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REPORT

Institute of Terrestrial Ecology

Natural Environment Research Council

Report of the Institute of Terrestrial Ecology 1989/1990

Natural Environment Research Council

Contents

Environmental pollution

This Research Programme aims to study the input of pollutants to terrestrial and freshwater ecosystems, their transfer through these systems and through food chains, and their impact on plant and animal populations.

A group at ITE Edinburgh has been investigating the deposition of atmospheric pollutants for more than 15 years. Early estimates of the amount of acidic deposition falling on the different parts of the UK were based mainly on collection and analysis of rainfall in open collectors. Working with others, the Edinburgh group has shown that this approach is unsatisfactory as it ignores, or grossly underestimates, the contribution of a number of important deposition processes. The first article in this section discusses one of the processes that leads to enhanced deposition of acidic pollutants in upland areas. This kind of work has led to new estimates of the amounts of acid pollutants being deposited in the UK, and has shown that in some areas the total deposition is almost double the earlier estimates.

The amount of acidic pollution deposited at a given location is partly determined by the nature of the vegetation canopy. The composition of the incoming rainfall is then modified as it passes through the vegetation canopy and the underlying soils. The second article illustrates the impact that variations in tree species can have an atmospheric deposition and on the changes in chemistry which take place as solutes are transferred through the soil/plant system. The choice of species can have a major impact on inputs and solute transfers to waters.

Acidification of surface waters in parts of the UK has led to a decline in populations of salmonids and in the diversity of invertebrate populations. There has been little work, however, on the impact of acid waters on amphibians. The third article describes experiments which examined the response of captive populations of the common frog to variations in acidity; it illustrates the difficulties inherent in any attempt to assess impacts of pollutants on populations.

The next report discusses another, although very different, impact study which examines the influence of agricultural pesticides on non-target insects in areas adjacent to sprayed ground. Such information is important because many of our insect species survive in refuges such as hedgerows, and because many protected sites, eg Nature Reserves, where insects breed are surrounded by agricultural land. The results of such studies help to define the size of the buffer zone required to protect sites from the impacts of drifting spray.

The final paper illustrates an area of work which will become increasingly important in ITE in the coming years – the assessment of the impacts of climatic change. In this example, the influence of the mild winter of 1988–89 on plant, insect and animal populations is examined for indications of the changes which might be expected if such mild winters become a regular feature of British weather.

The effect of hill cloud on pollutant deposition

(This work was partly funded by the Department of the Environment)

The deposition of acidity and sulphate in rain is being monitored routinely throughout the UK (Review Group on Acid Rain 1990). The geographical pattern in mean acidity, along with the concentrations of major anions, sulphate (SO_4^{2-}) and nitrate (NO^{3}_{-}), with which it is associated, shows largest values in the east Midlands and East Anglia and the smallest values in north-west Scotland. In marked contrast, the wet deposited acidity shows largest values in the high-rainfall areas of north and west Britain. The areas most sensitive to acidic inputs include many of the high-raiinfall, high-altitude regions of Wales, Cumbria and western Scotland (Acid Waters Review Group 1986). However, the rainfall chemistry monitoring networks from which the acidic inputs are estimated are confined to low ground (<400 m). In order to estimate wet deposition on hills, rainfall composition has been assumed to remain constant with altitude.

A collaborative project between ITE and the University of Manchester Institute of Science and Technology (UMIST) is testing this assumption, in field studies of the rain chemistry and hill cloud composition with altitude in Cumbria and southern Scotland. The measurements show that, in the presence of hill cloud enveloping the high ground, rainfall from higher levels intercepts the hill (cap) cloud droplets and increases the amount of rain at the higher elevations by the well-known seeder-feeder process (Figure 29). This process is the principal cause of the orographic enhancement in rainfall over the uplands in western Britain. Although the seeder-feeder mechanism is widely recognised, the ionic composition of the hill cloud and its effect on wet deposition is new. In

	Cap cloud	Rain 200 m	Rain 800 m
SO_4^{2-}	100-2000	42	60
NO_3^-	30-2000	45	65
H^+	10-1000	25	40

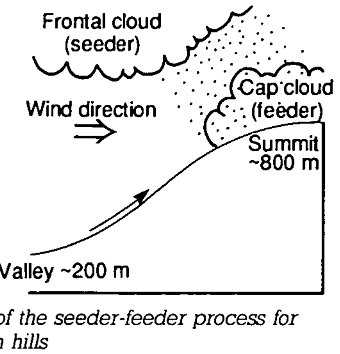

Figure 29. Diagrammatic representation of the seeder-feeder process for enhancing concentrations of ions in rain on hills

addition to marine-derived sodium ion (NA^+), chloride (Cl^-) and sulphate (SO_4^{2-}), the atmospheric aerosols contain SO_4^{2-}, NO_3^- and hydrogen ion (H^+), resulting from anthropogenic emissions of sulphur dioxide (SO_2) and oxides of nitrogen (NO_x). These aerosols are present in the size range 0.1–1.0 μum radius; they are too small to deposit from the atmosphere by gravitational sedimentation, and are not washed efficiently from the atmosphere by falling rain. They do, however, form efficient nuclei for the formation of cloud droplets, and are readily activated into cloud droplets as moist air is lifted over the hills. The cloud droplets are typically 3–15 μm radius and, unlike the aerosols on which they were nucleated, they are efficiently washed out by falling rain. At the sites of measurements in Cumbria (Great Dun Fell and Corney Fell), the concentrations of major ions in hill cloud are large relative to those in rain, as shown in Figure 29.

The larger concentrations in cap cloud than rain upwind of the hill lead to an increased concentration of major ions in rain with altitude (Fowler *et al.* 1988). The magnitude of this increase varies with meteorological conditions but is typically a factor of two between the valley (<200 m) and the summit (847 m) sites. The hills in Cumbria at 850 m above sea level are in cloud on some part of 220 days in each year, and the annual duration of cloud at such sites is in the order of 2000 h; these sites are generally in cloud during frontal rain. The enhancement of wet deposition is, therefore, a common feature of this area. The mechanism of seeder-feeder enhancement of wet deposition over Great Dun Fell has been simulated using a mathematical model (Choularton *et al.*

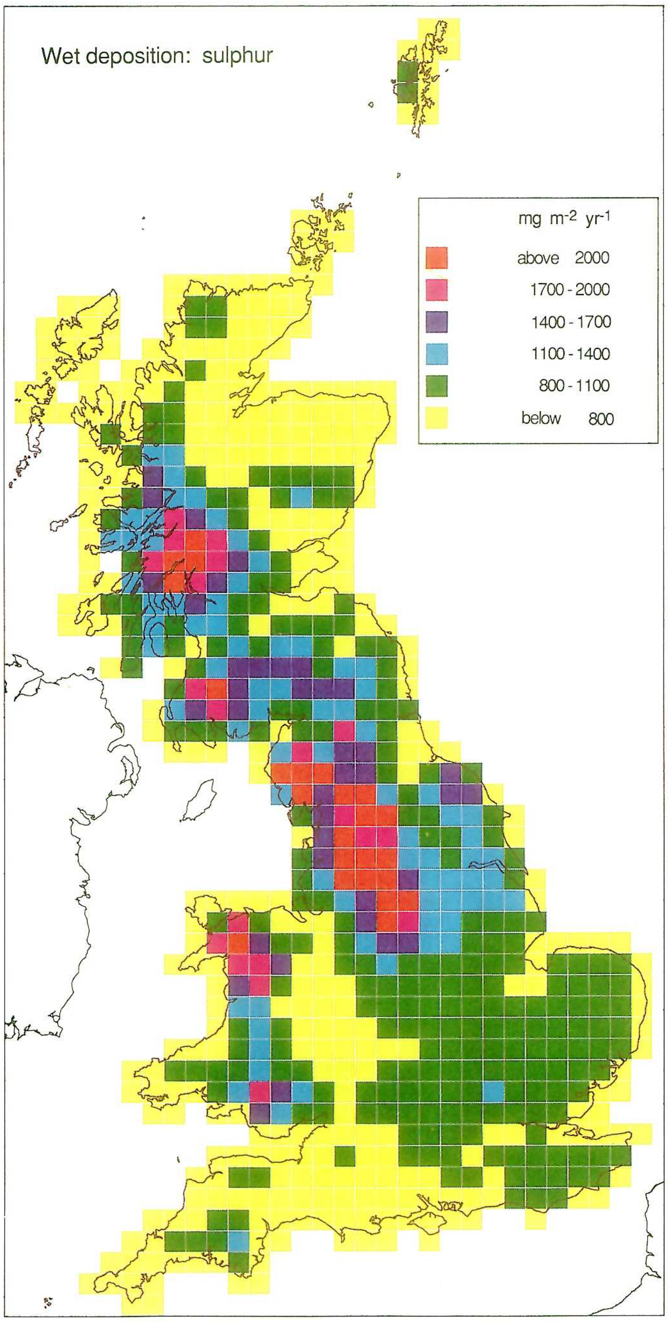

Figure 30. Annual inputs of atmospheric sulphur in rain and snow to the UK (excluding marine sources). The map includes the effects of seeder-feeder 'scavenging' of hill cloud, 1986–88

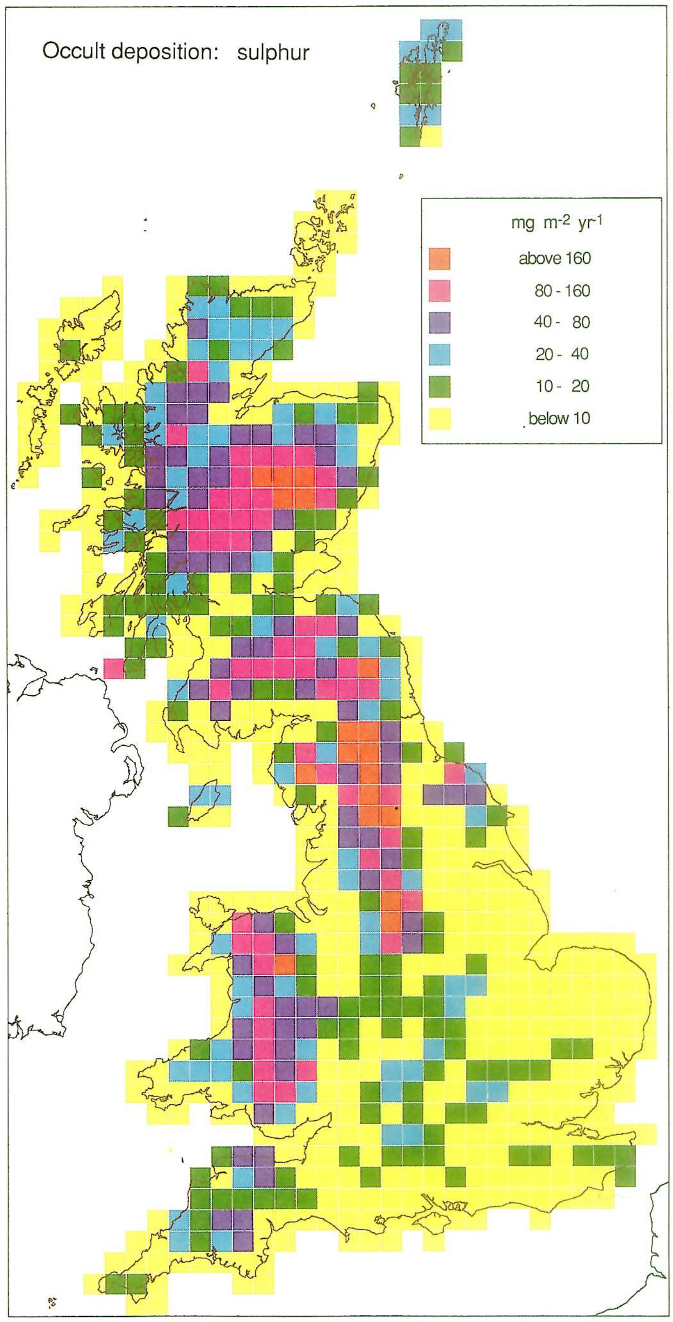

Figure 31. Annual inputs of atmospheric sulphur by cloud water deposition to the UK (excluding marine sources), 1986–88

1988) which reproduces quantitatively the observed changes in wet deposition with altitude. Both the experiments and the model have been successfully extended to a series of hills across Cumbria, from the coast at Corney Fell to the Pennines at Great Dun Fell.

The satisfactory simulation of the observed wet deposition from these studies has been used to extrapolate to the upland areas of the rest of the country (Fowler *et al.* 1990). For this extrapolation the average concentration of individual ions in the 'scavenged' feeder cloud water was assumed to be a factor of two larger than that in the seeder rainfall (at Great Dun Fell the average concentration of feeder cloud was four times that of the seeder rain). The enhanced rainfall at upland sites over coastal rainfall rates was assumed to result entirely from seeder-feeder scavenging. Using these simplifying assumptions, revised wet deposition estimates incorporating seeder-feeder effects have been calculated for the entire country, and Figure 30 shows the results for non-marine sulphate. At mountain-top sites in Snowdonia, Cumbria, and the west central Highlands of Scotland, the wet deposition of sulphate, nitrate, ammonium and acidity is increased by up to 70% over the earlier estimates. On the lower ground (<300 m), the effects are very small and do not significantly alter the map.

Plate 11. Equipment to measure rates of cloud droplet deposition on a high-elevation forest in the Scottish borders, using micrometeorological techniques

These new estimates of wet deposition are particularly important for studies of stream- and groundwater chemistry in catchments. The improved understanding of inputs is being used to construct catchment budgets for sites being monitored intensively in Wales. However, further work is necessary to show whether the extrapolation to remote areas of north and west Scotland is correct.

The hill cloud droplets are deposited efficiently on vegetation, and studies of droplet deposition in collaboration with the Department of Applied Physics at UMIST have shown the drop size dependence of the deposition rate. The measurements use micrometeorological techniques above the plant canopy to estimate rates of droplet deposition. The equipment shown in Plate 11 includes profile anemometers, three-dimensional sonic anemometers, cloud droplet sizing instruments (Knollenberg FSSP), and a rapid-response cloud liquid water content instrument (PVM). These studies have enabled a model to be developed of the deposition of cloud water on hills in the UK (Gallagher *et al.* 1988; Fowler *et al.* 1990). The model uses the aerodynamic roughness of vegetation, deduced from vegetation height with wind speed and cloud statistics, to estimate annual inputs to each 20 km grid square for the country. The results for cloud deposition of sulphur are shown in Figure 31.

These studies of wet deposition and cloud water deposition form a component of the Department of the Environment's pollutant deposition and effects research programme, and have been incorporated in the recent review of acid deposition in the United Kingdom (RGAR 1990).

D Fowler

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Variations in solution chemistry under four tree species at Gisburn

It is well established that the acidity and chemistry of rainwater change as it passes through a forest canopy, and that the proportion of such water flowing down the main branches and bole (stemflow) may be modified to a different extent from the water falling only through the canopy (throughfall). These modifications to water chemistry are not, however, the only ones occurring as the water passes further through the ecosystem, prior to leaving the site as drainage water: the forest floor and different horizons of the soil also exert their influence. Few studies compare the relative importance of these various modifications to solution chemistry for different species at the same site. Data for acidity and solute chemistry are presented here for stands of four tree species – Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), alder (*Alnus glutinosa*) and oak (*Quercus petraea*) – established at Gisburn in 1955.

The comparisons between throughfall and stemflow were made in the two-year period, November 1983 to October 1985. The more complete water chemistry profiles for bulk precipitation, throughfall (only), forest floor leachate and soil leachates from the base of the Ah horizon and from within the B/C horizon were determined in 1987 as part of a CASE studentship by M Iles, jointly supervised by ITE and Professor H G Miller (University of Aberdeen).

Stemflow and throughfall comparisons

The contributions of stemflow, per unit area of stand, to the total input of throughfall and stemflow are shown for each tree species and year in Table 6, in terms of both water volume and deposited acidity. Relatively more water is contributed by stemflow in spruce (15–16%) than in the other stands (10–12%), although this difference is not reflected in the acidity. The proportion of the total annual acidity reaching the forest floor as stemflow is higher for both deciduous broadleaves (*c* 25%) than in the two conifers – not through absolute increases in stemflow acidity, but because of reductions in throughfall acidity during the summer in-leaf period. The stemflow percentage for Scots pine (*c* 14%) is the smallest in acidity terms, with Norway spruce intermediate at *c* 20%. For all four stands, between-year variation was slight, suggesting that stemflow percentage (volume and acidity) is a function of stand characteristics rather than weather. This finding contrasts with interception percentages, which are very dependent on the pattern and intensity of rainfall.

Table 6. Contribution of stemflow as a percentage of total annual input (stemflow + throughfall) to the forest floor, Gisburn

	Water volumes				Acidity			
	Scots pine	Norway spruce	Oak	Alder	Scots pine	Norway spruce	Oak	Alder
Nov 1983–Oct 1984	10.5	15.0	11.4	11.5	14.7	22.4	24.4	25.9
Nov 1984–Oct 1985	9.8	16.3	12.1	10.6	13.9	18.9	23.8	26.0

As an example of the importance of stemflow in the transfer of other ions from the canopy to the forest floor, the data for alder are shown in Table 7. Such transfer depends not only on the relative quantities of water involved, but on ionic concentrations. Because stemflow contains higher concentrations than throughfall of sodium (Na), chloride (Cl), sulphate (SO_4^{2-}) and calcium (Ca), in addition to acidity, the importance of the stemflow pathway for these ions is greater than that indicated by the proportion of stemflow water alone. Conversely, stemflow represents a smaller than expected route for both forms of nitrogen (N), phosphate-phosphorus (PO_4-P) (averaged for the two years) and potassium (K).

However, whereas the above percentages apply to the unit area of a stand, stemflow is concentrated round the bases of the trees. Therefore, the localised effects of stemflow must be considerable, especially in respect of acidity inputs.

Water chemistry profiles

The acidity of water measured at any stage in its passage through the profile, from incident rain to soil runoff, will be the net outcome of acidifying and neutralising processes. The former include acid pollutants captured by the canopy (mainly SO_4^{2-} and nitrate (NO_3)), the creation of organic acids associated with organic matter turnover and the release of NO_3 (especially following N fixation in the case of alder), and the imbalance in ion uptake by roots. In practice, inputs of gaseous ammonia (NH_3) – converted to the ammonium (NH_4) ion and, therefore, having some theoretical neutralising potential – also have an acidifying effect. Its nitrification to NO_3 by bacteria in the forest floor or soil, and its role in enhancing the canopy absorption of sulphur dioxide (SO_2) through co-deposition can both lead to *increases* in acidification. The various acidifying influences are mainly counteracted by exchange and adsorption processes. The different species of tree at Gisburn appear to vary considerably in these respects, and an attempt is made here to interpret the variations in acidity (with both species and profile position) by reference to the changes in the other measured ions.

Figure 32 summarises the acidity (shown as H ion concentration) in the water of the various sampled strata (Figure 33) under the four tree species. In the throughfall, there is a clear distinction between conifers, in which acidity is identical and appreciably greater than in the incident rain, and broadleaves, which also have almost identical acidities to each other, although appreciably less than the conifers and marginally less than in the rain. In the forest floor waters, the conifer/broadleaf split disappears: acidity under pine and alder rises sharply, that under oak much less so, and spruce scarcely at all. Relative differences between species alter yet again as some neutralisation occurs in the upper mineral

Table 7. Contribution of stemflow as a percentage of total annual flux (stemflow + throughfall) to the forest floor for other ions. Alder stands, Gisburn

	Na	K	Ca	Mg	PO_4	NO_4	NH_4	Cl	SO_4^{2-}
Nov 1983–Oct 1984	11.7	8.8	12.7	12.4	5.9	4.7	4.7	11.5	18.7
Nov 1984–Oct 1985	11.8	7.9	14.6	10.0	11.3	4.1	4.5	12.4	19.2

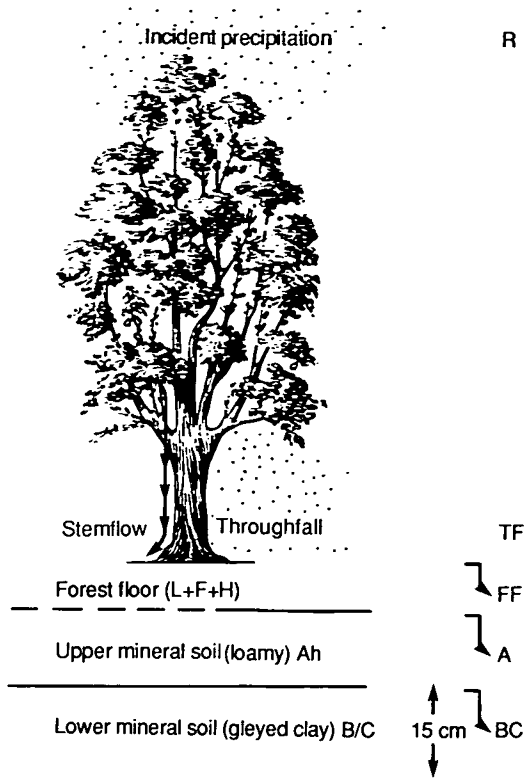

Figure 32. Profile showing strata in which waters were sampled for chemical analysis

soil, acidity under alder falling especially steeply. Only in the deeper, clayey B/C horizon is the buffering marked enough to cause convergence of all four species to a level of acidity less than that of the incoming rainwater. How are these differences reflected in the other ions, presented as concentrations in Table 8?

The potentially acidifying Cl ion is more-or-less fully balanced by its associated Na ion, and hence both of these ions can be ignored in the present discussion. Similarly, in the rain, throughfall, and (except for alder) the forest floor water, NO_3 is balanced by NH_4, PO_4 levels range from insignificant to small, and hence SO_4^{2-} represents the main acidifying anion, except in the mineral soil strata where NO_3 may appreciably exceed NH_4. Despite the greater concentration of SO_4^{2-} in spruce throughfall compared with that of pine (the denser spruce canopy possibly trapping more pollutant sulphate-sulphur (SO_4^{2-}-S) through dry and occult deposition and/or having a more leaky canopy for SO_4^{2-}), the resulting net acidity is identical in the two conifers. This result can be attributed to the greater leaching from spruce canopies, relative to those of pine, of all three bases, Ca, Mg, and especially K, in exchange for some of the SO_4^{2-}-generated acidity. The forest floor is the main seat of organic acid production for all species, reflected in the steep rises in concentrations of total organic carbon in waters from this horizon, followed by sharp falls in soil waters. Spruce again apparently counteracts this potential acidification in the forest floor much better than pine, by additional Ca release (in this stratum, Mg and K releases are similar): the two conifers thereby diverge markedly in acidity terms within this stratum.

The large rise in acidity associated with the forest floor waters of alder, which become almost as acid as those of pine, mainly relates to the fixation of N and its subsequent nitrification to NO_3. Despite the partial neutralisation of this NO_3-based acidity by a large concomitant increase in the release of all three bases, the net acidity remains high. Waters under oak are the least acid of the four species throughout the profile. As a deciduous broadleaf, pollutant SO_4^{2-} (and NO_3) inputs are low under oak, and the concentration of NO_3 in both the forest floor and soil waters remains as low as that in rain, reflecting low organic matter turnover and associated N mineralisation in this species.

Although the high levels of acidity in the forest floor are subsequently reduced in the Ah mineral soil horizon, in all four species, this reduction is not generally associated with any overall change in the total concentration of base cations. Although Ca levels do rise slightly, this increase is counterbalanced by the sharply reduced release of K in this stratum. Rather, in this upper soil horizon, aluminium (Al) mobilisation plays the major neutralising role, the different levels of which – in this horizon only – reflect those for acidity in the four species. In contrast, in the B/C mineral soil horizon, Al concentrations decline again, and buffering is provided by considerable increases in Ca release,

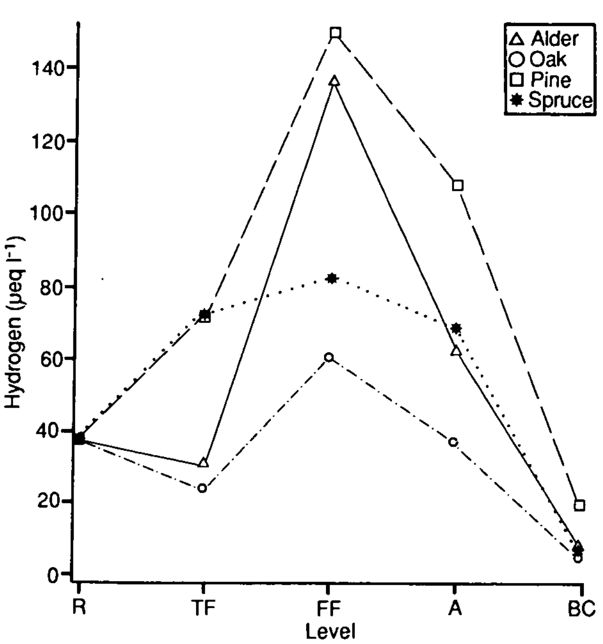

Figure 33. Annual means of acidity (H ion concentration µeq l^{-1}), based on fortnightly sampling, December 1986–December 1987, at Gisburn

Table 8. Mean annual concentrations (μeq l^{-1}) of major ions in water profiles under four tree species at Gisburn, 1987
TF = throughfall; FF = forest floor leachate; A = Ah horizon (upper mineral soil) leachate; BC = B/C horizon (lower mineral soil) leachate

Species	Level	SO_4-S	NO_3-N	PO_4-P	Cl	Na	Ca	Mg	K	Al	NH_4-N	H	pH
	Rain	71	24	2.2	92	94	26	16	8	<1	27	37	4.43
Oak	TF	113	25	13.2	129	113	55	34	34	<1	43	23	4.63
	FF	138	22	6.7	131	130	113	66	34	20	39	60	4.22
	A	202	21	1.0	175	184	132	49	10	58	1	37	4.43
	BC	238	8	0.9	209	229	296	51	6	18	0	5	5.29
Alder	TF	114	20	2.7	144	129	69	39	32	<1	25	30	4.52
	FF	170	247	6.1	190	162	186	87	66	40	44	136	3.87
	A	197	265	1.0	159	180	240	71	20	119	<1	63	4.20
	BC	207	174	0.8	159	193	344	65	7	24	0	9	5.04
Spruce	TF	328	76	8.5	274	240	130	79	95	7	99	72	4.14
	FF	299	55	7.1	241	217	194	74	74	40	61	82	4.09
	A	356	19	0.8	316	304	193	72	15	105	1	70	4.16
	BC	474	24	0.6	389	344	506	81	8	34	0	7	5.15
Pine	TF	242	70	7.1	265	231	88	60	57	14	99	71	4.14
	FF	278	127	14.2	262	258	108	81	72	38	136	150	3.82
	A	373	99	1.1	327	342	160	79	33	167	3	107	3.97
	BC	444	77	0.5	439	409	452	95	13	80	0	20	4.70

Note: Pine data based on only six replicates per 26 occasions; other species 18 replicates
Aluminium is assumed to be Al+++

which is especially high in the two conifer soils where it is supplemented by some increase in magnesium (Mg). K levels are low in all B/C waters.

The soil water data provide an indication of the chemistry of drainage waters from the different stands. In general, high levels of acidity, Al and NO_3 are to be avoided from the point of view of aquatic biota and water potability; losses of base cations also represent reductions in the site's fertility status. (The soil waters contain zero or negligible levels of PO_4 and ammonium-nitrogen (NH_4-N).)

As a result of the acidifying influences within these four ecosystems, and the release of other ions in response to them, the chemistry of the drainage waters is likely to vary appreciably according to tree species. In addition, however, because the chemistry of the soil waters usually differs markedly between the Ah and the B/C horizons, the depth at which the drainage originates will also be important in terms of potential losses of solutes. At present, this depth is not known for Gisburn, but is likely to vary with season, water probably flowing mainly from the less-buffered upper soil very wet conditions) in winter when these gley soils are normally saturated lower down. Waters under pine are the most acidic and most Al mobilisation occurs at either soil depth, together with high levels of total base cations (comparable with those from spruce); NO_3 mobilisation is second only to that under alder. Conversely, levels of acidity and most other ions are lowest in the soil waters under oak.

The likely predominance of drainage from the B/C horizon in summer would permit the greater buffering of the acidity in this deeper clayey soil in all four species, but at the cost of increased Ca losses. In contrast, relatively large species differences remain in the B/C waters for NO_3, Mg, and Ca. These differences can be summarised as follows.

Acidity of Ah horizon waters:
pine > spruce = oak

Al concentration in Ah horizon waters:
pine > alder = oak

NO_3 concentration in Ah and B/C horizon waters:
alder > pine = oak

Base cation concentrations in B/C horizon waters:
spruce = pine > alder > oak

Can these tree species differences for Gisburn be extrapolated to other sites? Such extrapolation would need great care because the relative degree of 'scavenging' of acidic atmospheric pollutants by the different species of tree – notably the apparently large difference between evergreen conifers and deciduous broadleaves – may vary with pollution levels. The relative responses of the trees to these potentially acidifying pollutant anions by cation exchange could also vary with tree age. Further, the endogeneous acidifying factors related to organic matter turnover (production of NO_3 and organic acids) will almost certainly vary with site, as may the acidifying imbalance between cation and anion uptake. Nevertheless, for polluted sites, evergreen conifers are likely to have more adverse effects than deciduous broadleaves on the acidity of soil waters and the other associated solute levels noted here. Similarly, through its N fixing properties, alder is likely to lead to more of the undesirable consequences than other native broadleaves. Its use as a buffer between conifer stands and watercourses could well, therefore, be counter-productive.

A H F Brown

Effects of acid waters on the survival of frogs

(This work was funded by the Central Electricity Generating Board and the Nature Conservancy Council)

In certain upland regions in Britain, surface waters are either naturally acid or susceptible to acidification: many such waters have become more acid as a result of the deposition of airborne pollutants, and changes in soil water and drainage associated with afforestation. Numerous laboratory studies have demonstrated sublethal and lethal effects of acid conditions on embryonic and larval amphibians, and evidence of acid-related stress and mortality has been found in the field. However, a lasting impact of acid conditions on amphibian populations has only been inferred.

ITE has a long-standing commitment to carry out ecotoxicology studies where the primary objective is to benefit wildlife. As part of a study of the impact of acidification on the common frog (*Rana temporaria*), an experiment was carried out at ITE Monks Wood in 1989 which was designed to evaluate the single and combined effects of some conditions associated with acid waters on the quality and quantity of froglets arising from populations of tadpoles.

Earlier laboratory experiments had shown that low pH and elevated levels of dissolved aluminium could reduce rates of growth and development of individual tadpoles (Cummins 1989). The laboratory results supported the hypothesis that lowered tadpole density, resulting from acid-related embryo mortality, could lead to faster growth and development among surviving tadpoles, in spite of the direct suppressive effects of low pH. The latest experiment was performed out-of-doors, with larger populations of tadpoles, and included a greater number of variables than previous experiments.

Common frog tadpoles were raised to metamorphosis in 54 pools, each of 200 litres, arranged in three blocks of 18, in which initial tadpole density and water chemistry were manipulated. Water in the pools was made up to simulate acidified and unacidified natural soft waters. In each block, one-third of the pools were initially circumneutral (pH 7), and two-thirds were acid (pH 4.1 or pH 4.3); aluminium (800 g Al l^{-1}) was added to six of the 12 acid pools. Two further treatments – initial calcium concentration (1 or 4 mg Ca l^{-1}) and initial tadpole density (90, 180 or 360 tadpoles $pool^{-1}$) – were applied factorially to the six pools with each combination of pH and aluminium. The experiment thus comprised 18 treatment combinations in an incomplete factorial design, which was replicated in three randomised blocks (A, B and C).

Early in the experiment, tadpole survival (Figure 34) was reduced by low pH P<0.0001), and reduced further by the addition of aluminium (P<0.006). In non-acid pools, early survival did not differ significantly between calcium treatments, but in the acid pools early survival was lower at the lower level of calcium (P=0.08) – the effect of calcium on survival was greatest in the block where acid pools began at pH 4.1 (A) rather than pH 4.3 (B and C). Calcium has been shown to ameliorate sodium loss by acid-stressed tadpoles (Freda & Dunson 1984).

The proportion of tadpoles surviving the early part of the experiment, prior to the earliest metamorphosis, decreased with increasing density. This effect of density was weakest in acid pools with additional aluminium, where early mortality was high. Thus, density-dependent mortality appeared to be ameliorated by mortality caused by acid conditions. Mortality was strongly density-dependent later in the experiment; there was a significant negative correlation between the number of pre-metamorphic survivors in a pool and the proportion of those tadpoles that achieved metamorphosis (Figure 35).

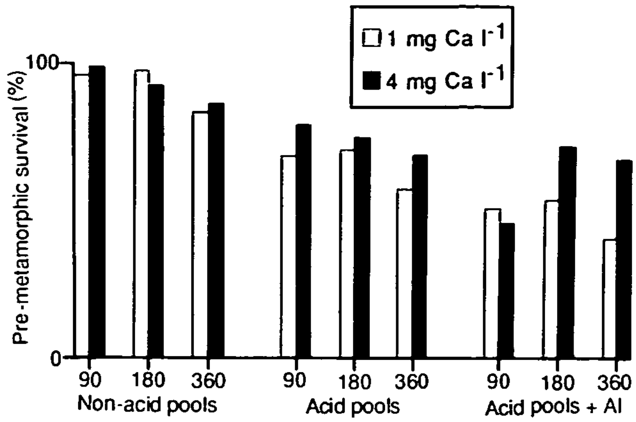

Figure 34. Tadpole survival during the period prior to the earliest metamorphosis. Each bar shows the mean for three pools. Values below bars show initial numbers of tadpoles per pool. Early survival was lower in acid water than in neutral water, and lower still in acid water with aluminium added. In acid water, survival was lower at the lower of the two calcium concentrations replicated in three randomised blocks (A, B and C).

Acid pools in block A were more acid than those in blocks B and C. In blocks B and C, early mortality in acid pools was offset by a reduced density-dependent mortality, to the extent that there was no significant net effect of acid conditions on the proportion of introduced tadpoles metamorphosing. In block A, early mortality in acid pools was greater than the resultant reduction in density-

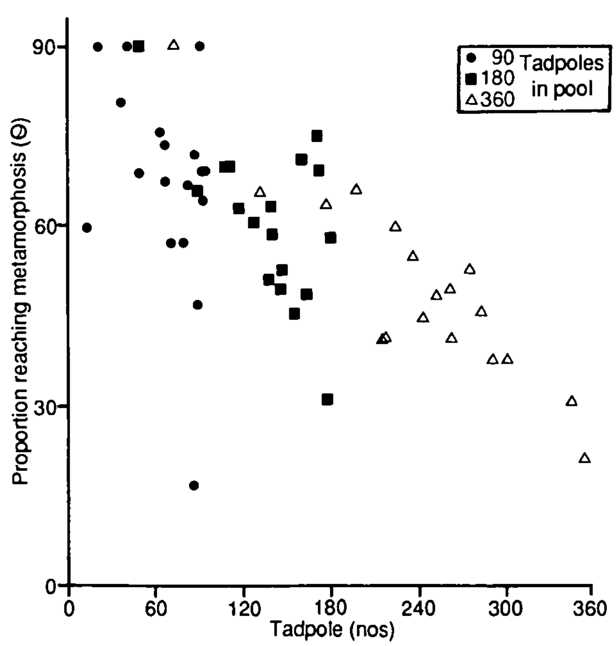

Figure 35. The relationship between number of tadpoles surviving in a pool prior to the earliest metamorphosis (n_i) and the proportion of those tadpoles reaching metamorphosis ($p = n_t/n_i$). In the Figure, 0 = arcsin p. Different symbols distinguish initial tadpole densities: 90 tadpoles $pool^{-1}$; 180 tadpoles $pool^{-1}$; 360 tadpoles $pool^{-1}$. The greater the number of tadpoles in a pool at the time when metamorphosis began, the smaller the proportion of those tadpoles that survived to become froglets

dependent mortality later on, and survival to metamorphosis was significantly lower in acid pools than in non-acid pools.

In acid and non-acid pools, the mean size of froglets decreased as initial tadpole density increased. Mean size at metamorphosis was greater in acid pools than in non-acid ones; furthermore, among acid pools, mean size at metamorphosis was greater when aluminium was added, and also at the lower of the two levels of calcium. These effects of pH, aluminium and calcium can all be attributed to reduced tadpole density, resulting from mortality caused by the acid conditions. In acid pools, most of the mortality that occurred took place early in the experiment, and the consequent reduction of density allowed surviving tadpoles to grow more rapidly than tadpoles in equivalent, non-acid pools. In the non-acid pools, survival was high initially, leading to poorer growth and greater mortality in the later stages of development. Consequently, even though survival to metamorphosis in acid and non-acid pools was similar under some treatments, the greater mean size of tadpoles in acid pools meant that froglet biomass was greater there than in non-acid pools (Figure 36).

Overall, increasing initial tadpole density led to an increase in the biomass of froglets produced. However, there was a significant interaction between density and low pH. In acid pools, biomass increased as density was increased, whereas, in non-acid pools, the intermediate initial density produced the highest biomass of froglets (Figure 36). Thus, within the range of conditions in this experiment, froglet biomass was limited by density effects at circumneutral pH, and by effects of acid conditions at low pH.

High tadpole densities in non-acid pools also led to delayed metamorphosis. Analyses of the numbers of froglet that had left pools by the time an unscreened, control pool dried up indicated a greater impact of desiccation on non-acid pools than on acid ones.

These results demonstrate that simple comparisons of the outputs of froglets from pools in more or less acid areas may fail to detect acid stress on frog reproduction. A range of acid conditions may exist in which acid-related mortality, in the embryonic or early larval stages, is offset by a consequent relaxation of crowding effects. Although the relative importance of these factors is likely to vary, according to resource availability and predation pressure, for example, the absolute effect of acid conditions on early survival ultimately limits the scope for successful reproduction. Acidification within the range of conditions in which compensation can occur may have a much smaller impact on recruitment to frog populations than would be predicted from simple laboratory studies – it may even prove beneficial in some respects, but further acidification could produce a sudden and rapid decline in recruitment as early, acid-related mortality became critical.

C P Cummins

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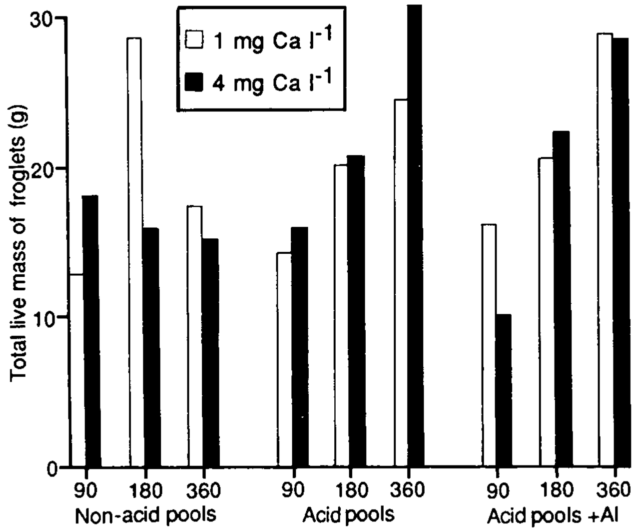

Figure 36. Total live mass (biomass) of newly metamorphosed froglets. Each bar shows the mean for three pools. Values below bars show initial numbers of tadpoles pool⁻¹. Biomass was limited by crowding effects in non-acid pools, whereas initial tadpole density limited biomass in acid conditions. Overall, in spite of the early mortality caused by acid conditions, acid pools were capable of producing a froglet biomass at least as great as that from non-acid pools
for diagram

Spray drift impacts on non-target organisms

(This work was partly funded by the Nature Conservancy Council and the Department of the Environment)

Agricultural sprays are designed to kill pests, weeds and diseases within the crops where they occur. Some compounds are effective against a wide range of species, and are therefore likely to affect non-target plants or invertebrates, including those of conservation value which occur in field margins and adjoining habitats. The hazard to such species depends on their intrinsic susceptibility to a compound, and to the extent of spray drift downwind of a sprayed area. The possible effects of spray drift were reviewed by Williams *et al.* (1987), but data are needed in order to assess buffer zones for protecting sensitive species. Research has, therefore, been done on this topic with respect to higher plants, ferns, lichens, terrestrial and freshwater invertebrates, and initial work on native plants is described by Marrs *et al.* (1989). This report summarises the work done on insecticides and terrestrial insects.

There are three main aspects:

1. choosing species whose phenology and behaviour may render them vulnerable to insecticides;
2. measuring the relative toxicity of different compounds to these selected species;
3. measuring drift deposition and mortality profiles downwind of sprayed areas in relation to site factors and operating conditions.

Butterfly larvae were chosen as the test organisms because of their conservation interest, and because there is good information available on their occurrence in field margins (Dover 1986) and on their general ecology (eg Thomas 1986; Pollard, Hall & Bibby 1986). For experimental purposes, the large white butterfly (*Pieris brassicae*) (Plate 12) was found to be particularly suitable as it can be bred continuously and its larvae are produced in large numbers. Three other, non-pest, species were used for comparison, namely green-veined white (*Pieris napi*), common blue (*Polyommatus icarus*) and hedge brown (*Pyronia tithonus*), all of which occur in field margins or adjacent habitats.

Laboratory experiments were carried out initially on two-day-old large white larvae (Plate 12 inset) with nine insecticides to determine LD_{50} from topical applications. Fewer insecticides were similarly tested on the other three species but, because of their smaller size at hatching, the tests were made when the larvae had reached a comparable size.

Plate 13. Spraying carrots with triazophos

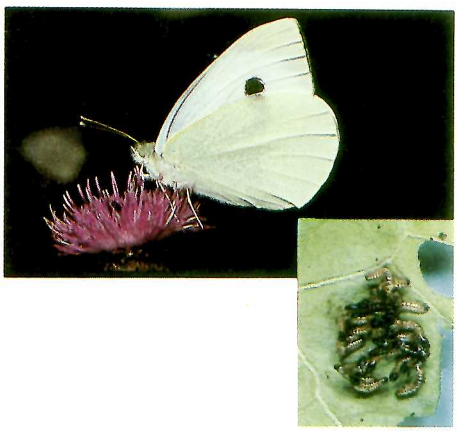

Plate 12. Large white butterfly, with (inset) larvae killed by spray drift

Field bioassays were then done under experimental conditions at ITE Monks Wood. Commercial insecticide formulations were sprayed on an open area of short grass, using standard hydraulic equipment and maximum recommended application rates (boom length 6 m, height above ground 80 cm, pressure 2 bar, speed 6 km h^{-1}, discharging spray at 200 litres ha^{-1}). Four passes were made covering an area of 70 m × 24 m to simulate the cumulative effect of drift from the outer zone of a sprayed field. Wind speed and direction were monitored on a portable anemometer. Target insects on cabbage (*Brassica* spp.) plants or on horse-radish (*Armoracia rusticana*) leaves were placed at intervals between 0 m and 32 m downwind (Plate 13). After spraying, the insects were taken back to the laboratory, and mortality was assessed over three to four days. Experimental and logistic models were fitted to the data to estimate 'LD_{50} distances' and 'LD_{10} distances', ie the distances at which 50% and 10% mortality would occur under the prevailing conditions. LD_{10} distances are more appropriate for determining buffer zones but can be estimated less accurately than LD_{50} distances.

This approach was also used to assess the effects of drift from actual crop spraying. Two bioassays were done for triazophos applied to carrots for carrot fly control (525 g ai ha^{-1}) at the Arthur Rickwood Experimental Husbandry Farm at Mepal, Cambridgeshire (Plate 14). One bioassay was done for cypermethrin (25 g ai ha^{-1}) plus demeton-S-methyl (325 g ai ha^{-1}) applied to brussels sprouts at Upper Caldecote, Bedfordshire.

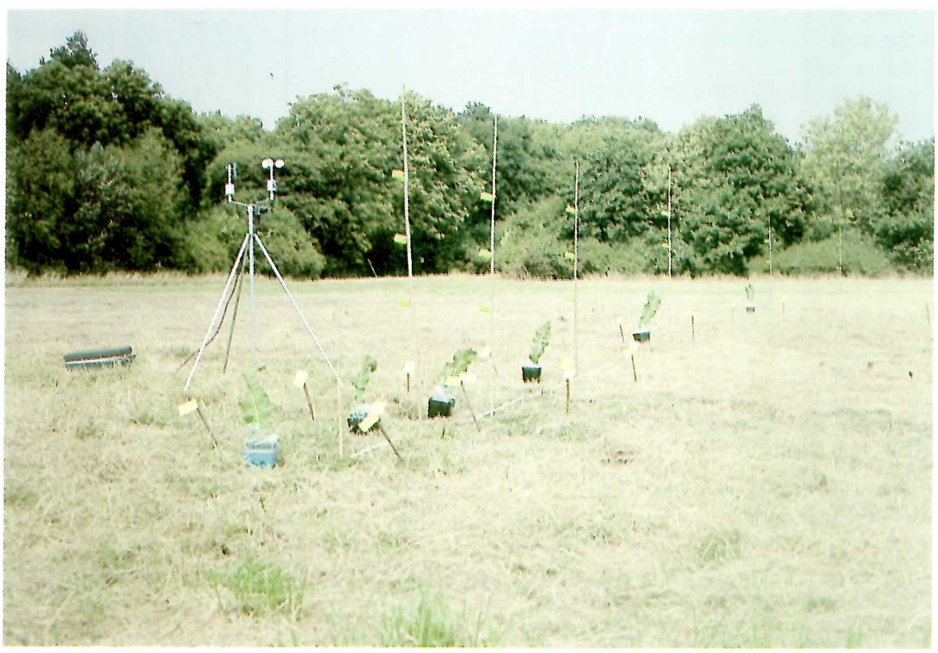

Plate 14. Experimental array of horse-radish leaves and caterpillars, with anemometer and collectors for measuring spray drift deposits 0–32 m downwind of a sprayed area

Table 9. Topical LD_{50} doses (µg $insect^{-1}$) of nine insecticides for young larvae of four butterfly species
(OP=organophosphorus, Ca=carbamate, OC=organochlorine, Py=pyrethroid, CH=chitin inhibitor)

Insecticide	Group	Large white	G-v white	Common blue	Hedge brown
Dimethoate	OP	0.439	0.834		
Pirimicarb	Ca	0.386			
Phosalone	OP	0.0270	0.0686		0.0273
Endosulfan	OC	0.0155			
Fenitrothion	OP	0.0029	0.0077	0.0240	0.0051
Pirimiphos-methyl	OP	0.0025			
Fenvalerate	Py	0.0013			
Triazophos	OP	0.0011			
Diflubenzuron	CI	0.0006	0.0013		

Water-sensitive papers (Ciba Geigy 5.2 cm × 7.6 cm) were placed on both sides of the target plants at Monks Wood to register drift deposition. These papers gave a quick visual guide to drift, and image analysis provided relative estimates of deposition at different distances downwind.

The laboratory tests with the large white butterfly showed a 700-fold range in toxicity, from dimethoate (least toxic) to diflubenzuron (most toxic) (Sinha, Lakhani & Davis 1990). Three-day-old green-veined white were found to be two to three times less sensitive, and a field trial with large white and green-veined white together confirmed this finding. The other two butterfly species were likewise less sensitive weight for weight (Table 9).

In an initial series of field trials with four compounds (Sinha *et al.* 1990), diflubenzuron was again the most toxic. At a rather high wind speed of 4.25 m s^{-1}, it gave an LD_{50} distance of 6.7 m for large white. In all other cases, the LD_{50} distance was <1 m (Table 10). Likewise, the estimate for LD10 distance for diflubenzuron was almost 16 m, while for the other compounds it was <2 m.

A second series of field trials compared drift effects from diflubenzuron at five different wind speeds. The drift deposition, as determined from the water sensitivity papers, was clearly related to wind speed (Figure 37). Thus, approximately equal deposits were recorded at 2 m, 4 m, 8 m and 16 m distances for wind speeds of 2.5 m, 3.5 m, 4.0 m and 5.3 m s^{-1} respectively. At the lowest wind speed of 2.0 m s^{-1}, the LD_{50} distance for large white was about 1 m and there was negligible kill beyond 4 m. At the highest wind speed of 5.3 m s^{-1}, the drift killed over 95% of larvae up to 16 m, and no LD_{50} distance could be estimated. Intermediate wind speeds gave intermediate results, with high kills for the first few metres and then a decline (Table 11, Figure 38).

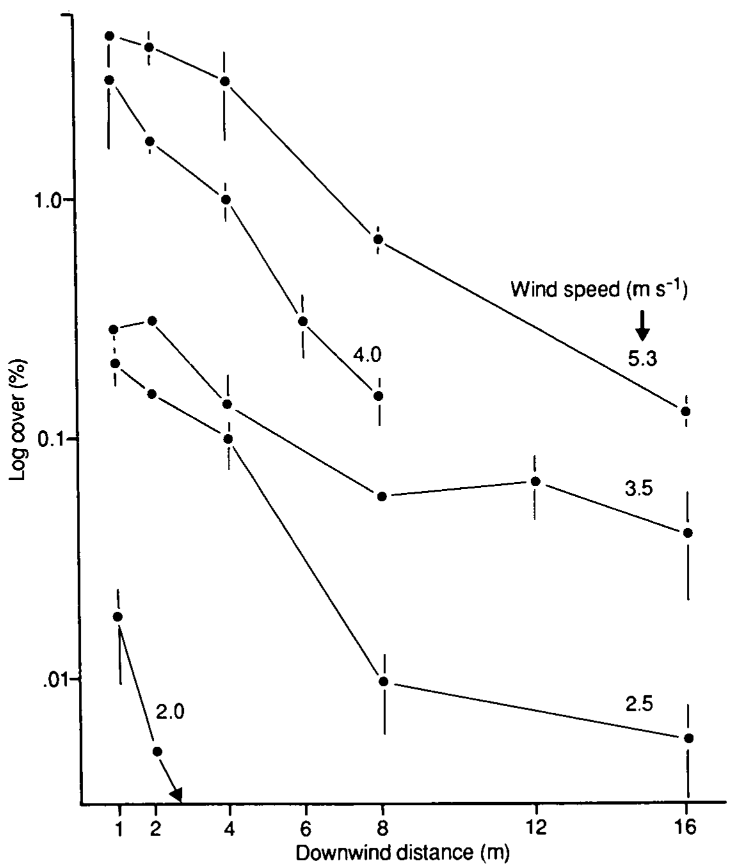

Figure 37. Spray drift deposition on water-sensitive papers at different wind speeds. Five trials with diflubenzuron. Means and ranges from paired receptors

Table 10. Estimated downwind distances (d_{50} and d_{10} from exponential models) at which 50% and 10% of large white butterfly larvae are killed by spray drift from four insecticides under similar experimental conditions. (Mortality assessed after one day for fenvalerate and after three days in other cases)

Insecticide	*Application rate*	*Wind speed*	*Estimated distances (m)* d_{50}	d_{10}
Phosalone	*700*	*4.0*	*0.28*	*0.66*
Fenitrothion	*1050*	*3.0*	*0.82*	*1.94*
Fenvalerate	*30*	*3.0*	*0.57*	*1.32*
Diflubenzuron	*100*	*4.25*	*6.70*	*15.84*

This effect was also seen in the field bioassay for cypermethrin plus demeton-S-methyl. The estimated LD50 distance here was about 5 m for a wind speed of 2.5 m s^{-1}, while estimates for LD_{10} distance were between 14 m and 20 m, depending on the model used. The two field bioassays for triazophos gave

Table 11. Estimated downwind distances (from logistic and exponential models) at which 50% and 10% of large white larvae are killed by spray drift from diflubenzuron at different wind speeds under similar experimental conditions

Wind speed (m s^{-1})	d_{50} Logistic/ exponential	d_{10} Logistic/ exponential
4.0	5.6/5.4	5.5/15.7
5.3	>16	No estimate
2.0	1.1/1.0	2.6/3.2
3.5	7.6/7.7	26.9/25.3
2.5	8.0/9.3	17.3/28.0

estimates for LD_{50} distance of 2.4 m and 4.1 m at similar low wind speeds.

On the basis of contact toxicity and maximum approved rate of application, pirimiphos-methyl and triazophos would appear to be the most hazardous to large white larvae in the field, followed by fenitrothion and then diflubenzuron. However, the last three of these compounds also act as stomach poisons, while pirimiphos-methyl has strong vapour action, so their overall relative toxicity in the field may be different. Of the four compounds tested experimentally – phosalone, fenitrothion, fenvalerate and diflubenzuron – only diflubenzuron produced significant mortality of larvae more than 2 m from the sprayer.

The results for diflubenzuron, at wind speeds of 2.0–4.0 m s^{-1}, were comparable with those for triazophos (at half the full recommended application rate) and for cypermethrin at wind speeds of 1.5–2.7 m s^{-1}. The highest logistic estimates of LD_{10} distance for these three sprays, in the absence of hedges, etc, were 27 m, 11 m and 20 m respectively. Buffer zones which are adequate for large white are likely to be adequate for green-veined white, common blue and hedge brown larvae under similar conditions of exposure.

The most extreme case of drift hazard was recorded when the mean wind speed was 5.3 m s^{-1} (at the upper limit of force 3 on the Beaufort scale). Diflubenzuron spray drift caused 97% kill at 16 m under these conditions, which should clearly be avoided.

The study shows that some of the most widely used insecticides, such as pirimicarb, phosalone and dimethoate, pose very little risk to butterflies. Diflubenzuron is extremely toxic but is little used in Britain. The greatest field hazards to butterflies may, therefore, be from triazophos, cypermethrin, fenitrothion and pirimiphos-methyl, which are all used quite widely. Buffer zones of the order of 20 m may be needed for triazophos and cypermethrin under conditions of moderate wind.

More field-scale tests are required on these compounds. Further work is also needed on the effects of hedges in deflecting or trapping spray drift deposits, and on the extent to which spray drift may penetrate woodland margins. Most important, however, is the need to measure the effects of spray drift from aerial spraying, as desk study estimates suggest that buffer zones should be considerably greater for some insecticides to afford protection to sensitive species.

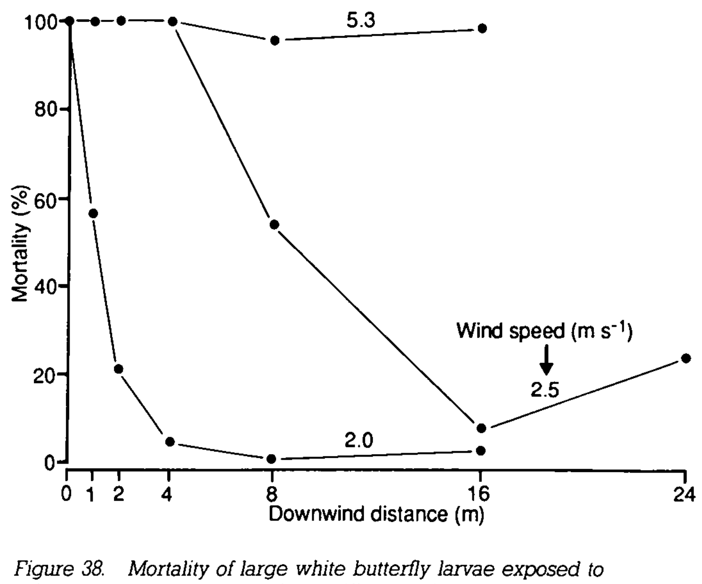

Figure 38. Mortality of large white butterfly larvae exposed to diflubenzuron spray drift at three different wind speeds (see Table 11)

Dr S N Sinha, from the Indian Agricultural Institute, made a valuable contribution to the work in 1988. He was supported by a British Council fellowship.

B N K Davis, T J Yates and K H Lakhani

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Climate change – the mild winter of 1988–89

(This work was funded by the Department of the Environment)

The exceptionally mild winter of 1988–89 provided an opportunity to observe the responses of the UK flora and fauna to the type of warm conditions that could occur in the 21st century as a result of an enhanced greenhouse effect. This co-ordinated project collected observations on temperatures (University of East Anglia), hydrology (Institute of Hydrology), ecological impacts (ITE and the Unit of Comparative Plant Ecology (UCPE), University of Sheffield), freshwater impacts (Institute of Freshwater Ecology), and impacts on agriculture and horticulture (University of Nottingham). Over 100 people were consulted.

The mean temperature in central England in the period December 1988 to March 1989 was 2.6°C above the 1961–80 average, and was the second mildest

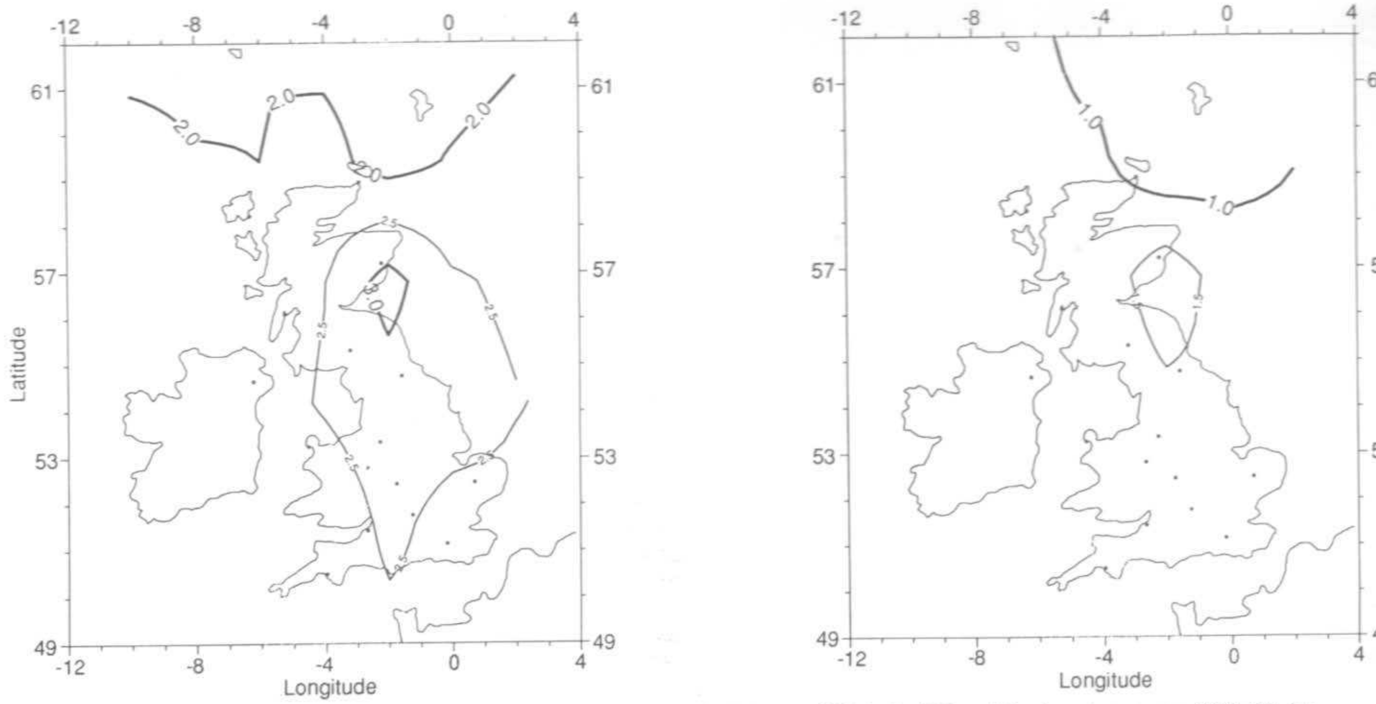

Figure 39. Difference between the mean temperatures in December 1988–February 1989 in the UK, and the long-term mean (1961–80) for December–February (°C). The greatest temperature anomaly is shown over the Firth of Forth (data by courtesy of P D Jones, Climatic Research Unit, University of East Anglia)

winter recorded since 1659. In December–February there were 29 fewer days below 5°C than the 1961–80 mean, including 23 consecutive days above 5°C during the Christmas–New Year period. The centre of the greatest anomaly (warmest compared with 1961–80) was over north-eastern England and eastern Scotland (Figure 39). The winter was characterised by westerly air flows (18 more westerly days than normal).

Mild winters in Britain tend to be relatively wet: 1988–89 was especially unusual in being dry. Over England and Wales, the period from November to January was the driest since 1879, and followed a relatively dry autumn. By contrast, the north-west of Scotland recorded more rain than usual (Figure 40), with incessant driving rain causing heavy red deer (*Cervus elaphus*) mortalities. By mid-February, there was concern over the water resources in England, but groundwater levels increased following heavy rainfall in March and April.

Observations of up to 17 native plant species at the six ITE Stations, and of over 200 plants in East Lothian (by Professor F T Last), showed that most species that normally flower before April flowered several days or weeks earlier than normal in 1989 (Figure 41).

However, some plant species flowered or came into leaf at the same time as

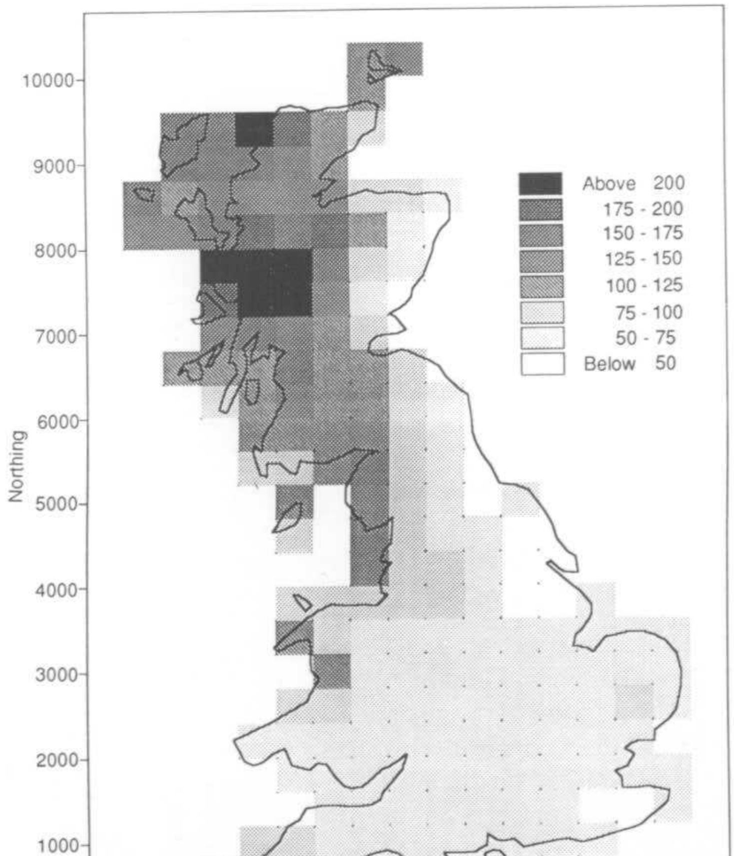

Figure 40. Precipitation in December 1988–February 1989 as a percentage of the 1961–80 average (data by courtesy of N W Arnell, Institute of Hydrology)

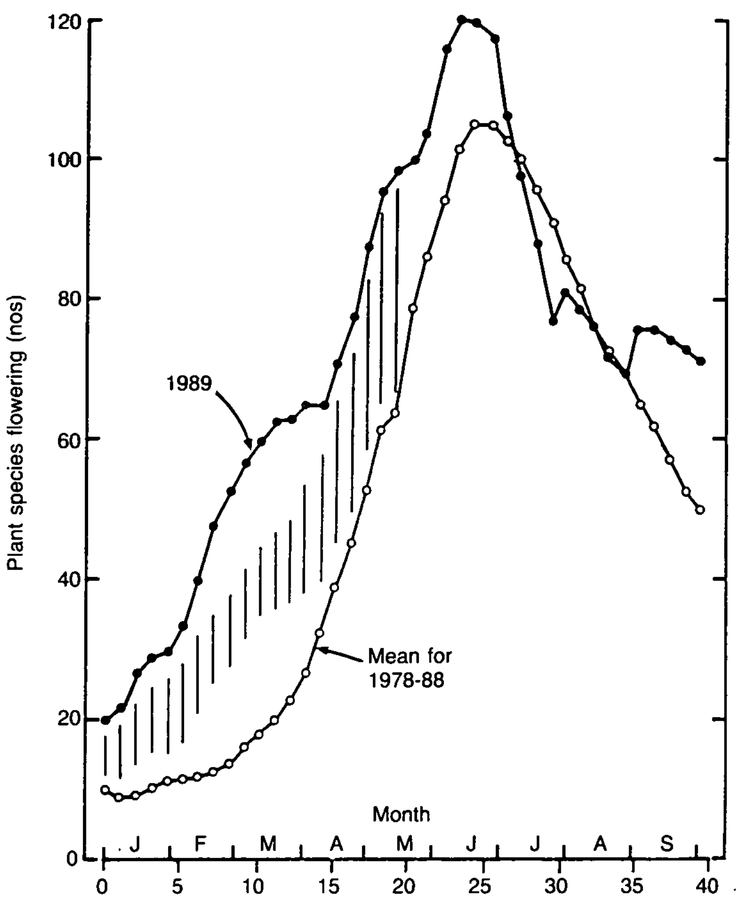

Figure 41. Number of species flowering during 1989 in a garden in East Lothian compared with the mean number in 1978–88. The vertical bars denote two standard deviations (data by courtesy of Professor F T Last)

normal, presumably because their spring phenology is controlled more by daylength and winter chilling than by spring temperatures. For example, blackthorn (*Prunus spinosa*) flowering and horse chestnut (*Aesculus hippocastanum*) leafing were very early, whereas honesty (*Lunaria annua*) and most apple (*Malus* spp.) varieties flowered at the same time as in previous years.

Observations on plant growth during March in Derbyshire supported the theoretical expectation of UCPE that species with small amounts of DNA per cell grew much earlier than normal, and hence competed more vigorously with vernal species which have large DNA amounts.

Conifer seedlings in forest nurseries did not 'harden off' as expected. About 2–3 million transplants died in cold storage, and a similar number died after outplanting.

Many invertebrate species were active during the winter. Black and green aphids built up large populations, and aphicides were quickly sold out to farmers. There were also major outbreaks of the green spruce aphid (*Elatobium abietinum*) on spruce (*Picea* spp.). Moths were unusually active in March–April, and many hibernating butterfly species were sighted during the winter. Species such as the red admiral (*Vanessa atalanta*) and painted lady (*Vanessa cardui*) successfully overwintered in southern England. Slug populations were higher than for about ten years, partly as a result of the wet summer and autumn of 1988 and the continued growth of vegetation and crops during the mild winter.

The Royal Society for Nature Conservation recorded common frogs (*Rana temporaria*) spawning several weeks or months earlier than in previous years (Figure 42). Reptiles were also active during the winter, but some suffered from fungal disease or from cold weather in March–April 1989.

Bird movements and behaviour were unusual. Oystercatchers (*Haematopus ostralegus*) returned to their breeding grounds early; and many bird species exhibited full breeding behaviour in mid-winter.

Freshwaters were about 2°C warmer than average, and no ice cover was recorded on most lakes. However, the mild winter had no dramatic effect on freshwater biology. Model simulations suggested that

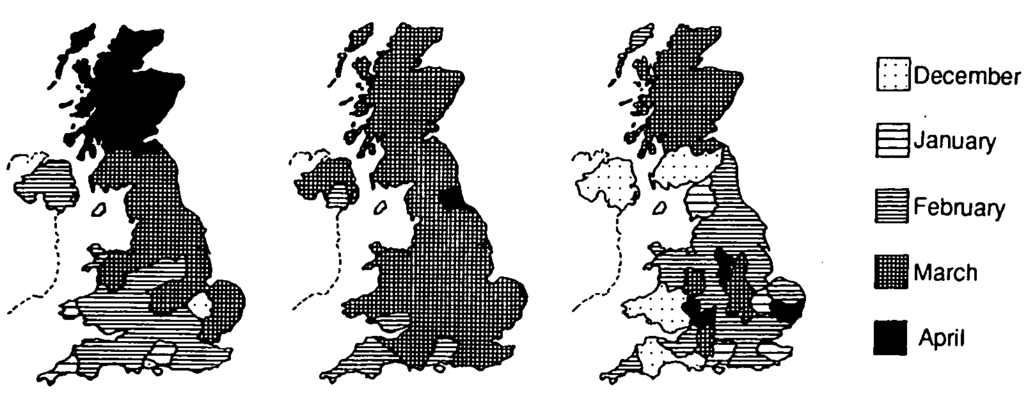

Figure 42. Phenological records of first date of spawning of the common frog in 1984, 1985 and 1989 (data by courtesy of the Royal Society for Nature Conservation)

the warm temperatures in 1988–89 would have had little effect on the seasonal dynamics of *Daphnia*, or on the long-term survival of brown trout (*Salmo trutta*).

The mild winter had large effects on agriculture, partly by affecting crop growth and development, and partly by affecting the spread and survival of diseases, pests and weeds.

Pigeon (*Callumba* spp.) numbers were high, but pigeon damage was generally less than normal on crops like oilseed rape because alternative food supplies were plentiful. In contrast, rooks (*Corvus frugilegus*) damaged many autumn-sown crops as they foraged for leather-jackets (Tipulidae) that were usually active. Rat (*Rattus* spp.) and mouse (*Apodemus* spp., *Micromys minutus*) populations were higher than normal, and Rentokil reported record sales; however, the mild winter may have been only one of several contributory factors. Many weeds survived the winter, as did volunteer cereals and potatoes which could carry pathogen inoculum.

Winter wheat crops were 2–3 weeks more advanced in the early part of the season, but they flowered only 7–10 days early and yields were near normal. However, some cereal crops were affected early and severely with mildew, yellow rust and barley yellow dwarf virus. Unusually large quantities of fungicides (as well as aphicides and molluscides – for slugs) were used.

Grass continued to grow throughout the winter, and sheep, which cause less trampling damage, were kept out late and turned out early. Some stock keepers were deceived by the lushness of the grass, and failure to feed supplements led to pregnancy toxaemia, milk fever, and hypomagnesaemia.

In general, early vegetables and flowers were oversupplied and prices were low. Disease and early regrowth caused problems in stored onions.

Overall, the mild winter revealed many aspects of the natural and managed environment that respond to unseasonally warm winter conditions, and those aspects that fail to respond. It also revealed a complex pattern of 'winners' and 'losers': some organisms benefitted from growth, development or activity in the winter, others did not. The complex set of observations posed many questions that need to be addressed in a more scientific manner and to be confirmed by further observations. To that end, a programme of research on the impacts of climatic warming on the UK flora and fauna has begun in ITE, and the Department of the Environment has commissioned a further set of observations on the impact of the hot summer of 1989 and the mild, wet winter of 1989–90.

M G R Cannell

Population ecology

Most of ITE's research on population ecology is concerned with understanding the factors that influence the abundance and distribution of wild plants and animals. Such an understanding is essential for the effective conservation of wildlife, and is helpful in the design of control programmes for pest species. It also enables us to predict more accurately the effects of land use changes on particular species.

The six projects described below are all concerned with species of importance to man, either as pests or as conservation priorities. Thus, the rabbit is a widespread pest of farmland whose reproductive rate is legendary. The work described forms part of a larger project designed to understand the various factors which influence rabbit breeding rates. The work on squirrels is concerned with factors affecting numbers, and examines why the introduced grey squirrel has so successfully replaced the native red squirrel in most of Britain. Another popular mammal which has declined in numbers is the otter. However, a good population still remains in Shetland and in other parts of Scotland, where the effects of habitat, food supply and pollutants are being studied to provide information of use in conservation.

The article on butterflies examines the impact of road construction on populations. It shows that several species can thrive on the flowers present on verges, and that roads are less of a barrier to dispersal than was once feared. It also suggests ways in which road verges could be adapted at the construction stage to support a wider range of butterfly species.

The last two papers discuss some effects of land use changes on certain bird species, showing how the lapwing has declined under modern agriculture, while the oystercatcher has increased. The effects of modern forestry on the capercaillie are also examined, as are the effects of changed grazing pressure on certain moorland species.

These projects form a small part of a much wider programme aimed at understanding the various pressures on plant and animal life in present-day Britain.

The effect of a plant compound on reproduction in rabbits

Research begun in the 1960s in the USA on the montane vole (*Microtus montanus*) first suggested that a plant compound may affect mammalian reproduction. This vole inhabits upland grasslands in western North America. Breeding begins each year within days of the first flush of grass growth, yet the time that this flush occurs can vary by more than one month between years. Consequently, the voles must use some cue other than, or in addition to, the change in daylength to time their breeding. It has been suggested that some factor in the new plant growth itself may trigger breeding, and, eventually, a compound was isolated which seemed to act in this way (Sanders *et al.* 1981). Field studies using food treated with the compound appeared to confirm the hypothesis (Berger *et al.* 1981), although the experimental design was open to criticism.

The compound isolated was 6-methoxy-2-benzoxazolanine (6-MBOA). This is an indoleamine, and, as such, has a similar structure to melatonin, which is a hormone in vertebrates. Melatonin is important in the photoperiodic responses of mammals, and is produced by the pineal gland which lies just beneath the top of the skull. Melatonin synthesis is inhibited by daylight, so large amounts are only produced during the night. Consequently, there is a daily cycle of melatonin concentrations in blood, with high levels at night and low levels during the day. In addition, there is a seasonal cycle, with high levels for a longer period of each day during winter, and for a shorter period during summer. It has been demonstrated in a number of mammals that this annual cycle modulates the timing of seasonal breeding.

Unlike most mammals, rabbits do not have oestrus cycles, and consequently do not ovulate spontaneously. The surge of luteinizing hormone (LH), which induces ovulation, only occurs in response to, and immediately following, copulation. Thus, the reproductive condition of female rabbits cannot be determined simply by measuring plasma levels of reproduction hormones, as in other female mammals. However, an assessment of reproductive condition can be obtained by giving a single injection of gonadotrophin-releasing hormone (GnRH), which causes a surge of LH in exactly the same way as copulation. LH levels reach a peak 15 minutes after injection, and this surge causes the ovaries to produce the steroid hormone progesterone, which itself reaches a peak about 60 minutes after injection.

Most of the work on photoperiodic control of seasonal breeding in mammals, and the involvement of melatonin, has involved species which show spontaneous oestrus cycles. The objectives of this study were (i) to investigate the seasonal cycle of response to GnRH in a reflex ovulator, the rabbit; (ii) to determine if melatonin modulates this cycle; and (iii) to see if the plant compound 6-MBOA affects the cycle by mimicking the action of melatonin. Compounds of similar molecular structure to natural hormones often act either in the same way as the natural hormone (agonists) or by inhibiting the natural hormone (antagonists). Whether a compound acts as an agonist or antagonist depends on the exact molecular structure and its effect on metabolism and binding to natural receptors.

Experiment 1

Female European rabbits (*Oryctolagus cuniculus*) were kept individually in large cages, with free access to food and water. The cages were kept outdoors, protected from rain and wind, but exposed to natural daylight. Each rabbit was given a monthly injection of GnRH, and blood samples were collected in the hour following the injection. Concentrations of LH and progesterone were measured in the plasma from these samples by radioimmunoassay.

At the beginning of the experiment in spring, the GnRH injections caused a large peak of LH at 15 min and of progesterone at 60 min (Figure 43). Both responses declined rapidly immediately after the summer solstice. The LH response gradually increased during autumn, but that of progesterone did not increase again until the following spring. The decrease in response after the solstice is due to the decrease in daylength (food availability was constant), and may be mediated by melatonin. It is perhaps paradoxical that a decrease in daylength inhibits the response, and yet the response resumes under the shorter days of autumn. The short days appear to switch on the reproductive system in rabbits and other species, in terms of endogenous GnRH synthesis in the hypothalmus, but subsequent exposure to long days seems to render them responsive to a decrease in daylength causing a transient switch off. The delayed return of the progesterone response is because the ovaries do not mature until spring, and so are unable to respond to the LH surge.

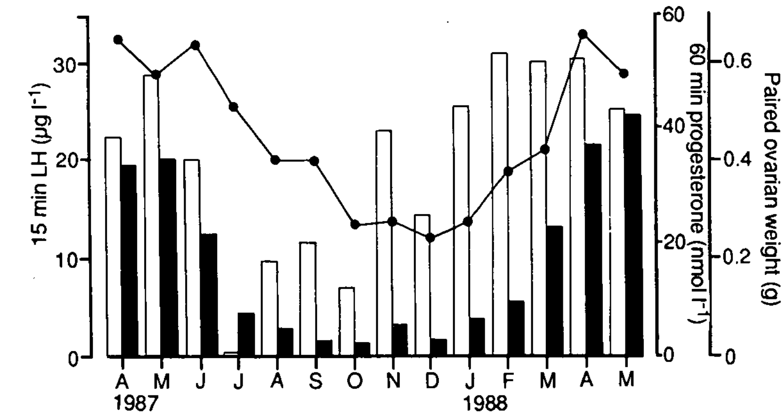

Figure 43. An injection of gonadotrophin-releasing hormone (GnRH) causes release of luteinizing hormone (LH) from the pituitary gland. Maximum concentration of LH in blood occurs about 15 min after injection. This LH surge causes release of progesterone from the ovaries, which reaches maximum concentration in the blood about 60 min after injection. This Figure shows seasonal changes in the response of female rabbits to an injection of GnRH (n=8). The open bars show plasma concentrations of LH 15 min after injection, and the solid bars progesterone concentrations 60 min after injection. The line represents change in ovarian weight in free-living rabbits (from Boyd & Myhill 1987)

Experiment 2

Female rabbits were kept individually in cages indoors and exposed to artificial long days. Each was given an injection of GnRH, and blood samples were taken. The animals were then assigned to one of four groups. The first group was kept on long days; the second group was kept on long days and treated with melatonin; the third was kept on long days and treated with 6-MBOA; and the last group was transferred to short days. Two further injections of GnRH were given, the first two weeks after the beginning of treatment and the second four weeks later. Again, blood samples were taken and plasma levels of LH and progesterone measured.

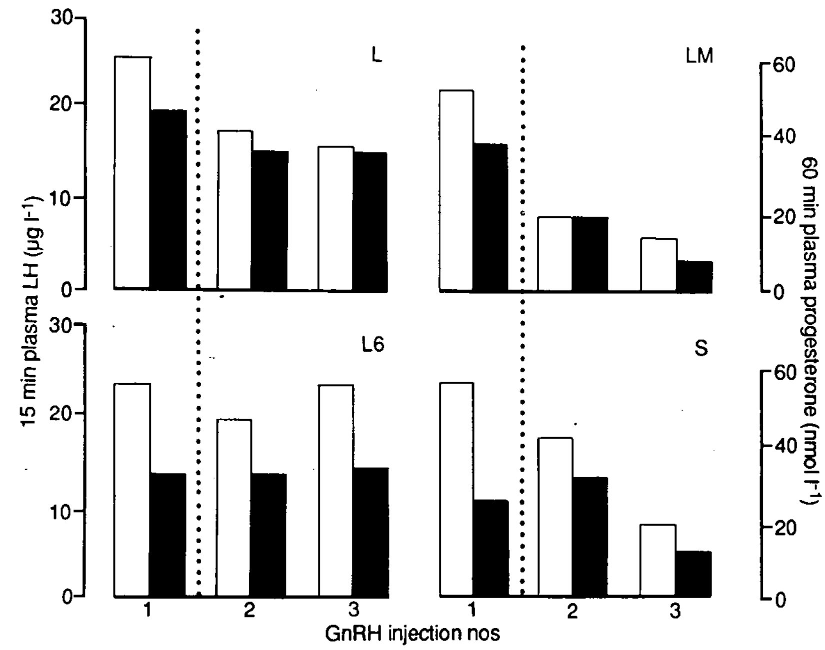

Figure 44. Responses of female rabbits to injections of GnRH. All rabbits were initially kept on long days and given an injection of GnRH. Two weeks later, the different treatments began. Group L (n =5) was kept on long days, group L6 (n=6) was kept on long days and treated with 6-MBOA, group LM (n=4) was kept on long days and treated with melatonin, and group S (n=5) was transferred to short days. Another injection of GnRH was given two weeks after treatment began, and a further injection was given four weeks later. The open bars show plasma LH concentrations 15 min after injection, and the solid bars progesterone concentrations after 60 min

The rabbits kept on long days showed no significant change in response to GnRH, neither did those treated with 6-MBOA (Figure 44). Those treated with melatonin and those transferred to short days both showed decreases in the response of LH and of progesterone. So, the effect of short days is mediated by melatonin, but 6-MBOA does not mimic this effect.

These two experiments are examples of a series done on female rabbits. Several experiments also involved male rabbits. The conclusions were that rabbits are highly photoperiodic and that melatonin mediates the effects of daylength. However, 6-MBOA had no effect whatever: it did not mimic short day effects in animals on long days, and so was not a melatonin agonist, neither did it mimic long days in animals on short days, and so was not a melatonin antagonist. The original work suggesting possible effects of 6-MBOA is open to criticism, and, since our study began, other results have been published which were either inconclusive or contradictory.

A S Dawson and C J Bray

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Competition between red and grey squirrels

(This work was partly supported by an NERC CASE studentship with Royal Holloway and Bedford New College, London)

North American grey squirrels (*Sciurus carolinensis*) may have been released in Britain as early as the 1830s, but only became permanently established following an introduction to Woburn in 1890. After 30 years, the species was established in 20 different areas, but its major range expansion occurred during the 1940s and 1950s (Lloyd 1983). From the late 1940s onwards, there was a corresponding rapid contraction in the British range of the native red squirrel (*Sciurus vulgaris*). By 1989, red squirrels were abundant only south of Yorkshire, in some Welsh conifer forests, and on the Isle of Wight, with small populations in East Anglia and on three islands in Poole Harbour.

Why have the red squirrels been replaced? It is important to answer this question, because, if the mechanism can be understood, then steps might be possible to halt or even to reverse the process. An important clue is that red squirrels can persist in conifers despite the presence of greys, and even recolonise such areas, but seem never to recolonise deciduous or mixed woodland from the edge of their range. This fact suggests that their disappearance is not simply a matter of disease, or of aggression by grey squirrels (Gurnell 1987). On the other hand, a mathematical model incorporating a coefficient of competition fitted quite well to the observed pattern of red squirrel replacement (Okuba *et al.* 1989).

Squirrels are dependent for food on tree seed crops during much of the year. MacKinnon (1978) noted that red squirrel densities tended to be lower than grey squirrels, and suggested that red squirrels were conservative breeders in order to reduce the scramble for food when seeds were few. However, when British Petroleum commissioned ITE to survey red squirrels on Furzey Island, where Scots pine (*Pinus sylvestris*) trees were producing heavy crops beside the oil rigs, red squirrels could breed as well as grey squirrels at similar densities in deciduous woodland (Figure 45).

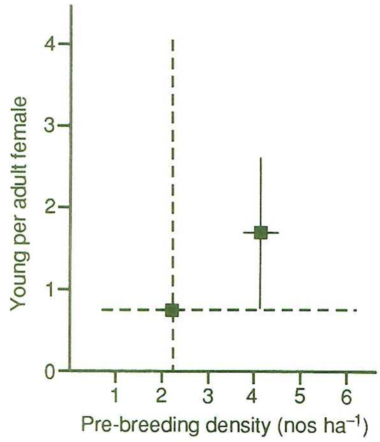

Figure 45. The range of densities, and of numbers of young produced per adult female, for red squirrels in Scots pine on Furzey Island (——), compared with grey squirrels in oak/hazel woods (----). Mean values are where the lines cross

Nevertheless, there are marked differences between red and grey squirrels in deciduous woodland, both in foraging behaviour and demography. The first evidence came from comparing radio-tagged grey squirrels in Monks Wood with red squirrels studied at Merlewood by M Tonkin, a CASE student with the University of Bradford. Monks Wood is predominantly oak (*Quercus* spp.), ash (*Fraxinus excelsior*), field maple (*Acer campestre*), and hazel (*Corylus avellana*), fairly similar to the oak, ash, yew (*Taxus baccata*) and hazel woodland near Merlewood. Grey squirrel foraging was 86% on the ground, which is appropriate for recovering fallen tree seeds in deciduous woodland, their native habitat in North America. Red squirrels, in contrast, did only 33% of their foraging on the ground. Arboreal foraging is appropriate for much of the red squirrel Eurasian range, where seeds are available in conifer canopy throughout the year, but did this feeding behaviour prevent them from competing with grey squirrels in deciduous woods?

From 1983, another CASE studentship enabled J L Holm to work on red squirrels in three oak/hazel woods on the Isle of Wight, for comparison with grey squirrels in three similar woods on the mainland. Squirrel numbers and breeding success were monitored by trapping in each wood (Plate 15), and foraging was assessed by recording 30-fix ranges about four times a year. The abundance of the main tree seeds was estimated each winter by counting acorn cups and hazel shells in 50 cm × 50 cm quadrats under oak and hazel canopy.

The number of hazel bushes was counted too, in four grids of 25 m × 25 m, spaced equally through each 100 m grid square. Oaks were either counted in the centre of each square, in a 50 m × 50 m quadrat, or mapped throughout the whole wood.

Grey squirrels ate many hazel nuts before they were ripe, and had generally consumed this crop by October, after which they fed mainly on acorns (Plate 16). Red squirrels ate some acorns, but often left them part-eaten. They fed mainly on hazel nuts through the winter or, when these were scarce, foraged in

Plate 15. Trapped red squirrel in oak/hazel woodland

Plate 16. An excellent acorn crop: not such good food for red squirrels

Table 12. Squirrel pre-breeding density, breeding success (with standard errors for both) in oak/hazel woods, plus mean tree seed availability. Correlations of squirrel parameters to tree seed availabilities are also given

	No. of site years	Squirrels ha^{-1} Mean	Correlation Acorn	Correlation Hazel	Young per adult female Mean	Correlation Acorn	Correlation Hazel	Tree seeds ha^{-1} Acorns	Tree seeds ha^{-1} Hazel nuts
Grey squirrel	15	2.31 (0.40)	P<0.02	NS	0.69 (0.28)	P<0.002	NS	37000 (17000)	9000 (2000)
Red squirrel	9	0.86 (0.09)	NS	P<0.002	0.37 (0.17)	NS	P<0.001	76000 (23000)	17000 (11000)

oaks for the fungus *Vuilleminia*, which grows under dead bark. The foraging preferences were quantified by a computer program, which used tree density in each 100 m square to estimate the mean tree density at each radio-location, for comparison with mean tree density within each polygon range outline (Figure 46). Where there were significant

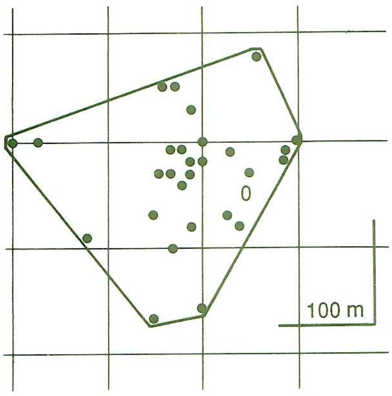

Figure 46. Structure analysis of a grey squirrel range in Monks Wood, showing the radio-locations (+) and convex polygon range outline of a grey squirrel overlain on the 100 m × 100 m grid squares used to estimate tree and seed densities. 0 marks the main drey

preferences, these were always for red squirrels to forage in hazel-rich areas, but for grey squirrels to forage where oak density was relatively high.

The foraging preferences were reflected in squirrel demography. The pre-breeding density and spring breeding success were significantly related to the density of hazel nuts but not acorns for red squirrels, and to acorns but not hazel nuts for grey squirrels (Table 12). Although there were, on average, more than twice as many acorns for red squirrels as for grey squirrels, red squirrels did not exploit this food, and had only 37% of the density and 54% of the productivity of the grey squirrels (Table 12) – far less than their densities and productivity in conifers on Furzey Island (Figure 45).

Acorns contain polyphenols (tannins), which inhibit digestion and can kill horses. This ingredient is probably a defence against seed-eating animals.

However, pigs thrive on acorns, and it seemed possible that grey squirrels had evolved a similar adaptation to their native deciduous habitat. Six young squirrels of each species were, therefore, tested for a month in captivity on an acorn diet, three at a time, while the others remained on a mixed diet of hazel nuts, peanuts, sunflower seeds, apple and carrot. Unlike grey squirrels, red squirrels on the mixed diet did not eat acorns, but both species gained weight, as did grey squirrels on the acorn diet. In comparison, red squirrels eating acorns alone showed significant weight losses and reduced survival. Analysis of faeces showed that the longest-surviving red squirrel was digesting acorns only 78% as efficiently as the grey squirrels. The most dramatic difference, however, was that red squirrel faeces contained 87% of the polyphenols in the original acorns, whereas faeces from the grey squirrels had only 37%.

The findings confirm the hypothesis that red squirrels are the victim of a plant defence mechanism, which grey squirrels can overcome. Red squirrels in deciduous woods appear to depend on hazel, which, like conifers, was an early coloniser of northern Eurasia as the ice sheets retreated, and which was being lost through coppicing just when red squirrels were disappearing most rapidly from British woodland. In winter, after the hazel crop has been eaten, red squirrels would have less suitable food than the invading grey squirrels, because most British deciduous woodland is still rich in oaks.

This study suggests a bleak future for red squirrels in British deciduous and mixed woodland, but many questions remain unanswered. Can oak varieties be found with less toxic acorns, or could one develop 'seed-less' oaks to annul the grey squirrel advantage, which could also reduce bark-stripping? Alternatively, are there polyphenol-tolerant red squirrels elsewhere in Eurasia which could be introduced to Britain? Could such squirrels be produced by gene transfer from grey squirrels? There is a pressing need to compare red and grey squirrels in conifers. If red squirrels have an advantage there, reintroductions might be practical in new southern conifer forests, at least where there has been no public pressure to plant oak fringes.

R E Kenward, T Parish and J L Holm

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Predator/prey relationships and species conservation: the otter

(This work was partly funded by the World Wide Fund for Nature)

The numbers of otters (*Lutra lutra*) have declined dramatically over the last few decades; the animal has now disappeared from several countries in Europe, and it is rare in many others where it was previously common. Several reasons are put forward for the decline, but evidence is generally lacking. Environmental pollution is considered to be important, as well as habitat change, disturbance, and mortality caused directly by man. As otters are at the top of a food chain, they can be important indicators of environmental change. Furthermore, the otter is considered to be an endangered species, and it attracts much public interest and concern. To understand the possible mechanisms for the change in its fortunes, ITE is studying factors limiting otter populations, their interactions with the fish on which they prey, and the role of habitat. These factors were first studied in a relatively healthy population in Shetland, and research is currently being carried out in an agricultural area in mainland Scotland.

Numbers in Shetland

Previously, there have been no successful attempts at estimating numbers of otters because of the problems of observing the animals. In Shetland, otters live along the coast, are normally active in daytime, and individuals can be recognised. One study area contained several otter ranges, and a good correlation was found between the number of otter dens or 'holts', and the number of resident adults. On average, there were 3.0 holts per resident female, which made it possible to use the numbers of holts along the 1400 km of Shetland coast to estimate the total numbers of otters on the islands. The coast was classified into six habitats (strata), which were sampled for holts with different intensities; the best habitat was sampled most intensively, and the holts were counted in about one-third of the coast. It was estimated that there were 1185 holts in Shetland (n=13, 95% confidence limits); allowing for observed sex ratios and numbers of non-resident otters, this estimate translated into 700–900 animals. Although the Shetland population is probably one of the most important in Europe, it is almost totally isolated, fairly small, and therefore vulnerable (for instance to disasters such as an oil spill or epidemic).

The large majority of these otters lived on undrained coasts with peat, where they had easy access to freshwater, which the animals need for washing. A series of experiments with captive otters showed that regular washing in freshwater is essential for otters living in seawater, in order to maintain the thermo-insulation of their fur. Numbers of otters were very low on Shetland coasts which had been drained for agriculture, and the absence of freshwater is a probable cause. The low numbers of otters on coasts elsewhere, such as in Orkney and the east coast of Scotland, can be similarly explained.

Prey populations

The Shetland otters fed mainly on small, bottom-living species of fish, especially eelpout (*Zoarces viviparus*) and five-bearded rockling (*Ciliata mustela*). These fishes were active at night, and easiest for otters to catch during the inactive phase of the fishes in daytime, which probably explains the diurnal activity of otters in Shetland. Fish biomass was assessed with small funnel traps, over a three-year period; it was highest in mid-summer, and lowest in early spring. The main food species of otters were found in different habitats; for instance, eelpout was found mostly along sheltered coasts and in the summer, rockling mostly in exposed areas and more often in winter. As expected, this pattern of food availability affected the extent and success of foraging by otters in different parts of their ranges.

Social organisation and reproduction

The spatial organisation of the otter was complicated, a demonstration of the difficulty in distinguishing between social and solitary species of carnivore. There were small female group territories (4 km of coast, or larger), in which group members were probably related (mothers/daughters, or sisters) (Plate 17), where each had a different core area, and all had access to the various habitats with different prey at varying times of year. Male ranges were larger, and overlapped with several female group ranges. Males also used a different habitat from females: they were much more likely to be found on the exposed coasts, whilst females used the sheltered bays. Within a female group range, several or all females reproduced, mostly in mid-summer. Litters were small (mean 1.8), and the numbers of cubs reared in the study area over the winters correlated closely with fish densities the previous summer (Figure 47), ie at the time of year when the mothers suckle their cubs. This correlation suggested that fish populations, and year-to-year changes therein, had an important effect on the recruitment of young otters.

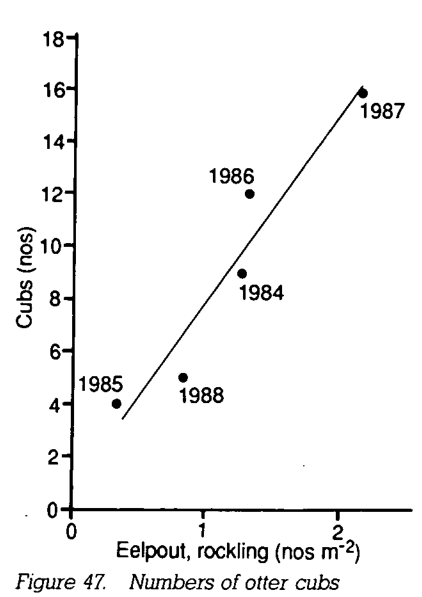

Figure 47. Numbers of otter cubs present in winter in a study area in Shetland, in relation to different prey densities the preceding summer

Mortality

Adult mortality was studied using corpses collected from all over Shetland. Most otters died naturally, although traffic also took a substantial toll. Most natural deaths occurred in spring (Figure 48), during

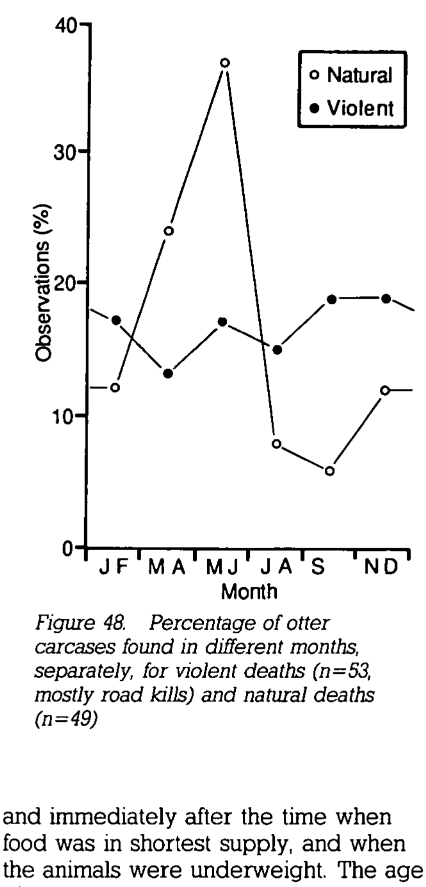

Figure 48. Percentage of otter carcases found in different months, separately, for violent deaths (n=53, mostly road kills) and natural deaths (n=49)

and immediately after the time when food was in shortest supply, and when the animals were underweight. The age of dead otters was determined from incremental rings in the teeth. Although the potential lifespan of otters is 15 years or more, the mean life expectancy of an adult otter in Shetland was only three years. Annual mortality increased linearly with age, unlike mortality in most mammals. This increase was possibly a result of the accumulating effects of toxic compounds in the body. However, the available evidence pointed to food shortage as the most important ultimate cause of death.

The livers of dead otters contained traces of DDE, HEOD (dieldrin), BHC (lindane), cadmium and lead, but none in concentrations which would have affected

Plate 17. Female otter with four cubs in Shetland, in winter. The numbers of cubs in an area are correlated with fish densities earlier in the year

the animals. Some contained enough PCBs to have had a possible negative influence on reproduction, but, of the compounds studied, only mercury was likely to have affected the overall level of mortality. Mercury occurs naturally in the sea, especially in the Shetland area, and otters do not have the detoxification mechanism for methyl mercury, involving selenium, which is found in other marine mammals. Mercury accumulated in otters with age (Figure 49), and in several otters aged five years or more sufficient mercury was found to have had a possibly toxic effect. This observation suggests that, although otter populations in the sea reach densities higher than anywhere else, the species is not optimally adapted to this habitat.

The correlations found in the Shetland studies suggested that, in areas where otters were common, fish populations were likely to have profound effects on recruitment and mortality, whatever the exact mechanisms. Toxic compounds may play a role secondary to that of food shortage, but the data suggest that a relatively small increase in the level of some compounds, as pollutants, could cause accumulations affecting overall mortality. An important conclusion for the conservation management of otter habitat was the effect of land drainage: otters need freshwater, especially underground, eg in peat, in order to be able to exploit the fish populations in the sea.

Otters in north-east Scotland

The populations of otters living in lakes, rivers and small streams in north-east Scotland show important similarities and differences with the otters in the sea in Shetland. As the animals in freshwater are largely nocturnal, they are being studied with the aid of radio-location, using implanted radio-transmitters (under licence from the Nature Conservancy Council and Home Office). The ranges are very much larger in freshwater than in Shetland: 25–40 km for females, and up to 70 km for males. Again, several females may share a range, especially in lakes. Interestingly, the habitat of the males appears to be different from that of females in freshwater also, adult males being more likely to inhabit the large rivers, females the small burns as well as lochs. Both sexes are much less likely to use 'holts' than the coastal otters; in fact, some litters are born in reed couches, and some otters rarely, if ever, sleep underground.

Plate 18. Otter habitat in NE Scotland. Reed beds are an important component of the habitat, especially for providing shelter

The radio-location studies have revealed the importance to otters of reed beds, even as far as several kilometres from open water, for resting and breeding as well as for feeding (Plate 18). The animals' use of such habitat has largely gone unnoticed in studies relying on the distribution of faeces ('spraints') as an indicator for habitat selection. Faeces were found to be an unreliable indicator of otter distribution and activity. Reed beds, incidentally, have disappeared in many parts of the country, which could mean the destruction of an important part of the otters' habitat. Small islands in rivers were also shown to be important.

Conclusions and future research

The present study demonstrated aspects of the food limitation mechanism in a population of mammals, with the possibility of prey availability affecting both mortality and recruitment. However, with the dispersion of otter populations, it also indicated that there were overriding effects of habitat. Moreover, effects of compounds such as methyl mercury in the environment suggested that there could be a complicated interaction

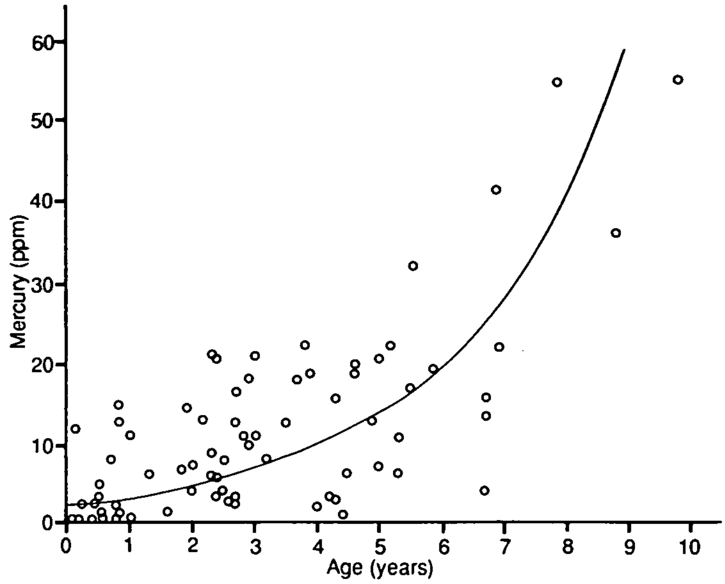

Figure 49. Concentration of mercury (ppm dry weight) in livers of otters in relation to age

between food availability and other factors affecting otter populations.

These mechanisms, *mutatis mutandis*, are likely also to affect populations in freshwater. The food of otters in the various study areas of north-east Scotland consists very largely of salmonid fishes (*Salmo* spp.) at all times of year, with eels (*Anguilla anguilla*) predominant in the lakes, and frogs (*Rana temporaria*) for a short period in spring. The effects of otters on prey populations, and *vice versa*, are currently being analysed, to determine the role of food as a factor limiting numbers in this more agricultural habitat, and possible interaction with other predators of salmonids.

The role of toxic compounds in the environment (especially pollutants) is also being studied in freshwater, although present data suggest that direct effects on otters are not of overriding importance, at least in north-east Scotland. However, it is possible that pollutants affect otter populations in a much more subtle way than has previously been assumed. Several metals, including mercury, may affect thermoregulation in mammals in the laboratory, even when present at relatively low levels, and preliminary studies on otters suggest that the demands of thermoregulation may play a vital role in the adjustment of otter populations to energy resources.

These complicated relationships will be the subject of future studies, and the results of this research in Scotland are expected to be relevant also in many other parts of Europe, especially in areas where numbers of otters are declining. In terms of conservation, the studies show which types of habitat need to be protected and why; they indicate which fish species may limit numbers, and how at least some pollutants can affect otter numbers in their interaction with the prey populations.

H Kruuk

Effects of roads on butterfly and burnet populations

There has been much speculation about the effects of roads on butterflies. On the one hand, it is often argued that new constructions will harm species that breed on neighbouring land, even if the route itself does not destroy existing breeding sites. The main concerns are that exhaust fumes might poison nearby populations, and that sites on either side of a road will become isolated, with adults reluctant to cross this supposed barrier. On the other hand, developers argue that butterfly habitats are created by new road schemes, because the verges and cuttings that are generated are usually won from intensively farmed land that supports few, if any, species.

Proponents and opponents of road schemes have been able to use butterflies as a cause célèbre mainly because few data existed on which to base their cases. For example, there was sufficient concern for butterflies to be a contributary factor in decisions to reroute the M40 near Oxford, and to delay the extension of the M3 at Winchester. In both cases, serious consideration was given to building a 'butterfly bridge' across the route.

An initial investigation of this problem was made in the summer of 1989, on major trunk and holiday routes in Dorset and Hampshire (Munguira & Thomas 1990). The verges of 12 roads were analysed for 14 weeks, and the density and diversity of butterfly and burnet moth populations were measured along fixed transects. The results were compared with the volume of traffic on these roads, the nature of the adjoining land, and five characteristics of the verges themselves: their topography, width, the abundance of nectar sources, the number of breeding habitats of different species that each contained, and whether the verges were sheltered by hedgerows. Studies were also made to determine whether the species found along roadsides were breeding on and supported by the verges, or were simply temporary visitors to flowers. Finally, two sites were intensively studied to discover whether adults crossed the roads and, if so, how many were killed by vehicles, using standard mark-release-recapture (MRR) techniques on the adults.

It was immediately clear that the verges of some very busy roads contained large populations of butterflies and burnets. For example, more than 2770 adults of the meadow brown (*Maniola jurtina*) were recorded per hectare on the peak day of emergence on one dual carriageway – a higher density than has been measured in any of the studies of this species in 'natural' habitats. High densities of marbled white (*Melanargia galathea*) (Plate 19), common blue (*Polyommatus icarus*) and Essex skipper (*Thymelicus lineola*) were also recorded on some roadsides. In addition, some verges supported a wide range of species. The richest example was a cutting for a bypass excavated six years earlier through intensive farmland that had previously been almost bereft of butterflies. This site now contained at least 23 species of butterfly (40% of the UK species) and two species of burnet. Most were breeding in self-contained populations that were wholly supported by the verge, with eggs and larvae found within 1 m of the busy road. Other verges had an extremely poor fauna.

When the reasons for this variation were analysed, it became clear that neither the volume of traffic nor the nature of the adjacent land had any bearing on the density or diversity of butterflies and burnets on the verges in between. Indeed, both measurements of Lepidopteran richness were negatively (but not significantly) correlated with the

Plate 19. Marbled white: found breeding in large numbers on the verges of several major roads in Dorset

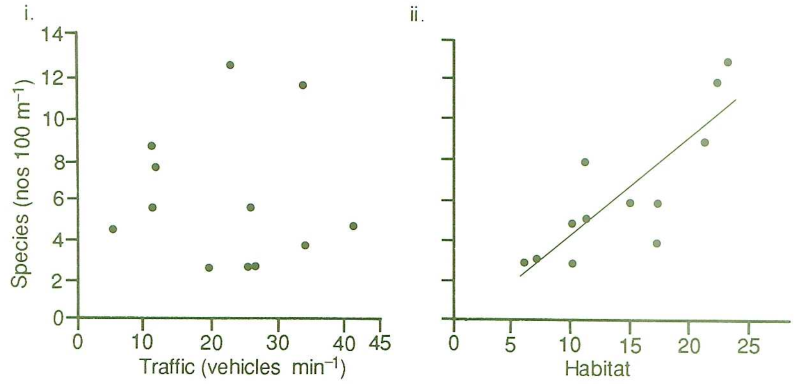

Figure 50. The number of different species of butterfly and burnet moth found on 12 southern road verges compared with (i) the volume of traffic on each road, and (ii) the variety of butterfly and burnet breeding habitats that each verge contained

richness of the adjoining land for butterflies and with the volume of traffic (Figure 50i).

In contrast, the condition of the verge had a strong bearing on the butterflies and burnets that were present: the five variables measured together explained 82% of the variation in the number of species found on different verges, and 90% of the variation in the density of adults. The variety of species present was particularly closely correlated with the range of different breeding habitats that existed on the 12 verges (Figure 50ii), although variation in the density of Lepidoptera was more closely correlated with verge width. Thus, the wider verges held significantly higher densities of adults per unit area of land, but only supported a large number of species if the specialised (and differing) breeding requirements of many species were present.

It was surprising to find how slight an impediment these roads were to the movement of butterflies, and how few of the adults were killed by vehicles. In some cases, there was no discernible barrier effect (Figure 51), although a small reduction in movement was usually recorded. Nevertheless, between 10% and 30% of all the marked adults that were later recaptured had crossed roads in the study area. These high figures suggest that the existence of a busy route between two populations does not add significantly to their isolation, although it should be noted that most of the butterflies studied were common species. Some rarities are notoriously sedentary, and additional research is needed on whether new roads form a significant barrier for such species.

Plate 20. Small blue: at least five colonies of this rarity are supported by the verges of major southern roads or motorways. It is a species whose requirements could easily be incorporated into the design of many more road cuttings

It was possible to record the mortalities inflicted by car strike on only one busy road. Cars killed between 0.6% and 1.9% of the adults of those species that live in closed populations, and about 7% of species that are migratory or nomadic. These figures are insignificant compared to the other natural mortalities experienced by adult butterflies.

The overall conclusion of the study is that many of the fears that have been raised over proposals for new roads are groundless, although there are certain qualifications. Most of this research involved fairly common species of

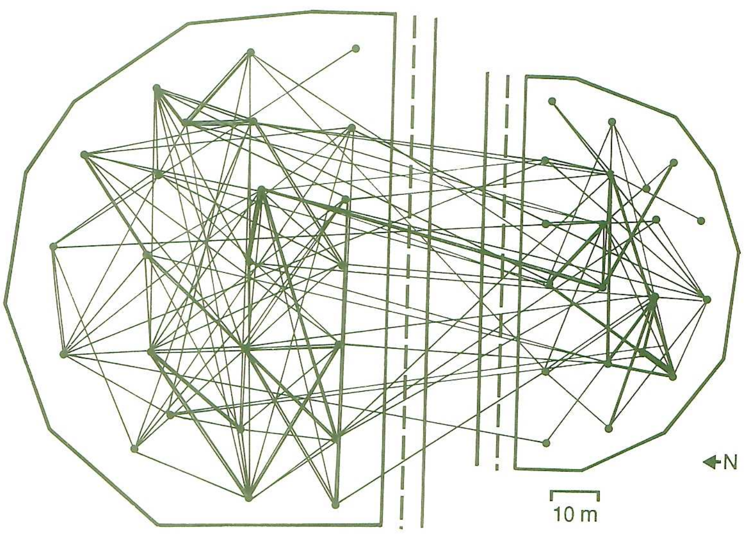

Figure 51. The movements of marked meadow brown butterflies between 42 subareas of an access roundabout on either side of a dual carriageway. The road formed no barrier to movements even though a vehicle passed approximately every 30 seconds

Plate 21. Adonis blue: at least two colonies of this rarity breed on road verges. It is a species whose requirements could be incorporated into the design of several proposed road schemes

butterfly and burnet, and inadequate data exist on the mobility of rarities. It is clear, however, that entire populations of local or rare species can be supported by road verges, so long as their specialised habitats exist there. We recorded grayling (*Hipparchia semele*), silver-studded blue (*Plebejus argus*) and brown argus (*Aricia agestis*) on the 14 study sites in Dorset and Hampshire, and elsewhere found several large populations of small blue (*Cupido minimus*) (Plate 20) and two of Adonis blue (*Lysandra bellargus*) (Plate 21) that were wholly supported by the verges of busy roads.

At present, however, it is very rare for roadsides to support scarce species, because most new verges and cuttings are uniformly graded, given a thick layer of (expensive) topsoil, and then often seeded with alien grasses or cultivars – practices which provide the requirements only of common species of butterfly and burnet. It is now clear that a much wider range of butterfly habitats could be created, including those of national rarities, if the traditional smooth topography of roadsides were altered to provide sheltered pockets containing patches of thin and deep soils, and if these pockets were seeded with wild flower mixes. Cuttings in the chalk and limestone of southern England offer the greatest potential, but probably almost every new scheme could be improved upon. However, to fulfill the potential of a new roadside, butterfly and other wildlife habitats must be incorporated into the original design, before the earth-moving plant has departed. ITE is uniquely qualified to advise on this potential enrichment of the British countryside, because of its pioneering research on the establishment of wild plant swards (Wells, Bell & Frost 1981) and its detailed analyses of the requirements of different butterflies (Thomas 1984, 1989; Munguira & Thomas 1990).

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Land inheritance and population cycles of red grouse

In some parts of their range, the numbers of red grouse (*Lagopus l. scoticus*) fluctuate in cycles of fairly regular periodicity of about six years and of varying amplitude. What are the causes of the cyclicity? Moss and Watson (1985) considered, in turn, the effects of food, cover, predation, parasites and disease. They concluded that each of these factors can be ruled out as proximate causes of the cyclic pattern in numbers. It is now proposed that the pattern could be explained by the joint action of two factors: territorial competition and differential behaviour towards kin and non-kin. The evidence leads to the assumption that the cycle in red grouse is driven by the male sex. Each autumn, old cocks and young cocks hatched the previous spring join in the contest for territories. The cock has the dual role of defending his territory from the incursions of other cocks (Plate 22), and of attracting and guarding a hen; the hens are attracted to cocks with larger territories.

The function of territorial behaviour may be to provide an adequate supply of some resource, such as food, cover, and space for sexual display, or for some other purpose. Whatever its function, one can reasonably suppose that the size of a cock's territory affects his reproductive success, ie the number of his sons recruited to the breeding population in the following year. If the reproductive success of the whole population, in any one year, is averaged, the proportion of young cocks recruited to the spring population in the following year is related to the average territory size of cocks in the current spring population.

This argument is based on a preliminary analysis of data on individual grouse territories and performance on a 1.8 km^2 study area at Kerloch Moor, Kincardineshire. The data include the mapped territorial boundaries of individually tabbed cocks and, wherever possible, the relative positions of fathers and sons (Figure 52).

As a rule, males remained on the same site. Those old cocks that survived and were still territorial the following spring (40–60% of the autumn number) usually retained a part of, or augmented, the territory which they had held the previous year. Out of 213 records of the central co-ordinates of the territories of cocks surviving to the following year, the distance moved in 195 records was equivalent to less than one territory away.

Paternal and fraternal proximity was also normal. In 14 out of 38 records of territoriality in surviving fathers and their sons, the sons gained territories adjacent to their father's territory and a further 14 settled at a distance equivalent to less than two territories away. In the case of orphaned cocks, eleven out of 28

Plate 22. A cock red grouse

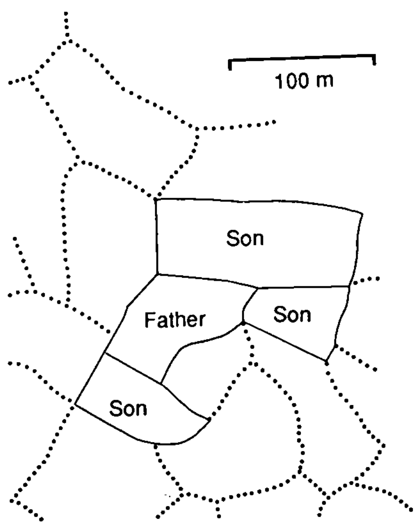

Figure 52. Territories of a red grouse father, his three sons and other neighbouring cocks at Kerloch Moor in spring 1974

territories established on the study area were more or less coincident with their natal territory, and a further eleven settled at a distance equivalent to less than two territories away. Of the 29 instances of marked full brothers obtaining territories, eight were adjacent and only five settled at a distance equivalent to more than four territories away.

A model has been built based on these observed factors, but most statements are speculations which have yet to be tested.

The data are consistent with the idea that competition amongst father and sons is less intense than that between unrelated cocks. Father, sons and brothers may be relatively tolerant in the territorial contest, directing their aggressiveness to unrelated neighbours.

With increasing population densities and smaller territory sizes, however, the tolerance between fathers, sons and brothers is likely to decrease, but competition between the members of a family group will probably still be less than that between unrelated cocks. In order of priority, a cock is likely first to attempt to meet his own territorial requirements, then those of his father/son/brother, and last of all to accept unrelated cocks as neighbours.

The outcome of the territorial contest presumably determines the cock's subsequent success at mating with a hen and producing offspring, and the mutual tolerance of father and son should give them an advantage in inclusive fitness over a pair of unrelated, and consequently more hostile, neighbours.

These speculations on differential behaviour between kin and non-kin of red grouse are consistent with the observations of Green (1983) on the red-legged partridge (*Alectoris rufa*).

In any one year, the chance that a territorial father has a son in the territorial population in the subsequent year is assumed to be directly related, first, to the size of the father's territory and, second, to the family relatedness of the neighbours, to the extent that they recognise each other as father, son or brother. The interplay of these two factors, territory size and kinship, is sufficient to explain the cyclical rise and fall in population size.

It is suggested that, at the low point of the cycle, the territory holders are few and well spaced out, territory sizes are large, young cocks can more easily establish territories close to those of their fathers, and the level of recruitment is high. As the population increases, the average territory size decreases, and smaller territories will lead to a reduced recruitment rate of young cocks. This reduction, in turn, together with the average 57% loss through the mortality of older cocks, will reduce the degree of kinship between neighbours. As his own territory becomes smaller, an individual cock, though still behaving differentially towards kin and non-kin, would be more likely to attack or threaten other cocks. Combined with the shrinkage of territory size, a reduced degree of kinship would thus lead to a further reduction in recruitment rate. As the population further increases, this falling recruitment continues, until the recruitment rate equals the replacement rate. At this point, the male territorial population is at its peak. Then, the effect of the greater aggressiveness between neighbours, associated with the continuing decrease in kinship, is likely to tip the population into decline. The population should continue to decline until the effect of increasing territory size cancels that of decreasing kinship. Cock numbers thus reach a low point, after which the recruitment rate rises again, and the next cycle begins.

The ITE mathematical model shows cycles with a period of about six years (Figure 53).

The hen's strategy seems quite different. She apparently invests little effort in the establishment of territory, but chooses between the male territories on offer, and then directs most of her energies to the production of young. If the territory is too small relative to others nearby, she moves on in search of a more attractive territory (Moss, Watson & Parr 1988).

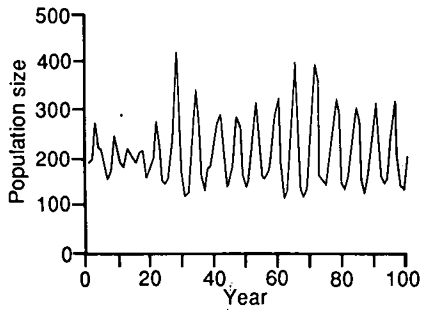

Figure 53. Segment of simulated population fluctuations for a survival rate distributed randomly as a normal variate, with mean=0.5 and SD=0.05

There is no need for a change in the rules governing the behaviour or in the genotype of the cocks, as suggested by Chitty (1967), between low and high densities; the slowing of recruitment and the decline in population size can be explained simply by variations in the level of aggressiveness between neighbours. According to the model, this aggressiveness depends upon the degree of family relatedness and upon territory size. This conclusion may apply more generally. Any species exhibiting fidelity to natal territory and differential behaviour between kin and non-kin has the potential to show cyclical fluctuations in population size.

Cyclical fluctuations in vole (*Microtus* spp.) numbers may be similarly explained. Charnov and Finerty (1980) suggested that aggression between unrelated individuals may be a factor causing population cycles. Subsequently, Boonstra *et al.* (1987) demonstrated that fidelity to natal territory, usually among females, occurs in most microtine species. The situation is thus similar to that found in red grouse, except that, in voles, it may be the female which drives the cycles.

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Effects of land use changes on wildlife

(Part of this work was done in collaboration with the Macaulay Land Use Research Institute (MLURI), and was funded by the Department of Agriculture and Fisheries for Scotland)

The effects of changes in land use upon wildlife can be immediate, ie when a grass field is ploughed for cereal production, or longer term, through, for example, afforestation or the removal of sheep from hill grazings. Some animals are favoured, while others cannot adapt and disappear. Some species may be 'pre-adapted' to exploit novel, man-modified environments, especially when the changed environments closely resemble their ancestral habitats. Others, such as ungulates, are able to modify their own environment, especially when their populations are uncontrolled.

Whatever the cause, a change in land use affects the species composition of the vegetation, and, equally important for wildlife, the structure of the habitat provided by the plants usually changes also. 'Structure' may be considered as having vertical and horizontal components. Vertical structure is concerned with the depth and layering of the vegetation, from the soil surface up to the canopy of ground layer, shrub or tree. Horizontal structure involves the shape (slender, branching, bushy) and patchiness of individual plants or associations of plants within the overall community. Techniques are being developed for quantifying these concepts so that the significance for wildlife of change in land use can be inferred from vegetation composition and structure.

In the following contrasting examples drawn from recent studies on Scottish farmland, conifer forest and moorland, aspects of adaptability, land use change, and habitat structure are illustrated in three major environments.

Farmland

The oystercatcher (*Haematopus ostralegus*) is a wading bird which nests around the British coast, mainly on bare or stony ground. In northern Britain, particularly NE Scotland, it spread inland along river systems in the last century, nesting on banks and shingles. A progression from riverine habitats to nesting on farmland far inland has been noted especially since the 1940s. On these farmlands, the oystercatcher nests alongside the lapwing (*Vanellus vanellus*), which, in contrast, is decreasing in number, as in many other parts of Britain. Both species were studied near Banchory, Kincardineshire, on land farmed on a 5–7-year rotation of leys, root crops and spring-sown cereals, and on the adjoining moorland edge. The two species differed in their use of habitat during the breeding season in two important respects.

First, although they nested on all available substrates, there was a clear and consistent preference by oystercatchers for recently cultivated land, and by lapwings for the wetter, broken ground, particularly that of the moorland edge. Many early lapwing nests on farmland were destroyed by cultivation, but, as oystercatchers started to nest 22–45 days later than lapwings, they avoided most field operations. The flat, bare, open fields closely resemble the ancestral coastal sites of oystercatchers, at least when the nests were initiated; indeed, so do the flat roofs of some buildings in Aberdeen, where up to 120 pairs of oystercatchers now nest each year.

Second, lapwing chicks are largely dependent upon wet and/or grazed fields with a short sward to which they are taken by their parents. As more land is drained or used for the cultivation of autumn-sown cereals, and less grazing land is required for cattle, suitable fields to rear young have declined. Oystercatchers, however, are unusual among waders in that they may carry food back to their young. They are, therefore, better adapted to exploit habitats normally considered unsuitable for wader chicks. In summary, the lapwing, once so typical of the British farming scene, is not as well adapted as the oystercatcher to overcome changes in farming practice, with the result that its numbers are decreasing in many areas, whilst those of the oystercatcher are increasing.

Forest

Throughout Europe and the USSR, most populations of capercaillie (*Tetrao urogallus*) are closely associated with old coniferous forests. The bird probably became extinct in Britain in the eighteenth century. It was successfully reintroduced in 1837 in Perthshire, and spread rapidly through the new conifer plantations which were, at that time, mainly of Scots pine (*Pinus sylvestris*). Large-scale planting from 1919 by the Forestry Commission and, more recently, by private concerns used a high percentage of fast-growing North American species, notably Sitka spruce (*Picea sitchensis*). This practice has resulted in large tracts of closely spaced, uniform, even-aged trees which shade out the ground vegetation when the canopy closes (although a mosaic of mixed-age trees may develop in the second rotation).

Droppings consisting entirely of spruce needles have been found in forest with 64% Sitka spruce and 7% Scots pine, and captive birds seem to subsist as well upon spruce as on pine. The structure of the forest and the growth form of the trees may be as important for capercaillie as the food value of tree species which comprise the forest. Our objective is, therefore, to determine which features in the structure encourage and support populations of males (females appear to be more adaptable in their choice of habitat). To this end, cocks were counted on their display grounds (leks) in spring in a wide range of forest types. Habitat maps are being made covering a circle of 1 km radius from each lek, which should include the home range of most of the displaying birds. These maps are used as a basis for sampling the forest structure in relation to capercaillie use. The height, spacing, shape and clumping of the trees are measured, as well as features of the ground vegetation. Principal component scores derived from these measurements will be used to describe forest structure quantitatively.

There is an early indication that the openness of a forest is important for capercaillie. Not only are adults able to fly between the trees, but sufficient light reaches the forest floor for a ground layer of vegetation to grow. This ground layer is typical of old forests and of great importance for chicks, which feed on the vegetation (notably blaeberry (*Vaccinium myrtillus*)) and associated insects.

Moorland

The grazing of rough grasslands and moorland by sheep has played a major role in determining the vegetation composition and structure of the Scottish uplands. Decades of continuous grazing and burning to provide fresh growth for sheep and red grouse (*Lagopus l. scoticus*) have prevented the establishment of shrubs and trees. Large areas of heather (*Calluna vulgaris*)-

dominant moorland have been converted to grassland, sometimes through intentional 'improvement', but often as an unplanned consequence of overgrazing and overburning. A gradual change is currently taking place, in which sheep stocks are being reduced in the uplands as production is increased in the lowlands. The effects of this change on the vegetation and the consequences for wildlife in the uplands need to be understood.

Although the main pathways for secondary vegetation succession after the removal of sheep have been studied for the main upland vegetation types (Miles, Welch & Chapman 1978), much of the component work on which our understanding has been based was done on a small scale and involved exclosure plots. Extrapolating from these plots to entire hillsides is difficult, as exclosures take no account of the ranging behaviour of the herbivores which can change the habitat. Furthermore, workers have paid scant attention to the vertical structure of the vegetation, which is likely to have far-reaching effects on ground-dwelling fauna.

In the collaborative study with MLURI, the changes in vegetation composition and structure on hillsides are being quantified, following the short-, medium- and long-term removal of sheep (Figure 54). The data are being compared with changes in indices of abundance of key wildlife species. The sampling procedure involves measuring the height, cover and layering of all the plant species in such vegetation communities as wet or dry heath, grassland, flushed grassland and bracken (*Pteridium aquilinum*). The numbers of pellet groups in sheep, deer, lagomorph and grouse droppings are counted, and a search is made for runs of field vole (*Microtus agrestis*) and other signs of their activity. Sites in eleven areas in eastern, western, and northern Scotland have been chosen, covering regions with different soils and climate. Each site has an 'experimental' area where sheep were removed from one to 20 years ago, and a control area which is still grazed by livestock.

On heaths and dry grasslands, the general effects of sheep reduction, in the absence of other factors, are that the vegetation grows taller, moss and litter strata increase in depth, heather invades grassy sites, and woody shrubs and trees eventually enter the community. The increase in bulk of the grass, litter and moss layers provided habitat for voles in 1989, a year of low vole numbers; a significant increase in vole activity was found only one year after grazing had been reduced on a recently fenced site.

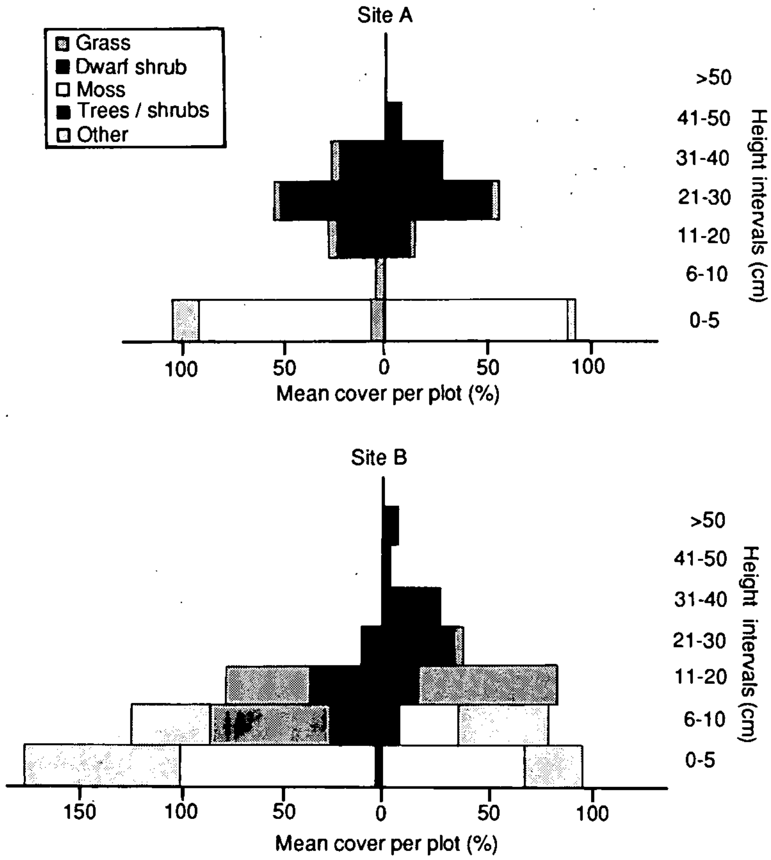

Figure 54. Vegetation profiles of dry heathland at two locations where sheep grazing was removed over 20 years ago (reduced treatment), compared with adjacent control areas. Red deer graze both reduced and control treatments at site A; these sites have very similar profiles. Red deer have been excluded from the reduced area at site B, and the profiles differ markedly

Factors which complicate this basic pattern include burning and the presence or absence of red deer (*Cervus elaphus*) and lagomorphs. At several sites, virtually no changes in vegetation were found, even after 20 years without sheep (Figure 54, Site A), but at most of these sites there was significantly more red deer dung on the areas where sheep had been removed. One effect of removing sheep appears to be an increase in the distribution and numbers of red deer, with the result that little structural change in the vegetation occurs on such sites.

Conclusion

Such studies as these described are improving our ability to predict the effect of land use change on certain species which might be at risk, or which may benefit from such changes. The definition of habitat structure in relation to animals' requirements also provides targets for management to enhance wildlife populations, eg in Environmentally Sensitive Areas.

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Community ecology

Community ecology is a complex area of science concerned with the interactions between plant and animal communities. The increasing anxiety over regional and global issues has led to a growing demand for predictive work at the community level.

The following three articles illustrate the broad nature of ITE's approach to the subject. All have conservation value.

The study of beetles in Snowdonia relates the distribution of beetle species to altitude, especially the factors limiting such distribution. Knowledge of the climatic limits on their range and about their interactions with one another are important in order to predict the consequences of any possible climatic change.

The second study of scrub succession shows the value of long-term studies in ecological research and manipulative field trials. The study followed the succession of vegetation for 16 years after clearance of old dense scrub, with particular emphasis on rotational management for conservation purposes. Seral communities such as scrub are dynamic and must be treated so, and not as static systems, as in a plagioclimax. Too often, scrub communities arise by chance, following changes in land use or grazing pressures. Active rotational management provides a means of creating habitats and landscapes to maximise species and habitat richness.

By contrast, the third article describes nitrogen cycling in a montane tropical rain forest in Costa Rica. Field and laboratory trials were conducted to determine if soil nitrogen processes were reduced with increasing altitude, and to identify the factors affecting those processes. The raising of temperature alone had little effect on mineralisation or nitrification, the important determinants being soil aeration and moisture. This study is relevant to the conservation of tropical forests, as drying of the soil following clearances could result in increased mineralisation and leaching losses, making regeneration in montane areas difficult.

Beetles on Snowdon

The work of the montane ecology group at ITE Bangor includes research on the effects of gradients of altitude (and thus of climate) on plants and animals, and studies of exclusively montane habitats and species. Current research on beetles on Snowdon can thus be divided into an examination of the relationship between beetle species and altitude, and a study of the rare Snowdon rainbow beetle (*Chrysolina cerealis*).

Beetle species and altitude

The objective is to determine why high-altitude species occur where they do, and why lowland species are unable to extend farther up the mountains. The answers to these questions should provide some indication of the beetle's likely response to changing climate.

In 1989, weekly collections of beetles on Snowdon were made by pitfall trapping in closely grazed montane fescue (*Festuca*) grassland at altitudes of 660 m, 860 m, 980 m and 1055 m above sea level.

Some species were found only at the higher altitudes, others mainly at lower altitudes, and yet others at a wide range of altitudes. The ground beetle *Patrobus assimilis* and the rove beetle *Geodromicus longipes* are both exclusively high-altitude species (Figure 55). The ground beetle *Pterostichus madidus*, however, is a very common low-altitude species (Figure 55), which is found at the lowest of the four sites. The species *Carabus problematicus*, similar to the common violet ground beetle (*Carabus violaceus*), is known to be a wide-ranging species, found above altitudes of about 300 m. The fewer number of beetles found in the lower

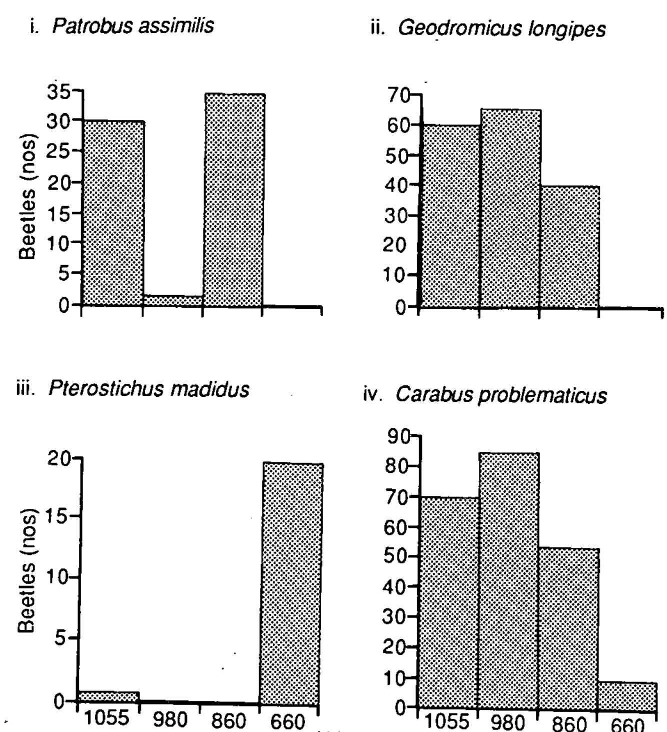

Figure 55. Numbers of four beetle species collected in 1989 at four sites of decreasing altitude on Snowdon

sites on Snowdon seems to be related to the lack of shelter for this large species (about 20 mm in length) at these particular sites (Figure 55).

Differences in life cycles are also apparent between species. For example, some species, such as the ground beetle *Nebria gyllenhali*, appear to be autumn breeders, whereas others, such as the rove beetle *Othius angustus*, appear to be spring breeders (Figure 56). Differences in the timing of the life cycle can also occur within a species, in populations at different altitudes, and these differences are now being examined.

To what extent does climate limit the distribution of the species? The responses of the beetles to gradients of temperature and humidity are currently being studied. At the same time, the microclimatic conditions of the various sites, and, within the sites, beneath stones and in crevices where the beetles shelter from severe conditions, are also being studied.

The Snowdon rainbow beetle

The Snowdon rainbow beetle (Plate 23) is a leaf beetle found in Snowdonia but nowhere else in Britain. It is also found in central Europe.

Our present interest in the species is because it is one of the protected species (Schedule 5 of the Wildlife and Countryside Act 1981) for which the Nature Conservancy Council in Wales is preparing a monitoring strategy. In particular, we need to know the optimal time of year and time of day at which it can be found, in order to estimate changes in its population from year to year.

There are several interesting problems relating to the Snowdon beetle. It is restricted to one main site, and yet its host plant, wild thyme (*Thymus drucei*), is common in the uplands and near the coast of Britain.

The beetle's life history is to be studied in captivity. In particular, its behaviour at different times of day and night will be monitored to see when it is most likely to be found in the field. Its behavioural response to microclimatic conditions, especially temperature and humidity, will be examined. The microclimatic conditions of the site will also be compared with apparently similar sites on Snowdon, to determine whether this particular site has any peculiarities.

A Buse

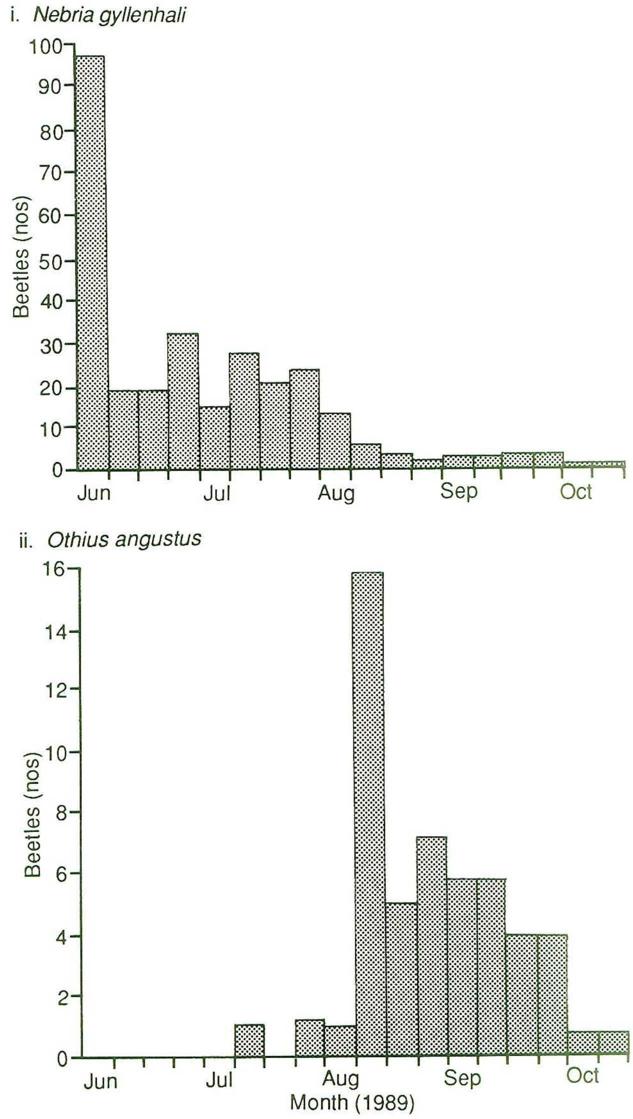

Figure 56. Numbers of two beetle species collected on Snowdon at different dates in 1989: (i) an autumn breeder, and (ii) a spring breeder

Plate 23. The Snowdon rainbow beetle

Scrub succession at Castor Hanglands NNR

(The Nature Conservancy Council collaborated in the setting up and general management of the plots at Castor, and provided some financial contributions to the research in 1973–76 and 1985)

In ecological studies, it is rarely possible to follow changes in the field over a long period of time. Although the long-term approach provides key information in understanding factors which maintain biodiversity, there are few examples of such data in the scientific literature because of the resources required in terms of manpower, time and finance for continual monitoring (Likens 1987). Results may not be produced quickly; also, such work is often empirical because of natural events which cannot be foreseen, and which prove to have a vital bearing on later events. Any disadvantages, however, are outweighed by new insights gained, as long as the recording has clear objectives, and quantitative, reproducible methods of data collection are adopted.

Plate 24. Aerial photograph of plots 1–10 at Castor Hanglands NNR in 1988. (Plot 1, top right, was only a trial plot and is an irregular clearing: plot 2, top left, was cleared in 1974 and has been in succession since 1979: positions of transects are visible from trampling during recording, and some deer paths can be seen)

Since 1974, successional vegetation following clearance of old dense scrub in sequential plots has been studied at Castor Hanglands National Nature Reserve, near Peterborough. The objectives are to record colonisation and change in a rotational management system for the conservation of seral scrub communities. One plot of 50 m × 50 m of the old scrub (*c* 30 years in 1974) was cleared every year from 1974 to 1988 (Plate 24). All plots have four random permanent belt transects, of 0.5 m × 25 m, one in each quadrant. The transects are marked by buried metal markers (an important feature of long-term work is reliable permanent marking systems in the field). All woody plants in the transects were recorded by searching through each metre of vegetation; seedlings and regrowth were distinguished and heights measured. The dominant flowering plants were noted, together with total numbers in transects and plots.

Plots received differing initial treatments after clearance, because it was decided that immediate regrowth of the shrubs should be reduced. The first four plots were mowed in July and September for four years after clearance. Such frequent mowing seriously reduced the seeding of early successional plants. Therefore, a second group of four plots was mowed once in late September for four years after clearance. The remaining four plots were left unmown.

It is not possible here to describe all the work at Castor Hanglands, but some results and discussion follow.

Initial responses to clearance

The old scrub before clearance was dense, casting heavy shade, and only 57 flowering plant species were recorded. Even in the first year after clearance, the mean number of species per plot was 108 (a total of 244 species for all 12 of the first year plots). In the second year, the mean numbers were 122 (240 species overall). There were many interesting species of disturbed ground (Plate 25), some of which had rarely or never previously been recorded from the Reserve. Annuals or biennials were frequent, eg henbane (*Hyoscyamus niger*), fluellen (*Kickxia* spp.), stone parsley (*Sison amomum*), mullein (*Verbascum thapsus*) and mignonette (*Reseda* spp.). Others persisted for longer, eg milk-vetch (*Astragalus*

Plate 25. Early successional plants in the second year after clearance of plot 13 in 1987

glycyphyllos), deadly nightshade (*Atropa belladonna*) and pepper saxifrage (*Silaum silaus*). Many of these species apparently germinated from the soil seed bank, responding to the opportunities presented by the bared ground following clearance.

Twenty-two species of woody plants have been recorded. Most of the common species occurred predominantly as seedlings in the first year. Blackthorn (*Prunus spinosa*) regrew from cut stumps and suckers. Figure 57 shows the total numbers of woody plants in the plots and the subsequent losses. There were striking differences between plots in the initial numbers recorded. These differences were partly related to meteorological factors, because seedling numbers were correlated in the different plots in particular years: 1979 and 1985 were good years for several species (Table 13). Preliminary analyses show that seedling numbers relate more to the volume of seed produced by the parent bushes than to the weather for germination. Another aspect of initial seedling occurrence was the relationship to topography. Where plots had ancient ridge and furrow, there were generally more woody plants on the ridges (Figure 58); few species were associated with the hollows, notably willow (*Salix* spp.).

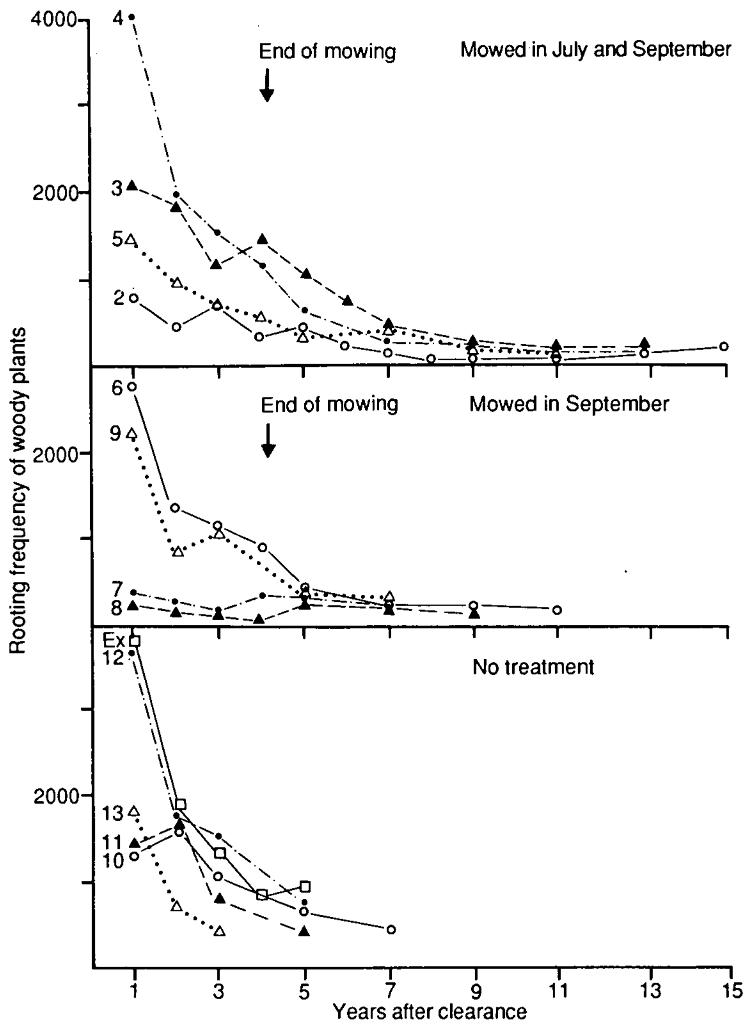

Figure 57. Total numbers of woody plants, as rooting frequency, in the transects of plots 2–12 and the deer exclosure (Ex) for all years of recording. (Plot 1 was a trial plot and recording was discontinued: deer exclosure had only two transects and figures doubled for direct comparison)

Succession in later years

Species numbers were highest in the first or second years and then fell slowly, reaching a mean of 76.8 per plot after ten years. From the results so far, the untreated plots are losing species faster than the mowed plots. The sequence of dominants was from dog's mercury (*Mercurialis perennis*) and rough-stalked meadow-grass (*Poa trivialis*) (with disturbed ground species, eg stinking groundsel (*Senecio viscosus*), St John's wort (*Hypericum* spp.), creeping buttercup (*Ranunculus repens*), ground ivy (*Glechoma hederacea*), creeping thistle (*Cirsium arvense*) and musk thistle (*Carduus nutans*)), through to Yorkshire fog (*Holcus lanatus*), tufted hair-grass (*Deschampsia cespitosa*), and towards bush grass (*Calamagrostis epigejos*) and woody plants. The speed of the change depended greatly on the initial colonisers, and transition matrices are being used to analyse the process in more detail. Tall dense grasses suppress the establishment of most woody plant seedlings, and, if the initial woody plants fail to grow on, succession can be deflected to a longer phase of grassland (Ward 1990). This deflection has occurred at Castor because of the mowing and deer (*Cervus nippon*) browsing (eg plot 2 is still grassland eleven years after mowing ceased – Plate 26). In the next few years, vegetative reproduction by suckering is expected to become more important; indeed, there was a slight rise in numbers of woody plants in the oldest plot (Figure 57).

The influence of deer on the woody plants has proved far greater than expected, and so a deer exclosure was set up in 1985. The contrast in growth has been remarkable. For example, after five years, the mean height of unbrowsed

Table 13. Total numbers of seedlings of six species in the first three years after clearance to show years of abundance

Year	Plots	Cornel	Hawthorn	Species Ash	Rose	Bramble	Willow
1977	2–4	51	64	1	336	740	3
1978	3–5	48	34	0	284	76	0
1979	4–6	97	93	35	1160	693	50
1980	5–7	35	27	6	106	41	1
1981	6–8	13	21	18	27	40	10
1982	7–9	155	14	16	928	328	7
1983	8–10	51	9	7	87	54	0
1984	9–11	236	32	378	318	333	0
1985	10–12	495	91	21	1296	1089	27
1986	11–13	145	67	63	505	180	0

blackthorn was 75.9 cm (n=229, SD 38.8), while the browsed plants were 22.5 cm (n=463, SD 10.6). In 1989, all woody plants in the transects were examined for damage, revealing that 40% (n=1939) had been browsed. Many undamaged plants were short and hidden in the denser grass, or were protected by clumps of thorny bramble (*Rubus*) and gorse (*Ulex*) which acting as 'nurse shrubs', shielding the more palatable woody species. Spacing patterns generated in this way probably persist through to older scrub.

Conservation of seral communities

Management of seral communities like scrub must take account of dynamic change: it is not practical to maintain a steady state like a plagioclimax. The management of succession requires information about the timing of colonisation and the persistence of species of plants and animals during seral change. The initiation phase and the subsequent early competition between herbs and grasses and woody plants are critical to the course of the succession. Indeed, scrub-resistant tall dense grassland might have a function in some species-poor amenity grasslands for reducing scrub invasion.

Ephemeral early successional communities of bare/disturbed ground are less often included in management plans for Nature Reserves, and in some cases could be combined with rotational scrub management (Ward 1990). The old scrub should continue until there is a high proportion of bared ground caused by shading, to enable greater activation, with less competition, for species of the soil seed bank following clearance. Early successional species need to set seed well to replenish the seed bank for a later rotational clearance.

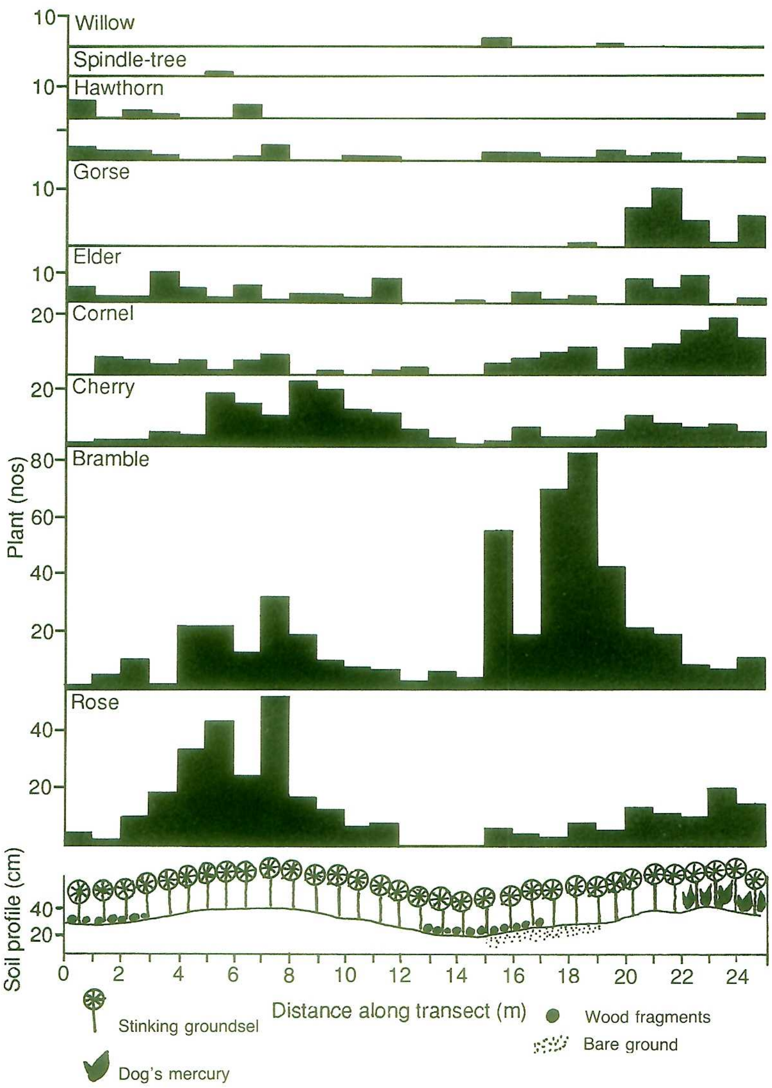

Figure 58. Numbers of woody plants in each metre of transect D in plot 12 in the first year after clearance (1985) (with soil profile of ridge and furrow, and key to dominants)

Plate 26. Transect A in plot 2 in 1989, eleven years after mowing ceased, with tall dense grasses and herbs suppressing colonisation by woody plant seedlings. Marker canes stand in buried metal tubes at each end of the transect

Browsing and grazing animals may greatly influence the course of succession. In management terms, it is advisable to consider whether the objectives of scrub rotational management should include the early control of deer and/or rabbit (*Oryctolagus cuniculus*) numbers.

The Castor trial has stimulated the development of ideas about the relationships between management and the landscaping of dynamic systems. Too many scrub communities have resulted by chance in areas which have remained ungrazed. The rotational management of structurally diverse vegetation provides an opportunity for reshaping and landscaping on Nature Reserves and amenity sites in ways which will also maximise the species richness of seral communities.

L K Ward

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Nitrogen cycling in montane tropical rain forest

(This project was part of a multidisciplinary study on the ecology of tropical mountains, and was done in conjunction with Operation Raleigh and colleagues from the Organization of Tropical Studies (OTS) at La Selva Field Station in Costa Rica. The study was partly funded by the award of a Travelling Fellowship to R H Marrs from the British Ecological Society)

It is well known that the species composition and structure of moist tropical forests change with altitude (Grubb 1977), and one of the hypotheses put forward to explain these changes is that nutrient cycling is reduced at high altitude. In particular, the transformations of nitrogen (N) in the soil were thought to change with altitude (Marrs *et al.* 1988). In most ecosystems, soil nitrogen occurs mainly in organic matter, and it is made available for plant uptake through the processes of mineralisation and nitrification. Mineralisation is the process where soil organic nitrogen is broken down by soil micro-organisms to produce inorganic ammonium-nitrogen, and nitrification describes the subsequent reaction which forms nitrate-nitrogen.

Both ammonium- and nitrate-nitrogen can be taken up directly by plants. Mineralisation and nitrification are, thus, key processes likely to control the productivity of trees. Both processes are mediated by soil micro-organisms and are reversible. Generally, mineralisation occurs when the soil organic matter and soil micro-organisms act as a source of inorganic nitrogen, ie when the reaction is positive, and immobilisation takes place when soil organic matter acts as a sink, ie the reaction is negative.

This study tested the hypothesis that soil nitrogen processes were reduced at altitude in moist tropical rain forest on a single mountain, Volcan Barva, in Costa Rica, Central America, and assessed the environmental factors which might affect such processes. At six altitudes (100 m, 500 m, 1000 m, 1500 m, 2000 m and 2600 m) on the mountain, permanent study plots of 1 ha were established (Table 14). In January 1986, ten replicate surface soil samples were collected from the plots, and treated as follows:

1. extracted with 1 M KCl for an initial measure of inorganic ammonium- and nitrate-nitrogen concentrations;
2. incubated under field conditions at the collection site for between 12 and 15 days and then extracted with 1 M KCl, as above;
3. incubated under laboratory conditions at the base of the mountain and extracted as in treatment 2 above.

Field and laboratory mineralisation and nitrification rates were then calculated by difference (incubated – initial concentrations) and expressed on a 14-day basis for comparative purposes.

4. air-dried, sieved to pass through a 2 mm mesh and brought back to Britain for chemical analysis. The rate of mineralisation was estimated in incubations made under 'improved' conditions, ie where soil aeration and moisture conditions were ameliorated by adding acid-washed sand and a known volume (6 ml) of deionised water.

The three ways of measuring mineralisation, therefore, represent a series of estimates where two environmental parameters which were thought most likely to limit the

Table 14. Some characteristics of the six 1 ha plots sampled on Volcan Barva, Costa Rica

Plot altitude (m)	Prevailing slope (°)	Prevailing aspect	Basal area of woody species (≥10 cm dbh) (m^2)	Height of main canopy (m)	Height of tallest tree (m)	No. of individuals of woody species (<10 cm dbh)	No. of species of woody plants (>10 cm dbh)	The five leading families ranked by number of woody species (≥10 cm dbh)
100	5	E	23	35–40	45	494	112	Mimosaceae Lauraceae Annonaceae Euphorbiaceae Meliaceae
500	0	–	24	38–43	50	391	121	Mimosaceae Meliaceae Rubiaceae Lauraceae Annonaceae
1000	20	NE	31	35–40	45	546	106	Lauraceae Mimosaceae Rubiaceae Moraceae Meliaceae
1500	15	N	27	30–35	38	553	63	Lauraceae Euophorbiaceae Myrtaceae Rubiaceae Cyatheaceae
2000	15	NW	27	25–30	35	448	59	Melastomataceae Lauraceae Rubiaceae Euphorbiaceae Piperaceae
2600	15	N	25	20–25	32	503	32	Lauraceae Melastomataceae Araliaceae Cunoniaceae Symplocaceae

mineralisation process in montane soils were alleviated: temperature in the laboratory incubations, and both temperature and moisture/aeration in the 'improved' incubations.

Nitrogen mineralisation under the 'improved' conditions increased markedly with increasing altitude (Figure 59i), from 150 µg to 760 µg N g^{-1} 14 days^{-1} between 100 m and 2600 m. Under field conditions, the opposite result was found, the rate declining with increasing altitude from 38 µg to -2 µg N g^{-1} 14 days^{-1} (Figure 59ii).

Under field conditions, there was a change from mineralisation to immobilisation at the highest altitude, and similar results were found in the laboratory study (Figure 59ii).

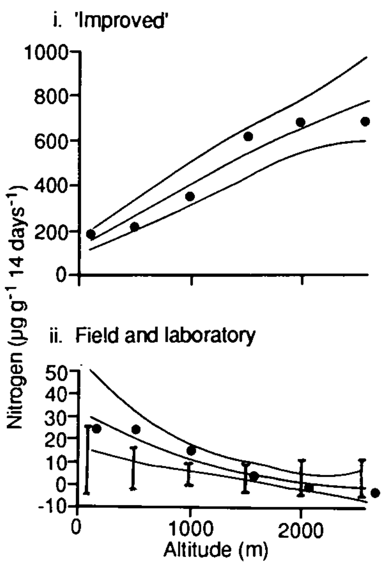

Figure 59. Changes in nitrogen/mineralisation in soils along the altitudinal transect on Volcan Barva, Costa Rica, under (i) 'improved' incubation conditions, and (ii) field incubation (fitted curve and approximate 95% confidence limits) and laboratory incubation (solid vertical lines = means + 95% confidence limits). The closed circles represent the mean values of the raw data for the respective curves

Under field and laboratory conditions, the nitrification rate also decreased with increasing altitude (Figure 60), from 22 µg to 3 µg N g^{-1} 14 days^{-1}.

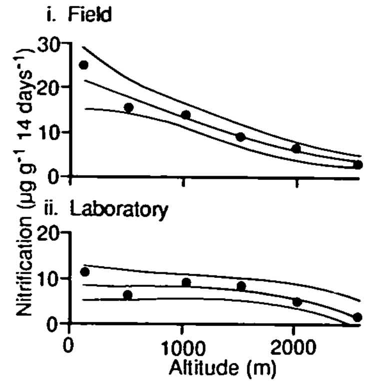

Figure 60. Changes in nitrification rates under (i) field, and (ii) laboratory incubation along the altitudinal transect on Volcan Barva, Costa Rica; the outer lines show the approximate 95% confidence limits, and the closed circles represent the mean values

A major conclusion from this study was that the rates of nitrogen mineralisation, or indeed of nitrification, did not improve when temperature alone was ameliorated. When the soils were dried and aeration improved, the relationship between altitude and mineralisation was completely reversed, and the rates were between one and three orders of magnitude greater. The implication of this finding is that soil structure and aeration may be the major factors limiting the breakdown of soil organic nitrogen in these montane soils. The soils from high altitude in Costa Rica were very wet, with moisture contents (80%) double those found in the lowland forest sites. Moreover, the montane soils had much higher concentrations of total nitrogen and carbon, and extractable cations (Marrs *et al.* 1988).

These conclusions have some relevance for the wise resource management of montane tropical forest vegetation. The combination of high rainfall and the high store of both nutrients suggests that such ecosystems will be particularly vulnerable to erosion and leaching losses after forest destruction. This vulnerability was to be expected. However, the dramatic increase in breakdown of the soil organic nitrogen under the 'improved' conditions implies that any management change which dries out the soil, either directly by draining or indirectly if the soil surface dries when soil temperatures are increased following forest clearance, could stimulate mineralisation and intensify leaching losses. Thus, the regeneration of montane tropical forests may be particularly difficult, and may take much longer than forests at low altitude.

R H Marrs and M D Mountford

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Scientific services

Large areas of work of ITE's are underpinned by ideas and equipment developed and supported by scientific services. Many of the newly emerging problems of the environment require more precise ways of measuring, before solutions can be suggested.

The three articles in this section highlight one aspect of the work of scientific services. They illustrate how instruments are being deployed by themselves, in purpose-built structures and in laboratory conditions, to solve some of the current problems.

The atmospheric deposition of pollutants takes place both in the wet and dry state. It is important to distinguish between these two states as they have been found to affect vegetation in different ways. The first article describes an instrument which is able to separate wet and dry deposition by the use of an automatically activated cover. It is able to sense when raindrops start falling, and then moves its cover over the collecting funnel.

In modern pollution research, emphasis is now concentrating on the more subtle effects of long-term low-level exposures of phytotoxic gases on vegetation. The second article describes the facilities at ITE Bangor for carrying out this type of research. A range of equipment has been specially designed to fit into hemispherical glasshouses. Gas control and delivery systems are housed in a separate building, with gas analysers and a sampling system for monitoring dome gas levels, and the supply and sample lines are ducted underground to the glasshouses.

The final article discusses the services provided by the Institute's analytical chemistry group, and illustrates its response to the high demand for the analysis of aqueous solutions, as a result of increased interest in water quality. Autosamplers and computerised control with data processing systems have been used to increase throughput.

These three articles emphasise how a wide range of instruments and technical knowledge are being used to solve some of today's pressing environmental problems.

Automated dry/wet deposition separator of aerial precipitates (ADDSOAP)

Much research is dependent on instrumentation. However, apparently simple requests can be technically demanding and require an iterative sequence of development and trial. One illustration is an application of research on atmospheric deposition, where it became increasingly important to distinguish wet deposition in rain from the dry deposited gases and particulates, and occult deposition, ie mist, fog and cloud water. It is often preferable to separate the 'true' wet deposition by covering the funnel between rainfall events, or providing some means to wash down the funnel at the start of a rain event in order to remove accumulated dry deposits, keeping these washings separate from the following rainfall. Manual control of a funnel cover is neither practical nor cost-effective. Collectors have, therefore, been developed with automatically activated covers, the movement of the cover being controlled via some form of rainfall sensor.

The commonest form of sensor detects the moisture from raindrops, generally as a conductive path between electrodes/conductors. However, a large sensing area is required if the initial and most contaminated raindrops of a shower are to be captured. There are also other practical problems, eg detecting raindrop size, contamination and power requirements. As a result, this form of sensor was rejected at an early stage in the development of ADDSOAP.

Ideally, a sensor should detect, within seconds, the start and finish of a rain event and the type of rainfall. It should require no maintenance, be reliable, and have low power consumption if battery operation is considered. These requirements have been fulfilled in the current form of ADDSOAP in field trials over the past five years.

During initial development, solutions focused on the detection of air moisture, surface wetness, and impact. The latter, although novel, appeared promising. Experiments with thin stretched diaphragms and a microphone exploited the self-resonance effects of metal sheet structures and vibration transducers in contact with them. Selective filtering of transducer signals and summing vibration patterns produced a programmable precipitation sensor, where the size and rate of impacts, or their combined effect, could be set as a threshold for cover opening. It is this precipitation sensing module which has been named ADDSOAP; it can be linked to a variety of cover mechanisms, can drive motorised valves, and can even drive a motor-powered wheel or pulley for moving a structure when a pre-selected precipitation threshold occurs.

Development of ADDSOAP has progressed over the years, from the original metallic funnel cover which acted as a vibration sensing board when rain landed on it. The vibrations were transmitted down the cover support to an electronic sensor. The processed signal then controlled the motor drive to position the cover. Although this device was compact and battery-powered, the cover did not fit tightly on the water collection funnel, and insects were able to seek shelter and add to the nutrients of the collected sample. Also, although the device responded quickly to impacts, it did not detect fog or fine drizzle. Modifications were made which largely overcame these problems. The modified instrument had a separate rain impact sensing box, a ventilated wet and dry thermistor psychrometer to open the cover under high humidity conditions, and a counterbalanced cover plate which revolved through about 220° to form a good fit on the funnel. However, this design was not ideal in windy conditions; the cover could be buffeted as it swung over between the open and closed state, or could be lifted from the seating on the funnel. In the open state, deposits on the exposed underside of the cover could be transferred to the funnel. The psychrometer also posed maintenance problems, with a lack of water to the wet wick and thermistors changing their characteristics.

In 1986, an improved device was built (ITE Annual Report 1985/86, p139) for research into acid waters in Wales, using experience gained from the two previous models. It incorporates a separate sounding board, which houses the control electronics and a synthetic fibre humidistat for moisture detection. The funnel cover is designed on a four-rod support, offset parallelogram principle, so that the top of the cover is always exposed to the elements; the cover lifts off the funnel but remains horizontal until almost clear of the funnel, when it tilts down the side out of the way below the funnel rim. An optional system has two funnels, one for wet and the other for dry collection, with the parallelogram arms moving the cover from one funnel to the other. Years of field trials have shown that wind or insect problems are of little significance, and the ventilated humidity sensor has proved reliable and maintenance-free. The stainless steel impact sensor has no moving parts or surfaces to contaminate, and thus requires no maintenance. The electronics control the mechanical positioning of the cover, so there are no switches to go wrong or out of alignment. The electronics can be programmed for the desired size and frequency of impacts to operate the cover; the cover is replaced over the funnel within a minute of these conditions ceasing. Use of the humidistat with impact sensing will capture almost all wet deposition; using the humidistat and impact sensor in opposition, the cover will open only when fog, dew or mist (occult deposition) occur, closing as soon as impacts are detected. The cover can operate equally well in the reverse mode, keeping the funnel dry or discarding occult deposition.

An eight-bottle carousel and timer have also been produced to sample portions of a shower, or for daily sampling. The whole apparatus can run for several weeks from a charged car battery, which can be routinely changed or, for continuous use, recharged from a solar panel or domestic mains supply.

A number of ADDSOAPs are now in operation around Britain, and, although such a device has a specialised and limited market, current trends towards pollution control and environmental consciousness are likely to extend the market. Applications of ADDSOAPs have, so far, included building weathering, acid rain, nutrient input, airborne metals and trace element studies. Integration with a wind direction sensor and time recorder would allow the catchment of plumes of industrial pollutants. Warren Springs Laboratory is currently evaluating a range of precipitation sensors, including the ADDSOAP, with a view to uprating the performance of their nationwide distribution of wet-only precipitation sensors.

The ADDSOAP concept has developed over the years to its present reliable form. One can only guess at future requirements, and adapt the device accordingly.

D G Benham

Pollution research facilities at ITE's Bangor Research Unit

(The experimental work was partly funded by the Welsh Office)

Assessments of the potential toxicity of pollutants to vegetation have changed substantially in recent years. Emphasis has moved away from studies of acute injury to plants, caused by high concentrations of the phytotoxic gases – sulphur dioxide (SO_2), nitrous oxide (NO_2) and ozone (O_3) – to investigations of the more subtle effects of long-term low-level exposures. In addition, the importance of wet deposition has been recognised as a major route for the influx of potentially damaging levels of sulphur, nitrogen and hydrogen ions into ecosystems. The importance of this route is particularly evident in the uplands, where high levels of rainfall occur, and vegetation may be cloaked for prolonged periods in highly acidic mists. ITE's new pollution research facilities at Bangor have been designed to allow studies of the effects on plants of both low, controlled concentrations of gaseous pollutants and acidic mists.

Studies of the effects of gaseous pollutants on vegetation are conducted in four hemispherical glasshouses, manufactured by Rosedale Engineering Ltd, of Filey, Yorkshire, and marketed under the tradename 'Solardome 1' (Plate 27). The system is based on one originally designed in 1976 at the University of Lancaster (Ashenden *et al.* 1982) and later modified (Lucas, Cottam & Mansfield 1987). The domes of the Bangor glasshouses are smaller, which provides a number of operational advantages. Each dome has a diameter of 3.05 m, a floor surface area of 7.31 m^2, and is constructed of glass mounted in an anodised aluminium framework (Figure 61). The domes are ventilated by two 'Sonoxcarb' fan filter units (Machine Control Ltd, Horsham, Sussex), each of which supplies two domes. Ambient air is drawn through charcoal filters, to remove any background levels of pollutants, and then pushed, via a flow splitter, along the main air supply trunking to each dome. The air then enters a mixing chamber where controlled quantities of pollutant gases may be added before it is pushed into the dome and released around the circumference via a ring of lay-flat perforated polythene tube. Finally, the air leaves the system via a central chimney cowl at the top of the dome. The rate of air movement through each dome is

Plate 27. 'Solardome' fumigation system

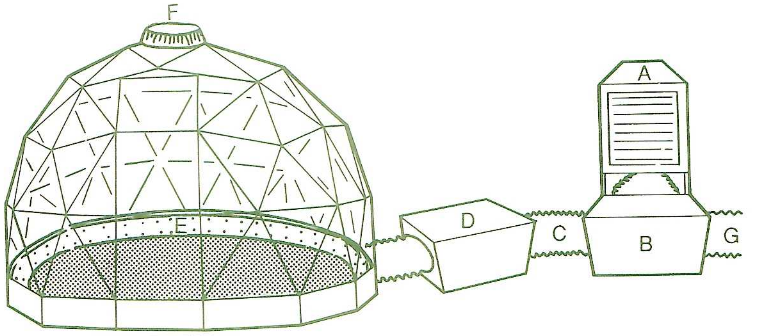

Figure 61. Diagram of 'Solardome' fumigation chamber. A, fan filter unit; B, flow splitter; C, air ducting; D, mixing chamber; E, lay-flat tubing; F, ventilation cowl; G, duct to second Solardome chamber

adjustable up to two complete air changes per minute.

Gas control and delivery systems, together with gas analysers and a sampling system for monitoring dome gas levels, are housed nearby in the systems control building, and all supply and sample lines are ducted underground to the domes. Ozone is generated by a laboratory ozonator (Wallace & Tiernan, Tonbridge, Kent); SO_2 and NO_2 are supplied from cylinders of compressed, pre-diluted gas, as opposed to the pure gases used in the earlier, larger 'Solardome' systems (see Lucas, Cottam & Mansfield 1987). The advantage of this system is an easier control of pollutant concentrations, without the need for expensive mass flow controllers. Instead, flows are maintained using constant differential regulation-type controllers with needle valves (Rosemount Ltd, Stockport, Cheshire). All domes are fitted with supply lines for the three pollutants and PTFE sampling lines. The levels of pollutants in air sampled from the domes are measured using Monitor Laboratories analysers for O_3 and NO_2, and a Meloy flame photometric analyser for SO_2.

Studies on the effects of acid mists on plants are conducted in a closed 7.3 m × 3.3 m polythene tunnel, divided internally by polythene sheeting into four treatment bays. Each bay is fitted with a Sonicore atomising station (Lucas Dawe Ultrasonics, London), which can provide low volumes (0.4–8.0 l h^{-1}) of treatment solutions at particle sizes in the range 5–30 μm (equivalent to fogs/clouds). Treatment solutions are made up in the systems control building and pumped underground to the treatment bays, where they are ultrasonically atomised in a compressed air stream (Plate 28).

The facilities have been used for a range of experiments aimed at determining the effects of pollutants on the growth and physiology of plants. One example is an investigation of the effects of low concentrations of SO_2, NO_2 and O_3, together with the additional stresses imposed by wet acid deposition, on the growth of white clover (*Trifolium repens*) cv 'Grasslands Huia'. The experiment was conducted on 6-week-old seedlings grown in 7.5 cm diameter pots containing John Innes no. 2 potting compost. Atmospheres within the glasshouses were set to provide treatments of:

i. charcoal filtered air (control)
ii. SO_2+NO_2
iii. O_3
iv. $SO_2+NO_2+O_3$.

Concentrations of SO_2 and NO_2 were maintained at 40 ppb, except for two additional peaks, one of 3 h at 80 ppb on Thursdays, and one of 3 h at 80 ppb, immediately followed by 1 h at 110 ppb O_3, on Tuesdays. Monitoring the dome atmospheres ensured that concentrations remained +2 ppb of the desired levels.

There were three experimental blocks of 20 plants in each dome, the positions of which were rotated weekly. Five plants from each block were allocated to receive one of four acid mist treatments. For all misting treatments, plants were

Plate 28. Misting unit in operation

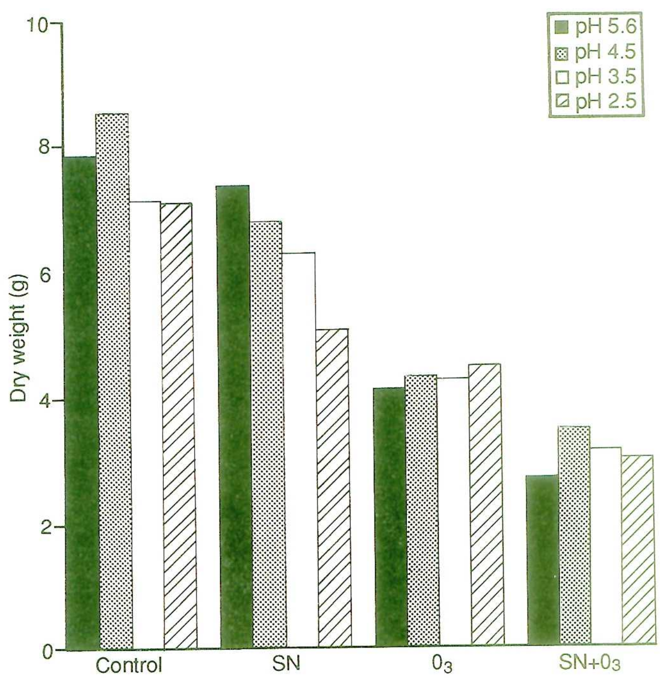

Figure 62. Mean dry weight yields of white clover after being exposed for 15 weeks to different aerial pollutants and acidified mist treatments

taken from the domes and transferred to the polythene tunnel misting system. The mist treatments were three 4 h exposures (Mondays, Wednesdays and Fridays each week) of:

i. pH 2.5
ii. pH 3.5
iii. pH 4.5
iv. pH 5.6

which provided a total wet deposition of 6 mm per week. Mist solutions were made in deionised water by adding equimolar concentrations of ammonium nitrate and sulphuric acid. Supplementary watering of plants was done by watering can at a rate of 24 mm per week, using a simulated acid rain solution of pH 4.5 (made up by additions of sulphuric acid and nitric acids in the ratio of 7:3, by volume).

Plants were removed from the treatments after 15 weeks of exposure, their roots washed free of soil, and then dry weights obtained. The results are shown in Figure 62. An analysis of variance of the data revealed significant differences ($P<0.001$) between both gaseous and acid mist treatments, and a significant ($P<0.001$) interactive effect of gases × mists on total plant dry weights. Averaged over all misting treatments, there were reductions in total plant dry weights of 16.6% for SO_2+NO_2, 43.6% for O_3 and 59.4% for $SO_2+NO_2+O_3$, in comparison with control plants. For misting treatments, a lower yield was averaged over all gas treatments at pH 2.5, compared to pH 4.5 and pH 5.6. The significant interaction of gas × mist treatments revealed that yield reductions which were attributed to the more acidic mist treatments (pH 2.5 and 3.5) were not significant in the O_3 and $SO_2+NO_2+O_3$ treatments; the severely harmful effects of these gaseous pollution treatments appear to override any effects of the mists.

T W Ashenden, C R Rafarel and S A Bell

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Analytical chemistry group

Over the past few years, the group has been going through a process of review and change. Reviews have been necessary to respond to the heavy and changing demands for analytical services from ecological scientists and to update the book *Chemical analysis of ecological materials* (Allen 1989), which has become a standard text since it was first published in 1974.

This text was based on the routine methods pioneered and developed from agricultural and water quality methods, applied and modified in ITE's Merlewood laboratory for conservation experimental work. The book contained separate sections on soil, vegetation and water analysis, and covered all aspects from sample collection to calculation of results. Full practical details were provided for well-tried and tested methods, with manual and semi-automated options to allow users to select a procedure to match their facilities. The second edition now includes theory, methodology and practical hints, based on 30 years of experience in supplying chemical data, a vital component to ecological research. The text has been completely revised and updated to reflect the rapid growth in technology and the change in emphasis from conservation to applied ecology. The section on instrumental procedures has been extended to incorporate liquid chromatographic methods and a vast experience in automated methodology. Advances in computing, statistics and data evaluation procedures promoted a radical revision of the final chapter, whilst the emphasis in water analysis was shifted towards the handling of solutions from nutrient cycling and pollution studies.

Several of the analytical facilities available to the group have been upgraded over the last three years. During 1989, the major commissioning work on an inductively coupled plasma/optical emission spectrometer (ICP/OES) was completed. This instrument uses a sequential scan to perform multi-element analysis for the wide range of applications required. Methods have been developed and tested for routine analysis of major cations on aqueous solutions (sodium, calcium, magnesium, iron and aluminium). ICP/OES has been particularly useful for trace metal analysis in soil and vegetation. In some instances (eg boron), the sensitivity and performance of the instrument have proved far superior to other methods available.

High demand for the analysis of aqueous solutions has also required reorganisation of the anion determinations, previously carried out on dispersed continuous flow equipment. Upgrading the equipment and the addition of a large capacity autosampler and computerised control/data processing system have enabled the grouping of all water methods, and provided the option to operate the analysers unattended overnight.

Improving laboratory operations to increase sample throughput inevitably results in greater demands in terms of data handling and report preparation. In anticipation of these demands, our strategy has been to upgrade each analytical instrument to incorporate a personal computer (PC)-based data handling package, thus enabling the use of purpose-designed software from the different manufacturers, and then to link each data system to the main Station computing network. Thin-wire ethernet has been installed, and each PC communicates with the Station's VAX mainframe computer via PCSA, which provides a network communication for automatic and transparent file storage. Data collation/manipulation and report generation can then be completed using any of the extensive range of facilities and packages available on the mainframe machine.

It is still too early to assess the full benefits of upgrading the automated analytical equipment, but, even during the difficult commissioning period, there has been a gradual increase in throughput. Our records show that 9000 samples (7000 natural waters) have been analysed for 70 000 determinations, an increase of 40% over the last two years, at similar staffing levels.

During the last year, the group made a major contribution to cycling/leaching studies carried out under contract in Devilla Forest, by developing a methodology to measure sulphur and S-35. Labelled S was applied to soil under trees, and its progress was followed through the ecosystem. Sample preparation techniques were developed for leachates (throughfall and stemflow solutions), pine needles, and soils to overcome interferences in the counting procedure. Pre-concentration of leachates was required to detect precisely both the S-35 by alpha counting (using a high ionic tolerant fluor) and the sulphate ion chromatographically. Matrix interference proved to be a major problem in vegetation acid digests, but was eventually avoided by using an oxygen bomb combustion procedure. Soil leaching was simulated by sequential aqueous extraction, pre-concentration of combined extracts, and then measurement of S components.

As a laboratory involved in long-term studies, it is important that the chemical data produced are reliable and of consistent quality. In addition to the rigorous internal quality control procedures developed, the group participates in national and international standardisation schemes to monitor performance and contribute to the scientific community as a whole. This year we have advised on the methodology for EEC certified reference material, and set up a scheme for a large international programme studying tropical soil fertility. Our work has also extended to the Sudan, where we have advised on the development of ecological analysis and provided technical support to commission equipment.

In addition to supporting contract work led by other ITE scientists, the group itself continues to generate income for the Institute by providing a service for sister organisations, such as the British Antarctic Survey and the Nature Conservancy Council, as well as universities and private companies.

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