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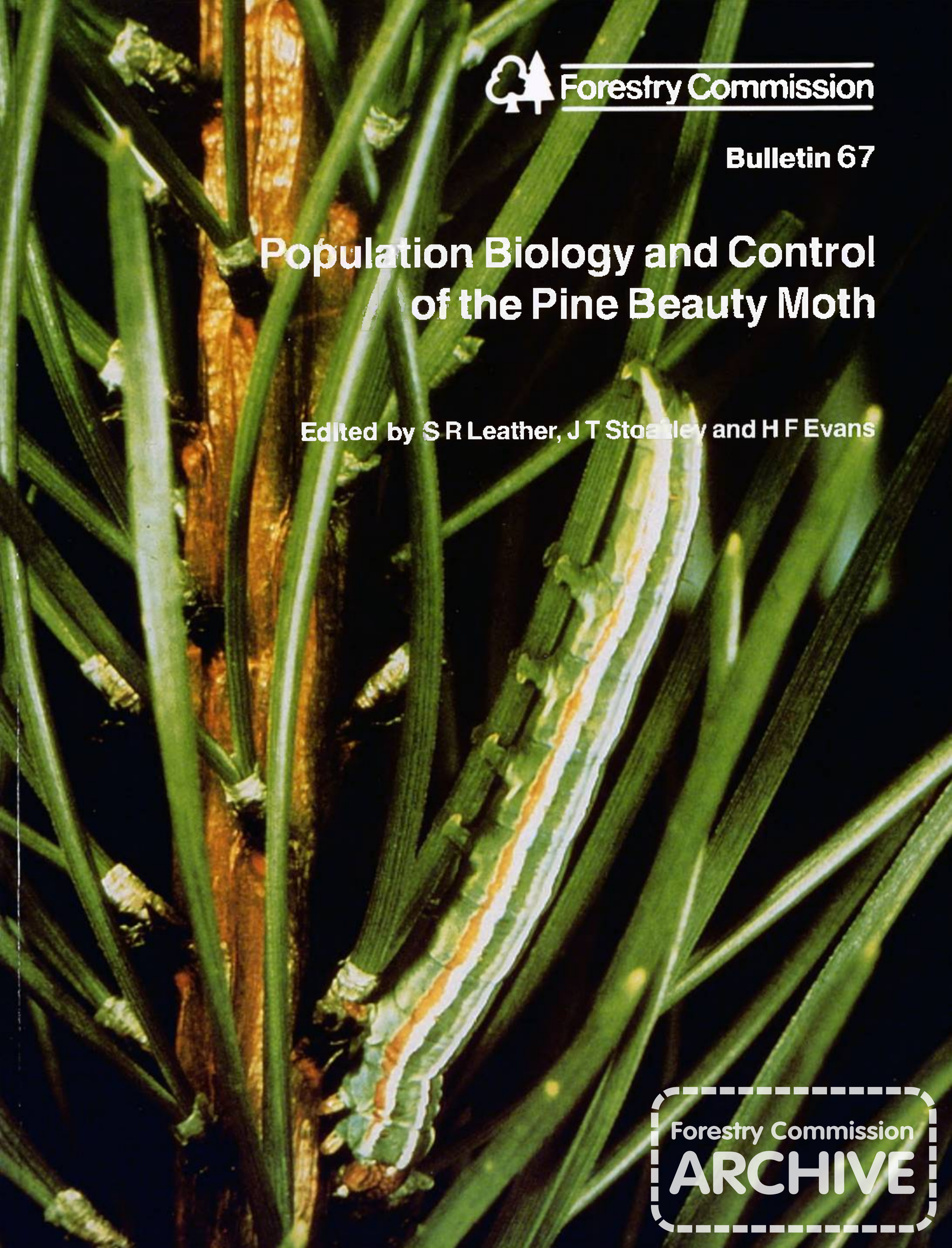
Population Biology and Control of the Pine Beauty Moth

Edited by S R Leather, J T Stoakley and H F Evans



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Population Biology and Control of the Pine Beauty Moth

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FRONT COVER: Mature larva of the Pine beauty moth *Panolis flammea* on Lodgepole pine foliage. (*33323*)
Copyright : Dr R. Parks

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Introduction

The following papers were given at a Workshop held at the end of 1984 to bring together a wide range of researchers, within and outwith the Forestry Commission, working on problems presented by the new and sudden occurrence in the late 1970s of large scale and severe outbreaks of the Pine beauty moth, *Panolis flammea* (D. & S.), in Lodgepole pine *(Pinus contorta* Loud.) plantations in Scotland.

South (1962) stated that Pine beauty moth is found in all counties of Britain except Caithness and Sutherland. Elsewhere in Britain Pine beauty has frequently been recorded from routine pupal surveys to monitor Pine looper moth, *Bupalus piniaria* L., populations in Scots pine, *P. sylvestris* L., and Corsican pine, *Pinus nigra* var. *Calabrica* (Loud.) Schneider, crops mainly in lowland forests on sandy soils but here Pine beauty numbers have always been low. However from the mid 1950s onwards increasing areas of acid, infertile upland soils, particularly peats, were planted with Lodgepole pine, a species introduced from western North America which appeared well suited to its new environment. Corresponding with the distribution of soil types most of the afforestation with this species took place in Scotland and particularly in the far northern counties. In 1973 and 1974 Pine beauty larvae were found for the first time, quite commonly, feeding on Lodgepole pine in Sutherland and in 1976 the first outbreak occurred in the Rimsdale block of Naver Forest, now part of Dornoch Forest District (Highland Region) (Stoakley, 1977).

In 1977 an attempt to prevent the further spread of this outbreak within the same block using a formulation of *Bacillus thuringiensis* failed and in that year and the following, three further serious outbreaks occurred, resulting in the destruction of 320 ha of plantations and, perhaps more significantly, in the need for control measures over some 10 000 ha during the years 1978-81 to prevent further loss of plantations. These were the largest aerial spraying operations ever carried out in British forestry, although very small by North American and even Central European standards, and involved: the rapid development of methods of population monitoring, the introduction of ultra low volume spraying techniques and of an electronic track guidance system for controlling lane separation by the spray aircraft, and the co-ordination of much research by a multitude of bodies in order to determine the safety and effectiveness of aerial application of the organophosphorus insecticide fenitrothion under forest conditions (Holden and Bevan, 1979, 1981).

This initial activity left few resources for acquiring the very thorough understanding of the biology of the insect and of the causes of outbreaks which is necessary if the incidence of Pine beauty attack is to be reduced in the future although it did become clear that high populations are particularly associated with the worst of upland peat sites. Time was also needed for investigations of further means of population monitoring using sex-attractant pheromones and of alternative control agents, and for development of improved methods of pesticide application. However, populations generally fell to low levels in the years 1981-83 and a start was made on essential research, much of which is reported here. The importance of this work has been reinforced by the commencement in 1984 of a fresh round of outbreaks continuing to the date of this publication and necessitating substantial control programmes in 1985 and 1986. These recent high populations go a long way to confirm the cyclical nature of the outbreaks – already clear in Central European experience of this insect and strongly suspected by analogy with the population dynamics of many other forest insect defoliators. They also further illustrate an association with what can now be considered 'problem sites' from the entomological viewpoint.

Since the first round of Pine beauty outbreaks there has been a considerable but not universal move away from afforestation with pure Lodgepole pine in favour of planting mixtures of Sitka spruce, which is expected to be the important element in the final crop, with Lodgepole pine (or sometimes other species). The risk and importance of Pine beauty moth in such mixtures remains to be discovered in practice, although there is evidence that the provenances of Lodgepole pine favoured for the purpose are the least susceptible.

However, the existing Lodgepole pine plantations on Pine beauty prone sites are extensive and many of them are only now reaching susceptible age. A continuing problem can thus be foreseen for several decades at least. This could be met at three levels:

1. By relying on application of pesticides, repeated as required.
2. By rapid, and therefore necessarily arbitrary, replacement of Lodgepole pine by other species.
3. By continuing research on the silviculture, ecology and entomological associations of existing and alternative species and mixtures, and methods of management, on these rather difficult sites.

We are grateful to Mr D.T. Seal, former Chief Research Officer (North), for allowing us to use the facilities at the Northern Research Station. Thanks are also expressed to all contributors.

S.R. LEATHER, J.T. STOAKLEY and H.F. EVANS

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Pine Beauty Moth Population Dynamics

General Considerations and Life-table Work

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Introduction

Panolis flammea is a widespread, indigenous moth in the British Isles, where it has historically been known to maintain only rather moderate population levels on Scots pine, *Pinus sylvestris,* a native conifer. Our experience of it as a pest dates from very recent years, coincident with the planting since the late 1950s of large areas of Lodgepole pine, *Pinus contorta,* on poor upland soils. However, on the continent of Europe *P. flammea* has a long history as a severe pest of *P. sylvestris,* being particularly associated with areas of continental-type climate (Schwenke, 1978). Before discussing the population dynamics of *P. flammea* in the novel ecosystem of young *P. contorta* plantations, it may be helpful to review what is known of the interaction with its indigenous host, both on the continent and in Britain.

Germany

Records of defoliating forest pests in North Bavaria and the Palatinate have been presented and analysed very fully (over a period going back to 1800) by Klimetzek (1979). Outbreaks of *P. flammea* on *P. sylvestris* occurred repeatedly and rather regularly at intervals of about 8 years, as illustrated (Figure 1) for the district of Mittelfranken. Twenty-one outbreaks ('gradations') occurred in the overall territory of North Bavaria during 1800-1970, and 19 of these are represented in the records for Mittelfranken. The mean periodicity calculated from this is 8.1 ± 0.4 years. Temporal occurrence of *P. flammea* in the three districts of Bavaria and in the Palatinate was highly significantly correlated, with simultaneous occurrence in the four areas. *P. flammea* outbreaks showed a significant degree of synchrony with those of the Nun moth, *Lymantria monacha,* in the same area, but not with those of the Pine looper moth, *Bupalus piniaria,* the other major pest of pine.

The factors determining this cyclic pattern of *P. flammea* populations are reviewed by Schwenke (1978). Climate and weather appear to have a predisposing role for the initiation of outbreaks; low rainfall areas (500-800 mm per year) are the most affected, and so-called 'wine years' with high temperatures and low rainfall precede or coincide with the severest outbreaks. In general, though, abiotic factors are of less significance for *P. flammea* population dynamics than biotic factors. Of these the most important are insect parasitoids – 85 recorded species of Ichneumonidae, 7 Braconidae and 11 Tachinidae. The single most important parasitoid is the Tachinid fly, *Ernestia rudis,* which has been definitely identified as the chief agent in the collapse of certain gradations in the past. Several insect predators are recorded, though being less specific to *P. flammea* they are less likely than some of the parasitoids to interact cyclically. Two species of fungal diseases, *Empusa aulicae* and *Spiralia (Isaria) farinosa* contributed significantly to the collapse of some outbreaks.

In other parts of Germany, as in Britain, *P. flammea* has persisted at moderate population densities for long periods of time without giving rise to outbreaks. Gauss (1975) reviewed its population behaviour over a 16-year period (1958-1973) in which the population density in south-west Germany remained low. Pupal parasitism was notably high, often in excess of 50 per cent, and Gauss's data give strong support to the idea that the population density was to some extent regulated by the action of parasitoids (Figure 2).

However, Gauss believed that additional factors were needed to explain the long 'latency' of the population. He stressed the likely importance of climatic factors, and of forest composition, particularly the practice of underplanting pine with hardwood trees.

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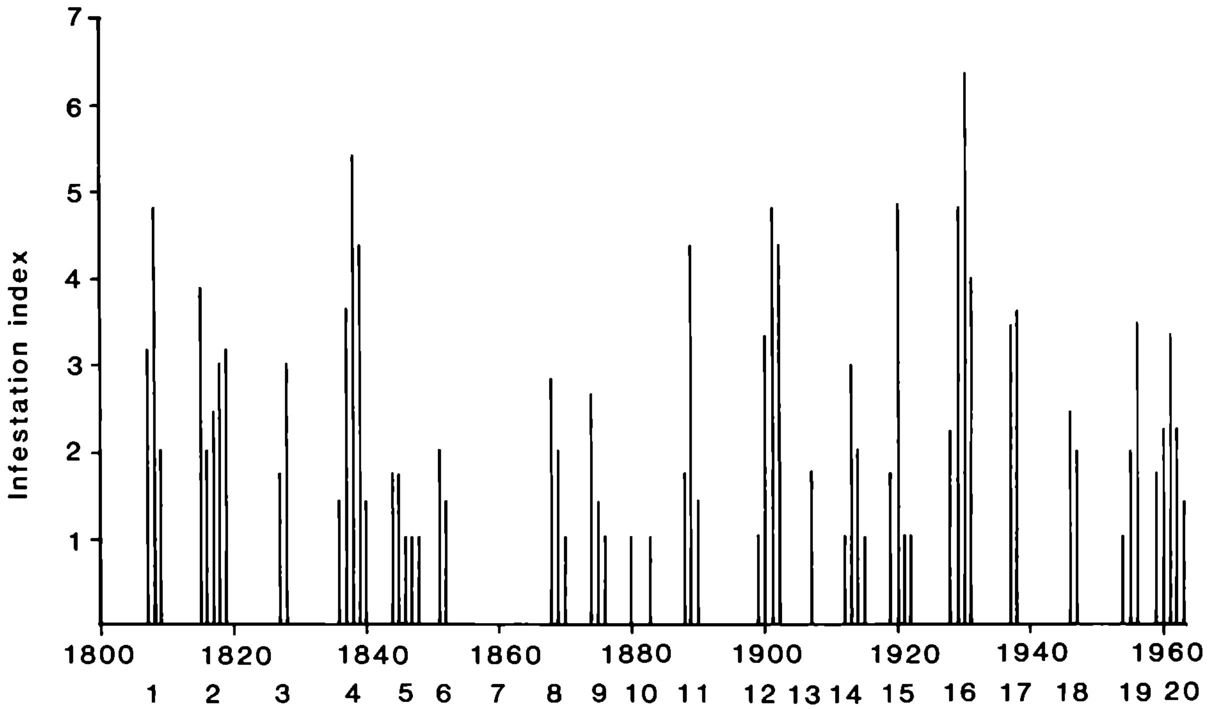


Figure 1. Historical sequence of *P. flammea* outbreaks in Mittelfranken (from data of Klimetzek, 1979). The infestation index calculated for each year is the square root of Klimetzek's index 'i'.

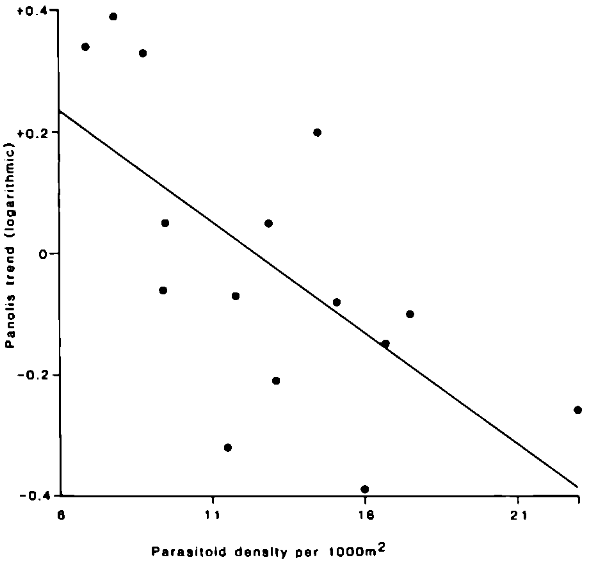


Figure 2. Correlation of *P. flammea* population trend (year n to year n + 1) with abundance of parasitoids in year n (from data of Gauss, 1975). Regression is $y = 0.458 - 0.037x$, $r = -0.650^{**}$.

Britain: Populations in Old Scots Pine Woods

In older pine plantations throughout Britain an annual pupal survey has been carried out since 1954 to monitor the populations of Pine looper moth, *Bupalus piniaria* (Bevan and Brown, 1978). The survey is carried out in the January-March period and records all lepidopterous pupae in the forest soil. *P. flammea* pupae are recorded regularly, as the adults do not emerge until late March-April. Detailed information from this survey is available from about 50 survey areas throughout the country, and in many cases the *P. flammea* data are continuous for the period back to 1955.

Two things are striking about the *P. flammea* data obtained from the survey results. First, the uniformity of the mean density level recorded for populations in different parts of the country: levels of 0.1 per m² or a little lower seem to have been general in virtually all areas. Secondly, the low amplitude of fluctuation: deviations of more than three-fold above or below the mean level were extremely rare. The impression given is of a well-defined, fixed equilibrium density about which only small random fluctuations occur. The *P. flammea* data for four widely-separated forest areas surveyed are shown on a logarithmic scale in Figures 3a-d.

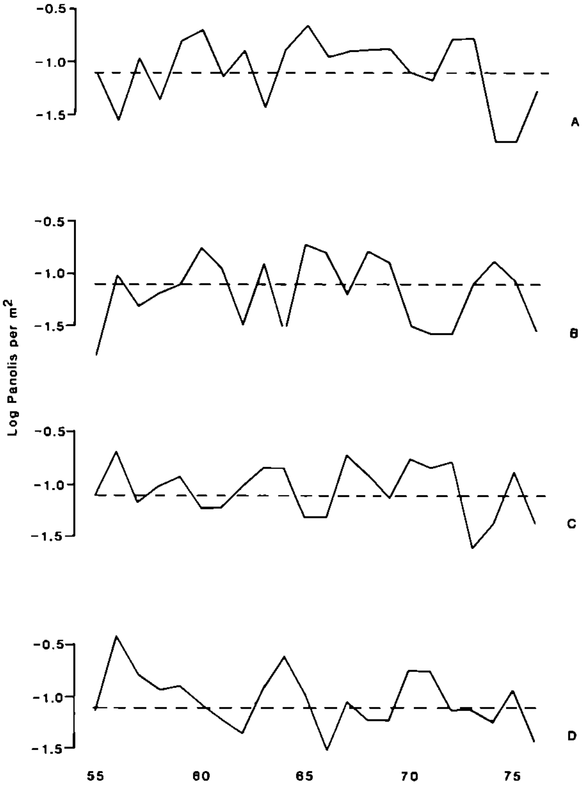


Figure 3. Pupal density of *P. flammea* (pupae per m² on log scale) from four different pine forests over 22 years
a) Black Isle, north Scotland
b) Montreathmont, east Scotland
c) Delamere, north-west England
d) Laughton, east England
The dotted line represents a common 'equilibrium density' at 0.08 per m².

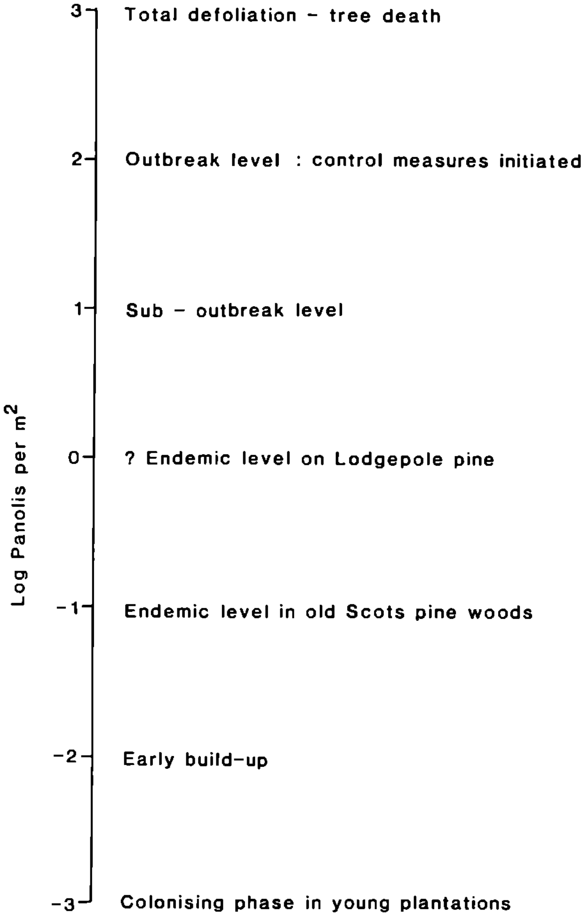


Figure 4. Numerical scale of fluctuations of *P. flammea* population density in British pine forests.

The reasons for this pattern of population behaviour are not known. As in the Gauss study in Germany, parasitism of the pupae was high, frequently 50 per cent or over. So it seems likely that natural enemies played an important role in maintaining the low, constant level of the population.

The data from Black Isle Forest in north Scotland are of particular interest for comparison with the *P. flammea* populations on Lodgepole pine in north Scotland during the same years. The Black Isle population varied within an approximately 10-fold range in the 22-year period. Populations in some Lodgepole pine plantations increased by a million-fold during the same years (see below).

Numerical Scale of the Fluctuations

Field assessments in connection with the *P. flammea* programme in the last 8 years have shown a very wide range of population density. At one extreme this may be as low as one pupa per 1000 m², at the other as high as 1000 *P. flammea* individuals per m² of plantation (Figure 4). The seven levels indicated in the figure differ by successive factors of ten:

-3 1 per 1000 m². This very low level probably relates to the initial colonization of young plantations in areas remote from pre-existing pinewoods. Such a population is too low to be measured directly, but comparative figures from the pheromone-trapping programme suggest that such low levels do occur.

-2 1 per 100 m². This still represents an extremely sparse population, but pupal densities as low as this have sometimes been directly measured in the course of extensive surveys.

-1 1 per 10 m². As shown above, this approximates to the long-term equilibrium density observed in all the old Scots pine woods sampled for the looper survey. Quite frequently such a pupal density has also been recorded in Lodgepole pine plantations.

0 1 per m². This density of pupae is commonly recorded in Lodgepole pine areas, though hardly ever achieved in old Scots pine woodland. Some Lodgepole areas that have been monitored over a period of years, without outbreak, have fluctuated approximately about this level.

1 10 per m². This comes very close to the level of 15 pupae per m² which has been regarded as the 'danger level' where spraying becomes necessary (Stoakley, 1979). On the other hand, populations have been known to decline naturally from 10 per m² with no observable damage to trees.

2 100 per m². The population is now well in excess of the critical level. Spraying is urgently necessary to protect trees. However, pupal levels of 100 per m² may well be found under trees which show little outward sign of feeding damage in the current generation. This explains the tendency for *P. flammea* damage to appear suddenly, quite 'without warning', in the absence of a proper monitoring programme.

3 1000 per m². This level represents a 'population ceiling' at which all foliage is stripped from the trees resulting in their death. Such a pupal density has been recorded only in rare instances, on the fringes of totally-defoliated areas (e.g. Stoakley, 1977).

This million-fold range of numbers is the more remarkable when it is realised that populations span the entire range in a period of just a few years. This can be seen in Table 1, which compares the age at death of the six major areas of trees killed in outbreaks to date. Nearly all these sites were plantations in remote areas well away from pre-existing pinewoods. Nevertheless colonization, population build-up and total defoliation occurred in a span of time typically between 12 and 15 years.

Table 1. Comparison of age at death of trees killed in major outbreaks to date

	Planted	Killed	Age at death
Rimsdale	1958-1967	1976	9-18
Strathy	1965	1977	12
Torrachilty	1956	1978	22
Annabaglish	1966	1978	12
Pollie Hill	1969-1970	1984	14-15
North Dalchork	1965	1984	19

The rate of population increase required to achieve this can be calculated quite simply. Two alternative scenarios are presented below (Figure 5). In one, the population increases just over three-fold from year to year throughout the period. This allows it to increase from 10^{-3} up to 10^{3} in a period of 12 years. A more realistic model makes use of the observed fact that very young trees (below about 10 years) are less favourable hosts for *P. flammea* than older ones. So we suppose the *P. flammea* population only doubles from year to year up to the age of 10 years after planting. Thereafter it quadruples each year until the ceiling is reached. This allows the transition from 10^{-3} to 10^{3} per m² to be completed in 15 years.

From this it is clear that *mean* rates of population increase of two-, three- or four-fold must be postulated to account for the observed long-term build-up of populations. Of course, the exact yearly increase will be a variable quantity influenced perhaps by weather and by biotic factors; but the overall pattern must be one of progressive, rapid, almost unrestricted increase. Year-on-year increases of this magnitude have been observed at a study plot in the N. Dalchork block of Shin Forest in four generations from 1981 to 1984 (see below).

To sum up, the observed population behaviour of *P. flammea* in young Lodgepole pine plantations is very different from what is seen typically in old Scots pine woods. Numbers at first build up rapidly, and may or may not decline naturally before serious defoliation is inflicted on the trees. The factors favouring or counteracting this build-up can be investigated by the standard techniques of insect population dynamics, in particular by life-table studies, and such a study on *P. flammea* has been in progress for 4 years in Scottish plantations.

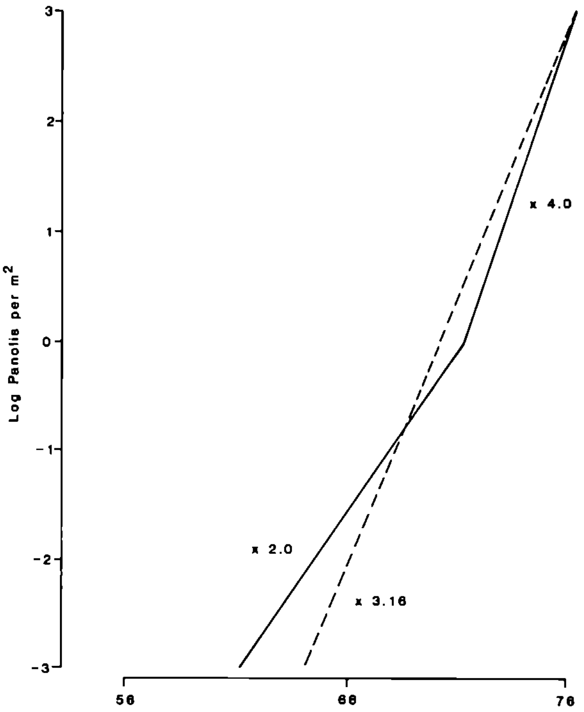


Figure 5. Two alternative scenarios for the increase of *P. flammea* population density in the Rimsdale plantation leading up to the first outbreak in 1976.

Solid line: annual increase x2 in first 10 years, thereafter annual increase x4.

Dotted line: annual increase x3.16 throughout period.

Compare Figure 3(a) on the same scale, for a stable population in north Scotland during the same period.

Life-table Study

The life-table work, commenced in 1981, aimed to investigate population dynamics of *P. flammea* on typical outbreak sites – that is, on Lodgepole pine of 10 years and older growing on deep unflushed peat soils. Two sites were selected initially, one in the Borgie block of Naver Forest, and one in the N. Dalchork block of Shin Forest (both in Sutherland). Subsequently the Borgie plot was discontinued and a new plot initiated in Elchies block of Craigellachie Forest (Moray).

Each year assessments were made of population density at the following stages of the life cycle:

1. Pupae in early spring. Twenty-four strips each of 2 m², randomly positioned within the one hectare plot were searched to a depth of approximately 15 cm, and all pupae (healthy, parasitized, or dead) were collected and recorded.

2. Adult emergence (March-April). Fifty emergence traps each of 0.2 m² collecting area, were randomly positioned within the plot. The trap consisted of an inverted metal funnel pressed into the surface of the ground, with a collecting pot fitted with sticky card attached to the apex.

3. Eggs on foliage (May). Twenty-five randomly-selected trees were felled after completion of egg-laying and before the beginning of egg hatch. The leading shoot and one branch from each alternate whorl of branches down the tree were carefully examined for eggs. This enabled an accurate estimate to be made of the total number of eggs on each sample tree (J. T. Stoakley, unpublished data).

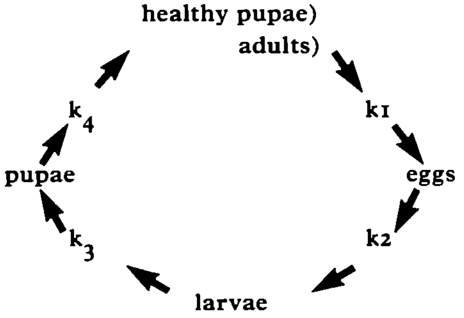
4. Larvae (June). The larvae were assessed on the basis of number of cast head-capsules falling into 50 metal funnels (each 0.2 m² collecting area), randomly placed beneath the trees. The fourth-instar capsules (i.e. the largest to be shed in this way) were used for the standard comparison because smaller capsules could not be so readily extracted and counted.

5. Prepupae descending from trees (July-August). These were trapped in basins filled to a depth of about 6 cm with water. One hundred basins, each of 0.08 m² collecting area, were randomly placed in each plot.

6. Prepupae in early autumn. As for the spring pupal count, 24 strips were searched totalling 48 m².

These six estimates were reduced effectively to four in each generation. There was no significant difference between the number of emerging adults and the number of live healthy pupae in the spring count, so these were combined to give a single estimate for the start of a generation. The number of prepupae in basins consistently over-estimated the true numbers present, apparently because prepupae descend more than once before settling on a site for pupation, and so these counts were not used in constructing life-tables.

The four remaining stages were as follows:



The mortality intervening between successive stages was expressed as the logarithm of the proportional reduction in numbers, respectively k_1, k_2, k_3, and k_4.

Upon completion of the 1984/5 fieldwork, there will be seven completed life-tables from this work, namely Dalchork 1981, 82, 83, 84; Borgie 1981; Elchies 1983 and 84. Until then the results in relation to the 1984 generation are provisional and incomplete, but it is possible to describe in very general terms the main findings which emerge.

Dalchork and Borgie both started in spring 1981 from a level of about 1.0 emerging adults per m². That year they diverged strongly, the Dalchork population increasing moderately over the season, while the Borgie population crashed to a very low level indeed resulting in this site being abandoned for further sampling. At Dalchork further 3-fold increases were seen during 1982 and 1983, with a much stronger increase (almost 10-fold) in 1984. The Elchies population started at around 0.5 emerging adults per m² in 1983 and showed an almost unchanged density after one generation. 1984 saw a moderate increase there.

The k-values from these seven life-tables were analysed by the key-factor technique of Varley and Gradwell, as modified by Podoler and Rogers (1975). The key-factor is that particular mortality-factor which most strongly determines the overall generation mortality and thus the trend of population increase or decrease. Podoler and Rogers determined this by regression of each of the k-values on K, the overall generation mortality. The regression coefficients of all the constituent ks should sum exactly to 1.0, and that k which shows the highest regression coefficient is by definition the key-factor.

The analysis for the seven life-tables is presented diagrammatically in Figure 6. On this analysis k_3, the mortality of late larvae and prepupae, emerges clearly as the key-factor. That it does so is due almost entirely to a single case, that of Borgie in 1981, when the 'crash' in population numbers occurred at that stage. The reasons for that crash are not known, as no larval corpses were found and there was no evidence of intensive parasitism or disease.

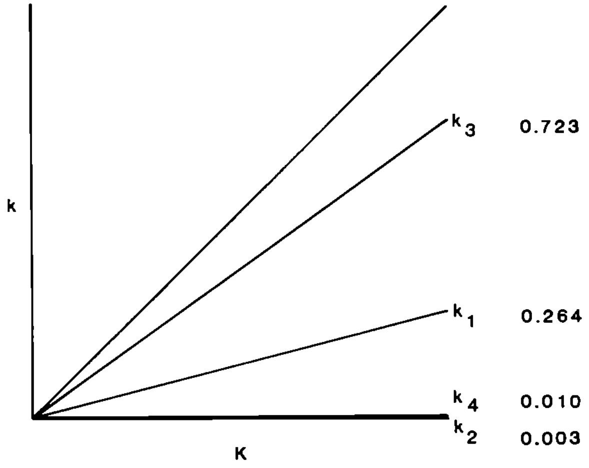


Figure 6. Key-factor analysis of *P. flammea* life-tables (all data). Regression coefficients of k on K calculated according to the method of Podoler and Rogers (1975).

By contrast with the Borgie example, the six other cases all represent populations in the increase phase of their natural cycle. So it is instructive to analyse the data for these six cases separately. The regression analysis now shows a different order of importance of the four k-values, and k_1 now outweighs k_3 to emerge as the apparent key-factor (Figure 7).

k_1 represents the mortality of adult moths and failure to lay the full complement of eggs under field conditions. It appears that where only increasing populations are considered, this factor has the greatest impact on overall generation trend. This is consistent with the finding of Leather (1984) that egg-laying by adult *P. flammea* is strongly dependent on temperature and is likely to be a major factor in the population dynamics of *P. flammea* under the conditions typical of Scottish plantations.

However, where decreasing as well as increasing populations are considered in the analysis, other stages of the life-cycle assume dominating importance. These might, for example, be those at which natural enemies take their toll; but as only a single case has been studied and the actual mortality agent there was not identified, it is not possible to draw firm conclusions about this. Clearly in any continuing life-table work it will be particularly valuable to look at populations which are declining naturally, and to take steps to identify actual mortality agents as well as the life-cycle stage at which they operate.

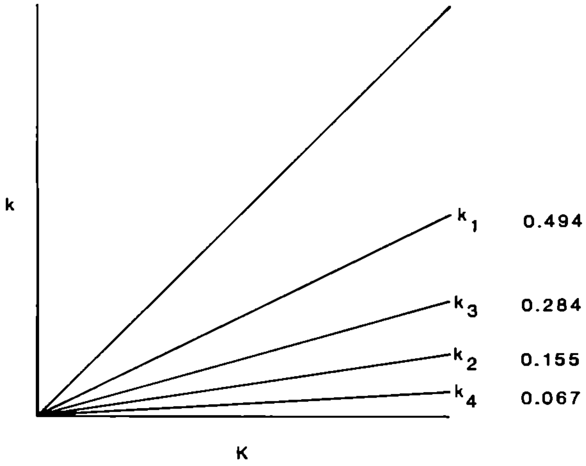


Figure 7. Key-factor analysis of *P. flammea* life-tables (increasing populations only). Regression coefficients of k on K calculated according to the method of Podoler and Rogers (1975).

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Pine Beauty Moth Outbreaks:

Associations with Soil Type, Host Nutrient Status and Tree Vigour

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Introduction

Nearly all of the *Panolis flammea* outbreaks which have occurred in the north, south and east of Scotland have been centred on areas of Lodgepole pine *(Pinus contorta)* over the age of 8-10 years growing on deep unflushed peat – either as hill peat or raised bog with *Calluna vulgaris* and *Scirpus caespitosus* as the dominant vegetation (Stoakley, 1979). The sites of two particular outbreaks, Bareagle Forest in south Scotland and Craigellachie Forest in east Scotland have been studied in an attempt to elucidate those factors which might predispose stands of Lodgepole pine to infestation by *P. flammea*.

In 1978-79 an outbreak in the Annabaglish Moss block of Bareagle Forest (Dumfries and Galloway Region) destroyed a clearly defined area of 50 ha near the centre of that block. In 1982-83 a retrospective investigation was carried out of trees within and around the area of severe defoliation. The stem radii and annual radial increments in the years preceding the outbreak were determined from core samples and foliage samples were taken for nutrient analysis. Also, since it appeared that the outbreak had occurred particularly in a low-lying wet area, a survey of ground levels was carried out. The outbreak site could thus be characterised in terms of previous tree growth and current foliar nutrients and these can be related to the topography of the area.

In the Elchies block of Craigellachie Forest (Grampian Region) highest *P. flammea* populations have been associated with areas of Lodgepole pine growing in deep peat. In the winters of 1981-82 and 1982-83, and during the period of larval feeding in summer 1982 a series of foliage samples was taken from trees on deep peat and on the two other major soil types present – mineral ironpan and surface water gley. Needles and developing shoots were analysed for foliar N, P and K concentrations. Foliar nutrient contents of trees on the three major soil types could therefore be compared with the previously observed abundance of *P. flammea* on these soils and susceptible sites characterised.

Additionally the effect of foliage nutrient levels on larval survival was investigated in a field experiment at Glentress Forest (Borders Region).

Methods

I. Annabaglish Moss

Site

The area studied was within an extensive crop of Lodgepole pine and Sitka spruce, in equal proportions, planted in an intimate mixture. The whole block is covered by deep peat (> 45 cm) but the outbreak occurred on what was evidently a raised bog. On broad rides, where conditions had not been modified by ploughing, drainage and tree growth, there was surface water in all but the driest periods (Stoakley, personal communication).

Within the outbreak area Sitka spruce, which is considerably more site demanding than Lodgepole pine, was largely in check and therefore not competing with the pine in the canopy; elsewhere in the block the two species were growing at similar rates. No significant defoliation was reported from the area prior to 1978 and this is consistent with other observations that Pine beauty outbreaks are sudden events.

Sample locations

Seven sample locations were selected along a transect running through the defoliated area and extending beyond it to the north and south. One location was sited within the severely defoliated area, with three locations

(N1, N2 and N3) at increasing distances to the north and three locations (S3, S2 and S1) at increasing distances to the south.

At each of these seven locations a pair of increment cores was taken at breast height, using a Pressler borer from a number of live, dominant and co-dominant sample trees. In the severely defoliated area, where there were few live trees, 25 scattered trees were used, and at the remaining locations 15 trees regularly spaced along the south-facing side of a ride, were sampled. Mean stem radii were calculated and annual increments for the years 1973 to 1982 inclusive were measured using a travelling microscope.

Foliage sampling and analysis

During November one unshaded fourth whorl branch was removed from each of the trees selected for core sampling at each sample location. This is the standard date for routine foliage analysis since nutrient concentrations are then most stable. The terminal 30 cm of each branch was sealed in a polythene bag and stored at -20°C within 24 h of sampling. Subsequently samples of needles from the shoots were oven dried at 85°C for 48 h, ground, weighed, digested with acid and analysed colorimetrically for total N, P and K. Results were expressed as percentages of dry weight.

Needle biomass and surface area

From the shoots collected as above, samples of 100 needles were removed, weighed and then oven dried at 85°C for 48 h and reweighed. Mean water content and dry weight per needle were then calculated. Further samples of 100 needles were measured using a Li-cor Area Meter and the resultant total projected surface area used to calculate the mean projected surface area per needle.

Levelling survey

A line of levels was run along the transect, in order to relate tree growth to topography. For this a surveyor's level, tripod and levelling staff were used, measurements being taken to 1 cm accuracy with collimation points 5 to 60 m apart depending on terrain. From these, the heights were recalculated against the lowest point, to give a Relative Ground Height above that point.

II. Elchies

Foliage sampling and analysis

Single branch samples were taken from each of 20 sample trees at locations representing the three soil types – deep peat, mineral ironpan and surface water gley. Samples were taken on eight occasions during the period February 1982 to March 1983, with the most frequent sampling during the period late May to mid July. On all occasions samples of the most recent mature needles were taken for analysis. During the early summer sampling period samples of new current shoots were also taken from the tips of branches for analysis. This soft shoot material represented that on which the early larval stages of *P. flammea* feed from about late May until towards the end of June. Samples of (a) needles and (b) current shoots were prepared and analysed for total N, P and K as described for Annabaglish. Needle and shoot dry weights were also determined as for Annabaglish.

III. Glentress

Larval survival in relation to host nutrient status

Groups of 15 larvae were sleeved, directly after hatching, on branches of Lodgepole pine growing on different plots of the Forestry Commission's Deficiency Garden, with nutrient treatments as listed in Table 1. The larval numbers were re-counted at third or fourth instar and again towards the end of the fifth instar just prior to pupation. Samples of foliage from each of the trees used were taken for analysis of N, P and K.

Table 1. Analysis of foliar nutrients and survival of larvae in Glentress Forest Deficiency Garden

Treatment	% dry weight composition			N : P : K ratio	Number larvae/instar			% survival to final instar
	N	P	K		I	III/IV	V	
– P	1.16	0.07	0.48	17 : 1 : 7	30	14	14	46.7
– K	1.02	0.13	0.22	8 : 1 : 2	30	21	21	70.3
– N	1.13	0.13	0.50	9 : 1 : 4	30	22	22	73.3
– NPKCaMg	0.97	0.06	0.35	16 : 1 : 6	30	19	19	63.3
– 0	1.15	0.12	0.37	10 : 1 : 3	60	44	44	73.3
'deficient'	<1.1	<0.12	<0.3-0.4	10 : 1 : 3 (optimum)				

Results

I. Annabaglish Moss

Core sampling

Stem radii and rates of growth for the seven sample locations are shown in Table 2 and Figures 1 and 2. Trees in locations S1 and S2 and N2 and N3, further from the defoliated area, were significantly larger in diameter than those in or nearer the defoliated area (S3, D and N1). The trees showing poorest growth were in the severely defoliated area (represented by location D) and at N1 where some 50 per cent of trees had been defoliated and killed. Differences in tree growth between locations S1 and S2, N2 and N3, and N1 and D were not significant. Trees in the outbreak area (D) showed only about half the annual rate of radial increment of trees growing at the best location (S1), prior to the insect outbreak in 1978 in each of the years measured.

Foliar analysis

Figure 1 shows that tree growth from 1973 to 1982 at each location was generally consistent from year to year except in the outbreak area where there was a dramatic increase in radial growth of surviving trees from 1979 onwards – probably due to release of nutrients by defoliation and/or reduction of between tree competition. For this reason results of foliage analysis for location N1 are taken to represent conditions in the oubreak area since tree growth was similar to that area prior to infestation and had been consistent since. Foliar nutrients present in November at N1 are compared with those at locations N3 and S1 which were unaffected by *P. flammea* (Table 3).

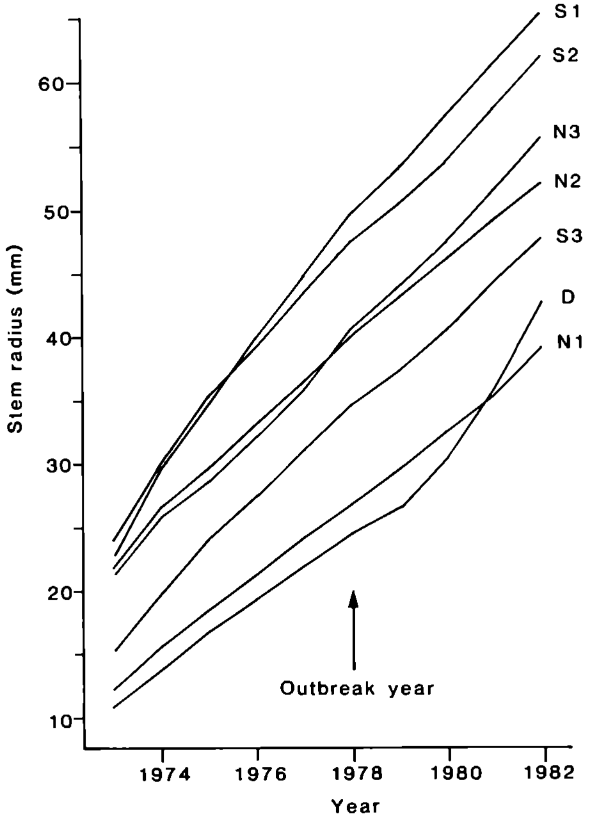

Figure 1. Growth of Lodgepole pine (P66) at seven sites at Annabaglish Moss, 1973-1982.

Table 2. Mean stem radius and annual radial increment of trees at Annabaglish, 1974-1978

	Sample location						
	N3	N2	N1	D	S3	S2	S1
Mean stem radius 1978 (mm)	40.5 (3.1)	40.3 (3.3)	26.8 (2.6)	24.5 (3.0)	34.7 (3.6)	47.4 (3.8)	49.6 (4.5)
Annual radial increment 1978 (mm yr^{-1})	4.6 (0.8)	3.5 (0.5)	2.6 (0.5)	2.5 (0.5)	3.6 (0.4)	4.0 (0.5)	4.8 (0.7)
Mean annual radial increment 1974-78 (mm yr^{-1})	3.8 (0.2)	3.7 (0.2)	2.9 (0.2)	2.7 (0.2)	3.9 (0.3)	4.7 (0.3)	5.3 (0.3)
Mean annual radial increment 1974-78 (% of maximum)	71.7 (3.8)	69.8 (3.8)	54.7 (3.8)	50.9 (3.8)	73.6 (5.7)	88.7 (5.7)	100.0 (5.7)

Figures in parentheses are ± 95% confidence limits. Data for 1978 are mean of n = 15 for undefoliated trees (defoliated n = 25); for 1974-1978 n = 75 for undefoliated trees (defoliated n = 125).

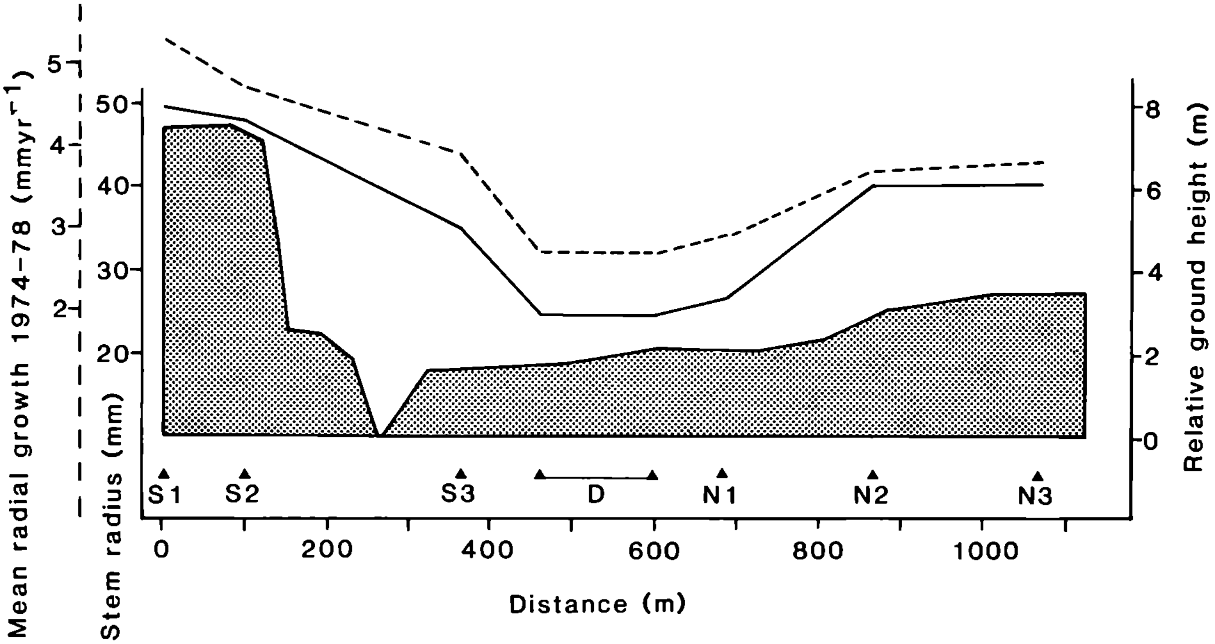

Figure 2. Growth of Lodgepole pine at Annabaglish Moss in selected years, showing the relative positions of the seven sample sites.

Table 3. Foliar nutrient levels at Annabaglish, November 1982

	Sample location		
	N3	N1, 'Defoliated'	S1
Needle content (μg/mg dry weight)			
N	10.39	9.58	10.77
P	1.05	1.12	0.97
K	5.23	4.59	5.00
N:P ratio	9.90	8.55	11.10
Needle content (μg/cm^2)			
N	0.308	0.297	0.327
P	0.031	0.035	0.030
K	0.155	0.143	0.152
N:P ratio	9.94	8.49	10.90

Needle dry weights and areas were not significantly different (Students t-test, $p > 0.05$), $n = 15$.

Tree growth, nutrients and topography

The site-related nature of the Annabaglish outbreak is apparent from Figure 3. Stem radius at breast height was found to be strongly correlated with relative ground height: for growth up to the 1978 outbreak $r = 0.87$, $p < 0.01$, and for growth up to 1982 $r = 0.99$, $p < 0.001$.

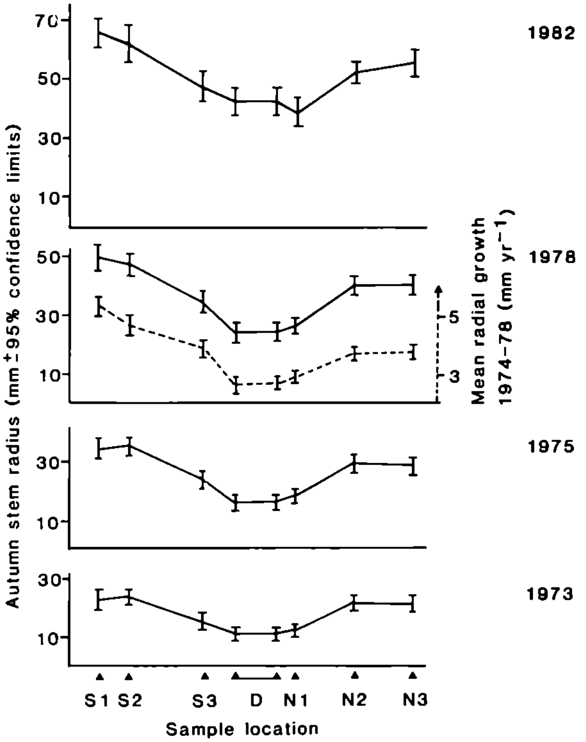

Figure 3. Site of Annabaglish Moss outbreak of *Panolis flammea* (1978) showing stem radius (—) and annual radial increment (----) of trees at that time.

Similarly mean annual radial increment prior to 1978 was closely correlated with relative ground height, $r = 0.88$, $p<0.001$. In the present context relative ground height is to be taken as a measure of the degree of waterlogging of the site rather than having any evident intrinsic significance. Tree growth also corresponded with November 1982 foliar nutrient concentrations. The radii of the trees (measured at breast height) in 1982 and 1978, correlated with the nitrogen:phosphorus ratio in the foliage: $r = 0.80$, $p<0.05$ and $r = 0.77$, $p<0.05$, respectively. Mean annual growth of the trees over the period 1974-78 was similarly correlated with N:P ratio: $r = 0.85$, $p<0.05$ (excluding data from the defoliated site where conditions have changed greatly since the outbreak in 1978). Needle nitrogen levels were also in good agreement with mean annual radial increment 1979-82: $r = 0.89$, $p<0.01$, and with tree growth in the previous year (1982): $r = 0.87$, $p<0.05$.

Foliar nutrient levels at the north and south sample sites are correlated with the relative ground height in two important respects: N:P ratio, $r = 0.87$, $p<0.01$ and %N, $r = 0.65$, $p<0.05$.

Tree growth on sites N1-3 and S1-3 has been generally consistent from 1973 to 1983 (Figure 1). It is probable, then, that the relationships of foliar nutrients and of tree growth present in the 1978 outbreak or just prior to it were similar to those found at the sample locations in 1982-83.

Needle biomass and surface area

Needle dry weights and areas were not significantly different between the sample locations whose foliar nutrient levels were compared (N1, N3 and S1); Students' t-test, $p<0.05$, $n = 15$.

II. Elchies

Foliar analysis

The nutrient concentrations found in needles and young shoots over a full year are shown in Figures 4 and 5. On the first two dates of sampling, 25 May and 6 June, shoot nitrogen concentrations were significantly higher for trees on deep peat than on the surface water gley and ironpan soils (Students' t-test, $p<0.05$). Also on these dates shoot P and K were in higher concentrations from deep peat trees, though the differences were not statistically significant. Nutrients were thus not only present in greater concentrations in shoots than in needles, especially during May and early June when shoots comprise the larval food, but also in greater concentrations in those trees on deep peat as compared with those on surface water gley or ironpan soils (see also Table 4). On the other hand nitrogen:phosphorus ratios were at all times lower in both shoots and needles on the deep peat site than on ironpan or surface water gley. Needles on trees on deep peat sites were smaller than on other soil types (Figure 6).

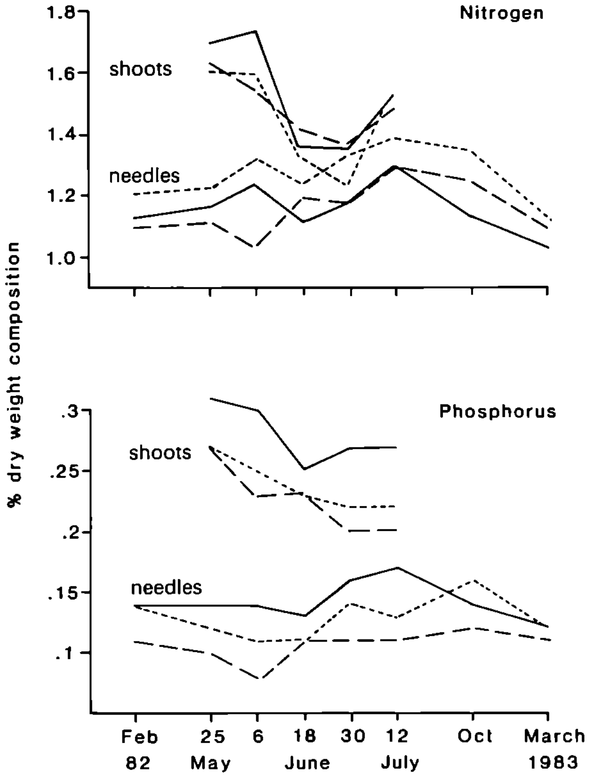

Figure 4. Site variation of foliar nitrogen and phosphorus at Elchies 1982-1983 (— deep peat, ... mineral ironpan, - - - surface water gley).

Table 4. Factors by which shoot nutrient concentration was greater than needle concentration over all site types at Elchies

	Date 25 May	6 June	18 June	30 June	12 July
Nutrient N	1.4	1.4	1.2	1.1	1.1
P	2.3	2.4	2.0	1.6	1.6
K	2.1	1.4	1.4	1.3	1.8
Approximate larval instar	I	II	III	IV	V
Larval food type	←---- shoots----→			←-----needles-----→	

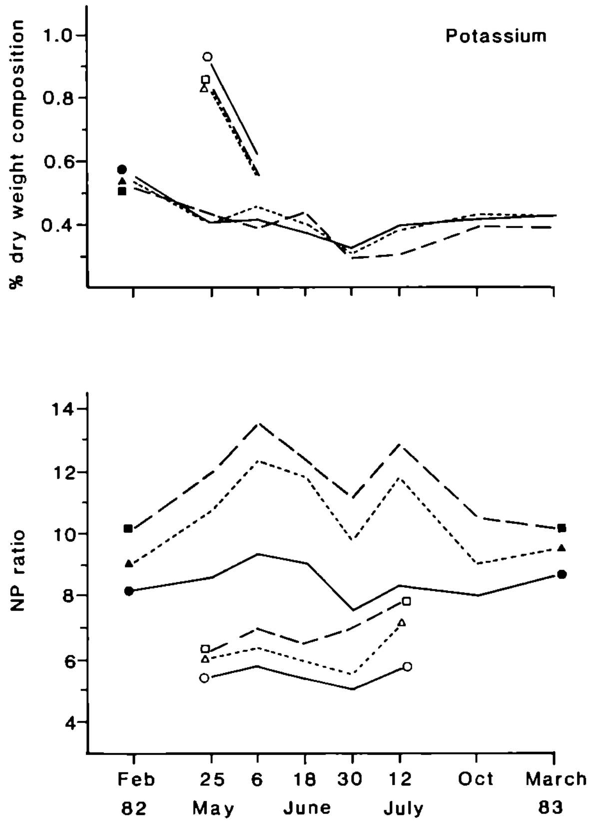

Figure 5. Site variation of foliar potassium and of nitrogen:phosphorus ratios at Elchies 1982-1983 (○ △ □ shoots, ● ▲ ■ needles; – deep peat, ... mineral ironpan, - - - surface water gley).

III. Glentress

Larval survival in relation to host nutrient status

Numbers of larvae surviving at third/fourth instar and in the fifth instar immediately prior to pupation, and the results of analysis of foliar N, P and K for each treatment are given in Table 1. Larval survival was greatest on those trees with lowest foliar N:P ratios. For all treatments the entire larval mortality occurred between establishment on new shoots and the third or fourth instar rather than in the later stages when feeding was on older needles. Unfortunately the data do not permit statistical analysis.

Discussion

In the period 1976 to 1984 there have been seven outbreaks of Pine beauty moth in upland forests in Scotland, in which severe defoliation leading to death of trees has occurred prior to any insecticidal treatment of the area. In each case the boundaries between such severe defoliation and crops suffering comparatively

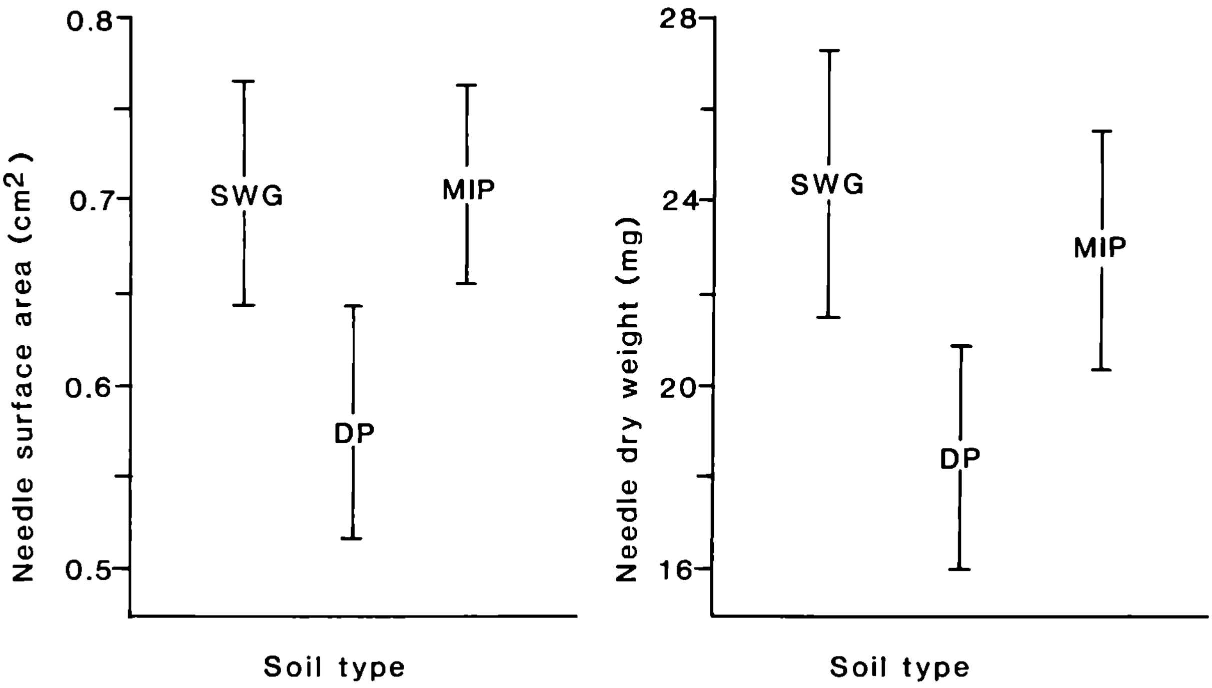

Figure 6. Comparison of needle surface area and dry weight from Lodgepole pines growing on surface water gley (SWG), deep peat (DP) and mineral ironpan (MIP) soils at Elchies. (Mean ± 95% confidence limits, n = 20 for each soil type).

unimportant damage have characteristically been well defined. In all instances except one it was observed that severe defoliation coincided more or less precisely with the extent of deep unflushed peat of the most infertile type. In some cases infestation seemingly spilt over from deep peat on to apparently more hospitable shallow peat; in others the boundaries were remarkably coincident (Stoakley, personal communication). In the remaining instance defoliation was shown to correspond well with shallow unflushed peat and to be largely absent from more fertile soil types in the forest block (Gordon, 1979).

The above observations have given rise to a number of hypotheses about the causes of Pine beauty moth outbreaks in Britain:

a. Unflushed peat may favour survival of overwintering pupae.
b. Parasites and predators may be relatively scarce in crops growing on the most infertile soils.
c. Females may select impoverished trees for oviposition.
d. Larval survival may be greater on such trees and possibly larval weights and consequently adult fecundity in the next generation may also be greater.

The investigations at Annabaglish confirm and document the observation that the outbreak there was associated with a raised bog of apparently low fertility by showing the previously poor growth of trees on the attacked area and linking this with their poor nutrient status, particularly low nitrogen levels and low nitrogen:phosphorus ratios, as determined in winter foliage samples.

Foliage analysis for different soil types at Elchies shows that during the earlier part of the larval stage when they are feeding on young shoots, such shoots from trees on deep peat have significantly higher concentrations of nitrogen than the other two soil types studied – surface water gley and ironpan. On the other hand it was found that nitrogen:phosphorus ratios were at all times lower in both shoots and needles from the deep peat site compared with the other two. This agrees with the essentially low nitrogen status of trees on the least productive ground at Annabaglish. There is thus an apparent paradox – that the most impoverished trees nevertheless have the highest levels of nitrogen at the site of larval feeding. However this characteristic of stress in trees and its association with infestations has been described by many authors (e.g. White, 1974, 1984). In relation to this the results of the investigation at Glentress showing highest larval survival on trees with the lowest N:P ratios in foliage is interesting. Clearly it would be valuable to repeat this experiment with adequate replication to allow statistical analysis and analysis of shoots at the time of feeding. A positive result would then indicate for Pine beauty moth a direct influence of poor nutrient status on population dynamics. This of course would not preclude the possibility that other factors are also of importance.

Acknowledgements

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Pine Beauty Moth Outbreaks:

The Influence of Host Species, Plant Phenology, Soil Type, Plant Stress and Natural Enemies

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Introduction

Between 1976 and 1978 Pine beauty moth *(Panolis flammea)* outbreaks affected almost 10 per cent of the Lodgepole pine crop in Scotland (Stoakley, 1983). In 1984 two serious outbreaks occurred and there were firm indications from population assessments in 1984 that further outbreaks would occur in 1985. Moreover it appeared that serious outbreaks were always on one type of site: Lodgepole pine growing on deep unflushed peat. This paper considers both the temporal and the spatial aspects of the population dynamics of the Pine beauty moth: why do outbreaks occur when and where they do?

Temporal Aspects of Pine Beauty Outbreaks

There are two alternative explanations for the outbreak behaviour of *P. flammea*.

1. Its population fluctuates in accordance with a cycle of about 8 years in length. This cycle may arise in two ways. (a) During the increase phase, population growth is unaffected by natural enemies and restricted only by the occasional occurrence of poor spring weather. Eventually the population is reduced by spraying with insecticide or host death occurs and the population is limited by lack of foliage. If the population is sprayed it may recover immediately or decline further (as in a true cycle) due to a time-lag in the effect of natural enemies or to a deterioration in host-plant quality. (b) It is possible that the effects of natural enemies or deteriorating host quality become felt during the population increase phase so that complete defoliation may be avoided in some cycles, as is the case for the Pine looper moth (Barbour, 1980).
2. The Pine beauty moth population may be held at low endemic levels by natural enemies or poor host plant quality or by their combined effect. Occasionally the population escapes these constraints and rises to epidemic levels.

In an epidemic model, population outbreaks may occur in three ways:

(a) through the action of weather conditions on plant quality,
(b) as a result of coincidence of plant and insect phenology, or
(c) as a result of weather conditions more suitable for *P. flammea* than its natural enemies.

These three hypotheses will now be assessed in turn.

Plant stress

The theory that plant stress is a cause of insect outbreaks has been developed in detail by White (1969, 1974, 1984). White postulated that plant condition is usually too poor to allow any significant rate of population growth. However, if plants are water stressed (by summer drought or winter waterlogging or both) their nitrogen levels rise; this provides better nutrition for insect herbivores which is manifest in better survival, fecundity and, therefore, in faster population growth. This theory has been used to explain the outbreaks of many different insects, including pine feeding Lepidoptera (White, 1974).

To test this hypothesis, a stress index (White, 1969) was calculated for the Elchies block of Speyside Forest, where pupal counts were available for the last 8 years (Barbour, personal communication). The calculation revealed that the index, which is a measure of drought in April-June and waterlogging during January-March, was not correlated with population growth (R = 0.02).

However if population growth was compared with late spring and early summer rainfall alone a larger correlation coefficient (R = 0.63) was obtained (Figure 1). That is, the less rainfall that occurred during April-June the greater was the population growth rate. However, the relationship was not significant at $p < 0.05$.

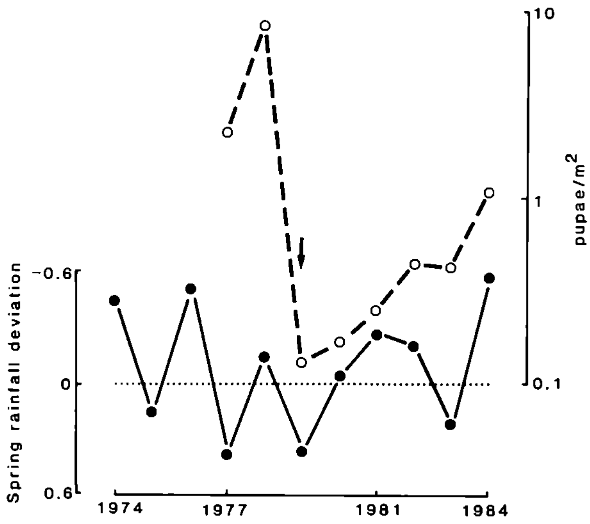

Figure 1. Pine beauty pupae numbers in the Elchies block of Speymouth Forest (– ○ –) and the proportional deviation in April-June rainfall at Glenlivet between 1974 and 1984 (– ● –): points above the dotted line indicate years where rainfall was less than the average of 125 mm. Population growth rate (N_t/N_{t-1}) and rainfall deviation were negatively but not significantly correlated (R = 0.63). (The arrow denotes an insecticide spray in 1979).

One explanation for the failure to achieve a simple correlation between water stress and population growth is that if the epidemic model for *P. flammea* is a valid description of its population dynamics the impact of stress will be at its greatest at low population densities. Once the population has been released from its endemic level stress may play only a minor part in determining overall population growth. If this is so, the drought of 1976 may have been significant in the Elchies outbreak of 1979 (by driving the population from the endemic to the epidemic region of population behaviour in 1976), and similarly the 1984 drought may prove to be the trigger for a second outbreak in Elchies in 1987 or 1988.

The evidence for the effect of water stress on temporal patterns of abundance of the Pine beauty moth is therefore, at present, completely circumstantial. In addition the stress hypothesis is more applicable to mature foliage-feeding insects than to flush feeders such as *P. flammea* (White, 1984).

Phenological coincidence

An alternative hypothesis which would explain epidemic behaviour is that of phenological coincidence. If egg hatch occurs when the host plant is at an unsuitable growth stage, population failure occurs; but if egg hatch coincides with the availability of the optimum stage of the host plant, rapid population growth is possible. This is an important factor in the population dynamics of a number of Lepidoptera including *Operophtera brumata* (Feeny, 1970) and *Tortrix viridana* (Schütte, 1957). If phenological coincidence has an influence on the population dynamics of *P. flammea* it is necessary to show that the survival of newly hatched larvae is influenced by the growth stage of Lodgepole pine and Scots pine. Laboratory experiments have shown that young *P. flammea* larvae were unable to survive on one-year-old needles but that their ability to survive on mature needles increased gradually as they grew older (Figure 2). The ability of young *P. flammea* larvae to survive on the current year's shoots was found to rise to a peak in May and decline thereafter.

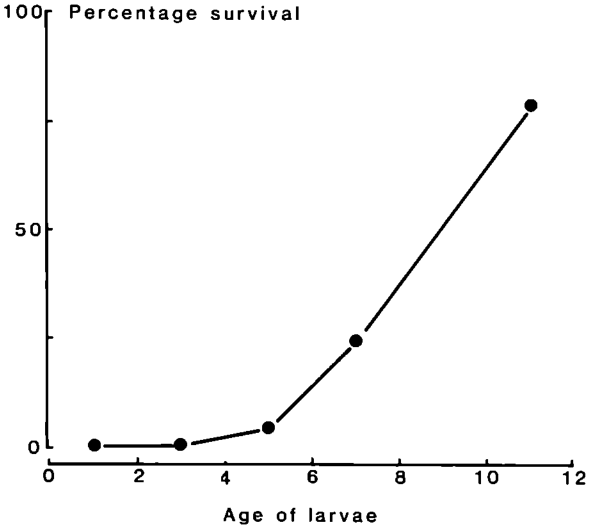

Figure 2. Survival of Pine beauty larvae of different ages on mature Scots pine needles (after feeding on young shoots).

Weather

A final possible explanation for the occurrence of Pine beauty moth outbreaks under the epidemic model is that natural enemies normally limit the survival and reproduction of *P. flammea*. The kind of weather which may allow *P. flammea* to escape from its natural enemies is warm weather during mating and oviposition (Leather, Watt and Barbour, 1985). This provides an alternative explanation for the observations in Figure 1. Another possibility is that warm weather during the summer months speeds development and thus reduces the time during which *P. flammea* is exposed to predation by birds and other natural enemies. This factor has been shown to be important for other Lepidoptera (e.g. Greenbank, 1956; Pollard, 1979). However, the available evidence indicates that weather is important in determining year-to-year variations in population growth but it does not act to 'release' *P. flammea* from endemic levels.

It may be concluded that *P. flammea* outbreaks on Lodgepole pine do not fit into the epidemic framework, although more work needs to be done, particularly in areas where outbreaks are infrequent or absent. At present it appears that population outbreaks in susceptible sites are inevitable; natural enemies, weather and phenological coincidence only influence the frequency of these outbreaks, and if these outbreaks are not controlled, *P. flammea* numbers are limited by depletion of their food resource. This is explored further in the paper by Watt and Leather, pp. 41-45.

Spatial Aspects of Population Behaviour

Although *P. flammea* poses a severe threat to Lodgepole pine, its outbreaks appear to be restricted (in their early stages at least) to areas of deep unflushed peat (Stoakley, 1979). In addition, Scots pine has never been threatened by this pest in Scotland. The reason for the association between *P. flammea* outbreaks and Lodgepole pine growing on deep peat may be a nutritional one. That is, trees growing on deep peat may be more susceptible to stress which causes an increase in the nitrogen level of their foliage, and hence increased suitability as a food source for *P. flammea*. Support for this view comes from the large number of examples of forest pests apparently associated with stressed host plants (Mattson and Addy, 1975; Rhoades, 1983). Moreover, detailed studies have found that there is an interaction between site condition (e.g. soils with poor drainage properties) and susceptibility to drought stress (White, 1974; Larsson and Tenow, 1984). However in the case of *P. flammea* the evidence for temporal patterns of stress-induced changes in population growth is equivocal (see above). Instead, retrospective surveys of outbreak sites have suggested that trees on deep peat always provide better conditions for *P. flammea* (see the paper by Barnett, pp. 14-20).

In 1983 and 1984, experiments were carried out in the Elchies block of Speyside Forest to examine the association between *P. flammea* outbreaks and Lodgepole pine growing on deep unflushed peat. The aim was to test the foliage quality hypothesis: to find out whether *P. flammea* survival differed between hosts growing on different soil types and also between Lodgepole pine and Scots pine.

Elchies was chosen because it is a typical *P. flammea* outbreak site. (An outbreak started to develop in the deep peat areas of the block in 1978 (see the paper by Barnett, pp. 14-20).) Two methods were used:

1. *Manipulative life-tables*
Because of the low density of *P. flammea* in Elchies in 1983 and 1984, plots of Lodgepole pine and Scots pine were infested with *P. flammea* eggs. Twenty-five trees per plot were used and approximately 1000 eggs, laid on short pieces of foliage, were placed in the upper crown of each tree. In 1983, one deep peat and one ironpan site were infested and a variety of sampling methods was employed. Egg numbers on the trees were counted weekly until egg hatch; larval densities were estimated by collecting head capsules in funnel traps and by removing branches for direct counts; pre-pupal and pupal numbers were assessed by water traps and ground quadrats respectively. In 1984, three plots in each Lodgepole pine category were used and three Scots pine sites were also infested. Less intensive sampling was carried out because the different methods used to assess larval numbers in 1983 had given consistent estimates of population change.

2. *Natural enemy exclusion cages*
In 1984, five Lodgepole pine trees on deep peat, five on ironpan soil and five Scots pine were each infested with *P. flammea* eggs in sleeve cages. Survival was assessed in late June (instar 2 to 4). The results obtained are summarised below.

P. flammea on Lodgepole pine

In 1983 the life-table analysis revealed no significant difference in survival between *P. flammea* populations on Lodgepole pine on different soil types (Figure 3). The 1984 experiment gave the same result (Figure 4). In both these experiments *P. flammea* survival was poor, particularly at two phases of the life cycle: during the egg and early larval instars, and during the pre-pupal stage. Therefore, no evidence was found for a difference between the nutritional suitability of Lodgepole pine growing on different soil types. The only important reservation to be made is that 1983 and 1984 may have been years during which water stress was insignificant,

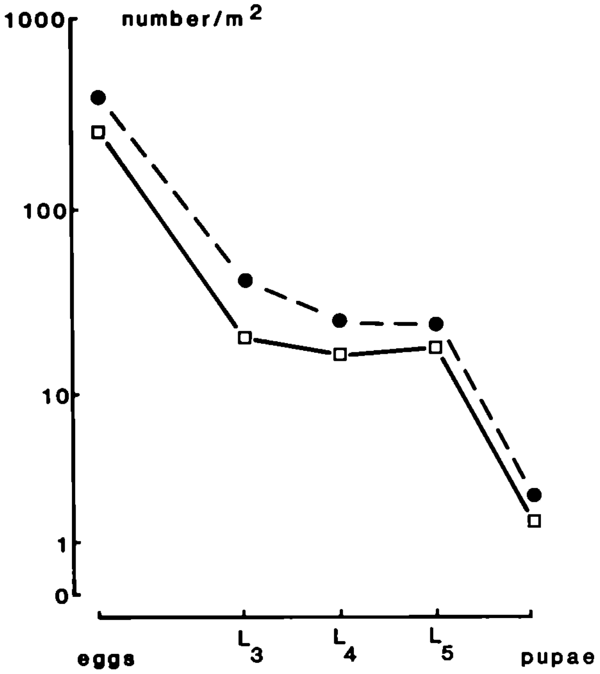

Figure 3. Survival of artificially introduced Pine beauty moth populations in Elchies during 1983 on trees growing in deep peat (– □ –) and in an ironpan soil (– ● –).

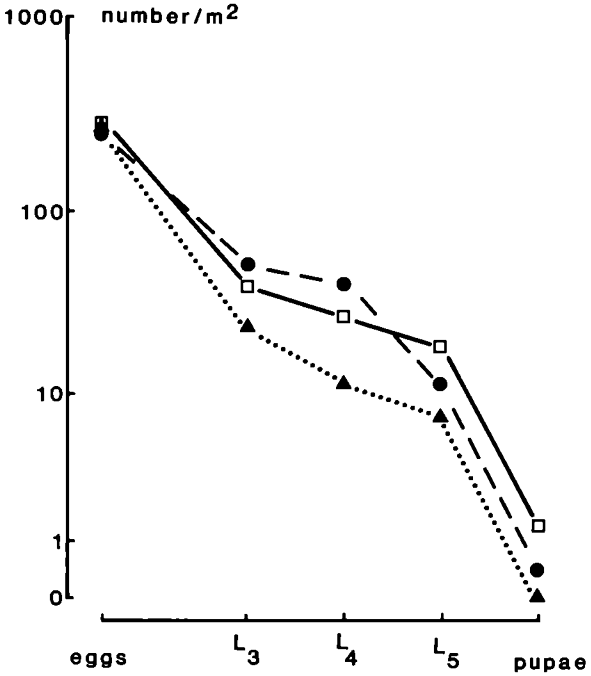

Figure 4. Survival of artificially introduced Pine beauty moth populations in Elchies during 1984 on Lodgepole pine growing in deep peat (– □ –) and in an ironpan soil (– ● –), and on Scots pine in a variety of soils (..▲..). Each line is the average of three populations.

but this is unlikely since the period April to June in 1984 was the driest for 22 years.

Another possible criticism of the life-table results is that natural enemies may have masked the effects of host plant condition. (The exceptionally poor survival of *P. flammea* at certain periods of the study was probably due in part to natural enemies, although the loss during the pre-pupal stage may have been caused by dispersal from the study sites.) However, the natural enemy exclusion experiment ruled out this possibility. *P. flammea* survival was considerably better inside natural enemy exclusion cages but, as with the exposed populations, there was no difference between soil types (Figure 5). The quality of Lodgepole pine, insofar as it affects the Pine beauty moth, does not differ between soil types.

In the absence of any evidence of long-term effects of host condition (which will be assessed in 1985) it has to be concluded that the development of *P. flammea*

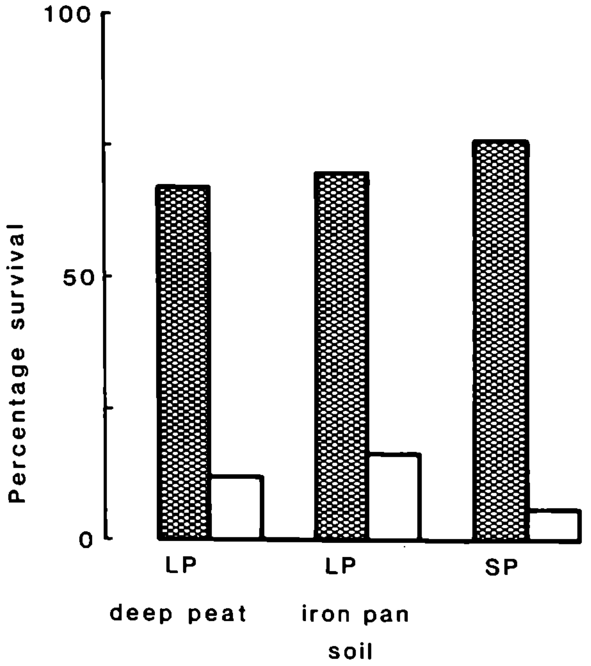

Figure 5. Survival of Pine beauty moth from egg to third instar inside natural enemy exclusion cages (shaded histograms). The survival of exposed cohorts in 1984 is shown for comparison (open histograms).

outbreaks on Lodgepole pine on deep peat (Stoakley, 1979; and see the paper by Barnett, pp. 14-20) is due to some factor other than the effect of host plant stress, through foliage quality, on *P. flammea* population development. This factor could be pupal survival which is known to be greater in peat than in soil (Leather, 1984), or it could relate to different pupal eclosion phenologies in different soil types (which would relate to phenological coincidence). It is also possible that Lodgepole pine is at risk on more soil types than was previously thought.

P. flammea on Scots pine

The life-table study in 1984 showed that *P. flammea* survival was poorer on Scots pine than on Lodgepole pine (although once *P. flammea* left the tree to pupate this difference disappeared) (Figure 4). However the survival of *P. flammea* inside the natural enemy exclusion cages was marginally (although not significantly) greater on Scots pine than on Lodgepole pine (Figure 5). In addition, larval growth and development were considerably better on Scots pine.

It appears that Scots pine is a better host than Lodgepole pine for *P. flammea* but that the survival of *P. flammea* populations is poorer on Scots pine. It may be concluded that natural enemies act to maintain *P. flammea* at low densities on Scots pine but further research is clearly required.

Acknowledgements

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Lodgepole Pine Provenance and the Pine Beauty Moth

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Introduction

Lodgepole pine (*Pinus contorta* Douglas) occurs as a number of different provenance (seed origin) types, all of which originate from North America (Lines, 1966, 1976). Each provenance, as well as being chemically distinct (Forrest, 1980a) also possesses characteristic growth forms and habitat requirements (Aldhous, 1976). South Coastal Lodgepole pine (SLP), for example, grows vigorously in British upland conditions, whereas Alaskan (ALP) and other North Coastal (NLP) provenance types are slower growing under the same conditions (Lines, 1976).

Although Lodgepole pine was first introduced into Britain as long ago as 1853, it was not widely planted until the late 1950s and early 1960s. It now makes up over 20 per cent of the total trees planted (Lines, 1976) and is thus of considerable economic importance in the United Kingdom, particularly in Scotland where the majority of the planting has taken place. There has, however, been a tendency to plant Lodgepole pine in areas of deep unflushed peat, where other conifer species cannot grow satisfactorily (Lines, 1976). It is in these areas that the Pine beauty moth (*Panolis flammea* D&S) flourishes (Stoakley, 1979; Leather, 1984).

Recent work suggests that certain provenances of Lodgepole pine may be more susceptible to insect attack than others (Bejer-Petersen and Esbjerg, 1972; Eidmann, 1982), coastal provenances being more susceptible. There is also evidence that *P. flammea* is attracted to certain Lodgepole provenances more than others and that high moth populations may develop in areas dominated by specific provenances (Leather, 1985; Leather, Watt and Barbour, 1985; Leather, unpublished). Certainly, the initial outbeaks of *P. flammea* in the 1970s (Stoakley, 1979) were associated with those provenances arising from the south coastal regions of British Columbia (Lines, 1980).

Egg Laying Behaviour in Relation to Lodgepole Pine Provenance

Laboratory experiments to investigate the influence of Lodgepole pine provenance on the egg laying behaviour of *P. flammea* showed that *P. flammea* responds differently to different provenances (Leather, 1985). Newly moulted, mated, adult female moths were liberated in cages (15 moths/cage) containing potted 2-year-old saplings of SLP, ALP, NLP and Skeena River (KLP) Lodgepole pine in an insectary during the month of April. The number of eggs laid by the moths on each plant was counted and the eggs were removed daily. Most eggs were laid on SLP and least on NLP. To see if the moths were responding to the provenance of the plant on a chemical or physical level, needle pairs of each of the four provenances of similar size and form were removed from the plants and placed upright in the bases of cages containing 15 female moths at either 20°C or 15°C under controlled long day conditions. At both temperatures, needles of SLP had the most eggs laid on them and needles of NLP and ALP the least.

In a further experiment, adult female *P. flammea* were given a choice of five Lodgepole pine provenances, ALP, KLP, SLP, Central Interior (CI) and Southern Interior (SI), and of Scots pine, *Pinus sylvestris* L. (SP). Potted, 2-year-old saplings in large cages were used as before but the foliage of each plant was intermingled to provide a less easily delineated choice between plants and the whole experiment was carried out at 20°C and under long day conditions. *P. flammea* females were still able to make consistent choices in egg laying sites, but SI was the most preferred provenance and CI and SP the second and third choices. ALP was the least preferred oviposition site.

Leather (1985) hypothesised that the female moths were responding to the chemical composition of the plants and suggested that the monoterpenes were the most probable candidates for attractant chemicals. Monoterpenes have been correlated with the severity of attack by other insects on Lodgepole pine, e.g. *Pissodes validirostris* (Annila and Hiltunen, 1977), and scale insects on *Tsuga* species (McClure and Hare, 1984). In addition, stressed *Pinus taeda* which are more susceptible to Southern pine beetle attack *(Dendroctonus frontalis)* than unstressed trees, show marked changes in their monoterpene content, especially in relation to α- and β-pinenes (Hodges and Lorio, 1975). Multiple regression analysis on the respective preference indices and the monoterpene composition of the test plants (monoterpene results were derived from Forrest, 1980a, 1980b) implied that this was indeed the case and that β-pinene was perhaps the most important single constituent. Leather, Watt and Barbour (1985) in a follow-up to this work showed that the relative preferences of the moths for different coniferous plants were strongly linked to the ratio of β-pinene to α-pinene within the plants.

It is likely that the chemical composition of a host plant as well as acting as an attractant for the herbivore also has an effect on the growth and development of that herbivore (Chew, 1977, 1979). Leather (1985) presented data on the growth and survival of *P. flammea* larvae on different Lodgepole pine provenances and on Scots pine. Large differences in mean relative growth rates (MRGR) and survival were attributable to the provenance and species of host that the larvae were reared on. By combining the two measures of larval performance it is possible to assign a value of tree suitability to each provenance/species used in that experiment. A plot of host preference (as defined by egg laying choice) and tree suitability (MRGR/mortality) demonstrates that the female moths are indeed laying their eggs on those hosts that are most suitable for their offspring's growth and survival (Figure 1). This ability to select host plants that are more suited to their offspring's growth and survival is a trait shared by other Lepidoptera (Wiklund, 1975; Myers, Monro and Murray, 1981; Holdren and Ehrlich, 1982; Williams, 1983). However, *P. flammea* appears to be able to distinguish much more closely between different qualities of closely related host plants than other Lepidoptera and this must represent a distinct evolutionary advantage.

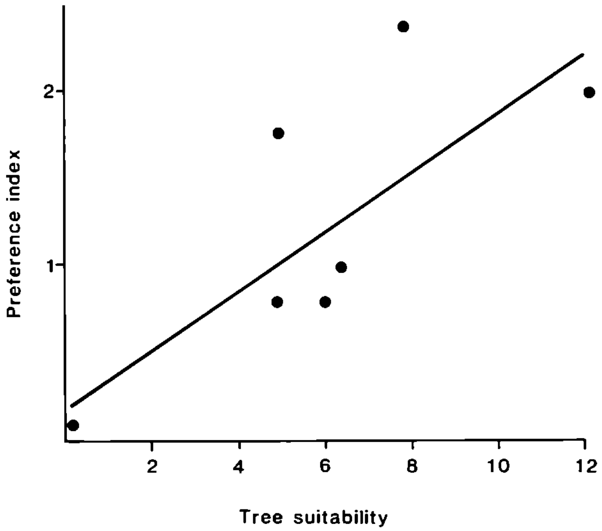

Figure 1. Relationship between egg laying preference index of *P. flammea* and suitability of the tree for growth and survival of their offspring ($y = 1.70x + 0.18$, $r = 0.75$, df = 5, $p < 0.02$).

Influence of Lodgepole Pine Provenance on the Fecundity and Lifespan of the Pine Beauty Moth

Lodgepole pine provenance also has a marked effect on the fecundity (total number of eggs laid) and lifespan of *P. flammea* (Leather, Watt and Barbour, 1985). When confined to a 'good' host, on which the larvae grow and develop well, e.g. SLP, female moths lay more eggs than when confined to a 'poor' host, e.g. ALP or Sitka spruce. At 15°C and under long day conditions daily rates of egg laying varied from approximately 12 eggs/female on KLP to approximately 4 eggs/female on Sitka spruce. Other Lodgepole pine provenances produced intermediate rates. The lifespan of the moths ranged from just over 14 days on KLP to 10 days on NLP. The pre-reproductive delay (the time between emergence and the laying of the first eggs) also varied significantly between hosts, being inversely proportional to host quality, for larvae i.e. shorter on better hosts than on worse hosts. The pre-reproductive delay on SLP was only 2.3 days whereas on Sitka spruce it was 5 days exactly. On NLP the pre-reproductive delay was 4.1 days. Both the fecundity and the pre-reproductive delay of *P. flammea* were strongly linked to the monoterpene composition of the host plant, with the β:α pinene ratio showing the strongest effect (Figures 2 and 3). Lifespan

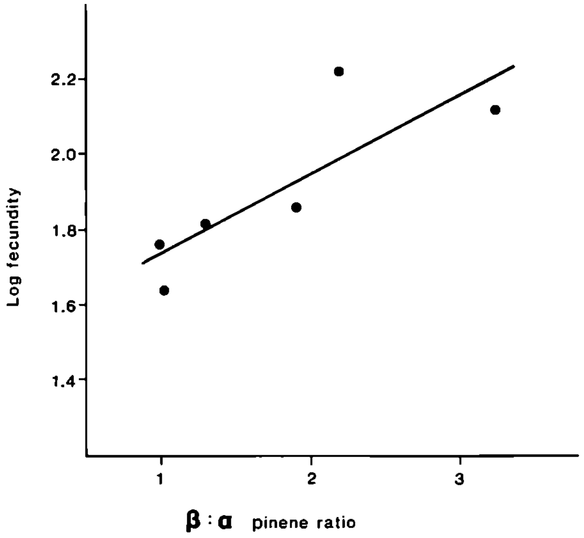

Figure 2. Relationship between the fecundity of *P. flammea* and the monoterpene composition of its host plants ($\log y = 0.21x + 1.53$, $r = 0.83$, $df = 4$, $p < 0.05$).

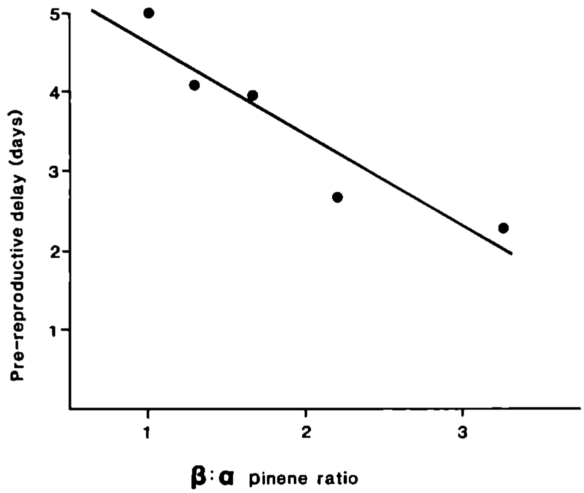

Figure 3. Relationship between the pre-reproductive delay of *P. flammea* and the monoterpene composition of its host plants ($y = -1.17x + 5.82$, $r = 0.93$, $df = 3$, $p < 0.02$).

of the moths was also linked to the monoterpene composition of the host plants but was more strongly correlated with the fecundity and pre-reproductive delay of the moth itself. In general, the more suitable the host for larval growth and survival, then, the shorter the period of time before the moth began to lay its eggs, the more eggs it laid, and the longer it lived. Thus the moths are responding to a set of subtle stimuli and their fecundity is consequently highest on the preferred hosts.

Pine Beauty Moth Abundance and Lodgepole Pine Provenance

All the preceding results and speculations are based on data obtained in the laboratory or semi-field conditions. How does the situation occurring in the field under non-controlled environmental conditions compare with these laboratory findings? Lines (1980) found that the initial phase of *P. flammea* outbreaks was associated with SLP, a provenance found to be of high suitability in the laboratory. The results of a pupal survey carried out in Craigellachie Forest (north Scotland) during the 1978-79 outbreak found that the highest *comparable* pupal numbers were associated with those compartments containing Central Interior (CI) and Southern Interior (SI) provenances (Leather and Barbour, 1988). Both these provenance types were highly preferred in the laboratory investigations. There is thus a *real* and demonstrable relationship between Lodgepole pine provenance and Pine beauty moth preference in both the laboratory and field.

An important question arising from these results is what effect, if any, does Lodgepole pine provenance have on Pine beauty moth population dynamics and can it be used in pest management strategies? Leather, Watt and Barbour (1985) presented a simulation model which examined the interactions between Lodgepole pine provenance and delayed mating at the time of egg laying. They also showed the importance of temperature at that time of the year. They concluded that by the use of provenances of varying susceptibility to *P. flammea,* differences in the number of eggs laid could be as much as threefold between KLP and NLP under similar conditions. Another model encompassing the whole life cycle of the moth has shown that two populations of the same initial size on KLP and NLP will result in an outbreak in the former stand and a static population in the latter stand (see paper by Watt and Leather, pp. 41-45).

However, these models, although showing very promising and realistic results require further validation before any long term sweeping changes are made in silvicultural practice. The evidence suggests that the incidence of Pine beauty moth outbreaks could be reduced by the planting of more resistant Lodgepole pine provenances. It remains to be seen whether this prediction is borne out in practice and this is the purpose of future research.

Acknowledgements

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Larval Behaviour of the Pine Beauty Moth

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Introduction

Knowledge of *Panolis flammea* larval behaviour and distribution is of particular relevance to aerial spray control strategy, both in terms of encounter with spray droplets and, in the case of control using entomopathogenic viruses, the possibility of dissemination of secondarily generated virus inoculum. This paper summarises a recent research study which will be discussed in more detail in two forthcoming papers (Ballard, in preparation). All of the effects described here have been shown to be statistically significant.

Materials and Methods

Three Lodgepole pine plots at the North Dalchork block of the Shin Forest were chosen for the distribution studies. A 50 x 40 m plot was marked out in an area of high *P. flammea* population at Forestry Commission block 359 – 19-year-old closed canopy trees (4-5 m high) on drained peat. To the north, two 100 x 50 m sites were chosen at Forestry Commission blocks 373 and 376 – areas of lower *P. flammea* population density in open canopy 13-year-old Lodgepole pine (3-4 m high). Aerial spraying of nuclear polyhedrosis virus (NPV) in Actipron® took place at block 373, using helicopter-mounted Micron X-15 ultra low volume (ULV) applicators. The prevailing wind at the time of spraying, coupled with the plot separation, protected the untreated plots from contamination.

Larval populations were sampled by beating branches removed at random from designated heights in the forest canopy. Trees were picked at random, avoiding the two rows adjacent to the forest rides. Two branches were sampled from each of the designated height zones in each of the sampled trees. The effect of variation in larval numbers between trees was taken into account in the statistical design. Careful dissection of the branches before beating allowed larvae to be subsampled for their position on old or current year foliage. In each branch, the total *lengths* of new and old foliage were recorded ('foliage length' being the summation of branch, twig and twiglet lengths, excluding those areas of bare wood). This proved to be an effective and convenient unit for comparison. Trees were visually assessed for foliage vertical distribution; this was supported by a detailed foliage assessment of a felled tree.

For the detailed studies of behaviour, larvae were taken randomly from the forest population. Individual larvae were distinguished using fluorescent marker dusts. These were available in six colours visible by day, or by night using a portable ultraviolet lamp (Fiesta Fluorescent Colours, Swada, London, Ltd.).

Results and Discussion

Distribution of *P. flammea* within the forest canopy

P. flammea eggs and larvae were sampled for vertical distribution in both the 19 and 13-year-old plantations. The survey continued through the season from egg to fifth instar, scoring individuals as numbers per metre of foliage (see Materials and Methods), within four height zones (only two, upper and lower, in the 13-year-old plots).

Vertical distribution of larvae was related to the forest canopy structure. For the 5 m closed canopy plantation both egg and larval (all instars) density (No./m foliage) was markedly increased towards the canopy top (Instars I and II; Figure 1). In combination with these results, an assessment of foliage distribution within each of the sampled trees allowed an estimate of the larval population in each of the four height zones. For all five instars, the preference for the upper branches, combined with the greater foliage bulk in the upper zone, resulted in a massive proportion of the larvae occurring in the upper height zone (3.5-5.2 m). Seventy per cent of the first and second instars, at which control measures are aimed, occurred in this top height zone (Figure 2).

The four height zones correspond to degrees of shading, from unshaded branches with full shoot

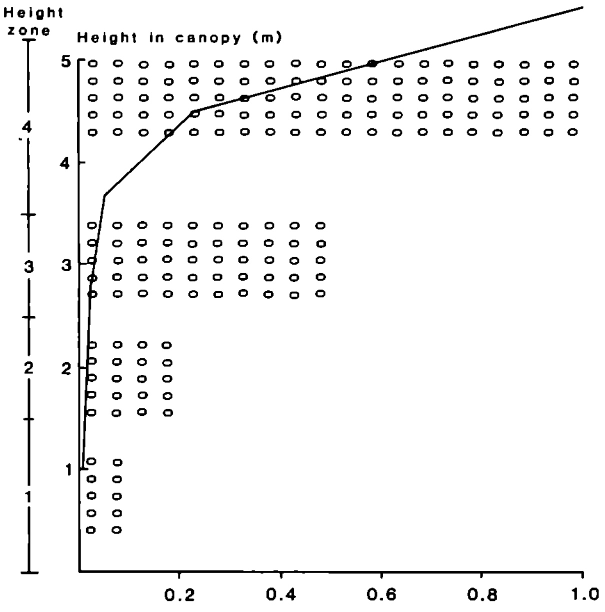

Figure 1. Larval density and ULV spray penetration in 5-5.5 m Lodgepole pine canopy (— relative spray dose capture at different heights in canopy (after Schaefer and Allsopp, 1983); ooo, relative larval density at four height zones).

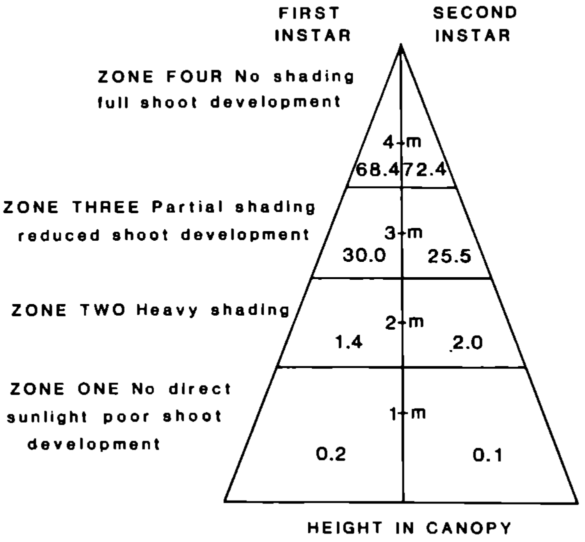

Figure 2. Vertical distribution of *P. flammea* larvae in 5-5.5 m closed canopy Lodgepole pines. (Figures refer to the percentage of the total larvae occurring in each of four height zones.)

development in the top zone, to almost complete shading in the bottom zone where shoot development was very poor. By contrast, in the younger 3-4 m open canopy plots, shading of the lower branches was much less, and shoot development was consequently greater. In this canopy the distribution of larvae, of all instars, was more uniform, with little difference between larval densities recorded at 1.5 and 3.0 m height branches.

In both canopy types the distribution of larvae was largely determined by the proportion of current year foliage in each branch and this alone accounted for most of the observed statistical variation. Thus larval distribution within the canopy is correlated with the distribution of current year foliage. In the open-crowned trees, larval distribution is therefore more uniform, corresponding to the more uniform occurrence of current year foliage. The first three instars feed mainly on current year foliage thus explaining this described correlation.

The additional variable of height in the canopy, after allowing in the statistical design for the effect of current year foliage distribution, explains some of the remaining variation. Its effect is much less important than the distribution of new foliage, and may be attributed to a possible oviposition preference for upper branches influencing to some extent the subsequent larval distribution, coupled with the possible poorer quality of shoots on lower branches.

Feeding behaviour of *P. flammea* larvae

Despite the correlation of larvae with new foliage distribution, the survey revealed that for both open and closed canopies larvae of all instars were considerably more common on the old foliage of any particular branch (Table 1).

Using fluorescent marker dusts, which were shown to have no effect on development of fifth instar observed behaviour, the behaviour of a number of individuals from each instar was studied over 24 hours on 1.5 m tall

Table 1. The time spent and distribution of *P. flammea* larvae on old Lodgepole pine foliage

	Larval instar				
	I	II	III	IV	V
Field distribution on old foliage (%)	89	84	75	87	96
Time spent on old foliage (%)	82	72	79	51	47

Lodgepole pine trees. Activity and position of each larva was scored at 15 or 20 minute intervals (consistent within each trial). From these results 24-hour time budgets were constructed for each instar. The overall time spent on different foliage types (Table 1) compares well with the observed distribution at the forest canopy for instars I, II and III. First and second instars spent 82 and 72 per cent respectively, of their time on old foliage and this did not change significantly with time of day.

Laboratory experiments produced no evidence of first and second instars feeding on old foliage. How does the apparent paradox between the distribution preference for old foliage and the feeding preference for new foliage in young *P. flammea* larvae relate to their behaviour? By studying their activity throughout the day, first and second instars were seen to make excursions from old to new foliage and back again. These excursions were variable in length, lasting from 15 minutes to 6 hours, and averaging 2.5 hours. The combined figures suggest that first instar larvae make approximately 2, and second instars 2.5, excursions every 24 hours, although a continuous survey lasting several days would be required to determine how this varies from day to day between individual larvae. Excursions occurred throughout the day but at different times for different larvae.

Larvae were not static, although the proportion of time spent walking was low. First and second instar larvae were too small to observe actual chewing in the field but excursions to shoots were presumed to mark feeding. By remaining on old foliage whilst not feeding, the larvae may derive protection against desiccation and predation; this may be enhanced by a lack of feeding synchrony between larvae. Young larvae are certainly less apparent to the human eye whilst on old foliage.

Actual chewing was monitored in third, fourth and fifth instar larvae. For these, and for first and second instars if we assume 'excursions' to indicate feeding, the amount of time spent feeding was only a small proportion of the total. Third instar excursions to new foliage were also observed, lasting from 20 minutes to 8 hours (mean = 2 hours). Third instar larvae were observed feeding on old foliage but showed a marked preference for new needles. Fourth and fifth instar larvae showed no significant preference for foliage type throughout the day. Fifth instar larvae tended to remain on the same sprig for most of the day, apparently not requiring a change of foliage type. Fourth and fifth instar larvae spent 12 and 15 per cent, respectively, of their total time chewing, at the tip or sides of new or old needles. Feeding bouts were short (less than one hour), and of the remaining time, larvae were commonly stretched out along a needle (old or new) with their heads down against the brown base of the needle pairs and their stripes parallel to the needle. This camouflaged position may confer protection as in the younger instars. After resting in this position, feeding usually required their turning around completely.

Fifth instar larvae were observed feeding at all times of the day and night. Night feeding was not observed in fourth instar larvae. However, owing to experimental problems, the fourth instar results were based on only seven larvae.

Spinning down off the branches was not observed in any of the 2250 observations (all instars) and generally occurs only after disturbance, but may be overridden by population density. In all instars activity varied significantly between individuals; perhaps depending on the previous day's feeding. Individuals were comparatively inactive for many hours prior to and after moulting.

The preference for old foliage seen in fourth and fifth instar larvae was not reflected in the study of time spent on foliage in these instars, there being no observed preference (Table 1). This was probably due to differences in the trees on which the observations were made. In the high *P. flammea* density closed canopy Lodgepole plot used in the distribution study, new foliage was largely defoliated by the time of the late instars, thus providing only a small food resource. By contrast the young undamaged trees used in the time budget experiments maintained full shoot development, offering a choice of old and new foliage.

Larval redistribution

Local movement to new foliage is observed in young *P. flammea* larvae, but is there movement over longer distances? The progress of larvae marked with fluorescent dye was followed from a known starting point on an accurately mapped tree. This enabled calculation of the minimum distance that each larva must have travelled by the first recording, and the minimum number changing their position on subsequent days. Figure 3 summarises this information for each instar.

The proportion of larvae in each instar moving daily to new positions did not differ significantly from day to day, negating the possibility of crowding influencing redistribution. Many larvae moved considerable distances, and some first instar larvae, only 6 mm in length, moved as far as 80 cm in the first 8.5 hours, moving *up, down* and *across* the tree. Third instar larvae were most active in this respect and were fully distributed throughout the 1.5 m tree after only 3 days. In several instances traces of fluorescent dust marked the path of redistributing individuals.

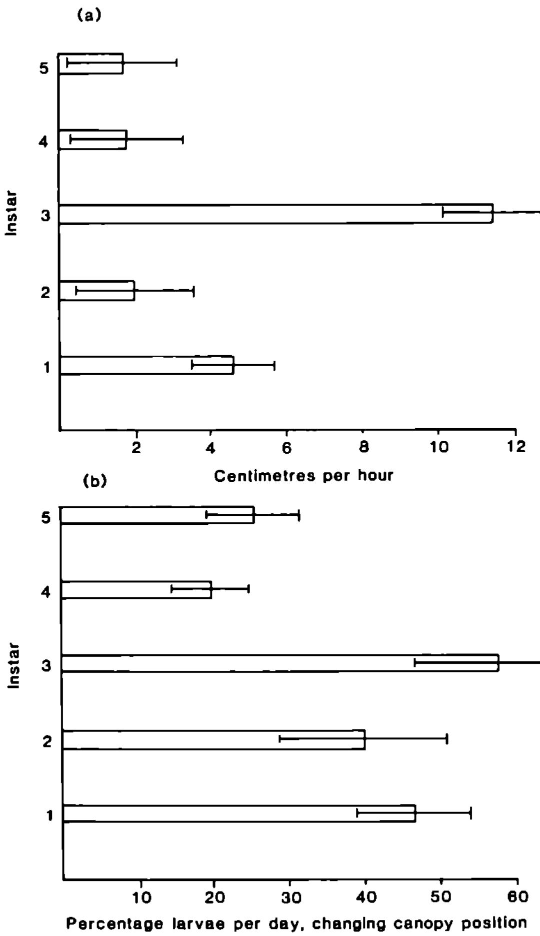

Figure 3. Net distance travelled per larva per hour (a) and percentage of sample population changing position in the canopy each day (b), in 1.5 m Lodgepole pines over the entire larval life.

Fourth and fifth instar larvae moved the least, and positional changes were mainly local, typically as sprigs became defoliated. Since these larvae are able to eat old and new foliage, there is less need for them to move further afield to find a suitable nutritional substrate.

In order to assess the importance of larval redistribution to control strategy, a similar experiment monitored the redistribution of marked second and third instar larvae, from two starting heights on a 5.3 m closed canopy Lodgepole pine. Larval positions were monitored after 57 hours. Redistribution of larvae was considerable. Of the 20 second and third instar larvae recovered after introduction at a one metre high branch, five had climbed to the apical branch of the 5.3 m tree. One second instar and three third instar larvae had moved to an adjacent tree, and two of these were found well into the neighbouring tree canopy. Third instar larvae are liable to ascend greater distances, and the tendency to climb is greatest in larvae introduced lower in the tree. Shortage of edible foliage in the lower branches seems the most likely cause. Ascent from an open starting position, high in the canopy at 3.5 m, was insignificant, the incentive to climb presumably being less in an area of good shoot availability.

Food finding

Although young *P. flammea* larvae spend more time on old foliage, one of the first priorities of a newly hatched first instar would be to locate suitable food: new shoots and male flowers (Escherich, 1931). Simple choice chamber tests revealed an attraction towards light but an indifference to gravity. Preference for food material over non-food material (old needles) was demonstrated by allowing larvae to walk over a moistened filter paper 'arena' impregnated with a standard mass of food or non-food. These preference tests (based on over 2500 recordings of 184 larvae) demonstrated that favourable substrates decrease larval movement and, by walking away from non-food substrates, a larva would increase its chance of finding and remaining in an area of adequate resources. Shoots are more likely to occur in illuminated areas but these are not necessarily in the upper branches, so the larval indifference to gravity is, perhaps, not surprising.

Implications for control strategies

In the 1978 and 1979 aerial spray programme in Scotland, the dose of fenitrothion (an organophosphorus insecticide) was calculated to hit each larva with at least one droplet; this view was later modified on noting spray cloud induced movement (Joyce *et al.*, 1981). Even without this induced movement we have seen that young *P. flammea* larvae do make short 'excursions' to new foliage as well as more widespread redistribution, presumably to locate fresh feeding areas. A reduced insecticide dose can be calculated if the foliage is designated as the spray target, and larval movement is considered to enhance contact with spray droplets.

Using fluorescent particles to label spray droplets in an ultra low volume spray operation, Schaefer and Allsopp (1983) demonstrated a rapid attenuation of droplet capture with depth in the canopy. Droplets were captured on 3 mm diameter cylinders and figures have been converted to give the relative dose captured per unit cylinder length at various heights in the canopy, thus comparable to the current data on larval distribution (Figure 1).

The attenuation of spray droplets towards the lower canopy is more rapid than the tail-off in larval numbers. Redistribution of larvae from lower branches, as demonstrated, could mean that many larvae would escape control and subsequently defoliate the upper canopy. This was indeed suggested as a possible explanation for the defoliation of some of the sprayed trees in the fenitrothion trials (Joyce *et al.,* 1981; Schaefer and Allsopp, 1983). However if the control agent had a degree of persistence, larval redistribution would aid contact despite poor coverage.

Before the use of fenitrothion against *P. flammea* outbreaks, the stomach acting biocontrol agent *Bacillus thuringiensis* (B.t.) was under trial. A lack of success was attributed to the larvae "feeding on internal tissues" of young needles, thus failing to contract an adequate dose (Stoakley, 1979a,b). Schaefer and Allsopp (1983) considered the importance of the larvae "feeding at the base of young needles creating a very difficult target reached only by good small droplet coverage." Might the use of nuclear polyhedrosis virus (NPV), also stomach acting, be subject to these same drawbacks?

A detailed laboratory analysis of feeding behaviour revealed that larvae would not be hidden from spray droplets whilst on young buds; furthermore, most of the time is spent on old needles. First and second instar larvae were found to make *several* circular or oval 'chew-holes' in the young needles within the duration of the instar, increasing the likelihood of contracting a lethal dose. Holes were more common in the middle and top thirds of the young needle. Table 2 summarises the findings.

First instar larvae made only slightly more holes on the outward facing needle surface (directly exposed to the spray cloud) than on the inward face, whereas the larger size of the second instars probably accounted for the sparsity of inward facing holes. First instar larvae were able to feed equally on both closed (needles still covered by their brown sheath) and open (young needles protruding) buds which reduces the need for hatching to be synchronised with 'bud-burst'. (First instar larvae can survive starvation for only 2.9 days, SE = 1.6.). The figures for the surface area consumed are important for the calculation of the required spray dose of aerially applied NPV or B.t.

Feeding in third, fourth and fifth instar larvae is no longer by chewing holes in the sides of the young needles, but by a more general devouring, from the side or tip of new or old needles.

There is no preferred time of day for feeding in the first and second instar larvae (the instars most suitable for control), thus the behavioural studies indicate no ideal time of day for application of NPV. Spraying late in the afternoon or evening might prolong the effectiveness of the NPV which decreases with exposure to solar ultra violet radiation (though on a fairly extended time course) (see the paper by Killick, pp. 69-75).

Table 2. Feeding activity of *P. flammea* larvae

First instars:	Mean number of holes/larva = 4.75 Mean total area/larva = 1.18 mm^2
Second instars:	Mean number of holes/larva = 6.5 Mean total area/larva = 4.54 mm^2

The secondary dissemination of NPV has not yet been thoroughly studied. However a third distribution study at one of the virus treated Lodgepole pine plantations revealed that virus infection, determined histologically, did not affect the spatial pattern of larval distribution on trees. By contrast larval distribution is modified by virus infection in other defoliator species; e.g. NPV infected larvae of the Nun moth, *Lymantria monacha,* are known to climb to the tree tops prior to death (Wahl, 1909; Zethner, 1976).

Acknowledgements

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Genetic Variation Between Populations of *Panolis flammea*

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Introduction

The accidental introduction of exotic insect pests is generally considered to be the most serious potential threat to productive forests in Great Britain. This is not surprising because our forest estate includes a substantial proportion of exotic conifers (Carter, 1983) which may be attacked by a wide range of insects in their native habitat. The recent introduction of *Dendroctonus micans* from Europe (Bevan and King, 1983) is a good example of the concern and expense that such introductions can generate. However we must also assume that our own indigenous forest insects may be able to exploit this large resource of non-native trees. Indeed, there have been some recent examples of considerable damage to exotic forest trees by native insects, some of which are given in Table 1.

The adoption of new host plants or new habitats by insects is likely to be affected by a number of behavioural and ecological factors, some of which are discussed in the present proceedings in relation to *Panolis flammea*. In this paper we report on a preliminary study to assess the extent of variation between populations of *P. flammea* in an attempt to determine whether those attacking Lodgepole pine are distinct from those endemic on the native Scots pine. This was done by examining isoenzymes which in certain cases can be assumed to be the products of different alleles. Screening individual moths for particular isoenzymes from different populations allows comparison of gene frequencies for the populations sampled (e.g. Fincham, 1983). Although only limited data are available and the provisional nature of the analysis is emphasised, we feel that the results offer some additional insights into the ecology of *Panolis flammea* in Britain.

Table 1. Examples of forest insects native to Britain attacking exotic host trees

	Indigenous host	Exotic host
Pine beauty moth *Panolis flammea*	Scots pine	Lodgepole pine
Winter moth *Operophtera brumata*	Oak, apple and other broadleaves	Sitka spruce
Vapourer moth *Orgyia antiqua*	Polyphagous on broadleaves	Sitka spruce, Lodgepole pine

Methods and Materials

Populations were sampled at six sites, detailed descriptions of which are given in Table 2. The location of each site is shown in Figure 1. The two Lodgepole pine sites suffered severe infestations of *P. flammea* in 1979 and 30-50 per cent of each area was sprayed with fenitrothion. During this study, however, *P. flammea* was at an endemic level at all sites and collecting males by attraction to pheromone traps was the only practical method of obtaining a sufficiently large sample of live adult insects. Six to eight funnel-type pheromone traps baited with a mixture of 5 mg of Z−9− and 0.5 mg of Z−11−tetradecenylacetate were deployed at each site and live males removed every few days during April and early May 1984. They were stored at approximately −18°C for up to 14 weeks before analysis. At the Lodgepole pine sites, the pheromone traps were deployed in the previously sprayed areas. It was assumed that dispersal of moths between the sprayed and unsprayed areas in the intervening 5 years would have

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Table 2. Description of pheromone trapping sites for *Panolis flammea*

	Forest site	O.S. map reference	Description
Scotland	Amat	NH 466 896	Relict natural Caledonian pine forest. Fairly open woodland with birch interspersed. Age? 150+ years.
	Roseisle	NJ 120 669	Plantation of predominantly Scots pine, some Corsican pine in general area. Planted 1931-36.
	Dalchork	NC 549 201	Plantation of predominantly Lodgepole pine, some Scots pine, Sitka spruce, larch and other species also present. Planted 1960-72.
	Elchies	NJ 199 462	Plantation of predominantly Lodgepole pine. Some Scots pine present, remote from traps. Planted 1961.
England	Bramshill	SU 800 580	Predominantly Scots pine with some Corsican. Isolated plots of Lodgepole pine, remote from traps. Mixed age: planted 1925-63.
	Tilford	SU 872 422	Predominantly Scots pine with a little Corsican. Mixed age, but mostly planted 1950s and 1960s. Much natural regeneration.

minimised any effect of spraying on gene frequencies in the populations.

Starch gel electrophoresis using a continuous buffer system was used to separate isoenzymes. Details of gel preparation, operating conditions and recipes for stains are based on those outlined by Shaw and Prasad (1970). Preliminary studies on 18 enzymes have shown that eight are polymorphic but in most of these further work is required to optimise separation and resolution of bands. However, one locus determining production of malate dehydrogenase (M.D.) has been studied in some detail for all the populations sampled and these results are presented here.

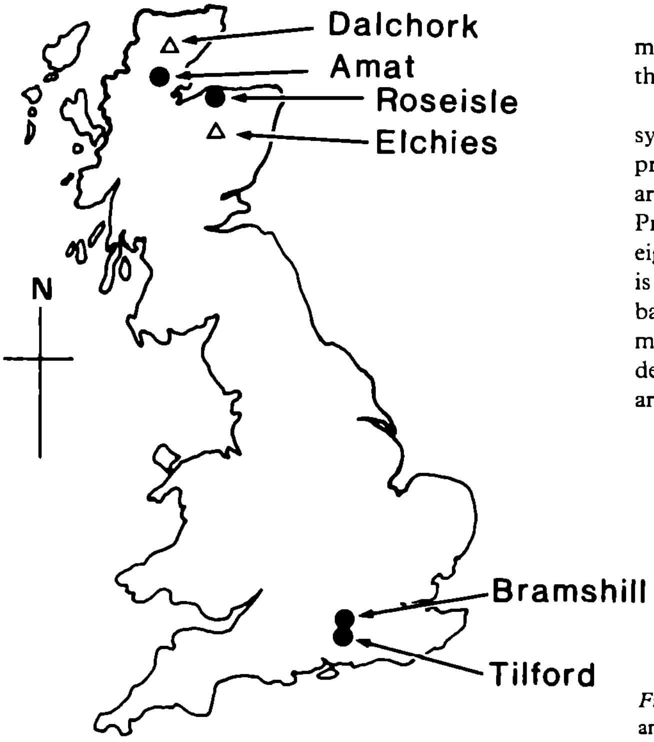

Figure 1. Location of pheromone trapping sites in England and Scotland in 1984. ● Scots pine, △ Lodgepole pine.

Results

A group of bands, apparently controlled by a single locus, was identified at the cathodal end of the gel, an example of which is shown in Figure 2. The isoenzymes consisted of densely staining single 'slow' or 'fast' bands or a more lightly stained group of three bands consisting of slow and fast bands separated by a hybrid band of exactly intermediate mobility. This pattern is typical of that produced by a dimeric enzyme, i.e. one with the protein molecule composed of two polypeptide chains, such as found in M.D. The homozygotes for either the slow or fast allele have enzymes composed of identical sub units. The heterozygote with both alleles present produces some hybrid dimers of intermediate electrophoretic mobility (Fincham, 1983; Moss, 1979). On the basis of random association, twice as much of the hybrid dimer is formed as the pure dimer and this is sometimes seen on the gels as a slightly darker staining of the intermediate band, reflecting its greater concentration.

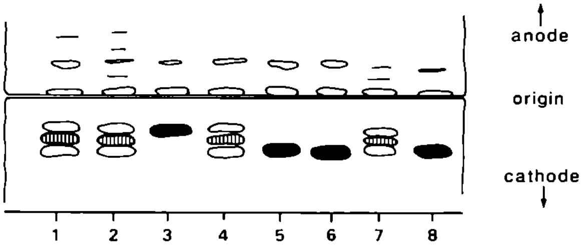

Figure 2. Cathodal bands of isoenzymes of malate dehydrogenase. Positions 1-8 are individual insects from Elchies showing homozygotes for slow (3) and fast (5, 6, 8) alleles and heterozygotes (1, 2, 4, 7).

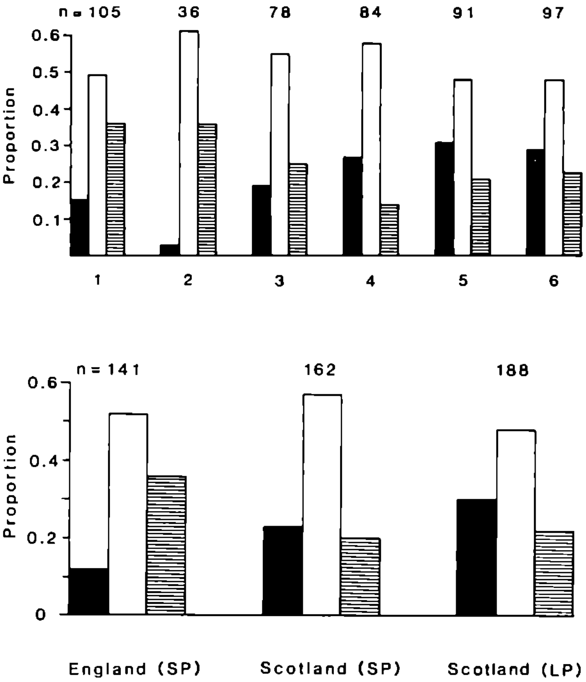

Figure 3.

a) The proportion of homozygous (slow ■, fast ▤) and heterozygous (☐) individuals in populations from the six sample sites: 1 Bramshill (SP), 2 Tilford (SP), 3 Amat (SP), 4 Roseisle (SP), 5 Elchies (LP), 6 Dalchork (LP). SP = Scots pine, LP = Lodgepole pine, n = number of individuals in sample.

b) Data from 1 and 2 were pooled for England (SP), 3 and 4 pooled for Scotland (SP), and 5 and 6 pooled for Scotland (LP).

The proportions of slow (S) and fast (F) and three banded heterozygote (H) bands for the six sites are shown in Figure 3a. The frequency of the homozygotes and heterozygotes in each population was tested for conformation to the Hardy-Weinberg equilibrium. Only moths from Tilford showed significant departure from the expected proportions ($\chi^2 = 5.07$; $p<0.05$), possibly due to the small sample (n = 36) taken at this site. Differences in numbers of the three genotypes trapped were tested by χ^2 analysis for each site and by pooling data from different sites. The only significant differences ($\chi^2 = 19.08$; $p<0.001$) were those found between the English and Scottish populations, pooling data from the two English and four Scottish sites respectively. In Figure 3b data were combined for the pairs of sites representing Scots pine in England and Scotland and Lodgepole pine in Scotland. The differences in proportion of genotypes between the Scots pine and Lodgepole pine sites in Scotland were not significant, but together with data from the English sites appear to form a trend of increasing proportion of the slow allele from Scots pine in England to Lodgepole pine in Scotland.

Discussion

The data provide evidence for distinct 'southern' and 'northern' populations of *P. flammea*. Clearly, more sites need to be examined to confirm this and to determine whether there are two distinct populations with a zone of inter-breeding or a cline of gradually changing proportions of alleles.

With such limited data available, it is only possible to speculate on the possibility of differentiated populations of the moth on Lodgepole pine. However, results suggest that a search for differences in ecology or behaviour between populations from the two host plants might prove fruitful. It may be that the geographical difference observed between populations in the present study has in some way pre-adapted the northern populations to attack Lodgepole pine in Scotland. We feel that such intra-specific variation may play an important role in determining pest staus and should not be neglected in considering the threats to our forest trees.

Acknowledgements

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Pine Beauty Moth Population Dynamics:
Synthesis, Simulation and Prediction

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Synthesis

Outbreaks of the Pine beauty moth *Panolis flammea* typically develop, in their early stages at least, on deep unflushed peat (Stoakley, 1983). The reason for this is unclear. It has been suggested that the nutritional quality of Lodgepole pine for *P. flammea* larvae is better in trees growing on poor soils in a manner similar to that supposed for the host plants of a number of other pests (White, 1984). Support for this comes from the association between peat depth, topography, poor tree growth, and *P. flammea* incidence (Stoakley, 1979; and see the paper by Barnett, pp. 14-20). In addition, the lower N:P ratio in the foliage of trees growing in deep peat suggests that they are nutritionally better for *P. flammea* larvae (see the paper by Barnett, pp. 14-20; also, Leather, unpublished; Watt, unpublished). However the only available evidence of the actual performance of *P. flammea* on trees growing in different soils shows that their survival, growth and development are as good on trees growing in an ironpan soil as they are on trees growing in deep peat (see the paper by Watt, pp. 21-26). Therefore, the occurrence of outbreaks on trees growing in deep unflushed peat is probably due to some other factor. There is evidence that pupal survival is better in peat than in soil (Leather, 1984). Additionally, it may be that adult *P. flammea* actively select poorly growing trees in a similar manner to the way they select different provenances of Lodgepole pine in the laboratory (Leather, 1985).

The selection by adult *P. flammea* of different provenances of Lodgepole pine is paralleled by differences in the growth rate and survival of *P. flammea* larvae on different provenances: the adult moths lay more eggs on those provenances on which their offspring perform best (Leather, 1985). This egg-laying behaviour is particularly significant because it occurs even when the adults are only offered plants of a single provenance on which to lay their eggs (Leather, Watt and Barbour, 1985). It is therefore not surprising that *P. flammea* numbers appear to be particularly high on certain provenances of Lodgepole pine in the field. So, although considerable field testing is required, there is merit in evaluating the potential use of less preferred and less nutritious (for *P. flammea* larvae) provenances as a silvicultural control strategy against *P. flammea.*

The situation for Scots pine is somewhat different; it is a better host than Lodgepole pine for larval survival, growth and development (Watt, 1986). Thus it is surprising that only very low, rather constant population densities typically occur in stands of Scots pine in this country (see the paper by Barbour, pp. 7-13). This, together with the high survival of *P. flammea* inside natural enemy enclosure cages (see the paper by Watt, pp. 21-26) indicates that natural enemies keep *P. flammea* at low endemic levels on Scots pine (Figure 1, curve b). However, if there is an invasion by large numbers of *P. flammea* from infested stands of Lodgepole pine nearby, natural enemies will be swamped and severe defoliation is likely, as seen in the Rimsdale outbreak in 1977.

The population dynamics of *P. flammea* on Lodgepole pine has received intensive study in a small number of deep peat sites since 1981 (see the paper by Barbour, pp. 7-13). At these sites there were no significant density-related restrictions to population growth and life table analysis revealed that the key factors (i.e. the factors which explained most variation in population size) were the number of eggs produced by adult moths in the spring and mortality of older larvae and pre-pupae. The general lack of restraints on *P. flammea* growth has been confirmed by other studies at the Elchies block of Speyside Forest (see the paper by Watt, pp. 21-26; also Leather, unpublished). The population dynamics of *P. flammea* on Lodgepole pine growing on deep peat may therefore be considered to take the form

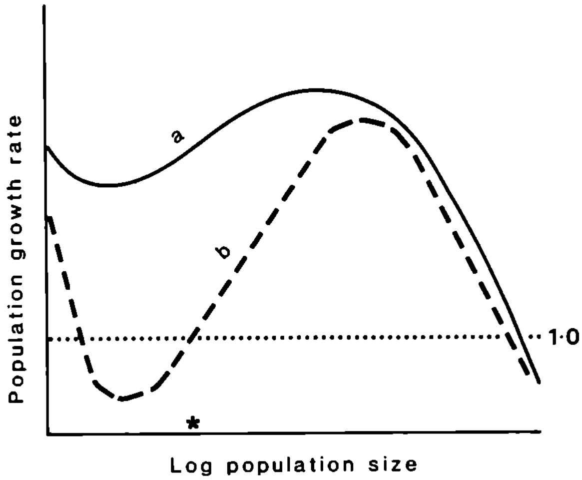

Figure 1. The relationship between population growth and population size of *P. flammea:* (a) on Lodgepole pine growing in susceptible sites (population growth is restricted only by intraspecific competition during severe defoliation) and (b) on Lodgepole pine growing in non-susceptible sites and on Scots pine (population growth is restricted by natural enemies at low *P. flammea* densities, but if immigration from susceptible sites raises population size above the release point (*) an outbreak will occur).

shown in Figure 1 (curve a). Its dynamics on better soils probably take the form shown in Figure 1 (curve b): some factor, or factors, keep it at an endemic level but trees on heavily colonised sites would be (like Scots pine) still susceptible to attack.

Simulation

Recent findings in the study of *P. flammea* population dynamics have been used to create a population simulation model. This model was built to gain a better understanding of the dynamics and pest status of *P. flammea*, to predict its future population development under existing and alternative management strategies, and to identify critical areas for future research. The model considers three stages of the moth life cycle:

1. autumn pupae to adult moths
2. adult moth egg production
3. eggs to autumn pupae.

Winter mortality is assumed to be 40 per cent in accordance with findings in field populations (Huggins, 1979; Leather, 1984; and see the paper by Barbour, pp. 7-13). The level of egg production varies according to host provenance, spring temperature, adult mortality and the timing of mating. Estimates were obtained from Leather, Watt and Barbour (1985). Larval and pre-pupal mortality depend on provenance, natural enemies and other factors. Values were taken from Leather (1985) and Barbour (pp. 7-13).

The model allowed various options to be considered. In particular it permitted the examination of the use of different provenances, control by mating disruption and the impact of different weather conditions.

Under average conditions of spring weather on a susceptible provenance of Lodgepole pine *P. flammea* outbreaks can be expected to occur every 7 years (Figure 2). (This outcome required two further assumptions: first, that control measures would be carried out when autumn pupae exceeded 15 m^{-2} and second, that control measures would be as effective as those described in Holden and Bevan (1981).)

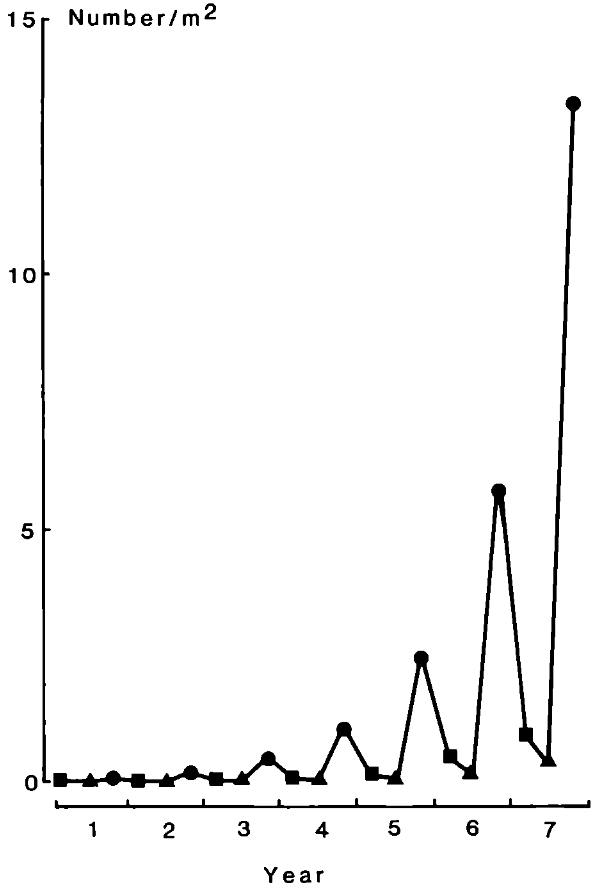

Figure 2. Population development of *P. flammea* under average weather conditions in northern Scotland as generated by a population model: pupae (■), adults (▲), eggs (●).

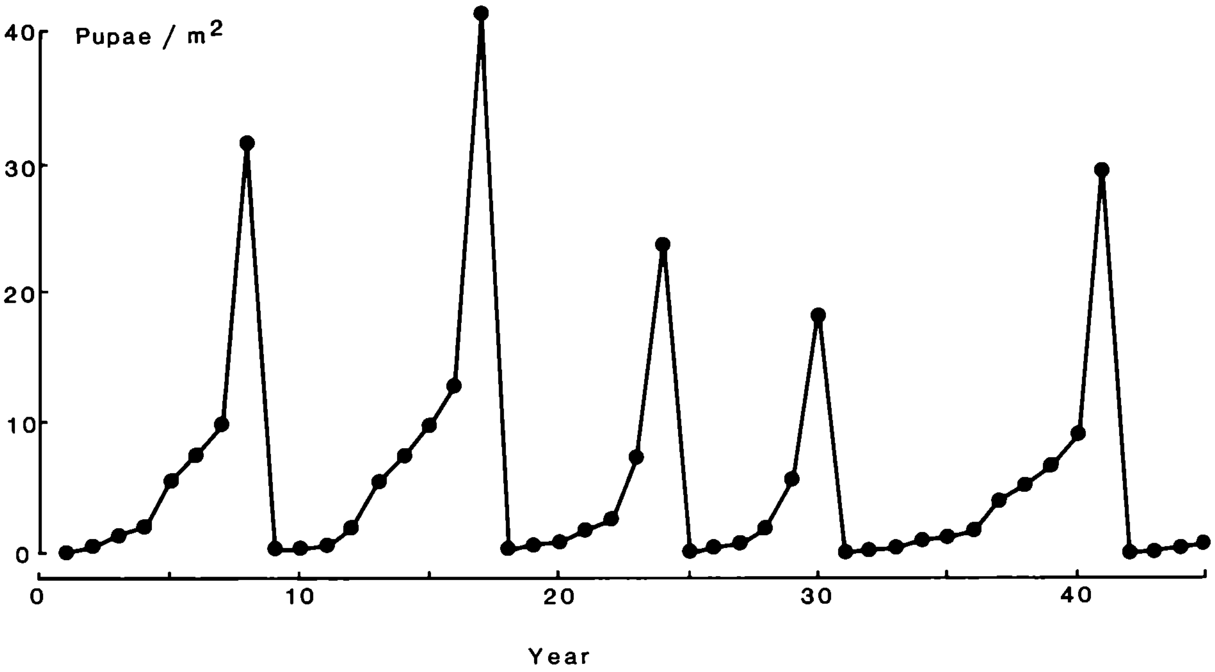

Figure 3. Population development of *P. flammea* during 45 years of variable weather conditions (based on the recent frequency of different weather conditions in northern Scotland, see text). When the population exceeded 15 pupae m^{-2} it was assumed that control measures would be carried out.

A more realistic simulation of *P. flammea* can be carried out by considering the effects of varying frequencies of good (e.g. 1981, 1984) and bad (e.g. 1982, 1983) spring weather (rather than assuming that average conditions exist each year, as in Figure 2). If there were an equal frequency of good and bad spring weather an outbreak could be expected, on average, every 9 years. However, the model showed that it is possible for outbreaks to develop in as few as 6 years and as long as 14 or more years (but with an extremely low probability – see below) (Figure 3). This conforms well with experience to date in Scotland and has therefore encouraged the use of the model for predictive purposes.

Prediction and Control

The *P. flammea* simulation model emphasises the cyclic nature of *P. flammea* outbreaks in susceptible areas and provides a basis from which an estimate can be made of the extent of control measures required during the life of a Lodgepole pine crop. Also, it has the potential ability to accurately predict short-term population trends from actual spring temperatures.

A rather different use of the model is to examine the population consequences of different management strategies. In particular it enables the results of planting different Lodgepole pine provenances to be examined. Figure 4 shows the results produced by the model when run with the appropriate fecundity and larval survival figures for each of four provenances, together with the effect of weather on egg production. Outbreaks on KLP would occur on average every 5 to 7 years, and on SLP every 6 to 9 years. In contrast, neither ALP nor NLP appears to be at risk from Pine beauty moth. Full probability patterns for outbreaks on KLP and SLP based on the current variability of spring weather in northern Scotland are shown in Figure 5. This model obviously requires further validation before any definite recommendations can be made concerning sweeping changes in silvicultural practice. But there is enough evidence to suggest that Pine beauty moth outbreaks could be delayed – if not prevented – by the planting of less susceptible Lodgepole pine provenances, and that the planting of south coastal, southern interior and central interior provenances will exacerbate the problem. It is up to the forest manager to weigh up the silvicultural benefits of certain provenances against the risks of substantial *P. flammea* outbreaks and associated control measures on those provenances.

A final use of the model is to indicate how successful the introduction of new control techniques might be.

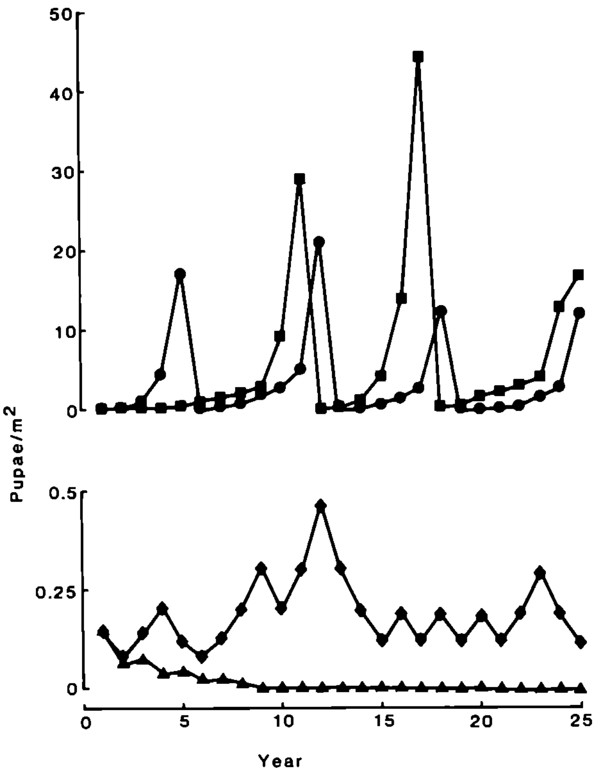

Figure 4. Population development of *P. flammea* on four Lodgepole pine provenances during 25 years of variable weather conditions (as Figure 3): KLP (●), SLP (■), NLP (◆), ALP (▲).

One possible control practice is pheromone disruption of mating. Leather, Watt and Barbour (1985) showed, in laboratory experiments, that if mating was disrupted so that a delay of 5 days occurred there was a 44 per cent reduction in the production of fertile eggs. This was not as great as the reduction in fecundity which sometimes occurs naturally in the field. It was concluded that, in practice, poor spring weather causes a reduction in egg production by increasing adult mortality as well as through a delay in mating. This conclusion was supported by the results of an adult egg production model. The influence of pheromone disruption can also be shown in the population simulation model. This was modelled with the assumptions that the disruption would cause a 5 day delay in mating in good springs, and that there would be an additional reduction in egg production equivalent to a 5 day delay in mating in poor springs. The model demonstrates that mating disruption might be an effective control measure on the more resistant provenances (Figure 6). However, a more thorough evaluation of pheromone disruption can be

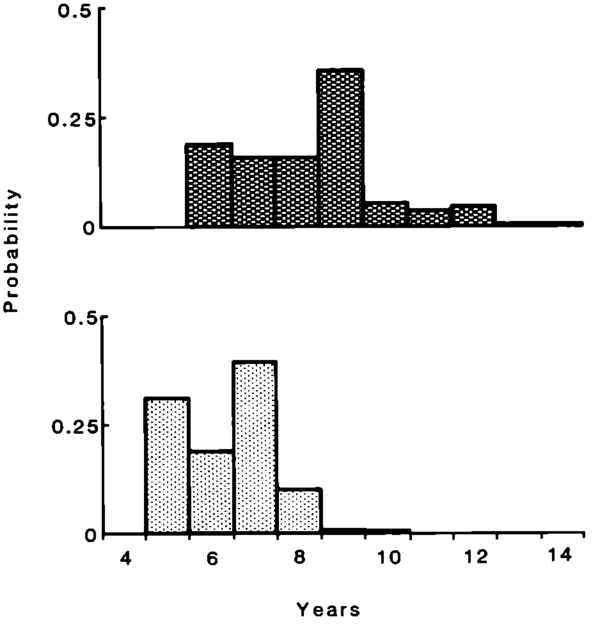

Figure 5. The probability of *P. flammea* outbreaks at different time intervals on SLP (▩) and KLP (▒) in northern Scotland assuming that current weather conditions continue. (On SLP there is an extremely small probability ($p<0.001$) of an outbreak taking 15 to 19 years to develop).

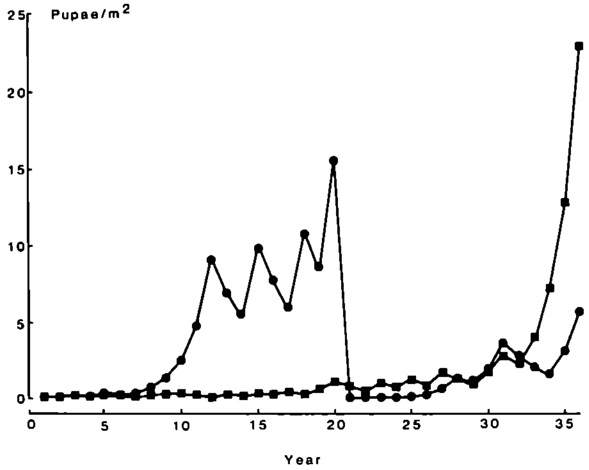

Figure 6. Population of *P. flammea* on KLP (●) and SLP (■) during a mating disruption programme which causes a 5-day delay in mating (and weather conditions as for Figures 3 and 4). The model predicted that outbreaks would still occur but that their frequency would be substantially reduced. For example, the probability of an outbreak developing on SLP in 10 years or less fell from 0.91 to 0.01.

made only from an accurate estimate of its effect on egg production in the field and an analysis based on the full costs and benefits.

It is planned that this simulation model will be developed further and will then form a basis from which management strategies against the Pine beauty moth can be proposed.

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The Use of Pheromone Traps in Monitoring Pine Beauty Moth Populations

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Introduction

Pheromone-baited traps are now widely used for monitoring populations of adult insects. Such traps can be used to show:

(i) the presence or absence of the pest species being monitored, or its spread;
(ii) population increases and decreases;
(iii) the optimal application times for pesticides;
(iv) the relationship between population and damage.

The above uses increase in complexity from (i) to (iv) both in terms of data interpretation and in the accuracy of predictions. In the case of the Pine beauty moth (*Panolis flammea*) a pheromone-based monitoring system was envisaged which would show not only population changes (ii) but also how those changes related to the damage produced by the subsequent larval generations (iv).

Background to Present Pheromone-based Monitoring System

Following the elucidation of the sex pheromone components of *P. flammea* by Priesner *et al.* (1978) and Baker *et al.* (1982) a potent attractant was made available for the establishment of a monitoring system for this species. Prior to this development, areas requiring control measures against this species could only be established by extensive pupal surveys followed by selective egg counts in some cases. Due to the obvious labour-saving advantages that a pheromone would bring, a pheromone-based trapping system was quickly developed. Bradshaw *et al.* (1983) recently described the experiments and results upon which the current system using delta sticky traps was based. In that study, relatively few trapping systems were investigated and all involved sticky materials as an entrapment mechanism. All such systems, however, suffer from problems of low trapping capacity; Bradshaw *et al.* (1983) showed that the capture efficiency in the delta trap eventually adopted decreased rapidly when 40 or more moths were caught. To try to overcome this problem, the amount of pheromone used to bait the trap was reduced so that in most areas with sub-outbreak population levels trap saturation would not be a problem.

The Pheromone-based Monitoring Systems Used 1981-1984

From 1981 to 1984 up to 1000 pairs of triangular shaped sticky traps were deployed in all the Lodgepole pine plantations of the United Kingdom thought to be at risk; about 40 000 ha in total. At each monitoring station, two triangular traps were placed 50 m apart, one baited with 25 μg and the other with 5 μg of Z−9−tetradecenyl-acetate (TDA), the major component, together with 10 per cent of the minor component Z−11−TDA, in each case. It was hoped that if the higher-dose trap became saturated, the low dose would then continue to catch, and if this caught high numbers too, then the possibility of an outbreak was thought to be high.

Mean trap catches rose steadily from 1981 to 1983, probably reflecting the cyclical nature of this pest, but in 1984 mean trap catches decreased even though outbreaks were recorded in some forests in the Highlands of Scotland. The hope that low dose traps would take over the catches from saturated high-dose traps was not fulfilled in any site in any year.

Factors which could have Affected the Performance of the Trapping System

All pheromone traps are made up of two basic elements:

1. a pheromone formulated in a controlled release device;
2. an entrapment mechanism.

In the case of *P. flammea* both of these elements could have produced inconsistent captures. As regards the pheromone components to be included in the lure an optimal ratio was not conclusively established, probably because of the type of controlled release devices and traps used in the early experiments. Natural rubber septa or polyethylene capsules were used extensively as controlled releasers for *P. flammea* pheromone in the UK and continental Europe. In essence, the pheromone is soaked into these releasing matrices, from where it then diffuses out according to first order kinetics where the rate of release from the lure is proportional to the amount remaining. An exponential decline in the amount remaining is therefore experienced with up to 70 per cent of the initial loading of pheromone released during the first 48 h. Ideally, a controlled release device is required which has a constant release rate throughout its period of use in the field, with a corresponding straight-line decline in the amount of pheromone remaining at the source, i.e. zero order kinetics. Such release rates are possible in membrane systems now being developed for controlled trans-dermal drug delivery. The main effect of a non-constant release rate of pheromone over the whole flight period of a pest being monitored is that it over-estimates the population initially and under-estimates the population towards the end of the flight period. This error is compounded further if the emergence pattern of the species is skewed towards the beginning or the end of the flight period; further complications can also arise if the skew pattern of emergence changes from year to year.

As regards the entrapment mechanism, in the case of *P. flammea* the delta trap plus its sticky base, errors can arise due to trap saturation; beyond a capture of 40 moths a true reflection of population levels using this system is not possible. Likewise, trap orientation will affect capture since it is not of an omni-directional design. Positional effects in the case of *P. flammea* standard monitoring traps should not, on the other hand, affect catch variability since they are located every year on the same stakes in the same locations. Work with other species has shown that the material from which the traps are constructed can also affect both the controlled release device and the responding insect. It has been seen, for instance, that a translucent plastic trap produces warmer conditions within its confines compared with an opaque one as a result of the 'greenhouse' effect produced as light passes through the translucent trap. These warmer conditions in turn accelerate the release of pheromone from the controlled release device.

A third factor which affects trap capture variability is the environmental conditions that prevail during the flight period of the insect. Wind speed and direction, temperature, relative humidity and sunshine can all affect the performance of a pheromone-based monitoring system by acting on the controlled release device, the plume of the pheromone produced by the trap, and/or the behaviour of the responding insect.

Many of the above factors have only come to light during the last few years from work with *P. flammea* and other species. It is clear that improvements need to be made to the present system for usable information to be gained from its use.

Development Work Required for an Improved Pheromone-based Monitoring System

Ratios of pheromone components

Because the trap design and controlled release devices were not optimal when ratios of pheromone components were first studied, it is advisable to look at this aspect again with new formulations and traps so that the ratio is optimised conclusively.

Controlled release device

Since novel controlled release devices are now becoming available for use with pheromones, comparative studies should be made to evaluate their potential as replacements for currently used devices.

Trap design and entrapment mechanism

Non-saturating trap designs should be evaluated which are omni-directional and optimised for material and colour. The need for a killing agent for retention of moths caught in the trap should also be investigated.

Environmental factors and insect behaviour

A long-term study is required into the effects of environmental factors on trap catch variability. Whereas the three factors mentioned above are fundamentally technical in nature, and therefore theoretically capable of being solved within a comparatively short period of time, a study of environmental and behavioural effects on trap catch variability has to be a long-term commitment. Many of the key factors which affect trapping performance can only be established from data collected over several years. Experience gained from similar studies with the Olive moth (*Prays oleae*) has shown, however, that once the environmental and behavioural parameters which influence trap catch have been established, then suitable correction factors can be developed for use with the trapping system to make it more reflective of the true population changes which it is designed to monitor (Ramos *et al.*, papers in preparation).

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Monitoring Pine Beauty Moth by Means of Pheromone Traps:

The Effect of Moth Dispersal

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Introduction

The Pine beauty moth *Panolis flammea* (D. & S.) has been a severe pest of Lodgepole pine *Pinus contorta* in upland areas of Scotland since 1976. Monitoring of populations has been carried out in the first instance by pupal surveys (counting the overwintering pupae in the soil in permanent 0.3 ha plots evenly distributed over the susceptible areas of plantation). More recently extensive monitoring has been attempted using pheromone-baited traps developed by the Chemical Entomology Unit of Southampton University (Stoakley, 1983).

Optimization trials have been carried out in relation to trap type, trap placing and dosage of the pheromone lure (Bradshaw, Baker, Longhurst *et al.*, 1983). More detailed studies have been made of the specific behavioural responses released by different components of the three-component pheromone system (Bradshaw, Baker and Lisk, 1983). However, a major practical problem which remains is that of relating catches of male moths in the pheromone traps to real population densities per unit area, so as to be able to use pheromone monitoring as a genuine early-warning system for the detection of outbreaks. This paper is an attempt to approach this problem of 'calibrating' pheromone traps with respect to true population density, using data collected at the Elchies block of Craigellachie Forest, during the 1979 flight season.

Materials and Methods

In autumn 1978 a routine pupal survey was carried out over the whole Elchies block (see Stoakley (1979) for method). This yielded counts of healthy pupae ranging from 0 to 49 per square metre (Figure 1). The highest counts were concentrated in a distinct epicentre in the west-central area of the block, around which numbers fell away rapidly particularly to the east.

In March 1979, 32 pheromone traps were set up at widely scattered points within the Elchies block, each of which was adjacent to a sampling area in which pupae had been counted. Traps were of Pherocon IC (Zoecon Corp.) design, baited with 100 µg (Z)−9−tetradecenyl acetate and 5 µg (Z)−11−tetradecenyl acetate loaded on to rubber stoppers. Each was suspended from a post at head height, in an open position in an internal ride of the plantation. Traps were visited at intervals of 3-5 days throughout the flight period, the trapped moths removed and trapping-surfaces 're-stickied' when necessary. Thus trap-filling was effectively prevented.

Results

Male moths were first caught in the traps during the period 9-12 April. Trap catches increased rapidly to a maximum in mid-April, then decreased in a period of colder weather (Figure 2). During a very cold period 30 April -3 May no moths were caught; thereafter there was a second peak of activity in the 5 days 8-13 May, and a final cessation of captures during 18-23 May.

The mean number of moths caught in a trap was 80, with a range from 4 to 260. The distribution of counts across the block is shown for the April catches in Figure 3 and for the May catches in Figure 4. In both cases there was again a distinct centre of high numbers corresponding very broadly to the original epicentre as defined by pupal counts. However the two periods

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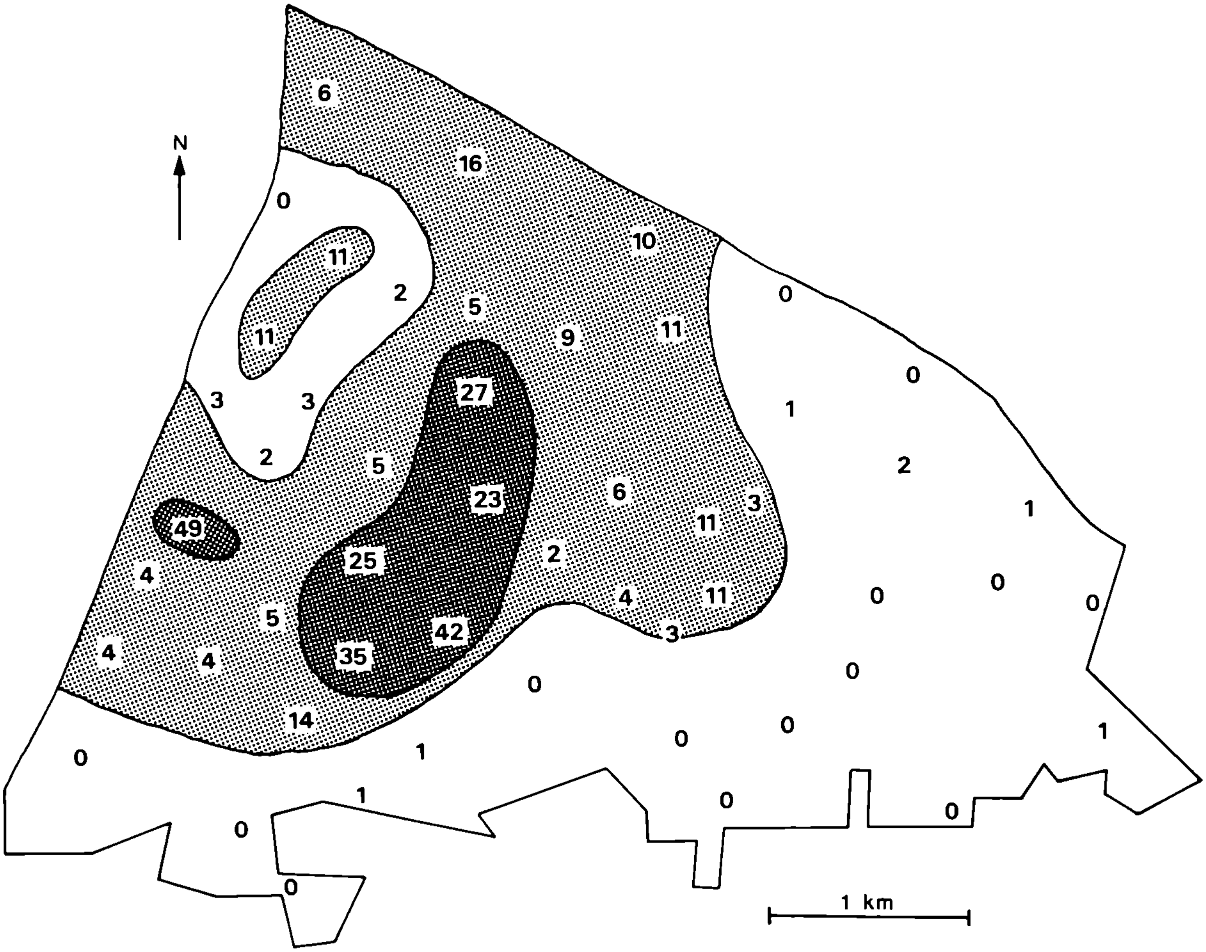

Figure 1. Counts of healthy pupae per m² in 53 sampling sites throughout the Elchies block, autumn 1978.

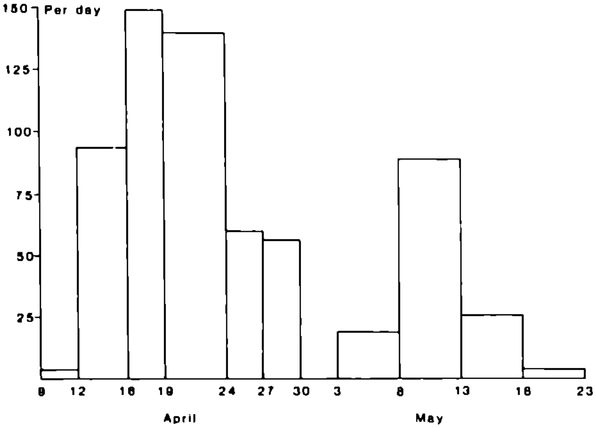

Figure 2. Total catches of male moths in 32 pheromone traps, April and May 1979.

showed quite different trends when compared with the pupal numbers.

April catches

The 32 values for April pheromone catches and corresponding pupal counts are listed in Table 1. The overall correlation between them is poor ($r^2 = 15.8\%$) though significant ($p < 0.01$). The regression is:

$$y = 45.0 + 1.26x$$

There may be several reasons for the poorness of fit: high sampling error associated with the pupal sampling method; variability of topography and intrusion of non-pine areas of plantation near some sample points; and the dispersal of adult male moths resulting in their being trapped some distance from their point of origin.

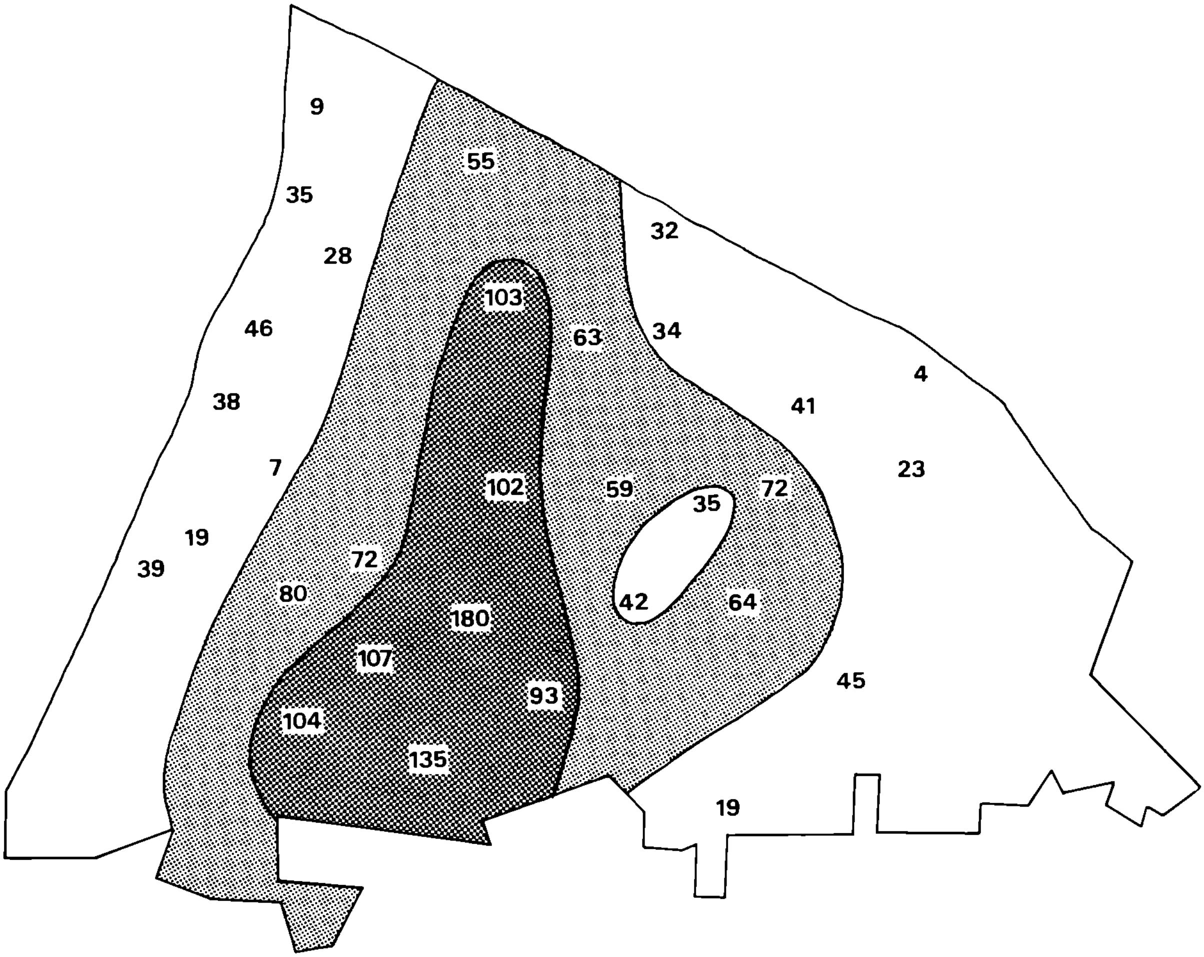

Figure 3. Numbers of male moths caught in the 32 pheromone traps during the April flight period.

The last factor in particular can be appreciated through examination of the contoured density maps of the area showing respectively the pupal counts (Figure 1) and the pheromone trap catches (Figure 3). In both cases there is a well-defined centre of high density in the central part of the block. In the map of pheromone catches, however, this centre is seen to have spread out southwards and eastwards from its original position as defined by pupal counts.

A closer examination and comparison of the two maps shows that this movement of population is evident over the whole area of the block. The ratio of pheromone catch to pupal count increases progressively in passing from one side of the block to the other. Figure 5 shows the 32 points which have been divided (by inspection) into four 'sectors' in which the ratio

mean pheromone catch : mean pupal count

changes from only 2.2 at the west end to 44.0 at the east end of the Elchies block. It is difficult to avoid the conclusion that there has been a substantial movement of male moths, whereby pheromone traps in the eastern and south-eastern parts have been flooded with male moths originating in the high-density centre of population. Conversely pheromone traps near the western edge may have been 'starved' of male moths which moved away eastwards.

The movement of population over the whole block can best be summarized by calculating the 'centre of gravity' (C of G) of *P. flammea* population based on each of the two sets of figures for the 32 points. In each case a mean easting and a mean northing were calculated from coordinates of the sample points and numbers of *P. flammea* recorded. The C of G calculated using pheromone catches was found to be displaced from the C of G using pupal counts by a distance of 350 m, in an ESE direction (to be exact 114°).

This direction is readily explainable on the basis of prevailing wind direction during the moths' flight period. Data for wind speed and direction were taken

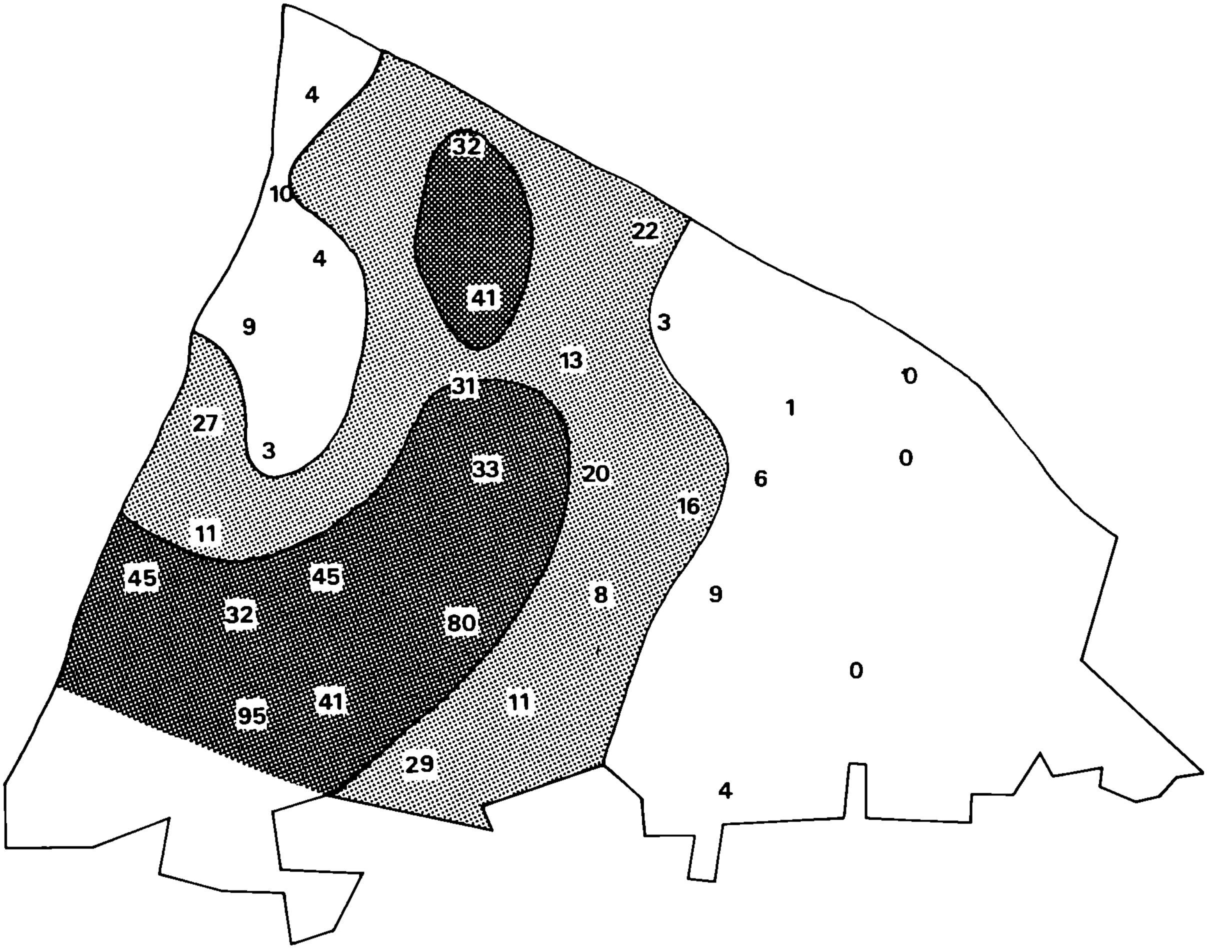

Figure 4. Numbers of male moths caught in the 32 pheromone traps during the May flight period.

from Meteorological Office daily reports covering the period April-May 1979. Data used were those for Dyce, the nearest synoptic reporting station listed in the reports. During the 18-day period 12 to 29 April the wind was rather consistently in the west and north-west, with a mean direction (weighted by wind speed) of 288°. So it appears that in this part of the flight period the population of male moths drifted a significant distance downwind and that this is reflected in the overall pheromone trap catches.

May catches

The May pheromone catches are illustrated in Figure 4 and listed along with the original pupal counts in Table 1. As for the April catches, the correlation with pupal density is low ($r^2 = 21.7\%$). The regression is:

$$y = 12.4 + 0.834x$$

Once again, the comparison of maps (Figures 1 and 4) shows that the ratio of pheromone catch to pupal count varied widely in passing from one side of the block to the other. Figure 6 shows three sectors in which the ratio

mean pheromone catch : mean pupal count

was respectively 0.29, 1.58 and 9.7. The low ratio represents a zone near the north-east corner of the block, and the high ratio represents an area in the south and south-west. It is noteworthy that the latter lies just outside the epicentre of high numbers indicated by the original pupal counts.

In terms of movement of the centre of gravity, the May catches show a displacement of 170 m in a SSW direction from the original centre. This displacement was most strongly marked in the 3-8 May collecting period; the centre of gravity calculated for this period only had moved as much as 570 m to SSW.

The comparison of these results with wind data from Meteorological Office reports is more difficult than it was for the earlier period. In the 15 days 3-17 May wind

Table 1. Catches of male *Panolis* in April and May 1979 in relation to previous pupal counts (per m^2)

Ref. no.	Pupal count	April catch	May catch
1	4	39	45
2	49	19	11
3	3	38	27
4	11	46	9
5	2	7	3
6	0	35	10
7	5	80	32
8	14	104	95
9	6	9	4
10	11	28	4
11	25	72	45
12	35	107	41
13	1	135	29
14	27	92	31
15	16	55	32
16	42	180	80
17	5	103	41
18	23	102	33
19	0	93	11
20	9	63	13
21	6	59	20
22	4	42	8
23	10	32	22
24	11	34	3
25	11	35	16
26	11	64	9
27	0	19	4
28	3	72	6
29	1	41	1
30	0	45	0
31	2	23	0
32	0	4	0

Table 2. Adjusted pupal densities (i.e. densities integrated over 20 ha catchment area for each trap) for April and May catches

Ref. no.	Adjusted pupal density for April catches	Adjusted pupal density for May catches
1	4	22
2	12	18
3	1	5
4	5	8
5	5	4
6	1	4
7	15	11
8	12	24
9	2	5
10	3	4
11	15	19
12	25	32
13	12	15
14	15	16
15	8	7
16	32	26
17	5	10
18	24	16
19	14	5
20	10	10
21	15	8
22	8	6
23	6	4
24	10	7
25	10	4
26	10	6
27	1	1
28	7	2
29	4	1
30	2	1
31	2	1
32	0	0

direction changed frequently from day to day, and temperature fluctuated strongly above and below the threshold value (about 6°C according to Zwölfer (1931)) for *P. flammea* flight. No good correlation can be seen in this period between wind direction and moth displacement, but given the changeability and the distance from the Dyce weather station this is perhaps not surprising.

Pheromone Trap Calibration

If we accept the above as evidence that moths have been trapped from a catchment area of many hectares lying predominantly to windward of each pheromone trap, it is possible to return to the question of pheromone catch in relation to population density with a fresh approach. The contoured density maps of pupal counts give an indication of the very considerable density variation in two dimensions over the entire area of the block. From contour patterns it is possible to interpolate the probable density of pupae at any given point within the area, and by extension of this to sum (or rather, integrate) these densities over any required two-dimensional area. A logical way of approximating the catchment area of any one pheromone trap is to take a 90° sector of a circle, of radius, say 500 m, centred on the trap position and extending in a windward direction away from it. This area contains approximately 20 ha of forest from which

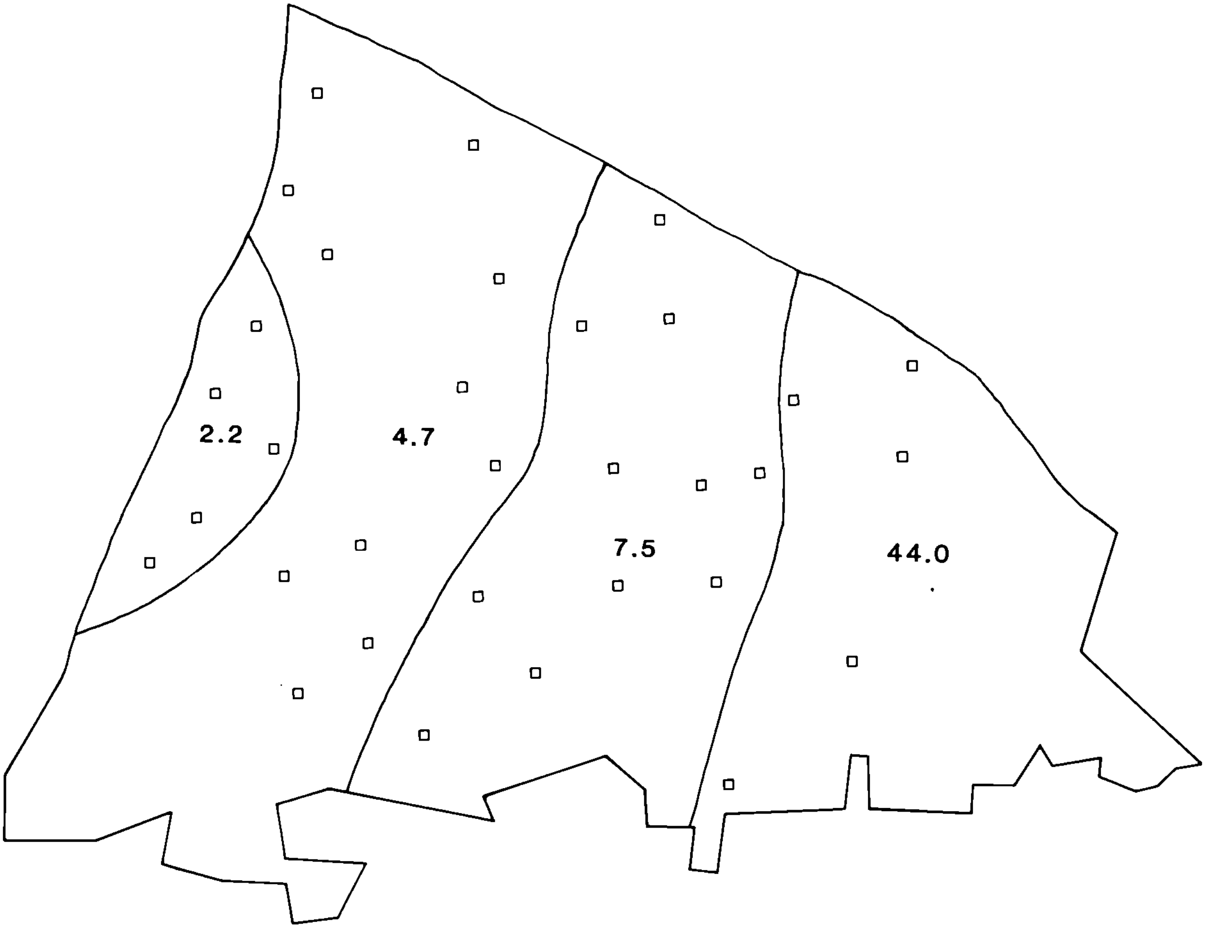

Figure 5. Ratio of mean pheromone catch : mean pupal count in four sectors of the Elchies block (April).

moths caught in the trap may be thought to have originated. By integrating the probable pupal density over this 20 ha catchment area we obtain a more meaningful independent variable on which to regress the observed values of pheromone trap catches. Pupal density values for each of the two periods, integrated by visual inspection of contour maps, are listed in Table 2. April values are based on a catchment area to WNW of each trap (Figure 7) and May values on a catchment area to NNE.

The regressions of pheromone catch on these figures are now dramatically improved:

APRIL $y = 20.4 + 4.15x$ ($r^2 = 61.5\%$)
MAY $y = 0.75 + 2.19x$ ($r^2 = 64.0\%$)

Neither of these regressions is significantly different from a straight line through the origin, consistent with a constant ratio of pheromone catch to population density at all density levels. On *a priori* grounds we might expect a more curvilinear fit, with catch increasing less steeply at higher population densities. This would correspond to a 'competition effect' with resident female moths starting to out-compete pheromone traps in attraction. However within the limits of variability of the present results a straight line fit seems to be quite an adequate model.

Discussion

The practical implications of this finding for the development of an effective pheromone monitoring scheme are considerable. The rather discouraging results obtained from direct regressions of pheromone catches on pupal counts may not after all be a bar to developing more precise 'calibrations' of the traps with respect to true population density. However in trying to establish such calibrations it will be necessary to consider

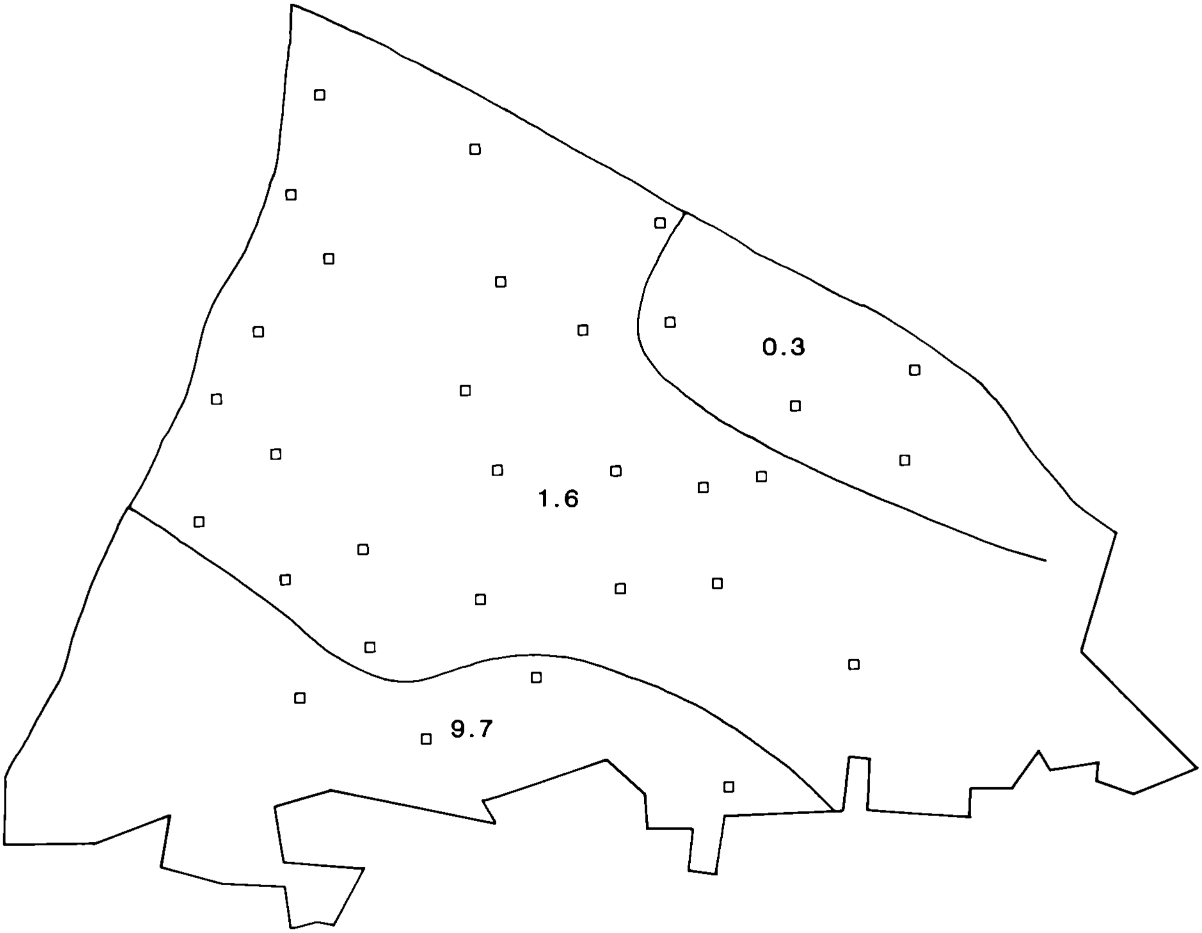

Figure 6. Ratio of mean pheromone catch : mean pupal count in three sectors of the Elchies block (May).

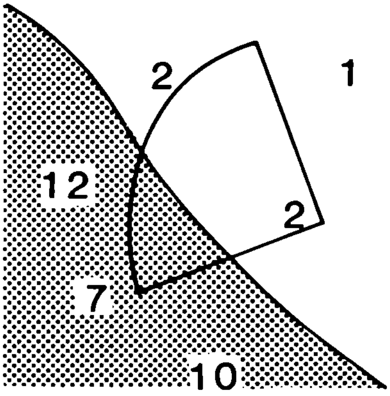

Figure 7. Method of integrating probable pupal density over 20 ha 'catchment area' of a pheromone trap.
Original pupal counts = 2/m²
Integrated pupal density = 4/m²

population density not as single-point measurements, as we have done hitherto, but more in terms of area-wide values. A logical corollary of this is that it may be more instructive to compare widely separate blocks of plantation, with different population levels, than to try to make comparisons between different points within a block.

Conclusions

1. Catches of male moths in pheromone traps showed a rather low degree of correlation with population density as indicated by earlier pupal counts. Part of the reason appeared to be dispersal of male moths from one part of the forest block to another.
2. In each of two distinct periods of moth activity the pattern of pheromone trap catches suggested there had been a uniform uni-directional displacement of

the moth population over the entire area. In one of the periods this corresponded closely to the direction of the prevailing wind.

3. By taking account of the evident displacement of moths from their place of origin it is possible substantially to improve the correlation of trap catches with population density as shown by pupal counts.

Acknowledgements

I should like to thank the Forestry Commission staff at Craigellachie (now Speyside) Forest for practical assistance with fieldwork. The Chemical Entomology Unit of Southampton University supplied the Pherocon IC traps and pheromone lures with which to bait them. I am grateful to my colleagues Dr S. R. Leather, Dr A. D. Watt and Mr J. T. Stoakley for helpful comments on this paper.

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Defoliation by the Pine Sawfly *Neodiprion sertifer:*

Effect on Growth, and Economic Consequences

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Introduction

Defoliating insects can cause tree mortality, deformed crowns and stems, and increment loss, which in turn will result in economic losses. The following discussion will be restricted to increment loss, with comments on a few general principles and with special reference to some Scandinavian investigations on the consequences of defoliation by *Neodiprion sertifer*.

Growth Pattern Following Defoliation

After a defoliation, the annual growth will decrease, reach a minimum and then increase until it reaches (usually) the same level as before defoliation. Thus the growth pattern will describe a U-shaped curve, in principle like the one shown in Figure 1. This graph shows that the total increment loss is determined by (1) the length of the recovery period and (2) the minimum level of growth during the period. It is obvious then that the complete growth loss can be recorded only when tree measurements are undertaken after the recovery period is ended. In the literature one will frequently find information on growth loss based upon measurements undertaken during a mass-outbreak or immediately afterwards. Such information is insufficient when economic consequences are to be considered.

The growth development after defoliation is influenced by several factors: the degree of defoliation; time of the year when defoliation occurs; latitude and climate; the insect species (Kulman, 1971). The effect of the latitude is clearly demonstrated when comparing the growth development between tropical and northern latitudes (Figure 2). The graphs are based on results from experiments with artificial defoliation of young pine trees (Austarå, 1970; Austarå, in preparation). In Norway, 100 per cent defoliation resulted in reduced diameter growth for 6 years, while after a similar treatment in Uganda, where the trees grow continuously throughout the year, normal growth was resumed after 12 months. In both cases the diameter growth was reduced to 50 per cent, on average, for the recovery period. This means that in Norway the actual diameter loss equalled 3 years of normal growth; in Uganda only half a year. But even less drastic differences in latitudes may affect the length of the recovery period. This effect has also been recorded within Scandinavia. After attacks by the Pine shoot beetle *Tomicus piniperda* (when the buds are removed) investigations have shown that the recovery period can last 8-10 years in southern Sweden and 12-14 years in northern Sweden (Nilsson, 1976).

Effects of Defoliation of *Pinus sylvestris* by *Neodiprion sertifer*

When mass outbreaks by *N. sertifer* continue for several years in succession, the trees may be completely stripped of their needles at the end of the larval period which normally occurs around the middle of July in the southern parts of Norway. At this time, the needle elongation is still not completed. And, because the larvae do not bore into the needle sheaths, the basal intercalary meristem is left intact, and the amputated needles continue to elongate after the larval feeding has ceased. Therefore, at the end of the growing season, there will exist a certain amount of foliage on the current year's shoots. For this reason the pine can survive even several years of heavy defoliation; usually only weakened and suppressed trees will die; but there is also a risk of tree mortality, especially when trees grow in exposed coastal areas.

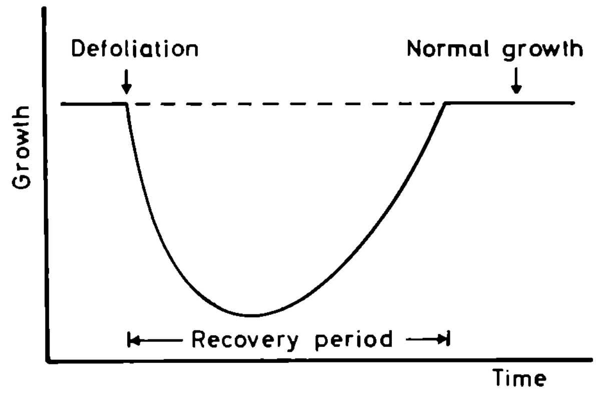

Figure 1. Principles of growth pattern after defoliation.

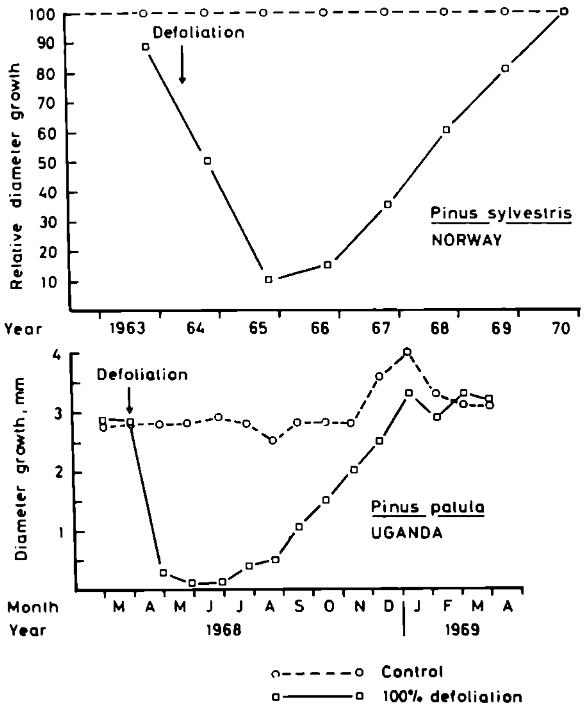

Figure 2. Comparison of recovery periods in northern and in tropical latitudes.

Increment loss

In Table 1 are listed results from some Nordic investigations on growth reduction following defoliation by *N. sertifer* and from one experiment with artificial defoliation.

The results found by Orlund and Austarå (in preparation) are derived from measurements following mass-outbreaks in west Norway during the years 1973 and 1974. In 1973 the current year's needles were not attacked, but in 1974 the larvae also partly defoliated the current year's shoots. These mass-outbreaks resulted in a volume loss equal to 3 years of normal growth during the preceding 9-year period. For a one year defoliation Tiihonen (1970) found a volume loss of one year in Finland. Here the degree of defoliation was very variable in the outbreak areas, and not particularly high. Tiihonen also found that the trees were not completely recovered at the time of measurements, 5 years after the attacks started.

The experiment with artificial defoliation (Austarå, in preparation) simulated a defoliation by *N. sertifer*. Defoliation was carried out during the period 8-30 June 1964. The treatment '100 per cent defoliation' also included complete removal of the current year's needles, which were clipped off near the needle sheaths at the end of June. The main reason for the greater increment losses found in this experiment (Table 1) is probably that artificial defoliation of 100 per cent is a more severe treatment than defoliation by *N. sertifer* usually is. Probably a 'heavy' defoliation by *N. sertifer* compares more to an artificial treatment where most of the old needles are removed. That is, a heavy defoliation by *N. sertifer* for one year most likely results in an increment loss equal to approximately 2 years of normal growth.

If it is assumed that the data given from Sweden by Forsslund (1945) and Eklund (1964) (Table 1) represent the average relative increment loss for a period of 5 years, it can be seen from Table 1 that the data for diameter and height growth loss correspond reasonably well to the Norwegian data for old and young stands.

On the basis of these data, it may be concluded that one year's heavy defoliation by *N. sertifer* results in a loss of volume production equal to 2 years of normal growth; and when heavy attacks continue for a further year, the corresponding loss equals 3 years.

Economic consequences

The economic consequences of increment loss can be calculated by a somewhat simplified method, taking into consideration the compound rate of interest. First one will have to know the increase in rotation age due to the increment loss following defoliation, i.e. the number of years of lost increment. Then the economic loss is found by discounting the net values of the future cutting revenue with and without increment loss back to the year of defoliation, and calculating the difference between these two values (Austarå, 1968). Table 2 shows, for Norwegian conditions, the results of such calculations for various assumptions (Veidahl, 1982). The figures represent the economic loss in N.Kr. per ha for one year's loss of volume increment. If the increment loss is equal to 2 or 3 years of normal growth the figures are doubled or tripled (N.Kr. 100 = approximately £9).

Table 1. Growth loss in diameter, height and volume following defoliation for 1 and 2 years by *Neodiprion sertifer*

Author and stand age	Diameter 1	Diameter 2	Height 1	Height 2	Volume 1	Volume 2	Remarks
Forsslund, 1945 Stand ages: 15-60 years			3-30%	25-60%			Measurements undertaken the year after defoliation
Eklund, 1964 Stand ages: not determined, 'older' stands	39%	52%					Measurements undertaken the year after defoliation
Tiihonen, 1970 Stand ages: 40-105 years					1 year		Measurements undertaken 5 years after defoliation
Austarå (in preparation) Stand age: 10-15 years Artificial defoliation							Measurements undertaken 8 years after defoliation
a) 100% defoliation					4.8 years		
b) Previous years' needles					2.1 years		
c) All needles except current					2.2 years		
Orlund & Austarå (in preparation)							Measurements undertaken 9 years after defoliation
Stand ages: 80-115 years		2.7 years		4.2 years		3.0 years	
Stand age: 40 years		5.1 years		2.3 years			

Table 2. Economic loss to date with one year's growth loss. N.Kr. per hectare.

Assumptions: Current timber prices, and 50% of the lumber as prime and 50% as second-rate.
Logging costs N.Kr. 75 per m³ and N.Kr. 6 per tree.
Growth model program 2 for pine.

Site class*	F17		F14		F11		F8	
Rate of interest	2%	3%	2%	3%	2%	3%	2%	3%
Rotation age (years)	85	75	95	85	105	95	115	105
Stand age								
10	310	230	180	120	100	70	60	40
20	390	310	230	160	120	90	70	50
30	490	420	280	210	150	150	80	60
40	600	570	350	300	180	210	90	70
50	730	760	420	400	230	280	110	100
60	890	1020	510	530	290	380	130	130
70	1080		620	700	350	510	170	180
80			750		430		210	240
90					530		260	
100								

* Yield capacity (m³/ha/year) of F 17 = 7.0, F 14 = 5.0, F 11 = 3.5 and F 8 = 2.0

In the south-eastern parts of Norway, heavy mass-outbreaks of *N. sertifer* were reported in 1979. The infestations spread, and in one county a total of 17 000 ha of pine forest had been defoliated by the end of 1983. In various districts, the attacks lasted 2 or 3 years. Therefore one may assume that the volume increment loss amounts to approximately 3 years of normal growth. Using Table 2 the economic loss at the time of defoliation can be estimated. Assuming a site quality of F 11, which means an average volume growth of 3.5 m³ per ha per year, and assuming that the attacks started at stand ages averaging 70 years, and choosing the rate of interest to be 2 per cent, one finds an annual loss of N.Kr. 350, which has to be multiplied by three, giving an actual loss of N.Kr. 1050 per ha. Since 17 000 ha were defoliated, the total loss amounts to N.Kr. 17 850 000 when discounted to today's value.

The figures in the table also dictate what sum of money could be invested in control to prevent defoliation of pine forests in south-eastern Norway. Provided control measures cost less than these figures, control is profitable. In the above-mentioned example, one could have invested up to N.Kr. 1050 per ha in control. However, to prevent serious and widespread defoliation, methods for monitoring the sawfly populations are needed. Infestations often start in small centres gradually spreading over large areas during the following years. Such centres might be detected with the help of an effective monitoring system. If control measures were capable of stopping the dispersal of the sawfly population from these initial outbreaks, large areas could be saved from heavy defoliation at low control costs.

In Norway the first recorded mass-outbreak of *N. sertifer* was in 1886. Since then, infestations have been recorded at more or less regular intervals. In Ostfold County, south-east Norway, eight outbreaks have occurred since 1898. This means that a stand may have suffered defoliation eight times during less than one rotation. The economic loss caused by *N. sertifer* may therefore be considerable.

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Trials on the Control of *Panolis flammea* with a Nuclear Polyhedrosis Virus

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Introduction

Viruses in the family Baculoviridae (BV) and especially the subgroup A nuclear polyhedrosis viruses (NPV) have been widely and successfully employed as sprayable entities for the control of forest defoliators (Entwistle and Evans, 1985). In the United Kingdom one NPV, that of *Neodiprion sertifer* the European pine sawfly, was the object of intensive field control experimentation between 1977 and 1983 (Cunningham and Entwistle, 1981; Entwistle *et al.*, 1985), leading to commercialisation and the successful treatment of approximately 3100 ha in Scotland in 1983.

In the context of the relatively low economic returns from forestry, the financial acceptability of control by viruses is strengthened by the facts that, at least in temperate areas, most forest defoliators are univoltine and express long interval outbreak cycles, commonly 5 to 7 years. Furthermore, as one virus application is in general sufficient to suppress a larval population it is realistic to anticipate only infrequent spraying in any one area. The high specificity of BVs means that beneficial insects are not adversely affected and consequently host population resurgence may be less rapid than following chemical insecticide applications. Nor do BVs cause environmentally unacceptable effects: indeed terrestrial habitats are commonly heavily exposed to BVs generated in natural epizootics. In Scottish pine forests, for instance, epizootics of NPV disease occur in *N. sertifer* the European pine sawfly and *Orgyia antiqua* the Vapourer moth. NPV disease is also expressed naturally in *P. flammea* populations but has not been observed to rise above 15 per cent infection before either population collapse due to tree death or the application of control by chemical sprays (Entwistle and Evans, unpublished).

In view of the low epizootic capacity of *P. flammea* NPV (PfNPV), application of the virus by spraying was investigated as the most promising approach to control using this virus.

Nuclear polyhedrosis viruses

The virus particle, or virion, is a rod approximately 250 nm long by 50 nm in diameter. The nucleocapsid consists of a DNA core enveloped in a protein coat, the whole contained by a membrane, the virus envelope, to form the virion. Replication is restricted to the nuclei of host cells where groups of virions are enclosed in polyhedral crystals of protein (approximately 1-5 µm in diameter), the polyhedral inclusion bodies (PIB), production of which is a virus coded function. The PIB is bounded by a glycoprotein envelope. Two types of NPV are recognised; those in which there is a single nucleocapsid per virus envelope (singly enveloped NPVs) and those in which some envelopes contain two, three or more nucleocapsids (multiply enveloped NPVs). PfNPV is of the latter type.

In general, infection of larvae follows ingestion of PIBs during feeding. Virions are liberated in the host midgut when PIBs break down in the presence of alkaline digestive fluids. The ensuing infection pathway has not been precisely identified in *P. flammea* but commonly in Lepidoptera a brief replicative phase in midgut secretory cells is followed by a more general viraemia in which fat body, hypodermis, tracheal matrix and haemocytes are especially involved. Eventually the larval body collapses and on rupture liberates PIBs. A full grown larva of *P. flammea* may contain approximately 1×10^9 PIBs.

The environmental persistence of NPV in PIBs may extend over years especially in situations, such as the soil, unexposed to solar UV.

Many aspects of BV structure, replication, the epizootiology of BV diseases and their application in pest control are treated in Entwistle and Evans (in press).

Methods

Production and purification of PfNPV

Due to problems of culture, *P. flammea* is not an ideal species in which to produce PfNPV on a large scale. The virus was therefore produced in larvae of the closely related cabbage moth, *Mamestra brassicae* (Lepidoptera: Noctuidae) bred under controlled conditions on a modification of Hoffman's Tobacco hornworm diet (Hunter *et al.*, 1984). Infected larvae were harvested at or shortly before death and deep frozen pending treatment. Extraction and purification of PIBs was by trituration in a Colworth stomacher and passing the triturate through a coarse filter to remove larger particles. Low speed centrifugation was then used to sediment host detritus following which impure preparations of PIBs were pelleted at higher speeds. Resuspended pellets were then highly purified through two cycles of sucrose density gradient centrifugation. The PIB concentration was measured by Wigley's (1980a) dry smear technique and batches stored at −20°C.

Restriction endonuclease (REN) mapping of the viral genome revealed that the inoculum sprayed in the 1983 trial was heavily contaminated with *Mamestra brassicae* homologous NPV (MbNPV) but retrospective REN analysis indicated that inoculum used prior to 1983, and yielded in samples of infected larvae collected in spray trials, was in fact PfNPV.

Timing spray applications

Because of the innately greater susceptibility to infection of young larvae, the hatch of eggs was carefully monitored so that spray applications could be made not later than at 95 per cent hatch. Emergence from the egg tended to be closely synchronised, mostly occurring in a period of one week.

Field application of PfNPV

Four types of spray equipment were employed.

a. The MicroUlva (Micron Sprayers Ltd.), a hand-held spinning disc controlled droplet applicator (c.d.a.) was set to produce droplets of 50 µm diameter with a flow rate of 0.43 ml s^{-1} and was used for applications from the ground
b. The X-15 (Micron Sprayers Ltd.), an electrically driven device similar in principle to the MicroUlva, in which 15 discs are mounted on a single axle perforated to permit delivery of spray fluid to each disc. It was first used on a helicopter for aerial application in 1983. The droplet spectrum was closely grouped around 100 µm.
c. The Mini Micronair (Micronair Ltd.), a propeller driven cage small droplet producing device, was employed for helicopter applications in 1981. The droplet size allegedly centred around 50 µm diameter.
d. A Simplex boom and hydraulic nozzle system was used for low volume spraying. Nozzles were fitted with 57 T-jets, D3 tips, No 13 cores and slotted strainers using a tank pressure of 50 psi. On impaction on spray cards, droplets were found to be 147 ± 67 µm in diameter, which is in fair agreement with the predicted emission diameter of 180 µm.

An emulsifiable light oil (successively trade named Ulvapron, Dessipron and Actipron: British Petroleum Ltd.) of very low volatility was used at 20 per cent with all equipment except the Simplex system spraying.

Assessment of spray droplet capture

Most monitoring was in experiments in which 0.5 per cent nigrosine had been added to the spray fluid. Droplet capture was assessed by counting the resultant black droplets on pine foliage which had been painted white using aerosol cans of paint. Capture was expressed as droplets/cm of mature needles. Results are referred to only in the Discussion section of this paper.

The experimental sequence

All experimental treatments are listed in Table 1.

1981 aerial trial

Six Mini Micronairs were employed. Plots were one hectare each and mutually separated by a buffer zone 100 m wide. Flying across wind at 50 knots two swathes were applied to each plot. The upwind swathe was 10 metres beyond the plot edge and the downwind swathe was therefore 40 m into the plot, a lane separation of 50 m. The helicopter flew about 2 m above the crop. The wind speed during spraying fluctuated between 6 and 9 knots.

Table 1. Summary of PfNPV PIB dosages and volumes per hectare employed in trials for the control of *Panolis flammea**

1981 aerial 17/5/81		1981 ground 18 & 26/5/81		1982 ground 26/5/82		1983 aerial 10 & 11/6/83	
PIBs/ha	l/ha	PIBs/ha	l/ha	PIBs/ha	l/ha	PIBs/ha	l/ha
1×10^{12}	9.0	1×10^{13}	9.0	1×10^{13} H_2O#	2.2	8×10^{11} Mc[c]	4.5
1×10^{11}		1×10^{12}		5×10^{12} SDS		4×10^{11} Mc	4.5
1×10^{10}		1×10^{11}		1×10^{12} SDS		4×10^{11} Lc	2.25
1×10^{9}		1×10^{10}		5×10^{11} SDS		8×10^{10} Mc TL	4.5
		1×10^{9}		1×10^{11} H_2O		8×10^{10} Mc	4.5
				1×10^{11} SDS		4×10^{10} Mc	4.5
				5×10^{10} SDS		8×10^{10} HN	9.25

*All trials included two control treatments: one sprayed with water/Ulvapron in a ratio of 4:1 and one unsprayed treatment.

#PIBs purified with water only (H_2O) or 0.1% sodium dodecyl sulphate (SDS).

[c] Mc – Maximum coverage to produce at estimated minimum droplet number per cm of foliage and achieved by four passes along each swathe.

Lc – Least coverage; two passes/swathe.

HN – Hydraulic nozzles.

TL – Tate and Lyle Research and Development PIB formulation.

1981 ground trial

Apart from the inclusion of one extra dose level at 1×10^{13} PIBs/ha, this trial duplicated both the dosage and volume rates of the 1981 aerial trial. Applications were with a MicroUlva on plots of 0.01 ha, spaced 50 m apart. There was no replication, but to assess the width of the application 'window' treatments were made at 95 per cent hatch on one series of plots and one week later on a second series.

1982 ground application trial

This had a replicated (x 5) randomised block design in which each plot was of approximately 0.02 ha with 30 m plot separation. Using MicroUlvas, a spray application system was devised whereby the central five trees in each plot were sprayed at a rate of 2.2 l/ha.

1983 aerial application trial

In addition to a stepped dosage series, the trial incorporated a contrast of c.d.a (using X-15s) and wide spectrum droplet size (using hydraulic nozzles) and a first commercial formulation (produced by Tate and Lyle Research and Development, UK, now Microbial Resources Ltd., UK). To inspect the effect of reduced droplet numbers the spray volume in one of the stepped dosage series was reduced to half. Plots were each one hectare and mutually separated by a distance greater than 80 m. There was no replication. Four pairs of electrically driven X-15s (= 8 spray heads) were used to drift droplets downwind into plots. There was a lane separation of 50 m with the two upwind lanes respectively 50 and 100 m from the plot. To allow for deviation in wind direction during application, swathes were 200 m long as compared with a plot side length of 100 m. Wind speed fluctuated between 12 and 25 knots at 2.5 m above the crop. The helicopter flew 6 metres above the crop.

Sampling larval populations

In all except the 1981 aerial trial, the innate density of egg populations in the trial areas was too low to be likely to yield adequate numbers of larvae in subsequent samples. Therefore eggs, on needles, were introduced and taped in groups to the trunk and main branches. This time consuming process limited the number of trees available for sampling in each plot to two in the 1981 ground trial, five in the 1982 ground trial and 49 in the 1983 aerial trial. The 1981 aerial trial was sampled using a quick knock down insecticide (S-Bioallethrin synergised with piperonyl butoxide). Each sample consisted of larvae falling from one quarter of the canopy of four adjacent trees on to a plastic sheet. Five such points were sampled in each plot each week using random numbers and a grid system to locate points. No point was sampled twice. In all the other trials a destructive sampling system was used: all branches of each sample tree were carefully removed and beaten over a 2 x 2 m sheet. Due to the threat of total defoliation of the 1981 ground control trial area by *Zeiraphera diniana*, all *P. flammea* larvae were removed on 23 June and 1 July, from the early and late sprayed plot series respectively, and maintained in individual containers on clean foliage until expression of NPV disease symptoms.

In the 1982 trial, plots were sampled on five occasions at intervals of 10 days commencing 6 days after spraying. On each occasion one tree per plot, hence five per treatment, was sampled. Following each sample the larvae collected were divided into equal batches, one batch being frozen pending NPV diagnosis and larvae of the other batch reared in individual isolation until expression of NPV disease, pupation or parasite emergence. In the 1983 trial, sample trees were ordered into seven cross plot strata at right angles to the wind direction pertaining during spraying. Plots were sampled weekly for 7 weeks involving one tree per stratum (seven trees per plot) in each plot on each occasion. All larvae were frozen pending NPV diagnosis.

Diagnosis of NPV disease

Smears of larval tissue were fixed and triple-stained to permit differentiation between the inclusion bodies of PfNPV and a cytoplasmic polyhedrosis virus (Wigley, 1980b). Smears were examined using a compound light microscope with an oil immersion objective at a magnification of more than x 1000. Before smearing, the instar of each larvae was determined.

Site of virus acquisition trial

An experiment was conducted to determine the relative levels of NPV infection in larvae on trees which had been sprayed overall and those where, by covering the current year's shoots with plastic bags, the spray had been restricted to other tissues. Twelve trees were first reduced each to 15 branches. Two trees were designated as unsprayed controls and the other ten sprayed (five each in the bagged and non-bagged categories) at a rate of 5×10^{12} PIBs/ha in 2.2 l/ha. Following removal of bags each tree was infested with 40-50 neonate larvae and 20-30 mature eggs. Sixteen days later all larvae were harvested and inspected for NPV disease symptoms.

Results

With the exception of the 1981 aerial trial the results of all experiments are presented comparatively in terms of log dose-probit mortality analyses (Finney, 1971) in Table 2 and in Figure 1 as log dose-percentage mortality.

1981 aerial trial

Infection levels in any one week or treatment did not exceed 6 per cent, and there were no statistically significant treatment differences.

Table 2. Computed LD_{50}s for field infection responses to PfNPV applications and extrapolated (calculated) LD_{95}s

Year of trial	LD_{50}	Slope	Intercept	LD_{95}
1981	6.1×10^{10}	0.45	0.17	1.0×10^{14}
1982	1.8×10^{11}	0.47	−0.34	2.1×10^{14}
1983	2.15×10^{11}	1.27	−9.43	3.0×10^{12}

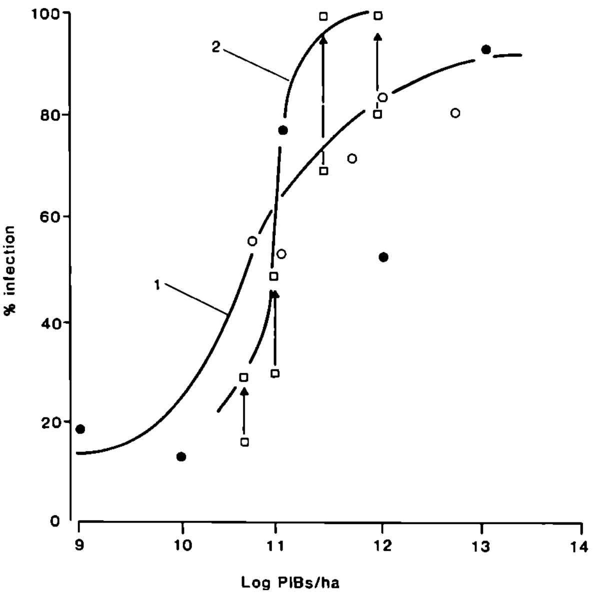

Figure 1. Log PIB dose of *Panolis flammea* NPV/hectare and percentage infection response in larvae in the 1981 (●) and 1982 (○) ground application trials and the 1983 (□) aerial application trial for which the data have been transformed to terms comparable with 1981 and 1982 using the relationship shown in Figure 2.

1981 ground trial

Comparison of the results of the two times of spray application suggested that the later application was slightly the more effective. However, because larval numbers were low, for purposes of log dose-probit mortality analysis the results of the two application series have been combined. On this basis the highest rate of application, 1 x 10^{13} PIBs/ha, yielded an infection level above 95 per cent (Figure 1).

1982 ground trial

The data employed here for purposes of analysis are from larvae which, following sampling, were retained until full expression of NPV disease since this is most directly comparable to the 1981 trials' results. The top two doses, 1 x 10^{12} and 5 x 10^{12} PIBs/ha, both yielded mean infection levels of around 80 per cent, data which conceal the higher levels reached on some trees.

An analysis of the relationship between infection detectable at sampling in the field (x) and 'real' infection (y) in the retained portion of each larval sample was explored. The ratio y/x initially fell rapidly with time to a minimum at approximately 35 days post spraying, irrespective of the dose applied. This presumably reflected the tendency with time to increasingly express peak real infection in the field. Thereafter the ratio increased, probably indicating the onset of a secondary cycle of infection. In Figure 2 the changing mean y/x ratio is contrasted with the mean time to field expression of infection.

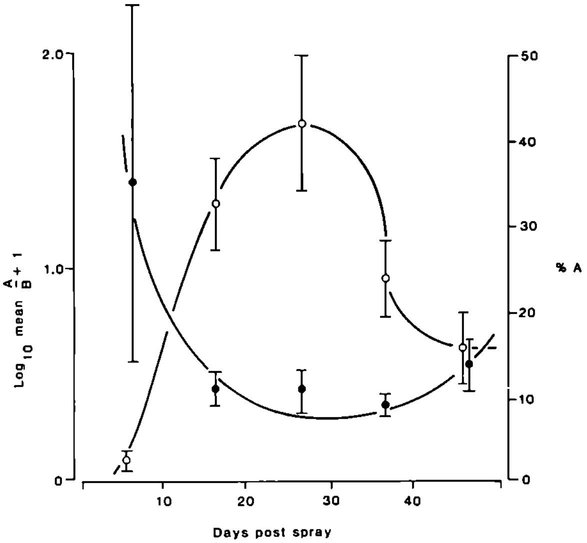

Figure 2. 1981 ground application trial. The relationship between infection of NPV disease in *Panolis flammea* larvae at collection (A) and as finally expressed (B) (●) contrasted with the mean infection picture for all dosage treatments (○). Bars represent standard errors of the means.

1983 aerial control trial

As larval samples were frozen within hours of collection, the infection parameter determined is x (see above trial). The relationship y/x derived for the 1982 trial has been employed in Figure 1 to convert 1983 infection values so that they are comparable with the y values of the 1981 and 1982 trials.

Figure 1 and Table 2 demonstrate the much steeper response in 1983 leading to greater infection in the upper dosage range. Maximum infection levels achieved with hydraulic nozzle applications are compared in Table 3 with equivalent doses of purified and formulated PIBs using X-15 application. Drifting of four swathes of droplets downwind into the plots resulted in an uneven pattern of droplet capture, the infection response to which will be the subject of detailed analysis elsewhere.

Table 3. Comparison of maximum infection recorded in three treatments at the dosage rate of 8 x 10^{10} PIBs/ha in the 1983 aerial trial

Treatment	Application method	Percentage infection x	y
Pure NPV	X-15	29.3	49.52
Commercial formulation	X-15	11.5	19.44
Pure NPV	Hydraulic nozzle	10.2	17.24

x = infection at time of sampling.
y = infection corrected by relationship given in Figure 2.

Site of acquisition trial

Approximately 20 per cent of the larvae used to infest the trees were recovered, there being no significant treatment related loss of larvae. No infection was found in control larvae but 51.5 ± 18.6 and 76.6 ± 74.3 per cent of larvae were infected on trees, respectively, where only the old foliage and all the foliage had been sprayed with PfNPV (not significant at $p<0.05$; Students 't' test).

Discussion

The problem of NPV control of *P. flammea* may essentially be defined in terms of the restricted ingestion of needle surface by young larvae and the matching of spray deposits to this and the overall distribution of larvae on trees. First and second instar larvae largely feed internally on needle tissue of the current year's growth so that the chances of encountering spray droplets are less than for species, e.g. *N. sertifer*, which browse generally on foliage. The strongly asymmetric droplet deposition pattern on canopies which is consequent on drifting spray directionally downwind would, in theory, exacerbate this problem. However, despite such established strong asymmetry (Entwistle and Evans, unpublished) high levels of infection of *P. flammea* larvae have been achieved.

To account for this effect it seems necessary to postulate that young larvae move widely over the canopy. The observations of Ballard (see pp. 31-36) indicate considerable within and between canopy wandering in first and second instar larvae but much more sedentary behaviour in older larvae. Additionally, evidence from the site of acquisition trial suggested that despite feeding being concentrated on the current year's needles larvae may acquire virus elsewhere. It is quite possible PIB deposits on trees are not static (Evans and Entwistle, 1982) and once applied to old tissue may come to contaminate new needles, though it seems unlikely this could entirely account for the high levels of infection found on trees where new foliage was not sprayed. However Ballard found that though young larvae spent 80 per cent of their time on older tissue there was evidence for feeding only on new shoots. Clearly this question requires further examination.

The second question concerns the extent to which it is feasible with available spraying technology to ensure that the vertical pattern of droplet capture and its density can be optimised. What is meant by optimisation may depend greatly on the contribution to droplet encounter provided by horizontal and vertical components in early larval movement. Assuming no larval density interactions and no differential uv degradation of PIB deposits with tree height (see the following paper by Killick, pp. 69-75), in the hypothetical case where larval movement approaches zero, equal infection of larvae throughout on the tree will be achieved only by a vertically even distribution of spray droplets.

Reference to Figure 3 reveals that the vertical distribution of droplets in the 1982 trial (determined by spraying nigrosine-labelled spray fluid) was far from uniform. However, both peak droplet density and the bulk of the larval population were in the upper part of the trees, a situation which, combined with the movement of early stage larvae probably explains the observed high infection levels. Furthermore if larval movement has a strong vertical as well as horizontal component, such a spray pattern would be of high efficiency in bringing young larvae into contact with high concentrations of spray deposits. Closer attention, therefore, to the geometry of larval movement and to the period defined jointly by their susceptibility and the natural degradation of NPV deposits, might pay dividends in terms of understanding both the larval infection response to observed spray deposition patterns and the optimal desirable pattern. Such ideal spray patterns may well vary with the overall pattern of canopy form in any one area and the related distribution of *P. flammea* larvae.

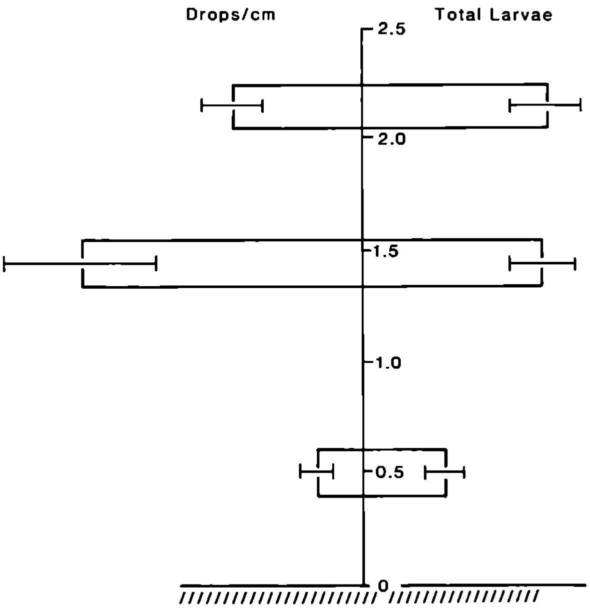

Figure 3. 1982 ground application trial. The relative distribution of spray droplets (droplets/cm of mature needle) and of total larvae of *Panolis flammea* on trees 2.5 m tall. Bars represent standard errors of the means.

The practical relevance of the trials' results

With the exception of the 1981 aerial trial all the studies indicated the practical possibility of achieving high levels of infection by spraying suspensions of PfNPV PIBs. This is now briefly inspected in the light of within-trials response variation.

1981 and 1982 ground application trials

In terms of the area of trees sprayed in each plot these trials were very small scale. Serial overlap of sequential spray swathes impacting on very few sample rows resulted in some trees having much lower droplet densities than others. For instance in 1982, for any one of three height profiles compared on four successively downwind rows, deposit densities varied by a factor of from x 4.35 to x 7.34. This level of variation would not be expected in the operational treatment of a larger area and it is therefore suggested that the overall response of these trials was lower than would result in an operational context.

1983 aerial application trial

Within all the virus treated plots, the infection picture fluctuated downwind with the density of droplet deposition. The extent of such within-treatment variation

$$\text{ratio } y = \frac{\text{greatest \% infection}}{\text{least \% infection}}$$

differed with the PIB dose (x) applied (Figure 4) being adequately described by several models, e.g.

$$\frac{1}{y} = a + bx \qquad (r^2 = 0.996)$$

where $a = -3.67$ and $b = 0.36$

and

$$y = ax^b \qquad (r^2 = 0.980)$$

where $a = 5.78$ and $b = -14.45$

This general relationship seems predictable in terms of the sigmoid dose-per cent infection response curve. In the light of this it seems that the ratio y would be least at very low dose responses (not represented in Figure 4), greatest in the central, exponential zone of the curve, and low again at very high doses. It must be an objective in future trials to minimise such variation by achieving more spatially even distribution of spray droplets.

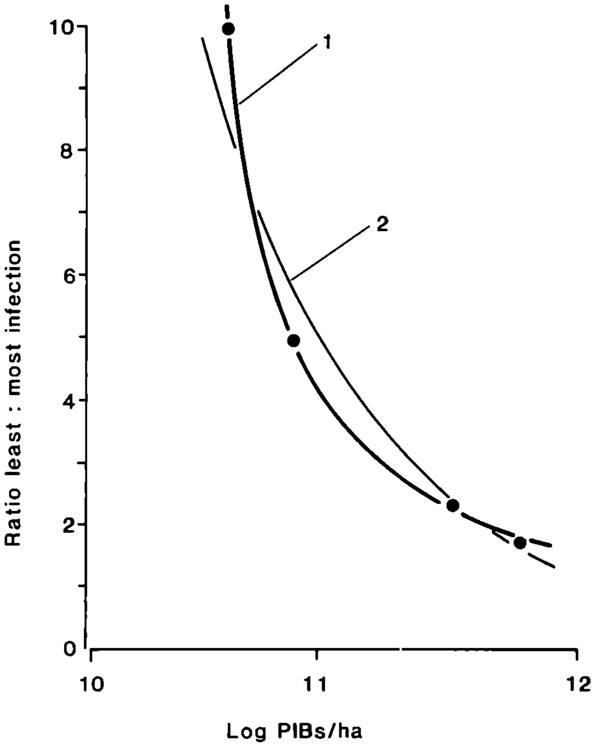

Figure 4. 1983 aerial application trial. Relationship between variation in the NPV infection of larval *Panolis flammea* downwind across plots (y) and the dose of NPV PIBs/hectare applied (x). Two possible models are shown:

1. $\frac{1}{y} = 0.36x - 3.67 \quad (r^2 = 0.996)$
2. $y = 5.78x^{-14.45} \quad (r^2 = 0.980)$

Acknowledgements

These studies were conducted with the express permission of the Pesticides Safety Precautions Scheme, MAFF, under licences: PSPS 1981/10459, 1982/12141 and 1983/13903a. They would not have been possible without the very considerable level of day to day co-operation of the Forestry Commission (FC). We would in particular like to thank the Conservator of Forests, North Scotland, within whose jurisdiction the work proceeded, Mr J.T. Stoakley of the FC Northern Research Station, Mr H. Mackay then of the Lairg and now of the Dornoch Forest Office and Mr N. Davidson of the Lairg Office. Conduct of the studies was very greatly assisted by the following students: Mr D.F. Barrett, P. Edwards, A. Hayes, D.J. Methley, M.A. Thompson and R. H. Veal. The Bioallethrin formulation was kindly supplied by the Wellcome Foundation.

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Ultraviolet Light and *Panolis* Nuclear Polyhedrosis Virus:

A Non-problem?

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Introduction

There is widespread concern about the effects of solar ultraviolet (UV) light on the viruses used to control insect pests which can sometimes halve the activity of the virus in a few hours (e.g. David *et al.*, 1968). Entwistle and Evans (see previous paper, pp. 61-68) have described experiments on the control of *Panolis flammea* larvae by a nuclear polyhedrosis virus (NPV). Some 1984 trials concerned a specific aspect – the possible harmful effects of solar UV light on the virus, and the use of spray additives to reduce them. This paper discusses how much *P. flammea* NPV activity is lost at an experimental site at a high latitude (58°N) in a dense, three-dimensional crop *(Pinus contorta)*.

The nature and quantity of solar UV

Solar UV can reach the ground in two ways – in a direct straight line from the sun (incident or I-radiation), and as diffuse or sky radiation (D-radiation). The two combined are known as global (G-) radiation.

The UV of greatest biological interest lies in the 'UVB' range, 320-280 nm. On a sunny midday at Davos, Switzerland (Bener, 1960) the global energy reaching the ground falls steeply below 330 nm, that at 305 nm being only 0.04 times as much (Figure 1). Also, as the sun rises higher in the sky, more UVB reaches the ground; as the solar elevation rises from 30° to 50° the amount of 320 nm radiation is doubled but that of 305 nm is multiplied five-fold.

Because solar elevation is important, the season, time of day and latitude are likewise important. Figure 2 shows the relationship between the solar elevation on 29 May in the N. Dalchork block of Shin forest, the experimental site referred to above, and the observed UVB input on the same day. There are complicating factors. Altitude is one; the incident UVB at 3000 m is twice that reaching sea level. Cloud is another. Atmospheric ozone decreases the UV reaching the ground, and removes a bigger proportion of the shorter wavelengths. Harder to identify are the effects of haze and dust.

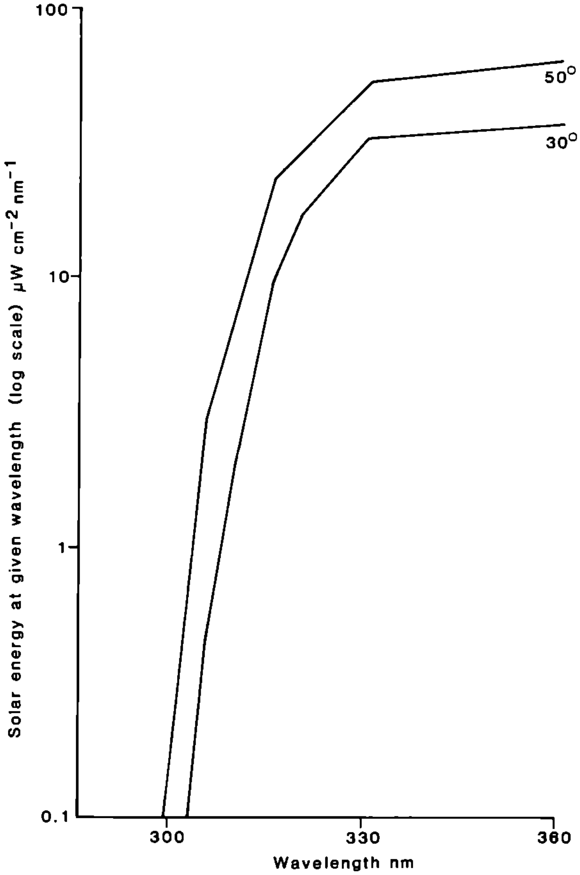

Figure 1. Solar ultraviolet global radiation at various wavelengths at solar elevation 50° and 30° and 0.250 cm of atmospheric ozone (Bener, 1960).

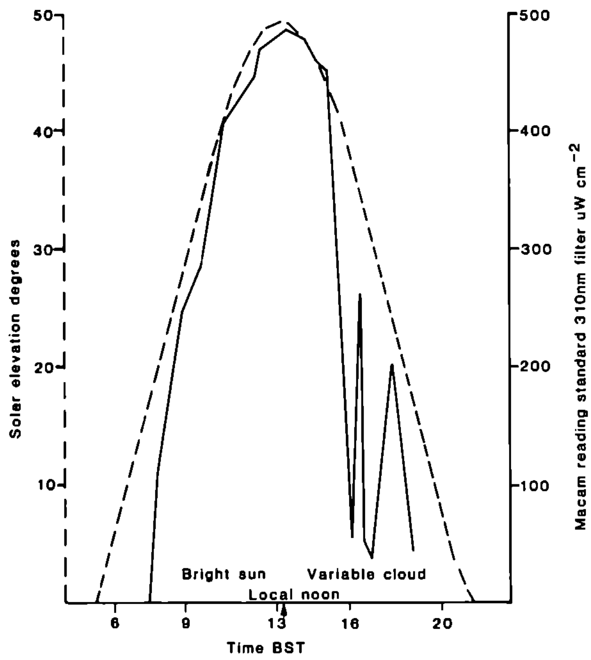

Figure 2. North Dalchork Forest, 29 May 1984: solar elevation and UV recordings. UV data from Macam UV103 radiometer using standard 310 nm filter pointed directly at the sun.

How UV affects the virus

There is much good evidence to show the damaging effect of UV on DNA which is the genetic basis of many viruses including NPVs. The damage per unit energy increases sharply as the wavelength falls (Harm, 1980; Figure 3). The relationship between solar UV and human sunburn (erythema) is also well documented, and erythema per unit dose also increases with decreasing wavelength (Figure 3) reaching a peak at 280 nm (Anon., 1972).

It is also well documented (Harm, 1980) that the damage to DNA can be reversed by visible light. This process is slower, so a net damage to the DNA results, especially at lower wavelengths. Where the DNA is repaired, its biological activity can resume. The shortest wavelength at which repair can happen in insect viruses has not been systematically studied, but is claimed to be as low as 320 nm for the NPV of the cabbage looper *in vitro* (Ramoska *et al.*, 1975).

These three lines of evidence, if valid for the *P. flammea* NPV, focus attention on UVB. More precise information can be gained by multiplying the amount of solar UV at a given wavelength by its damaging power (Figure 4). For solar elevation 50° (midday elevations in June in Sutherland are 50-55°) the important wavelength is likely to be 307 nm. A similar result is obtained by employing the erythema data.

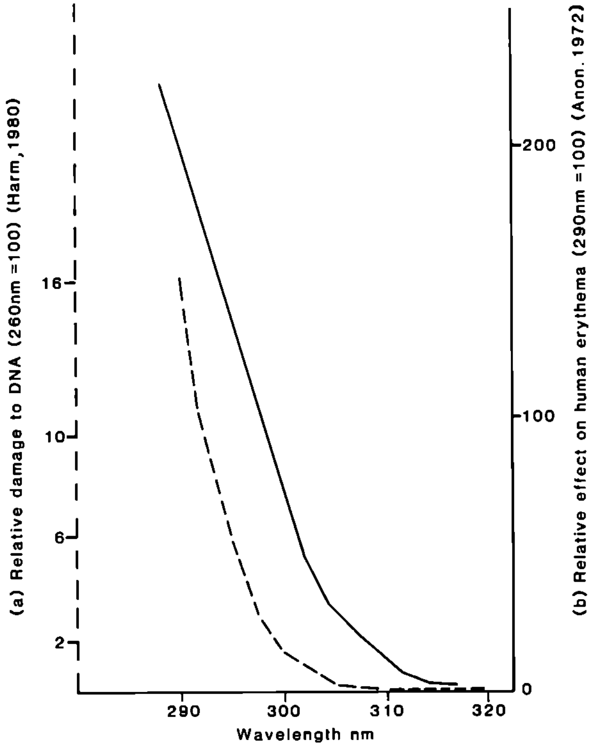

Figure 3. Relationship between wavelength and (a) relative UV damage to DNA and (b) erythema of human skin.

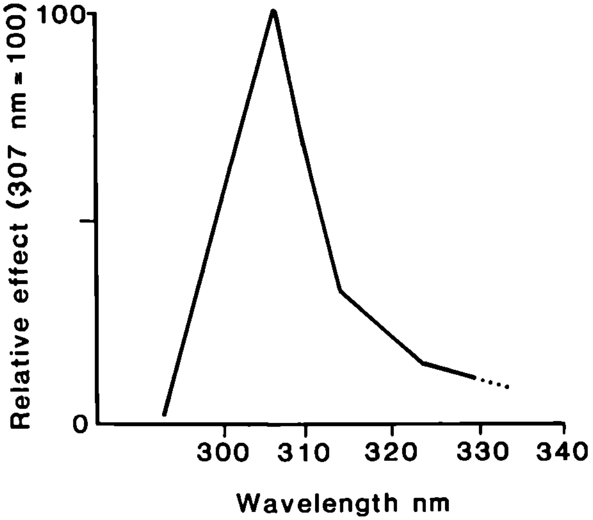

Figure 4. Product of the amount of solar UV energy (global radiation at 50° elevation; Bener, 1960) and its relative damaging power to DNA.

Methods

Field measurement of solar UV

A Macam UV Radiometer UV 103 (Macam Photometrics Ltd., Livingston, Scotland) was used following other workers (e.g. Timans, 1982). It is simple to operate but records a cone of light, vertex angle 55°, and not the full 180° used by meteorologists measuring solar radiation.

Its standard UVB filter, nominally 310 nm has a broad band-width (half strength b.w. 34 nm) and the maximum transmission is actually at 313 nm. Taking account of the light the filter transmits at given wavelengths and the energy delivered by the sun at those wavelengths, the mean wavelength actually recorded was calculated; and, using the Davos data for 50° elevation, found to be 325 nm.

Interference filters IF310 and IF320 with narrower band-widths near 10 nm, and mean calculated solar inputs near 312.5 and 322 nm, became available late in the season. The best available measure was then the IF310 filter reading. The radiometer was pointed in various directions: towards the sun gives approximately the direct UV and vertically gives a relative value of the diffuse UV. Readings were mostly taken in the open but also within small trees – under tufts of leaves, part-way up or in the shade at the base.

Table 1. Effects of some treatments in 1984 UV trials on *P. flammea* larval survival at N. Dalchork

(Trees (1.6 m) sprayed on 28 May, 31 May or 5 June with Micron Mini Ulva. NPV at 6 x 10^7 PIBs/ml and 1% egg albumen (EA) unless otherwise stated; at 2.7 ml/tree)

Plot	Treatment	Crude % infected[a]	Final % mortality[b]	% larval survival[c]
1	20% Actipron (no EA)[d]	18.7	38	52
2	1% Tinopal CBS-X[e]	22.4	60	45
4	2% charcoal	23.0	43	17
5	EA and virus only	22.5	55	90
7	2% indian ink	19.6	47	78
9	0.5% nigrosine[f]	7.1	16	54
6	EA only (control)	1.3	4	81
11	Unsprayed control	0	0	64

[a] Mean of trees harvested at 3 dates, 25 June, 2 July, 9 July.

[b] Calculated assuming that all larvae infected at first harvest had died by the second, etc.

[c] Healthy larvae on 9 July, divided by total larvae on 25 June. % mortality should be 100 minus this figure.

[d] BP Oils Ltd., London, SW1.

[e] Ciba-Geigy Ltd., Manchester.

[f] BDH Chemicals Ltd., Poole.

Measurements of UV penetration of trees

Direct radiometer measurements were supplemented by comparing on 8 July the leaf area of four trees approximately 1.6 m high (one side of needles only) with field measurements of the area of shade they cast. The ratio suggests how many layers of foliage the UV must pass before reaching the ground. Data were also obtained on 8 July of the percentage of old foliage remaining on the trees after a variable amount of defoliation by pine sawfly, *Neodiprion sertifer*, since the sprays were applied.

1984 spray experiments

The 1984 experiments used small (1.6 m) trees, sprayed with a Micron Mini-Ulva sprayer (Micron Sprayers, Bromyard, UK). A trial run used microslides (Camlab Ltd., Cambridge, UK), paper targets and painted foliage to reveal the coverage of spray labelled with nigrosine. Virus suspensions, with various adjuvants (Table 1) were sprayed at different times to allow natural UV to degrade them over 0, 5 or 8 days before about 40 newly hatched *P. flammea* larvae, whose development had been slowed by storage at 5°C until 5 June, were put on each of nine trees per treatment. Trees within a treatment were 30 m apart, and between treatments at least 80 m apart to minimise effects of downwind spray drift. The wind was strong (typically 6-7 m s^{-1}) during nearly all of the three spraying operations, from the north for the first spray and from the east for the second and third.

Results and Discussion

Strength of solar UV on sunny days

Calculations from the literature (Table 2) suggest that on sunny days with solar elevation 50°, N. Dalchork should receive 67 per cent of the 310 nm UV falling at the equator. Macam readings with IF310 filter, pointed at the sun, suggested 77 per cent and those with standard 310 nm filter, 87 per cent. However, 50° elevation is near the limit for N. Dalchork at the time of spraying, while near the equator the sun rises to 70° and above for long periods.

Davis *et al.* (1978) used a UV-sensitive polysuphone film to give integrated daily totals of 'biologically active'

Table 2. UV radiation: 310 nm at N. Dalchork and elsewhere

Solar elevation	Calculated from literature allowing for altitude and ozone		Observed at same elevation, µW cm^{-2}		
	Location	µW cm^{-2} nm^{-1}	Location	IF310 filter	310 std filter
50°	Davos 1700 m	8.8			
(Bener, 1960)	N. Dalchork 200 m	6.0	N. Dalchork	104	384
	Equator 0 m	8.9	22 June		
50°	Equator 0 m	15.0	Dodo Creek 9°S[a]	135	440
(Baker *et al.*, 1982)			22 September		
70°	Equator 0 m	29.0	Dodo Creek 9°S[a]	216	608
(Baker *et al.*, 1982)			22 September		

[a] Data from P. F. Entwistle

UV. They found this to be twice as much at Innisfail, Queensland (17°S) in November as at Waltham Abbey, Essex (52°N) in July. The average noon elevations are respectively near 86° and 55°.

Thus the solar UV in N. Scotland is of the order of 2-5 times weaker than that of comparably sunny days near the equator.

UV in poor weather

The 1984 spray programme was followed by rainy as well as sunny days and the average cloud cover over 8 days was near 6/8. By graphing the readings and summing the area under the daily curves (e.g. Figure 2), the total UV energy inputs were approximately compared.

The UV recorded in the open under cloudy or rainy conditions was much less than that under sunny conditions. With the radiometer pointed at the sun the lowest rainy-day total (standard 310 nm filter) was only 7 per cent of the highest sunny day total; when pointed vertically the rainy-day total was relatively more, at 30 per cent. The percentage for global UV must lie between these values. It was less than that obtained in Florida by Green *et al.* (1974) who found that global radiation was reduced, by 5.6 per cent for each tenth of cloud cover, to 44 per cent on a rainy day with total cloud cover.

These data suggest a greater impact of rain and cloud cover in N. Scotland than under average conditions at the equator.

UV penetration of the trees

On a sunny day the within-tree radiometer recordings were a very small percentage of the direct-sun and vertical readings outside, respectively (Table 3).

Table 3. UV readings within and outside a 2 m *Pinus contorta* tree on a bright July day at N. Dalchork

(N. Dalchork, near UV trial plots. 5 July 1985; fairly bright; cloud cover 5 but sun visible through it. Readings from Macam spectroradiometer UV 103, in µW cm^{-2}).

Orientation of meter	310 standard filter		310 interference filter		
	In the open 1419 h	In/near tree 1425 h	In the open 1347 h	In the open 1438 h	In/near tree 1438 h
At sun	360	430	63	75	116
Vertical, open sky	90	40-80	17	7-9	
Below tufts of foliage at sun	–	3, 12, 13, 3, 5 ($\bar{x}$ = 7)	–	2, 2, 1, 0, 0 ($\bar{x}$ = 1.0)	0, 1, 2, 0, 2, 2 ($\bar{x}$ = 1.2)
(% of sun		1.6		1.3	1.0)
(% of vertical		11.3		12.5)	
(% of open vertical		7.7		5.9)	
Base of tree, at sun				0-5	0-5

The shade cast by a pine needle varies with its orientation; with a solar elevation of 45°, close to that recorded on 8 July, the ratio of leaf area to its shadow is 1:1. The ratio is the same for a horizontal leaf, and ranges from 1:nearly zero for one pointed at the sun to 1:1.41 for one normal to the sun's rays. For new shoots which grow nearly vertically the ratio is very near 1:1 and for old leaves of mixed orientation an overall ratio of near 1:1 is also likely.

On 8 July the ratios ranged from 1.2:1 to 2.5:1. A more speculative back calculation was made to the time of larval placement (5 June), when old foliage was denser, new foliage much smaller and solar elevation similar, giving ratios from 2:1 to 4.5:1 and the number of layers from 2 to 4.5. Assuming the under surface of the top layer and all the lower layers are shaded then 75 to 88.9 per cent of the total leaf surface was shaded on 5 June at noon. At that time any virus so shaded would have been protected from direct solar UV. The degree of shade on a particular surface must however vary with time of day.

Much slower inactivation would be expected than found by David (1968) who used leaves laid flat, singly and constantly exposed to UV. Timans (1982) noted that virus spread on slides was 50 per cent inactivated ten times as quickly as that on the leaves of small sprayed oak trees.

Tree size and UV penetration

The N. Dalchork data above refer to small (1.6 m) trees but the more serious *P. flammea* infestations are on bigger (*c.* 5 m) trees, where radiometer readings were not taken. On apple trees Richards (1984), in studies with different objectives, found that virus inactivation rates, presumed due to UV, were much faster in small (1.2 m) trees than in bigger (4 m) ones (Figure 5).

Thus internal shading could decrease the overall UV exposure of virus deposits on many leaf surfaces especially in larger trees.

Virus inaccessible to UV?

Richards' data also suggests that the virus decay curve flattens out and that a residue of the viral activity may persist beyond the critical period. This residual activity is proportionately larger on big trees (8 per cent) than on small ones (0.2 per cent).

Possibly some virus reaches sites permanently inaccessible to solar UV. An Australian paper (Reed, 1971) demonstrated that virus inclusion bodies (IB) had entered the stomata of potatoes: he used a surfactant, Tween 20 (Sigma Chemical Co., St Louis, Missouri, USA). Electron microscopy of *Pinus contorta* leaves shows that the stomata are big enough (near 12 x 8 μm) to admit IBs (approximately 1-3 μm) and they may account for as much as 0.3-0.5 per cent of the total area of leaf when the stomata are widely open. However IBs mostly arrive in spray droplets bigger than the stomata, and this may hinder their entry. Other possible refuges include crevices in the bark, especially in bigger trees, in leaf sheaths and between pairs of needles, and in the tightly packed leaves of new shoots.

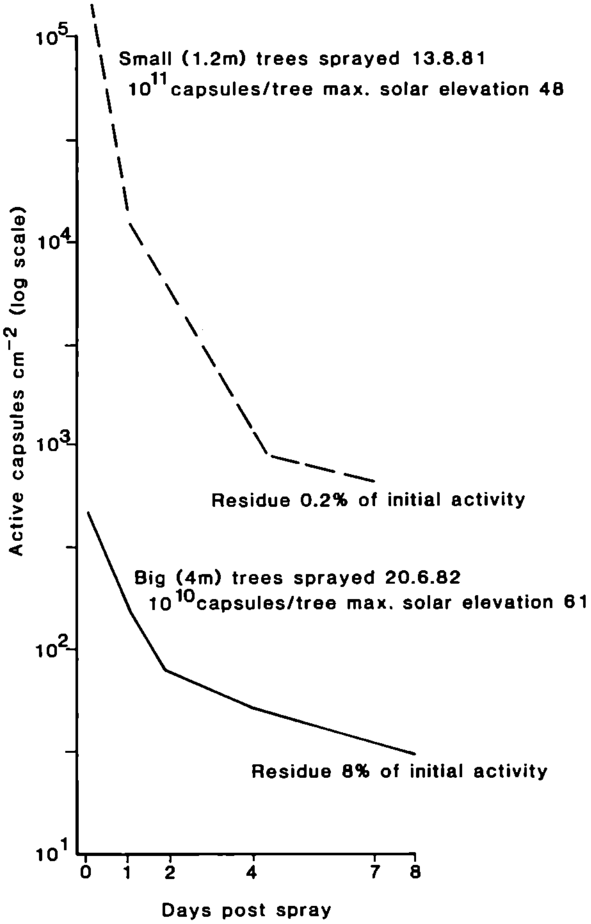

Figure 5. The decay of virus activity in large and small apple trees (Richards, 1984).

Leaf eating insects other than *P. flammea* may also temporarily protect the virus from UV within their bodies or in frass, though its subsequent fate is not known; e.g. the Pine sawfly *N. sertifer* consumed many virus sprayed needles.

Spray distribution and *P. flammea* behaviour

The trial run using nigrosine showed that spray could be recovered from any part of the tree. Furthermore, the wind during spraying (from east and north) is likely to have placed relatively more spray on their shadier sides, where the virus may remain active.

Much in practice depends on the behaviour of *P. flammea* larvae, and Ballard (see paper on pp. 31-36) has documented their migrations. If the larvae are always to feed on leaves on the sunny outer surface of the tree, then UV inactivation of the virus could save them from disease. If, as seems likely, they do much early feeding in new buds, then the initial dose of spray is, like the silhouette of the buds, small, but some virus has a good chance of being shaded within the buds against UV. Larvae that move, and early on eat enough virus elsewhere in the tree that is protected from UV, are at risk.

Practical observations

We have few data on how UV affects *P. flammea* NPV in practice. Entwistle and Evans (1985) used experimentally in 1983 4 x 10^{11} and 8 x 10^{11} IBs per ha and no UV protectants, and found high levels of larval infection but also virus shown to be ineffective 2 weeks after spraying. Two features may explain the lack of impact of UV at that time. For the week following the spray, the cloud cover was heavy, nearly 7/8 (Anon., 1983). Also, the 20 per cent Actipron spray additive may have conferred some UV protection; it was found to give high absorbance values at 310-320 nm but these varied unaccountably with concentration, batch and age of the material.

The 1984 UV trials gave equivocal results. The latest spray might have been expected to have the strongest effects and the earliest the weakest, but this did not happen (Figure 6). Cloud cover was again heavy. Likewise the UV-protected virus might have been expected to infect more larvae than that without protectants. In fact (Table 3) two formulations (Indian ink and charcoal, each with egg albumen), and also Actipron with no egg albumen, gave no higher infection than the virus with egg albumen alone. One with nigrosine gave lower infection. Only the treatment with egg albumen and Tinopal CBS-X gave a higher larval mortality, and even in this case the number of surviving larvae fell no more steeply than that of some other treatments.

Conclusions

The thesis that "UV on *P. flammea* NPV is a non-problem" remains unproven. It seems probable that the UV input on a sunny day in Scotland, though less than near the equator, is significant, but rainy days reduce it; that trees, especially big trees, give the virus considerable protection; that *P. flammea* behaviour affects its chance of acquiring an infective dose; and that some existing spray treatments used in Scotland are capable of succeeding despite the UV. These inferences need confirmation.

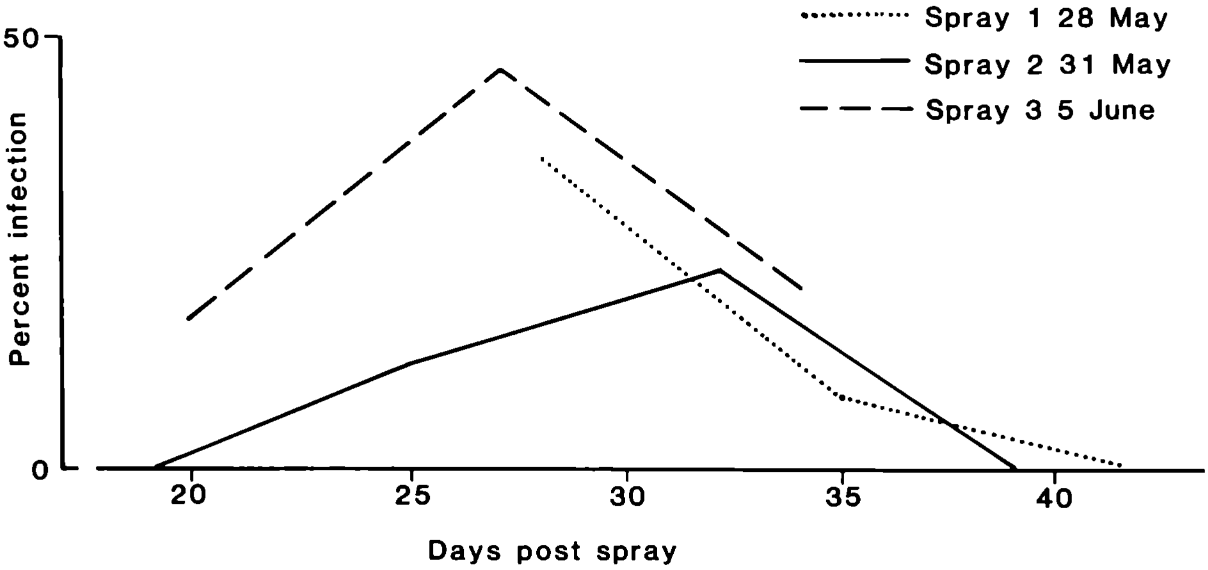

Figure 6. North Dalchork Forest UV trials 1984: the percentage infection of harvested larvae following spray applications on one of three different dates. Data for plots 1, 2, 4, 5 and 6 are combined for each spray separately. Each tree (1.6 m) received 2.7 ml of spray containing 6 x 10^7 polyhedra ml^{-1}.

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The Impact of Aerial Applications of Fenitrothion on Forest Bird Populations

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Introduction

Fenitrothion is an organophosphorus (OP) insecticide which kills animals by inhibiting the activity of acetylcholinesterase (AChE): nerves become unable to repolarise after a period of continuous stimulation due to a build-up of acetylcholine at synapses (Fleming and Grue, 1981). This mode of action is common to OPs and carbamates, the pesticide classes which have largely replaced organochlorines for forest pest control since the late 1960s (Symons, 1977; Peakall and Bart, 1983), although carbamates have never been used for this purpose in Britain.

Since 1967, in eastern Canada, fenitrothion has been sprayed aerially to control Spruce budworm (*Choristoneura fumiferana*) over large areas (Peakall and Bart, 1983). Subsequently and after due consideration and testing, fenitrothion was chosen by the Forestry Commission in Britain to control outbreaks of the Pine beauty moth (*Panolis flammea*) in Lodgepole pine (*Pinus contorta*) plantations in Scotland (Stoakley and Heritage, 1979). The history of spraying operations in Scotland is given elsewhere in this volume (see the following paper by Stoakley, pp. 87-90). It should be noted that although the Spruce budworm control programme, using fenitrothion, has become annual over large areas of Canada, Pine beauty moth control is considered to be much less intractable due to the Pine beauty's life history, mode of feeding and forest relations; furthermore, a much higher percentage kill can be expected from one application of fenitrothion (J. T. Stoakley, personal communication).

Despite its extensive use in Canada, two major Canadian reports on fenitrothion (NRCC, 1975; Roberts *et al.*, 1977) draw attention to large areas of ignorance about the fate and effects of the chemical in the environment after large-scale aerial spraying of forests. In 1978, limited clearance was given for aerial applications of fenitrothion in Scotland under the UK Pesticides Safety Precautions Scheme, subject to the condition that adequate environmental monitoring was undertaken, with special reference to any direct risks to people. The results of the environmental monitoring were detailed in Holden and Bevan (1979, 1981) and concluded that the effects on humans and wildlife were insignificant. However, some sublethal poisoning had been detected in forest passerine birds in 1979 and 1980 (Hamilton *et al.*, 1981) and a three-year study was initiated in 1981 to examine in detail the effects of fenitrothion applications on forest birds (Spray *et al.*, 1987).

In this paper, a general framework for studying the effect of fenitrothion on forest bird populations is suggested. The pathways through which birds could be poisoned are considered and a hierarchy of levels, from population to the individual, at which detrimental effects of fenitrothion might be observed, is constructed. At each level of the hierarchy, methods used to investigate pesticide impact are examined and their use in Scotland and elsewhere is discussed. In particular, the results of the three-year investigation mentioned above are summarised. It should be noted that most studies concentrate on small passerines, which occur in sufficient numbers to provide adequate sample sizes;

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larger species tend to be present at very low densities and therefore present logistical problems for their study.

Fenitrothion and Forest Birds: Poisoning Pathways

Pathways, timing of spraying and the duration of effects

Aerial application of fenitrothion by the ultra-low-volume technique deposits the majority of spray droplets in the forest canopy (Joyce *et al.*, 1981), and only 6 per cent of the droplets reach the ground under trees (Crick, 1986). Therefore canopy-dwelling birds are most exposed to direct contact with the spray cloud.

In addition to direct exposure, secondary poisoning is possible through the ingestion of poisoned food. Those birds which feed on lepidopteran larvae in the canopy are likely to ingest some poisoned prey. Scottish spraying operations are timed to occur when 90 per cent of Pine beauty moth eggs have hatched (Stoakley, 1981), at the end of May or beginning of June. At this time of year, most forest birds are part-way through nesting, although species such as crossbill (*Loxia* spp.) and crested tit (*Parus cristatus*) have usually finished. Nestlings of forest passerines are generally fed invertebrate prey by their parents and therefore may be at risk due to ingestion of poisoned food items.

Exposure to fenitrothion is limited by its persistence in the environment. Direct exposure of birds to the spray cloud can probably only occur within an hour of the application (Holden and Bevan, 1981). Exposure to fenitrothion through invertebrate food can occur probably only during a few days after spraying because deaths of Pine beauty moth larvae stop 2-3 days after spraying (Barbour, 1979). In Canadian studies, fenitrothion concentrations on conifer foliage decreased by 50 per cent after 4 days and by 70-85 per cent after 14 days (Yule and Duffy, 1971). Rapid environmental degradation of fenitrothion and a rapid insect kill reduces the period in which birds could be poisoned to not more than 7-14 days immediately post-spray. Throughout and after this period, birds may also be further affected by a reduction in the availability of their invertebrate prey.

A hierarchy of effects on birds

Fenitrothion spraying programmes could have detrimental effects on the population levels of forest birds, or relatively minor effects on individual birds, such as temporary decreases in nestling growth rates. It is possible to construct a hierarchy of effects on forest birds, to allow a graded assessment of environmental impact. The hierarchy used is outlined in Figure 1, and considered below are what can be done and what has been done in Scottish forests to assess fenitrothion impacts at each level of the hierarchy. Also, evidence from other countries of the effects of fenitrothion on forest birds is considered. Control operations in Scotland are relatively recent, and effects found during the long-running programmes in North America could be relevant to the former because fenitrothion has been mostly sprayed at ultra-low-volumes in both regions, although there are large differences in scale and in spraying regimes.

LONG-TERM REDUCTION IN BREEDING NUMBERS
APPARENT SHORT-TERM POPULATION CHANGES
ADULT DEATHS
NESTLING POISONING
BREEDING SUCCESS CHANGES
SUBLETHAL EFFECTS
Inhibition of Brain AChE
Adult Activity Changes
Changes in Nestling Growth, Parental Behaviour and Nestling Diet

Figure 1. A hierarchy of detrimental effects on forest birds due to aerial application of fenitrothion.

Do Fenitrothion Applications Affect Forest Birds?

Long-term reduction in breeding populations

There are several approaches to assessing changes in population densities of territorial forest passerines, including: (a) territory mapping, (b) transect and point counts; (c) capture-mark-recapture; and (d) nest counts. These can provide either relative or 'absolute' measures of bird density during the breeding season and full details of techniques can be found in IBCC (1970), Shields (1979) and Ralph and Scott (1981). However, only the first method has been used to assess long-term changes consequent upon fenitrothion spraying.

Territory mapping was used in a three-year experimental study in Scotland to detect year-to-year variation in population densities of breeding birds in an area sprayed with fenitrothion and in an adjacent unsprayed area (Spray *et al.*, 1987). This study showed that spraying had no effect on population densities in the next year: between two years there were parallel variations in population densities of five forest bird species in sprayed and unsprayed areas. The changes in density of territorial males singing were, in sprayed and unsprayed plots respectively: − 15.9 per cent and − 16.3 per cent for robins *(Erithacus rubecula)*, + 6.0 per cent and + 39.5 per cent for chaffinches *(Fringilla coelebs)*, − 14.9 per cent and − 15.0 per cent for willow warblers *(Phylloscopus trochilus)*, − 36.2 per cent and − 42.5 per cent for goldcrests *(Regulus regulus)*, and + 42.4 per cent and + 27.0 per cent for coal tits *(Parus ater)*; the differences between sprayed and unsprayed areas were not statistically significant. It must be noted that in this study the area sprayed (70 ha) was small and that movement into the 15 ha census plots from the surrounding forest could have occurred.

Apparent short-term population changes

a. Transect and point counts

Both transect and point count censuses have been used widely to assess short-term changes in population levels immediately following application of pesticides. Results from such census techniques are difficult to interpret since, in effect, they measure bird detectability, which is a composite function of activity, breeding phenology and abundance. A pesticide may affect the activity level of birds within a sprayed area, and hence their detectability to an observer, without any real changes in abundance, or indeed mortality (Grue and Shipley, 1981). Apparent activity levels of territory holders could decrease due to death, sublethal incapacitation, or out-of-area movements. Conversely, activity levels could apparently increase if resident birds increased singing levels following nesting failure; or if territories of dead or incapacitated birds were to be taken over by immigrants (e.g. Krebs, 1977; Edwards *et al.*, 1979). The use of these techniques in monitoring short-term changes in population levels cannot differentiate between these processes.

In Scotland, the first fenitrothion spray programme was monitored in sprayed areas only (Broad and Dennis, 1979) using transect counts. Willow warbler and robin numbers apparently declined after spraying, but began to recover after two weeks. However, these observations are only anecdotal due to the lack of any control counts. In 1983 and 1984, point count censuses were made in four 70 ha plots in Scotland, two of which were sprayed with fenitrothion at 300 g ha^{-1} (Spray *et al.*, 1987). These censuses revealed in each season broadly parallel changes in bird numbers in each pair of matched sprayed and unsprayed plots (e.g. see Figure 2). For the five commonest species of birds in Lodgepole pine plantations, this method did not detect any effect of fenitrothion.

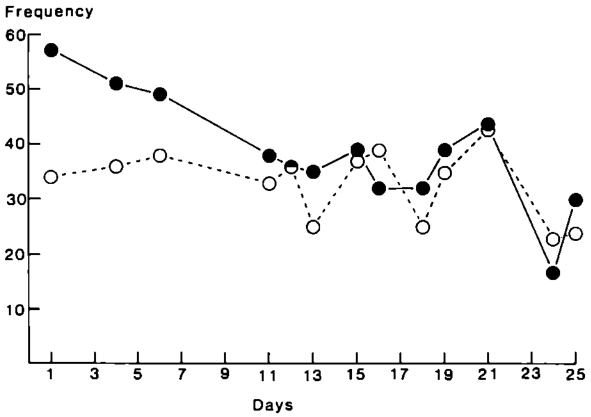

Figure 2. Total numbers of singing chaffinches recorded daily at 16 fixed points in a sprayed plot (filled circles) and a control plot (open circles) in 1984 in Elchies forest (fenitrothion spray applied on day 17).

In Canada, Pearce, Peakall and Erskine (1976) compared transect censuses made shortly before and after spraying with fenitrothion: a dosage rate of 175 g ha^{-1} caused significant decreases in ruby-crowned kinglets *(Regulus calendula)* and Cape May warblers *(Dendroica tigrina)*; but on a separate occasion fenitrothion at 280 g ha^{-1} caused significant decreases of the latter species only. Pearce, Peakall and Erskine (1979) found that two successive applications of fenitrothion (emulsifiable concentrate formulation) in water at 210 g ha^{-1} decreased ruby-crowned kinglet numbers in nine out of ten transects. When fenitrothion was sprayed twice at 210 g ha^{-1} in an oil solvent, then the impact on forest birds was much less: only the ruby-crowned kinglet decreased and then only in one of six transects (Pearce *et al.*, 1979).

Problems associated with the interpretation of transect counts have been suggested from studies of other pesticides. Moulding (1976) found that short-term declines in numbers of singing birds after a carbaryl application could have been due to out-of-area feeding, or perhaps to skips in spray coverage which had left food 'islands' for birds. Bracher and Bider (1982) used 'sand transects' to monitor aminocarb spraying in a forest: transects provided an index of animal activity as revealed by their footprints and other signs in a 305 m sand strip. Avian activity increased after spraying, probably because of the abundance of dead invertebrates on the ground. Birds may have shifted their foraging niche from amongst trees to the ground due to relative changes in food availability. This is another factor which could change the detectability of birds in standard transect and point counts.

b. Capture-recapture techniques

The use of mist-nets or other traps could allow assessment of the effects of fenitrothion applications on resident bird populations. Similarly, observations of marked birds, singing or otherwise active in an area, could reveal losses of resident individuals. In Scotland, however, neither technique was successful because low population densities resulted in low numbers of captures per unit effort (51 birds caught in 700 mist-net-hours). In addition, observations were severely limited by the impenetrability of the Lodgepole pine plantations (Spray *et al.*, 1987). The technique has not been used elsewhere to monitor forest spraying programmes.

c. Summary

Various techniques have been used to assess the changes in numbers of birds on a short-term basis, immediately before and after spraying. These methods suffer from severe practical and interpretational problems when used in the field and have limited capacity to detect less than major impacts (see also Peakall and Bart, 1983). In Scotland, no apparent short-term changes in bird numbers occurred after spraying with fenitrothion (Spray *et al.*, 1987).

Poisoning of adult birds

a. Measurements of whole-body fenitrothion residues

In the Scottish spray programme from 1978-80, fenitrothion deposits on birds and insects were measured by Hamilton *et al.* (1981). Fenitrothion was applied from a fixed-wing aircraft at 3000 g ai ha^{-1} using rotary atomisers at a volume application rate of 1 l ha^{-1} (ultra-low-volume). Whole body residues measured on the day after spraying in 1979 were 0.80 mg kg^{-1} body weight for chaffinches ($n = 7$), 7.45 mg kg^{-1} for coal tits ($n = 13$) and 1.90 mg kg^{-1} for willow warblers ($n = 12$). At least 95 per cent of the total body burden in each sample was on the skin and plumage. Coal tits received the highest dose of pesticide and the inhibition of their brain AChE was also highest at 47.1 per cent, consistent with the observation that they feed higher in the Lodgepole pine canopy than the other two species (Spray *et al.*, 1987).

b. Calculations of ingestion rates of fenitrothion

The majority of forest passerines are insectivorous during the summer. The minimum ingestion rate of fenitrothion by birds would be zero if they avoided dead or partially poisoned insects. In Scottish Lodgepole pine plantations, coal tits and goldcrests were most vulnerable to the ingestion of fenitrothion in their food. They are small, insectivorous, canopy-feeding species and laboratory studies have suggested that small species are most sensitive to the effects of an OP (Hill *et al.*, 1975). Coal tits were the more suitable study species, because they were present at higher population densities, were more audibly apparent and took readily to nestboxes. Calculations of ingestion rates of fenitrothion for coal tits were made below because they were likely to receive a relatively large (secondary) dose in their food.

Hamilton *et al.* (1981) measured the residue of fenitrothion on Pine beauty moth larvae to be between 1.3 and 2.7 mg kg^{-1}; on other invertebrates they found residues of between 0.5 and 25.0 mg kg^{-1}. Feeding rates of adult coal tits during breeding are unknown (Perrins, 1979) but Gibb (1957) showed that adult coal tits ate between 3.1 and 3.5 g wet weight of insects per day in winter. From the residues found on Pine beauty larvae (see above), such feeding rates could result in a daily intake of fenitrothion of between 4.03 and 9.45 µg. The mean weight of coal tits is 9.3 g (Perrins, 1979), thus the daily dietary intake of fenitrothion from Pine beauty larvae would be between 0.43 and 1.02 mg kg^{-1} body weight. From the highest residue values found on other invertebrates (Hamilton *et al.*, 1981), the maximum daily dietary intake would be 9.6 mg kg^{-1}.

In summary, Hamilton *et al.* (1981) have shown that coal tits may receive 7.5 mg kg^{-1} body weight of fenitrothion directly on the plumage, and the calculations above suggest that they could ingest up to a maximum of 9.6 mg kg^{-1} daily in their diet. The only passerine species for which toxicity tests of fenitrothion have been done is the red-winged blackbird *Agelaius phoeniceus.* This species is five times heavier than the coal tit and had an acute oral LD50 of 25 mg kg^{-1} body weight (Schafer, 1972). It seems possible, therefore, that adult coal tits could acquire a lethal or significant sublethal dose of fenitrothion within a few days of spraying.

c. Death of adult birds

In Canadian forests, searches produced no dead birds after fenitrothion applications at 140 g ha^{-1}; up to 0.9 dead birds h^{-1} (mean = 0.4 h^{-1}) at 280 g ha^{-1}; up to 4.5 h^{-1} (mean = 0.4 h^{-1}) at 420 g ha^{-1}; and up to 1.2 h^{-1} (mean = 0.7 h^{-1}) at 560 g ha^{-1} (Peakall and Bart, 1983). These figures were for birds such as kinglets, vireos and some parulid warblers which feed on sedentary canopy invertebrates, but pre-spray population densities of birds subjected to each spraying regime were not given.

The carcasses of three species of forest bird (magnolia warbler *Dendroica magnolia,* blackburnian warbler *D.*

fusca and American redstart *Setophaga ruticilla*) found in spray zones after fenitrothion applications at 206 g ha^{-1} had whole body (less head) residues of 1.11 to 5.22 mg kg^{-1} (NRCC, 1975). In other spray operations, involving fenitrothion at 206 g ha^{-1}, or two sequential applications at 138 g ha^{-1} dead forest birds (warblers, dark-eyed juncos *Junco hyemalis* and purple finches *Carpodacus purpureus*) carried residues of 0.1 to 4.7 mg kg^{-1} and their brain AChE was inhibited by 50-80 per cent (NRCC, 1975). After an accidental overdose of fenitrothion in Quebec, several dead tree swallows *Iridoprocne bicolor* were found which had high concentrations of fenitrothion on their plumage (197.2 ppm) and in their gizzards (2.28 ppm).

Reviews of Canadian research on fenitrothion forest spraying have concluded that applications at 275 g ha^{-1} killed some adult birds and that mortality increased sharply at 550 g ha^{-1} (Buckner, 1974; NRCC, 1975). After fenitrothion was sprayed twice at 210 g ha^{-1}, followed by aminocarb at 70 g ha^{-1}, Buckner and McLeod (1977) found no bird carcasses, although search hours were not recorded.

Searches for carcasses of small birds after Scottish fenitrothion operations have not been productive, although the man-hours spent searching were not detailed (Broad and Dennis, 1979; Hamilton and Ruthven, 1981b). One severely incapacitated chaffinch was found 24 h after spraying in 1980: it had a whole body fenitrothion residue of 1.38 mg kg^{-1} body weight, and its brain AChE activity was inhibited by 50 per cent (Hamilton *et al.*, 1981). However, while monitoring the growth rates of nestling coal tits in 21 nestboxes inside sprayed areas in Scotland during 1983 and 1984, no losses among parents attending the nest were observed (Spray *et al.*, 1987).

In summary: mainly from N. American experience forest bird mortalities have occurred at fenitrothion dosage rates of >206 g ha^{-1}. Whole body fenitrothion residues of birds found dead in sprayed areas have varied between 0.1 and 5.2 mg kg^{-1} and the activity of brain AChE in dead birds has been inhibited by 50-80 per cent. There is often little relationship between fenitrothion residues and brain AChE activity because fenitrothion is rapidly degraded and can be excreted after enzyme inhibition has occurred (Hamilton *et al.*, 1981; Busby, Pearce, Garrity and Reynolds, 1983; Peakall and Bart, 1983). Measurements of the level of AChE inhibition in field studies following application of other OPs, indicate that death due to poisoning can occur at levels as low as 57 per cent, but that the majority of values are greater than 80 per cent (e.g. White *et al.*, 1979; Felton *et al.*, 1981; De Weese *et al.*, 1983). These field data correspond well with fatal levels of brain AChE inhibition found in laboratory studies (e.g. Mehrota *et al.*, 1967; Grue, 1982; Evans and Rosenblum, 1984). In the Scottish spraying programmes there has been no evidence of bird fatalities due to fenitrothion applications at the dosage of 300 g ha^{-1}.

Poisoning of nestlings

Despite Dittrich's (1966) early observations on the mortality of nestling coal tits fed lepidopteran larvae poisoned with phosphamidon, this has been a neglected aspect of forest-spray monitoring. Nestling coal tits at 9 to 10 days old receive between 1.58 and 5.14 g day^{-1} of invertebrate food material (Gibb and Betts, 1963). Using residue values found in Pine beauty larvae (see above), nestlings could receive between 2.05 and 13.88 µg fenitrothion day^{-1}. Ten-day old nestlings in Lodgepole pine plantations weigh between 6 and 9 g (Spray *et al.*, 1987). Thus 6 g nestlings could be fed a daily dose of dietary fenitrothion in Pine beauty moth larvae at between 0.34 and 2.31 mg kg^{-1} body weight; and 9 g nestlings could be fed fenitrothion at between 0.23 and 1.54 mg kg^{-1}. Using the highest residues on other invertebrates recorded by Hamilton *et al.* (1981) the maximal intake of fenitrothion would be 21.42 mg kg^{-1} for 6 g nestlings and 14.28 mg kg^{-1} for 9 g nestlings. Given that nestling brain AChE levels are likely to be lower than in adult coal tits (Grue *et al.*, 1981; Grue and Hunter, 1984), and that juvenile birds are usually more sensitive than adults to OP-induced toxic effects (Ross and Sherman, 1960; Hudson *et al.*, 1972), our calculations suggest that nestling coal tits could be vulnerable to fenitrothion applications.

In the experimental fenitrothion application in Scotland in 1984, two coal tit nestlings found dead within 4 days of spraying contained residues of fenitrothion of 0.04 and 0.36 mg kg^{-1}, although their deaths could not be ascribed certainly to poisoning. A further six nestlings found dead 10 to 16 days post-spray had no detectable fenitrothion residues (Spray *et al.*, 1987). Thus the information available suggests that nestling coal tits are not exposed to lethal doses of fenitrothion, although it must be noted that there is no knowledge of LD50s from fenitrothion for nestling passerines.

Breeding success

In coniferous forests the nests of small passerines are very difficult to find and observer interference may increase the probability that they will be deserted or predated (Peakall and Bart, 1983). One way around these problems is to erect nestboxes at suitable densities to obtain an adequate sample of study nests.

In Canada, fenitrothion sprayed once at 420 g ha^{-1} and again, 'several days later', at 210 g ha^{-1} resulted in a high degree of nest desertion by female white-throated sparrows *Zonotrichia albicollis:* the proportion of eggs that produced fledged young was only 12 per cent, compared to 58 per cent in a control area (Peakall and Bart, 1983). Busby *et al.* (1981) reported that a 40-50 per cent inhibition of brain AChE in white-throated sparrows due to fenitrothion, caused increased nest desertion and nest predation. However, in these Canadian studies, no details were given of the timing of spraying in relation to the breeding cycle of the white-throated sparrow, or of the probabilities of renesting.

In Scotland, the breeding success of coal tits nesting in boxes was measured in areas sprayed with fenitrothion and in control areas (Spray *et al.*, 1987). During 1983 and 1984, there were no differences in clutch size, brood size at hatching, or brood size at fledging between 29 nests in the sprayed plots and 21 in the unsprayed plots. In the earlier Scottish spray programme, Broad and Dennis (1979) had seen one nest of willow warblers fledge successfully and had observed that fledging family parties of passerines were widespread and numerous later in the year. Similar observations were made after the experimental application in 1983, when also colour-ringed coal tits, which were known to have fledged from within the sprayed area, were seen later in the year (Spray *et al.*, 1987).

Sublethal effects

a. *Inhibition of brain AChE*

Sublethal poisoning of forest birds by fenitrothion can be monitored directly by measuring inhibition of brain AChE activity. After Scottish spray operations, the maximum AChE inhibition in a chaffinch was 74 per cent, and inhibition was still apparent in some chaffinches after 21 days (mean values are in Table 1) (Hamilton *et al.*, 1981). Individual coal tits and willow warblers had AChE activity inhibited by up to 62 per cent 2 to 4 days after spraying, and inhibition was still apparent in some birds at 11 and 21 days post-spray, respectively (Hamilton *et al.*, 1981).

In Canada, the mean values of brain AChE inhibition found in birds surviving fenitrothion applications have been up to 52 per cent (Table 1), although the majority were inhibited by less than 30 per cent. One should note that Table 1 includes species which are not just canopy feeders, but also birds such as chaffinch and white-throated sparrows, which forage mainly on the ground. Brain AChE inhibition following spraying increases to maximum levels after 2 to 3 days (Table 1), implying that secondary poisoning could have occurred in addition to an immediate effect due to exposure to the spray cloud. Recovery from AChE inhibition begins in the first few days after spraying, but it is not necessarily complete 21 days later (Table 1). This conforms to the time-scale of brain AChE recovery found under controlled conditions (Fleming, 1981; Fleming and Bradbury, 1981; Fleming and Grue, 1981).

b. *Activity of adult birds*

Very little work has been done in the field on the effects of aerial application of OPs on the behaviour of adult forest birds. Busby *et al.* (1981) reported that a fenitrothion application which inhibited brain AChE by 40-50 per cent in white-throated sparrows decreased their singing activity. Practical difficulties precluded such studies in the Scottish situation.

Laboratory work with other OPs has indicated that exposure to sublethal doses can lower feeding rates and increase weight loss in birds and that such changes vary in a dose dependent manner (Rattner *et al.*, 1982; Grue, 1982). A commonly reported effect of OP poisoning of birds is anorexia (Pope and Ward, 1972) and De Weese *et al.* (1983) have found supporting evidence for this in the field. Grue and Shipley (1981) have also reported that male starlings *Sturnus vulgaris* which had been dosed with dicrotophos such that their brain AChE activity was inhibited by 50 per cent, reduced flying time by 97 per cent, singing and displaying time by 50 per cent and foraging time by 28 per cent.

c. *Nestling growth, parental behaviour and nestling diet*

Nestling growth rates of white-throated sparrows in Canada decreased after fenitrothion applications (Busby *et al.*, 1981; Peakall and Bart, 1983). After an application at 210 g ha^{-1}, the rate of body weight growth in this species significantly decreased, though reductions in the growth of tarsus, bill and wing were not significant.

Measurements of the growth of nestling coal tits from seven boxes on areas sprayed in an experimental fenitrothion application in Scotland revealed a non-significant negative trend due to spraying (Spray *et al.*, 1987). Observations in 1984 using nestboxes fitted with cameras suggested that in two out of three nests under study, one of the parent coal tits temporarily decreased its visiting rate to the nest for three days after spraying. In addition there were complex changes, after spray date, in the proportions of different types of prey brought to nests in sprayed and unsprayed plots in both 1983 and 1984, although the consequences of these changes are unknown.

Nestling growth could be affected by changes in parental behaviour, physiological effects of secondary poisoning (e.g. reduced begging for food), and changes in diet brought to the young. These aspects are poorly understood and need further investigation.

Table 1. Levels of brain AChE inhibition in surviving wild birds after aerial application of fenitrothion

Reference	Species*	Time after spraying	Dosage rate g ha^{-1}	% AChE inhibition compared to controls	N
Hamilton *et al.* (1981)	Chaffinch	1 d	300	17.5	7
	Chaffinch	4 d	300	16.9	4
	Chaffinch	11 d	300	27.8	10
Hamilton *et al.* (1981)	Coal tit	1 d	300	47.1	4
	Coal tit	4 d	300	32.2	6
	Coal tit	11 d	300	12.1	2
Hamilton *et al.* (1981)	Chaffinch	1 d	300	42.7	13
	Chaffinch	2 d	300	37.9	10
	Chaffinch	7 d	300	33.5	11
	Chaffinch	21 d	300	13.0	12
Hamilton *et al.* (1981)	Willow warbler	1 d	300	26.6	12
	Willow warbler	2 d	300	30.0	12
	Willow warbler	7 d	300	5.0	12
	Willow warbler	21 d	300	9.2	13
Busby *et al.* (1981)	Tennessee warbler	6-48 h	280	2.0	22
	Tennessee warbler	6-48 h	280	7.6	23
	Magnolia warbler	6-48 h	280	20.7	9
	Magnolia warbler	6-48 h	280	12.7	16
	Blackburnian warbler	6-48 h	280	11.6	8
	Bay-breasted warbler	6-48 h	280	32.2	7
	White-throated sparrow	6-48 h	280	12.4	16
	White-throated sparrow	6-48 h	280	14.4	13
Busby *et al.* (1983)	White-throated sparrow	24 h	210	24.0	3
	White-throated sparrow	1 d	210	16.0	5
	White-throated sparrow	2 d	210	9.0	4
Busby *et al.* (1983)	White-throated sparrow	24 h	210 + 210 5 days later	6.0	15
	White-throated sparrow	1 d	210 + 210 5 days later	22.0	10
	White-throated sparrow	2 d	210 + 210 5 days later	33.0	5
Busby *et al.* (1983)	White-throated sparrow	24 h	420	52.0	10
	White-throated sparrow	1 d	420	30.0	5
	White-throated sparrow	2 d	420	34.0	5
Busby *et al.* (1983)	White-throated sparrow	24 h	420 + 210 8 days later	6.0	4
	White-throated sparrow	1 d	420 + 210 8 days later	34.0	6
	White-throated sparrow	2 d	420 + 210 8 days later	34.0	5
	White-throated sparrow	3 d	420 + 210 8 days later	44.0	3
NRCC (1975)	Tennessee warbler	Not given	138	16-32	Not given
	Bay-breasted warbler		138	16-32	
	White-throated sparrow		138	16-32	

*Scientific names: Chaffinch *Fringilla coelebs*, Coal tit *Parus ater*, Willow warbler *Phylloscopus trochilus*, Tennessee warbler *Vermivora peregrina*, Magnolia warbler *Dendroica magnolia*, Blackburnian warbler *D. fusca*, Bay-breasted warbler *D. castanea*, White-throated sparrow *Zonotrichia albicollis*.

Discussion and Conclusions

The application of fenitrothion against Pine beauty moth using ultra-low-volume techniques reduces the risk to wildlife in forests, compared with other application methods. This method is target specific: depositing the majority of droplets in the upper canopy, with only 6 per cent of the applied chemical reaching the ground under trees. Because of this, ultra-low-volume applications are likely to minimise the impact of pesticide on forest birds, many of which feed and nest close to the ground in plantations. Furthermore, exposure to fenitrothion is limited to about 2 weeks due to its relatively rapid degradation. Birds may be affected indirectly by prey losses in the canopy, but such losses are likely to be made up relatively rapidly by the emergence of alternative prey after spraying.

There is no evidence that fenitrothion applications have caused any reduction in numbers of the common breeding birds in pine plantations in Scotland and little evidence for any sustained decreases in the much more extensive spraying programmes in North America. Annual variations in populations of small temperate forest passerines are naturally large (Perrins, 1979), and mortality due to pesticide application may be of only minor importance. However such large scale annual variations could at times mask smaller losses due to pesticide usage, which in circumstances of low population density could be significant.

Although extensive work in Canada has suggested that major reductions in certain bird species occur immediately following treatment with fenitrothion (Pearce, Peakall and Erskine, 1979), statistically significant changes in bird numbers immediately after spraying have not been found in Scotland. In nearly all field studies the techniques used to assess short-term changes in abundance have, in reality, only been able to measure changes in detectability rather than numbers. Interpretation of the data is confounded by a combination of lethal, sublethal and behavioural responses to fenitrothion application all of which may affect detectability. It is impossible to isolate or identify their relative importance without detailed knowledge of the processes by which birds are affected by fenitrothion. Thus conclusions of major reductions in bird numbers in Canada are open to different interpretations.

Laboratory studies have shown that sublethal doses of fenitrothion and of other OPs which inhibit AChE activity affect the behaviour of adult birds. Observed effects include reduced feeding rates, decreased mobility, anorexia, reduced singing activity, and lowered responsiveness to predators. However, due to practical problems it has rarely proved possible to transfer such studies into the field, and little is known still of the consequences of such behavioural changes in response to forest spraying programmes. Sublethal and behavioural changes could become important in certain situations: for instance when the maintenance of a restricted population of a rarer species needs to be considered, or when environmental stress on birds is increased due to adverse weather and feeding conditions.

In Canada, Busby *et al.* (1981) have reported increased nest desertion and predation of white-throated sparrows (with 40-50 per cent AChE inhibition) after fenitrothion application. However, studies in Scotland revealed neither any changes in breeding success of coal tits in response to fenitrothion spraying, nor any significant effects on the growth rates of nestling coal tits. This species had been predicted to be vulnerable to the effects of spraying because of its foraging niche, small size and diet. It seems likely that if coal tits are not affected then neither will be other species.

The Scottish spraying programme is at present a relatively small scale and infrequent operation and although its impact on wildlife is negligible now, certain caveats should be made concerning its possible future use:

i. Experience in Canada has shown that heavy use of pesticides to control spruce budworm since the 1950s has shortened the interval between outbreaks and prolonged their duration (Dahlstein and Rowney, 1983). Although this situation is unlikely to develop in Scotland and there is no evidence for it in the intermittent use of control measures against the Pine beauty moth over a long period in continental Europe (J.T. Stoakley, personal communication) the consequences of repeat spraying on forest bird populations cannot be predicted.

ii. The dosage rate of fenitrothion applied in Scotland (300 g ai ha^{-1}) is higher than has been recommended for safe use in other situations, although dosage rates in excess have been used elsewhere (Peakall and Bart, 1983). Symons (1977) reported that the Pesticides Ecology Research Group, which has studied large-scale pest control programmes in New Brunswick, recommended in 1974 that spraying fenitrothion once at 210 g ha^{-1} or twice (one week apart) at 140 g ha^{-1} were the levels which were 'environmentally acceptable'. In a wide-ranging review of forest spraying, Peakall and Bart (1983) concluded that 280 g ha^{-1} was the critical dosage rate at which bird casualties could be found and that at this rate the safety margin for fenitrothion was small. Thus although the Scottish spraying programme has been found to be harmless to populations of common passerines, the dosage rate of 300 g ha^{-1} could be detrimental to birds when they are environmentally stressed, and consideration may have to be given to the effects on populations of rare species, because there is considerable interspecific variation in sensitivity to pesticides (Hill *et al.*, 1975).

In conclusion, fenitrothion applications at 300 g ha^{-1} by ultra-low-volume techniques have no measurable impact on the population levels of the common forest passerine birds in Scotland. Although studies in N. America have detected bird mortality and effects on short-term activity and breeding success at similar dosage rates, only minor sublethal poisoning has been detected in Scotland.

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Pine Beauty Moth Control:

Past, Present and Future

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Introduction

Protection of crops against attack by Pine beauty moth (*Panolis flammea* D&S) may be considered under two major headings: choice of insecticide (conventional or otherwise) and choice of aerial application technique, although the two are clearly interrelated. The target is normally the larval population; the objective maximum and rapid mortality.

Prior to the Pine beauty moth outbreaks of the late 1970s, large scale control of forest defoliators in Britain had been carried out only against Pine looper moth (*Bupalus piniaria* (L.)), using first DDT and later the organophosphorus insecticide tetrachlorvinphos. Application was by fixed wing aircraft, or helicopter, using conventional boom and nozzle equipment.

Development of Control Methods

The first attempt to control Pine beauty, in 1977, used a formulation of *Bacillus thuringiensis* (Dipel) applied by helicopter and boom and nozzle equipment at 1 kg ha^{-1} to early larval stages over an area of 540 ha. This choice of pesticide was, of course, strongly influenced by environmental considerations, particularly the possible risk, or appearance of risk, to salmon of using some of the conventional insecticides. The treatment was ineffective although it was established that an adequate dosage of the material had been deposited on the foliage. It was thought probable that the mode of feeding of early instars resulted in inadequate ingestion of surface treated material. At this point a thoroughly reliable insecticide was needed for the very large control programme necessary in 1978 (*c.* 5000 ha) and the choice, confirmed by laboratory screening trials, fell on the organophosphorus insecticide fenitrothion.

At this time we were extremely fortunate in making contact with Vernon Joyce, Professor of Bio-aeronautics at Cranfield Institute of Technology who was the leading exponent of target specific ultra low volume (ULV) spraying technique. He and his colleagues and successors have led a revolution in the understanding and methodology of aerial application of insecticides. All aspects of the development and application of this method for use of fenitrothion against Pine beauty have been very fully written up and a brief summary of the basic technique will suffice.

Wind strengths of 4-5 knots (2-2½ m s^{-1}) or greater over a forest canopy, which aerodynamically is a rough surface, result in a turbulent rather than linear airflow. Droplets below a certain size are carried in this turbulent flow until they impact on a collecting surface. Larger droplets fall rapidly to the ground where they obviously play no part in pest control while contributing to contamination of the environment. The impaction efficiency of droplets carried in the turbulent flow depends on the size and velocity of the droplets so that smaller droplets are carried further downwind than larger ones, but there is a greater probability of droplets being collected within a reasonable distance downwind in a stiff breeze than in a light one. For this reason fear of excessive drift is not soundly based and the description 'drift spraying' is not appropriate. Experimental evidence on downwind movement of droplets leads to selection of a lane separation which will give optimum overall distribution of spray droplets. It follows from the foregoing that the term 'swathe width', associated with boom and nozzle spraying is not descriptive.

Fine and irregular surfaces such as tree needles, small larvae, or the hairs on such larvae are better droplet collectors than large smooth surfaces over which a laminar airflow may develop. Another consideration in determining optimum droplet size is the nature of the target. In the use of fenitrothion against Pine beauty the original concept was that there should be a high probability of individual larvae receiving direct hits from a sufficient number of droplets of known insecticide concentration to introduce a lethal quantity of insecticide based on the size of the larvae and their LD_{90} or LD_{95}. If, as has since been suggested, young larvae habitually move about more than originally suspected, or do so especially after disturbance by spraying, this should increase their susceptibility and might enable the amount of insecticide required to be reduced. Given that a certain droplet size is considered optimal — 50 µm is specified for Pine beauty — it is necessary to ensure that as much of the spray liquid is converted into droplets of this size, or, more realistically, to a close size range. This is a problem in physics, aerodynamics and engineering, including aircraft engineering with which we are much concerned.

The standard specification for Pine beauty control developed for the large programmes 1978, '79 and '80 and used, successfully, over some 6600 ha was the application of fenitrothion (50 per cent e.c. formulation) at 600 ml (i.e. 300 g a.i. plus 400 ml of butyl dioxitol (a glycol) as a diluent of suitable viscosity and low volatility, giving a volume application rate of 1 litre ha^{-1}), using rotary atomisers set to give a droplet volume median diameter of 50 µm and flown at a lane separation of 50 m. The droplet size specification can be expressed in a different way by saying that 95 per cent of the spray volume should consist of droplets in the 40-60 µm range, the remaining 5 per cent consisting of droplets of a smaller size. This programme was carried out using a Pilatus Porter, which is a large single engine fixed wing aircraft with STOL capability, equipped with Micronair AU3000 rotary atomisers. These atomisers are propeller driven and their speed of rotation therefore depends upon forward airspeed. The production of droplets as small as 50 µm requires a high speed of rotation which can be achieved, with appropriate setting of flow rate and blade angle, at the normal operating speed of the Pilatus Porter, about 90 knots.

Control Programmes Using Fenitrothion

In 1978, the first year of fenitrothion application, clearance under the Pesticide Safety Precautions Scheme was granted only for areas more than 2 miles from habitations or public roads, with the result that only 1200 ha of a 4800 ha programme was treated in this way. The remainder of the programme was carried out at low volume (LV) again using 300 g a.i. ha^{-1} but with the e.c. formulation diluted with water to give a volume application rate of 20 litres ha^{-1} and using a lane separation of 25 m. This treatment also gave satisfactory results but was clearly less efficient technically and in terms of time and cost of application.

In 1979, following a detailed report on spray deposition and on a wide variety of environmental investigations PSPS clearance was given for the whole programme to be carried out by ULV application, with some comparatively minor restrictions relating to habitations and public roads. It was understood that LV application would not be an acceptable alternative.

In 1980 there was a control programme of only 66 ha. The positioning costs for the previously used equipment could not be justified and a locally based Hiller helicopter fitted with Micronair AU5000 (Mini-Micronair) rotary atomisers was employed. These atomisers were fitted with larger than standard drums to give a higher speed of rotation at the periphery. Even so it was found in trials that adequate rpm could only be achieved by flying at greater than the normal operating speed for a small helicopter. Also, this necessitates longer than usual turns at the end of each lane. Good control was achieved but the method of flying would not be satisfactory for large operations. In 1983 and 1984 the same means was used for application of fenitrothion at the standard specification over 142 ha for experimental purposes.

Choice of Spraying Equipment

From the operational viewpoint helicopters are very much to be preferred over fixed-wing aircraft for insecticide spraying operations in upland forests. Not only are suitable landing sites for fixed-wing aircraft scarce but the general conduct of spraying depends on local weather and in particular adequate wind is a critical requirement for ULV application. It is therefore best if the customer's supervisor, who is normally a Commission entomologist, the pilot and all equipment are 'on site' for each major block to be treated. Unfortunately, however, use of propeller driven atomisers on helicopters seems unsatisfactory and other possibilities also either present difficulties or are insufficiently developed. These possibilities are:

1. use of electrical power from the helicopter's supply;
2. use of pneumatic power from the helicopter engine;
3. the provision of a supplementary power supply, such as a small petrol engine, mounted on the helicopter to produce either electrical or pneumatic power.

Surplus electrical or pneumatic power from the smaller helicopters, such as a Bell or a Hiller is surprisingly limited and it seems that only more powerful machines such as the Llama are really suitable as a power source. However a system which can operate on electrical power from a Hiller has been developed and used experimentally by the Institute of Virology and is of potential value for applying conventional insecticides as well as viruses but requires engineering improvements and then Civil Aviation Authority (CAA) clearance before use on large operations. A pneumatic system with rotary atomisers driven by standard air motors has been developed for the Llama and has CAA clearance but has not yet been calibrated or tested under operational conditions. The use of a supplementary motor, although commercially available in the USA, is as yet only a gleam in the eye as far as British practice is concerned.

There are as yet few aerial spraying contractors in Britain equipped with rotary atomisers or having a good understanding of ULV application. Also, there are few contracting companies in Britain having helicopters equipped with an electronic track guidance system. These systems are expensive and there is generally a very conservative attitude to their use, although there is in fact good evidence that they are almost essential for good control of lane separation and thus ensuring full coverage. This is particularly true of course in rugged forest terrain. Undoubtedly use of an Agrifix system avoided many tedious problems in 1978-80 and the del Norte equipment available today is more satisfactory in that it can be positioned by helicopter. Also the track flown while spraying can be recorded on magnetic tape which will subsequently give a print-out to any convenient map scale. This permanent record is valuable for checking quality of work and resolving any problems or queries. Regarding application technique there is then an interesting blend of technical requirements and problems and commercial considerations and much proselytizing will be necessary to achieve adequate availability of suitable systems.

Alternative Insecticides

The use of fenitrothion with ULV application methods has been shown, over a period of years, to be an effective and relatively safe method of controlling Pine beauty moth. The specification is also available, 'off the shelf' for other defoliator outbreaks of economic importance. It has in fact been used against Winter moth (*Operophtera brumata*) on Sitka spruce and undoubtedly could be used against Pine looper. The cost of fenitrothion is appreciably less than that of some alternatives, although this should not be an overriding consideration. So why investigate alternatives? There are three possible reasons.

1. If fenitrothion should prove less satisfactory than appears at present, e.g. if there occurred a rapid population resurgence due to ill effects on natural enemies. So far there is no such evidence although it is interesting that in two small neighbouring blocks where high populations were successfully controlled in 1978 populations were again at or near outbreak level in 1981 and control was again judged advisable.
2. For use in areas where there are genuine environmental problems *or* intolerable environmentalist pressures, even if not soundly based.
3. Because conventional insecticides are always liable to become unavailable for environmental or purely commercial reasons.

There are three obvious environmentally safe pesticides — a nuclear polyhedrosis virus, preparations of *Bacillus thuringiensis* and diflubenzuron (Dimilin). All require to be ingested and the first question is — will young larvae with their specialised mode of feeding ingest them in lethal quantities? All are slow acting and, assuming adequate ingestion, the second question therefore is — will feeding cease sufficiently rapidly to prevent unacceptable damage, bearing in mind, firstly, the nature of the damage, which is destructive to current shoots, not mere defoliation and secondly the relatively short larval feeding period of about 6 weeks. For all three the timing of application may prove more critical than in the case of conventional insecticides and if so would be a real problem in large scale operations.

Ad hoc attempts at control by application of micro-encapsulated pheromone to disrupt mating have failed to give promising results and a more fundamental approach is now required if any progress is to be made in this direction. Choice of an alternative conventional pesticide might well fall, following fashion, on a synthetic pyrethroid, probably cypermethrin. Since efficacy is virtually certain the critical question is whether the PSPS would give approval for aerial application to upland forest.

Cultural Considerations

This paper has dealt with methods of controlling outbreak populations in order to prevent anticipated death of trees. This may be likened to fire brigade action although the simile is not exact. Clearly there are possibilities for cultural practices designed to minimise the chances of outbreaks occurring — in other words for prevention rather than protection. These include planting apparently less susceptible provenances of Lodgepole pine, planting alternative species (although the choice is limited and their success on limiting sites must also be uncertain) or even leaving the most susceptible sites unplanted. For several years now sites formerly thought suitable only for Lodgepole pine have generally been planted with mixtures, usually of Sitka spruce and Lodgepole pine, with the expectation of obtaining final crops of the former following 'self thinning'. However it is by no means clear that the pine component of such crops will be any less susceptible to

Pine beauty or indeed that there will be a reduced risk of other insect pest problems in such crops.

Four facts now deserve serious consideration.

Firstly, a second major outbreak is now occurring only 6 or 7 years after the first.

Secondly, all but one of the blocks which required treatment in 1985 had high populations and were sprayed in the previous outbreak except two private woodlands which were below the minimum susceptible age (of about 10 years) at that time.

Thirdly, the two outbreaks which caused severe defoliation strongly confirm previous observations that the highest populations are associated with areas of deep unflushed peat.

Fourthly, both earlier and current outbreaks are very largely confined to sites overlying Moine schists mainly in Sutherland and, for example, have not occurred to any significant extent on superficially similar soils overlying the Old Red Sandstone, where pupal numbers are markedly low at the present time.

In the longer term the wisdom and even the feasibility of continuing to support Lodgepole pine on the worst of the susceptible sites with a regime of pesticide application, however inocuous to the environment, is doubtful and the time has come to recognise a silvicultural problem in the broadest sense of that term.

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