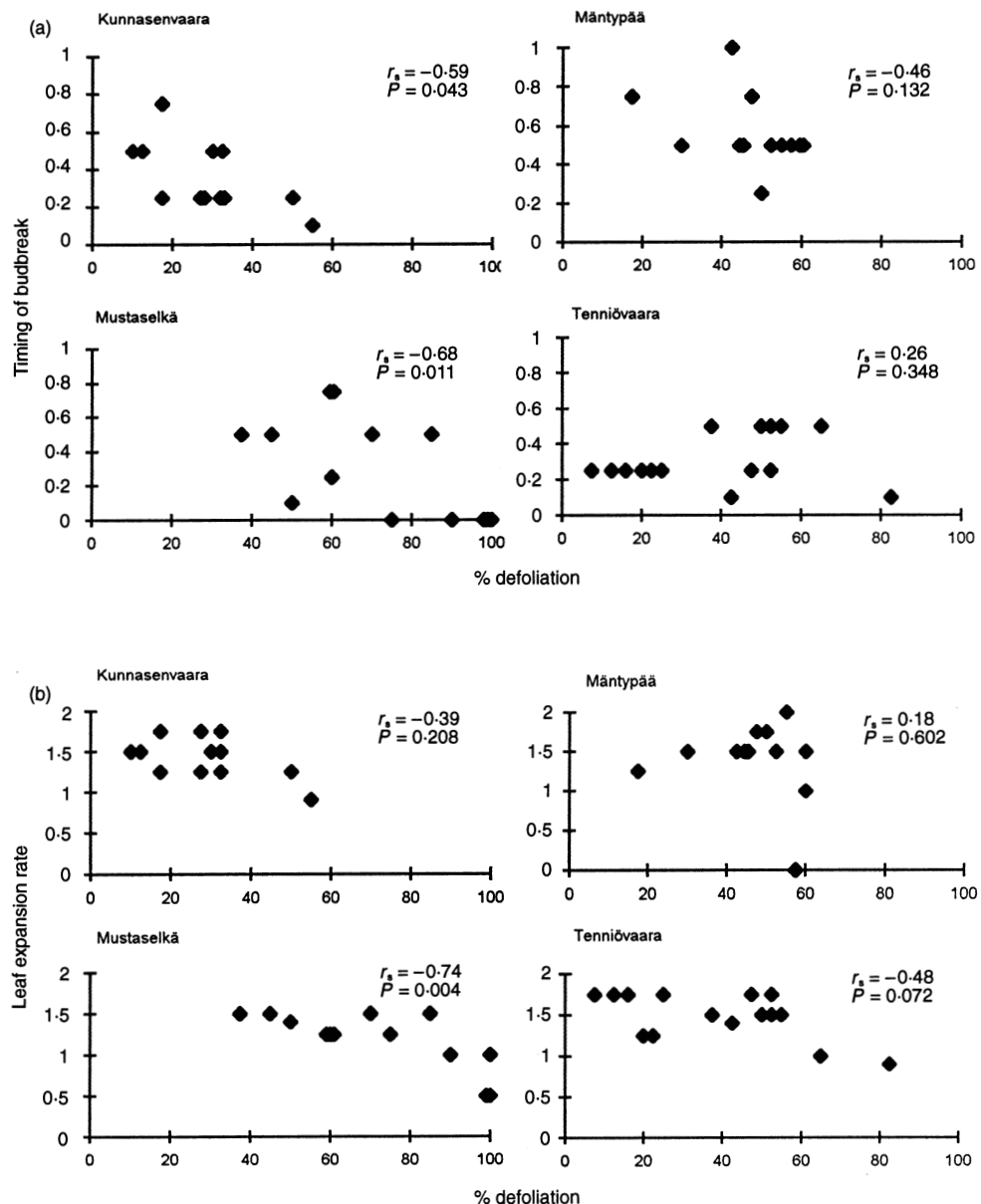


Fig. 1. Spearman correlation coefficients for the relationships of previous year's defoliation degrees (a) and leaf expansion rates (b) with timing of Mountain Birch budbreak (represented as the length of outcoming leaves in relation to the length of bud scales) at four sites within an outbreak area of *E. autumnata*. Leaf expansion rates are represented as the difference between leaf length on two dates in spring (see text for details).

RESPONSES OF *EPIRRITA AUTUMNATA* TO BUDBREAK PHENOLOGY

The degree of synchrony between *E. autumnata* larvae and Mountain Birch clearly affected *E. autumnata* performance. Larvae with delayed phenology had *c.* 30% smaller pupal masses than larvae whose hatch had been synchronized with birch phenology (Fig. 2). However, there was an exception: pupal masses of delayed larvae in totally defoliated trees at Mustaselkä were equal to those of synchronized larvae, and, according to a Dunnett's test, significantly higher than masses of delayed larvae on control trees (Fig. 2; for overall differences $F_{2, 16} = 17.38$, $P = 0.0001$). This anomaly was obviously caused by the later flushing of

those particular trees (Table 1): the delayed larvae were actually well synchronized with the totally defoliated trees. Similarly, performance of the synchronized larvae at Mustaselkä was also best in the totally defoliated trees, although the difference compared with the control was not significant (Fig. 2; for overall differences $F_{2, 26} = 2.57$, $P = 0.0956$).

At Kunnasenvaara, which had trees with less defoliation and no delays in budbreak in previously defoliated trees, the performance of delayed larvae in the defoliated trees was relatively poor (for trees common to both phenology groups: $F_{1, 25} = 3.06$, $P = 0.0926$) compared with the performance of synchronized larvae ($F_{1, 25} = 0.30$, $P = 0.5908$; Fig. 2).

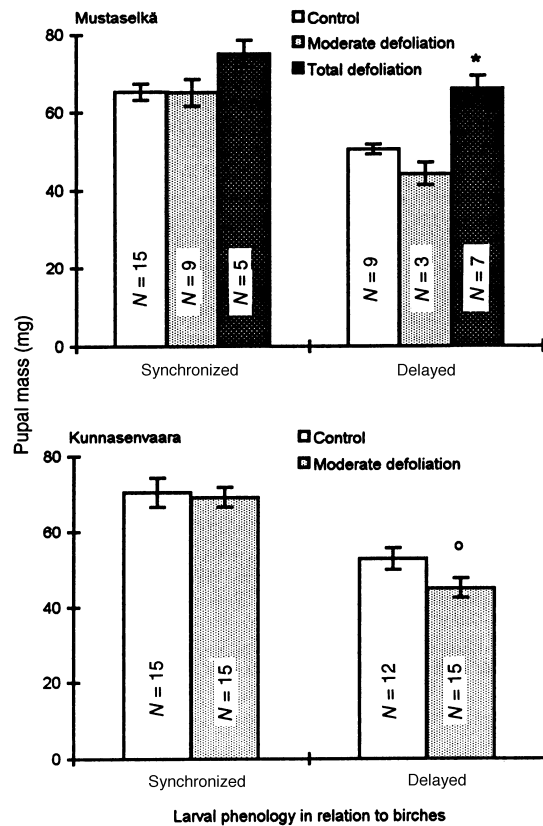


Fig. 2. Performance of *E. autumnata* with either synchronized or artificially delayed egg hatch in relation to budbreak of undefoliated Mountain Birches at two sites within an *E. autumnata* outbreak area in 1994. Defoliation of control trees in 1993 was prevented by insecticide sprayings. Trees defoliated totally in early summer 1993, and two trees with moderate defoliation, had a second flush of leaves. * shows a significant ($P < 0.05$, Dunnett's test) and ° a marginally significant ($P < 0.1$, *F*-test; see text) difference between control and defoliation. Means \pm SE are given.

Table 2. MANOVA table for the repeated measures tests of the effects of defoliation (Def), larval crowding and phenology on performance (pupal mass) of *E. autumnata* larvae. Pair is a term for adjacent pairs of control and defoliated trees sharing a common microsite

Source of variation	DF	MS	<i>F</i>	<i>P</i>
Def*	1	113.1	1.94	0.1917
Crowding†	1	4266.4	71.32	0.0001
Pair	13	79.3	1.50	0.3021
Def × Crowding	1	35.1	0.67	0.4416
Pair × Def	11	58.5	1.11	0.4623
Pair × Crowding	11	59.8	1.13	0.4494
Error	7	52.7		

	Roy's greatest root	<i>F</i>	Num df	Den df	<i>P</i>
Phenology	1.85	12.94	1	7	0.0088
Phenology × Def‡	0.11	1.19	1	11	0.2988
Phenology × Crowding§	1.27	13.95	1	11	0.0033
Phenology × Pair	3.20	1.72	13	7	0.2397
Phenology × Def × Crowding	0.17	1.19	1	7	0.3109
Phenology × Pair × Def	1.90	1.21	11	7	0.4147
Phenology × Pair × Crowding	1.34	0.86	11	7	0.6083

* Pair × Def used as an error term.

† Pair × Crowding used as an error term.

‡ Phenology × Pair × Def used as an error term.

§ Phenology × Pair × Crowding used as an error term.

The correlations of timing of budbreak and leaf expansion rate with pupal masses were close to zero or negative, and none of them reached statistical significance (Fig. 3). Presumably, the degree of defoliation had to approach 100%, as in the totally defoliated trees of Mustaselkä, to delay budbreak enough to affect *E. autumnata* performance.

PERFORMANCE OF *EPIRRITA AUTUMNATA* LARVAE AT DIFFERENT REARING DENSITIES

In accordance with the above results, the degree of synchrony between birch and larvae had a significant effect on larval performance: singly grown larvae with delayed phenology produced c. 15% smaller pupae than those with good synchrony in relation to birches (Table 2, Fig. 4). However, pupal masses of crowded larvae with different phenologies were nearly equal, which indicates that the effect of host phenology was overridden by the crowding effect (Table 2, Fig. 4). No significant indication of DIR was obtained, because all larvae performed as well on defoliated trees as on control trees. Thus, unlike on defoliated trees at Kunnasenvaara, no trend in the efficacy of DIR in relation to larval phenology could be detected (Table 2, Fig. 4).

Discussion

DETERMINATION OF MOUNTAIN BIRCH BUDBREAK AND *EPIRRITA AUTUMNATA* EGG HATCH

Primordial buds of Mountain Birch develop the year before leaf flush. The developing bud initials become visible during the latter half of the *E. autumnata* feeding period, and bud scales are still soft, when larvae stop feeding. Thus, *E. autumnata* defoliation can affect the development of buds, as does the prevailing weather (Senn *et al.* 1992). For example, defoliation may influence the amounts of carbon and nutrients available for developing buds (Tuomi *et al.* 1984), and it may affect their later ability to take up stored nutrients (Honkanen & Haukioja 1994).

Previous experiments have shown that delayed budbreak occurs in Mountain Birches in the year after total manual defoliation (Haukioja *et al.* 1988b; Tuomi *et al.* 1989). In the experiment of Haukioja *et al.* (1988b) the delay of budbreak after total defoliation was 17 dd5 (calculated from unpublished information). Our results also showed negative correlations between moderate natural defoliation due to larval feeding and the timing of budbreak, but these relationships did not necessarily exceed the normal among-tree variation in flushing phenology. Buds of trees that refoliated after total defoliation had the most delayed budbreak, with consequent effects on *E. autumnata* performance in the following year. They reached the same stage as the buds of the other trees approximately at the time as our delayed rearings were started, i.e. they burst almost 30 dd5 later.

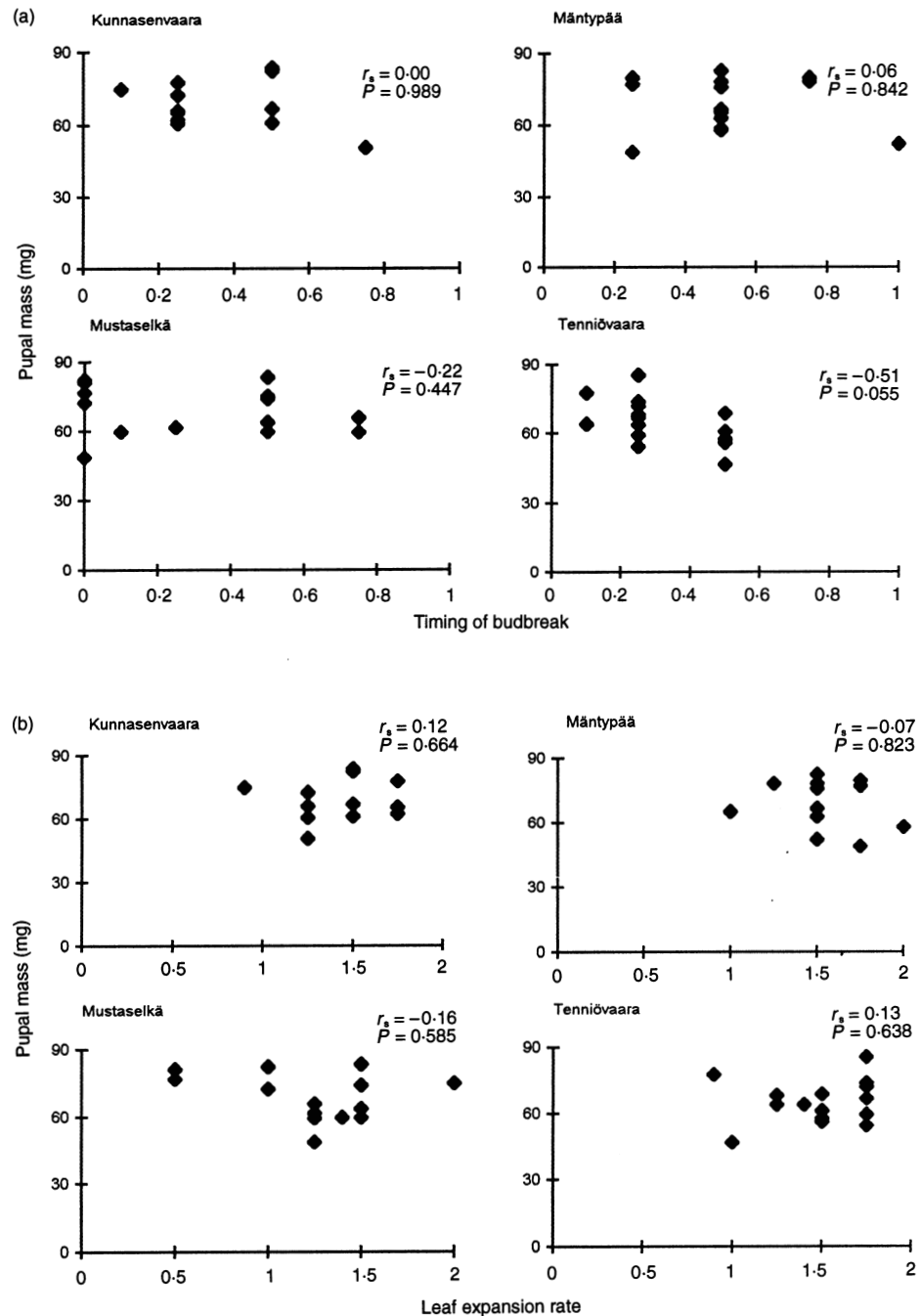


Fig. 3. Spearman correlation coefficients for the relationships of *E. autumnata* pupal mass with Mountain Birch leaf expansion rate (a) and the timing of budbreak (b).

The crowding effect, on the other hand, delays *E. autumnata* egg hatch in spring via later oviposition in the previous autumn, and thus promotes better synchrony of the offspring of crowded insects with previously defoliated host trees. The delay of egg hatch between the first and last laid broods in the experiment by Haukioja *et al.* (1988b) was 20 dd5 (calculated from unpublished information), which was almost equal to the delay in budbreak after total defoliation in the same study.

Although we have demonstrated the crowding effect only in laboratory, it is very likely that it exists

also at high *E. autumnata* densities in the field, because young larvae tend to concentrate at birch apices, where they necessarily meet each other (Kaitaniemi *et al.* 1997). In our study area, during the recent outbreak, which was not among the most severe known for *E. autumnata*, it was common to find more than one first instar larva consuming the same apical bud, and that kind of proximity is sufficient to induce the crowding effect (Haukioja *et al.* 1988b). In addition, this crowding effect is a general response in many lepidopteran species (Gruys 1970), and is not restricted to *E. autumnata* only.

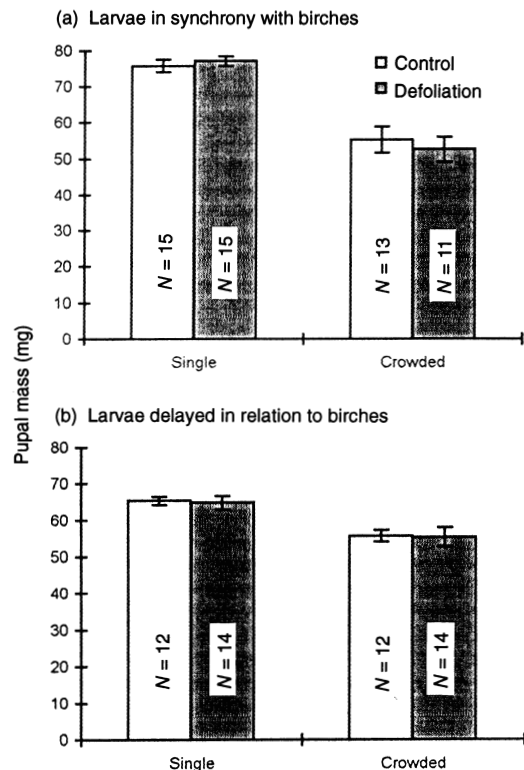


Fig. 4. Performance of solitary reared and crowded *E. autumnata* larvae at different phenologies in relation to Mountain Birches with or without previous year defoliation. Means \pm SE are given.

CONSEQUENCES OF PHENOLOGICAL MISMATCH FOR *EPIRRITA AUTUMNATA* LARVAE

Fifty per cent of *E. autumnata* larvae survived 10–20 dd5 without food at various constant temperatures under laboratory conditions (Haukioja *et al.* 1988a), which implies that hatching too early could increase larval mortality in birches with delayed budbreak. On the other hand, delayed hatching may also be harmful for larvae, although, unlike starving, it may not result in immediate death. Delayed larvae grow poorly, which drastically reduces their fecundity (Ayres & MacLean 1987), and first and second instar larvae may totally refuse to feed when delayed by more than 50 dd5 in relation to birches (personal observations).

Epirrita autumnata females are not known to use cues to predict host plant conditions on which their offspring will hatch (Tammaru *et al.* 1995), but crowding itself is an indication of a defoliation-induced delay in budbreak. Total defoliation commonly occurs during the outbreaks (Tenow 1972; Bylund 1995), sometimes with varying frequency as regards individual trees (Tenow 1975; and this study). Outbreaks have only rarely been reported to spread from the edges (Tenow 1972), and, owing to a poor flying ability, *E. autumnata* females probably lay most of their eggs near or on the trees where they were feeding (P. Kaitaniemi *et al.*, personal observations, see also Itämiies, Pulliainen & Siekkinen 1995). Thus,

the delayed hatch of eggs of females that experience crowding as larvae could provide a mechanism to enhance better synchrony of offspring in relation to the parental host trees. This may prolong the outbreak by enhancing larval performance in the year following severe defoliation.

As suggested by Ruohomäki, Hanhimäki & Haukioja (1993), laying eggs singly in varying microsites within and among trees (for more on oviposition sites, see Tammaru *et al.* 1995) can increase variation in hatching times and thus reduce the risk of all young larvae dying. The magnitude of hatching variation among microsites is not known, but it could potentially serve as a bet-hedging strategy to cope with the great phenological variation among trees. In any case, microsite variation probably brings about more variation in hatching time than within-brood hatching difference between the first and last laid eggs, which is 0.4 days at room temperature in the laboratory (Ruohomäki *et al.* 1993), corresponding to 6 dd5. Additional variation to hatching times is brought about by the large variation in dates of adult emergence and, consequently, in oviposition dates of both crowded and single larvae (Haukioja *et al.* 1988b).

DIR AND PHENOLOGY OF MOUNTAIN BIRCHES

The results of this study did not indicate a significant DIR response after defoliation, although DIR has been demonstrated in several previous studies in Mountain Birch. However, its magnitude has been shown to vary between different experiments and years for unknown reasons (for a summary, see Ruohomäki *et al.* 1992). DIR complicates the interaction between *E. autumnata* and Mountain Birch, because its consequences for *E. autumnata* performance are similar to those of phenological asynchrony: larval mortality increases and pupal mass decreases. On the other hand, the crowding effect seemed to override the effect of food quality in this study, because crowded larvae reared on foliage of birches in the experiment with experimentally generated defoliation performed equally well regardless of their phenology in relation to birches. This is in line with results by Haukioja *et al.* (1988b), indicating that unlike single larvae, crowded larvae could not gain benefit from good food quality. Their better performance on low quality foliage resulted from increased consumption (Haukioja *et al.* 1988b). This also means that crowded larvae may be relatively insensitive to DIR. However, this indifference of crowded larvae to low food quality is not a global result, because several bag rearings with grouped larvae have demonstrated strong DIR (Ruohomäki *et al.* 1992).

IMPLICATIONS FOR FUTURE STUDIES

Our results indicate that complex interactions exist between host plant phenology, host plant quality, her-

bivore performance and herbivore phenology. The most important methodological lesson of this study relates to larval crowding and to larval-induced changes in host plant phenology. Effects of larval crowding are usually not explicitly considered in plant–herbivore studies, although drastic effects are common (Klomp 1966; Gruys 1970; Lance, Elkinton & Scwalbe 1986; Cheke 1995; Goulson & Cory 1995; Harrison 1995). As studies of *E. autumnata* indicate, the crowding effect should be routinely considered in studies of plant–herbivore interactions, because it may greatly modify the larval responses to plant quality by making the larvae less sensitive to poor diet.

Induced changes in host plant phenology and foliage quality represent another complication which may modify larval responses in species that are sensitive to the degree of synchrony with their host plant phenology. For instance, if defoliation induces both a delay in budbreak and DIR, it is possible that the better synchrony of larvae with defoliated trees makes the defoliated trees actually better hosts than control trees. Therefore, the phenological states of host plants should be considered and reported in future studies.

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