Plant defenses and population fluctuations of forest defoliators: mechanism-based scenarios

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Among the factors contributing to defoliator population fluctuations the possible role of plant defenses depends on how defenses (secondary compounds, primary compounds, and defense cascades) are assumed to function. Delayed inducible production of secondary compounds does not seem to explain cyclic fluctuations in population density. Instead, properties of general plant defense cascades, especially of the octadecanoid pathway, suggest new potential mechanisms. Insect damage, and sunspot-related high ultraviolet radiation (UV-B), trigger the octadecanoid pathway. In birch it also contributes to defoliator immunocompetence. Therefore, the low rate of parasitism in the increase phase of an outbreak has potential connections to inducible plant defense. The octadecanoid pathway is also involved in the production of volatile plant compounds, known to modify defenses of other plants and the behavior of parasitoids. Accordingly, the octadecanoid pathway and other plant defense cascades suggest unappreciated plant-mediated connections between the environment, defoliator performance, parasitism, and spatial expansion of outbreaks.

Introduction

The most spectacular effects of insects in forest ecosystems relate to their multiannual population outbreaks or cycles, which often lead to large-scale defoliations. Herbivore-induced phenotypic changes in the quality of long-lived host plants represent a potential factor contributing to fluctuations in the population densities of the short-lived defoliators. Before we can proceed to realistic analyses of the spatial scales of host plant effects on defoliators, we have to know the range of different defenses employed by plants and the extent of temporal variation in defenses.

Studying the potential effects of plant defense on temporal and spatial aspects of defoliator population dynamics may not sound very interesting, since time series analyses have repeatedly indicated that variation in parasitoid numbers is enough to produce the observed fluctuations in insect density (e.g. Berryman 2002). This indirectly suggests that the role of plant defenses must be low. While long-term data concerning parasitoid numbers at different phases of population cycles are available, however, there exist no corresponding data concerning annual variation in plant defense. The reason is that there is no simple way to determine the level of plant defense (Haukioja 2005). Accordingly, the indices of plant defense levels, such as larch needle length (Turchin *et al.* 2003), have been extremely crude.

Ecologically the best known classification of plant defense is whether it is constitutive or induced. The level of constitutive defense does not depend on prior contacts with herbivores. The effects of a herbivore-induced response depend, in addition to the strength of the response, on the time lag between the induction and the time when its effects are experienced by the herbivore. This scale is huge, ranging from seconds (e.g. Bown *et al*. 2002) to years (e.g. Benz 1974, Neuvonen & Haukioja 1991). From the viewpoint of the population dynamics of temperate-zone defoliators, the critical difference is between herbivore-induced effects on the generation of herbivores that did the damage (rapid responses, no time lag, basically dampening population fluctuations) and on subsequent generations (delayed responses, with time lags, basically accentuating population fluctuations) (Haukioja 1982). A second classification of plant defenses is based on whether the plant effects are direct or indirect. For a long time the main action of plant defenses was implicitly assumed to be direct, i.e. plant quality was thought to directly modify herbivore performance, growth/fecundity and/or survivorship. During the last decade it became clear that plant defenses often operate indirectly; in other words, they change the likelihood of the herbivore being predated, parasitized or killed by pathogens. The best known, often fascinating examples of indirect defenses involve volatile plant compounds which can be used by invertebrate predators and parasitoids to obtain information concerning their prey animals (e.g. Dicke & Hilker 2003). The mere existence of indirect defenses suggests that the relative roles of bottom-up and top-down forces behind herbivore population fluctuations are not distinct (*see* also Denno *et al*. 2005).

In this paper I have two main goals. First, the assumed role of plant defenses in herbivore populations depends critically on how plant defenses are thought to function. I therefore briefly review the multiplicity of plant defenses. Many of my examples come from our long-term research on mountain birch (*Betula pubescens* ssp. *czerepanovii*), the main host of the geometrid *Epirrita autumnata*, known for its regular large-scale population cycles (Tenow 1972, Ruohomäki *et al*. 2000). *E. autumnata* shows

life-history features typical for an outbreak species (Hunter 1991), for instance it is indiscriminative in its oviposition behavior (Tammaru *et al*. 1995). Secondly, I discuss the implications of this information for spatial analyses of host plant effects on insect populations. This part is necessarily of a more speculative nature than the previous one. Still, it is important to appreciate the potential implications for population dynamic analyses opened up by some recently-found plant defense mechanisms. So far these mechanisms have been studied mainly in short-lived plants, well suited to laboratory studies. However, they seem to be ubiquitous in the plant kingdom, and offer new and physiologically sound mechanistic explanations for some long-known correlates of herbivore cycles.

Defenses in birch

Plant defenses against herbivorous insects can be traced to three broad classes of plant compounds, and to the mechanisms which produce variations in their concentrations (Haukioja 2005). The oldest, still viable explanation is that low levels of plant nutritive factors are crucial to the extent of herbivore damage on plants. The second explanation, dominant since the mid-1960s and 1970s, suggests that the crucial defenses are plant secondary compounds such as phenols, terpenoids and alkaloids. The most recent explanation, still unfamiliar to many field ecologists, is that plants share few broad-scale but versatile defense cascades which orchestrate defenses, including the toxicity of secondary compounds, against numerous biotic and abiotic challenges.

Nutritive traits

Especially the older German forest-entomological literature emphasized the importance of low levels of nutritive factors, particularly sugars, for forest defoliators (e.g. Schwenke 1968). More recently, low levels of foliage proteins and water have been seen as an important barricade against herbivore consumption, especially in woody plants (Scriber 1977, Scriber & Feeny 1979, Scriber & Slansky 1981, Haukioja 2003).

A major problem with the defensive role of low levels of nutritive leaf traits is that insects may compensate for the inadequacy of dietary nutrients by increasing consumption, which may actually lead to increased consumption of plants (Moran & Hamilton 1980). Accordingly, there is not much sound evidence demonstrating that low levels of leaf nutrients alone reduce consumption on trees, or even the performance of forest defoliators. This contrasts with experimental evidence showing that carbohydrate/protein ratios are very important to herbivores such as locusts, and may modify the effects of secondary compounds (Simpson & Raubenheimer 2001).

In birch leaves, nutrients show dramatic ontogenetic changes: proteins and leaf water go down in maturing leaves while the originally low content of sugars in young leaves tends to go up, and different sugars peak in just maturing or mature leaves (Riipi *et al*. 2002). The tightly intercorrelated traits (high water, high proteins, and low toughness and sugars) which characterize young birch leaves are important for the performance of those birch-chewing insects that are adapted to young leaves (Haukioja *et al*. 2002). On the other hand, the larvae of late season herbivore species, mainly sawflies, are fully able to utilize nutritionally-poor mature birch leaves, and may even be unable to survive on nutritious young leaves (Martel *et al*. 2001). Accordingly, seasonal trends in foliar nutrients alone cannot explain defoliator preference or performance.

Secondary compounds

In woody plants tannins and other phenolic compounds have been regarded as the main defenses since Paul Feeny's seminal paper on oak leaf tannins (Feeny 1970). Their popularity as an index of defense also depends on the availability of relatively simple analytical procedures, such as the Folin-Ciocalteau method, for quantifying "total phenols". Due to the high number of individual phenolics (more than 100 in birch leaves), however, such analyses do not necessarily reveal the importance of individual phenolic compounds. The probable compound-specific effects of phenols on insect defoliators are complex also because individual phenolic groups

display distinctly different seasonal dynamics (Haukioja 2003), and respond idiosyncratically to environmental factors (Haukioja *et al*. 1998, Koricheva *et al*. 1998). The foliar contents of condensed tannins (= soluble proanthocyanidins) increase dramatically with leaf maturation. Since they also form by far the largest category within the "total phenols" in birch leaves, both total phenols and soluble proanthocyanidins peak in August. This easily masks the fact that condensed tannins are synthesized during the period of most active growth of birch leaves (Riipi *et al*. 2002), while other phenolic compounds may peak in young or mature leaves or show no clear seasonal trends at all (Salminen *et al*. 2001, Riipi *et al*. 2002).

Insect performance on birch leaves characteristically correlates negatively with foliar total phenols or with some individual phenolic compounds or groups of them, such as hydrolysable tannins and phenolic glycosides (Ruohomäki *et al*. 1996, Kaitaniemi *et al*. 1998, Kause *et al*. 1999, Haukioja *et al*. 2002, Henriksson *et al*. 2003, Riipi *et al*. 2005). On young as well as on shaded birch leaves, for instance, insect growth tends to correlate negatively with galloylglucoses and ellagitannins, two groups of hydrolysable tannins, the peaks of which may occur at any time of the growth season (Salminen *et al*. 2001). High contents of surface flavonoids of young birch leaves may lead up to 100% larval mortality (Lahtinen *et al*. 2004). In more mature leaves, total phenols, proanthocyanidins, flavonoids, or hydrolysable tannins are most likely to display the strongest negative correlations with insect growth. The finding that condensed tannins, the largest fraction of total phenols, do not necessarily show the strongest negative correlations with insect performance seems to result from the ability of geometrids to pass condensed tannins through the gut, and of sawflies to digest them and to sequester some degradation products of phenols in their hemolymph (J.-P. Salminen unpubl. data).

Specific defense cascades

Contrary to the mainstream forest-entomological literature, the physiologically motivated lit-

erature on plant defenses against pathogens and insects heavily emphasizes the importance of specific defense mechanisms rather than of secondary compounds (e.g. Heath 1997, Baldwin *et al*. 2001). During the last ten years it has become increasingly clear that specific defense mechanisms against insects, pathogens and some abiotic stresses are governed in the plant kingdom by a small number of complex defense cascades, such as the octadecanoid and salicylic acid (Reymond & Farmer 1998) and the ethylene (e.g. Chang & Shockey 1999) signaling pathways. Since these cascades can switch up and down hundreds of genes, a small number of cascades can produce very flexible and specific outcomes. Accordingly, the same cascades are activated by a great variety of abiotic and biotic challenges. In entomological studies much attention has been devoted to oxylipins (oxidation products of octadecanoid fatty acids), for instance because jasmonic acid derivatives are nowadays widely used to trigger induced plant defenses without damaging the plants (Baldwin 1996). Different defense pathways show complex interactions; they may for instance interfere with each other, leading to so called crosstalk between different inducers and pathways (e.g. Thaler *et al*. 2002).

Interplay between different classes of defense

A key challenge to our understanding of plant defenses is the unraveling of the relative roles — and mutual interaction — of specific defense pathways and other metabolic routes with possible defensive implications, such as phenol metabolism and primary leaf nutrients (Haukioja 2005). Very few results are available towards this end, especially in woody plants (but *see* Constabel *et al*. 2000, Tscharntke *et al*. 2001).

I discuss one example from the birch system to illustrate some of the complexities which arise in trying to identify the relative roles of different types of defenses against insects. By applying gas chromatography (GC) and high pressure liquid chromatography (HPLC), close to 1500 peaks have been detected in the leaves of mountain birch (V. Ossipov unpubl. data). Preliminary analyses (E. Haukioja *et al*. unpubl. data), using

ca. 600 birch leaf traits detected by the HPLC and GC methods, suggest that different classes of foliar compounds are important against different insect traits. Phenolic leaf compounds were dominant among the leaf constituents showing the strongest negative correlations with the growth rate of the geometrid *E. autumnata*, and its final product, pupal mass. In contrast, the survivorship of *E. autumnata* larvae enclosed on branches of individual mountain birch trees, and therefore unavailable to predators and parasitoids, displayed the most negative correlations with fatty acids and oxylipins, indicating the role of the octadecanoid pathway. These results suggest that birch defenses correlating with defoliator mortality, presumably leading to reduced damage, result from the activation of the octadecanoid pathway, while birch leaf suitability (= value of leaves for larval growth) is more closely related to foliar phenols.

Direct *vs*. indirect defenses

In the entomological literature, much effort is nowadays directed to the capacity of volatile plant compounds to lure predators and parasitoids to protect the plants (Turlings *et al*. 1995, Thaler 1999, Kessler & Baldwin 2001, Hunter 2002). Volatile production involves the octadecanoid pathway, and is triggered by at least partially species-specific fatty acid–amino acid conjugates in insect saliva (Alborn *et al*. 1997, Pohnert *et al*. 1999). These studies have also demonstrated that plant volatiles do switch on defense-related genes in other plant individuals (Shulaev *et al*. 1997, Bate & Rothstein 1998, Arimura *et al*. 2000, Faraq & Pare 2002, Choh *et al*. 2004, Engelbercht *et al*. 2004), finally confirming at the level of physiological mechanisms the phenomenon of "talking trees", first proposed in the early 1980s (Rhoades 1983, Baldwin & Schultz 1983). Birches are also known to produce large amounts of volatile compounds (Hakola *et al*. 2001); the composition of these exudates depends on herbivore damage to these plants (Vuorinen *et al*. 2005). The same applies to mountain birch as well (T. Vuorinen pers. comm.).

Another indirect role played by plant defenses on insects is exemplified by the effect of birch
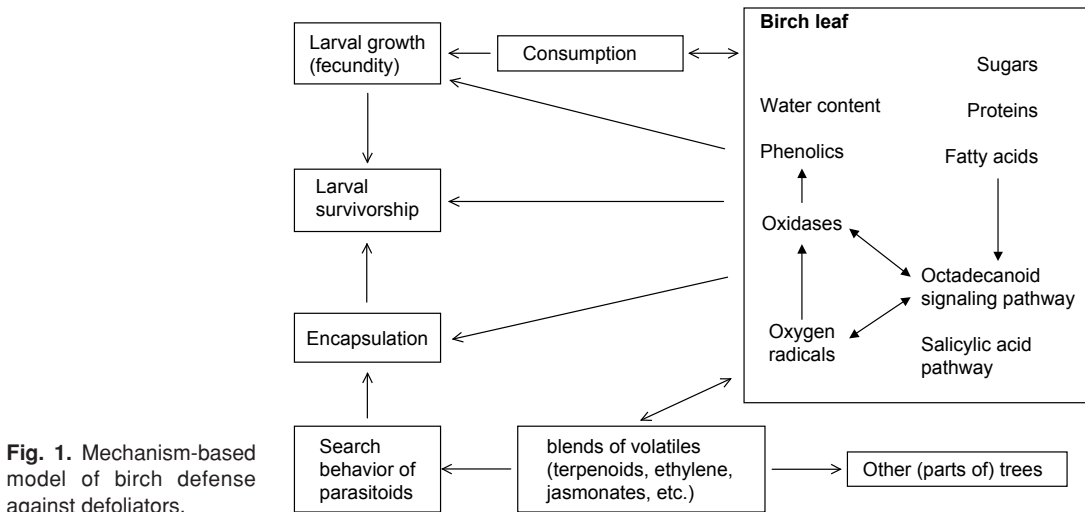
Fig. 1. Mechanism-based model of birch defense against defoliators.

foliar quality on the immune defense of *E. autumnata*. Insects in general defend themselves against multicellular invaders, such as parasitoids, by an immune response, in which hemocytes recognize an object as foreign and cause other hemocytes to aggregate on and capsulate it. The enclosed intruder dies from asphyxiation or cytotoxicity (Nappi *et al.* 1995). Encapsulation results from a cascade of biochemical reactions, employing phenoloxidases, and leads to the deposition of melanin and hardening of the capsule (Gillespie *et al.* 1997, Renault *et al.* 2002). The encapsulation response of *E. autumnata* varies significantly among larvae reared on different birch individuals, demonstrating that the immune resistance of the defoliator has a tritrophic level component (L. Kapari *et al.* unpubl. data). As such the dependence of the immune defense on the defoliator diet is not surprising, since the main limiting compounds for effective encapsulation and melanization, the amino acid tyrosine and the phenoloxidases, or their precursors, both come from the larval diet. The tyrosine content of birch leaves correlates significantly with the encapsulation ability of *E. autumnata*. Compounds in the phenoloxidase family are active both in birch leaves and in insect hemolymph, but comparisons between plant and insect phenoloxidases are complicated by the numerous variants among the phenoloxidase family. In any case, both the host plant and the insect are likely to utilize compounds of the

phenoloxidase family to transform relatively harmless compounds into highly reactive quinones.

Combining these indirect defenses into an explanatory model, the total effects of birch defenses on *E. autumnata* can be described as shown in Fig. 1.

Plant-based mechanisms behind population fluctuations of *Epirrita autumnata*

The first hypotheses proposing that induced plant defenses could contribute to fluctuations in herbivore densities (e.g. Haukioja 1980) were — compared with our present-day knowledge of how plant defenses operate — deceptively simple. Nevertheless, these scenarios, for instance the role played by phenolic compounds as defenses of woody and other plants, still often form the basis of how plant defenses are assumed to operate.

Models of population dynamics assume that population fluctuations are regulated by negative feedbacks with time lags. Accordingly, the role of plant defenses against herbivores has been sought in delayed induced resistance in the host. But the direct effects of delayed induced resistance on defoliators presumably are not strong enough to drive population cycles (Tanhuanpää *et al.* 2002). No long-term data are available

concerning possible variations in birch defenses at different phases of a cycle, but the obvious dependence of *E. autumnata* numbers on parasitoid numbers suggested the unimportance of plant defense: *E. autumnata* populations increase when the rate of parasitism is low, and crash when parasitoid numbers increase (Bylund 1995, Klemola *et al.* 2004). But such parasitoid data, used to elucidate the importance of parasitism, also leave open an important question: why does the incidence of parasitism remain low, close to 1%–2%, for several successive years during the increase phase of the cycle (Tanhuanpää *et al.* 2002: fig. 2, Turchin *et al.* 2003: fig. 3)? This problem is typically bypassed by assuming that parasitoids are unable to catch up with the increase of the defoliator. But this is not an explanation, merely a description of what happens. It does not offer any mechanism for the failure of any of the numerous parasitoid species or pathogens known to attack *E. autumnata* (Tenow 1972, Ruohomäki 1994, Tanhuanpää *et al.* 1999, Teder *et al.* 2000) to increase in numbers sufficiently to halt the explosive increase of the defoliator population.

As mentioned above, the level of immune defense in *E. autumnata* has a tritrophic component. Interestingly, in the increase phase of the population cycle the values of *E. autumnata* immunocompetence were significantly higher when larvae were reared in trees which had experimentally introduced larvae — and consequent foliar damage — in the previous year, as compared with those in trees without introduced larvae (L. Kapari *et al.* unpubl. data). Furthermore, in the batch of trees in which larvae had been reared in mesh bags in the previous year, the survivorship of the bagged larvae (being inaccessible for predators or parasitoids) correlated negatively with defoliator immunocompetence, but this was not the case in trees without the introduction of larvae the previous year. Taken together, these results suggest that larval-induced birch defenses led the surviving larvae to express, with a time lag, a higher immune defense than in trees without previous defoliation. Induced plant defense thus indirectly produced delayed positive effects on the immune defense of defoliators. A basically similar release of defoliators from diseases via induced plant defenses has been previously described for gypsy moth resistance against viruses (Hunter & Schultz 1993, Bakhvalov *et al.* 2002).

Although there are no controlled data as to the efficiency of immune defense of *E. autumnata* relative to other insects, two features observed by L. Kapari *et al.* (unpubl. data) suggest that the rate of encapsulation in *E. autumnata* is very rapid. First, they had to use an incubation time of one hour to obtain maximum variation in implant melanization at +14 °C, which strongly contrasts with the 48 or 24 hours at higher temperatures commonly used with other insects (e.g. Renault *et al.* 2002, Wilson *et al.* 2003). Second, the standard practice of counting hemocyte numbers forming the capsule around the implant did not function in *E. autumnata*; the capsule was so hard that it was impossible to crush the cells (M. Rantala pers. comm.*)*. In *E. autumnata*, the encapsulation response was high also in trees without introduced larvae in the previous year; I will return to this below.

The ecological relevance of these observations depends on how rapidly the encapsulation has to take place to really prevent parasitism, and this information is as yet lacking. Furthermore, the possible tendency of parasitoids to avoid ovipositing on larvae with high encapsulation efficiency is an open question. In any case, Münster-Swendsen (2002) reported that parasitoid probing of *Epinotia tedella* larvae, without oviposition, was a common cause of poor fecundity of the moth.

The above observations suggest that enhanced, host-plant mediated immune defense in *E. autumnata* may play a causal role in the increase phase of the defoliator population, potentially leading to a delayed positive feedback. The rapid, herbivory-enhanced encapsulation and melanization process offers so far the first mechanism-based explanation for the observation that during the increase phase of the *E. autumnata* cycle parasitism remains close to zero for several successive years (Bylund 1995). The encapsulation response correlates negatively with larval growth rate in *E. autumnata* (E. Haukioja *et al.* unpubl. data), just as in other insect species (e.g. Rantala & Roff 2005). Along with induced rapid host plant resistance, this offers a potential explanation for the declining

average size of *E. autumnata* during the increase phase of the cycle (Klemola *et al.* 2004).

At the low phase of defoliator population density, predators such as birds can be effective agents in gleaning larvae from individual trees with locally high prey densities (Marquis & Whelan 1994). This is facilitated by the ability of at least willow warblers to sense insect-induced changes in birch foliage (Mäntylä *et al.* 2004). This may make birds efficient predators at relatively low population densities of defoliators; if all the trees are infested by defoliators, however, this mechanism no longer helps, and even the numerical response of birds is not enough to curb the defoliator population increase.

Birch defense and spatial scales in defoliator populations

Potentially, the spatial scales of plant defenses range from within-plant variability to very large scales, for instance in the case of herbivore-induced plant volatiles. Scales at both ends of this spectrum are likely to be temporally variable, but there is scanty information about temporal (annual, seasonal, herbivore-induced) variation in the spatial patterns of woody plant quality for herbivores. I still see it as worthwhile to discuss the possible spatial effects of some plant defense functions, although there are so far no hard data demonstrating their importance in woody plants.

Small-scale effects of plant defenses

An individual host plant represents the logical basic spatial level for plant effects on herbivores. However, considerable variation in defensive traits is also found within individual host plants (Suomela & Nilson 1994, Gripenberg & Roslin 2005). This relates to the architectural complexity of plants, especially of large trees, and to seasonal asynchrony in leaf maturation in different parts of the tree canopy. Since leaves of different ages employ partially different defensive compounds, and because of phenological differences among tree individuals (Haukioja 2003), there may be extensive variation in the suitability of individual trees for defoliators at different times

of leaf expansion. This also leads to a spatial problem: the ranking of suitability of individual trees for herbivores may rapidly change in the course of leaf/larval development (Ruusila *et al.* 2005).

Differences in the strength of direct constitutive and induced defenses, in the absence of predation and parasitism, can lead to great variation (by almost two orders of magnitude) in the realized reproductive potential of *E. autumnata*. Such variation in suitability among individual host trees makes the tree population a spatially highly heterogeneous resource for the defoliator. This variation is hard to quantify, since even the best and worst tree individuals cannot be detected by visual inspection of the trees. When we also take into account the observed trade-offs between the survivorship of larvae in a tree and the parasitoid resistance of the offspring the following year, this variation is far from trivial.

Sunspot-related UV-radiation as a possible mechanism for the Moran effect?

Population cycles in *E. autumnata*, as well as in other defoliating insects (Liebhold & Kamata 2000), tend to occur synchronously over large areas. This may result from certain environmental variations synchronizing the cycle phase, i.e. from the Moran effect.

Long-term variation in the activity of sunspots is known to correlate with population fluctuations of herbivores. In *E. autumnata*, for instance, there is a significant tendency for new peak densities to be observed 3–4 years after sunspot minima (Ruohomäki *et al.* 2000: fig. 3). For many people this type of observation presumably represents an example of spurious correlations. However, Selås *et al.* (2004), using *E. autumnata* as a model species, have proposed that UV-B radiation, known to peak during troughs of sunspot cycles, may require plants to increase their radiation tolerance by producing higher contents of UV-B-protective phenolic pigments. They assumed that this decreased the production of herbivore-protective phenols, or increased contents of essential amino acids, increasing the nutritional quality of foli-

age. Results of my group do not support these predictions. As demonstrated by Klemola *et al.* (2004), individual performance of *E. autumnata*, measured as growth or fecundity, was low during the increase phase of the cycle.

Selås *et al.* (2004) based their argumentation about *E. autumnata* on mountain birch on a reported case of the preference of the related winter moth (*Operophtera brumata*) for UV-B treated foliage over control foliage on the related silver birch (*Betula pendula*) (Lavola *et al.* 1998). However, a detailed study using *E. autumnata* itself on mountain birch revealed just the opposite trend: UV-B radiation worsened the quality of the leaves of mountain birch for *E. autumnata* (Buck & Callaghan 1999). Furthermore, there is ample evidence from other systems showing that UV-B generally makes plants worse, not better, for herbivory (Rousseaux *et al.* 1998, 2004, Mazza *et al.* 1999). Even the mechanism whereby UV-B can make plants worse for herbivory has been known for almost a decade: Conconi *et al.* (1996) demonstrated that UV-B triggers the same signaling pathway, the octadecanoid pathway, as herbivory. Since then these functions have been studied in detail (e.g. Stratmann 2003, Izaguirre *et al.* 2003), and it is well established that a large proportion of the genes switched on by UV-B are the same ones that are activated by herbivore feeding as well. These results are fully consistent with the role of the octadecanoid pathway as a general defense cascade, operating against both biotic and abiotic challenges (e.g. Pellinen *et al.* 2002).

An interesting scenario emerges when we combine the above results from the literature on plant defenses with experimental data about *E. autumnata* immunocompetence (L. Kapari *et al.* unpubl. data): (1) during sunspot minima, UV-B activates genes belonging to the octadecanoid pathway; (2) insect survivorship, and to some extent larval growth, are negatively affected by the high activity of this pathway; but (3) simultaneously, and with a time lag, this triggers increased immunocompetence in the defoliator. Together these observations suggest that high UV-B activity, and the sunspot cycles behind it, may be mechanistically involved in the low incidence of parasitism and diseases during the increase phase of the cycle.

Spread of population outbreaks: potential connections with plant defense?

Plant defenses, via sunspots and the variation in UV-B which they give rise to, may bring synchrony into population cycles over very large spatial scales, and represent a possible causal explanation for the Moran effect. The dispersal of insects is another logical choice in explaining the large-scale synchrony of cycles. However, although dispersal undoubtedly drives individuals from high density to low density sites, the spread of outbreaks seems to be independent of the dispersal capacity of the defoliator species (Peltonen *et al.* 2002), casting doubt on the generality of this explanation.

Dispersal, however, is not the only alternative for a biological mechanism for the synchronous spread of population outbreaks. Plants do emit huge amounts of volatile compounds; Lindfors and Laurila (2000) estimated that the average annual production of organic volatiles by Finnish forests was around 2 tonnes per km². Since the contents and concentrations of these volatiles depend on herbivory, clouds of insect-induced plant volatiles offer a neglected candidate for large-scale effects, one that might produce the same end result as dispersal. Volatiles are known to switch on defensive genes in other plant individuals (as discussed above), offering a mechanism for the rapid synchronization of plant defenses. Because of trade-offs between plant defense and insect immunocompetence on those plant individuals, volatile compounds may decrease the susceptibility of insects to higher trophic levels, and synchronize population expansion over large areas. This offers a potential explanation for two features of local cycles. First, the annual expansion in the range of defoliator outbreaks is very rapid, over 200 km per year in the larch budmoth (Bjørnstad *et al.* 2002). Dispersal is a possible explanation, but it would demand huge numbers of dispersing individuals. Furthermore, the dispersing individuals would have to be predominantly females, and they are usually less mobile than males. Second, population outbreaks are more common and pronounced in continuous monocultures as compared with those in mixed stands and fragmented habitats (Ruohomäki *et al.* 1997, Roland

2005). This might result from the easier spread of volatiles in monocultures as compared with that in mixed and fragmented habitats.

Discussion

Plant defense mechanisms suggest novel explanations for several temporal and spatial aspects of defoliator outbreaks. They do not falsify old explanations, but offer more mechanisms than have been assumed to operate in the field, and may balance the current strong emphasis on delayed negative feedbacks with an equal emphasis on positive ones.

I have included in Fig. 2 the key plant-related mechanisms which are likely to contribute to *E. autumnata* outbreaks, and which could help in explaining a large number of traits associated with cyclic fluctuations. Findings with *E. autumnata* suggest that it may be the combined effect of insect damage and the sunspot-cycle-related increase in UV-B which activates the octadecanoid pathway. This also participates in the production of volatile compounds, which may lead to large-scale changes in plant defense. If these defenses can be exploited by defoliators for their own defense against higher trophic levels, they would help the defoliator population to escape the control of higher trophic levels. This suggests that the resistance of defoliators against parasitoids and diseases would be high in tree populations under, and after, high sunspot activity, and would be further enhanced by feeding-induced feedbacks. In this scenario, the "cause of an outbreak" is in mechanisms which allow the defoliator population to escape from the control of parasitoids and pathogens. After the population has enjoyed practical freedom from parasitism and pathogens for several generations, one or more factors put an end to the density peak. Among the possible candidates are starvation as such, deprivation of food, known to lead rapidly to declining immune defense (Fellowes *et al.* 1999, Siva-Jothy & Thompson 2002, Rantala *et al.* 2003); decline in sunspot-related UV-B; the emergence of parasitoids able to block the encapsulation/melanization process by means of specific polydnaviruses; or pathogens able to resist encapsulation/melanization
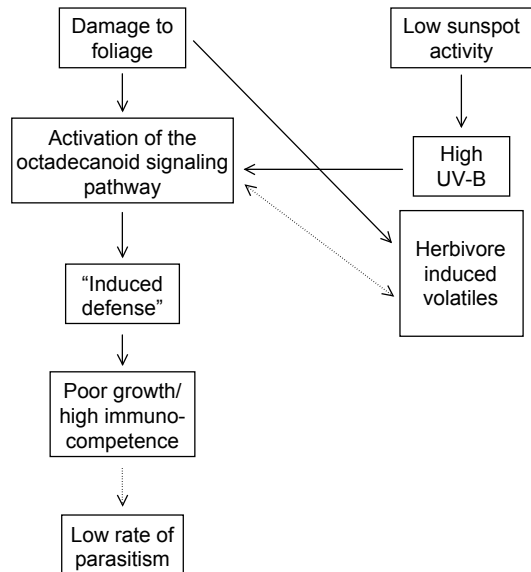

Fig. 2. Mechanism-based scenario of an *Epirrita autumnata* population outbreak. Dashed arrows describe phenomena known from other systems than birch–*Epirrita autumnata*.

(*see* Beckage & Reynolds 2003, and articles in this issue).

All in all, this scenario proposes a switch in what demands explanation in herbivore cycles: from the factors responsible for the crash to the actual mechanisms which promote the multiannual population increase: in a finite environment, some factor(s), usually parasitoids, disease or lack of foliage, will terminate the peak. It is interesting to realize that different factors (different species of larval parasitoids, pupal parasitoids, pathogens) really have put an end to individual population peaks of *E. autumnata* (Ruohomäki *et al.* 2000) and *Zeiraphera diniana* (Baltensweiler 1993), the two species with the longest time series.

As regards the potential synchronizing agents for population outbreaks, herbivore-induced volatile compounds are likely to be important in all systems, but may probably spread easiest in monocultures. The relative importance of sunspot-activity-related UV-B radiation is likely to be highest in high altitude areas. It is precisely in these areas (high altitude monocultures) that the most regular population fluctuations of defoliators have been observed (Baltensweiler *et al.* 1977, Ruohomäki *et al.* 1997).

To sum up: our present-day knowledge of plant defenses proposes a wide array of potential mechanistic links with herbivore densities, which can operate at different spatial scales — from millimeters to perhaps hundreds of kilometers. Possibilities to take these factors into account have emerged during just the last few years with our progress in understanding how plant defenses function. Not surprisingly, these findings have made hardly any contribution to the ways in which the factors underlying the population fluctuations of herbivorous insects are analyzed. Whether or not they are taken into account in the models, however, these invisible operators, such as cyclic UV-B with connections to plant defense and plant-emitted volatile info-chemicals, do in fact operate in the field.

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