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The ecology of the pine beauty moth in commercial woods in Scotland

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1 Introduction

The pine beauty moth (*Panolis flammea*) is a noctuid which occurs throughout the UK, Scandinavia and the rest of Europe. Scots pine (*Pinus sylvestris*) is its natural host and outbreaks of the moth occur on Scots pine on the continent. In Scotland, it is a pest of lodgepole pine (*Pinus contorta*), but no outbreaks have been recorded there on Scots pine. This paper is concerned with the factors which influence the temporal and spatial population dynamics of the pine beauty moth in commercial pinewoods in Scotland, and discusses conclusions reached from research in progress.

2 Temporal dynamics of pine beauty moth

In 1976, 120 ha of lodgepole pine were defoliated and killed by the pine beauty moth (Stoakley 1979, 1981). In the next 5 years, another 200 ha were destroyed and 10 000 ha were sprayed with insecticide. Outbreaks occurred in areas as far apart as Naver Forest (Highland Region) and Bareagle Forest (Dumfries and Galloway Region). Between 1982 and 1983, no further control measures were needed, but 2 serious outbreaks occurred in Highland Region in 1984. In 1985, 4700 ha were sprayed and there were firm indications from population assessments in 1985 that further control would be necessary in 1986. It is now clear that the moth poses a serious threat to the successful growing of lodgepole pine in Scotland. Indeed, it is probable that outbreaks did not occur earlier only because lodgepole pine was not widely planted in Scotland until the late 1950s and early 1960s (Lines 1976) and was not susceptible before the early 1970s.

The numbers of pupae at one site, the Elchies block of Speyside Forest, over a 9-year period are shown in Figure 1. This population was sprayed with fenitrothion in 1979 (Stoakley 1981) but started to increase in size immediately thereafter. However, the population trend since 1979 has been rather erratic; numbers increased by varying degrees in 4 years but declined in 2 years, most notably in 1985. Elsewhere, as mentioned above, the pine beauty increased rapidly after control operations in 1977–79 to outbreak levels in 1984–85.

The variability in the moth's performance from one year to the next is demonstrated by the survivorship curves shown in Figure 2. In 1984, the population in a study plot in the North Dalchork block of Shin Forest (Highland Region) showed a fecundity of 123 eggs per female and the mortality in the successive stages was low at 56.5% (Barbour 1985). However, in Elchies in 1985, the fecundity was only 35 eggs per female, and

the mortality in the subsequent stages was much higher at 99.3%. A number of factors could be responsible for these different patterns of fecundity and mortality. These factors include host plant condition, natural enemies, competition, and weather acting directly or indirectly through other factors. They are discussed below, using North Dalchork 1984 and Elchies 1985 as examples.

2.1 Host plant condition

Host plant condition may be defined as the level of nitrogen and other indicators of the nutrient content of plant foliage, and tannins or other chemicals which are known to be detrimental to some insect herbivores. Changes in host plant condition are thought to be responsible for different temporal patterns of population behaviour, from irregular eruptions to regular cycles (Rhoades 1983; White 1984). White (1969, 1974), for example, postulated that when plants are stressed they become a better source of food for insect herbivores because stress, usually caused by water shortage or waterlogging, results in an increase

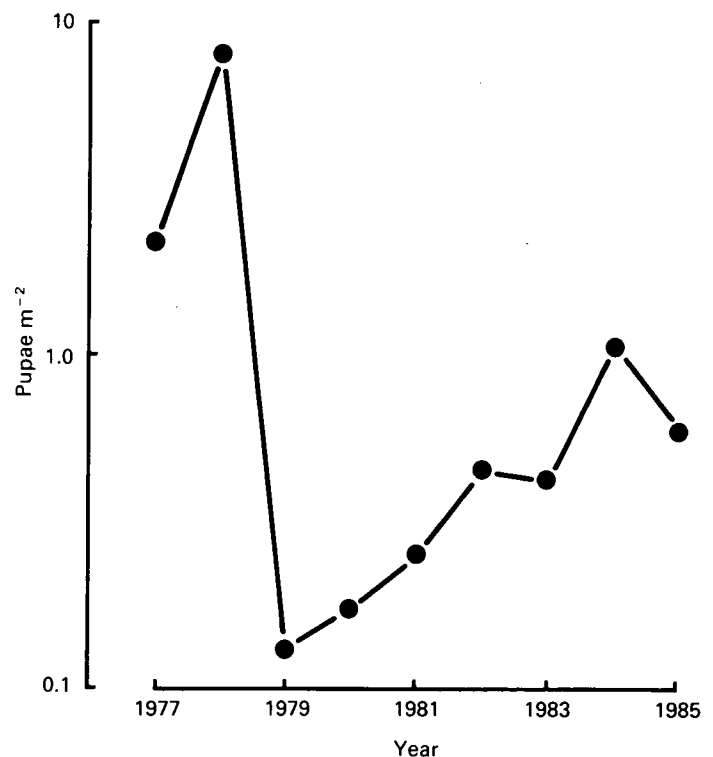


Figure 1. The number of pine beauty moth pupae m^{-2} in the Elchies block of Speyside Forest (an insecticidal spraying operation was done in 1979) (source: D A Barbour & J T Stoakley pers. comm.)

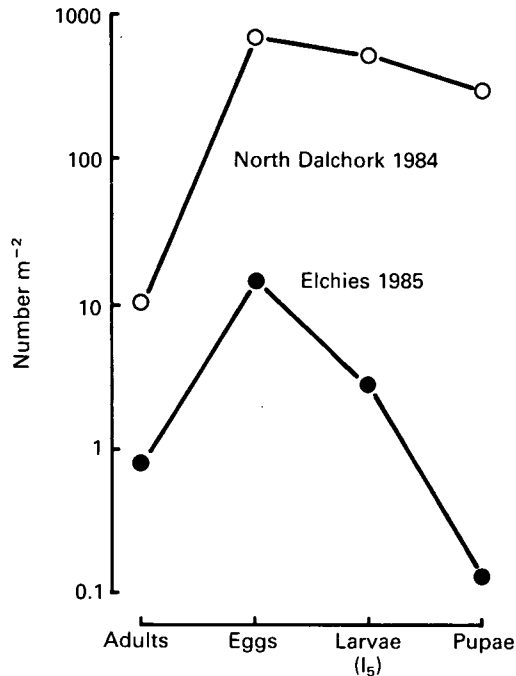


Figure 2. Survival of 2 contrasting generations of the pine beauty moth at North Dalchork (Shin) 1984 and Elchies (Speyside) 1985 (source: Barbour 1985; original data)

in the amount of nitrogen available for immature herbivorous insects. White (1974) found that certain insect populations fluctuated in accordance with a stress index which was a measure of winter waterlogging and summer drought. When a similar exercise was done for the pine beauty population in Elchies, population growth was not found to be correlated with January–March waterlogging and April–June drought when these 2 factors were considered together (Watt 1986). However, a much better correlation was found between population growth and late spring–early summer drought alone (Figure 3): population growth was highest in years when rainfall amounts were low. Is this correlation due to the effect of drought stress on plant nitrogen, and hence on insect survival?

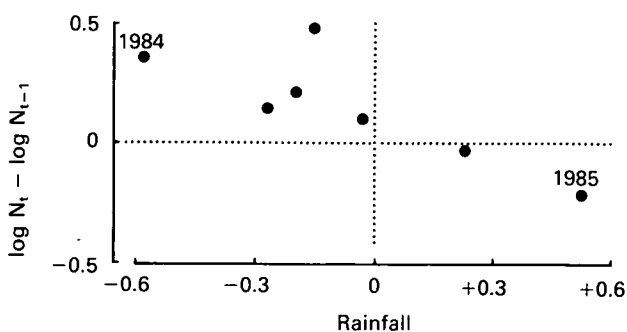


Figure 3. The relationship between the population rate of increase of pine beauty moth in Elchies ($R = \log N_t - \log N_{t-1}$) and the deviation from average of rainfall in April, May and June at Glenlivet (source: original data)

To examine the role of plant condition further, chemical analyses of pine foliage were done in Elchies during the feeding period of larvae from 1983 to 1985. Also, in 1984 and 1985, the effects of host plant condition and natural enemies were examined by using cages to exclude natural enemies. The results show that nitrogen levels in the current year's needles did not vary significantly even between years such as 1983, when the 'stress index' was low, and 1984, when it was high (Figure 4).

Larval mortality in the absence of natural enemies was measured in 2 contrasting years, ie 1984 and 1985, which had even higher rainfall than 1983 in April, May and June. Larval mortality was 32% in 1984 and 29% in 1985. From this evidence, it may be concluded that host plant condition plays no significant role in the temporal dynamics of the pine beauty moth. One possible exception is that sublethal levels of insect damage may cause a reduction in host plant quality (as found elsewhere, eg Rhoades 1983). Although herbivore-induced plant defences (or merely reactions) cannot prevent moth outbreaks, it is possible that they may extend the time between outbreaks.

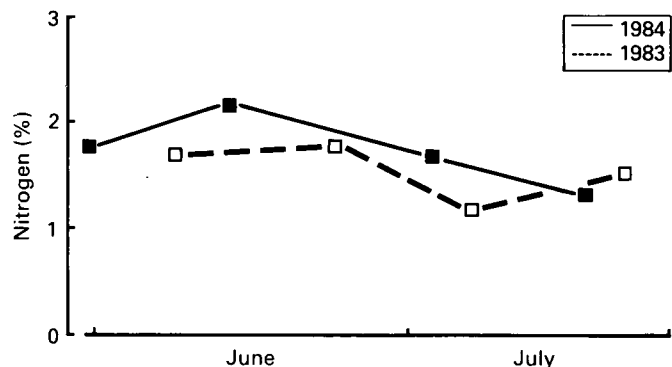


Figure 4. The nitrogen content of the current year's growth of lodgepole pine in Elchies, 1983 and 1984 (source: original data)

2.2 Natural enemies

A variety of natural enemies feed on the different stages of the pine beauty moth (Table 1). Parasitism by ichneumonid and braconid wasps and tachinid flies has been recorded at both low and outbreak densities. However, the proportion of moth larvae parasitized each year does not appear to increase as moth numbers rise. At North Dalchork, for example, parasitism between 1981 and 1984 never exceeded 7%, and was only 2.7% in 1984 when the average number of larvae per tree was 1700 (Barbour 1985). In contrast, parasitism in Elchies in 1984 and 1985 was 48% and 50% when larval numbers were 42.8 and 9.4 per tree respectively. It is as yet unclear whether these differences were site-related or whether parasites are generally more effective at low densities of the pine beauty moth.

Table 1. Natural enemies of pine beauty moth recorded, up to 1985, in Scotland (source: Barbour 1985; Stoakley 1979; H Crick pers. comm.; R H Dennis pers. comm.; original observations)

i. Parasites	
<i>Aphanistes xanthopus</i>	(Ichneumonid, pupal parasite)
<i>Banchus hastator</i>	(Ichneumonid, pupal parasite)
<i>Zele albiditarsus</i>	(Braconid, pupal parasite)
<i>Ichneumon septentrionalis</i>	(Ichneumonid, pupal parasite)
<i>Therion circumflexum</i>	(Ichneumonid, pupal parasite)
<i>Meteorus</i> spp.	(Braconid, larval parasites)
<i>Ernestia</i> spp.	(Tachinid, pupal parasites)
ii. Predators	
Redwing (<i>Turdus iliacus</i>)	(pupal predator)
Fieldfare (<i>Turdus pilaris</i>)	(pupal predator)
Robin (<i>Erithacus rubecula</i>)	(pupal predator)
Raven (<i>Corvus corax</i>)	(pupal predator)
Great tit (<i>Parus major</i>)	(adult & larval predator)
Coal tit (<i>Parus ater</i>)	(adult & larval predator)
iii. Fungi	
<i>Isaria farinosa</i>	
iv. Viruses	
<i>Panolis flammae</i> NPV	(nuclear polyhedrosis virus)

Unlike the effect of parasitism, the mortality caused by fungal and viral diseases has been found to be directly proportional to the density of the moth. For example, the number of diseased pupae at North Dalchork rose steadily from 3% in 1981 when there were 100.6 larvae per tree to 46% in 1984 when 1700 larvae per tree were found (Barbour 1985). Disease mortality was clearly density-dependent. However, it has never been found to reach a level high enough to prevent the moth from destroying its host plant.

The role of specific predators in the population dynamics of the pine beauty is poorly understood. However, life table and predator exclusion studies have given an indication of the level of predation at different stages of the life cycle. Predation during the egg and early larval instars, for example, has been studied with the aid of predator exclusion cages placed over individual branches. During the egg laying period, eggs were taken from heavily infested trees and placed, at known densities, within these cages. The cages were later examined and the development, growth and mortality of the larvae within each cage noted. In 1985, 60 cages were placed on lodgepole pine in Elchies. The mean level of survival to the third instar was 71%.

Precisely comparable figures for natural populations could not be obtained because it is difficult to assess density in the first 3 larval instars. The mean level of survival to the start of the fourth instar in the natural population in 1985 was 52%. Therefore, predation during the egg and larval stages in that year was less than 20%. Predation in subsequent stages could only be assessed by natural population counts. While most mortality in the late larval stages may be attributable to predation, some caution is needed in interpretation because there are few causes of mortality whose

impact can be separately assessed by population counts alone. Two such causes of mortality are larval starvation and failure to find a suitable pupation site. Returning to the 1985 example, it was found that, although mortality due to predation was less than 20% in the egg and early larval instars, it reached 61% in the fourth instar alone and then soared to 96% in the fifth instar and pre-pupal stage. Such high losses of older larvae are unusual but they have been encountered before, at Borgie (Naver Forest) in 1981 (Barbour 1985). A contrasting example is shown in Figure 2, North Dalchork 1984, where the egg to pupal mortality was 56.5% compared to 99.3% at Elchies in 1985. It is notable that, unlike disease but like parasitism, the level of predation has not been found to be density-dependent.

2.3 Intraspecific competition

Intraspecific competition clearly plays an important role in unsprayed outbreaks through larval starvation. However, there is no indication that competition exerts any significant effect on reproduction and survival in the years prior to an outbreak. In one of the examples given above, North Dalchork 1984, when there were on average 1700 larvae per tree, mortality attributable to both predation and starvation was only 56.5%. Similarly, there appears to be no reduction in the fecundity of the moth as its population density increases, at least until widespread defoliation occurs. Even then, the number of eggs laid in a defoliated area appears to be largely determined by moth dispersal (see below).

2.4 Weather

It may be concluded from recent research that the numbers of pine beauty moths are limited by the availability of its food resource, and that this limitation is only felt when there is substantial damage to the host plant. There is considerable variation in fecundity and mortality at different stages of the life cycle between different years, but little of this variation is related to the density of the moth. So, although pine beauty moth outbreaks are not everywhere as frequent as might be expected, density-dependent regulation does not appear to be the reason.

The remaining possibilities are that populations behave in an endemic/epidemic manner or that density-independent factors act to prevent or delay outbreaks. The density-independent action of weather in particular is now known to play a major role in pine beauty moth population dynamics. The phenology of the moth is such that critical parts of its life cycle occur when the year-to-year variation in the weather is large. In particular, adult emergence and egg laying are vulnerable to the weather in March, April and early May.

Adult emergence is dependent on temperature. Figure 5 shows the emergence of adults at North Dalchork in 1985. Emergence started in early April but was interrupted by cold weather on 10–15 April. Interrup-

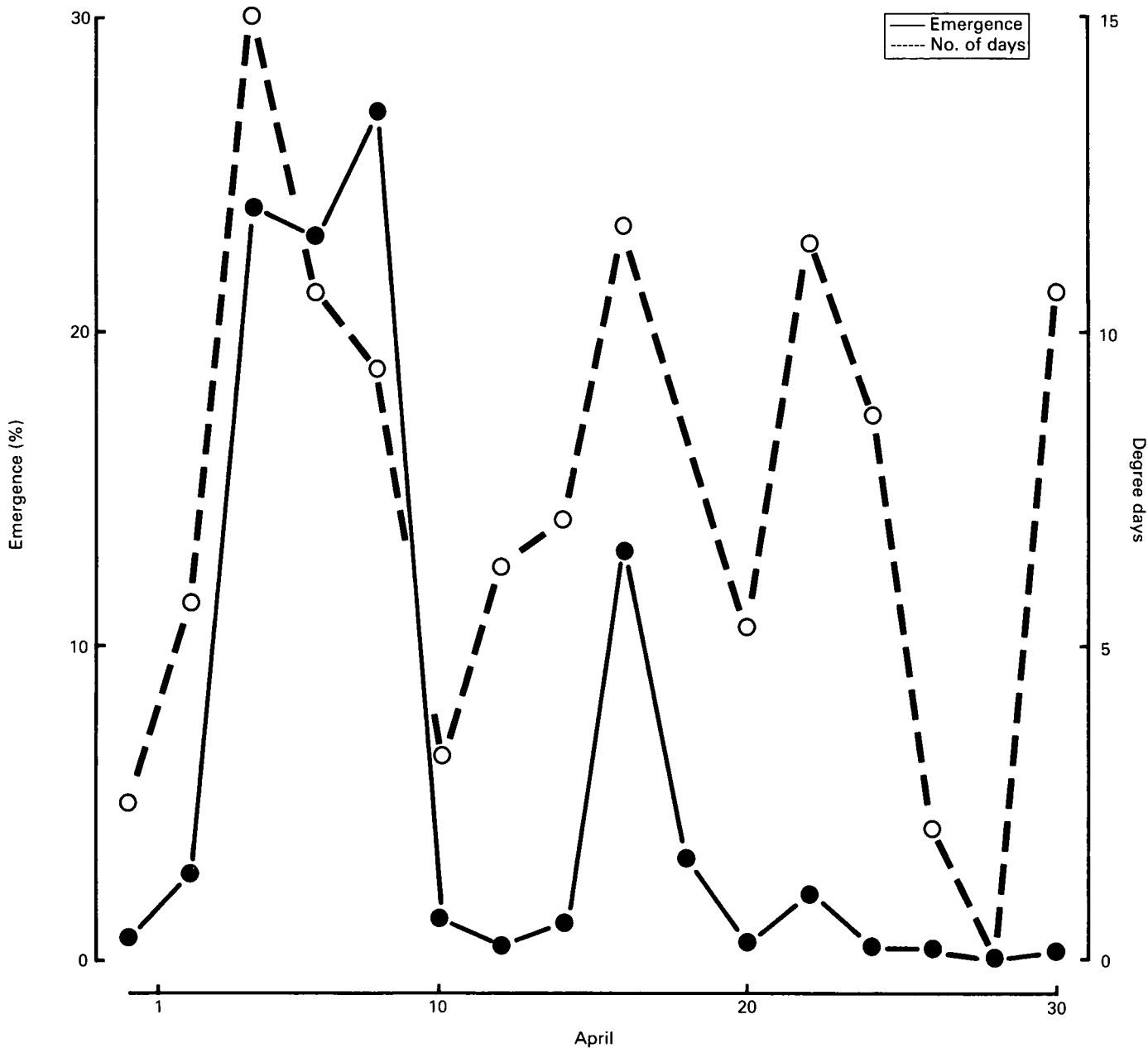


Figure 5. The emergence of pine beauty moth adults at one site in North Dalchork in 1985 and the number of degree days accumulated over 7°C at Lairg (each point is the sum of 2 consecutive nights' catches or day degrees (source: S R Leather & A D Watt unpubl.)

tions in emergence, and cold weather after emergence are both likely to cause a delay in mating, and this delay in turn is known to affect the pattern of egg production and the fertility of the eggs laid (Leather *et al.* 1986). Poor weather is also likely to affect adult mortality, and any decrease in adult longevity will result in a disproportionate effect on moths which have experienced a delay in mating (because of their different pattern of egg laying). The result is that the moth's fecundity is lower in cool springs than in warm springs (Figure 6).

Very little is known as yet about the effect of weather at other stages of the life cycle. The levels of parasitism and disease, for example, appear to be

unrelated to weather conditions, even though correlations have been noted in other studies. However, it may be that predation of older larvae and pre-pupae is more severe during cool summers because such weather causes larval development to be extended, and therefore makes the insect vulnerable to predation for a protracted period. This possibility is supported by the fact that the unusually high level of predation of older larvae and pre-pupae in Elchies 1985 occurred during an unusually cool summer.

The pine beauty moth has now been shown to be capable of rapid population growth, so rapid that in some forests control measures have been required twice in the last 7–8 years. Elsewhere, on the other

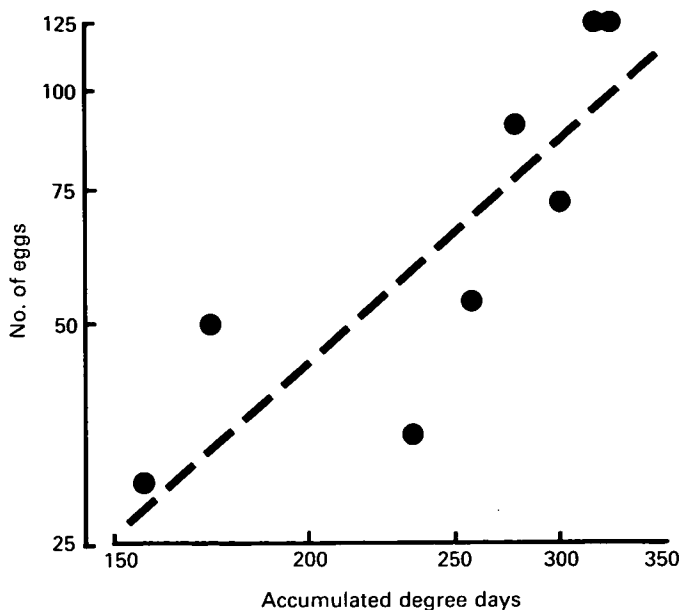


Figure 6. The relationship between the fecundity of pine beauty moth and day degrees accumulated above 7°C at North Dalchork (1981–85) and Elchies (1983–85) (source: Leather *et al.* 1986; original data)

hand, its density has remained below outbreak levels. Some understanding of this species' population dynamics has been gained by looking at temporal patterns of abundance but, given the differences in population behaviour between, and even within, forest blocks, it is also appropriate that spatial patterns of abundance should be studied.

3 Spatial dynamics of pine beauty moth

Two aspects of the spatial dynamics of a forest pest are important. First, are outbreaks more likely to start in some places than in others and, if so, can we explain why and then predict which sites are at risk? Second, when an outbreak has started, how far and how fast is it likely to spread?

3.1 Soil type

Forest entomologists have often tried to identify areas at risk from pest attack. 'Site hazard rating' systems have been developed for coleopterous, hemipterous and lepidopterous pests (eg Berryman & Stark 1985). It was quickly noted that outbreaks of the pine beauty moth in the early stages were associated with lodgepole pine growing on deep unflushed peat (Stoakley 1977). Moreover, it was suggested that this association was because trees growing on deep peat are 'stressed', and therefore are a better food source for the larvae. This suggestion was largely prompted by White's (1974) convincing evidence for the effect of soil conditions and plant stress on the population dynamics of the looper *Selidosema suavis* on Monterey pine (*Pinus radiata*) in New Zealand.

Therefore, in 1983, a series of experiments was started to see whether soil type had any influence on

the population biology of the pine beauty moth. These experiments were set up in the Elchies block of Speyside Forest because an outbreak developed in an area of deep unflushed peat in that block in 1978. Two techniques were used: (i) population monitoring and the construction of life tables, and (ii) predator exclusion experiments. For both these approaches, treatments were set up in areas of deep peat and ironpan soils. In 1983 and 1984, populations were monitored on artificially infested trees, but in 1985 observations were made on the natural population. The predator exclusion experiments were done with single branch cages placed within the top 5 whorls of trees 23–26 years old.

No significant differences were found in the population development of pine beauty moth on lodgepole pine growing in different soils between 1983 and 1985, either in exposed or caged populations (Watt 1985, 1986). Therefore, the observed outbreak behaviour of the moth in areas of deep unflushed peat does not appear to be the result of any improvement in pine foliage quality associated with deep peat. The tendency for outbreaks to develop on deep peat must be due to some other factor. It may be that pupal survival is greater in deep peat. Leather (1984) found that soil and peat were equally good pupal substrates, but that lodgepole pine needle litter was significantly better than either. As the needle litter layer is deeper and more persistent on deep peats than on sandy mineral soils (Blatchford 1978), and because pupation occurs at the needle litter/soil interface, pupal survival is likely to be greater in deep peat areas.

Alternatively, adult emergence from deep soils may be better synchronized with the development of the host plant, or adult moths may lay their eggs preferentially on trees growing on deep peat. A further possibility is that some trees in deep peat act as a 'sink', 'collecting' moths from surrounding areas because of their topography, associated temperature profiles and the wind patterns they experience. Greenbank *et al.* (1980) described one way how this may occur for the spruce budworm (*Choristoneura fumiferana*) in Canada. Moth dispersal in New Brunswick mainly follows the south-west to north-east direction of the prevailing wind. Moths tend to collect in the north central highlands of New Brunswick where decreasing night temperatures limit both the emigration of local moths and the re-emigration of invading individuals. There is, unfortunately, very little evidence concerning any of these possibilities for the pine beauty moth.

At present, then, certain areas of lodgepole pine can be said to be more at risk from pine beauty moth attack than others, but there is no clear reason why.

3.2 Host plant species

To try to explain why pine beauty outbreaks are frequent on lodgepole pine, which is a North American species, yet absent from Scots pine (Barbour 1986a),

which is a native host, natural and caged (from which natural enemies were excluded) populations of the moth were monitored in Scots pine as well as in lodgepole pine in 1984 and 1985. The exclusion experiments clearly showed that the survival of caterpillars was slightly (though not significantly) higher on Scots pine than on lodgepole pine, and that larval growth and development were better on Scots pine (Watt 1985). The monitoring of natural populations, however, showed that the species survived less well on Scots pine than on lodgepole pine, at least during the egg and early larval stages (Watt 1986). Thereafter, the difference disappeared. Mortality in the late larval and pre-pupal stages was as high on lodgepole as on Scots pine. This particular study is in its early stages, but it is already evident that the observed lack of outbreaks on Scots pine in Scotland is not due to the nutritional quality of Scots pine as a host plant. In fact, Scots pine appears to be a better host than (at least some provenances of) lodgepole pine in terms of larval growth and development, and perhaps for larval survival also.

A number of other possibilities may explain the absence of outbreaks on Scots pine. First, the phenology of Scots pine may be such that Scots pine shoots are likely to be at an unfavourable stage of development at the time of egg hatch. This was not the case in either 1984 or 1985. It is nonetheless a matter requiring attention as the development of shoots of Scots pine lags behind that of lodgepole pine, and the survival of young larvae could be poorer on Scots pine in years when the eggs hatch early in relation to shoot development. A second possibility is that the structure of Scots pine is such that newly hatched larvae have more difficulty in finding suitable feeding sites on Scots pine than they do on lodgepole pine. In 1984, sticky traps were placed under both lodgepole and Scots pine trees to see how many larvae fell from the canopy during the early instars. This experiment showed that only a small percentage of larvae was lost from the canopy during the early instars, but that significantly fewer were lost from Scots pine than from lodgepole pine (Table 2). There is no evidence that Scots pine is a poorer host for the moth than lodgepole pine: at present, the reverse appears to be true.

A third possibility is that the soil or litter, or both, is less suitable for pupae under Scots pine than under lodgepole pine. There is no information on this

Table 2. Number of young pine beauty moth larvae caught under lodgepole and Scots pine on sticky traps (Elchies block, Speyside, 1984) (source: original data)

	Eggs m ⁻² (artificially infested)	Larvae trapped m ⁻²	Larvae trapped as % of eggs
Lodgepole pine	264.2	20.0	7.6
Scots pine	282.7	11.3	4.0

hypothesis to date, but it obviously requires investigation, given that Scots pine tends to be planted in different soils from lodgepole pine. A fourth possible reason why outbreaks of pine beauty do not occur in Scots pine plantations is that natural enemies may be causing greater mortality on Scots pine than on lodgepole pine. The life table and exclusion cage studies referred to earlier indicate that the moth suffers heavier mortality on Scots than on lodgepole pine during the egg and early larval stages, but that the reverse may be true for the late larval and pre-pupal stages. In 1984 and 1985, the difference between the mortality of the early stages on the 2 host plants was not large and was, in any case, masked by the mortality acting upon the later stages. However, as pointed out earlier, this late larval mortality was exceptionally high in 1985 and the technique used in 1984 may itself have exaggerated late larval mortality.

The significance of mortality of eggs and early larvae of pine beauty moth on Scots pine has yet to be assessed fully. In both 1984 and 1985, the mortality of late larvae was higher on lodgepole pine than on Scots pine. This was in contrast to the mortality of eggs and early larvae, perhaps because of the faster development of pine beauty larvae on Scots pine which would leave them vulnerable to predation for less time than on lodgepole pine.

It may be concluded that, although it is known where pine beauty moth outbreaks start, ie on lodgepole pine rather than on Scots pine and on unflushed peats rather than other soils, the reasons are only just beginning to be understood. Consequently, population monitoring should be restricted to these 'at risk' sites with caution. Experience of pine beauty moth is still fairly limited, so that the observed associations between outbreak behaviour and site characteristics may be misleading. Moreover, until the reason why outbreaks are centred on certain areas are discovered, there will be no basis for pest management other than by chemical, viral or bacterial spraying.

Two examples are relevant to current research into the pine beauty moth. First, if the association between outbreaks and deep peat had been found to be nutritional, fertilizer application or thinning might have been tried in order to make the foliage less suitable for the caterpillars. Second, if outbreaks of pine beauty moth are absent from Scots pine because natural enemies are more effective on Scots pine than on lodgepole pine, the planting of the 2 species in mixture might lead to the prevention of outbreaks, or a reduction in their frequency. If, on the other hand, pine beauty outbreaks centre on certain areas because the soil conditions there are more suited to pupal survival, both these control practices will be ineffective.

3.3 Spread of pine beauty moth outbreaks

Although outbreaks of pine beauty moth tend to start in relatively small areas within forest blocks, they

spread rapidly to larger areas. For example, in 1984 an outbreak occurred in the North Dalchork block of Shin Forest, killing trees over 30 ha. By the following year, however, 1550 ha had to be sprayed. The development of such an outbreak is the sum of 2 processes. First, insect populations grow and decline at slightly different rates in different parts of a forest (ie what might appear to be a spreading outbreak is really a population reaching damaging levels at different times in different parts of the forest). Second, moths disperse from areas of high densities into surrounding parts of the forest.

Both these processes occurred in the development of the pine beauty moth population in North Dalchork, where annual surveys of pupae have been done by the Forestry Commission (FC) since 1977. In 1985, a joint ITE/FC study was undertaken on adult emergence and egg laying in different parts of the forest. In 1979, an insecticide spraying operation was carried out in the older parts of the forest block where densities had risen to a maximum of 40 pupae m^{-2} . In all parts of the forest, pupal densities declined or remained at low levels until (after no counts were done in 1981) an appreciable rise was noted in 1982. During 1983, a small increase in pupal density occurred in most areas, but a marked increase in numbers occurred throughout the forest in 1984. The high densities found in 1984 were, as already mentioned, only great enough to cause substantial defoliation in one part of the forest. However, the rate of population increase in that part of the block in 1984 was only marginally greater than that found in other areas. Moreover, the annual rate of increase in previous years was not consistently higher in the area defoliated in 1984 than in other areas. The reason why an outbreak centred on this part of the forest in 1984 seems to have been mainly because the numbers of pine beauty moths did not drop to such low levels there in 1979 and 1980 as elsewhere. Thereafter, with the rate of population increase being more or less the same throughout the block, the next outbreak was almost inevitably going to be centred in the place where the numbers of moths were high initially.

In the autumn of 1984, the pupal survey in North Dalchork showed that almost the whole block was at risk from defoliation by the pine beauty moth in 1985. In spring 1985, a study was done to see whether dispersal by moths out of the area defoliated in 1984 would lead to an even greater risk of damage in the surrounding parts of the block.

There was substantial pupal mortality during the winter of 1984–85 but the average number of moths which emerged in April 1985 was 29.4 m^{-2} , almost double the damage threshold of 15 m^{-2} . In the defoliated area, 181.5 moths m^{-2} emerged but average densities in 7 sites 1–3 km distant ranged from 12.4 to 21.9 moths m^{-2} . Later, there was much less variation in the numbers of eggs laid (1202–5496 eggs

per tree), but the number of eggs laid per emerged female ranged from 18 to 163. Only 18 eggs per female were laid on the defoliated trees, but 57 to 163 eggs per female were laid at the other 7 sites. The greatest numbers of eggs per female were found at the 3 sites nearest the area defoliated in 1984. Apparently moths emigrated from the defoliated area, laying the equivalent of at least two-thirds of their eggs elsewhere, so that the number of eggs laid on trees surrounding the defoliated area was approximately twice as great as expected.

The 'spread' of the outbreaks of pine beauty moth in North Dalchork in 1984–85 was therefore the sum of 2 processes, ie the slightly different population trends over a number of years in different parts of the block, and the dispersal of moths from the severely defoliated area in the spring of 1985. It would be wrong, however, to conclude that the only moth movement of any significance occurs after severe defoliation. Barbour (1986b) showed that adult pine beauty moths in the Elchies block of Speyside (then Craigellachie) Forest in 1979 underwent significant dispersal so that there was a large difference between the distributions of pupae, adults and eggs. This redistribution was not a response by adult moths to defoliation but could be explained by the direction of the wind during the flight period.

4 Discussion

A number of factors is now known to affect the temporal and spatial dynamics of the pine beauty moth. The most notable effects on temporal dynamics are by natural enemies, intraspecific competition and weather. There is good evidence that parasites and predators are more effective at low densities of the pine beauty moth. Fungal and viral diseases cause significant mortality at high densities but their impact is not great enough to prevent complete defoliation of host plants, and sharp population declines result from intense intraspecific competition. At this stage of research, the population dynamics of the pine beauty moth can be described either completely by a resource limitation model or, because of the possibly greater role of natural enemies at low densities, by an endemic/epidemic model. Whichever of these models is a truer representation of pine beauty moth dynamics, the role of weather must not be underestimated. Its effect on moth fecundity is particularly marked, but its effects on other stages of the life cycle are yet to be evaluated.

Although outbreaks of the pine beauty moth appear to be cyclical, a number of factors can be seen to be acting to make it very difficult to predict the length of time between successive outbreaks. This prediction was attempted by Watt *et al.* (1986), who used a simple simulation model incorporating the relationship between fecundity and weather together with the frequency of different patterns of spring weather found in northern Scotland. The model was used

primarily to assess the susceptibility of different provenances of lodgepole pine. It did not, however, include the large variability in larval mortality which was seen particularly in 1984 and 1985. Further research will be needed before the impact of late larval mortality and other factors can be satisfactorily included in a population simulation model. As such models are necessary for the strategic planning of pest control (Leather *et al.* 1986; Watt *et al.* 1986), a further commitment to the study of pine beauty moth populations through the life table approach is clearly needed.

The spatial aspects of the population dynamics of the pine beauty moth also require further attention. Outbreaks seem to be limited to lodgepole pine growing on certain soils, but the reason or reasons are unclear. The extensive approach to studying this pest must therefore continue to accompany the intensive approach, and future research must include the effect of crop age and further work on plant species mixtures.

Are there any wider implications from current research into the population ecology of the pine beauty moth? First, it has been confirmed that the pine beauty moth has become an integral part of the lodgepole pine ecosystem. The numbers of the moth are determined in part by several other organisms, and the abundance of these organisms is also certain to be affected by fluctuations in the density of the pine beauty moth. The same is likely to be true of other pests so that it would be wrong to consider the ecology of many of the other fauna of forests in isolation from forest pests.

Second, the prospect for the control of the pine beauty moth is, at present, limited to the use of insecticides, whose side-effects on other organisms are giving cause for concern. Further research should be done to develop less harmful pest control techniques and to improve the tactic of chemical control so that it is used as efficiently as possible. An important example is the timing of chemical application. A joint ITE/FC programme of research is attempting to predict pine beauty moth emergence, egg laying and egg hatch so that insecticidal application can be timed more easily and more effectively. This technique has been used for the control of a number of other pests, with the emphasis on trying to apply insecticides when the pest is most vulnerable. In future, the emphasis might be placed on trying to avoid harming the vulnerable stages of butterflies, dragonflies and other insects which are worth preserving within woodlands. This aspect would, however, require a far greater knowledge of the population ecology and behaviour of these insects.

Third, forest management practices designed for ensuring the conservation of wildlife within woodland or promoting the amenity value of woodland are

extremely unlikely to have no effect on the population dynamics of the pine beauty moth and other insect pests. For example, mixtures of tree species will promote insect diversity but may also decrease the abundance of certain pests. The mixed planting of different pines may be an effective management strategy against pine beauty moth, but more research is needed on its population ecology on Scots pine before this strategy is seriously considered.

Other mixed planting combinations such as pine/spruce, pine/birch and conifer/broadleaf combinations will, in general, lead to greater diversity among insects and probably other wildlife. There is, perhaps, a feeling that such diversity will lead inevitably to decreased pest problems. However, it must not be forgotten that the reason for fewer pest problems in some polycultures is not diversity *per se*, but some factor such as greater mortality during dispersal, or enhanced natural enemy action due to a predator or parasite being particularly associated with one of the plant species in the polyculture. These factors are not necessarily present in a species mixture which is chosen for conservation or amenity reasons.

Indeed, there is a risk that pest problems could be increased by mixed planting, because a number of serious forest pests are both polyphagous and phenological specialists. That is, they can feed on a number of plant species but they must hatch from the egg stage at a certain stage of the host plant's development: individuals hatching early and late may fail to become established. For example, if 2 or more host plant species are available with different phenologies, they will present the pest with a longer period during which it can successfully appear. One example is pine beauty moth on lodgepole and Scots pine which flush at different times. Two other examples are winter moth (*Operophtera brumata*) and vapourer moth (*Orgyia antiqua*), which have extremely wide host ranges including both broadleaved and coniferous trees. These examples provide a further reason why research into the management of forests for wildlife must include an assessment of how particular species mixtures, and indeed any other aspect of forest structure, will affect the incidence of insect pests. Moreover, this aspect and any other work done on insects for conservation or amenity reasons must be done rigorously. In particular, population surveys of insects must take note of the fact that insect abundance varies greatly from year to year, from month to month and, indeed, between superficially similar areas at the same time.

There are, therefore, good reasons why mixed planting would lead to both increased and decreased pest problems. A programme of research is urgently needed to find species mixtures which have fewer pest outbreaks.

Fourth, and finally, it should not be forgotten that the

exotic tree species which form so much of plantation forestry in the UK have been shown to be vulnerable to hitherto harmless indigenous insects which can become pests serious enough to jeopardize not just the economic value of forestry, but its wildlife and amenity values as well. At present, we do not even have complete records of which insect species currently feed on trees in commercial plantations. This basic gap must be filled, but a species list will not enable us to predict which insects will be pests in the future. Some indigenous insects can rapidly achieve pest status on exotic conifers, as in the case of the pine beauty moth. Other insects may adapt over a number of years before becoming pests. We therefore need to monitor and try to understand the population fluctuations of insects in woodlands.

5 Summary

The temporal and spatial population dynamics of the pine beauty moth are affected by host plant condition, natural enemies, competition, weather and dispersal. Natural enemies and weather are the principal factors affecting the sub-outbreak dynamics of the pine beauty moth, but their roles are still poorly understood so that adequate medium- and long-term prediction is as yet impossible. Unsprayed outbreaks are terminated by competition in the face of extreme food shortage. Fungal and viral diseases do not prevent complete host plant defoliation. Outbreaks of pine beauty moth are restricted to certain areas for reasons that are unclear, so that the classification of sites at risk still requires a firm scientific basis. The spread of outbreaks of the pine beauty moth is caused by slight differences in dynamics between different parts of forest blocks (apparent spread) and also by dispersal from heavily defoliated areas (actual spread).

The pine beauty moth forms an integral part of the pine ecosystem. Any forest management plan for whatever purpose (timber production, wildlife conservation, amenity) must take into account the fact that this and indeed many other pests are likely to be affected incidentally in ways that cannot yet be predicted.

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