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Performance of the cyclic autumnal moth, *Epirrita autumnata*, in relation to birch mast seeding

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Abstract The mast depression hypothesis has been put forward to explain the 9- to 10-year population cycle of the autumnal moth (*Epirrita autumnata*; Lepidoptera: Geometridae) in northern Fennoscandia. We analysed long-term data from Finnish Lapland in order to evaluate the critical assumption of the mast depression hypothesis: that better individual performance of herbivores, followed by high annual growth rate of populations, occurs in the year following mast seeding of the host, the mountain birch (*Betula pubescens* ssp. *czerepanovii*). Since mast seeding has been suggested to occur at the expense of chemical defence against herbivores, we bioassayed the quality of birch leaves from the same trees by means of yearly growth trials with autumnal moth larvae. We also measured the size of wild adults as a determinant of potential fecundity of the species in different years. The relative growth rate of larvae was poorer in post-mast years compared to other years, rather than better as assumed by the hypothesis. Conversely, a slight indication of the increase in potential fecundity was observed due to the somewhat larger adult size in post-mast years. Population growth rate estimates, however, showed that

the increase in fecundity would have to be much higher to facilitate population increase towards a cyclic peak with outbreak density. Accordingly, our two data sets do not support the assumption of a higher annual growth rate in autumnal moth populations subsequent to mast seeding of the host, thereby contradicting the predictions of the mast depression hypothesis. Temperatures, when indexed by the North Atlantic Oscillation and accumulated thermal sums, were observed to correlate with the abundance or rate of population change of the autumnal moth. The factors underlying the regular population cycles of the autumnal moth, however, remain unidentified. Overall, we suggest that the causal agents in cyclic insect population dynamics should be clarified by field experimentation, since trophic interactions are complex and are further modified by abiotic factors such as climate.

Keywords Fecundity · Larval growth rate · Population cycle · Population growth rate · Mountain birch

Introduction

In northern and mountainous parts of Fennoscandia, populations of the autumnal moth, *Epirrita autumnata* Borkhausen (Lepidoptera: Geometridae), fluctuate periodically, reaching outbreak densities at intervals of 9–10 years (Tenow 1972; Haukioja et al. 1988; Ruohomäki et al. 2000; Neuvonen et al. 2001; Selås et al. 2001a). These subarctic regions are dominated by mountain birch, *Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti, which is the main host for the spring-feeding larvae of the autumnal moth. Autumnal moth outbreaks may lead to severe defoliation of mountain birch (Tenow 1972; Kallio and Lehtonen 1973; Bylund 1995; Ruohomäki et al. 2000), at worst transforming vast areas into treeless tundra (for instance a 500-km² area in northern Finnish Lapland subsequent to a massive outbreak in the mid-1960s; see Fig. 1 in Ruohomäki et al. 2000). In southern Fennoscandia, populations of the autumnal moth gener-

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ally remain at low densities (Tenow 1972; Haukioja et al. 1988; Ruohomäki et al. 2000; Klemola et al. 2002).

Several mechanisms have been suggested – though none of these has been adequately verified – to explain cyclic fluctuations in the density of the autumnal moth (for reviews see Haukioja et al. 1988; Ruohomäki et al. 2000). According to one of the most prominent hypotheses, that of delayed inducible resistance (DIR), larval defoliations cause poor foliage quality for the subsequent moth generation(s) as a result of unfavourable changes in the chemical composition of mountain birch leaves (Haukioja 1982, 1990, 1991). Since recovery of the foliage quality may take 1–4 years after defoliation (Haukioja 1982; Kaitaniemi et al. 1999a, 1999b), the DIR hypothesis involves a time-lag in the interaction between birch and moth. According to the conventional theory of population ecology, such a delayed density-dependent feedback is a prerequisite for cyclic population dynamics (Varley et al. 1973; May 1981; Haukioja et al. 1983; Berryman et al. 1987).

An alternative view of the host plant-mediated population cycles of the autumnal moth was recently taken by Selås et al. (2001a) who reported that moth population increases towards outbreak density seem to start in the year *after* mast reproduction of mountain birch. Selås et al. (2001a) proposed that abundant and synchronous birch flowering and seeding are triggered by climatic conditions and occur at the expense of chemical defence against herbivores. The reduced chemical defence in birch leaves then enables a higher annual growth rate of autumnal moth populations, allowing outbreaks (Selås et al. 2001a). During the outbreak, birch reproduction remains low until the moth population has declined due to the induced defence mechanism of mountain birch (Selås et al. 2001a). The cycle may recur when mast seeding is again favoured (Selås et al. 2001a). Accordingly, the mast depression hypothesis states that it is the mast seeding of mountain birch that is responsible for the regular autumnal moth outbreaks in northern Fennoscandia (Selås et al. 2001a; see also Selås 1997, 1998, 2000a, 2000b; Selås and Steel 1998; Selås et al. 2001b).

In this article, we evaluate the mast depression hypothesis concerning the population cycle of the autumnal moth by testing its critical assumption of better individual performance in populations occurring the year following birch mast seeding. Our data consist of the instantaneous leaf quality of 20 mountain birches bioassayed annually with autumnal moth larvae. During the study period of 1987–1999 (excluding 3 non-mast years in the early 1990s), two clear flowering peaks of mountain birch occurred in northern Fennoscandia, 1989 and 1998; this gives us 2 independent mast years, 2 independent post-mast years and 6 non-mast years. Since birch flowering seems to be temperature-dependent (Gross 1972; Perala and Alm 1990; Holm 1994; Dahl and Strandhede 1996; Masaka and Maguchi 2001; Selås et al. 2001a), we also consider weather data (as did Selås et al. 2001a) affecting the performance of the autumnal moth. We further provide data on the size of wild adults

as a determinant of potential fecundity of the species in different years. Using simple calculations, we translate size-dependent fecundity into a hypothetical population growth rate; we thereby evaluate the likelihood of achieving outbreak density during just a few generations, as typically takes place in nature.

Materials and methods

Study area and determination of mast years

The study was conducted at the Kevo Subarctic Research Station in northern Finland (69°45'N, 27°01'E). Based on the amount of dispersed birch pollen (Fig. 1), which has been recorded yearly at the Aerobiology Unit of the University of Turku, clear flowering peaks of the mountain birch can be determined for the Kevo area in the summers of 1989 and 1998, a lower peak in 1985, and perhaps a very low peak in 1978 (Fig. 1; Hicks et al. 1994). Since the same peak years from 1985 onwards were also recorded as pronounced mast years in the study of Selås et al. (2001a) for the Ammarnäs study area (65°58'N, 16°03'E) in northern Sweden, birch flowering seems to be synchronous over large areas in northern Fennoscandia. Furthermore, our data on annual birch pollen sums (Fig. 1) correspond well [$r_s=0.48$, $P=0.024$, $n=22$ years] for visually ranked data points from Fig. 1A in Selås et al. (2001a)] to data on birch flowering (pooled number of male and female catkins) at Ammarnäs. All in all, we can thus assume that the annual amount of pollen dispersed is proportional to the abundance of male flowers, which in turn has been shown to correlate positively with the annual seed crop (Dahl and Strandhede 1996; Masaki and Maguchi 2001). In this article, we use the term “mast seeding” for a large reproductive effort of the mountain birch. This is by definition not necessarily a matter of true masting, since there is no inherent switching mechanism from vegetative growth to reproduction or the ability to accumulate resources over years to be used in a large reproductive effort (Kelly 1994; Dahl and Strandhede 1996).

Larval growth rate

Twenty mature mountain birch trees (1–4.5 m in height) were chosen and marked individually in spring 1987. Senn et al. (1992) provide details of tree characters, such as leaf morphology and

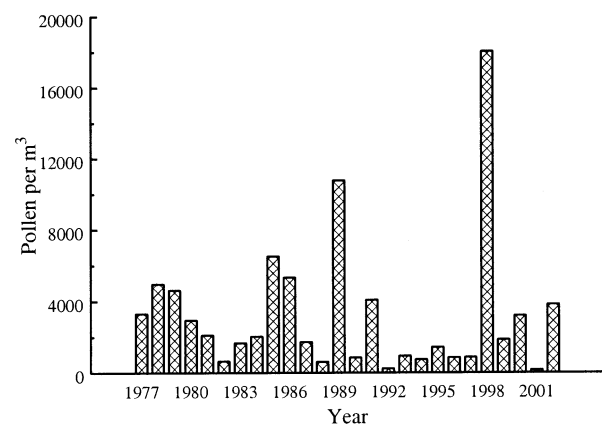


Fig. 1 Total annual sums of birch pollen (pollen in m³ of air) in the Kevo area, 1977–2002. The effect of pollen transport over long distances was reduced by excluding days before the onset of the local flowering period (Hicks et al. 1994). Pollen counts were measured with a 7-day volumetric Burkard sampler (Burkard Manufacturing; see Mäkinen 1981 for methodological details)

phenology. Each year, several larval broods (three in 1987, four in 1988–1990, five in 1995 and 1999, six in 1994 and 1996–1998) were bioassayed under similar laboratory conditions with leaves from the study trees (one larva from each brood per tree). The relative growth rate (RGR) of the fifth instar autumnal moth larvae was used as an index of tree quality. In the autumnal moth, it is the fifth instar that is responsible for most of the gain in final body mass and potential reproductive capacity (Tammeru 1998).

Experimental leaves were always collected early in the morning and kept in a cooler. The growth trial was started without delay and run in a growth chamber at a constant 12°C and under continuous light. Freshly moulted fifth instar larvae were weighed to the nearest 0.1 mg at the beginning and end of the growth trial. In a 48-ml transparent plastic vial, each larva had an excess of fresh leaves (i.e. one to two leaves) to feed on for 24 h (timed to the nearest minute). The RGR ($\text{mg} \times \text{mg}^{-1} \times 24 \text{ h}^{-1}$) was recorded for each larva: $\text{RGR} = [\ln(\text{final mass}) - \ln(\text{initial mass})] / \text{time}$. Before the statistical analysis of the RGR values, we calculated tree-specific means within a year and then used them for the grand mean of each study year. Throughout the study, the larvae were reared solitarily and were fed before the growth trials with leaves from non-experimental trees. The rearing procedure was kept as similar as possible in each year. The experimental larvae originated from eggs laid the preceding autumn (see e.g. Hanhimäki and Senn 1992; Tammeru 1998; Kause et al. 1999 for details of standard growth trials for the autumnal moth).

Adult size and density

Adults of the autumnal moth fly at Kevo during the autumn, i.e. from mid-August until late September, and were caught by light and pheromone traps (Linnaluoto and Koponen 1980; Tammeru et al. 1996a; Kaitaniemi et al. 1999b). Trapped individuals were sexed and measured under the microscope. The size of an adult correlates with its potential fecundity (number of eggs laid), and can be used as a proxy for the reproductive performance in between-year comparisons (Tammeru et al. 1996a; Kaitaniemi et al. 1999b). Our data for the adult size (hind femur length in mm) consist of males trapped with light-traps from 1989 to 1992 and with pheromone-traps from 1993 onwards (data from 1991 and 1998 are lacking). For an index of the autumnal moth density in the Kevo area (number of adults counted per light-trap during the whole flight season), light-trapped individuals have been used throughout since 1972 (Linnaluoto and Koponen 1980; S. Koponen unpublished data).

Climatic indices

Temperatures measured at the Kevo Meteorological Station (operating within the research station) were used to facilitate comparisons between the years. Although all growth trials were conducted with the same final larval instar (17 June–11 July inclusive, depending on the advance of the summer season), there were between-year differences in the accumulated thermal sums (above the baseline of +5°C; termed “DD5” in the following) prior to the growth trial. This seemed to lead to a clear quadratic trend in larval growth rates (Fig. 2A). To remove the trend caused by the timing of the trial in relation to leaf maturation (Ayres and MacLean 1987), we fitted a polynomial regression ($\text{RGR} = 0.02 \times \text{DD5} - 0.000077 \times \text{DD5}^2 - 0.99$), explaining 51% of the variation in the RGR values (Fig. 2A). Residuals of the regression, when added to the grand mean, provided corrected RGR values (Fig. 2B). These were then used in all further analyses.

To find relationships between autumnal moth performance and weather data, several cross-correlation coefficients were calculated (Box and Jenkins 1976), using the ARIMA procedure of the SAS statistical software (version 8.2) for data standardised to zero mean and unit variance. DD5 was used as a temperature index for the whole summer period. In northern Finland, DD5 starts to accumulate in late April or early May and reaches its final level in late

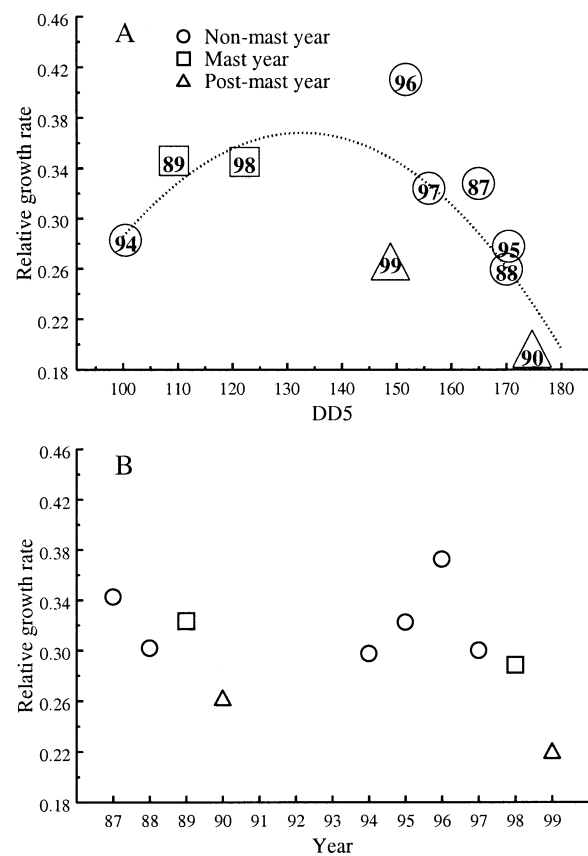


Fig. 2 A Mean relative growth rates (RGRs) of autumnal moth (*Epirrita autumnata*) larvae in relation to accumulated thermal sums prior to growth trial. The curve is fitted by a polynomial regression and explains 51% of the variation. B Mean RGRs after removal of quadratic trend. Study years grouped into three categories according to birch flowering

September or early October. In addition, the North Atlantic Oscillation (NAO) was used as a temperature index for the winter period, i.e. the mean of December, January, February and March (Hurrell 1995; Hurrell et al. 2001; data from <http://www.cru.uea.ac.uk/cru/data/nao.htm>). The NAO, measured as an alternation in the pressure difference between the Azores and Iceland in the Atlantic Ocean, is most pronounced during winter and correlates positively with winter temperatures and precipitation in the northern hemisphere (Hurrell 1995; Selås et al. 2001a). NAO seems to affect many aspects of the ecological dynamics in both marine and terrestrial systems (for reviews see Ottersen et al. 2001; Stenseth et al. 2002). In addition to the actual density index of the autumnal moth, another variable used in the cross-correlation analyses was the realised per-capita rate of population change over a year $[\ln(X_t / X_{t-1})]$, where X_t is the density index for autumnal moth adults at Kevo in the autumn of year t .

Results

Performance of the autumnal moth

There was a statistically significant difference in the RGR values of the fifth instar larvae when the study years were grouped according to birch flowering (one-way ANOVA: $F_{2,7} = 5.9$, $P = 0.032$, $R^2 = 0.63$). The least square mean of

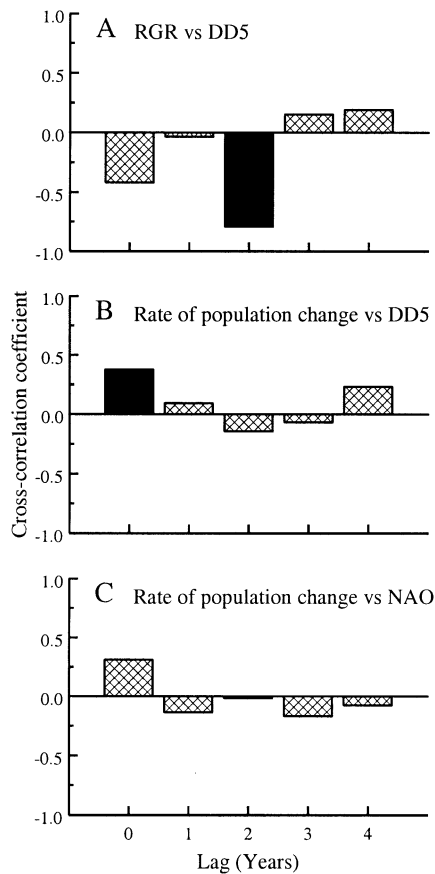


Fig. 3 **A** Cross-correlation coefficients for RGR of autumnal moth larvae (as in Fig. 2B) and thermal sums above the baseline of +5°C (*DD5*), **B** for rate of population change of autumnal moth and *DD5* thermal sum, and **C** for rate of population change of autumnal moth and winter index (December–March inclusive) of the North Atlantic Oscillation (NAO). Solid bars indicate correlation coefficients significantly different from 0, by exceeding 2 respective SEs (Box and Jenkins 1976). Only lags of up to 4 years in which weather data precede the biological attribute are given as relevant

RGR was 0.32 (95% confidence limits: 0.30 and 0.35; $n=6$) for non-mast years, 0.31 (0.26 and 0.36; $n=2$) for mast years, and 0.24 (0.19 and 0.29; $n=2$) for post-mast years (Fig. 2B). A multiple comparison test (Tukey) revealed that the significant difference was between the non-mast and post-mast years ($P=0.026$), since larval growth was poorer the year after mast seeding than in other years (Fig. 2B). This finding is clearly contrary to the predictions of the mast depression hypothesis (Selås et al. 2001a).

The relative larval growth rate correlated negatively with the summer temperature prevailing 2 years earlier (Fig. 3A); low RGRs were recorded in post-mast years, while high summer temperatures were recorded a year prior to abundant birch flowering (Fig. 4A). A positive correlation without lag was detected between the rate of population change of autumnal moth adults and accumulated summer temperatures at Kevo (Fig. 3B). Winter temperatures, when indexed by the NAO, did not correlate with the rate of population change of autumnal

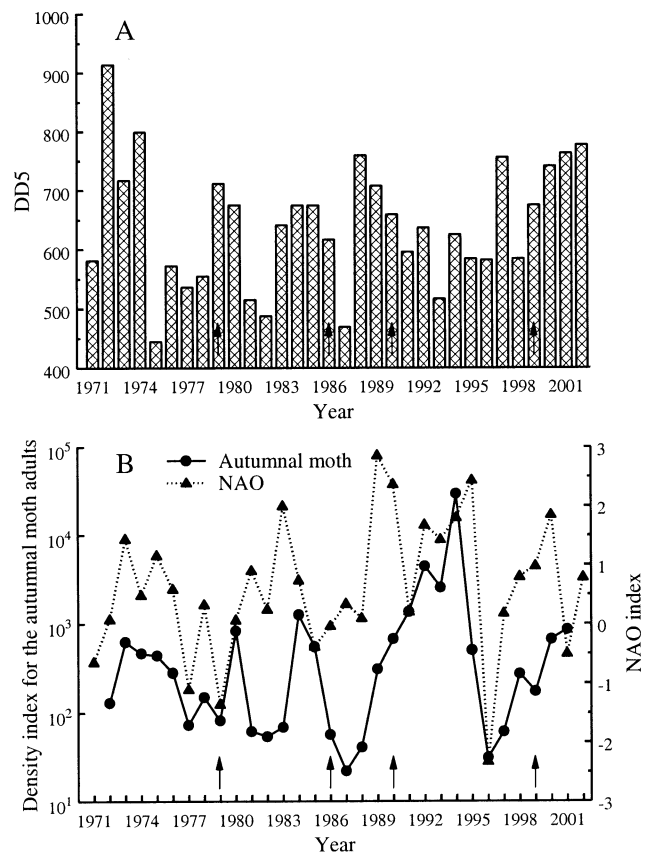


Fig. 4 **A** *DD5* thermal sum at Kevo Meteorological Station 1971–2002. **B** Annual density index (number of adults counted per one light-trap during whole flight season) of autumnal moth at Kevo during 1972–2001, and winter index (December–March inclusive) of NAO during 1971–2002. → Indicate post-mast years considered in this study (see Fig. 1)

moth adults (Fig. 3C). However, winter temperatures correlated positively ($r=0.46$, $P=0.010$, $n=30$) with the ln-transformed density index of adults, the latter representing the growth season following a particular NAO index. This finding can be attributed to the vulnerability of overwintering eggs to cold (note the years 1977, 1979 and particularly 1996 in Fig. 4B) (Niemelä 1979; Nilssen and Tenow 1990; Tenow and Nilssen 1990).

Adult size, as defined by femur length, varied in the Kevo area from year to year (Fig. 5A). Both post-mast years ranked among the years with the largest adult size (Fig. 5A). The increase in potential fecundity due to larger adult size in post-mast years, however, was a matter of only a few eggs in comparison to the grand mean of potential fecundity over all years (Fig. 5B). Adult size correlated negatively with population density ($r=-0.67$, $P=0.034$, $n=10$). However, this relationship disappeared when the extremely high-density year of 1994 was excluded from the analysis ($r=-0.21$, $P=0.59$, $n=9$) (Figs. 4B, 5A).

catkins, as well as the survival of later instar larvae, which feed on female catkins (K. Ruohomäki and P. Kaitaniemi unpublished data). Although these observations deserve further evaluation, they do not provide new insight into the mast depression hypothesis, since there are very few catkins available on birches in post-mast years (Gross 1972; Dahl and Strandhede 1996; Koenig and Knops 2000; Masaka and Maguchi 2001; Fig. 1).

We are not convinced that the logic of the assumed trade-off between defence against herbivores and flowering is true. Although the effects of flowering per se were not focused, Riipi et al. (2002) demonstrated a positive relationship between leaf growth and the production of phenolics in mountain birch. Other recent studies have similarly demonstrated that the assumed defence vs. growth (or reproduction) trade-off may not be generally valid (Messina et al. 2002; Siemens et al. 2002). Nor does it seem likely that defensive compounds in any simple way determine the larval growth of the autumnal moth on mountain birch. Haukioja et al. (2002) have demonstrated that water content and leaf toughness were more important for larval growth than any of the individual phenolics analysed, and that most leaf phenolics which had a significant association with larval performance operated interactively with leaf water content, toughness and the sugar/protein ratio rather than displaying direct correlations with herbivore traits. These findings emphasise the difficulties inherent in the operational definition and measurement of plant defence levels, and suggest potential problems in reasoning based on simple trade-offs between defence, growth and flowering (see Koricheva 2002).

Our growth rate simulations show that a slight increase in adult size does not lead to sufficiently rapid population growth. The density difference between peaks and troughs in cyclic moth populations, such as those reported in our Kevo series (Fig. 4B) as well as in the Ammarnäs and Budal series (Hogstad 1997; Selås et al. 2001a), is at least 1 order of magnitude but often considerably more than 2 orders of magnitude (up to 5 orders of magnitude; see Neuvonen et al. 2001). During the hypothetical increase phase of 5 years, the R_0 should be about 2.5–6.3 in order for the population to reach outbreak density, which is 100–10,000 times greater, respectively, than the low density. Such high reproductive rates are not possible for the autumnal moth without clear changes in survival, besides minor changes in fecundity. Thus larval survival in relation to mast seeding warrants future studies. At the moment, however, we are not aware of any mechanism that might greatly increase the survival of the autumnal moth in post-mast years within the context of the mast depression hypothesis. It is also unlikely that relatively poor larval growth, as measured for the post-mast years in our study (Fig. 2), would be associated with exceptionally high larval survival. In a study conducted at Kevo in summer 2002, the survival rate of autumnal moths reared from neonate larvae to pupae in branch-wide mesh-bag enclosures correlated positively with the RGR of the fifth

instar larvae which were bioassayed with leaves from the same 50 study trees (L. Kapari et al., unpublished data).

The post-mast years studied at Kevo were not generally followed by an initiation of density increase of the autumnal moth (Fig. 4B). We admit, however, that this pattern was obvious in the data presented by Selås et al. (2001a) for two sites (Ammarnäs in Sweden and Budal in central Norway) within the Fennoscandian outbreak range of the autumnal moth. Since our data do not support the trade-off between defence against herbivores and flowering, alternative mechanisms, some of which are briefly outlined by Selås et al. (2001a), are needed to explain the coincidence between mast seeding and outbreaks in Ammarnäs and Budal. Our density indices for adult moths at Kevo may include migrating adults from asynchronously fluctuating moth populations and thus may not be fully comparable to the more local density indices of Selås et al. (2001a). If the mast depression hypothesis is adopted, however, synchronous birch flowering between Kevo and Ammarnäs also presumes synchronous population fluctuations of the autumnal moth in a rather large area around the light-traps used.

Warm summer temperatures in the previous year seem to prompt abundant birch flowering (Hicks et al. 1994; Holm 1994; Dahl and Strandhede 1996; Masaka and Maguchi 2001; Fig. 4A). Warm summer temperatures, however, are not associated with high growth rates of autumnal moth larvae (Fig. 3A). The rate of population change correlated positively with the summer thermal sum (Fig. 3B). This correlation was unexpected; earlier studies have indicated the partial dependence of autumnal moth outbreaks on low summer temperatures (Niemelä 1980; Virtanen and Neuvonen 1999; Selås et al. 2001a). The most obvious explanation for our result could be a warm autumn period, increasing the success of oviposition or flight activity and “trappability” of adults. However, we did not find significant cross-correlations between the accumulated thermal sum during the flight period (15 August–30 September) and the rate of population change ($r=0.16$ and $r=0.20$ for time-lags 0 and 1, respectively) or ln-transformed density index of adults ($r=-0.03$ and $r=0.13$ for time-lags 0 and 1, respectively). Accordingly, the mechanisms of the positive correlation between the rate of population change and summer temperatures are not known.

The minimum winter temperature affects autumnal moth densities through increased egg mortality in cold winters (Ruohomäki et al. 1997). This is explained by the minimum temperature (-36°C) below which over-wintering eggs die (Niemelä 1979; Nilssen and Tenow 1990; Tenow and Nilssen 1990). A positive winter index of the NAO coincides with a high temperature and a thick snow layer. Proportionally more eggs laid on the trunks and branches of trees may be protected from cold air during mild and snowy winters (positive NAO), whereas during cold and dry continental winters (strong negative NAO) (Hurrell 1995), egg mortality significantly reduces the abundance of the autumnal moth (Niemelä 1979; Bylund 1995; Ruohomäki et al. 1997; Virtanen et al. 1998;

Fig. 4B). Accordingly, we suggest that the mechanisms affecting mortality are important if autumnal moth outbreaks are to be predicted on the basis of weather data (see also Virtanen and Neuvonen 1999).

Conclusions

Since the assumption of better individual performance in autumnal moth populations subsequent to mast seeding was not supported by our data, the factor(s) underlying regular outbreaks at intervals of 9–10 years in northern Fennoscandia remain unidentified. In this paper, we have focused only on the trophic interaction between the host and the herbivore, leaving all interactions with natural enemies out of consideration as factors behind the cyclic dynamics (see Bylund 1995; Ruohomäki et al. 2000; Klemola et al. 2002). For example density-dependent larval parasitism by hymenopteran parasitoids offers an explanation worth future study (Ruohomäki et al. 2000; Tanhuanpää et al. 2002).

In general, the mast depression hypothesis, as proposed for several plant and herbivore species (Selås 1997, 1998, 2000a, 2000b; Selås and Steel 1998; Selås et al. 2001a, 2001b), needs further experimentation. Without field experiments, causal relationships cannot be identified in complex trophic interactions which are further modified by abiotic factors like weather and climate. Abiotic factors, for instance, may affect the phenology of the autumnal moth, its parasitoids, and its host plant, the mountain birch, in different ways (Kaitaniemi and Ruohomäki 1999; see also Visser and Holleman 2001; Stenseth and Mysterud 2002), thus generating conditions that favour the survival of the moth and initiation of an outbreak.

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