DO DIFFERENCES IN INDUCIBLE RESISTANCE EXPLAIN THE POPULATION DYNAMICS OF BIRCH AND PINE DEFOLIATORS?

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INTRODUCTION

Damage inflicted by insects may trigger responses in their host plants resulting either in immediate effects on herbivores either rapidly or in effects upon subsequent herbivore generations. Differentiation between rapid and delayed inducible resistance is essential since the two responses affect the population dynamics of herbivores in fundamentally different ways (Haukioja 1982). Rapid inducible resistance (RIR) tends to stabilize herbivore population dynamics. On the other hand, delayed inducible resistance (DIR) introduces a time-lag into the negative feedbacks regulating the population dynamics of insects and may generate cyclical fluctuations in density (Benz 1974, Haukioja 1980, Berryman et al. 1987).

Experiments have shown that rapid and/or delayed inducible resistance exists in some tree-herbivore systems while other systems apparently lack such responses (Haukioja and Neuvonen 1987). The variation in inducible responses may help us to understand differences in the population dynamics of defoliators on different host trees. For example, both white birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*) suffer large-scale defoliation in Fennoscandia. However, the outbreaks on birches and pines show different temporal and geographic patterns. This paper compares inducible resistance mechanisms and patterns in the population dynamics of defoliating insects Scots pine and birch.

DEFOLIATING INSECTS ON SCOTS PINE AND BIRCH

Scots pines and birches are abundant and widespread in northern Europe. Thus the species richness of insects feeding on these trees is great (Larsson and Tenow 1980, Neuvonen and Niemelä 1983), though, only some of the insects cause serious damage to their host. The most important defoliators of Scots pine in Fennoscandia (*Neodiprion sertifer* and *Diprion pini*) belong to the sawflies (Symphyta: Diprionidae) (Table 1). In other areas, however, such as Central Europe and Siberia, these

[1]Order of authorship determined by tossing a coin.

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are also lepidopteran species (*Bupalus piniarius, Panolis flammea, Dendrolimus pini*) which can become predominant defoliators of pine.

The mountain birch forests in northwestern Europe are periodically defoliated by geometrid larvae feeding mainly during the early season (Table 1). Several species (*Epirrita autumnata, Operophtera* spp., and *Erannis defoliaria*) fluctuate greatly and fairly synchronously in density (Tenow 1972, Haukioja et al. 1988). Local defoliations may also be caused by a late season sawfly, *Dineura viridiorsata* (Koponen 1981).

OUTBREAK PATTERNS

Birch-Feeding Insects

An extensive record of geometrid defoliation of Fennoscandian birch forests has been compiled over the years from 1862 to 1968. During this span of time outbreaks have occurred at 9- to 10-year intervals (Tenow 1972). The duration of these outbreaks is short, 2 to 3 years. Distribution of the outbreaks shows a number of varying patterns. Outbreaks of *Epirrita autumnata* are restricted to the mountain birch forest zone of northern Finland and the Scandinavian mountain chain. In the birch forests along the Norwegian coast, *Operophtera* spp. are the most important defoliators, and *E. autumnata* occurs mainly at higher altitudes and at inland localities with a more continental climate (Tenow 1972). Outbreaks of *Operophtera* spp. and *Erannis defoliaria* have been recorded on isolated islands in the southwest archipelago of Finland (Tenow 1972, Laasonen and Laasonen 1987). Birches are also regularly defoliated in other areas of the world, e.g. *Rheumaptera hastata* on *Betula resinifera* in Alaska (Werner 1981).

Furthermore, defoliation by *Epirrita* larvae is often topographically restricted, patches of undefoliated birch forests typically occur at the bottom of river valleys while birches at higher altitudes are usually heavily defoliated (Kallio and Lehtonen 1973, Tenow 1975).

Pine-Feeding Insects

In Fennoscandia outbreaks of diprionid sawflies are restricted chiefly to southern regions and are, with few exceptions, absent from northern areas (Christiansen 1970, Löyttyniemi et al. 1979, Juutinen and Varama 1986). Diprionid outbreaks on pine are not cyclical as are the well-known 9-year cycles of the tortricid, *Zeiraphera diniana*, on European larch (Baltensweiler et al. 1977, Hanski 1987, Geri 1988). In Sweden and Finland local outbreaks of diprionids occur every year (Larsson and Tenow 1984, Juutinen and Varama 1986). Large-scale outbreaks occur irregularly in 10- to 20-year intervals (Kangas 1963, Hanski 1987).

The duration of outbreaks in a given habitat is variable. According to Juutinen and Varama (1986), outbreaks of *N. sertifer* last 3 to 4 years in southern Finland. In the middle region of Finland the duration is 4 to 6 years. In the Saariselkä mountain chain in northern Finland, an outbreak has been chronic for the last 20 years (Juutinen 1967, Juutinen and Varama 1986).

N. sertifer outbreaks in Fennoscandia and in parts of the U.S.S.R. characteristically occur following dry summers and are restricted mainly to dry sites or dense stands (Juutinen 1967, Larsson and Tenow 1984, Sharov, this volume). Interestingly, several successive large-scale outbreaks of *N. sertifer* occurred during the warm period in the 1930s (Kangas 1963, Hanski 1987).

Defoliations by other insect pests in Fennoscandia are more sporadic than those caused by *N. sertifer*. In more southern areas of Europe, such as Germany and some parts of Britain, some populations of *Bupalus piniarius* and *Panolis flammea* show more or less regular cycles of 6 to 11 years (Schwerdtfeger 1968, Barbour 1987), while other populations are relatively stable or fluctuate irregularly, e.g. most British populations (Barbour 1988).

Table 1. Outbreak species of Scots pine (*Pinus sylvestris*) and birches (*Betula pendula* and *B. pubescens*) in Fennoscandia

Species	Family	Larval period
	Scots pine	
Neodiprion sertifer	Diprionidae	May-July
Diprion pini	Diprionidae	July-September
Gilpinia pallida	Diprionidae	June-August
Microdiprion pallipes	Diprionidae	June-August
Bupalus piniarius	Geometridae	June-August
	Birches	
Epirrita autumnata	Geometridae	May-July
Operopthera spp.	Geometridae	May-July
Erannis defoliaria	Geometridae	May-July
Dineura virididorsata	Tenthredinidae	July-September

EXPERIMENTAL EVIDENCE OF INDUCIBLE RESISTANCE

Experiments on Birch

Rapid Inducible Resistance

Mechanically damaged birch foliage is less suitable for the growth of larvae of several lepidopteran and hymenopteran species than undamaged control foliage (Haukioja and Niemelä 1977, 1979, Hanhimäki 1989). Larvae grew for a longer time and the pupal masses were the same or lower on damaged than on control foliage (Table 2). When the total impact of RIR on the capacity of *E. autumnata* to increase were estimated by combining the effects on survival and fecundity, the reduction ranged from 0 to 22 percent (Haukioja and Neuvonen 1987). Rapid inducible resistance against *E. autumnata* seems to be equal in birch provenances from both outbreak (northern Finland) and nonoutbreak (southern Finland) areas (Haukioja and Hanhimäki 1985).

Rapid inducible resistance in birch foliage can be triggered by damaging early, but not late-season birch leaves (Haukioja and Niemelä 1979, Wratten et al. 1984). However, the responses may have such a long relaxation time that they also affect insects feeding later that season (Neuvonen et al. 1988, Hanhimäki 1989). On the other hand, not all types of damage to birch trees result in deterioration in foliage quality. Increased densities of insects have been observed on birches browsed, either artificially or by moose, during the previous winter(s) (Danell and Huss-Danell 1985), though the performance of *Epirrita* larvae was affected only slightly (Neuvonen and Danell 1987, Haukioja et al. 1990).

Table 2. The existence of rapid (RIR) and delayed induced resistance (DIR) on mature Scots pine needles and birch foliage (see Haukioja and Niemelä (1979) and Hanhimäki (1989) for more examples). 0 = no statistically significant effect, + significant increase, - significant decrease. Some statistical tests may suffer from sacrificial pseudoreplication. Damage on Scots pine needles occurred during mid or late season (for the effects of early season damage, see Neuvonen et al. 1988).

Insect species	Development/ growth rate	Pupal weight	Larval survival	References*
Scots pine needles				
RIR				
Neodiprion sertifer	+	0	+	1
Gilpinia virens	0	0	0	1
Microdiprion pallipes	0	0	-	1
Diprion pini	0	0	0	1
DIR				
Neodiprion sertifer	0	0	0	1
Diprion pini	0	+/0	-/0	10
Birch foliage				
RIR				
Epirrita autumnata	-	-	0	2,3,4
Dineura viridorsataa	0	0	0	3,5
DIR				
Epirrita autumnata	-	-	-	6,7,8
Dineura viridorsataa	+	?	?	9

*References: 1) Niemelä et al. (1984), 2) Haukioja and Niemelä (1977), 3) Haukioja and Niemelä (1979), 4) Haukioja and Hanhimäki (1985), 5) Neuvonen et al. (1988), 6) Haukioja et al. (1985), 7) Haukioja and Neuvonen (1985), 8) Neuvonen et al. (1987), 9) Neuvonen (pers. observ.), and 10) Niemelä (pers. observ.).

British experiments have concentrated on reporting chemical changes induced by foliage damage and their effects on the feeding preferences of herbivores (Wratten et al. 1984, Hartley 1988, Hartley and Lawton 1991). These studies have shown the existence of RIR, as evidenced by increases in phenolics, in British birch provenances, although the feeding bioassays have yielded variable results. Some British studies have also reported negative effects of foliage damage on the performance of insects (Bergelson et al. 1986, Fowler and MacGarvin 1986).

Delayed Inducible Resistance

Decreased quality of foliage during years following simulated or real insect attack, or delayed inducible resistance, can be triggered by mechanically damaging the birch leaves or by depositing feces of *Epirrita* larvae beneath/at the base of the birches (Haukioja et al. 1985). Insect damage induces a stronger delayed inducible response than does manual damage (Haukioja and Neuvonen 1985, Neuvonen et al. 1987). Both survival of *Epirrita* larvae and pupal weights were reduced on defoliated trees (Table 2). Performance, as measured by combined effects on survival and fecundity, of *E. autumnata* on partially defoliated trees may be over 70 percent below that on control birches. Mountain birches which had been artificially defoliated 2 to 4 years earlier still caused a reduction of 16 to 38 percent in fecundity (Haukioja and Neuvonen 1987). Birch provenances outside the usual outbreak range of defoliating insects may not express DIR (Haukioja 1980, Haukioja et al. 1983), and it is difficult to say whether this is a cause or a consequence of the distribution of outbreaks.

The foliage of defoliated mountain birches has lower nitrogen and higher phenolic content than that of control trees in the years following damage (Tuomi et al. 1984). Because of the high negative correlation between nitrogen and phenolic concentrations in birch foliage, it is difficult to evaluate which of these factors is more important in determining the success of *Epirrita* larvae. However, when the nitrogen content of birch foliage has been accounted for in models explaining variation in the pupal weight of *Epirrita*, the additional contributions of phenolic content have not appreciably improved the explanatory power of the models (Haukioja et al., unpubl. observ.).

Experiments on Pines

Studies of 20- to 25-year-old Scots pines in Finland have suggested that neither RIR nor DIR apparently develops in the mature foliage, the normal diet of diprionid sawflies (Niemelä et al. 1984). For example, four sawfly species survived and grew equally well on mature needles from control and defoliated (in the spring of the same and in previous years) branches. Geri et al. (1990) reached nearly the same conclusions working in France on the sawfly, *Diprion pini*. But, surprisingly, they discovered that female fecundity declined substantially on previously but not concurrently defoliated trees even though all other performance parameters (survival, growth, developmental rates, diapause rates) showed little response to defoliation. This is evidence for DIR, but not RIR. Because Niemelä et al. (1984) did not measure fecundity, which is usually positively correlated with insect growth, it is not known whether this performance variable declined due to defoliation. However, Sharov (this volume) found no changes in the fecundity of *Diprion pini* during outbreaks on Scots pine in the Rostov region of the U.S.S.R., as would be expected if there were strong DIR responses in pine.

In the case of other evergreen conifer species and other defoliators, there is some evidence for either weak RIR or DIR (Wagner and Evans 1985, Leather et al. 1987, Wagner 1988, Mattson et al. 1988). The study of Thielges (1968) has often been cited, though incorrectly, as an example of induced resistance. What he actually observed, however, was only that an "abnormal compound" occurred in the foliage of Scots pine heavily damaged by *N. sertifer*. It is not possible to evaluate whether this compound resulted from defoliation or existed prior to it, nor whether it was harmful to the larvae.

We conclude that there is at best only a weak DIR in Scots pine. Otherwise, one should be able to measure significant reductions in insect growth, developmental rates, and survival, none of which has been found.

HYPOTHESES EXPLAINING INDUCIBLE RESISTANCE

Owing to fundamental physiological differences between deciduous and evergreen coniferous trees (Dickson 1989), one would expect differences in their defensive responses to folivores. Tuomi et al.

(1988) suggested that the plants' carbon-nutrient balance (sensu Mattson 1980, Bryant et al. 1983) could largely determine the nature of the DIR occurring in the foliage. For example, an increase in resistance is expected when defoliation causes a relatively greater deficiency of minerals than carbon--leading to enhanced carbon-based secondary metabolism. This is presumably the case for deciduous trees growing on nutrient-deficient soils and having large carbon reserves in their stems and roots. On the other hand, for evergreens, old needles serve both as important sources of carbon reserves, and current photosynthates (Bryant et al. 1983), and hence their removal by herbivores may cause a relatively greater carbon than nutrient deficiency and hence suppress accumulation of carbon-based secondary metabolism. Furthermore, defoliation tends to increase the N content of the needles in evergreen conifer trees (Piene 1980, Piene and Percy 1984, Långström et al. 1990) which supports the thesis of a defoliation-induced carbon shortage. However, chronic, severe defoliation may eventually cause substantial rootlet mortality and result in a serious mineral deficiency thereby leading to enhanced secondary metabolite buildup.

Though differences in the effects of first defoliations on the plants' relative carbon/nutrient balance may explain differences in DIR in evergreen and deciduous trees, it is not sufficient to explain their apparent differences in RIR. Moreover, bioassays conducted with mountain birch have yielded results either difficult to predict from or inconsistent with the carbon/nutrient balance hypothesis (Haukioja and Neuvonen 1985, Haukioja et al. 1985). The facts that intensification of DIR is caused by cues from insects and that fertilization does not mitigate delayed inducible resistance triggered by manual defoliation are more consistent with a view of the responses as actual defenses against defoliators.

Although the carbon/nutrient balance hypothesis cannot explain all the details of delayed inducible resistance in birch, it is possible that the incidental responses suggested by it may have become truly more defensive in areas where heavy defoliations occur.

INDUCIBLE RESISTANCE AS A FACTOR IN THE POPULATION DYNAMICS OF PINE AND BIRCH DEFOLIATORS

The apparent absence of strong DIR in mature needles of Scots pine may explain why diprionid sawfly outbreaks can continue for several years in the same stands (Juutinen 1967, Juutinen and Varama 1986) and why several successive outbreaks are possible (Kangas 1963). Furthermore, the apparent lack of regular cycles in the population dynamics of diprionid sawflies is consistent with the lack of delayed negative feedbacks via foliage quality.

Some populations of pine defoliators show more or less regular cyclical fluctuations (Barbour 1988). It seems probable that other delayed feedback mechanisms than inducible changes in foliage quality are involved in these cases. The existence of DIR in those pine provenances has to be tested before any firm conclusions are possible, however.

As compared with other possible regulating factors, the importance of DIR is well established in birch/herbivore systems showing cyclical fluctuations in insect densities (Haukioja et al. 1988). These responses introduce time-lag negative feedback into the population dynamics of *Epirrita*. The importance of RIR is far less clear, on the other hand. DIR may be a key factor in the cyclical density fluctuations of birch defoliators in some areas, though this does not obviate the importance of other factors (e.g. parasitoids, diseases). DIR also contributes to the relatively short duration of *Epirrita* outbreaks.

SUMMARY

Both the presence and the absence of induced resistance in tree foliage can explain the population dynamics of defoliating insects. White birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*) suffer large-scale defoliation in Fennoscandia. Outbreaks of birch defoliators have occurred at 9- to 10-year intervals. Duration of the outbreaks is short, 2 to 3 years. On Scots pine, local outbreaks occur every year, and large-scale outbreaks follow irregularly in 10- to 20-year intervals. That DIR produces time-lag negative feedback in the population dynamics of herbivores can explain the cyclical fluctuations. The absence of inducible responses in the mature foliage of Scots pine may explain why outbreaks can continue for several years in the same stands and why several successive outbreaks are possible.

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