Agricultural and Forest Entomology (1999) **1**, 19–26

Effects of previous defoliation on pine looper larval performance

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Abstract

1 During outbreaks of the pine looper, *Bupalus piniarius*, its host, *Pinus sylvestris*, is severely defoliated. The larvae of this geometrid normally feed on mature needles. However, because trees are totally defoliated during outbreaks, the next generation is forced to feed on current-year needles.
2 *Bupalus piniarius* larvae feeding on previously defoliated trees may show lower performance either because of induced resistance or because larvae have to feed on needles not normally fed upon (current instead of mature).
3 These hypotheses were tested in an experiment where larvae were reared on (i) shoots naturally defoliated the previous year, and thus, bearing only current-year needles, (ii) non-defoliated shoots where larvae had access only to current-year needles, and (iii) control shoots with access to both current and mature needles.
4 There was no support for the induction hypothesis. Survival was lower on naturally defoliated shoots than on control shoots (81.3 vs. 90.9%), but survival was lower also on non-defoliated shoots where larvae had access only to current-year needles (78.8%). Data on larval feeding distribution showed a strong preference for mature needles.
5 Needle nitrogen concentration of current-year needles was 38% higher on defoliated trees than on non-defoliated trees.
6 It is concluded that defoliation affected larval performance primarily through the removal of the preferred type of needles and not because of an induced resistance. Effects of increased concentrations of allelochemicals in defoliated shoots, if present, were probably cancelled out by increased nitrogen concentrations.

Keywords *Bupalus piniarius*, delayed induced resistance, food preference, Geometridae, insect–plant relationship, natural defoliation, nitrogen, *Pinus sylvestris*.

Introduction

Outbreaks of folivorous insects frequently result in the complete defoliation of their host plants. Leaves of defoliated trees often differ in biochemical composition from leaves of non-defoliated trees (Tallamy & Raupp, 1991; Karban & Baldwin, 1997). Future generations of insects feeding on defoliated trees often suffer higher mortality, slower growth or reduced fecundity compared with conspecifics feeding on non-defoliated trees (Haukioja, 1990). Such effects, referred to as delayed induced resistance (Haukioja & Honkanen, 1997), could potentially affect insect population dynamics (Haukioja, 1990; Karban & Baldwin, 1997; but see Fowler & Lawton, 1985).

By depleting their preferred food resource, insects in an outbreak phase also alter their feeding conditions in other ways. Food shortage is one obvious consequence of total defoliation. In high-density situations the food supply may not be sufficient for insect individuals to complete their development. In fact, starvation due to overexploitation contributes to the population decline in many insect outbreaks (Berryman, 1988). However, depletion of the food resource can influence future insect generations in more subtle ways. For instance, defoliated plants often have the capacity for regrowth (Ostaff & MacLean, 1995; Krause & Raffa, 1996). From the insect's point of view, regrowth tissue may not be of the same nutritional quality (Hunter & West, 1990) as original tissue. Many insects, for

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example, are adapted to ovipositing and feeding on a particular age class of leaves (e.g. Ikeda *et al*., 1977; Bingaman & Hart, 1993). Different age classes of leaves often show large differences in chemical characteristics (Ikeda *et al*., 1977; Niemelä *et al*., 1982; Stamp & Bowers, 1994) and, consequently, differ in their suitability for insects (Raupp & Denno, 1983).

The pine looper (*Bupalus piniarius* L., Lepidoptera, Geometridae) is one of the most serious defoliating insects on Scots pine (*Pinus sylvestris* L.) in Europe. Outbreaks usually occur in pure pine stands on poor soils (Schwerdtfeger, 1941; Barbour, 1988; Šmits & Vilka, 1993), and, at least for some pine looper populations, seem to occur at regular intervals, indicating a cyclic insect population behaviour (Broekhuizen *et al*., 1993). Life-table analyses indicate that early larval mortality is an important factor in *B. piniarius* population dynamics (Klomp, 1966; Broekhuizen *et al*., 1994; Marchenko, 1994). Delayed density dependence seems to be important (Barbour, 1988; Broekhuizen *et al*., 1994; Ginzburg & Taneyhill, 1994); at high larval densities intraspecific interference competition results in poor growth and smaller pupae (Klomp & Gruys, 1965; Gruys, 1970), from which females emerge that lay fewer eggs and have fewer viable offspring than females emerging from larger pupae (Klomp & Gruys, 1965).

Bupalus piniarius is univoltine and, in Sweden, monophagous on Scots pine. Larvae develop very slowly, reaching the pupal stage after 3–4 months. There are five larval instars. Early instars feed on mature needles (Schwenke, 1978; Barbour, 1988; Straw, 1996). The feeding behaviour of late-instar larvae is less well documented, but it has been reported that old larvae consume current-year as well as mature needles (Straw, 1996; Broekhuizen *et al*., 1993). At outbreak densities *B. piniarius* larvae consume needles of all age classes. Because larvae feed late in the season no needles will be available at the start of the next growing season after a complete defoliation. According to Botterweg (1978), *B. piniarius* has a low dispersal ability (30 m per day and about 150 m during its lifetime). Thus, the year after complete defoliation, females will be forced to lay eggs on current-year needles, whereas eggs are usually deposited on mature needles (Schwenke, 1978). After a defoliation no mature needles are present at the time of larval hatching, forcing young larvae to feed on newly produced needles. Thus, a complete defoliation by *B. piniarius* can influence the next generation of larvae in two ways: (i) defoliated trees can be a less suitable resource for *B. piniarius* because of induced changes in needle chemistry, and (ii) defoliated trees can be unsuitable because the preferred resource, mature needles, is not available at the start of the larval feeding period.

These different, but not mutually exclusive, hypotheses were tested in a feeding experiment performed in connection with an extensive *B. piniarius* outbreak at Hökensås in southern Sweden. Larvae were fed: (i) shoots that were naturally defoliated the previous year (test of the induction hypothesis), (ii) non-defoliated shoots where larvae had access only to current-year needles (test of the resource type hypothesis), and (iii) control shoots with both current-year and mature needles present. We predicted that larvae would show lower performance (survival, growth rate, body size) on shoots with only current-year needles than on control shoots because current-year needles contain more noxious chemical compounds (Ikeda *et al*., 1977; Niemelä *et al*., 1982). It was also predicted that larvae raised on naturally defoliated shoots would show lower performance than those raised on non-defoliated shoots where larvae had access only to current-year needles. The reason for this is because larvae on the former type of shoot would suffer not only from feeding on the wrong type of needles but also from feeding on needles from shoots damaged in the previous year. Thus, the induction hypothesis would be supported if larval performance was best on (iii), poorest on (i), and intermediate on (ii). A result showing high larval performance on (iii) and lower but equal performance on (i) and (ii) would be interpreted as supporting the idea that larvae have difficulties in handling young needles but not supporting induction.

Materials and methods

Study site

The study was conducted at Hökensås (58°05′ N, 14°06′ E) in southern Sweden where an extensive outbreak of *B. piniarius* occurred in 1996. The area is characterized by pure Scots pine forests growing on extremely poor soils. The area has a history of extensive *B. piniarius* outbreaks, the last one occurring in 1943–44 (Butovitsch, 1946). In the present outbreak, about 4000 ha was heavily damaged in 1996. In the attacked stands most of the trees had been completely defoliated by the end of the 1996 growing season. In general, repeated defoliations by pine loopers result in high mortality in pine stands (Schwenke, 1978). Pupal counts at Hökensås in spring 1997 indicated that larval populations in 1997 were high enough to lead to another complete defoliation. Therefore, in early August 1997 the infested area was sprayed with *Bacillus thuringiensis.*

Effects of previous defoliation on larval performance

In 1997, a rearing experiment was carried out to investigate the effects of previous defoliation on *B. piniarius* larval performance. The experiment was conducted in a shadehouse built in the vicinity of the defoliated forest. In the shadehouse, larvae were exposed to ambient temperatures but were protected from rain and direct sun. Treatments included: (i) natural defoliation – naturally defoliated shoots from the previous year with only current-year needles present, (ii) limited access – non-damaged shoots with mature needles removed prior to the experiment, and (iii) control – shoots with both current-year and mature needles undamaged. Branches (about 1 m long), from which the shoots were taken, were sampled with the aid of a sky-lift from the mid-crown of mature pine trees at the start of experiment and at weekly intervals thereafter. Defoliated shoots were taken from a completely defoliated stand. Control and limited-access shoots were taken from trees of similar age growing in the same type of stand, but with no visible *B. piniarius* damage.

Sampled shoots were immediately placed in water and taken to the shadehouse where each shoot was placed in a plastic container filled with water. The shoot axis was inserted through a hole in the lid of the container and was recut under water to maximize its water uptake capacity. To prevent the larvae from mixing, each shoot was enclosed in a transparent plastic cylinder with the top covered by muslin. New shoots were offered to the larvae at weekly intervals.

At the start of the experiment (14–17 July), 10 newly emerged larvae or eggs just about to hatch, which had been collected from the naturally-infested forest, were transferred to experimental shoots. There were 18 replicates of each treatment. All transfers of larvae to experimental shoots were made in triplets (one corresponding to each treatment); each triplet was started on the same day, in order to facilitate comparisons among treatments.

Larval development was monitored until 15 August, by which time most of the larvae were in instar III–IV. Larval growth and survival were registered weekly in connection with changing the shoots. Missing larvae ($n = 15$, 2.8%) were scored as dead. This seems reasonable given the minute size of young *B. piniarius* larvae. We had originally planned to continue the experiment until pupation. However, due to accidental contamination by *B. thuringiensis* from the spraying operation the experiment had to be terminated at an earlier stage.

Repeated-measures ANOVA was applied to analyse variation in larval survival among treatments. The analysis was based on arcsin-square root transformed data on the proportion of dead larvae per cage. Tukey's honest significant difference (HSD) test was used for comparing mean survival rates at the end of the experiment.

Sleeve cage experiment

Because the experiment had to be terminated before the larvae had pupated it was not possible to estimate pupal weight; thus, no data on effects on future fecundity could be obtained from the shadehouse experiment. Therefore, an additional experiment was initiated in order to supplement the shadehouse data. We located a defoliated stand that was not treated with *B. thuringiensis* and was not contaminated. From that stand, where larvae had experienced defoliated shoots since egg hatch, larvae (most of them in the fourth instar) were knocked down from the canopy. The larvae were then put back on the trees in large sleeve cages. The same procedure was used on trees in the control stand. In each stand, eight replicates, with seven larvae in each cage, were established on 2 September. Another eight replicates were established in the two stands on 8 September. On 1 October, branches were taken down, and pupation was monitored daily. Branches were kept outside until all larvae had pupated. Pupae were then sexed and weighed.

Larval feeding distribution

To investigate how larvae distribute their feeding between current-year and mature needles when given a choice, feeding damage was scored for young (instars II–III) and old (IV–V) larvae. For both larval ages, data were collected for shadehouse-reared larvae as well as for larvae feeding under natural conditions. In all cases damage was assessed on twigs with both current-year and mature needles, thus enabling paired comparisons.

Feeding by young larvae from the shadehouse experiment was investigated on control shoots ($n = 12$ shoots) fed to the larval cohorts in the performance experiment during the period 23–31 July. Feeding by old larvae from the same experiment was studied on shoots ($n = 10$) fed to larval cohorts held on control shoots after the main performance experiment had been completed (3–11 September). Needles on all shoots were sorted into mature (1- and 2-year-old) and current-year needles. All needles were examined under a stereo-microscope, and the length of each feeding mark was recorded. Mean feeding mark length per needle was then calculated. An estimate of larval consumption rate was obtained by dividing the total feeding mark length by the number of larvae in the cages and number of feeding days. On average, 197 current-year (SD = 64, $n = 12$ shoots) and 277 mature (SD = 51, $n = 12$) needles were examined in order to estimate young larval feeding, whereas 463 current-year (SD = 141, $n = 10$ shoots) and 412 mature (SD = 130, $n = 10$) needles were examined to estimate old larval feeding.

Branches for assessing the distribution of feeding by young larvae in the field were sampled from mature trees on 1 August. Six trees, with branches having both current-year and mature needles, were selected in a partially defoliated stand. One branch was sampled from each tree. The branches were divided into twigs that contained shoots with both current-year and mature needles. A subsample ($n = 15$) of such twigs was taken from each branch. The number of needles as well as the number and length of larval feeding marks were recorded. On average, 1267 current-year [SD = 168, $n = 6$ branches (15 shoots/branch)] and 773 mature (SD = 181, $n = 6$) needles were examined.

Late-instar feeding in the field was assessed on branches sampled on 15 October from trees from the control plot (one mid-crown branch from each tree). To assess young-instar feeding, a subsample ($n = 20$) of shoots was taken from each branch. Every needle was examined visually, and the number of feeding marks per needle was recorded. On average, 1338 current-year [SD = 335, $n = 10$ branches (20 shoots/branch)] and 1180 mature (SD = 216, $n = 10$) needles were examined.

Needle nitrogen analysis

Needle samples for nitrogen analysis were taken in 1997 from five trees in a stand that had been completely defoliated in 1996 and from a control stand with trees of similar age growing in the same type of stand without visible *B. piniarius* damage. Samples were taken on 16 July, 20 August and 14 October. Needles were sampled from five branches from each tree; for the analysis, needles from each tree were pooled. Current-year as well as 1-year-old needles were sampled from control trees, whereas only current-year needles were available for sampling on defoliated trees. Needles were immediately frozen in liquid nitrogen and stored at – 20°C until analysis. Total nitrogen (on a dry weight basis) was determined with an NA 1500 Elemental Analyser (Rodano, Italy). Repeated-measures ANOVA was applied to arcsin-square root transformed data in order to analyse the variation in needle nitrogen concentrations. HSD was used for comparisons among means.

Results

Early instar larvae suffered somewhat higher mortality on the two types of shoots without mature needles than on control shoots. When the experiment was terminated after 5 weeks, by which time most larvae were in instar III–IV, survival rates were

90.9% on the control, 81.3% on naturally defoliated shoots and 78.7% on limited-access shoots (Fig. 1). Most of the mortality occurred during the first week; no significant difference in mortality rate among treatments was detected after the first week, as evidenced by the lack of a treatment–time interaction (Table 1).

Treatment effects on larval growth, estimated as the proportion of larvae that had reached instar IV by the end of the experiment (15 August), differed somewhat from the effects on survival. The proportion of fourth-instar larvae was lowest on limited-access shoots (14.4%) (Fig. 2). There was no significant difference ($\chi^2 = 1.28$, $P = 0.26$) in the proportion of larvae reaching the fourth instar between control shoots (23.9%) and naturally defoliated shoots (29.7%), but both of these values differed significantly from that obtained for limited-access shoots ($\chi^2 = 4.28$, $P = 0.039$, and $\chi^2 = 9.58$, $P \leqslant 0.002$, respectively).

The rate of needle consumption by young larvae differed among treatments. Larvae on limited-access shoots had a 17.5% higher consumption rate compared with those fed naturally defoliated shoots (Table 2). No significant differences in consumption rates were detected between control shoots and either of the other two types of shoots.

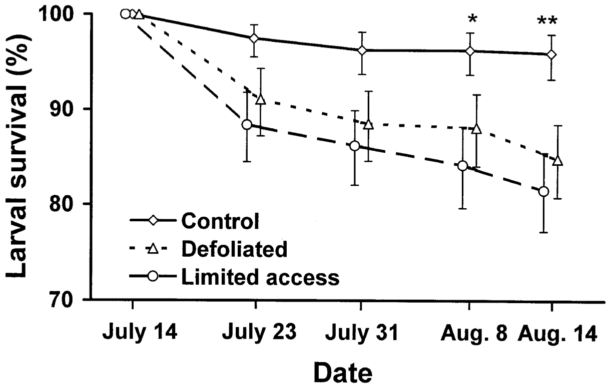

Figure 1 Survival of young larvae of *Bupalus piniarius* raised on different types of *Pinus sylvestris* needles: control – both current-year and mature needles present, limited access – only current-year needles, mature needles removed prior to the experiment, defoliated – only current-year needles, natural defoliation of mature needles in the previous season. On 14 August, larvae were in instar III–IV. Error bars represent standard errors. * and ** represent significant differences among treatments, $P < 0.05$ and $P < 0.01$, respectively.

Larvae raised in sleeve cages developed into larger pupae on defoliated trees than on control trees. Female pupae on defoliated trees were 22% heavier compared with those on control trees (Table 3). No significant difference in pupal sex ratio was found between defoliated and control trees (defoliated, 58.6% females; control, 48.2%; $P = 0.17$; *t*-test).

Mature needles were preferred as food over current-year needles by both young and old larvae. In the shadehouse experiment feeding damage caused by young larvae on mature needles was, on average, 2.5-fold higher compared with the damage they caused on current-year needles (Fig. 3a). Similarly, in the field, the damage cause by young larvae was, on average, 3.4-fold higher on mature needles compared with on current-year needles (Fig. 3b). Older larvae also fed more on mature needles than on current-year needles. In the shadehouse experiment mature needles sustained 4.6-fold more damage compared with current-year needles (Fig. 3c), and needles from field-collected shoots showed 3.2-fold more damage (Fig. 3d).

Needle nitrogen concentrations were higher on trees from the defoliated stand than on trees from the control stand. Averaged over the three sampling occasions, nitrogen concentrations in current-year needles were 38% higher on defoliated trees compared with control trees (Fig. 4). No significant differences in nitrogen concentrations were found between current-year and mature needles on control trees (Fig. 4). A significant decrease in nitrogen concentration occurred over the course of the season and was most pronounced in defoliated trees (see treatment–time interaction, Table 4).

Discussion

Our results provide no support for the induction hypothesis. Larval survival on shoots where larvae had access only to current-year needles (limited access) did not differ from that on shoots defoliated by *B. piniarius* larvae the previous year. Survival was lower on both limited-access and naturally defoliated shoots than on control shoots. Furthermore, in contrast to larvae on naturally defoliated shoots, larvae on limited-access shoots showed a reduced growth rate compared

Table 1 Repeated-measures ANOVA univariate test of hypotheses for between-subjects (treatment) effect and within-subject (time) effect on survival of young *Bupalus piniarius* larvae. Larvae were raised on different types of *Pinus sylvestris* shoots: control – both current-year and mature needles present, limited access – only current-year needles, mature needles removed prior to the experiment, defoliated – only current-year needles, natural defoliation of mature needles in the previous season (data arcsin-square root transformed).

Source	d.f.	Type III SS	F	$P>F$	Adj. $P>F$ G-G	Adj. $P>F$ H-F
Between subjects						
Treatment	2	1.7249	3.79	0.0293		
Error	51	11.6207				
Within subject						
Time	3	0.1715	14.38	0.0001	0.0001	0.0001
Treatment × Time	6	0.0242	1.02	0.4176	0.4062	0.4093
Error (Time)	153	0.6083				
			Greenhouse-Geiser $\varepsilon = 0.7192$			
			Huynh-Feldt $\varepsilon = 0.7815$			

with larvae on control shoots. We interpret this result as indicating that larvae suffer more from feeding on the wrong type of needles than from consuming needles on previously defoliated shoots.

Due to accidental contamination by *Bacillus thuringiensis* it was possible to monitor larval performance only up to instar III–IV. In general, insect larval mortality is highest in young instars (Cornell & Hawkins, 1995). In particular, life table analyses of *B. piniarius* populations indicate that early instar mortality is of great importance for *B. piniarius* population dynamics (Klomp, 1966; Broekhuizen *et al*., 1994). Thus, it seems likely that the 5-week experiment covered the critical phase of *B. piniarius* larval development and that we would have detected mortality strong enough to substantially influence *B. piniarius* population dynamics.

The experiment was carried out on cut branches in a laboratory setting. Ideally, tests of induction effects should be carried out on intact plants (Neuvonen & Haukioja, 1985). *Bupalus piniarius* defoliation is restricted to mature trees (Gralicki, 1986; Barbour, 1988). Tests of induction effects on the performance of young larvae in sleeve cages on mature trees are, in practice, impossible to carry out. Because shoots were changed every week and the focus was on delayed-induced responses, we believe that the amount of error resulting from the use of cut branches should have been minimal.

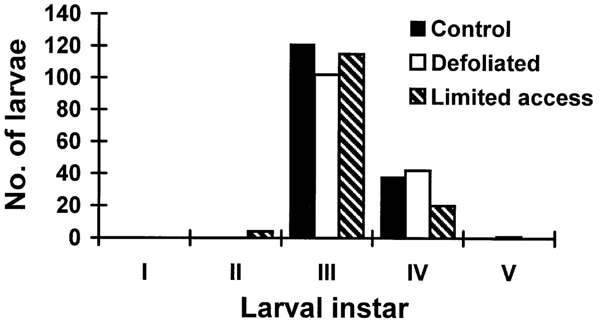

Figure 2 Distribution of *Bupalus piniarius* larvae in different instars at the end of a rearing experiment (14 August). Treatments are: control – both current-year and mature needles present, limited access – only current-year needles, mature needles removed prior to the experiment, defoliated – only current-year needles, natural defoliation of mature needles in the previous season.

Table 2 Consumption rate (mm of feeding marks per day per larvae) of *Bupalus piniarius* larvae (instar II–III) feeding on different types of *Pinus sylvestris* shoots. Treatments are: control – both current-year and mature needles present, limited access – only current-year needles, mature needles removed prior to the experiment, defoliated – only current-year needles, natural defoliation of mature needles in the previous season.

	Consumption rate (mm day^{-1} larvae^{-1})			
Treatment	Mean	SE	*n*	*P* = 0.05
Control	11.6	0.63	12	ab
Defoliated	10.8	0.39	12	a
Limited access	13.1	0.71	12	b

In the limited-access treatment, mature needles were removed immediately before the experiment was started and weekly thereafter, in connection with shoot replacement. It is possible that the removal of mature needles could have initiated rapid induced changes (Haukioja & Honkanen, 1997) in the remaining needles. Such changes, in turn, could have lowered the performance of *B. piniarius* larvae. However, even if rapid changes in the remaining needles did occur, it is unlikely that they would have affected the overall result since needles were also removed from control shoots so that they would fit into the rearing cages.

Defoliated shoots had higher nitrogen concentrations than non-defoliated shoots. It is possible that the improved nutritional quality ameliorated the effects of any induced increase in secondary chemicals that could, otherwise, have contributed a reduction in larval performance (Wagner & Evans, 1985; Långström *et al*., 1990). Several other insect species that occasionally reach outbreak levels, such as the larch moth (Baltensweiler & Fischlin, 1988) and the autumnal moth (Haukioja *et al*., 1988), induce chemical changes that have deleterious effects on subsequent insect generations. In pine-feeding insects delayed induced resistance has been found to reduce the performance of *Panolis flammea* (Leather *et al*., 1987), especially on young trees, but not the performance of pine sawflies (Niemelä *et al*., 1991). Tuomi *et al*. (1988) tentatively ascribed the lack of induction by pine sawflies to basic differences in responses to defoliation between deciduous and coniferous trees, with the former being more responsive. This explanation may also hold for the results presented here. Unfortunately, because we have no data on allelochemical concentrations in defoliated shoots, no conclusions can be drawn about the mechanisms behind the lack of induction effects in this study.

The fact that larvae grew more slowly on limited-access shoots than on naturally defoliated ones suggests that one or more current-needle traits deleterious to larval performance were more strongly expressed in limited-access shoots. Terpenoid compounds are known to be present in current-year needles at concentrations high enough to repel other needle-eating insect species (Ikeda *et al*., 1977; Niemelä *et al*., 1982); however, the extent to which these compounds influence *B. piniarius* performance is not known. Although the consumption rate in the present study was highest on limited-access shoots, larvae, nevertheless, grew slower on these shoots. This implies that there are chemicals present in current-year needles that make them less suitable for *B. piniarius* larval growth.

Table 3 Weight (mg fw) of *Bupalus piniarius* pupae formed by larvae raised in sleeve cages on defoliated and control *Pinus sylvestris* trees.

	Control			Defoliated			
	Mean	SE	*n*	Mean	SE	*n*	P
Female	76	2	32	98	3	46	< 0.01
Male	62	3	31	76	3	36	< 0.01

In the sleeve cage experiment, late-instar larvae performed better on defoliated trees than on control trees. By contrast, in the shadehouse experiment young larvae performed less well on naturally defoliated shoots than on controls, although the difference was small. We interpret the better performance in sleeve cages as further support for the hypothesis that there is an interaction between nutrient quality and concentrations of allelochemicals. The noxious terpenoids in current-year needles decrease in concentration as the season progresses (Ikeda *et al.*, 1977; Niemelä *et al.*, 1982). Needle nitrogen concentrations were consistently higher in defoliated trees than in non-defoliated ones. If *B. piniarius* larvae respond negatively to the putative deleterious compounds in current-year needles, one would expect the amelioration effect of high nitrogen to be stronger for old larvae late in the season when the negative effects of the terpenoids are less pronounced. The sleeve cage data, however, need to be interpreted with caution because not all factors in the experiment were controlled. By necessity, comparisons had to be made between larvae exposed to somewhat different environments. There were some indications that larvae in the defoliated stand grew faster, possibly owing to better microclimatic conditions. As a result these larvae might have gained weight more efficiently than larvae in the control stand. Although this effect relates to the defoliation event, and is interesting in itself, it could be a confounding factor when evaluating effects of needle quality. It is still interesting to note, however, that the results were opposite to our prediction, i.e. pupal mass was higher in the defoliated stand than in the non-defoliated one.

Larvae very clearly preferred to feed on mature needles over current-year needles. This observation is in agreement with published work on the feeding behaviour of young *B. piniarius* larvae (Schwenke, 1978; Barbour, 1988). The literature suggests, however, that old larvae largely feed on current-year needles (Straw, 1996; Broekhuizen *et al.*, 1993). Our data do not support this suggestion; feeding damage caused by old larvae

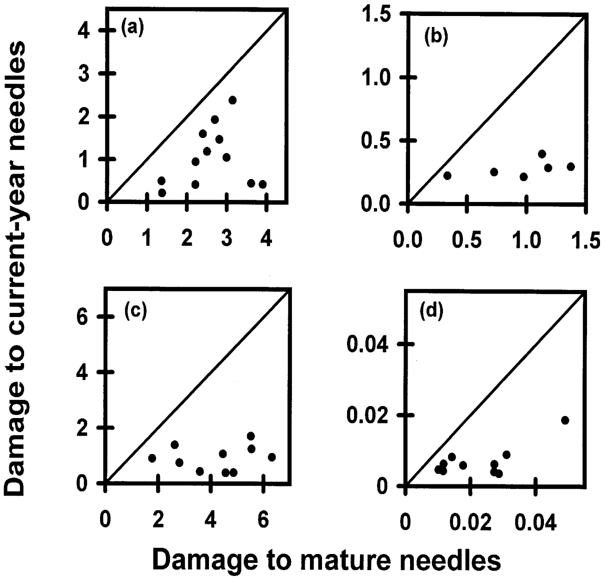

Figure 3 The distribution of feeding damage caused by *Bupalus piniarius* larvae on current-year and mature (one-year old and older) needles of *Pinus sylvestris* for: (a) early instar larvae in the shadehouse, (b) early-instar larvae in the field, (c) late-instar larvae in the shadehouse and (d) late-instar larvae in the field. Units are mm damage per needle (a, b, c), and number of feeding marks per needle (d). Each marker represents average damage density (based on subsample) on a branch.

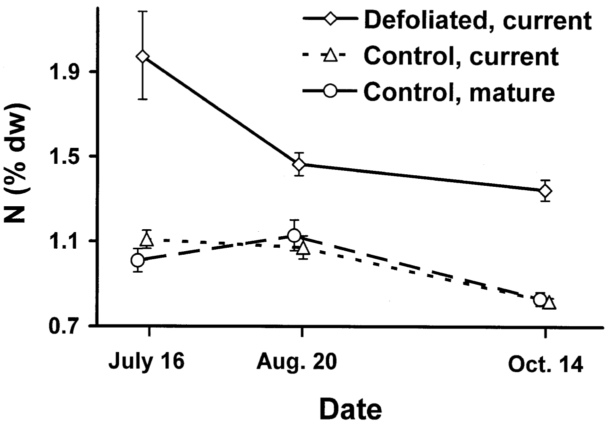

Figure 4 The dynamics of needle nitrogen concentrations in defoliated (current-year needles) and control (current-year and one-year old) *Pinus sylvestris* trees at Hökensås in 1997. Defoliated trees were completely defoliated by *Bupalus piniarius* in 1996. Error bars represent standard errors.

Table 4 Repeated-measures ANOVA univariate test of hypotheses for between-subjects (treatment) effect and within-subject (time) effect on needle nitrogen concentrations in defoliated and control *Pinus sylvestris* trees (data arcsin-square root transformed). Treatments are: current-year needles and mature needles (one-year and older) from control trees, and current-year needles from trees completely defoliated by *Bupalus piniarius* in the previous season.

					Adj. *P*>F	
Source	d.f.	Type III SS	F	*P*>F	G-G	H-F
Between subjects						
Treatment	2	0.00700	40.78	0.0001		
Error	12	0.00102				
Within subjects						
Time	2	0.00208	25.88	0.0001	0.0001	0.0001
Treatment × Time	4	0.00086	5.37	0.0023	0.0113	0.0057
Error (Time)	24	0.00096				

Greenhouse-Geiser ε = 0.6132
Huynh-Feldt ε = 0.7610

was clearly more abundant on mature needles than on current-year needles, both on shoots from the shadehouse experiment and on field-collected shoots. We are not aware of any data on feeding preferences for *B. piniarius* larvae at low population densities. It is certainly true that *B. piniarius* larvae feed on current-year needles at outbreak densities. Our data, however, indicate that this is suboptimal food. Larvae forced to feed on current-year needles in situations with no amelioration effects, i.e. for a population in an increase phase, could suffer reduced performance. Such reduced performance, e.g. lower fecundity, could then contribute to the delayed density dependence observed in population dynamics studies (Barbour, 1988; Broekhuizen *et al*., 1994).

It is possible that the amelioration effect in this study was unusually strong owing to favourable weather conditions in 1997. Plant nitrogen uptake on nutrient-poor soils may be favoured by high soil water availability (Karrou & Maranville, 1994; Nilsen & Orcutt, 1996). Rainfall was abundant in late spring to early summer 1997. This could have contributed to the high nitrogen concentrations in current-year needles on defoliated trees. However, if trees had suffered early summer drought, then nitrogen uptake could have been reduced, and the deleterious effects on larvae forced to feed on current-year needles would have been more pronounced. Under such a scenario negative effects of defoliation on insect growth and survival would be more severe under stressful conditions.

One of the main purposes of this study was to determine the extent to which the effects of previous defoliation can influence *B. piniarius* population dynamics. If individual performance differed significantly between defoliated shoots and non-defoliated shoots, then defoliation effects could be potentially important. The findings of several long-term population studies infer that young larval mortality is important in *B. piniarius* population dynamics (Klomp, 1966; Broekhuizen *et al*., 1994; Marchenko, 1994). To date, the data needed to test this hypothesis have not been available. The small effect of natural defoliation on insect growth and survival found in this study, however, seems marginal in a population dynamics context. In fact, defoliated trees could potentially be a better food resource if current-needle nitrogen concentrations generally increase as documented in this study. Still, defoliation could have a delayed influence on population dynamics by affecting egg-laying females. Such an effect could occur in cases where a complete defoliation depletes preferred oviposition sites, i.e. mature needles, for the next generation of females, resulting in a reduction in realized fecundity.

Acknowledgements

We thank Hökensås Häradsallmänning for permission to work in the study area, Ingvar Johansson for hosting the shadehouse and for assistance during the sampling, Margit, Ulf and Else-Marie Bertilsson for field accommodations, Åke Lindelöw, Peter Dalin, Peter Zonneveld and Karin Eklund for assistance in the field and laboratory, Erik Lindquist for nitrogen analyses, Christer Björkman for fruitful discussions throughout the study and Christer Björkman, Barbara Ekbom, Julia Koricheva, Pekka Niemelä and David Tilles for comments on earlier drafts of the manuscript. This research was supported by a grant from the Royal Swedish Academy of Science.

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Accepted 27 November 1998