

SPECIAL FEATURE: REVIEW

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Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice

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Abstract Creating multiyear cycles in population density demands, in traditional models, causal factors that operate on local populations in a density-dependent way with time lags. However, cycles of the geometrid *Epirrita autumnata* in northern Europe may be regional, not local; i.e., successive outbreaks occur in different localities. We review possible causes of cycles of *E. autumnata* under both local and regional scenarios, including large-scale synchrony. Assuming cyclicity is a local phenomenon, individual populations of *E. autumnata* display peaks but populations all over the outbreak range fluctuate in synchrony. This concept assumes that the peaks at most localities are so low that they do not lead to visible defoliation and easily remain unnoticed. In this scenario, populations are able to start recovery a few years after the crash, i.e., at the time of the mitigation of detrimental delayed density-dependent factors, such as delayed inducible resistance of the host plant or parasitism. In that case, the same factors that lead to crashes also explain the periodicity of cyclic fluctuations. According to the regional cyclicity scenario, different factors can be important in different phases of the cycle. The key is to identify the factors that tend to produce outbreaks with a periodicity of about 10 years. Initiation of the increase phase seems to coincide with maxima in sunspot activity, but causal connections remain unclear. Climatic factor(s) associated with the solar cycle could contribute to the large-scale geographic synchrony.

Key words Cyclic population dynamics · Host plant quality · Inducible resistance · Parasitism · Predation · Winter mortality

Introduction

Most natural populations of herbivorous insects do not reach outbreak densities (Mattson and Addy 1975; Mason 1987; Hunter 1995) while a few others (Baltensweiler et al. 1977; Ginzburg and Taneyhill 1994; Myers 1993; Berryman 1995) display irregular outbreaks or regular cycles, an outbreak being defined as an “explosive increase in the abundance of a particular species that occurs over a relatively short period of time” (Berryman 1987).

The geometrid *Epirrita autumnata* (Borkhausen) (earlier called *Oporinia autumnata*) displays outbreaks in mountain birch [*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti, earlier called *B. pubescens* ssp. *tortuosa* (Ledeb.) Nyman] forests that form the tree line in northwest Europe. During the outbreaks, northern birch forests may become totally defoliated in limited areas or defoliations may cover hundreds of square kilometres. Trees may occasionally die over vast areas (Fig. 1) (Tenow 1972; Kallio and Lehtonen 1973; Bylund 1995; Lehtonen and Heikkinen 1995). Outbreaks of *E. autumnata* do not usually spread out from epicenters and can thus be classified as cyclic gradients (Berryman 1987).

Olle Tenow published in 1972 an extensive survey of 12 successive outbreaks of *E. autumnata* in northern and mountainous Fennoscandia (Scandinavia plus Finland), covering the period from 1862 to 1968 (Tenow 1972). Later, three further outbreak periods occurred in the same area: in the middle of the 1970s (Hogstad 1997), in the middle of the 1980s (Bylund 1995; Ruohomäki and Haukioja 1992a; Itämies et al. 1995; Tenow 1996; Hogstad 1997), and in the first half of the 1990s (Bylund 1995; Tenow 1996; Hogstad 1997; Ruohomäki et al. 1997). By using published records, Haukioja et al. (1988a) demonstrated a statistically

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Fig. 1. Dead mountain birch forest in Finnish Lapland, destroyed by defoliation during an *Epirrita autumnata* outbreak in the middle of the 1960s



significant 9- to 10-year regional periodicity in outbreak dynamics in northern Fennoscandia.

Large-scale outbreaks of *E. autumnata* have been recorded only in northernmost Europe, i.e., in northern and mountainous Fennoscandia and northwesternmost Russia (Tenow 1972), although the species is common and abundant in many parts of its Holarctic range. The nonmountainous populations south of the polar cycle do not produce outbreaks (Tenow 1972). *E. autumnata* matches the larch budmoth (Baltensweiler et al. 1977) in that the same insect–host plant association displays both outbreaks and relatively stable densities in different geographic regions.

At a general level, stability versus fluctuations in population densities are well understood. Stability is achieved in traditional models by direct negative density dependence in population growth (Murdoch 1994; Krebs 1995): an increase in mortality or decrease in natality with increasing population densities. In contrast, cyclic dynamics results from *delayed* density-dependent factors (Berryman 1995). According to the traditional approach, for the relatively stable southern *E. autumnata* populations the primary causal forces leading to stability might be detrimental factor(s) that act in a direct density-dependent manner without time lags. In contrast, for the northern populations the critical factors are detrimental (during the decrease phase) or promoting (during increase) factor(s) operating in a delayed density-dependent way, with an appropriate time lag.

Models of this type have been used to analyze recorded density fluctuations, for instance in cyclically fluctuating forest insect and rodent populations, and with suitable parameterization they accurately describe past dynamics. Problems often start, however, when trying to identify the causal factors behind the delayed feedbacks and especially when trying to test the importance of particular factors. Two questions have to be separated. It is relatively straightforward to demonstrate that a certain factor contributes to

cyclicality (e.g., by showing that it can reduce the performance of the herbivore in a density-dependent way, with time lags), but it is much more difficult to determine whether the reduction is a cause or a consequence of the change in herbivore density (i.e., whether the factor really drives cycles under natural conditions) and to estimate its relative importance compared to other factors. However, these latter steps are necessary if our intention is to predict what happens in natural populations.

Occurrence of cyclic outbreaks in *E. autumnata* has stimulated several research projects, especially during the last quarter of the previous century. These projects, like many other projects on forest lepidopterans, have concentrated on factors that could lead to density-dependent time lags in population density. The key questions have been effects of inducible resistance of the host tree on *E. autumnata* and other herbivores and the efficiency of parasitism and predation. However, in the case of *E. autumnata*, a basic problem is encountered at a very basic level: while the cyclicality is statistically significant at the regional level (Haukioja et al. 1988a), it is not necessarily the same forest stands that experience successive outbreaks (Bylund 1995). In other words, even demonstrations of negative density-dependent factors with time lags, operating in a local scale, may not be sufficient when trying to explain regional cyclicality across a scale of hundreds of kilometers.

In this review, we first introduce the species and then the problem of regional versus local cyclicality. We then turn to possible mechanisms in the cyclic dynamics, treating separately the scenarios of local and regional cyclicality, including synchrony in population dynamics over vast areas. We also briefly discuss possible reasons why northern but not southern populations have outbreaks, as well as empirical pitfalls in practical research. Throughout this article, “northern” and “southern” populations (in Fennoscandia) refer to cyclic outbreaking and more stable nonoutbreaking populations, respectively.

The species

The spring-feeding green (cryptic) larvae with five instars are highly polyphagous, having been recorded on more than 15 species of deciduous trees, shrubs, and dwarf-shrubs (Seppänen 1970). In Fennoscandia, birches are the most frequently used hosts, apparently because of their abundance. The larvae eclose in spring in synchrony with birch leaf flush (Kaitaniemi et al. 1997a; Kaitaniemi and Ruohomäki 1999). The synchrony between larval and leafing phenologies is important for successful larval development because fast growth can only be maintained on young leaves (Haukioja et al. 1978; Ayres and MacLean 1987; Tammaru 1998; Kause et al. 1999b). The growth rate, in turn, is decisive in determination of larval period, pupal mass (Kause et al. 1999c) and – because adults generally do not feed – fecundity (Tammaru 1998). At least in the first instar, larvae can disperse by ballooning; this can be important because female adults oviposit indiscriminately, even on plants that are not suitable for larval development (Tammaru et al. 1995).

The duration of the larval stage is highly variable, from just over 2 weeks to almost 2 months, depending on temperature and forage quality. The larvae pupate before mid-summer within a thin cocoon in the litter at the depth of a few centimeters. The pupal stage lasts until autumn. The life cycle is adjusted for latitudinal changes in summer length by adjustments of the duration of the pupal stage. In Finland (1200-km south-north gradient), the duration of the pupal stage varies from more than 3 months in the south to about 1.5 months in the north (Haukioja et al. 1988a; Tammaru et al. 1999). The length of the pupal period is partially genetically determined but is influenced by environmental cues, at least by temperature (Harrison 1920; Peterson and Nilssen 1996; Tammaru et al. 1999).

The short-lived nocturnal adults have a weakly developed proboscis. They are able to imbibe water from suitable surfaces, but unfed females successfully lay most of their egg load (Haukioja and Neuvonen 1985a; Tammaru et al. 1996a). *E. autumnata* is thus a capital breeder (Tammaru and Haukioja 1996) in that potential and realized fecundity is directly dependent on resources (Haukioja and Neuvonen 1985a; Tammaru et al. 1996a) accumulated during the larval stage. Each milligram of additional mass is equivalent to ≈ 2.6 more eggs. Reproductive success of males is also positively correlated with their mass, but this variation probably has no consequences for population dynamics (Tammaru et al. 1996b). Males fly actively searching for females, which release a pheromone (Zhu et al. 1995), and large size may enhance flight ability. In contrast, females are poor flyers, at least when still fully loaded with eggs. The low mobility of *E. autumnata* females decreases the potential for behavioral responses to cues indicating high population density (Tammaru et al. 1995).

The reproductive potential of *E. autumnata* is high enough to allow rapid population increases ($r_m > 4$ females \cdot female⁻¹ \cdot year⁻¹; Haukioja et al. 1988a). Therefore, intrinsic factors allow *E. autumnata* populations to initiate out-

breaks. However, they are not sufficient to explain outbreaks (Tammaru and Haukioja 1996). For instance, the same basic features characterize populations within and outside the outbreak range (Ruohomäki 1991). Accordingly, the extent to which potential reproductive capacity is realized is critical, i.e., whether internal constraints, external environmental conditions, or their interactions allow an increase.

Local versus regional cyclicality

Epirrita autumnata population cycles vary in their amplitude (Tenow 1972). Thus, two alternatives can explain the causes for cyclicality. First, cyclicality may be a local phenomenon. In other words, individual populations of *E. autumnata* display peaks, and populations all over the outbreak range fluctuate in synchrony. This concept assumes that peaks at most localities must be so low that they do not lead to visible defoliations and easily remain unnoticed. In this scenario, populations are able to start recovery a few years after the crash, i.e., at the time when the detrimental delayed density-dependent factors are mitigated. In that case, the same factors that led to crashes also explain the periodicity of cyclic fluctuations. The alternative explanation is that recorded fluctuations (Tenow 1972) show regional but not necessarily local cyclicality (Haukioja et al. 1988a). In this scenario, the key is to identify the factors that permit new outbreaks at roughly 10-year intervals. This idea reiterates the notion by Price et al. (1990) and Tammaru and Haukioja (1996): to understand dynamics of outbreak populations, it may be at least as important to have information about the factors and conditions allowing some populations to achieve outbreak densities as to study factors terminating outbreaks.

Available data do not allow us to distinguish between these alternatives. Bylund (1995) has reported different birch stands becoming defoliated during successive outbreaks, which is consistent with the observation that severe defoliations take place in mature birch forests (Bylund 1995; Ruohomäki et al. 1997). The generality of these observations is unclear. However, there is evidence for local cyclicality (Enemar et al. 1984; Hogstad 1997). In addition, we have monitored larval densities within the same forest patches (within 1 ha) for 14 successive years in 12 populations widely distributed in northern Finland, Norway, and Sweden. Six of the populations gradually developed peak density during the early 1990s; only 2 of these populations attained an outbreak, and severe defoliation did not occur even in these populations. Of the other 6 populations, 4 were situated along the Atlantic coast, where *E. autumnata* populations are known to be relatively stable compared to the more continental (and mountainous) populations (although the related *Operophtera* spp. do reach outbreak densities there; Tenow 1972). The 2 continental populations without an obvious population peak in the early 1990s were from northern Norway, where the previous outbreak at the same birch stands occurred in the mid-1980s. The hypoth-

eses of regional cyclicality versus local cyclicality may not be totally exclusive. For example, factors important to the scenario of regional cyclicality may also affect local population dynamics.

Mechanisms in the local cyclicality scenario

In the local scenario, the cyclicality runs as proposed by the traditional theory (Berryman 1987; but see Kaitala et al. 1996): a new increase is possible after relaxation of delayed density-dependent factors that precipitated the previous peak. This theory means that there are one or more factors creating cyclicality and that increases, peaks (outbreak or not), and decreases are explained by the same factor(s).

In *E. autumnata*, two mechanisms obviously operate with delayed density dependence: delayed inducible resistance (DIR) of mountain birch and larval parasitism, which both have been studied intensively. Information about DIR mostly originates from experimental studies, whereas that for parasitism comes from long-term monitoring of parasitism rates in field populations. In our modeling effort, it has been easy to produce cyclic behavior in population density by realistic values of both induced resistance and parasitism.

Delayed inducible resistance of the mountain birch

DIR means that larval defoliations lead to poor foliage quality for the subsequent moth generation(s) (Haukioja 1990). The main approach in experimental studies on DIR has been to randomly allocate birch trees to treatments, manually defoliating (usually by tearing half of each leaf) the experimental trees at the natural feeding time of *E. autumnata* larvae. In subsequent season(s), larvae have been reared in the field in mesh bags on birch branches. The pupal size (and hence, indirectly, the potential fecundity) and survival rate have been used as indices of foliage quality. Manually devised DIR can cause up to 70%–80% reduction in the egg production capacity of *E. autumnata*, but the strength of DIR has been highly variable between different experiments (Haukioja et al. 1985; Ruohomäki et al. 1992). Figure 2 summarizes our current data set. Following defoliation, the quality of foliage may remain low for 1–4 years (Haukioja 1982; Kaitaniemi et al. 1999a,b).

These results demonstrate the potential of DIR to contribute to the cyclicality of *E. autumnata* populations. There have been two attempts to demonstrate DIR during a natural outbreak. In 1988, after the 1986–1987 outbreak in northern Norway, we tested the quality of mountain birch foliage at three sites, one heavily defoliated the previous years, one that was partially defoliated, and an undefoliated one. In a 24-h growth trial in the laboratory, larvae reared on foliage of the heavily defoliated site grew significantly slower (33%) than those reared on foliage from the undefoliated site (Haukioja et al. 1990). Although this observation supports the significance of DIR, it is a weak test

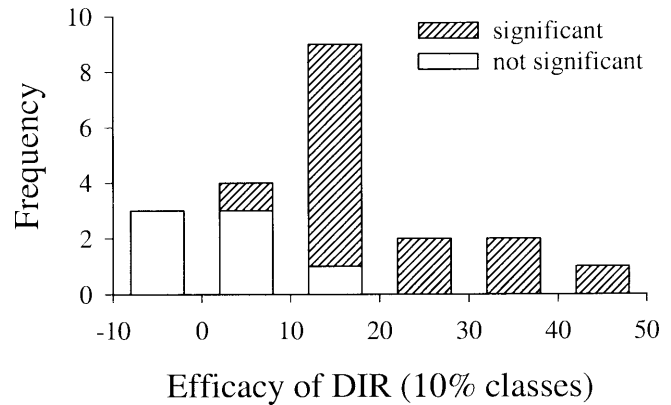


Fig. 2. Summary of experiments that have used artificial defoliation during the previous season to test the effects of delayed inducible resistance (DIR) of mountain birch on pupal mass of *E. autumnata*. The vertical axis shows the frequency of studies demonstrating statistically significant or not significant effect of DIR; the horizontal axis shows the efficacy of DIR as percentage reduction of the pupal mass of *E. autumnata* (positive value indicates a decrease in pupal mass)

because there was only one replicate (site) of each defoliation history. We made a further attempt to evaluate effects of DIR on population dynamics of *E. autumnata* in a natural situation during the 1992–1994 outbreak in central parts of Finnish Lapland. We used two complementary approaches to investigate the impact of DIR on moth performance. First, we introduced hatching eggs into mesh bags on naturally defoliated birches and on those protected from defoliation by an insecticide. Second, we pheromone-trapped wild males at sites where birches had been defoliated and at sites with no or only slight defoliation. Differences in size of *E. autumnata* were in accordance with DIR, as were chemical changes in foliage (see Kaitaniemi et al. 1998), but they were mostly not significant statistically and too small to have a marked impact on population dynamics (Kaitaniemi et al. 1999b). Therefore, DIR was not of primary importance during this outbreak. Because the 1990s peak declined without severe defoliations (mostly below 50% defoliation), this experiment did not elucidate well the general role of DIR.

In conclusion, although even a strong DIR has been repeatedly demonstrated experimentally, it still remains uncertain whether DIR is a generally important contributor to cyclicality of northern *E. autumnata* populations.

Inducible susceptibility of the mountain birch

Because an outbreak density cannot be achieved in one or two generations, the permissive conditions have to prevail for several generations. Therefore, it is logical also to look for positive density dependence as a reason behind the cyclicality. Herbivore-triggered susceptibility (Haukioja et al. 1990; Karban and Thaler 1999) is the only mechanism suggested thus far that might produce positive feedbacks into the population dynamics of the moth. Under this hypothesis, larger size and hence higher reproductive capacity of

moths can be expected in the increase phase than in the low-density phase. However, the field evidence is conflicting (cf. Hogstad 1996 and Ruohomäki et al. 1996). Our knowledge of the importance of inducible susceptibility is based mainly on experimental manipulations of birches. It is easy to break apical dominance of shoots and branches by destroying the apical meristems, e.g., by clipping. That technique leads to vigorous growth of extant leaves, with corresponding changes in foliage chemistry (Danell et al. 1997; Honkanen and Haukioja 1998); the outcome resembles that of nitrogen fertilizing. It is, however, not clear whether larvae in the field can produce the same response. We have demonstrated that larval damage during a natural outbreak tends to be concentrated on the most apical buds (Haukioja et al. 1990), which could improve foliage quality the next year, or at least eliminate induced resistance (Kaitaniemi et al. 1997b). However, our attempts to get bagged larvae to consume buds in an identical way have mostly failed.

Parasitoids

At least seven species of larval parasitoids (Ruohomäki 1994) and three pupal parasitoids (Tenow 1955; Tanhuanpää et al. 1999) (all hymenopterans) have been reared from northern *E. autumnata*. To contribute to cyclicity, at least some of the parasitoids have to be host specialists. We know that most, perhaps all, larval parasitoids of *E. autumnata* in Fennoscandia are potential generalists (see Ruohomäki 1994). However, because alternative hosts are scarce in subarctic insect communities, all the parasitoids associated with *E. autumnata* in the north are functional specialists and hence potentially important for cyclic dynamics.

Delayed density dependence is indicated in both long-term monitorings of larval densities and parasitism rates of *E. autumnata* (Ruohomäki 1994; Bylund 1995) as well as in trapping data of adult parasitoids during different phases of the cycle (Nuorteva and Jussila 1969; Gergely Várkonyi, personal communication). The delayed density-dependent variation in larval parasitism rate ranges almost from 0% to 100% (Bylund 1995). In adult trappings, some parasitoid species declined from very abundant to nearly undetectable within 2 years after *E. autumnata* outbreaks (Nuorteva 1971; G. Várkonyi, personal communication).

Pupal parasitoids, especially *Itamoplex armator* (Vill.) (earlier called *Trachysphyrus albatorius*), can also be important during some outbreaks (Tenow 1972) but not during others (Bylund 1995; see also Tanhuanpää et al. 1999). There is some indication that their effects exert delayed density dependence (Nuorteva and Jussila 1969).

Predators

There are few data describing the importance of predators for northern populations of *E. autumnata*. However, insectivorous birds show both numerical and functional responses to outbreaks of *E. autumnata* (Silvola 1967; Hogstad 1969; Lennerstedt 1973; Enemar and Nyström

1981; Enemar et al. 1984). Birds respond to larval densities without a time lag, and therefore their role in causing cyclicity is negligible. Furthermore, their densities are relatively low. However, it is less clear whether birds occasionally or locally control *E. autumnata* populations, thereby suppressing tendencies to cycle.

Voies and shrews are potentially important pupal predators of *E. autumnata* (Tanhuanpää et al. 1999). They are cyclic in northern Fennoscandia, displaying a 3- to 5-year periodicity (Norrdahl 1995). Neuvonen (1988) investigated the covariation between cycles of *E. autumnata* and voles (and shrews) during 1888–1968. The cross-correlations between *E. autumnata* and vole densities with different time lags were generally low (<0.1). When the *E. autumnata* series was shifted 1 year ahead of that of voles, the cross-correlation became somewhat stronger (-0.2) (Neuvonen 1988). These results do not suggest any direct effect of small mammals on population dynamics of northern *E. autumnata*. Results of pupal predation experiments support this conclusion (Tanhuanpää et al. 1999).

Among invertebrate predators, wood ants, especially *Formica aquilonia* Yarrow, as predators of larvae, and pupal predators are the only ones for which published information is available on the field effects on *E. autumnata*. During outbreaks, wood ants can protect mountain birches around the mounds from defoliation by *E. autumnata* larvae (Laine and Niemelä 1980; Karhu 1998). Accordingly, they may, if the mound density is high enough at favorable sites (Laine and Niemelä 1989), mediate local declines. Wood ants probably do not contribute to maintenance of population cycles because they respond functionally, without a time lag, and hence their effect should stabilize the population dynamics of *E. autumnata*. Experimental studies by Tanhuanpää et al. (1999) suggest that invertebrate pupal predators play a negligible role in population dynamics.

Diseases

There have been no explicit studies of disease epidemiology in *E. autumnata*. Field observations suggest that diseases are only rarely involved in population declines (Tenow 1972, and personal observations). This idea is consistent with the low incidence of diseases in *E. autumnata* rearings; it is not necessary, for instance, to sterilize rearing vials or leaves to successfully rear larvae.

Intrinsic factors

Chitty (1960) proposed intrinsic characteristics to drive rodent cycles, and later the explanation was extended to forest lepidopterans (Wellington 1960; Pimentel 1968). The mechanism of these changes could be maternal or genetic, both of which could operate with a time lag (Mitter and Schneider 1987; Ginzburg and Taneyhill 1994). Cycle phase-dependent differences in fitness-related life history traits, such as reproductive capacity, have been searched for and found in several lepidopteran species (Mason et al. 1977; Myers 1990, 1998). The most obvious of these is the

small size of the moths, and consequently their low reproductive capacity, during the peak and decline phases. However, it is difficult to know whether this is the result of intrinsic factors (maternal or genetic), extrinsic environmental factors, or their interactions (Haukioja et al. 1988b).

In *E. autumnata*, we have been generally unable to attribute differences in reproductive capacity, wing-loading (indicating flight ability), or host plant use (Ruohomäki and Haukioja 1992a,b; Ruohomäki 1992; see also Berryman 1996) among *E. autumnata* populations to cyclic changes in maternal or genetic effects. A single exception is that Haukioja and Neuvonen (1987) found an increased ability of larvae to feed on low-quality foliage expressing DIR when their mothers had been reared on DIR foliage. This study has been recognized by advocates of the maternal hypothesis (Ginzburg and Taneyhill 1994; Myers et al. 1998). However, subsequent tests have not supported this hypothesis for *E. autumnata* (Ruohomäki and Haukioja 1992a).

Mechanisms in regional cyclicality scenario

In the regional scenario, it is assumed that the 9- to 10-year cyclicality is not experienced at a local scale; i.e., after a severe defoliation episode birch stands become unsuitable for further outbreaks for longer times than the cycle length of *E. autumnata* populations. Accordingly, successive peak densities occur mostly at different localities, or birch stands. This condition is clearly satisfied in cases in which severe defoliations kill mountain birches and decades are required for the forests to recover (Bylund 1995).

In both the regional and local scenarios, the same factors can explain the crash of the population and the beginning of the early low phase. However, in the regional scenario, it is less easy to understand such factors being responsible for the initiation and intensity of a new peak, because the traditional delayed density-dependent factors that could be important in the case of *E. autumnata* cannot operate in regional scales. For example, if DIR is triggered in a birch stand it cannot explain a new increase in another stand 100 km distant. Therefore, the regional scenario must emphasize factors and conditions that allow initial increases in density at the start of an outbreak.

Predation, parasitism, and diseases

As regards the higher trophic level, the only published data concerning areas where no *E. autumnata* outbreak has occurred for a long time (longer than the cycle length) are those for pupal predation (Tanhuanpää et al. 1999). For the regional cyclicality scenario, the most valuable information would be that from the density increase phase. Although we lack that information, the data show 65% mean pupal survival for a northern area, whereas survival in southern stable populations was only 34% (Tanhuanpää et al. 1999). Therefore, pupal predation is less limiting in the north.

Foliage quality

There are three ways in which leaf quality could contribute to initiation of outbreaks: external conditions may modify foliage quality differently in different years, synchrony between larval and leaf development may cause annual variations into foliage actually consumed by larvae, and larval feeding may induce better foliage quality for the same or the following generations of the moth. The latter possibility has already been discussed in the section on local cyclicality.

High-quality foliage is necessary for rapid larval growth leading to high pupal weights and high fecundity. In spite of our long-term research on the quality of foliage, we still believe that for *E. autumnata*, as well as for other defoliators, this continues to be the least understood contributor of population fluctuations. Because of the rapid changes in foliage quality during leaf growth, it is extremely difficult to collect comparable leaf samples to reveal whether the constitutive resistance of birch leaves varies between years. Accordingly, we do not have reliable data for solving this problem. In the mountain birch, leaf quality profoundly changes during leaf growth, and even the chemical and physical correlates of foliage quality for *E. autumnata* larvae change completely during leaf development (Nurmi et al. 1996; Ossipov et al. 1997). The change is so total that young, half-grown, and mature leaves do not share a single group of chemical compounds significantly affecting performance of larvae (Kause et al. 1999b). In young leaves, concentration of hydrolyzable tannins is the main hurdle for larval performance, although larvae can decrease their importance by compensatory feeding. On half-grown leaves, condensed tannins are the main determinants of leaf quality, and during the final instar, low water and protein content and high toughness indicate poor growth.

Synchrony of larval hatching and leaf burst is essential for *E. autumnata* larvae (Haukioja et al. 1978; Ayres and McLean 1987). There is an inherent discrepancy in timing because leaf burst obviously depends on temperature sum of the spring only while larval hatch depends on temperature sum accumulated both during autumn and spring (Haukioja et al. 1988b; Ruohomäki et al. 1993; Kaitaniemi and Ruohomäki 1999). Both early and late hatching of larvae in relation to leaf development are potentially hazardous for larvae. During warm spells in early spring, larvae may hatch before the budburst (Bylund 1995), causing ballooning larvae to perish on the snow surface. Late and prolonged eclosion period is also risky: during the 1990s outbreak, Kaitaniemi and Ruohomäki (personal observation) found numerous newly hatched larvae on rapidly maturing foliage together with earlier hatched larvae already in their third instar. Larvae delayed to that extent never reach the pupal stage because of high parasitism rate and being forced to feed on foliage rapidly declining in quality (Kaitaniemi et al. 1997a; Kaitaniemi and Ruohomäki 1999; Kause et al. 1999b).

Forest age

Epirrita autumnata outbreaks take place mostly in mature mountain birch forests (Tenow and Bylund 1989; Bylund 1995, 1997; Ruohomäki et al. 1997). The most obvious explanations are low rates of parasitism or high foliage quality in mature forests, but these have not survived empirical tests (Bylund 1997). Bylund (1997) also suggested that old forests provide more suitable oviposition sites (e.g., more lichens). However, although females tend to lay eggs singly in physically protected microsites (e.g., beneath lichen lobes and in bark crevices on tree trunks and branches) (Tenow 1972; Tenow and Bylund 1989; Tammaru et al. 1995), they will lay their full egg loads even in the absence of lichens (Tammaru et al. 1995). High predation of eggs on lichen-free trees is unlikely because there are very few egg predators during the egg stage at high-latitude (and high-altitude) areas. In particular, we have shown that caged willow tits (*Parus montanus* Conrad) did not utilize even unnaturally large groups of seven eggs (Päivi Lundvall and K.R., unpublished data; for the size of winter food items of tits, see also Carlson 1992).

Within the regional cyclicity scenario, we have thus far been concerned with conditions and factors allowing initial increases in density of *E. autumnata*. However, we still need some factor(s) that make those conditions cyclical. The best candidate as a timer seems to be periodic variation in solar activity (10–11 years; see Waldmeier 1961). If solar activity influences population dynamics, it could explain the pattern of local cycles and simultaneously solve the puzzle of large-scale synchrony of population dynamics in *E. autumnata* (Tenow 1972) and many other moths (Hanski and Woiwod 1993; Myers and Rothman 1995; Liebhold et al. 1996).

Solar cycle: cause for synchrony and regional cyclicity?

The idea of a causal connection between herbivore and sunspot cycles has survived from Elton (1924) to the present (Sinclair et al. 1993; Myers and Rothman 1995; Myers 1998); the two latter papers discuss outbreaks of Fennoscandian *E. autumnata* in relation to sunspot activity. Alternative (or perhaps complementary) explanations for large-scale synchrony in population dynamics include dispersal and the Moran effect (Ranta et al. 1995; Myers 1998).

It may seem probable that an outbreak population would spread from its epicenter but in *E. autumnata* this rarely happens (Tenow 1972), apparently because of limited capacity for long range dispersal. Several sets of data support this conclusion. First, when eggs at low altitudes have been killed by winter frost (see following), the consequent boundary between defoliated and not-defoliated trees was retained sharply during the following summers (Tenow 1975; Tenow and Holmgren 1987); that is, just those trees were defoliated in which eggs were not killed by winter frost, indicating very limited larval dispersal (see also

Tammaru et al. 1995). The same phenomenon has been claimed to take place also within trees: trees with tops above the boundary of lethal winter temperature experienced heavy defoliation of tops while basal parts remained undefoliated (Tenow 1975). However, lacking or restricted movements within or among host trees does not necessarily prove that larvae could not start ballooning from nonhost species (Conchita Alonso, unpublished data). Second, in spite of some contradictory data for the related geometrid, *Operophtera brumata* L. (Edland 1971), results with other lepidopteran species with ballooning larvae indicate that the dispersal distances are too short to modify local population dynamics (Liebhold and Elkinton 1990; Harrison 1994; Dwyer and Elkinton 1995). Third, although it is known that large numbers of *E. autumnata* males may migrate long distances [Bruun's (1990) 200 migratory specimens were all males; checked by K.R., and personal observations], females are apparently poor fliers, especially when fully loaded with eggs (Itämies et al. 1995; Tammaru et al. 1995).

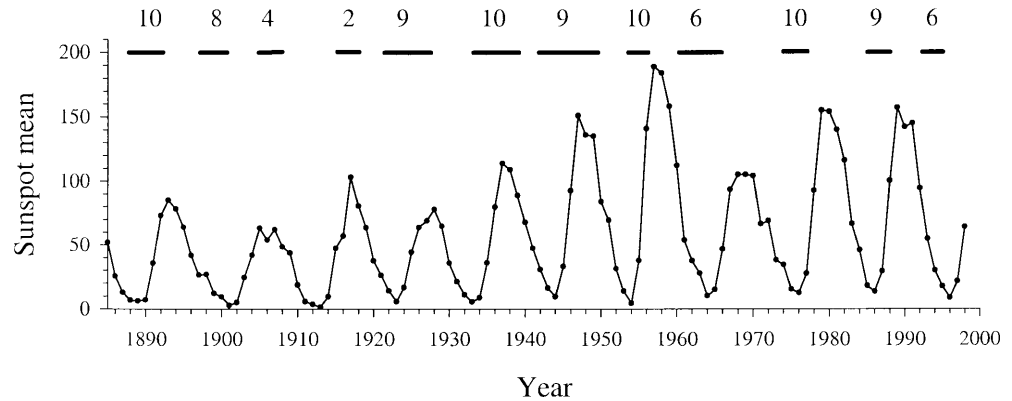
The Moran effect results from spatially correlated density-independent factors, such as weather. Accordingly, it does not offer any single causal factor, just the general principle. However, because the factor causing the spatial correlation can be produced by solar activity, Moran effect is not necessarily different from solar cycles. The Moran effect does not necessarily require periodicity in the exogenous factor that influences population dynamics; even a randomly occurring spatially correlated density-independent factor can synchronize different populations (Ranta et al. 1995). Testing these ideas requires empirical analyses of spatial patterns in the relevant factor(s). Of the plausible factors, weather records afford the most commonly available data.

Winter temperatures below -36°C kill eggs of *E. autumnata* (Niemelä 1979; Nilssen and Tenow 1990; Tenow and Nilssen 1990). Such temperatures are common in northern Fennoscandia and can obviously limit outbreaks both temporally and spatially (Tenow and Holmgren 1987; Tenow and Bylund 1989; Tenow and Nilssen 1990; Tenow 1996; Ruohomäki et al. 1997; Virtanen et al. 1998). Low winter temperatures occur, especially in river valleys and other low-altitude sites that experience temperature inversions in which cold air accumulates during calm winter nights and kills *E. autumnata* eggs. Consequently, *E. autumnata* outbreaks are characteristic of high-altitude sites (Tenow 1972; Ruohomäki et al. 1997) and are not possible immediately after cold winters.

As suggested by Bylund (1995) for *E. autumnata*, winter temperature is the most obvious density-independent factor spatially correlated at an appropriate scale. Cold winters cause low densities over large areas. When the populations begin to increase, this happens with enough synchrony to simultaneously reach peak densities in widely separated areas.

Neither dispersal nor Moran effect can, however, produce cyclicity without additional assumptions. It is here that the cyclic solar activity enters. Figure 3 relates *E. autumnata* outbreaks to sunspot activity. The first outbreak years of

Fig. 3. Occurrence of *E. autumnata* outbreaks in northern Europe (north of the 64° parallel) in relation to sunspot activity. Outbreak periods are shown as horizontal lines above the solar cycle. The numbers above the horizontal lines show the number of years since sunspot minimum to the first year of outbreak of the following *E. autumnata* outbreak period



the 12 outbreak periods are significantly associated ($G^2 = 5.6$, $df = 1$, $P = 0.018$) with the decline phases of sunspot activity (in the analysis, the first half of each solar cycle consists of the year of sunspot minimum and the following 5 years, and the latter half consists of the 6th to 11th years after the preceding sunspot minimum). In addition, also the results with three or four even-sized groups of years are significant ($P < 0.03$ in both), but the assumptions of the G -test are violated in both. The latter two analyses further indicate that the first years of the outbreak periods are associated with the end of the solar cycle, more specifically, with the last 3 or 4 years of the solar cycle (see also Fig. 3). One can extrapolate from this information to predict that the next outbreaks should take place in about 2003, but where these will occur is more difficult to predict. The conclusion remains elusive. It is logical, however, that the outbreaks lag behind the solar activity, because the solar events that lead to the beginning of the increase in density must occur a few years before the peak in population abundance.

Low winter temperatures covary with sunspot activity. Because variation in sunspot activity also correlates with outbreaks of forest lepidopterans that are not susceptible to winter temperatures (Myers 1998), we do not want to emphasize this specific mechanism as the explanation for cyclicity (local or regional) of *E. autumnata*.

Spring and summer temperatures are also associated with sunspot activity. *E. autumnata* outbreaks have not occurred during periods of high summer temperature (Niemelä 1980). The same trend was traced by Myers (1998): cool springs characterize outbreak periods of many species of forest lepidopterans. However, as commented earlier, we should not overemphasize the time periods when outbreaks are recorded.

The mechanisms through which solar activity could affect population dynamics of forest insects are not clear. However, we have demonstrated associations between plant stress, success of herbivores, foliar phenolic, and sugar metabolisms (Lempa et al. 2000). Because solar activity correlates with both photosynthetically active and UV-B radiation, this to our knowledge provides for the first time a potential mechanistic link between sunspots and plant traits relevant for herbivores.

Why do northern but not southern populations have outbreaks?

Although both birches and *E. autumnata* are common throughout Fennoscandia, outbreaks of *E. autumnata* are restricted to the northern parts of the area and to the Scandian mountains. As comparisons between outbreak and nonoutbreak populations might elucidate causes of outbreaks, we summarize here our knowledge of factors that maintain low densities in the southern populations.

In *E. autumnata*, we do not know of any intrinsic differences (including genetic ones), such as body size and hence reproductive capacity, between northern and southern *E. autumnata* that could explain the geographic pattern of outbreaks. However, southern forest communities are generally more productive and diverse; the concomitant increase in generalist predators offers a potential explanation for regional differences in population dynamics. In our studies, the highest mortality rates (close to 90%) occurred in the larval stage, mainly caused by passerine birds and parasitoids (see Tanhuanpää et al. 2000). However, patterns in larval predation (Tanhuanpää et al. 2000) and parasitism (Teder et al. 2000) suggest that they are of limited importance in the regulation of southern populations. Six successive years of data from 12 to 15 populations of southern *E. autumnata* reveal surprisingly constant annual parasitism rates of 28%–35% (Teder et al. 2000). Importantly, there was no hint of positive correlations among years between larval density and the proportion of parasitized larvae. The contrary was true in a 5-year study of pupal predation, which indicated rapid density-dependent mortality from small mammals (Tanhuanpää et al. 1999). The role of other predators may be in suppressing population densities sufficiently that pupal predators are able to regulate.

Differences in foliage quality between northern and southern birches offer another possible reason for regional differences in *E. autumnata* populations. For instance, northern birches might have lower constitutive resistance and therefore allow more rapid growth of *E. autumnata* larvae and of their populations. However, if anything, the reverse seems to be true, because natural *E. autumnata* larvae grow larger in the south than in the north

(Kaitaniemi et al. 1999b). Another attribute of southern forests that might contribute to lack of outbreaks is the relatively high diversity of tree species. For young ballooning larvae it must be more probable to land on a suitable host in northern homogenous mountain birch forests than in the more diverse southern forests. However, we did not find indications of higher polyphagy in southern larvae (Ruohomäki and Haukioja 1992b), and *E. autumnata* outbreaks do not occur even in monospecific southern birch stands.

Differences in induced resistance of birches between southern and northern tree populations also offer a potential explanation. Rapid inducible resistance (RIR) is triggered just like DIR, but it is experienced as reduced relative growth rate by the *same* larval generation that caused the response and its decay time is days or weeks and not years (Haukioja and Hanhimäki 1985; Hanhimäki and Senn 1992). Accordingly, it offers a negative feedback without a time lag and is a potential stabilizing factor in the population dynamics of *E. autumnata*. RIR could slow down population growth during such relatively high larval densities when larvae can trigger RIR in a large part of the tree. However, in experiments in the north, the efficacy of RIR has generally been less than 20% reduction in herbivore performance, and as for DIR, different experiments have produced variable results (Haukioja and Neuvonen 1987; Hanhimäki and Senn 1992). Furthermore, there are no studies of RIR for birch – *E. autumnata* system under natural conditions in the south or north.

In summary, the strongest candidate to control southern populations of *E. autumnata* is predation. Pupal predation by small mammals is the only factor known to operate in a density-dependent fashion. However, large-scale defoliations of southern birch forests take place by the phylogenetically and ecologically related *Operophtera* spp., which have very similar ecology as pupae to *E. autumnata*. However, *Operophtera* differ in other characteristics that may relate to their outbreak tendency. For instance, their females are wingless, and larvae live among loose-tied leaves. Therefore, we propose that controlling factors fail to keep densities of *Operophtera* spp., but not those of *E. autumnata*, low enough for pupal predation to regulate the densities in homogenous southern birch stands.

Practical problems

Our work on *E. autumnata* has lasted more than 25 years and, paradoxically, this has largely refuted simple explanations for cyclicity. In a sense, we have “too much” detailed knowledge about the multiplicity of possible contributing factors and about the variation in results. A part of the variation presumably results from complex interactions and context-dependent outcomes of experiments and a part from technical problems in conducting the appropriate empirical tests. We believe that it is worth discussing practical pitfalls in collecting the type of data needed. While some problems are generally recognized, others are not.

In studies of larval parasitism, exact timing of larval collections is critical. If the animals are collected too early, this results in underestimate of parasitism, and if too late, close to 100% parasitism rates can be obtained because of the retarded growth of parasitized larvae. Problems in timing of samplings easily prevent comparisons covering several, especially geographically scattered, populations. A logical test would be to eliminate for example DIR or parasitoids from large replicated areas and test for changes in population growth (Harrison and Cappuccino 1995; Myers and Rothman 1995; Kaitaniemi et al. 1999b), but this is difficult or impossible in practice. Problems arising from scale-related questions in population dynamics of *E. autumnata* are diverse. For example, long-range dispersal is difficult to directly study in many forest insect species, including moths (Nieminen 1996). An obvious scale-related problem manifests itself at a very basic level: in spite of our rather extensive knowledge of this system, it remains unresolved whether population dynamics are a product of local or regional processes.

Investigations of population dynamics of any species with 10-year cyclicity run into problems with time scale. For example, efficient statistical tests of cyclicity from a time series require at least 20 years of data (Woiwod and Hanski 1992; Turchin 1995). Furthermore, experiments replicated representatively in time are practically impossible. For example, the same factors (DIR, parasitoids, food quantity, etc.) seem to vary in their importance during different peaks and decreases of *E. autumnata* (Bylund 1995). Different parasitoid species may be involved with variable importance, perhaps because of initial stochastic differences in the abundance of parasitoid species, which are magnified during numeric responses to increasing host abundance. This difference may contribute to variability in the dynamics of different outbreak cycles.

Less obvious are pitfalls in trying to test the role of foliage quality for *E. autumnata*. For example, to study the induced resistance, a critical question is how well do manual defoliations mimic larval-made defoliations. We have some data (Haukioja and Neuvonen 1985b) indicating that larval-caused defoliations lead to stronger DIR than manual defoliations, but the true effects are still open. It has been repeatedly shown that branches and ramets responded individually to defoliation, nondefoliated branches representing better quality. However, results with pine indicated that defoliation of individual branches led them to respond more strongly than if whole trees were defoliated (Honkanen and Haukioja 1994). This counterintuitive result is consistent with the modular regulation of resource flows within the tree and may cause problems in practical work. Furthermore, our experiments to break apical dominance of birch branches, and thereby trigger inducible susceptibility, showed that larvae did not generally consume buds under experimental conditions. However, when they consumed buds in a particular tree, they did it in all branches. We have no good explanation for this result.

Interactions between traits of trees and larvae may seriously complicate the design and interpretation of experiments. For example, damage to foliage and damage to buds

(triggering DIR and delayed inducible susceptibility, respectively) interacted so that the harmful effects of DIR on *E. autumnata* were alleviated (Kaitaniemi et al. 1997b). An example of other types of pitfalls is that defoliation causes delayed bud break of birch; that might cause timing problems for hatching *E. autumnata* larvae. However, the necessary condition for defoliation is high larval density, and high larval density per se prolongs the pupal period and delays laying of eggs and thereby hatching of eggs in the following spring (Haukioja et al. 1988b; Kaitaniemi and Ruohomäki 1999) because late-laid eggs of *E. autumnata* naturally accumulate thermal sum for a short period in autumn (see Kaitaniemi and Ruohomäki 1999).

In addition to synchrony between leaf and larval development, crowding effects on larvae produce other nonobvious experimental problems. For instance, the chemical quality of foliage does not necessarily modify larval performance because larvae can exhibit physiological and behavioral adjustments that compensate for variation in diet quality (Suomela et al. 1995; Kause et al. 1999c), and these responses may be species specific (Kause et al. 1999a). Consequences may be nontrivial. For instance, experimentally crowded larvae of *E. autumnata* attained lower pupal weights than solitary ones on high-quality diets, but their larval period was short and they achieved similar or higher pupal weights under adverse conditions such as low-quality diets (Haukioja et al. 1988b; Kaitaniemi et al. 1997a). This realization exemplifies a potential pitfall in comparisons of foliage quality for larvae, and it also has evolutionary implications. For instance, the adaptiveness of the crowding response presumably is tested by standardizing all other factors, e.g., by providing larvae with homogeneous and good diets. The result resembles self-regulation at the population level: crowding decreases growth and the reproductive capacity of *E. autumnata*. If the performance is tested over natural gradients of resource quality, however, no support for population regulation emerges (Haukioja et al. 1988b).

Other important interactions are possible among the ecological processes that influence population dynamics. For example, plant quality can interact with parasitism (Werren et al. 1992; Johnson 1997). The scanty information for *E. autumnata* suggests no differences in parasitism rates between larvae living on different host plant species (Ruohomäki 1994) or between larvae collected from birches that were or were not defoliated in the previous season (K.R. and P.K., unpublished data). However, in the latter data, host tree quality (irrespective of earlier defoliation) was negatively correlated with the risk of becoming parasitized. This result is consistent with the observation that larvae experiencing prolonged development (e.g., due to poor foliage quality) are vulnerable to parasitoids for a longer time (Kaitaniemi and Ruohomäki 1999).

Our studies of interactions among these factors have mainly just begun but will include field studies of southern populations and modeling. A major challenge for both modelling and field studies is to identify the appropriate spatial scale.

General conclusions

Theories of population dynamics are most useful to identify the general conditions that promote stability versus fluctuations in population density. Identifying the ecological mechanisms that operate in the field, and characterizing their relative strengths, remains a major empirical challenge. This challenge is complicated by the potential for contributions from processes that act at both local and regional scale. For other reasons, too, it is not straightforward to infer which causal factors, and interactions between them, lead to the observed dynamics. First, there may be complex interactions between different factors during a given outbreak cycle, and different factors may be most important during different outbreaks (Hunter and Price 1992; Baltensweiler 1993; for *E. autumnata*, see also Bylund 1995). Second, most of the models are based upon elucidating the role of negative delayed density-dependent factors. However, for delayed density-dependent factors such as DIR and parasitism, it is not clear whether they are the causes or consequences of the cyclic dynamics. In addition, as causes of cycles, they apply only within the local cyclicality scenario. They can be critical for the minimum length of the low phase after the collapse, however, and have been amply tested. Models are particularly valuable in comparing the sensitivity of the system to different causal factors. Unfortunately, this logic does not flow in the opposite direction: the factors that produce the greatest effects in sensitivity analyses need not be those that actually determine fluctuations in nature. Models can tell what is possible given initial assumptions, but strong inference about nature requires critical experiments in the field.

Exclusive emphasis on factors that operate with delayed density dependence can constrain our understanding of complex population dynamics. We are not sure whether a new outbreak starts simply because of a relaxation in those density-dependent factors that act with a delay. Analyses of negative delayed density-dependent factors help to understand local but not regional cyclicality. Accordingly, if peak densities do not repeat themselves in the same areas and same populations (contrary to the situation for vole cycles), it seems appropriate to shift emphasis toward understanding factors that permit the early stages of population increase.

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