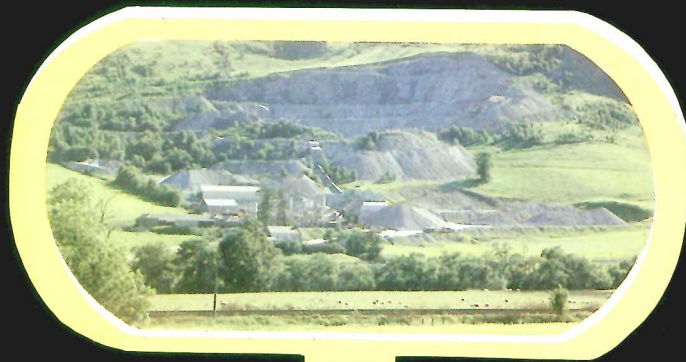# Natural Environment Research Council

# Institute of Terrestrial Ecology



# 1984

# Natural Environment Research Council

# Institute of Terrestrial Ecology

# Annual Report 1984

# Contents

# Research report

## Programme 1
## FOREST AND WOODLAND ECOLOGY

### HABITAT USE AND FEEDING BY DEER IN SITKA SPRUCE PLANTATIONS

Red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer can cause serious damage to commercial woodlands by eating leading and lateral shoots of young trees and by stripping bark from tree trunks. Because the extent of damage often warrants the introduction of deer control, there is a need for more information on the habits of deer in plantations, where the often thick cover helps these naturally secretive animals. For this reason, a wide-ranging study of the ecology of deer in Glenbranter Forest, in the Cowal district of Argyllshire, was begun in 1978. At Glenbranter, Sitka spruce (*Picea sitchensis*) is the most important tree species, with both second and first rotation crops being present, as will be the case in most of the upland forests of Britain in the near future. This report deals with the selection by red and roe deer of different habitat types within Glenbranter Forest, and also with their home range and feeding behaviour—an earlier report was concerned with browsing damage (Welch *et al.* 1983).

### The deer populations
Roe deer, living chiefly in deciduous woodlands, have been present in Cowal for a long time, while red deer, absent for most of the 19th century, reappeared following the start of commercial afforestation in 1906 (Staines & Welch 1984). As the number of forests in Cowal increased, both species of deer extended their ranges so that they are now widespread and abundant.

Stocks of deer (red and roe) at Glenbranter are similar in terms of density, reproduction and body size to those in comparable forests elsewhere in western Scotland. Densities of roe deer vary from 5 to 35 deer 100 ha$^{-1}$, depending on plantation age (Loudon 1982): those of red deer usually range between 5 and 15 deer 100 ha$^{-1}$, sometimes exceeding 30 deer 100 ha$^{-1}$ in favourable forests (Ratcliffe 1985). Compared to their counterparts on open ground (Mitchell *et al.* 1976), red deer females (hinds) and calves in Glenbranter Forest are 9-10 kg heavier. The Glenbranter hinds reach puberty as yearlings and breed every year (Ratcliffe 1985), whereas those on moorland usually mature one or 2 years later, with 30-40% of adults failing to breed each year (Mitchell *et al.* 1977).

### Deer distribution within the forest
Habitat selection and deer behaviour have been studied by (i) measuring accumulations of pellet groups on 300 permanent plots (Staines & Welch 1984), a technique generally accepted as providing reasonable estimates of the relative occupance of different sites (Neff 1968), (ii) direct observation, and (iii) radio-tracking marked individuals.

Broadly speaking, counts of pellet groups showed that red and roe deer utilized similar habitats (Table 1). Rides and open areas within 40 m of forests dominated by heather (*Calluna vulgaris*) were occupied by both species more than any other habitat type. Red deer had a greater preference than roe for the open areas close to the upper forest-edge and also for grassy rides, especially in summer.

Table 1. Preference rankings (10 is the strongest) of red and roe deer for the different habitats in Glenbranter Forest, which has a range of compartments with different planting dates. Rankings calculated from accumulations of pellet groups per unit time and area

| Habitat type | Mean ranks of habitat occupancy | |
| --- | --- | --- |
| | Red deer | Roe deer |
| Rides   Heather | 10 | 10 |
| Grassy | 8 | 6 |
| Open ground within 40 m of forest | 9 | 8 |
| Open hill | 3 | 4 |
| Establishment/restocked (0-8 years) | 7 | 7 |
| Pre-thicket (9-14 years) | 6 | 9 |
| Thicket (15-28 years) | 5 | 2 |
| Pole (29-44 years) | 1 | 1 |
| High forest (over 44 years) | 2 | 3 |
| Deciduous 'scrub' | 4 | 5 |

Of the forest stages, recently planted ground was very heavily used; pole-stage stands were the least used. Whereas thickets were used more by red than roe deer, the reverse was true of pre-thickets. In these areas, the sample plots with most bare ground, that is those with the most complete canopies, were used more by red than by roe deer (Table 2): in the event, the correlations between densities of dung and amounts of higher-plant cover were stronger for roe (r = 0·726) than for red (r = 0·601) deer. These conclusions, based on comparisons made between stands, are supported by the trends detected as the trees at specific sites passed from the establishment of pre-thicket stages, and so on. In part of the study area planted in 1973 and becoming pre-thicket in 1982, numbers of roe pellet groups counted increased by 180% in the winters between 1978 and 1982, and by 127% during summers. In contrast, roe deer usage of older pre-thicket stands decreased as their canopies started to close.

Direct and radio-telemetric observations have also indicated the importance of cover. Marked red deer were generally found in the denser parts of the forest

by day; they ventured out to feed in large open areas mainly from dusk to dawn. This pattern of behaviour is undoubtedly related to the effects of hunting pressures, because red deer in populations that have not been culled are often seen in the 'open' during daytime (Mitchell *et al.* 1977). In contrast, some roe deer fed throughout the day on recently replanted areas. Being smaller, roe, unlike red, deer can probably gain sufficient cover in these situations from the brash remaining after felling. Using spotlights in Glenbranter, Thirgood (1984) saw more deer in the larger restocked coupes during the night than during the day; more roe than red deer were seen by day and *vice versa* at night.

*Home-range behaviour*

The red deer hinds at Glenbranter have overlapping ranges which vary between 400 ha and 1100 ha. Range size, which, like range location, did not alter

i. **Red deer hind 15 Aug 1984**
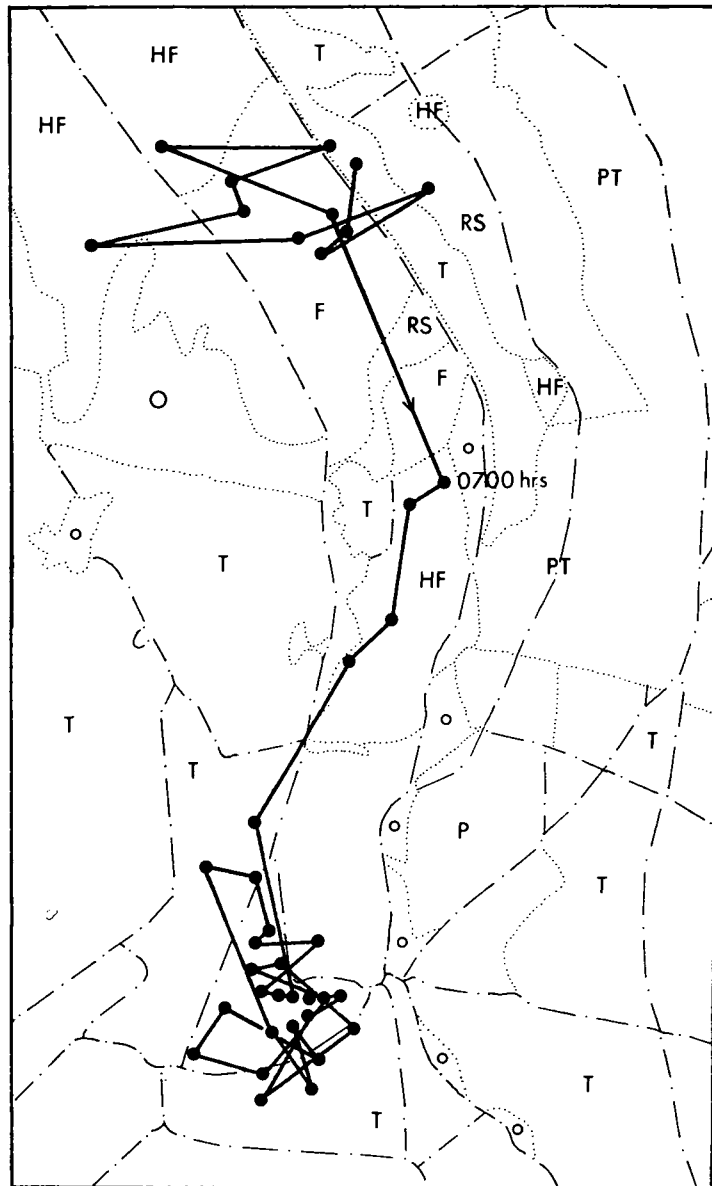
ii. **Roe deer doe 14 Sept 1984**
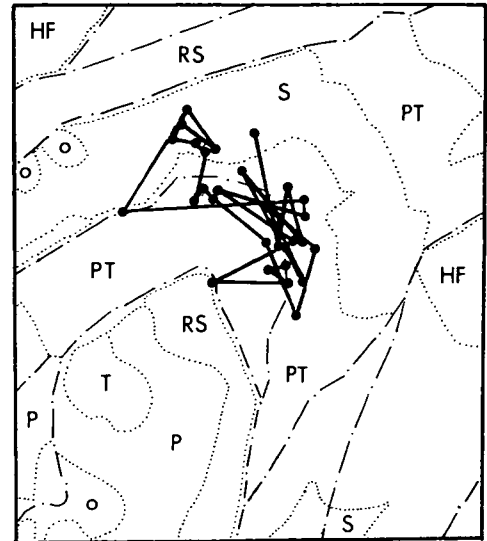
iii. **Roe deer buck 3 June 1983**
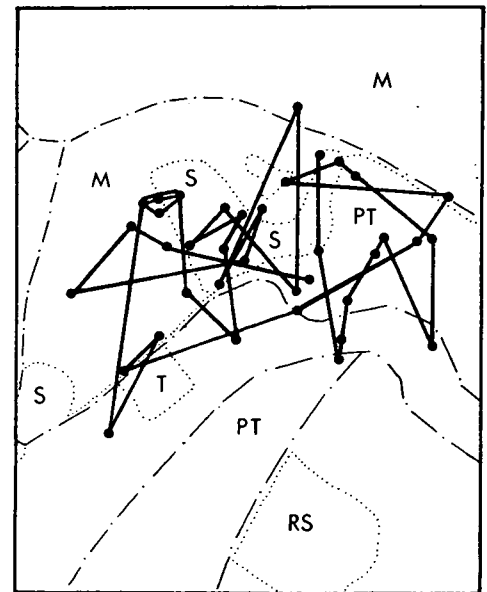
1 km

O = open ground     F = recently felled     HF = high forest

M = fields     P = pole     PT = pre-thicket

T = thicket     S = scrub     RS = restock

*Figure 1   Movements of marked (radio-tracked) red and roe deer in Glenbranter Forest mainly stocked with Sitka spruce*

i. Red deer          ii. Roe deer

Spring

Summer

Autumn

Winter

Graminoids      Other      Ferns      Conifers

Forbs      Other heaths      Calluna

Figure 2    Rumen contents of red and roe deer during different seasons of the year at Glenbranter Forest. Quantities of the different types of vegetation expressed as percentage of volume. Observations made on 283 and 325 red and roe deer respectively from 1979-83

*Table 2.* Differences, using pre-thicket, thicket and pole stages of a Sitka spruce plantation, between proportion of bare ground and numbers of pellet groups, direct indicators of the occurrence of deer (observations made between 1978 and 1982)

| Percentage of bare ground | Number of replicate plots | Number of pellet groups 100 m$^{-2}$ | | Significance of difference (P<0·05) between pellet groups of red, and roe, deer |
| --- | --- | --- | --- | --- |
| | | Red deer | Roe deer | |
| 0-15 | 28 | 31·6 | 43·0 | Significant |
| 6-15 | 7 | 21·9 | 49·0 | Significant |
| 16-30 | 10 | 9·6 | 18·0 | Not significant |
| 31-70 | 10 | 7·7 | 4·0 | Not significant |
| 71-95 | 20 | 6·1 | 4·4 | Not significant |
| 96-100 | 21 | 7·7 | 2·8 | Significant |

significantly between seasons and years, appeared to be related to habitat structure, being smallest where the proportion of restocked and pre-thicket stands was large and biggest where open ground was abundant (Staines *et al.* 1982). Few adult stags were seen in the study area, possibly because they are very secretive or because the habitat was unsuitable (Watson & Staines 1978). Marked stags born in Glenbranter, in fact, dispersed considerable distances, the longest so far recorded being 18 km. Roe had much smaller ranges than red deer, both daily (Figure 1) and seasonally. Areas occupied by adult roe females, during periods of 7 days, varied from 2·5 ha to 16·5 ha, compared with 13·5 ha and 71·5 ha for adult hinds. Some young roe deer moved 6 km from their birth places before establishing their adult ranges.
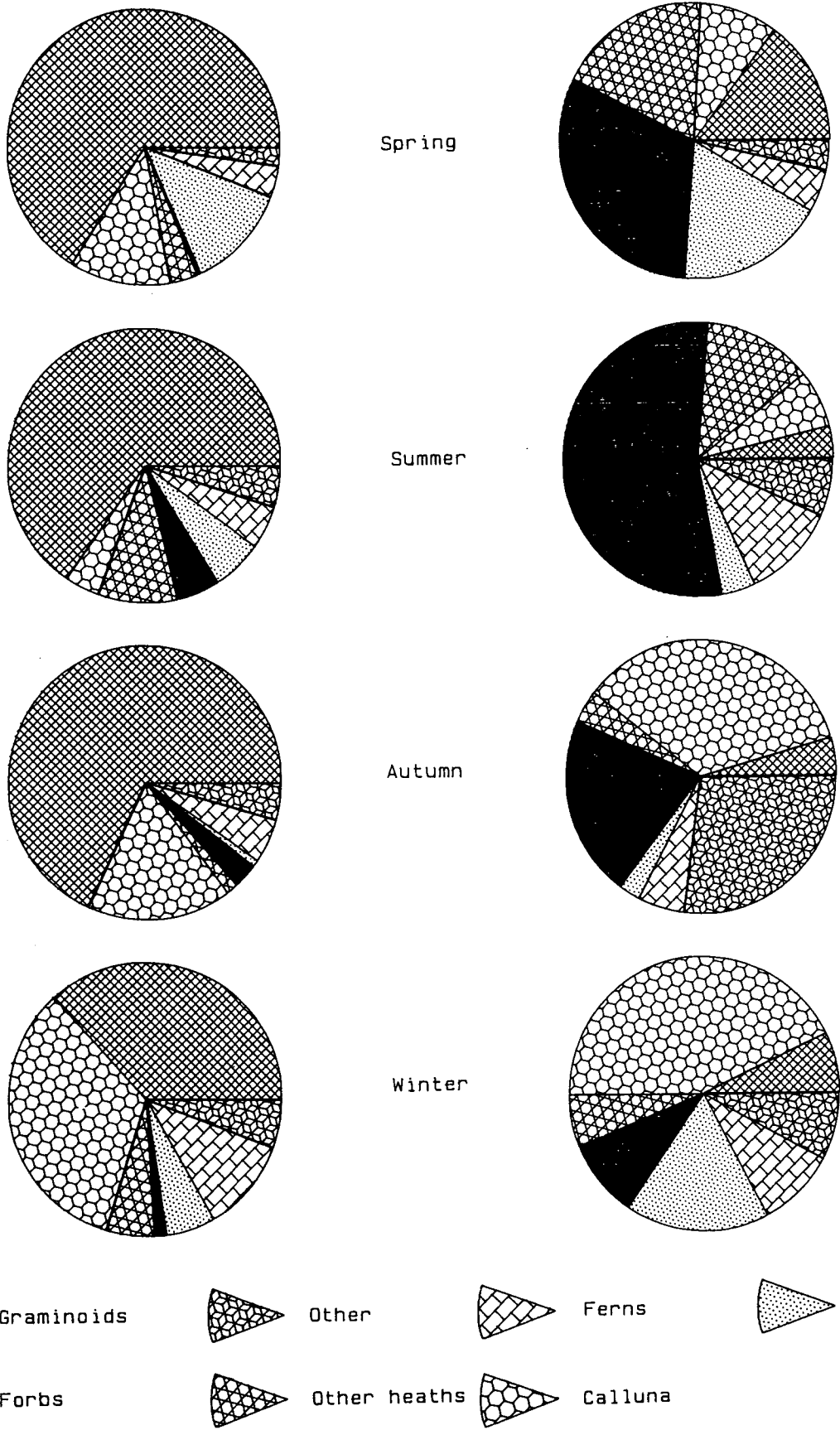
*Food and feeding behaviour*
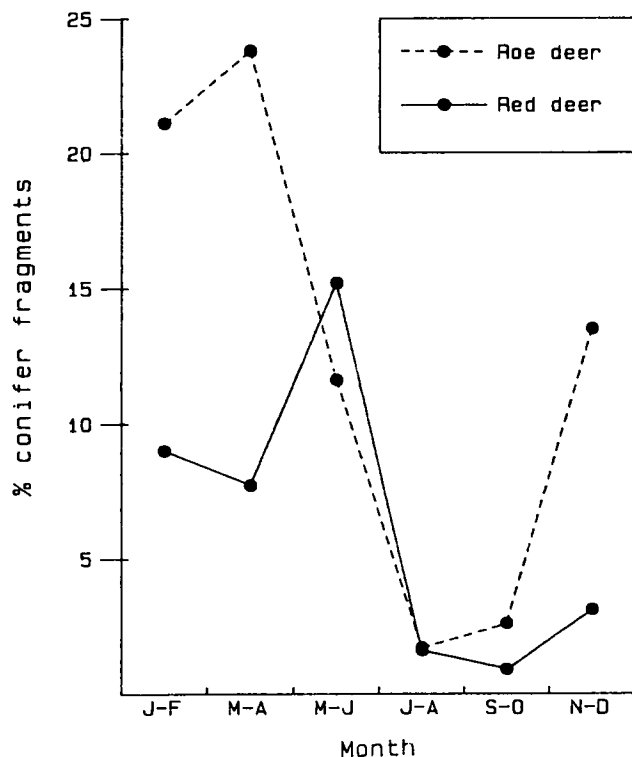The diets of red and roe deer differed greatly during



*Figure 3 Seasonal changes in the proportion of conifer material found in the rumen contents of red and roe deer. Observations made in Glenbranter Forest stocked mainly with Sitka spruce*

summer (Figure 3), but less so during the winter. During summer, red deer ate mostly grasses while roe consumed mostly forbs (non-graminaceous herbs) and bilberry (*Vaccinium myrtillus*). The forbs selected by roe included heath bedstraw (*Galium saxatile*), sorrels (*Rumex acetosa* and *R. acetosella*), tormentil (*Potentilla erecta*) and violets (*Viola* spp.), all being found in more than 40 of the 110 stomachs examined: the sorrels and tormentil often formed more than one third of the rumen contents. During winter, heather and ferns, particularly *Dryopteris*, increased in importance for both species of deer: red deer ate more sedges and rushes, notably *Eriophorum* and *Luzula*, than did roe deer. Also, the concentrations of the main nutrients in the food eaten were significantly larger in roe deer at this time.

Amounts of conifer browse in rumens varied seasonally: they were larger from mid-May to mid-June (when the trees were starting to grow) and in late winter (Figure 2). This pattern mirrors the loss of leading shoots (Welch *et al.* 1983). The proportions of conifers were significantly larger in the rumens of roe than in those of red deer from September to April (Figure 3).

Roe deer fed on more occasions during a 24-hour period than red deer, usually having 9 feeding periods compared with 5. During daytime, roe fed for shorter periods than did red: 80% were less than 2 hours, compared with 56% for red. No differences were obvious during night-time.

*Feeding strategies of red, and roe, deer*
Large ruminants such as red deer need smaller amounts of metabolizable energy per unit of body weight than small mammals like roe deer. The former can afford to eat poor forage, with small amounts of digestible energy, because the food can be held longer in their rumens for more thorough digestion (Kay & Staines 1982). Smaller ruminants, with a faster throughput, select more nutritious forage. Deer at Glenbranter conformed to these principles. Roe fed more often and ate a greater proportion of nutritious forbs; red deer fed less frequently, but for longer periods, eating a larger proportion of less digestible herbage. These nutritional differences may help explain the differences in habitat selection. Roe deer

were most abundant in areas where food and cover were closely interspersed (ie restocked ground and pre-thickets), while red deer, on the other hand, with their more capacious rumens, could afford to consume large amounts of the poorer herbage and then move considerable distances into thick cover to ruminate.

## Implications for forest management

Observations at Glenbranter have shown that the early forest stages are of great value to deer. With a 50-year rotation, as is common in upland Britain, the early stages comprise roughly 30% of the planted area, but, with a rotation of 120 years, as in many continental forests, this percentage is halved. For this reason, coupled with fast rates of deer reproduction, plantations in the UK are likely to support greater numbers than continental woodlands, and, as a result, there is a greater risk of serious damage. To counter this threat from secretive animals using thick cover and living in small, well-dispersed groups (Staines et al. 1982), it is essential to design forests with deer control in mind.

It is suggested that unplanted areas of heather, within or close to planted ground, should be kept and maintained to facilitate deer control, so complementing the frequent provision of grass swards for this purpose. Until now, the retention of heather has not been given adequate consideration. It is further recommended that the control areas should be small but widespread, because it seems that red deer in forests will not allow themselves to be lured long distances to improved sites. Some control areas should be adjacent to forest compartments with thick cover, which might entice deer to emerge during daytime; such a distribution should increase the options open to management.

*B W Staines, D Welch, D C Catt, D Scott and M D C Hinge*

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## CHANGES IN PLANTS AND ANIMALS IN THE FIRST 10 YEARS AFTER UPLAND AFFORESTATION

It is common knowledge that afforestation of moorland and grassland alters the assemblages of plants and birds, though there is often disagreement about the desirability of these changes. A 'tongue-in-cheek' article published in *The Scotsman* in 1971 advised that 'If you seek true silence, enter the heart of a conifer forest. No birds raise their discordant voices, save the smart black carrion crows rejoicing over a remaining lamb'. On the other hand, Chard (1972), a forester, suggested that 'New conifer forests encourage a much richer flora and fauna than the hill sheep farms they are replacing'. With these differing perceptions, it was clear, in the early 1970s, that more facts were needed to identify the role of new conifer forests as wildlife habitats.

Wildlife changes, resulting from changes in land use and maturing conifer plantations, can be inferred from short-term observations on series of sites, some unplanted and others at different stages of forest development. Observations of this kind have been reported by members of ITE, Hill and Evans (1979) dealing with plants and Moss (1979) working with birds.

In early 1972, we were fortunate to be in a position to implement a second approach to the problem. The owner and managers (Economic Forestry Group) of a small upland (167-260 m) afforestation scheme at Stone Chest, Cumbria (NY 480 790), have allowed ITE to monitor plant and animal changes after ploughing, draining and planting on 90% of the available land, formerly a sheepwalk. To improve the sporting potential of the plantation, the plantings of Sitka spruce (*Picea sitchensis*) were 'diluted' with other tree species, a pond was constructed, rides were made wider than usual and some improved arable land was left unplanted. It was thought that these measures would also improve the wildlife value of Stone Chest. For sampling, this location was divided, using a regular grid, into 139 squares, each of 1 ha, and marked by posts inserted at intervals of 100 m (Plate 2). By making a series of successive observations in time and space, it was hoped to define the detailed habitat requirements of animals, noting their arrival, population growth and, for some, their disappearance.

## Vegetation

Vascular plants have been recorded every 3 years in quadrats, each 200 m², at about half the grid intersections; numbers and heights of trees were also recorded. In 1972 and 1981, however, quadrats were recorded at every intersection, the data obtained being classified, using indicator species analysis (Hill et al. 1975), to pinpoint the temporal changes that have occurred. Before afforestation, 2 major types of vegetation, largely the product of past management, could be identified. The first, occupying about 40% of Stone Chest, and represented in Figure 4 by classes 3, 4, 2 and 1, occurred on stony surface-water gleys which had, in the past, mostly been ploughed, limed and used for cattle and sheep grazing. The vegetation contained rough grassland species such as common bent (Agrostis capillaris), tufted hair-grass (Deschampsia cespitosa), Yorkshire-fog (Holcus lanatus), and many herbs, including creeping buttercup (Ranunculus repens), meadow buttercup (R. acris), marsh thistle (Cirsium palustre) and common mouse-ear chickweed (Cerastium fontanum) (Table 3). The remaining area, with peaty soils, had heath-type vegetation represented by classes 6, 5, 7 and 8, the last of these occurring on the wettest and least fertile soils. The heath-type vegetation was characterized by dwarf shrubs such as heather (Calluna vulgaris), bilberry (Vaccinium myrtillus) and by wavy hair-grass (Deschampsia flexuosa), hare's-tail cottongrass (Eriophorum vaginatum), sedges and rushes. By 1981, the balance of vegetation had changed significantly, with an increased occurrence of classes 2, 1 and 5. The vegetation at the 2 extremes was markedly modified, the movement to classes 1 and 2, on the surface-water gleys, being attributed to the removal of grazing

and the consequent loss of small-stature grassland herbs. The movement to class 5 on the peaty soils probably occurred as a result of improved drainage and the consequent oxidation of peat.

Numbers of species of vascular plants at Stone Chest remained fairly constant between 1972 and 1981; of the original 100 species, 22 disappeared while 25 others appeared. Like several other plants of wet habitats, the marsh marigold (Caltha palustris) disappeared completely. The frequency of occurrence of many other plants decreased for a variety of reasons, including the elimination of grazing pressures, the effects of improved soil drainage, increased competition from coarse grasses, and the effects of shading concomitant upon the tree canopy development. Heath rush (Juncus squarrosus), common cottongrass (Eriophorum angustifolium), deergrass (Trichophorum cespitosum), common mouse-ear chickweed, creeping buttercup and common sedge (Carex nigra) decreased by more than 20%. Creeping soft-grass (Holcus mollis), which was not found in 1972, appeared in 41% of quadrats by 1981. Other plants to have increased their frequency include brown bent (Agrostis canina), creeping bent (Agrostis stolonifera), tufted hair-grass, broad buckler-fern (Dryopteris dilatata), and the foxglove (Digitalis purpurea) which was probably present as buried seed before afforestation. Interestingly, chickweed wintergreen (Trientalis europaea), a plant usually associated with the Scottish native pinewoods, has survived.

Sitka spruce and Japanese larch (Larix leptolepis) had reached an average height of 3·6 m by 1981 but there



Vegetation classes

| 3 | 4 | 2 | 1 | 6 | 5 | 7 | 8 |

Numbers of replicate quadrats allocated to the different classes

1972

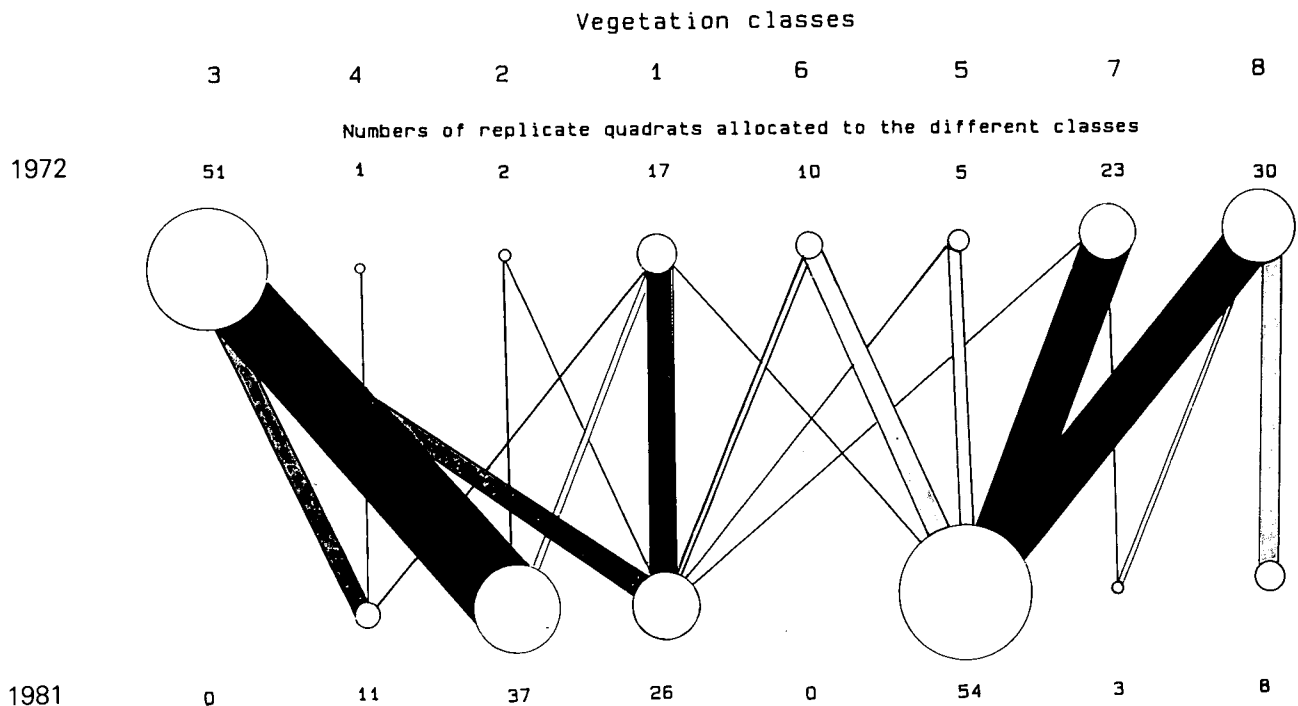| 51 | 1 | 2 | 17 | 10 | 5 | 23 | 30 |

1981

| 0 | 11 | 37 | 26 | 0 | 54 | 3 | 8 |

Figure 4 The effects of conifer afforestation in 1971-72 on the allocation of quadrats to 8 vegetation classes recorded in 1972 and 1981 at Stone Chest, Cumbria

*Table 3.* Species composition in constancy groups 1, 2 and 3, of 8 vegetation classes at Stone Chest, Cumbria

| | Vegetation classes | | | | | | | |
| | Rough pastures | | | | Grassy/shrubby heaths | | | |
| Constancy group | 3 | 4 | 2 | 1 | 6 | 5 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1<br>Frequency<br>100% to >80% | Anthoxanthum odoratum<br>Cerastium fontanum<br>Cirsium palustre<br>Festuca ovina<br>Holcus lanatus<br>Juncus effusus<br>Luzula multiflora<br>Poa nemoralis<br>Poa pratensis<br>Ranunculus acris<br>Ranunculus repens | Achillea ptarmica<br>Agrostis canina<br>Agrostis capillaris<br>Anthoxanthum odoratum<br>Cerastium holosteoides<br>Cirsium palustre<br>Deschampsia cespitosa<br>Epilobium spp.<br>Festuca ovina<br>Holcus lanatus<br>Juncus effusus<br>Poa pratensis<br>Ranunculus acris<br>Rumex acetosa | Agrostis capillaris<br>Anthoxanthum odoratum<br>Cirsium palustre<br>Deschampsia cespitosa<br>Epilobium spp.<br>Festuca ovina<br>Holcus lanatus<br>Juncus effusus<br>Poa pratensis<br>Potentilla erecta<br>Rumex acetosa | Anthoxanthum odoratum<br>Cirsium palustre<br>Deschampsia cespitosa<br>Epilobium spp.<br>Festuca ovina<br>Galium saxatile<br>Holcus lanatus<br>Juncus effusus<br>Luzula multiflora<br>Potentilla erecta<br>Rumex acetosa | Anthoxanthum odoratum<br>Carex nigra<br>Deschampsia flexuosa<br>Epilobium spp.<br>Eriophorum vaginatum<br>Festuca ovina<br>Galium saxatile<br>Holcus lanatus<br>Juncus effusus<br>Juncus squarrosus<br>Luzula multiflora<br>Molinia caerulea<br>Potentilla erecta<br>Stellaria alsine | Agrostis canina<br>Anthoxanthum odoratum<br>Deschampsia flexuosa<br>Dryopteris dilatata<br>Festuca ovina<br>Galium saxatile<br>Juncus effusus<br>Luzula multiflora<br>Molinia caerulea<br>Potentilla erecta<br>Vaccinium myrtillus | Anthoxanthum odoratum<br>Carex nigra<br>Deschampsia flexuosa<br>Eriophorum vaginatum<br>Festuca ovina<br>Galium saxatile<br>Juncus effusus<br>Juncus squarrosus<br>Luzula multiflora<br>Molinia caerulea<br>Potentilla erecta<br>Vaccinium myrtillus | Calluna vulgaris<br>Carex nigra<br>Deschampsia flexuosa<br>Eriophorum vaginatum<br>Molinia caerulea<br>Potentilla erecta<br>Vaccinium myrtillus |
| 2<br>Frequency<br><80% to >60% | Agrostis capillaris<br>Carex nigra<br>Cardamine pratensis<br>Deschampsia cespitosa<br>Epilobium spp.<br>Galium palustre<br>Galium saxatile<br>Juncus articulatus<br>Potentilla erecta<br>Stellaria alsine<br>Trifolium repens | Cardamine pratensis<br>Galium palustre<br>Holcus mollis<br>Juncus articulatus<br>Potentilla erecta<br>Ranunculus repens<br>Stellaria alsine | Agrostis stolonifera<br>Cardamine pratensis<br>Galium palustre<br>Holcus mollis<br>Juncus articulatus<br>Stellaria alsine | Agrostis stolonifera<br>Agrostis capillaris<br>Carex nigra<br>Deschampsia flexuosa<br>Digitalis purpurea<br>Molinia caerulea<br>Poa pratensis | Molinia caerulea<br>Poa nemoralis<br>Stellaria alsine<br>Vaccinium myrtillus | Agrostis stolonifera<br>Carex nigra<br>Eriophorum vaginatum | Calluna vulgaris<br>Eriophorum angusti-folium | Anthoxanthum odoratum<br>Erica tetralix<br>Eriophorum angustifolium<br>Festuca ovina<br>Galium saxatile<br>Juncus squarrosus<br>Luzula multiflora<br>Trichophorum cespitosum |
| 3<br>Frequency<br><60% to >40% | Cardamine flexuosa<br>Cynosurus cristatus<br>Juncus squarrosus<br>Lotus uliginosus<br>Myosotis spp.<br>Plantago lanceolata<br>Ranuculus flammula<br>Taraxacum officinale<br>Urtica dioica | Agrostis stolonifera<br>Cynosurus cristatus<br>Galium saxatile<br>Juncus conglomeratus<br>Lotus uliginosus<br>Luzula multiflora<br>Plantago lanceolata<br>Poa nemoralis<br>Prunella vulgaris<br>Rumex crispus<br>Succisa pratensis<br>Trifolium repens<br>Urtica dioica | Agrostis canina<br>Cardamine flexuosa<br>Juncus conglomeratus<br>Lotus uliginosus<br>Myosotis spp.<br>Plantago lanceolata<br>Ranunculus flammula<br>Taraxacum officinale<br>Urtica dioica | Agrostis canina<br>Cardamine flexuosa<br>Dryopteris dilatata<br>Galium palustre<br>Juncus articulatus<br>Ranunculus repens<br>Stellaria alsine<br>Urtica dioica<br>Viola palustris | Agrostis canina<br>Calluna vulgaris<br>Cardamine flexuosa<br>Cardamine pratensis<br>Cerastium fontanum<br>Cirsium palustre<br>Dryopteris dilatata<br>Poa pratensis<br>Ranunculus repens | Calluna vulgaris<br>Digitalis purpurea<br>Holcus lanatus | Polygala serpylli-folia | Juncus effusus |
| Total number of species recorded | 78 | 62 | 64 | 68 | 52 | 53 | 39 | 43 |

was a large variation, partly because of frost damage. Hybrid larch (*Larix eurolepis*) had an average height of 5·2 m but western hemlock (*Tsuga heterophylla*) was only 2 m on average, probably because of its susceptibility to late spring frosts and cold winter winds. It was estimated that 12% of the canopy in the study area was 80-100% closed in 1981; 35% of it was 60-80% closed. In about 20% of the area, crown closure was still less than 20%.

### Animals
The presence of vertebrates in each grid-hectare was recorded annually, using different methods for diffe-

rent species, some methods being modified as tree cover developed. Small mammals were assessed each summer using 4 Longworth live traps near each grid intersection. Crows (*Corvus corone*), wood pigeons (*Columba palumbas*) and pheasants (*Phasianus colchicus*), in addition to song birds, were recorded using, as far as feasible, the method employed in the Common Birds Census (Enemar 1959). Observations of bird behaviour (feeding, hunting, roosting, etc) were also noted. Records of song birds were made annually, mostly between 0430 and 0800 h on 3 mornings a week from the end of April to the beginning of July. Other species such as grouse (*Lagopus scoticus*) and

green plover (*Vanellus vanellus*) were recorded as breeding only when seen feeding chicks, or when eggshells were found in, or near, nests.

In 1972, 9 species of mammal were resident at Stone Chest; the number had increased to 16 by 1983, with 12 breeding regularly each year. In some years, mink (*Mustela vison*) and water voles (*Arvicola terrestris*) also visited Stone Chest, but neither stayed longer than a few months, bringing the total number recorded to 18.

Seventy-one bird species were recorded: in 1972, there were 36 species, while, in 1983, the number had increased to 43. In between times, 21 species were lost and 28 species gained; 9 were both gained and lost (Plate 3). Only the meadow pipit (*Anthus pratensis*), tree pipit (*Anthus trivialis*), pheasant, stock
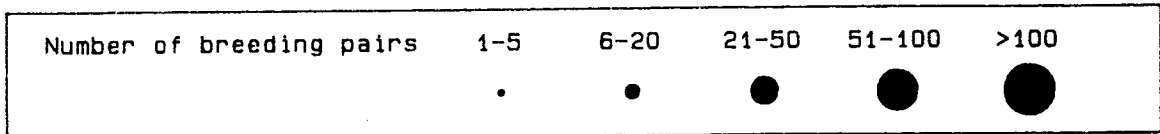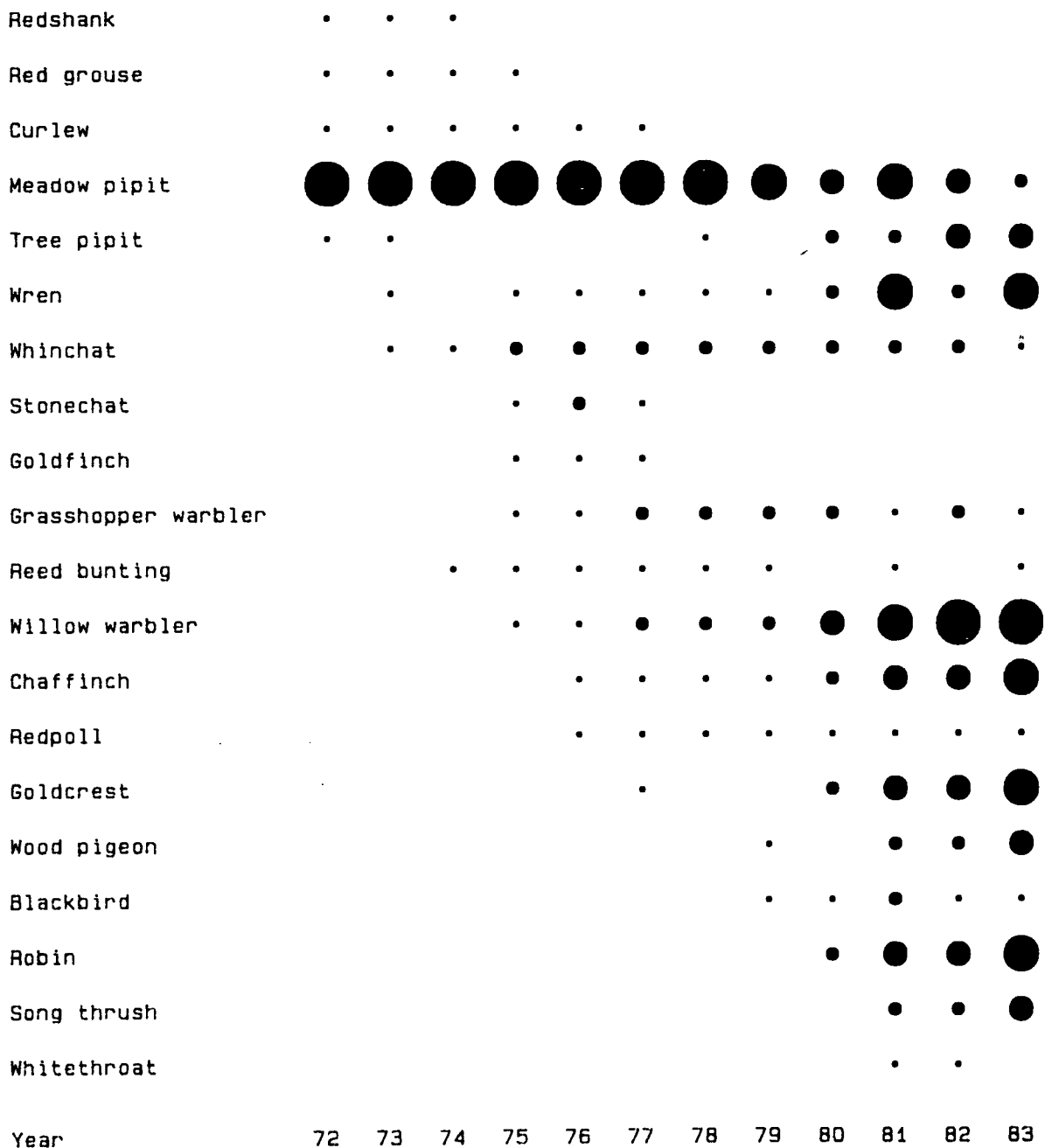


*Figure 5 Changes in number of breeding birds in successive years, following the afforestation of Stone Chest in 1971-72*

dove (*Columba oenas*), carrion crow and black-headed gull (*Larus ridibundus*) persisted throughout as breeding species. However, there was a distinct tendency for numbers of meadow pipits to decrease, while those of the willow warbler (*Phylloscopus trochilus*), chaffinch (*Fringilla cœlebs*), goldcrest (*Regulus reg-*

*ulus*) and robin (*Erithacus rubecula*) increased (Figure 5), presumably as a result of changes in the abundance of their habitats.

The effects of afforestation can be assessed (Figure 6) by examining the occurrence of a number of mammals
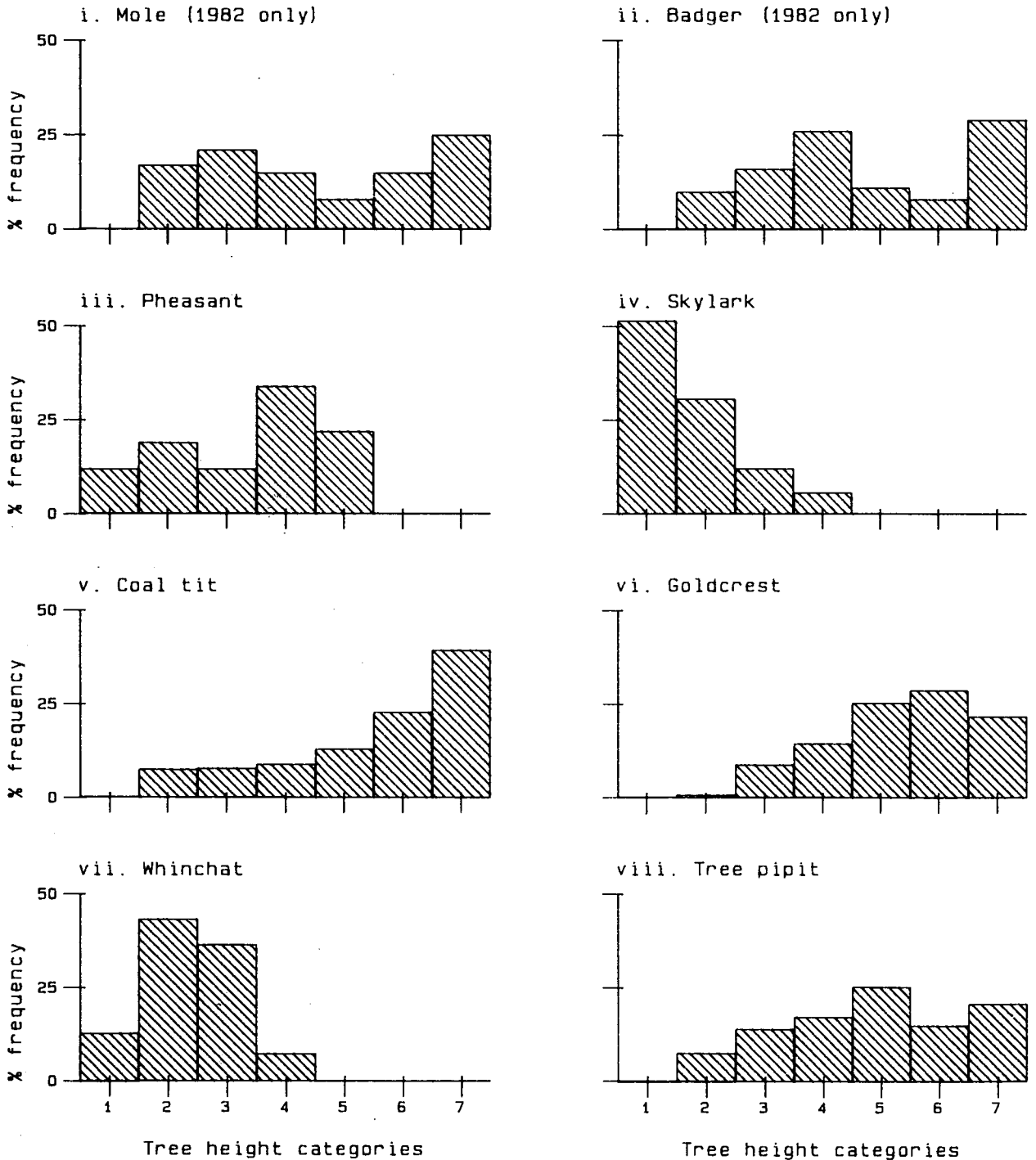


| Tree height categories (m) | | | | | | |
|---|---|---|---|---|---|---|
| 1 = <1.1 | 2 = 1.1-2.0 | 3 = 2.1-3.0 | 4 = 3.1-4.0 | 5 = 4.1-5.0 | 6 = 5.1-6.0 | 7 = 6.1-7.0 |

*Figure 6    Frequency of occurrence of some animals in different tree height classes, following afforestation at Stone Chest, Cumbria, in 1971-72*

and birds with widely differing habitat requirements: the mole (*Talpa europaea*) and the badger (*Meles meles*) representing below- and above-ground feeding mammals, the skylark (*Alanda arvensis*) and pheasant, ground-nesting birds already on the site in 1972, the whinchat (*Saxicola rubetra*), a representative of birds requiring small trees, the coal tit (*Parus ater*), goldcrest and tree pipit, birds of increasingly closed woodlands.

Moles, as determined from molehills in 1982, were significantly associated with stands of short, slowly developing trees (P<0·01). In contrast, numbers of badgers, as indicated by their scats, were maximal in association with trees 3·1-4 m tall. Skylarks were found (P<0·001) on newly planted ground but disappeared when trees reached 2 m in height. Whinchats were most abundant in the first few years after afforestation; most of them disappeared, with only 2 pairs remaining in year 11 after planting (1983) in areas where growth was slowed by summer frosts. Coal tits and goldcrests unexpectedly differed in their association with tree height classes, possibly because stands of the tallest trees, in this case the deciduous hybrid larch, were suitable for the ground-nesting coal tit but not for the tree-nesting goldcrest, an observation agreeing with those made in some pinewoods in Deeside and published by Jenkins *et al.* (1984), but at variance with the study of song birds made by Moss (1979). Whereas there were 45 pairs of coal tits km$^{-2}$ before trees at Stone Chest were 7 m tall (Table 4), densities in comparable stands in south Scotland were only 4 pairs km$^{-2}$. In contrast, the densities which Moss recorded for whinchats in trees 3-5 m in height were 3 times greater than the maximum recorded at Stone Chest, where few pairs of this species remained after trees were 3 m or more in height.

Because inconsistencies of this kind constantly occur in the literature, an attempt has been made to relate faunal changes to changes in site characteristics as indicated by vegetation. Significant associations (P<0·001) have been found between classes of vegetation and the occurrence of moles, badgers, skylarks, pheasants and whinchats, but not with coal tits, goldcrests and tree pipits.

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## PREDICTING SQUIRREL DAMAGE

Bark stripping was at first thought to reflect squirrel population density (Shorten 1957), perhaps because aggressive gnawing (Taylor 1966) or food shortage would be most common in dense populations. Because squirrel numbers are related to the availability of tree seeds (Gurnell 1983), the Forestry Commission issues warnings that damage is likely when there has been a good crop of acorns. On the whole, however, squirrel damage has remained unpredictable. Some young plantations of beech, oak and sycamore are never seriously damaged, whereas others are attacked so severely, either continuously or intermittently, that most of the trees die. After many years of absence, severe damage may suddenly be done. To be sure of avoiding damage, or even loss of these slow-growing trees, foresters have been obliged to waste resources for the control of squirrels in years when they would not have damaged the trees.

Since 1979, squirrel densities, spring breeding and damage have been recorded in 30 areas between Stamford, Northampton, Luton and Oxford in the southern midlands of England. Densities were esti-

*Table 4.* Maximum densities of some breeding birds (prs km$^{-2}$) at Stone Chest, Cumbria, which was afforested with conifers in 1971-72; (i) densities related to study area and (ii) height of trees with greatest density of birds

| Species | Year of maximum density | Height (m) class of trees with maximum bird density | Average bird density (prs km$^{-2}$) at Stone Chest | Bird density (prs km$^{-2}$) in most favoured tree height class in year of maximum density |
|---|---|---|---|---|
| Whinchat | 1978 | 1·1-2 | 10·1 | 11·6 |
| Coal tit | 1983 | 6·1-8 | 44·6 | 50·0 |
| Goldcrest | 1983 | 3·1-4 | 52·5 | 68·0 |
| Tree pipit | 1982 | 4·1-5 | 22·3 | 29·5 |

mated with grids of traps, 12-56 per site, operated during March or April, and again during June or July when the young had entered the population. Because male squirrels often ranged too far for their density to be estimated reliably (Kenward 1982a), numbers of trapped adult females, with a more restricted range, were doubled on the assumption that the ratio of males to females was about 1:1. Since 1981, the winter availability of food at the different sites has been assessed (scored), before trapping, by counting the numbers of tree species (eg oak, hazel, chestnut, conifers) providing moderate (= 1) or good (= 2) supplies of seeds, with a further 2 points being added if pheasants in the wood were being supplied with grain.

Damage was categorized on the following scale—0, no bark removed; 1, 5 cm of bark removed from a few trees; 2, 5-250 cm of bark removed from a few trees; 3, >250 cm of bark removed from a few trees; 4, >250 cm of bark removed from many trees; 5, most trees extensively stripped. In 1983, numbers of trees with fresh damage and numbers of separate attacks per tree were counted across transects of 50 trees.

In 1981, it was found (Kenward 1982b) that amounts of bark stripped from individual trees were correlated with the widths (volume/unit area) of sappy phloem tissue which squirrels eat. On examining this relation in greater detail in 1982 and 1983, damage was most strongly correlated at many sites with average phloem tissue widths between June 20 and July 10, when most damage was actually being done (Figure 7). The average phloem widths accounted for 69% of the variation in amounts of damage. When 24 areas were observed in consecutive years, it was found that damage in one year predisposed the area to damage the following year. Taken together, the amounts of previous damage and the current widths of phloem accounted for 81% of the variation in current amounts of damage. Average numbers of attacks made on individual trees were strongly related to current phloem widths, suggesting that squirrels repeatedly attacked trees that they found rewarding. In contrast, the percentages of trees attacked within a population were more strongly related to the intensity of damage in the previous season.

Numbers of squirrels per unit area (population densities) varied by a factor of × 5 in both 1981 and 1983. Adult densities were correlated with the locally available supplies of winter food. However, damage was not correlated significantly with densities of adult squirrels in either year. Instead, in 1981, it was correlated with densities of juvenile squirrels, whose numbers were only correlated significantly with winter food in 1983. These variable results suggest that the abundance of winter food is not a very good predictor of squirrel damage, compared with tree quality and the occurrence of previous damage. However, damage may be influenced more by extremes of winter food availability than by the intermediate, moderate levels recorded during the study. There is no doubt that plentiful supplies of seeds during winter enhance
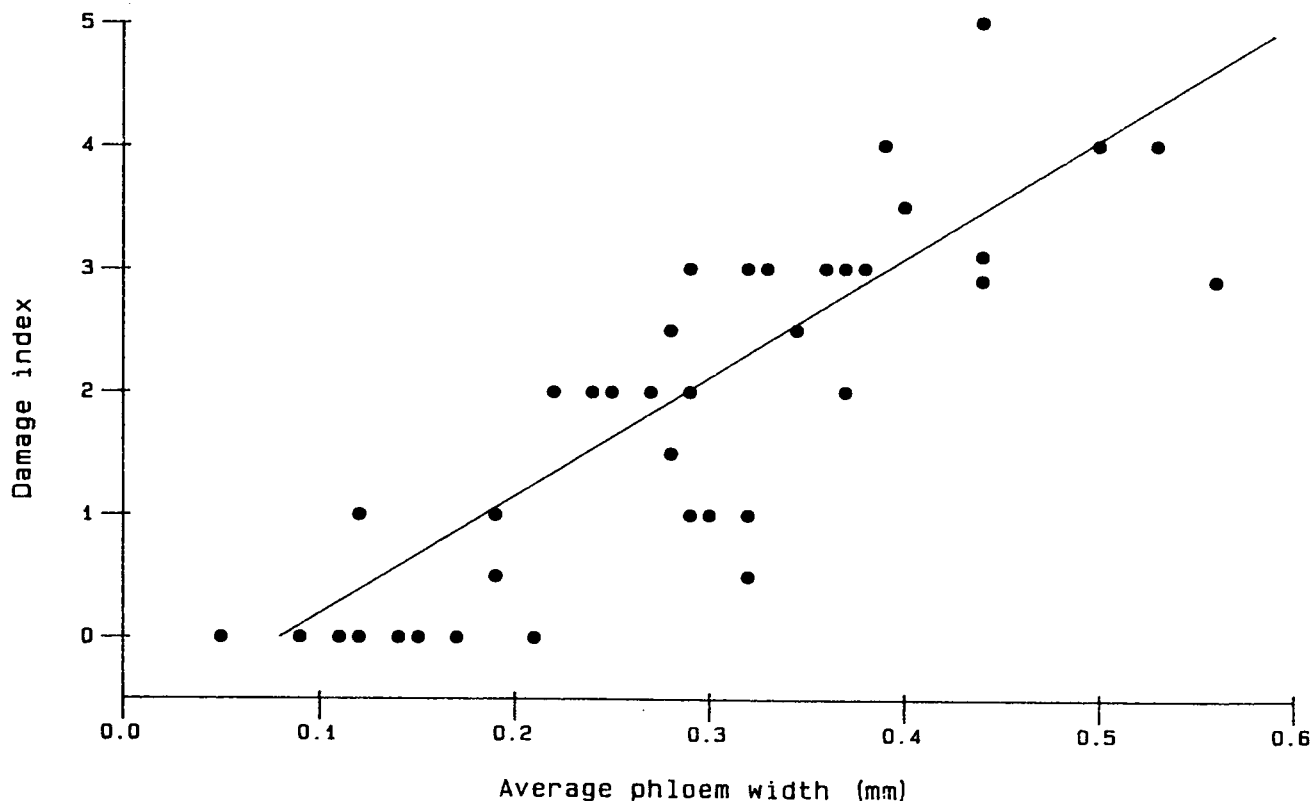


*Figure 7  Relationship between average phloem width and the damage (bark stripping) done to beech and sycamore trees*

squirrel breeding, while, in the absence of winter food, too few squirrels would be present to cause significant damage.

Our observations suggest that the extent of bark stripping can be predicted from estimates of phloem width, which seems to be minimal in closely spaced stands of saplings, such as develop from naturally regenerating sycamore. This finding suggests that, in conservation areas where fast growth is not a priority, squirrel damage might be minimized by maintaining dense stands of trees. Conversely, phloem width might be expected to increase soon after thinning, making this a time to institute squirrel control. Because we have been able to establish a relation between squirrel damage and phloem widths, in future we wish to see if phloem development can be predicted from weather and soil conditions in sufficient time to institute squirrel control before damage is done. Bearing in mind that all trees within a population are not attacked to the same extent, is it conceivable that resistant trees may be selected and exploited?

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## ECOTYPIC VARIATION IN OAK

The 2 British native species of oak, sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*), are important both ecologically and from a forestry viewpoint. Together with a largely unknown proportion of interspecific hybrids, they are major components of semi-natural woodlands on a wide range of soil types.

Ecologically, oak is unusual, as trees of this genus can be both pioneer and climax species. This characteristic probably accounts for at least part of the wide ecotypic variation that is readily apparent, but whose significance is little understood. *Quercus* is a largely sub-tropical genus and Jones (1974) suggested that our British native oaks show clear signs of being poorly adapted to cool-temperate climates. He cites features such as late flushing, frost sensitivity, and the production of large seeds that are easily damaged by cold and desiccation, and which often germinate precociously. The formation of a thick tap root, containing reserves, and the ability to produce successive flushes of growth during the growing season are regarded as attributes typical of sub-tropical species.

Work being done in ITE has the 2, sometimes conflicting, aims of investigating the characteristics of (i) different oak provenances (ie the progeny of trees from a specified location), and (ii) individual genotypes. The investigation of the latter will not be possible until the plants are large enough to provide sufficient vegetative material to initiate clonal propagation. Even then, there may be problems, because some characteristics may be linked to genotypes that are difficult to propagate.

The collection of acorns has been based on the approach adopted for birch by Gardiner and Pelham (1983), who used the Merlewood system of land classification (Bunce *et al.* 1981) as the basis of a system of stratified sampling. At present, collections have been limited to north Wales, where 11 of 17 UK land classes that occur were calculated as having a reasonable probability of containing oak. In the autumn of 1982, 4 randomly selected 1 km grid squares of each land class were searched for oak, and acorns from 40 trees representing 8 out of the 11 land classes were collected in sufficient numbers for use. Fifty acorns from each tree (seedlot) were planted in 3·5 inch (9·9 cm) pots. Other acorns were retained for dry weight determinations and chemical analyses. A variety of repeated measurements, height, leaf numbers and area, etc, was made on seedlings during their first year of growth (1983), with a destructive sample of 5 seedlings in each of 32 seedlots taken at the end of the season when roots were washed and plants dissected to find how assimilates had been partitioned.

From leaves and peduncles taken from the parent trees when the acorns were collected, it was found that 26 trees had predominantly sessile affinities, 8 pedunculate and 6 intermediate, one of which may be a hybrid with species of oak other than *Q. petraea* or *Q. robur* (Figure 8). These designations refer to the female parent, the nature of the male parent in this usually outbreeding genus being unknown.

Analysis of data collected from seedlings has been aimed at (i) the correlations between different growth parameters and their relationships with the different land classes, and (ii) identification of seedlots whose characteristics markedly deviate from average (Table 5). In the event, heights, stem weights, root weights, leaf numbers and areas were all strongly inter-related. They are also related to land class, as is acorn size. However, Jarvis (1963) established that acorn size

rather than provenance was the major factor determining the size of first-year oak seedlings which will have taken up comparatively small amounts of mineral nutrients from the soil (Shaw 1974).

*Table 5.* Coefficients of correlation (r) within a range of important growth parameters measured at the end of the first year of growth of oak seedlings grown from acorns collected from a range of habitats in Wales

| | Growth attributes | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| †1 Acorn weight | — | | | | | | |
| 2 Height | 0·75 | — | | | | | |
| †3 Stem weight | 0·86 | 0·90 | — | | | | |
| †4 Root weight | 0·89 | 0·68 | 0·85 | — | | | |
| †5 Total weight | 0·91 | 0·75 | 0·90 | 0·99 | — | | |
| *6 Number of leaves | 0·64 | 0·60 | 0·70 | 0·58 | 0·62 | — | |
| *7 Leaf area | 0·77 | 0·74 | 0·85 | 0·80 | 0·83 | 0·67 | — |

† Weights after drying at 80°C
* Primary leaves only (not lammas leaves). All correlations are statistically significant (P>0·001)

Because acorn size is positively related to land class, which in turn is related to soil type, it was anticipated that large acorns would have large concentrations of nutrients. Instead, chemical analyses of acorns unexpectedly showed that concentrations of most major plant nutrients, including Ca, Mg, P and N, are negatively correlated with acorn size.

Seedling characteristics such as the production of lammas shoots, flushing dates (spring 1984), root/shoot (R/S) ratios and relative growth rates (RGR) all seem to be independent of seedling size (and land class) and, to a large extent, of each other. While it is probably premature to assess lammas shoots and flushing dates after only one year, an examination of R/S ratios and relative growth rates shows some differences between provenances.

Previous experiments using mixtures of seeds from different trees show that the R/S ratio is a sensitive index of seedling performance (Shaw 1974). Adverse conditions, such as low light or damage by insects,



i. Pedunculate          ii. Sessile          iii. Intermediate          iv. Possible hybrid

*Figure 8* Leaves and peduncles illustrating the range of morphological variation found among the female parent oak trees, from which seed collections were made in north Wales

  i. Leaf and peduncle typical of sessile oak
 ii. Leaf and peduncle fairly typical of pedunculate oak, petiole tending to be long while fruiting stalk may be short
iii. Leaf and peduncle showing intermediate characteristics but more towards sessile than pedunculate
iv. An unusual tree with a typical sessile type of peduncle, but having a leaf shape similar to that of Turkey oak

markedly decrease the R/S ratio—while stems are only slightly affected, root growth is significantly decreased. The mean R/S ratios of seedlots being investigated at present range from 1·4 to 5·0 and of individual seedlings from 0·7 to 7·2. Interestingly, the seedlot with smallest R/S ratio (1·4) suffered 15% mortality in the first year. Seedlings from this seedlot grew unexpectedly tall for the size of acorn. Conversely, seedlings from the seedlot with the highest R/S ratio (5·0) were relatively short in relation to acorn size. The 8 fastest growing seedlots (RGR over 35%) had R/S ratios greater than 3·0.

Relative growth rates (total weights after leaf abscission divided by acorn weights) also varied considerably, the means for seedlots ranging from −14% to +77%. The fastest growing seedlots tended to be those with medium-sized acorns (1·6–1·8 g). Of the 4 fastest growing seedlots (RGR over 57%), 3 were derived from female parents with predominantly 'sessile' characteristics and 1 intermediate. The fastest growing pedunculate seedlot was ranked sixth. The tree with the fastest RGR (77%) was collected from a grid square in land class 19, the most environmentally extreme class in which oak normally grows in Wales, and in which we could locate only one tree. The progeny from this tree was also notable for being the earliest to flush and for having the second largest production of lammas leaves. Four trees from one grid square (land class 15, a fairly lowland class) were among the 8 fastest growing seedlots. Even among the fastest growing seedlots, there was a considerable range of growth strategies, from short, stocky seedlings with large R/S ratios to much taller, thinner seedlings with comparatively small R/S ratios.

Seedlings in seedlots from pedunculate female parent trees produced 10-20% more leaf area per unit weight of acorn than seedlots from sessile oaks. Although the former all grew faster than average, they were not, despite their enhanced leaf areas, the fastest.

For the future, the surviving oak seedlings will be planted individually into the field where successive measurements will be made, including assessments of form, wood quality and tolerance of pests and pathogens.

Apparently interesting genotypes will be clonally propagated and submitted to more detailed investigation.

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## DECLINE IN THE GROWTH OF THICK ROOTS AS FORESTS AGE: DOES IT INCREASE THE RISKS OF WINDTHROW?

Windthrow (the uprooting of trees by wind) is a major threat to British plantation forestry. As gales occur every winter, the minimization of the windthrow threat is a dominant aspect of silviculture, particularly in the uplands.

Normal thinning (from about year 20) increases the likelihood of windthrow. Consequently, thousands of hectares of upland forest have been designated 'non-thin' forests: they will carry the complete stock of trees from planting to harvest without incurring the disruption of canopy structure that was inevitable with thinning. However, 'no thinning' incurs a number of penalties. Without the selective removal of (i) small trees and (ii) larger trees of undesirable form, eg twisted stems or large branches, insufficient space exists to enable stand production to be concentrated on the vigorous straight-stemmed trees which would have been retained, when thinning, to form the final crop of large valuable sawlogs. The presence of these small and/or misshapen trees, of little or no value, increases harvesting costs. The net result is reduced profitability and a disincentive for the necessary expansion of British forestry if timber deficits, predicted to occur before current plantings reach maturity, are to be avoided.

The resistance of a tree to uprooting by wind (windthrow) depends on the properties of its stem and roots. Deans and Ford (1983) have shown that, where stem diameters (1·3 m above ground) of Sitka spruce (*Picea sitchensis*) are increased from 15 cm to 18·1 cm, as could occur where trees are planted at wider spacing, the displacement of the crown by wind will be halved, with the subsequent likelihood of its toppling being dependent upon the resistance of its roots and attached soil. The position of the fulcrum through which trees rotate is strongly influenced by the resistance of roots to compression and bending. The resistance to compression of a round section is a function of the fourth power of its diameter, and consequently small differences in root diameter can produce large differences in root resistance. Analysis of excavated whole-root systems at one site has suggested that the growth of thick roots starts to decline when trees are 15 years old (Deans 1981). This note describes the results of a more extensive study in

which root thickening was compared at different sites with trees of different ages.

The thick roots of duplicate trees in 3 stands of unthinned Sitka spruce, 9, 15 and 20 years from planting, were severed at their union with stems at weekly intervals from April until November, when numbers of cells were counted in 5 radial files in the current, and previous year's, annual rings at 0·25 m intervals along the detached roots. Adjacent pieces of root bark and cortex were dried and then analysed for starch. Stem radial growth was estimated weekly with vernier girth bands positioned at ground level and 1·3 m above ground; mid-canopy shoot elongation was measured.

Roots of old trees produced fewer root cells than those of young trees; numbers also decreased as the distance along the root from the stem increased. Thus, the numbers of cells produced along radial files of tracheids near stems decreased from 282 to 189 and 153 in trees 9, 15 and 20 years old respectively. In the 20-year-old trees, cell production in roots decreased from 153 near the union with stems to 41 and 12 at distances of 0·5 m and 1·0 m along the roots, a decrease reflected in a rapid root taper. Together, these differences are reflected by the larger increases in cross-sectional areas of roots of trees 9 years old than of trees 20 years old (Figure 9).

At all 3 sites, root and stem thickening began earlier in the year than budburst. The thickening of sections of roots, 1 m distant from stems, began 3, 8 and 5 weeks

later than thickening in the base of stems in trees 9, 15 and 20 years old respectively. Although the thickening of stems and roots proceeded rapidly early in the
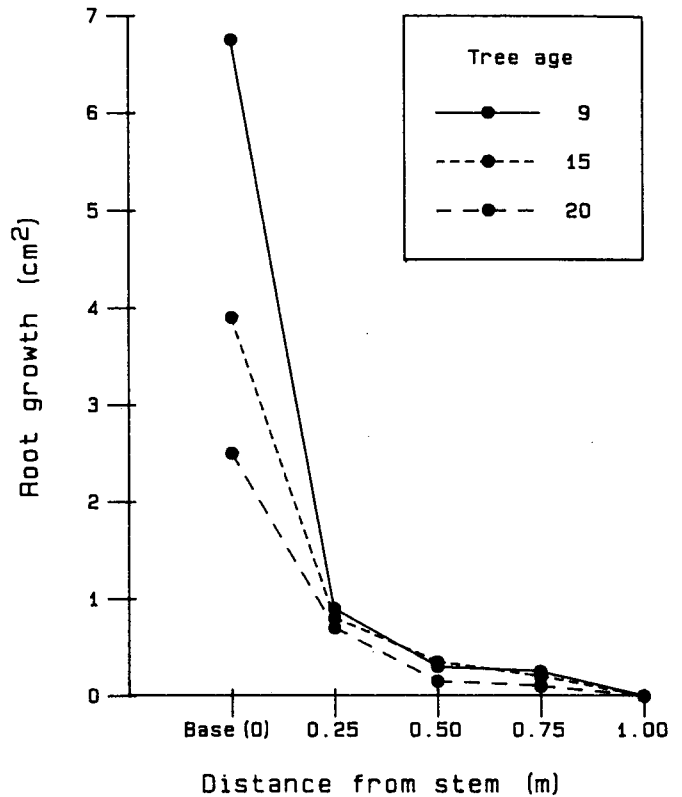


Figure 9   Cross-sectional area of Sitka spruce roots at 0·25 m intervals from stems at 3 sites where the trees were aged 9, 15 and 20 years
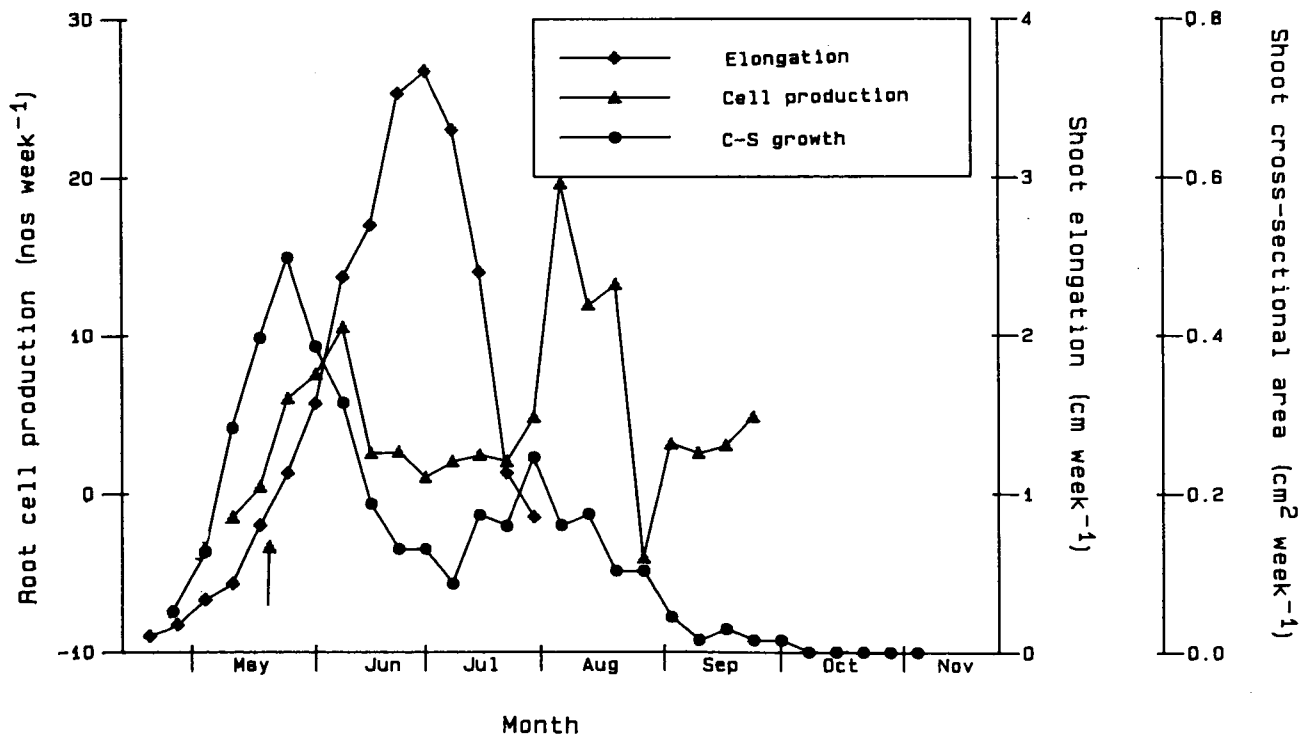


Figure 10   Annual course of shoot elongation, stem thickening 1·3 m above ground level (cross-sectional area) and root thickening 0·25 m from the stem (cell production) in a 15-year-old Sitka spruce plantation. The arrow indicates the occurrence of budburst and the onset of visible shoot elongation
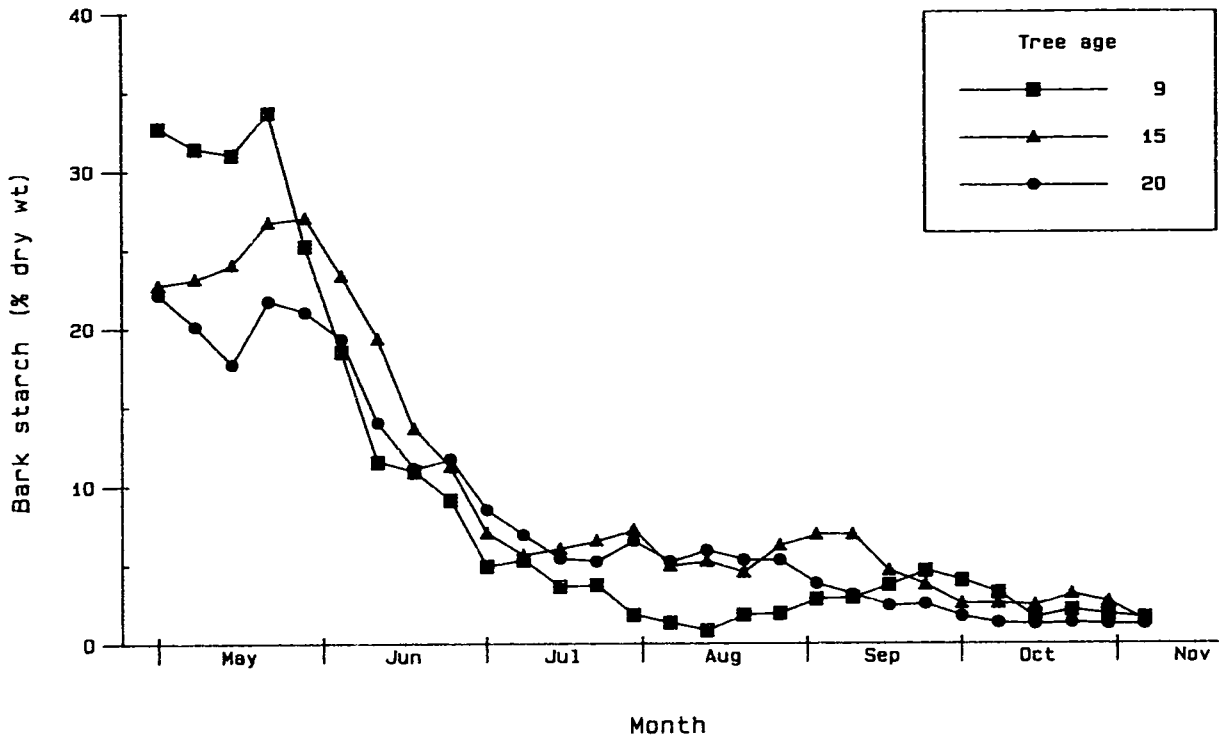
*Figure 11    Amounts of starch stored in the bark of Sitka spruce roots at 0·25 m from stems in plantations aged 9, 15 and 20 years*

season, it slowed as shoot elongation reached maximum rates (Figure 10), suggesting that stem elongation and associated needle growth have higher priorities for internal resources than root thickening.

The youngest trees, 9 years old, produced the largest root increments; they also contained the largest concentrations of stored starch within their roots (Figure. 11). The amounts of stored starch were depleted rapidly, irrespective of tree age, from maximum concentrations in May. By considering the weights of starch lost, and the weights of thick roots produced in June (Figure 12), it is clear that the root increments close (0·25 m) to stems were dependent upon an influx of carbohydrates during the period of growth itself. At 0·5 m from stems, roots of the oldest trees lost about twice as much starch as that required for thickening in that region: at greater distances from stems, this ratio of starch depletion to root production was much larger, suggesting that there was a substantial translocation of carbohydrates to other parts of the tree. In contrast, the youngest tree lost no amount of starch in excess of those required for root production at distances less than 0·75 m from stems. It is possible that the larger concentrations of starch stored in the young trees enabled their roots to grow faster.

This difference in root growth rates among trees of different ages may be attributable to the more complete illumination of the living branches of young trees than of those of older trees, many of which grow in dense shade. Consequently, the youngest trees have both relatively larger and more effective 'crowns' for producing photosynthates and shorter transloca-

tion pathways from needles to roots than were found in the oldest trees. On balance, these attributes of young trees are likely to ensure a greater surplus of
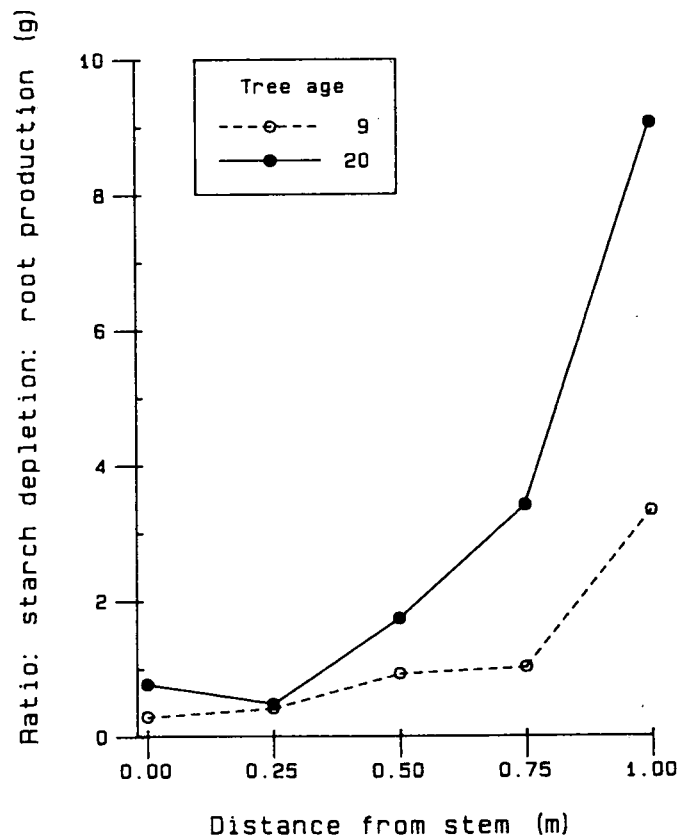


*Figure 12    Ratio of weight of starch depleted in June to weight of thick root produced in June at 0·25 m intervals along Sitka spruce roots aged 9 and 20 years*

photosynthates for root growth than occurs in older trees in stands with closed canopies. If this statement is correct, is it possible that the same result would be achieved in old stands if silvicultural management aimed to sustain active deep crowns? This characteristic could be achieved by wider initial spacing or by thinning plantations before they reach the height at which they become susceptible to windthrow.

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## THE INFLUENCE OF HOST PLANT SPECIES AND SOIL TYPE ON THE POPULATION ECOLOGY OF THE PINE BEAUTY MOTH

The pine beauty moth (*Panolis flammea*) is a serious pest of Scots pine (*Pinus sylvestris*) in mainland Europe but, in the UK, its depredations are confined to lodgepole pine (*Pinus contorta*). The first recorded damage by the pine beauty in the UK occurred in 1976 when 120 ha were destroyed in Naver Forest (Highland Region of Scotland). Between 1977 and 1979, a further 200 ha were completely defoliated in 4 separate areas, and 8700 ha were sprayed with insecticide (Stoakley 1979, 1981). Control measures were not applied between 1980 and 1983, but an outbreak occurred at Pollie Hill (Gordonbush Estate, Highland Region) in 1984 when 150 ha of
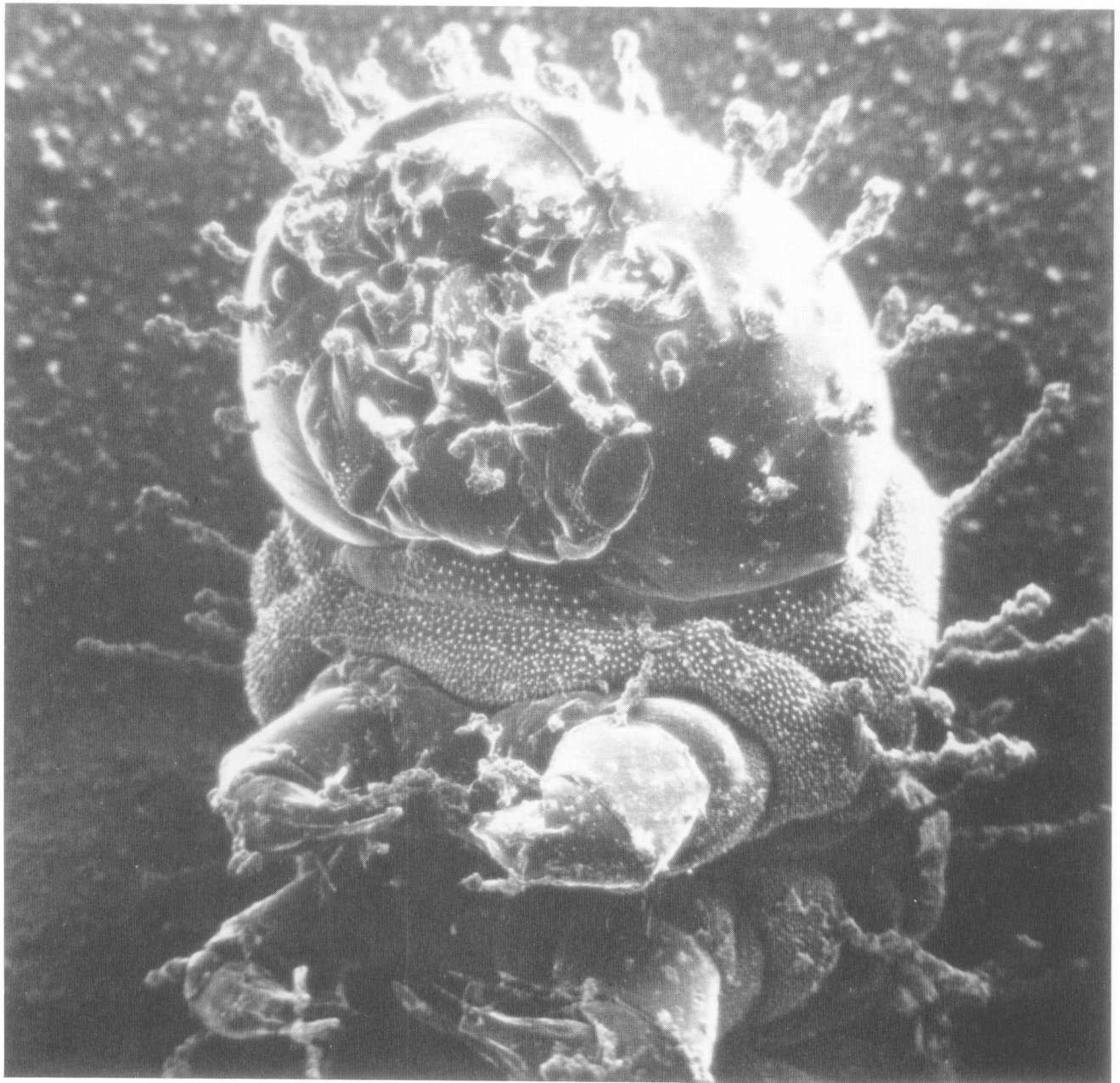


Plate 1    A pine beauty moth caterpillar one day old (actual length 2-3 mm). Despite its well-formed mouthparts, it is unable to feed on mature pine needles; it is restricted to new foliage until it is about 10 days old (Photograph A D Watt)

lodgepole pine were defoliated; 10 other sites have been identified as being at risk from defoliation in 1985 on the basis of existing population levels (D A Barbour, personal communication).

Observations of the 1976-78 outbreaks showed that they started on lodgepole pine growing on deep unflushed peat (Stoakley 1979). It has been suggested that trees on deep peat suffer water stresses, causing increases in the nutritional quality of pine foliage for pine beauty larvae, so leading to improved insect survival or fecundity (or both), and therefore to faster rates of population increase than occur on unstressed trees growing in other soils. Indeed, it has recently been argued that plant stress is the major cause of outbreaks of insect herbivores (eg Rhoades 1983; White 1984).

Life table studies of pine beauty moth were made in 1983 and 1984 to test the hypothesis that insect survival is relatively good on trees growing on deep unflushed peat. The work was done in the Elchies block of Speyside Forest (Grampian Region), where a pine beauty outbreak started to develop in 1978 in those parts of the block where lodgepole pine was growing on deep unflushed peat. In 1983, 2 plots of 25 trees were set up, one on deep peat near the epicentre of the 1978 outbreak, and the other on an iron pan soil about 1 km distant from the epicentre.

Because the density of pine beauty was too low to allow accurate population sampling, each tree was artificially infested with approximately 1000 eggs (laid on short pieces of foliage which were tied on to branches in the upper crown). Thereafter, population development was monitored using several methods: weekly egg counts until egg hatch; larval counts from excised branches and from head capsules (shed by pine beauty caterpillars (Plate 1) at each moult) collected in funnel traps at ground level; pre-pupal counts from water-filled basins, also at ground level; and pupal counts from ground quadrat sampling. Because methods for sampling larvae gave consistent results, a less intensive sampling programme was used in 1984, when 3 plots of 25 trees were studied on each soil type. Additionally, 3 plots of Scots pine, each of 25 trees and growing in a range of soils, were infested in 1984. To assess the survival of pine beauty in the absence of predators and parasites, 20 small cages with pine beauty moth eggs were placed on 5 trees in one of the replicate plots of (i) lodgepole pine in deep unflushed peat, (ii) lodgepole pine in an iron pan soil, and (iii) Scots pine.

There were no significant differences in the development of populations of pine beauty moth on lodgepole pine growing in deep unflushed peat and iron pan soils, either in 1983 or 1984 (Figure 13). It therefore seems that the hypothesis centred on the quality of lodgepole
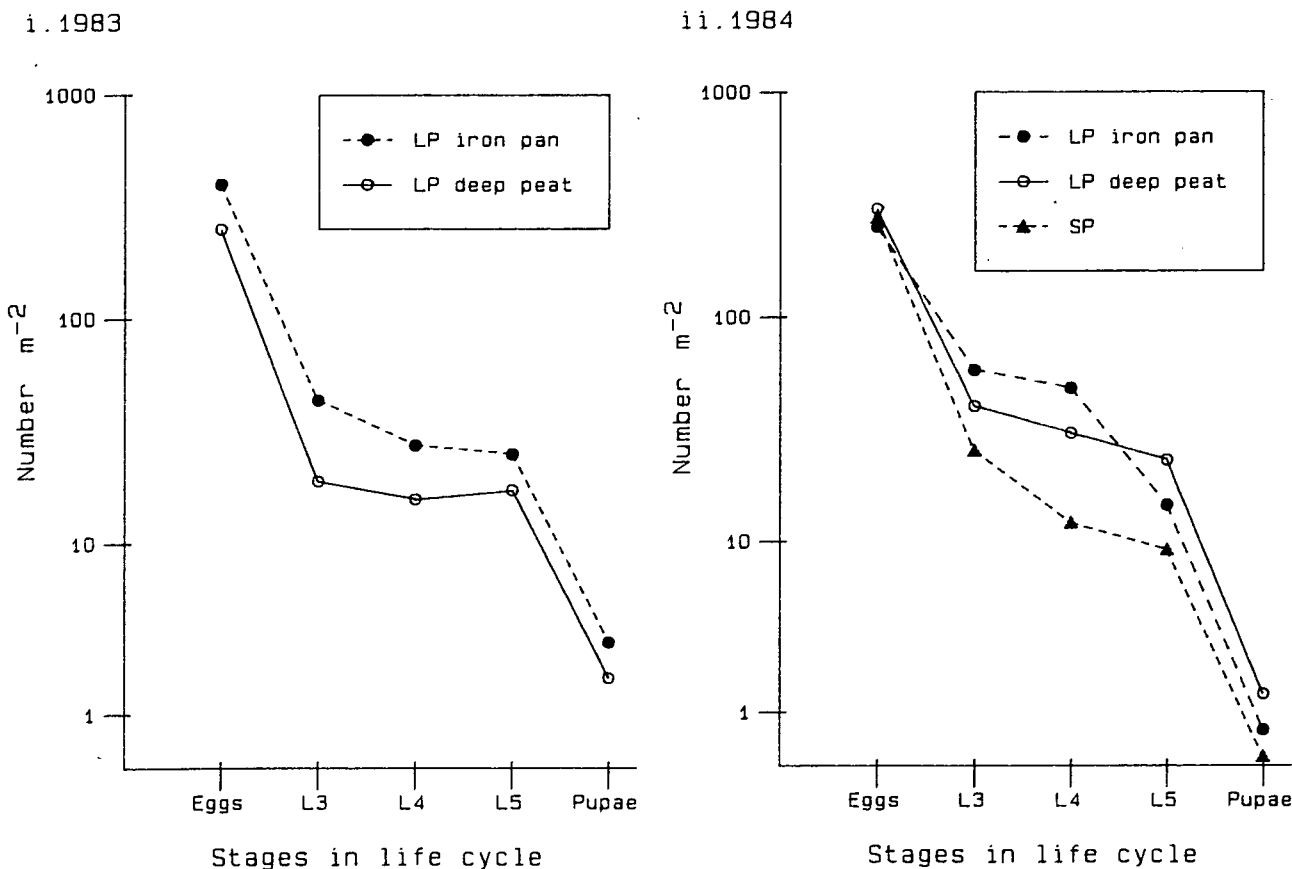


*Figure 13   Survival of manipulated populations of pine beauty moth in (i) 1983 and (ii) 1984 on lodgepole pine (LP) growing in an iron pan soil or in unflushed deep peat and Scots pine (SP) in a variety of soils*
$L_3$ = third instar larvae; $L_4$ = fourth instar; $L_5$ = fifth instar

pine foliage from trees growing in different soils is not tenable. However, there are 2 reservations. First, natural enemies appeared to aggregate and cause substantially greater mortality in the experimental plots than elsewhere; for example, pupal parasitism in the study plots was about 75%, compared with only 10% in the natural population in 1983 (D A Barbour, personal communication), a difference possibly masking the influence of different soil types. Second, although the period April-June 1984 was the driest for over 10 years, it is possible that the weather in 1983 and 1984 did not induce plant stress.

However, in the cages, in the absence of natural enemies, survival to the third instar larval stage was about 70% and did not differ between the 2 soil types (Table 6). This high survival rate, compared to those quoted in other studies of insects, suggests that lodgepole pine is an adequate food source for pine beauty moth, irrespective of soil type.

The tendency for pine beauty moth outbreaks to develop on deep unflushed peat therefore remains unexplained. It may be that pupal survival is better in deep peat (Leather 1984) or that adult emergence from deep peat is better synchronized with the development of lodgepole pine, its host. Alternatively, the entire crop of lodgepole pine in Scotland may be at risk from this pest.

The results of life table and caging experiments on pine beauty on Scots pine were contradictory. Fewer of the uncaged, exposed populations on Scots pine survived than was the case on lodgepole pine (Figure 13ii). In contrast, a greater proportion of the protected caged population survived on Scots pine than on lodgepole pine (Table 6). In addition, growth and development were greater on Scots pine than on lodgepole pine. It therefore appears that Scots pine is a better host than lodgepole pine for the pine beauty moth, but the outbreaks do not occur on Scots pine because of the greater activity of natural enemies.

*Table 6.* Survival of pine beauty moth from egg to third instar larvae in cages excluding natural enemies

| Host species/soil types | Number of eggs | Percentage of eggs yielding surviving third instar larvae |
|---|---|---|
| Lodgepole pine/deep peat | 296 | 66·9 |
| Lodgepole pine/iron pan soil | 298 | 69·8 |
| Scots pine/range of soil types | 305 | 76·1 |

This project forms part of a collaborative study with the Entomology Branch of the Forestry Commission. Valuable advice and assistance have been given by D A Barbour, S R Leather, J T Stoakley and A Thompson (all

of the Forestry Commission). C Beetham and J Clarke provided assistance in the field.

*A D Watt*

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## Programme 2
## FRESHWATER ECOLOGY

### SOME EFFECTS OF VARIATION IN EGG SIZE IN THE COMMON FROG

This report is concerned with a particular aspect of a study of the life history of the common frog (*Rana temporaria*). The rationale of the study as a whole is that, by understanding the ways in which individuals partition their resources between growth, reproduction and maintenance under various conditions, it should be possible to predict the responses of individuals and populations to environmental disturbances. Such disturbances might include changes in land use, atmospheric or aquatic pollution, or natural climatic variations.

Egg size is variable in the common frog, both within and between populations (Figure 14): during the course of this study, egg sizes ranging from 0·73 mg to 3·03 mg dry mass have been observed—more than a 4-fold difference in maternal investment per offspring. This degree of variation requires explanation. If tadpoles from large eggs do not have a greater chance of surviving to sexual maturity or, as mature frogs, have a greater reproductive capacity than those from the smallest eggs, we should expect there to be strong selection favouring the division of female reproductive investment between a large number of smaller eggs, rather than between a smaller number of large eggs. On the other hand, the range of possible combinations of number and size of eggs may be
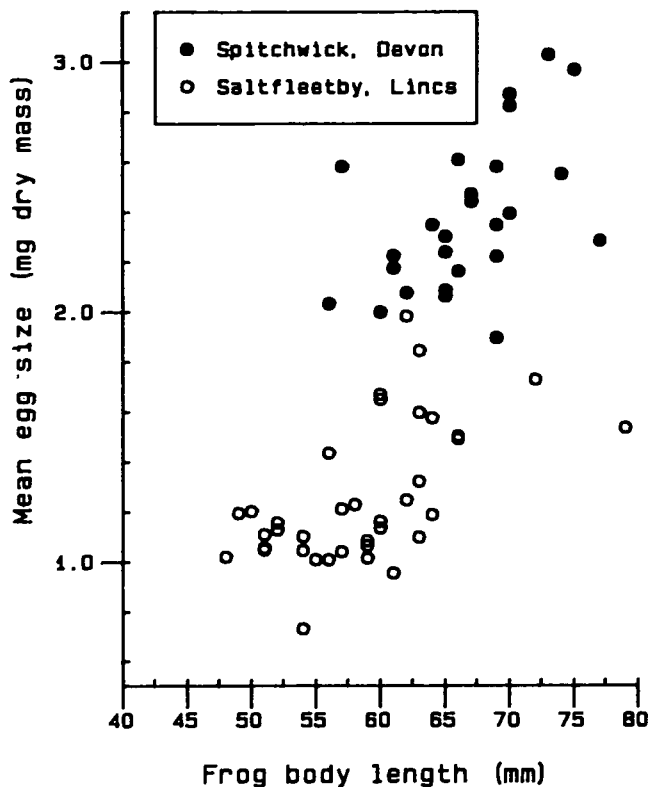
*Figure 14    Relationship between egg size (mean egg dry mass) and female body length in 2 populations of the common frog in 1984*

constrained by some aspect of the animal's physiology. The main source of variation in egg size within populations is female body size, with which egg size is positively correlated. There is little reason to suppose that the optimum egg size—that size at which the product of egg number and individual egg fitness is maximized—should be different for different-sized frogs. Furthermore, as frogs retain the capacity for growth throughout life, an individual female which survives to breed more than once may produce different-sized eggs each year.

Environmental factors can certainly influence the size of eggs produced. This effect was suggested by field data which showed that egg size, adjusted for female body size, was lower in 1984 than in 1983 in all of the 4 widely separated populations sampled. In 2 populations, annual differences in egg size, adjusted for body size, were in the order of 20%. More conclusive evidence, however, came from an experiment in which the number and size of eggs produced by female frogs were measured before and after a year in captivity on known rations of food. At the end of the experiment, all the frogs had produced eggs which were different in size from those laid in the previous spring. Final egg size could be related to the frogs' total food ration since the previous spawning. Environmental factors may account for observed differences in egg size, adjusted for body size, between populations. Frogs have been transplanted to enable egg

production by representatives of a single population to be compared in different locations, but results are not yet available. However, Berven (1982) found significant genetically based differences in egg size and age at maturity between 2 populations of a similar species, *Rana sylvatica*, in the USA.

Thus far, examples have been given of the range of variation in egg size and the major source of that variation, but what is its significance? This question may be approached in 2 ways. If we are primarily interested in the selective pressures operating to constrain egg size, or to bring about genetically based differences between populations, then we should ask how an individual's fitness is influenced by the size (ie the resource content) of the egg from which it develops. If, on the other hand, we are more concerned with population dynamics in the short term, then it might be more appropriate to ask how the size distribution of the eggs laid at a particular site influences the dynamics of the resultant tadpole cohort. In practice, the same information is required to answer both questions, and the relationships of most obvious potential importance are those between egg size and (i) time taken to reach metamorphic climax; (ii) size at metamorphic climax; (iii) cumulative risk of predation; and (iv) competitive ability.

Instantaneous risk of predation is generally inversely related to tadpole body size (eg Cooke 1974), and, in several experiments involving tadpoles of various sizes, crowding has been shown to affect the larger tadpoles less than the smaller ones (eg Rose 1960). Initial body size and growth rate will therefore be important variables influencing the cumulative risk of predation and competitive ability. Hatching size is highly correlated with egg size. In the following section are some results of experiments designed to investigate the influence of egg size on tadpole growth rate, body size at metamorphosis and time taken to metamorphose.

Two experiments were performed. The first used eggs from 6 females from the Devon population shown in Figure 14, egg sizes ranging from 2·03 mg to 2·97 mg dry mass. The second experiment used eggs from 10 females from the other population shown in Figure 14, egg sizes ranging from 0·73 mg to 1·84 mg dry mass. In both experiments, eggs from each female were fertilized by each of several males. Four tadpoles from each pairing (ie 20 from each female in the first experiment and 24 from each female in the second) were raised to metamorphosis in individual dishes, under constant daylength, at constant temperature, and with excess food.

The time taken for each tadpole to reach metamorphosis was recorded (t), as was its body size at metamorphosis (m), and a measure of growth rate during the pre-metamorphic period (g). The results of
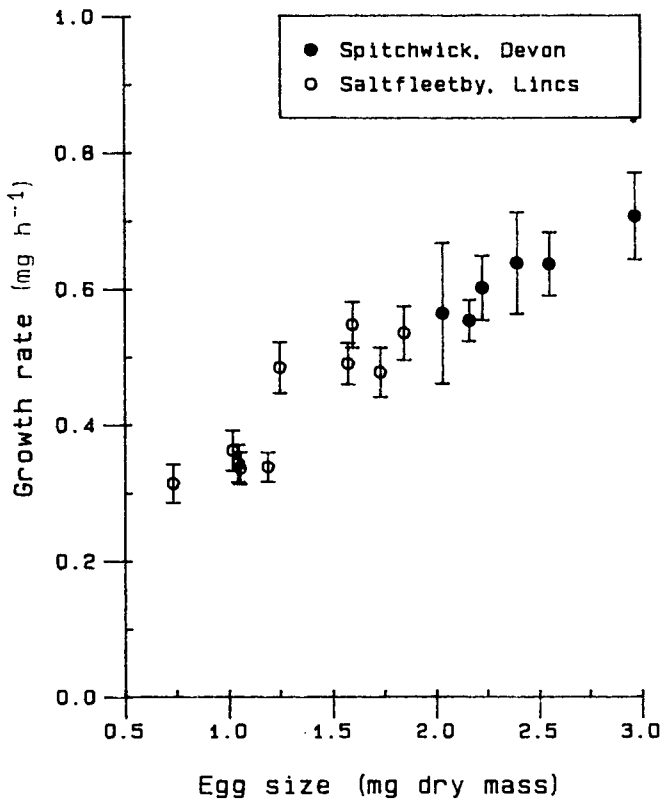
*Figure 15 Relationship between pre-metamorphic growth rate and egg size in experiments using eggs of the common frog from 2 populations. Points show mean values with 95% confidence limits for offspring of individual females paired with several males*

each experiment were analysed in 2 ways: a cross-classification analysis of variance was used to test for additive parental effects on g, m and t, and least-squares linear regression was used to investigate the relationship between egg size and the same 3 variables. It was assumed that all eggs from a particular female were the same size, so the effects of egg size could not be separated from maternal genetic effects. However, paternal effects could only have had a genetic basis, and therefore provided a baseline against which to measure maternal effects. The effect of egg size was also tested across the whole range of egg sizes by combining results from the 2 experiments (and thus ignoring parental effects). Significant paternal effects on growth rate were detected in the first experiment ($F_{4,87} = 6 \cdot 12$, $P<0 \cdot 001$), but not in the second ($F_{5,210} = 1 \cdot 90$, $0 \cdot 05<P<0 \cdot 10$). Maternal effects on growth rate were significant in both experiments ($F_{5,87} = 6 \cdot 13$, $P<0 \cdot 001$; $F_{9,210} = 37 \cdot 12$, $P<0 \cdot 001$), as was the effect of egg size ($F_{1,95} = 18 \cdot 37$, $P<0 \cdot 001$; $F_{1,223} = 202 \cdot 02$, $P<0 \cdot 001$). However, female parentage accounted for much more of the observed variance than egg size in the second experiment, but only very little more in the first. There were no significant differences between the regression lines fitted separately to the 2 sets of data and a common line fitted to the combined data (Figure 15).

Overall, it seems that this measure of growth rate was strongly related to egg size: significant parental

(genetic) effects were detected, but in the first experiment males were more varied than females, while the reverse was the case in the second experiment.

Significant paternal ($F_{4,87} = 6 \cdot 74$, $P<0 \cdot 001$; $F_{5,210} = 3 \cdot 66$, $P<0 \cdot 005$) and maternal ($F_{5,87} = 3 \cdot 66$, $P<0 \cdot 005$; $F_{9,210} = 4 \cdot 90$, $P<0 \cdot 001$) effects on size at metamorphosis were detected in both experiments. As with growth rate, a common regression line satisfactorily fitted the combined results (Figure 16).



*Figure 16 Relationship between tadpoles size at metamorphosis (Taylor-Kollros stage XX) and egg size in experiments using eggs of the common frog from 2 populations. Points show mean values with 95% confidence limits for offspring of individual females paired with several males*

When time taken to reach metamorphic climax (t) was plotted against egg size (Figure 17), it was clear that a single linear regression equation would not adequately describe the combined results. Analysing the experiments separately, virtually no relationship between egg size and t was detected in the first experiment ($F_{1,95} = 0 \cdot 02$), but the 2 variables were strongly related in the second ($F_{1,223} = 96 \cdot 46$, $P<0 \cdot 001$). As there was no overlap in egg size between the 2 experiments, it is not possible to say whether this result indicates different relationships in the 2 populations or, perhaps more likely, whether a common, non-linear relationship exists between egg size and time taken to metamorphose. Parental effects were significant, except in the case of males in the first experiment ($0 \cdot 05<P<0 \cdot 10$).
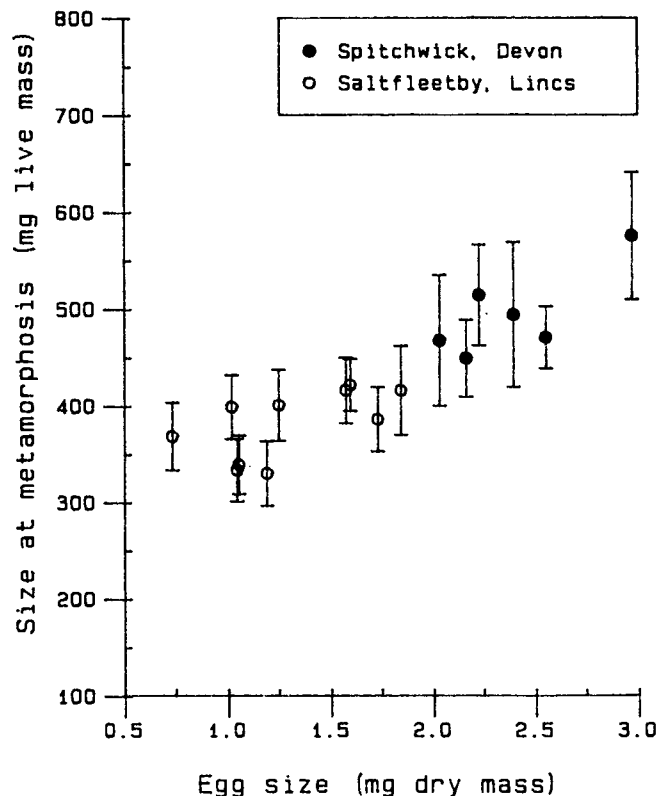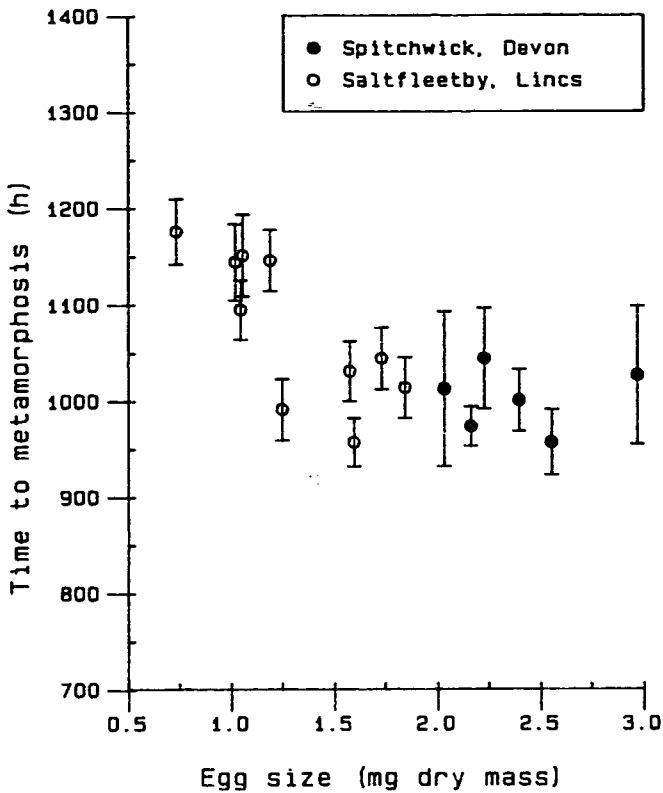
*Figure 17    Relationship between time taken to reach metamorphic climax (Taylor-Kollros stage XX) and egg size in experiments using eggs of the common frog from 2 populations. Points show mean values with 95% confidence limits for offspring of individual females paired with several males*

Although these findings do not represent definitive analyses of the results, it is clear that large eggs give rise to fast-growing tadpoles, which metamorphose sooner and at a larger size than tadpoles from small eggs. Likely advantages of early metamorphosis include the ability to escape desiccation or crowding in a drying pond, while large froglets will have a greater range of potential prey than small froglets. Future work will integrate these relationships into a model of tadpole cohort dynamics.

*C P Cummins*

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## THE INFLUENCE OF EVENTS ON POPULATION GROWTH

Environmental influences, such as floods, storms or frost damage, can cause sudden falls in population. The sediment on a river bed, for example, is stable so long as the stabilizing forces are greater than the disturbing ones. Once the equilibrium point is passed, the disturbance can be quite sudden and many bottom-dwelling invertebrates may be lost.

A preliminary investigation has considered the theoretical relationship between the intrinsic rate of increase, r, in a logistic growth model, the interval between events, $T_e$, and the fractional population loss, $\alpha$, resulting from an event. The post-event population is assumed to be a fixed fraction of that immediately before the event (Figure 18).
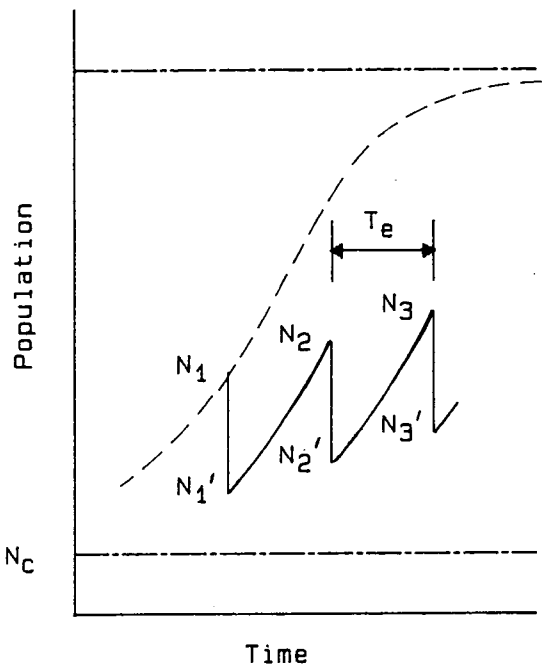


*Figure 18    Logistic population growth subject to sudden, catastrophic events*

—— = the growth that would occur in the absence of events

$N_c$ = the population at which extinction occurs due to other biological controls

$$\frac{N_1'}{N_1} = \frac{N_2'}{N_2} = \frac{N_n'}{N_n} = \alpha$$

When the interval between events is regular, the analysis starts by considering the conditions for a steady cycle, ie the situation where the recovery between events is exactly equal to the loss due to an event. This analysis can be extended to give general relations between r, $T_e$ and $\alpha$. When the loss is large, events frequent, and the growth rate low, extinction is inevitable. At the other extreme, the population is limited by the carrying capacity, events having little influence. Between these limits, the population settles

down to a regular cyclic pattern, irrespective of the initial population.

While regulated aquatic systems, for example, may generate events at regular intervals, most natural events occur at random, ie the interval between events is itself a variable, although its mean value is known. Hanson and Tuckwell (1981), starting from the same premises, calculated population survival times for a number of different conditions. Attention here centres on the construction of population risk curves, ie the relation between a population, growing logistically, and the probability of its extinction due to random, destructive events. It is assumed that there is a minimum critical population, $N_c$, such that, if the population is less than $N_c$, extinction is inevitable because of other biological controls. If the population is less than $N_c/\alpha$, then it will be destroyed if one or more events occur in the time it takes to grow from its current value to $N_c/\alpha$. This probability can be calculated. Even if the population survives to reach $N_c/\alpha$, it is still subject to the risk of extinction due to the occurrence of 2 or more events in the time taken to grow from $N_c/\alpha$ to $N_c/\alpha^2$. Similar arguments apply to initial populations greater than $N_c/\alpha$. Thus, the relationship between population and risk of extinction can be established.

As might be expected, population risk curves are hyperbolic, ie the risk is inversely proportional to the population. Unlike the regular interval model, the fate of a population subject to random events depends on the initial conditions. With random event intervals, there also exists a chance of survival under conditions in which extinction would be inevitable if the interval between events was constant.

Population risk curves are particularly useful in applied problems, such as impact assessment, but the great realism is obviously necessary for practical applications. Seasonal variations in event probability and a more realistic growth model than the logistic curve are starting points.

*I R Smith*

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## CRUSTACEAN ZOOPLANKTON COMMUNITIES OF STANDING WATERS: A THEME WITH VARIATIONS

Present-day pressures which lead to changes in the status of standing waters come from many sources: recreation, forestry, chemical run-off from agriculture, acid deposition, and so on. Surveys carried out by the freshwater group of ITE have been directed towards the examination of the flora and fauna of affected and unaffected sites, together with the measurement of many physical and chemical parameters that influence life in fresh waters. These surveys have been carried out in various parts of Scotland, from Shetland to Tayside, from the large lochs of the north and west to the smaller lochs of the Borders Region. One habitat selected for detailed study is the offshore water column which is occupied by crustacean zooplankton communities.

Data on such communities, especially their species composition and relative abundance, are now being collated in order to detect similarities and differences and, where possible, to attempt to relate these to environmental variations. The range of such variations in physical terms, at sites already examined, is considerable; from high-altitude peat pools in open moorland to medium-sized lakes in woodlands, from large and deep 'flooded valley' lochs to lowland or coastal ponds. A complete spectrum is represented. Despite this wide variation in environment, there is a nucleus of a few species, some or all of which occur in practically every water body and are usually the dominant species.

Three of the species which dominate the Scottish freshwater zooplankton are the calanoid copepod, *Diaptomus gracilis* Sars, the cyclopoid copepod, *Cyclops (strenuus) abyssorum* Sars, and the cladoceran, *Daphnia hyalina* Leydig.

Figure 19 shows that these species are found almost 'across the board', occurring commonly in lakes from a wide range of trophic conditions and sizes. The copepods mentioned above are, with the exception of one area, the only representatives of their groups to dominate the crustacean zooplankton, the exception being that, in the Shetland Isles and parts of north-east Scotland, a related species, *Diaptomus wierzejski* Richard, replaces *D. gracilis. Daphnia hyalina* is slightly more selective in its choice of a suitable environment, being superseded or occasionally accompanied by *Diaphanosoma brachyurum* Lieven in oligo- or mesotrophic lakes. Other Cladocera (eg *Bosmina coregoni* Baird) may be abundant, and sometimes numerically dominant, in oligotrophic or mesotrophic waters, but generally, in the richer lowland waters, they will be replaced, perhaps by closely related species (eg *B. longirostris* O. F. Müller).

Where groups of broadly similar lochs have been studied together, such as Scotland's 5 largest lochs (Maitland *et al.* 1981) and 5 Tayside lochs (Jones 1985), it has been possible to present diagramatically the relationship of the species to the lochs (Figure 20), and the results generate the idea of a 'theme with variations'. It was claimed by Maitland *et al.* (1981) that, given a sample from any one of the 5 lochs, they
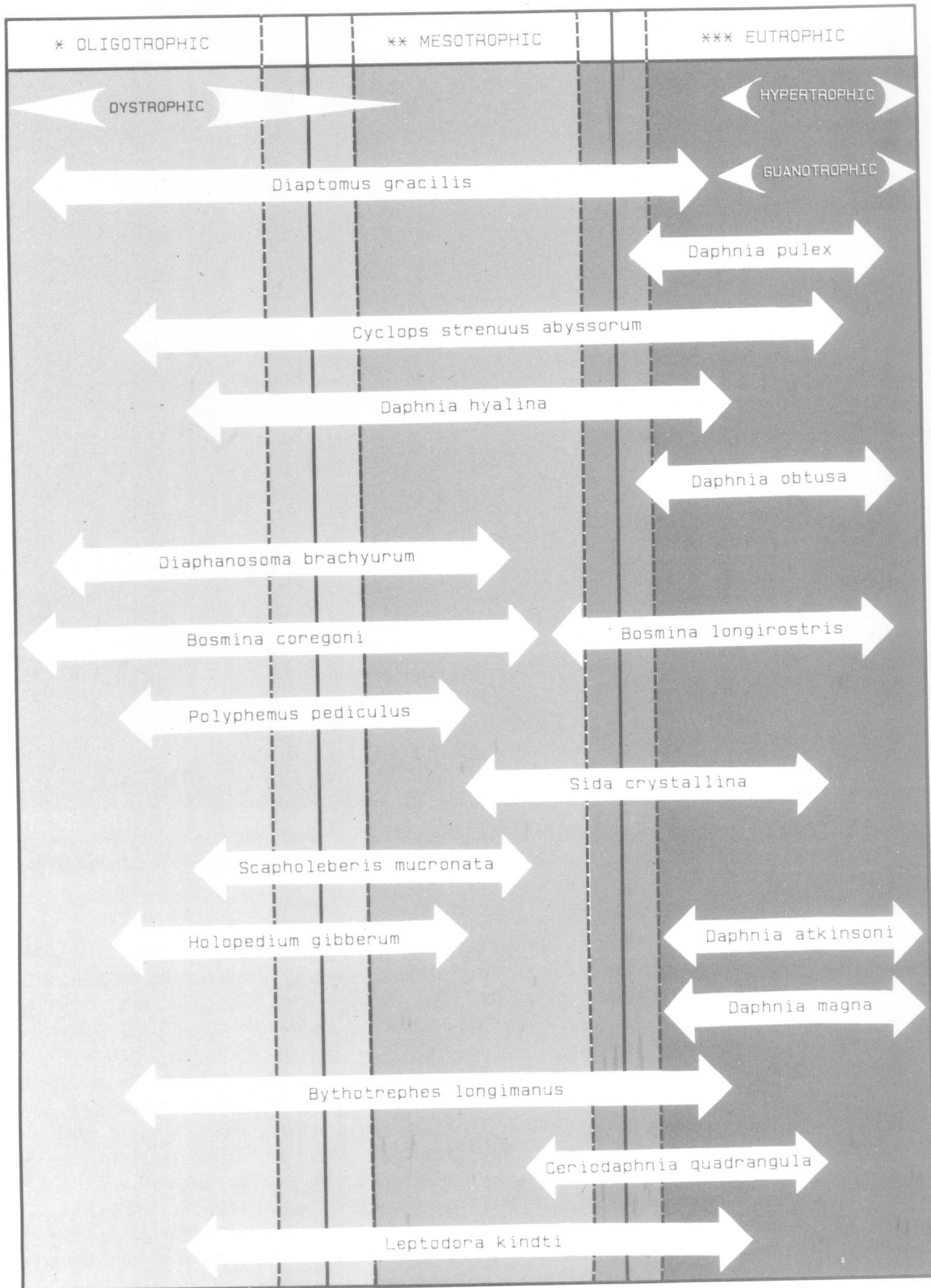
Figure 19   Seventeen crustacean zooplankton species from Scottish lakes arranged according to their apparent preference for trophic conditions

| * Oligotrophic: | clear colourless water, low in organic material |
| Dystrophic: | brown-stained due to humic acids, generally low pH and conductivity |
| ** Mesotrophic: | a full range of habitats, all moderately productive and species-rich |
| *** Eutrophic: | biologically very productive with a tendency towards fewer species, probably developing some chemical imbalance |
| Hypertrophic: Guanotrophic: | a markedly unbalanced system with exceptional chemical input and few species, although sometimes present in great abundance |
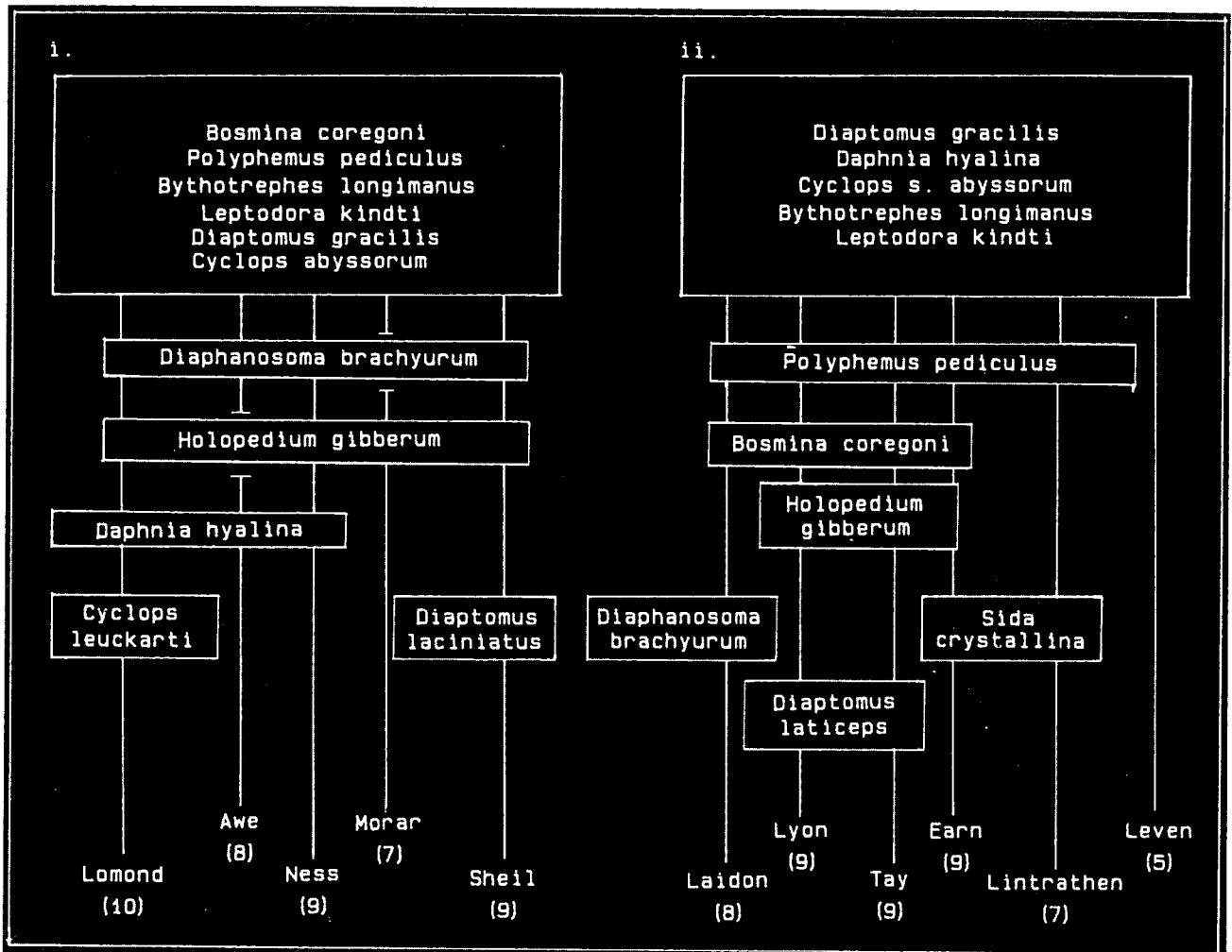
Figure 20    Zooplankton communities of (i) Scotland's 5 largest lochs (after Maitland et al. 1981) and (ii) 6 lochs in the Tayside Region (from Jones 1985, with unpublished data for Loch Tay). Figures in parentheses give the number of common species recorded in each loch

would be able to identify the loch from the species composition and the relative abundance of these species. This identification would also be possible for the Tayside lochs.

The species composition and relative abundance of crustacean zooplankton in lochs classified as eutrophic, hypertrophic or guanotrophic are generally very distinctive. Such waters are frequently undergoing comparatively rapid evolutionary changes, with the development of dense marginal and shallow-water vegetation, and a general shallowing of the loch due to the deposition of organic material. Much of this change is due to a marked chemical imbalance in the waters, which causes surges and troughs of productivity and decay. Consequently, it is not unexpected to find that the zooplankton is restricted to a few specialized or widely adaptable forms, or that waters of an apparently similar type have different species composition and are characterized by erratic bursts of production by a few species.

Some of the relatively small and shallow lochs in the Borders Region fall into this category, and one factor common to them is that they have a high population of

roosting or nesting birds. The resultant alteration of the natural chemistry of the waters influences the crustacean zooplankton (Moss & Leah 1982) and avian transport possibly introduces fresh species from outside their area of natural distribution (Jones 1984). Such species noted in Figure 19 are the daphnids, *Daphnia magna* Straus, *D. atkinsoni* Baird, *D. pulex* (De Geer) and *D. obtusa* Kurz. Of the 3 species given as the basic 'theme' of Scottish freshwater crustacean zooplankton (Figure 20), only the ubiquitous, adaptive and tolerant *Cyclops* (*strenuus*) *abyssorum* seems to accompany these less common species, and even then it appears, subjectively, to vary structurally from one loch to another.

So far then, it would be true to say that we have some baseline standards for species composition and relative abundance in the zooplankton communities of many of the larger lochs on the Scottish mainland, but much more information is needed from the medium-sized and smaller lochs before our knowledge of these aspects can be considered even reasonably complete. There is still much of interest and use to be obtained from the study of zooplankton communities in all types of standing waters, but, more particularly, it is neces-

sary to study those sites which are at risk of major change, such as waters where there is a high level of chemical enrichment, and consequently a high level of biological productivity.

*D H Jones*

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## THE USE OF A BBC MICROCOMPUTER TO RECORD PLANKTON COUNTS IN THE LABORATORY

Like many aspects of biological research, studies on freshwater plankton (free-floating plants and animals in lakes and ponds) involve the counting of organisms under the microscope. In the past, these counts have usually been recorded either by hand or on mechanical tally counters. In both cases, the final totals must be noted manually at the end of each count. Subsequently, these results may also be typed into a computer for storage, and the risks of transcription errors increase at every stage.

This article describes a microcomputer-based counting system used in our laboratory to automate the recording of plankton counts. The system consists of a BBC microcomputer, with disk drives, visual display unit and Epson dot matrix printer. With the keyboard placed close to the microscope and each alphanumeric key assigned to a different organism (species or life stage), counts can be registered quickly and easily by pressing individual keys.

The counting program (illustrated schematically in Figure 22) begins by asking the user for basic information on the sample to be analysed, including date, sampling station, sample and sub-sample sizes. Having recorded this information, the computer begins the count by setting all of the counters to zero and displays a blank results table on the screen. At this stage, the common species names can either be entered from the keyboard, or read from a named data file and assigned to appropriate keys. Additional species names, up to a maximum of 34 species, can be added to the list at any stage of counting. The results from different sub-samples of a given sample can be recorded separately within each count. The

maximum number of sub-samples is limited by the screen size, and the number of species being counted. Thus, 16 sub-samples can be counted for up to 17 species, because the whole screen width can be used for each species (Figure 21i). For 18 to 34 species, only one half of the screen is available to record each species and the maximum number of sub-samples is 6 (Figure 21ii).

i.

| Loch Leven - Routine Sample | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date: 19.8.84 | | | | Station: Reed Bower | | | | | | Depth: 3.5 metres | | | | | | | |
| Species | S1 | S2 | S3 | S4 | S5 | S6 | S7 | S8 | S9 | S10 | S11 | S12 | S13 | S14 | S15 | S16 | TOTAL |
| SP1..."2" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP2..."3" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP3..."4" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP4..."5" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP5..."6" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP6..."7" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP7..."8" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP8..."9" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP9..."0" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP10.."Q" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP11.."W" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP12.."E" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP13.."R" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP14.."T" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP15.."Y" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP16.."U" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP17.."I" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

ii.

| Loch Leven - Routine Sample | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date: 19.8.84 | | | | Station: Reed Bower | | | | | | Depth: 3.5 metres | | | | | |
| Species | S1 | S2 | S3 | S4 | S5 | S6 | TOTAL | Species | S1 | S2 | S3 | S4 | S5 | S6 | TOTAL |
| SP1..."2" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP18.."0" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP2..."3" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP19.."A" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP3..."4" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP20.."S" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP4..."5" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP21.."D" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP5..."6" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP22.."F" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP6..."7" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP23.."G" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP7..."8" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP24.."H" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP8..."9" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP25.."J" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP9..."0" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP26.."K" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP10.."Q" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP27.."L" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP11.."W" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP28.."Z" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP12.."E" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP29.."X" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP13.."R" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP30.."C" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP14.."T" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP31.."V" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP15.."Y" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP32.."B" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP16.."U" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP33.."N" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SP17.."I" | 0 | 0 | 0 | 0 | 0 | 0 | 0 | SP34.."M" | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

*Figure 21 Screen formats of results tables for plankton counts. Abbreviated species names (SP1-SP34) are shown and the corresponding input keys are indicated (i) for 17 species, and (ii) for 34 species. A hard copy of the results can be obtained from the printer at any time during the count*

Having reset the counters and allocated species names to keys, the count can begin. Each key press increments the counter for a particular species, and an audible signal, at a pitch characteristic of that particular key, is emitted. This facility hastens the work, as the observer can locate and increment the correct counter
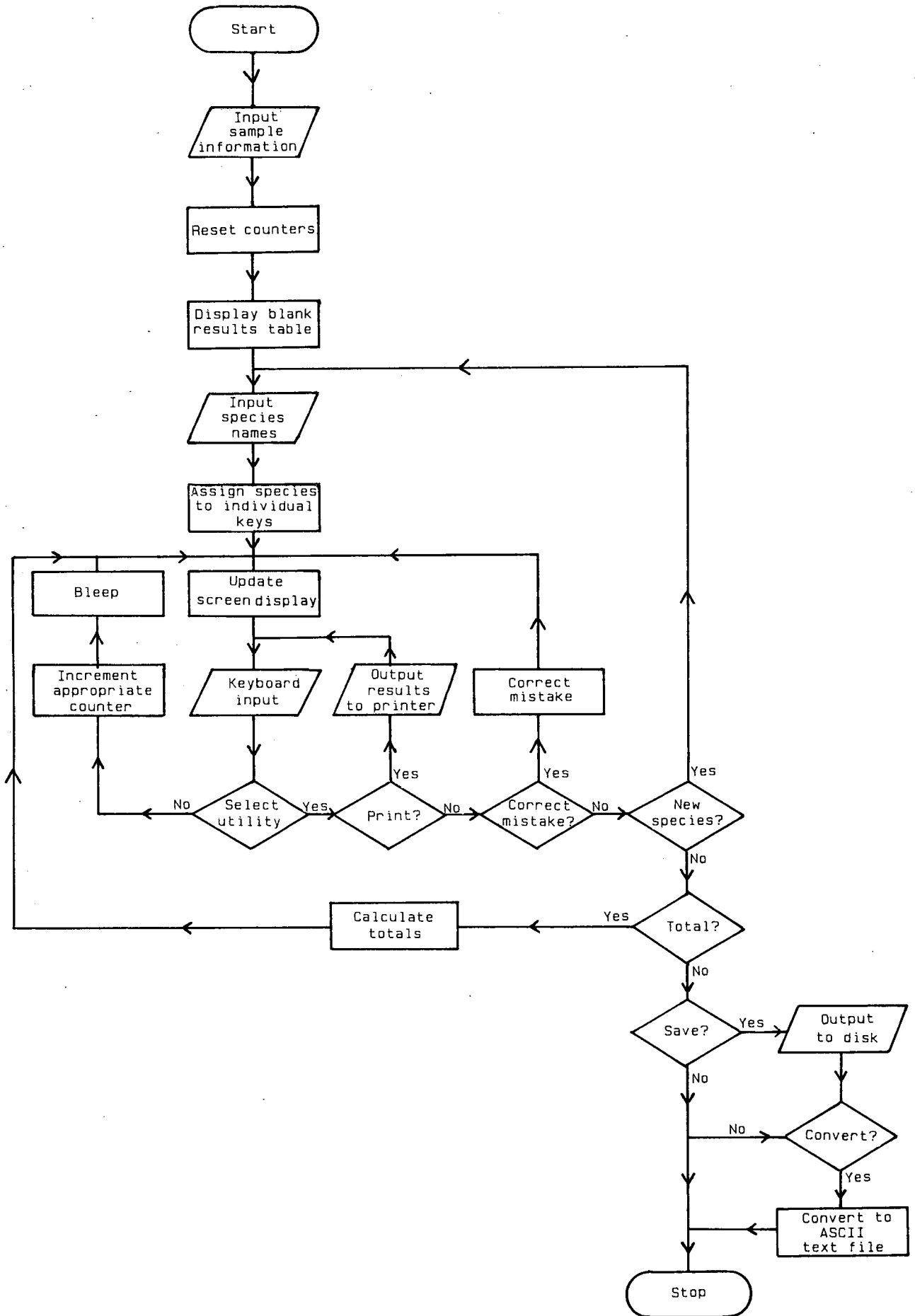
*Figure 22   Flow diagram of a BASIC program which enables the BBC microcomputer to be used for recording plankton counts*

without looking away from the microscope. Should a mistake be made, eg by pressing an incorrect key, the program allows the count to be corrected immediately. The screen display (Figure 21i, ii) is updated continually throughout and can be sent to the printer to supply a hard copy at any stage.

The count is terminated at the operator's discretion or when a predetermined sample volume or number of individuals has been examined. The latter is indicated audibly by the microcomputer. Several options are then available to the operator. First, the total number of each species in the whole sample can be calculated. Second, the results table displayed on the screen can be sent to the printer. Finally, the results can be saved on floppy disk for future use. The reduced risk of transcription errors, compared to the older methods of recording results by hand, is obvious. The method also represents a considerable saving in time.

The microcomputer-based counting system has one more important advantage over the older methods described. Data saved on floppy disk at the end of each count can be quickly and efficiently transferred to a mainframe computer over the telephone network, without retyping. The data files are first converted to text files, by a utility contained in the counting program, and then transferred directly using one of the commercially available communications packages. Again, this facility represents a considerable saving in operator time and decreases the risk of errors.

The system described above is similar to that of Cunningham and Purewal (1983), but has 2 important advantages. First, it uses standard hardware, which is readily available and can be set up without access to workshop facilities. The functions and utilities are generated from a disk-based program written in BASIC. Second, the system allows direct data transfer to a mainframe computer.

*Linda May*

Reference
**Cunningham, C. R. & Purewal, J. S.** 1983. A microcomputer-based aid for counting plankton samples. *J. Plankton Res.,* **5,** 783-786.

## Programme 3
# REHABILITATION OF DISTURBED ECOSYSTEMS

### RESTORATION OF *CALLUNA* ON A LOWLAND HEATH AFTER CONTROL OF DENSE BRACKEN BY ASULAM
(This work was largely supported by Nature Conservancy Council funds)

In recent decades, the area of lowland heath in Britain has declined rapidly (Moore 1962; Armstrong 1975; Webb & Haskins 1980) in response to powerful economic forces. The traditional low input/low output agricultural practices of burning, grazing, cutting, etc, which created and maintained heathland communities are no longer profitable. As a consequence, many former heathlands have undergone changes in land use to arable, improved pasture, forestry, mineral extraction, and industrial or residential development. Other heathlands have merely been neglected, and the absence of management has allowed succession towards a climax community to occur. Hence, the few remaining areas of heathland have become increasingly fragmented and isolated by changes in land use and by the development of secondary woodland. Furthermore, increases in the area and/or density of bracken (*Pteridium aquilinum*) have reduced the value of the remaining heathland sites for wildlife conservation.

It is therefore essential to establish active management programmes on remaining areas of heathland, based on sound scientific principles, if heathland communities are to be retained for future generations. Weed control is often the first priority in a management programme, and techniques for controlling birch and bracken have been studied under a contract from the Nature Conservancy Council (Marrs & Lowday 1983). However, once weed control has been achieved, for conservation purposes, it is particularly important to know how heathland vegetation is likely to develop subsequently; indeed, the restoration of native heathland vegetation on former 'weedy' areas is likely to be the most important long-term objective. Where light infestations of bracken and birch are controlled on established heathland, the former presence of these weeds may have a minimal effect on the subsequent development of heathland vegetation. However, where dense infestations of bracken occur, there is often a deep accumulation of litter, and the heathland ground flora is either sparse or absent, making restoration of heathland slow and unpredictable. The dispersal of litter and the sowing of locally collected *Calluna* seed have been investigated experimentally, on an area where a dense stand of bracken was controlled by asulam, at Cavenham Heath in the Brecklands of East Anglia.

An area of 0·1 ha of dense uniform bracken was sprayed with Asulox*, at the manufacturer's recom-

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*Asulox is a 40% w/v solution of the sodium salt of asulam, manufactured by May & Baker

*Table 7.* The effects of litter dispersal and seeding on (i) the percentage cover of *Calluna* 1981-83, and (ii) overall percentage vegetation cover 1979-83 at Cavenham Heath

| Litter dispersal | Seeding | Calluna cover 1981-83 (%) | | | Total vegetation cover 1979-83 (%) | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 1981 | 1982 | 1983 | 1979 | 1980 | 1981 | 1982 | 1983 |
| Untreated | Unseeded | 0·1 | 0·3 | 0·9 | 11·7 | 22·0 | 38·0 | 47·1 | 67·3 |
| | Seeded | 0·9 | 3·7 | 10·1 | 7·6 | 17·0 | 47·8 | 54·3 | 71·5 |
| Burnt | Unseeded | 0·1 | 1·5 | 3·8 | 11·4 | 20·3 | 53·3 | 63·8 | 68·8 |
| | Seeded | 4·9 | 16·1 | 29·0 | 2·8 | 6·8 | 31·5 | 44·9 | 64·8 |
| Litter removed | Unseeded | 0·3 | 1·7 | 4·6 | 10·2 | 18·9 | 48·3 | 60·4 | 72·1 |
| | Seeded | 18·5 | 40·9 | 68·4 | 2·6 | 14·5 | 40·4 | 60·9 | 83·7 |
| Rotavated | Unseeded | 0·5 | 1·7 | 5·5 | 2·9 | 7·2 | 37·3 | 59·4 | 70·6 |
| | Seeded | 15·3 | 40·5 | 51·3 | 2·0 | 4·2 | 28·8 | 58·5 | 81·7 |
| | LSD (P<0·05) between any 2 subtreatments | 7·4 | 8·7 | 16·0 | NS | NS | NS | NS | 11·7 |

mended rate of 4·4 kg a.i. ha$^{-1}$, during August 1978. Three bracken litter dispersal treatments were applied in early spring 1979—burning, raking off, and rotavating—and compared with undispersed litter. These experimental plots were then split to test a seedling subtreatment consisting of 20 000 *Calluna* seeds m$^{-2}$, and compared with unseeded plots.

*Growth of heather* (Calluna vulgaris)

*Calluna* seedlings were first observed on the experimental site in spring 1980, about one year after sowing. They were mainly confined to plots where the litter had been dispersed and *Calluna* seed sown. Very few seedlings occurred either on unseeded plots, or on seeded plots where the litter was undisturbed. Development of *Calluna* was most rapid on seeded plots where litter was raked off, and *Calluna* occupied 68% cover in July 1983 (Table 7). Establishment of *Calluna* from naturally occurring seed (the unseeded plots) was slow, attaining 3-5% cover in 1983, where litter was dispersed, but remained below 1% where the litter was undisturbed.

*Growth of other heathland species*

Widespread natural development of vegetation occurred on the experimental site, even where the litter was undisturbed. The principal naturally occurring species were sheep's sorrel (*Rumex acetosella*) and species of bent (*Agrostis* spp.), although early hair-grass (*Aira praecox*), wood small-reed (*Calamagrostis epigejos*) and *Dicranum scoparium* all increased. All these species were present, but sparse, within the litter layer at the start of the experiment. However, the growth of these naturally occurring species was closely related to the development of heather (Table 7). Where growth of *Calluna* was slow (where the litter was undispersed and on unseeded plots), the standing crops of sheep's sorrel and bent species were largest. Conversely, where *Calluna* had successfully established (where both seed was added and litter dispersed), the standing crops of other species were smallest.

Whereas the results of controlling bracken, either by herbicide or cutting, are relatively predictable (Lowday 1984a), the development of vegetation after the control of dense bracken is less certain. Vegetation development depends on the interaction of several factors, many of which are out of the control of the manager, for example:

i. survival of vegetative propagules underneath the bracken canopy;
ii. buried seed (Lowday 1984b);
iii. seed rain;
iv. depth of litter layer;
v. climate.

By manipulating at least 2 of these variables, this experiment has demonstrated that the development of post-asulam vegetation can be directed in favour of preferred species, in this case *Calluna*. Typically, *Calluna* is a colonist of disturbed areas, often after burning, and germination of seed is encouraged by both light at ground level and fluctuating temperatures, conditions which are characteristic of cleared or burnt areas (Gimingham 1972). Germination of *Calluna* is poor in its own litter, especially when the litter is fresh and loose, but is more vigorous when the litter is partly decomposed or compacted.

It is important to monitor the post-asulam vegetation development, because examination of buried seed has shown that potentially it can develop in several ways (Lowday 1984b). Indeed, further management may be needed to remove undesired species in order that vegetation development proceeds in a favourable direction. The manager may need to allocate as many, if not more, resources for subsequent vegetation management as were used for bracken control. Finally, an appropriate maintenance management regime will need to be imposed on the site in order to ensure the perpetuation of open heathland communities (Marrs & Lowday 1983); otherwise, weed control problems will recur.

*J E Lowday*

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## TOLERANT NATIVE TREES FOR OPENCAST COAL SITE REVEGETATION

### Background

The Opencast Executive of the National Coal Board (NCB) operates on the principle that the land from which coal is removed should be restored to its former condition, or better, as soon as possible after extraction ceases (Lindley 1979). Even in the case of restoration to agriculture, tree and shrub planting may be specified for practical reasons (hedges, shelterbelts), as well as to enhance visual amenity and wildlife habitat. Where afforestation is the aim, as in parts of the south Wales coalfield, native species of little commercial value may be specified for planting alongside roads, rides and watercourses, to blend in with the surrounding 'natural' vegetation and to reduce the visual impact of the site during the rehabilitation period, while also increasing the wildlife habitat. Where the land had no productive use prior to mining, and particularly where the site had previously been derelict, restoration may be aimed solely, or predominantly, at improving amenity. Trees and shrubs are often the major vegetation component of such schemes.

Over the years, problems have often been encountered in establishing trees and shrubs on restored sites, which is not surprising, given the relatively low quality land (nutrient-deficient (Plate 6), poorly drained (Plate 7), severely exposed) which is often reserved for tree and shrub planting. In an attempt to improve the situation, the NCB commissioned ITE to investigate the potential for using tolerant clones of native tree and shrub species for tree planting on such hostile sites.

### Research programme

Selected clones of a range of species, but particularly birch and willow, have been developed from saplings or cuttings taken from a variety of spoil heaps. The criteria for selection were as follows.

1. Only trees known to have originated by natural regeneration, and hence subject to site selection pressures, were considered.
2. Individuals growing in seemingly favourable niches were rejected.
3. Amenity features (form, bark colour, flowering, etc) were considered wherever possible, so that tolerant clones might also be virtually attractive (Plate 8).

More than 100 clones of 20 species have been selected, including 22 of birch and 10 of willow. Many of these clones and species were difficult to propagate vegetatively (Good *et al.* 1978), and the number of useful clones was reduced to about 25. Other clones have been derived vegetatively from plants obtained from standard commercial sources, with at least 3 clones for each species, and these clones have been used as the controls in field trials and glasshouse experiments.

The field trials have been planted on a range of restored sites throughout Britain. Some are hostile sites (Empire, Haigh, Tir-y-Gof, Whaupknowe 'B'), lacking topsoil and subsoil, and presenting drainage and/or wind exposure problems. Others are more hospitable sites (Radar North, Ty Cerrig), restored primarily to agriculture. A summary of the nutrient status and drainage characteristics of the sites is given in Table 8. The field trials have been augmented by pot experiments testing the responses of the selected clones to specific nutrients under controlled conditions. In addition, experimental inoculations of selected clones of birch with selected isolates of mycorrhizal fungi have been attempted under non-aseptic, glasshouse conditions.

### The field trials

In the field trials, most of the selected clones of birch and willow have achieved higher survival rates than the unselected clones (Table 9), although some (*Betula pubescens* clone 86 (BPu 86), *Betula pendula* clone 28 (BPe 28), *Salix caprea* clone 51 (SCa 51)) have not. The advantages gained by the best clones have been greatest on the more hostile sites, where 25% improvements in survival over controls have been commonplace, and 50% not uncommon, particularly in birch. It has been possible to draw up a list of selected clones which can be guaranteed to achieve high survival rates under a wide range of site conditions, and which are relatively easy to propagate vegetatively (Plate 9).

*Table 8.* Nutrient status, loss on ignition, pH and drainage characteristics of restored opencast coal spoils on which trials of selected clones of birch and willow have been planted

| Site | Depth of soil sampled (cm) | Loss on ignition (%) | pH | Water extractable nutrients (mg 100 g$^{-1}$) | | | Total N (%) | Drainage characteristics |
|------|------|------|------|------|------|------|------|------|
| | | | | N | P | K | | |
| Haigh | 0-10 | 5·7 | 6·5 | 0·027 | 0·02 | 0·45 | 0·12 | Very poorly drained |
| Ty Cerrig | 0-10 | 6·7 | 6·4 | 0·042 | 0·20 | 2·10 | 0·19 | Well drained due to slope |
| Radar North | 0-10 | 5·8 | 7·9 | 0·040 | 0·26 | 5·50 | 0·18 | Moderately well drained |
| Whaupknowe 'B' | 0-10 | 68·0[†] | 5·0 | 0·022 | 0·02 | 1·40 | 1·09[†] | Very poorly drained |
| Empire | 0-20 | 8·0 | 7·6 | 0·006 | 0·02 | 0·78 | 0·14 | Very poorly drained |
| Tir-y-Gof | 0-10 | 4·6 | 6·9 | 0·010 | 0·02 | 0·93 | 0·10 | Freely drained |

[†] High loss on ignition and total N due to large coal content

*Table 9.* Survival (%) of selected and unselected clones of birch and willow when planted on a range of restored opencast coal sites

| Species | Haigh[6] | Survival | | | | | Mean[†] |
|------|------|------|------|------|------|------|------|
| | | Ty Cerrig[6] | Radar North[6] | Whaup-knowe 'B'[5] | Empire[7] | Tir-y -Gof[5] | |
| **Birch** | | | | | | | |
| Unselected | — | 100 | 5 | 39 | 83 | 72 | 60 |
| BPu 7 | — | 100 | 89 | — | — | — | 95 (52)** |
| BPu 47 | — | 94 | — | 94 | — | 94 | 94 (70)** |
| BPu 86 | — | 67[5] | 22 | — | — | — | 44 (61) |
| BPe 28 | — | 50[5] | — | — | — | 94 | 72 (86) |
| BPe 34 | — | 100 | 83 | 61 | 92 | 89 | 85 (60)** |
| BPe 64 | — | — | 5 | 67 | — | — | 36 (22) |
| BPe 73 | — | 89 | 44 | — | 66 | — | 66 (63) |
| BPe 94 | — | 94[5] | — | 72 | — | 100 | 89 (70)* |
| Mean | — | 87 | 41 | 67 | 80 | 90 | 71 |
| **Willow** | | | | | | | |
| Unselected | 94 | 83 | 72 | 33 | 83 | 78 | 74 |
| SCi 12 | 94 | 100 | 94 | 61 | 100 | 67 | 86 (74)* |
| SCi 90 | — | — | 78 | 100 | — | 100 | 93 (61)** |
| SCa 16 | — | — | — | 78 | — | 94 | 85 (56)* |
| SCa 29 | 100 | 89 | — | — | — | — | 95 (88) |
| SCa 50 | 94 | 78 | 33 | 83 | 50 | — | 68 (73) |
| SCa 51 | 81 | — | 11 | — | — | — | 46 (83)** |
| SCa 76 | 83 | 94 | 89 | — | — | 72 | 85 (82) |
| Mean | 92 | 89 | 63 | 71 | 78 | 82 | 79 |

Superscripts [5, 6, 7] refer to assessments after 5, 6 or 7 seasons' growth respectively
[†]  Figures in brackets are means for unselected clones at the sites where the particular selected clone was planted
*  Means for selected and unselected significantly different (P = 0·05)
**  Means for selected and unselected significantly different (P = 0·01)
—  Clone not planted at this site

Some clones are more prone to shoot dieback following planting than others, but there is no consistent relationship between either survival and dieback, or dieback and subsequent growth. Clones should not, therefore, be rejected only because they are susceptible to dieback.

At most sites, mean growth increment of the leading shoots of control clones equalled, or exceeded, that of selected clones after 5 growing seasons (Table 10). Unselected willow, in particular, grew very well on the wetter, more fertile sites (Haigh, Ty Cerrig, Radar North). There were substantial differences in the performance of individual clones at different sites.

Thus, clone BPe 34 outgrew all other birch clones at Whaupknowe 'B', a site where growth was generally very poor, but grew least well of any at Ty Cerrig, the site where the highest mean growth rates of both birch and willow were recorded. Similarly, willow clone SCa 76 grew very strongly at the hostile Tir-y-Gof site, but less well than the average at the other 3 sites where it was planted.

Annual applications of a nitrogen:phosphorus (5:22) fertilizer at rates equivalent to either 20 kg ha$^{-1}$ N + 88 kg ha$^{-1}$ $P_2O_5$ ($F_1$) or 60 kg ha$^{-1}$ N + 264 kg ha$^{-1}$ $P_2O_5$ ($F_2$) have had no significant effect on survival or dieback of either selected clones, or

*Table 10.* Mean growth increment of the leading shoot (cm cm⁻¹) of selected and unselected clones of birch and willow after 5 growing seasons on a range of restored opencast coal sites

| Species | Haigh | Ty Cerrig | Radar North | Whaup-knowe 'B' | Empire | Tir-y -Gof | Mean† |
|---|---|---|---|---|---|---|---|
| | | | Mean growth increment of leading shoot (cm cm⁻¹) | | | | |
| **Birch** | | | | | | | |
| Unselected | — | 2·75 | 1·25 | 0·16 | 0·80 | 1·61 | 1·31 |
| BPu 7 | — | 1·55 | 1·39 | — | — | — | 1·47 (1·98) |
| BPu 47 | — | 4·30 | — | 0·54 | — | 0·83 | 1·89 (1·50) |
| BPu 86 | — | 1·22 | 2·02 | — | — | — | 1·62 (1·98) |
| BPe 28 | — | 2·20 | — | — | — | 2·66 | 2·43 (2·16) |
| BPe 34 | — | 1·19 | 1·53 | 0·58 | 0·76 | 1·64 | 1·14 (1·31) |
| BPe 64 | — | — | 1·04 | 0·29 | — | — | 0·66 (0·70) |
| BPe 73 | — | 3·39 | 1·07 | — | 1·30 | — | 2·23 (1·59) |
| BPe 94 | — | 1·68 | — | 0·02 | — | 0·16 | 0·62 (1·50) |
| Mean | — | 2·28 | 1·38 | 0·32 | 1·99 | 1·38 | |
| SED | — | 0·46 | 0·35 | 0·17 | 0·22 | 0·37 | |
| **Willow** | | | | | | | |
| Unselected | 4·92 | 5·03 | 3·90 | 0·16 | -0·34‡ | 3·00 | 3·40 |
| SCi 12 | 2·76 | 1·79 | 2·03 | 0·11 | 0·20‡ | 1·87 | 1·71 (3·40)** |
| SCi 90 | — | — | 2·09 | 0·87 | — | 2·90 | 1·95 (2·35) |
| SCa 16 | — | — | — | 1·75 | — | 3·10 | 2·42 (1·58)* |
| SCa 29 | 3·23 | 5·07 | — | — | — | — | 4·15 (4·97) |
| SCa 50 | 2·79 | 3·89 | 3·67 | 1·68 | -0·89‡ | — | 3·01 (3·50) |
| SCa 51 | 3·40 | — | 3·00 | — | — | — | 3·20 (4·41) |
| SCa 76 | 2·93 | 2·22 | 2·54 | — | — | 5·25 | 3·23 (4·21) |
| Mean | 3·34 | 3·60 | 2·87 | 0·91 | -0·34‡ | 3·22 | |
| SED | 0·26 | 0·68 | 0·33 | 0·47 | 0·17 | 0·67 | |

SED Standard error of the difference of the means for individual clones at a particular site
† Figures in brackets are means for unselected clones at the sites where the particular selected clone was planted
* Means for selected and unselected significantly different (P = 0·05)
** Means for selected and unselected significantly different (P = 0·01)
‡ Willows at Empire site severely grazed in 1981, not included in clone means
— Clone not planted at this site

unselected controls, of birch or willow, at any site. Fertilizer has produced significant growth responses, but only on the less fertile sites. The magnitude of the response has generally been similar in birch and willow, but some selected clones within each species have responded more than others. At Tir-y-Gof, for example, (Figure 23) willow clone SCa 76 was much more markedly affected than the unselected controls, or the other 3 selected clones. Such responses vary considerably from site to site, however, and, given the many variables influencing growth in the field situation, it is not possible to determine the likely growth response of individual selected clones from field trial data alone.

### The pot experiments

In pot experiments, all willow clones and unselected controls showed a more marked response to nitrogen in solution culture than birch (Figure 24). The proportionate response of each willow clone seemed to be similar, so that their ordering was the same by the end of the experiment, regardless of nitrogen level. It is notable that, at the 5 ppm level, all the selected clones had stopped growing by the tenth week, whereas the controls were still growing strongly after 12 weeks. In birch the response was different, all clones and the controls continuing to grow throughout the experi-

ment at the 5 ppm nitrogen level. Furthermore, at both 5 and 20 ppm nitrogen, unselected birches finished the experiment with lower growth rates than any of the selected clones. Only at 80 ppm nitrogen did the unselected plants outgrow the rest.

It seems, then, as if selected birches are better able to tolerate very low levels of nitrogen than selected willows, but they are not able to respond as much to additional nitrogen. The fundamental difference in response to the controls in birch and willow is interesting. The inability of unselected birches to respond as effectively as selected plants to very low levels of nitrogen, and their greater response to higher levels, is what might be expected. However, the ready response of unselected willow to very low levels of nitrogen is, so far, unexplained.

Another important factor to emerge from this experiment was the difference between birch and willow with regard to dry matter partition. Birches were generally more leafy than willows, and devoted less of their resources to root production. Furthermore, in willow, all the selected clones had consistently higher root/shoot ratios than the unselected plants. No such difference was found in birch. It is easy to imagine how high root/shoot ratios might favour plants growing
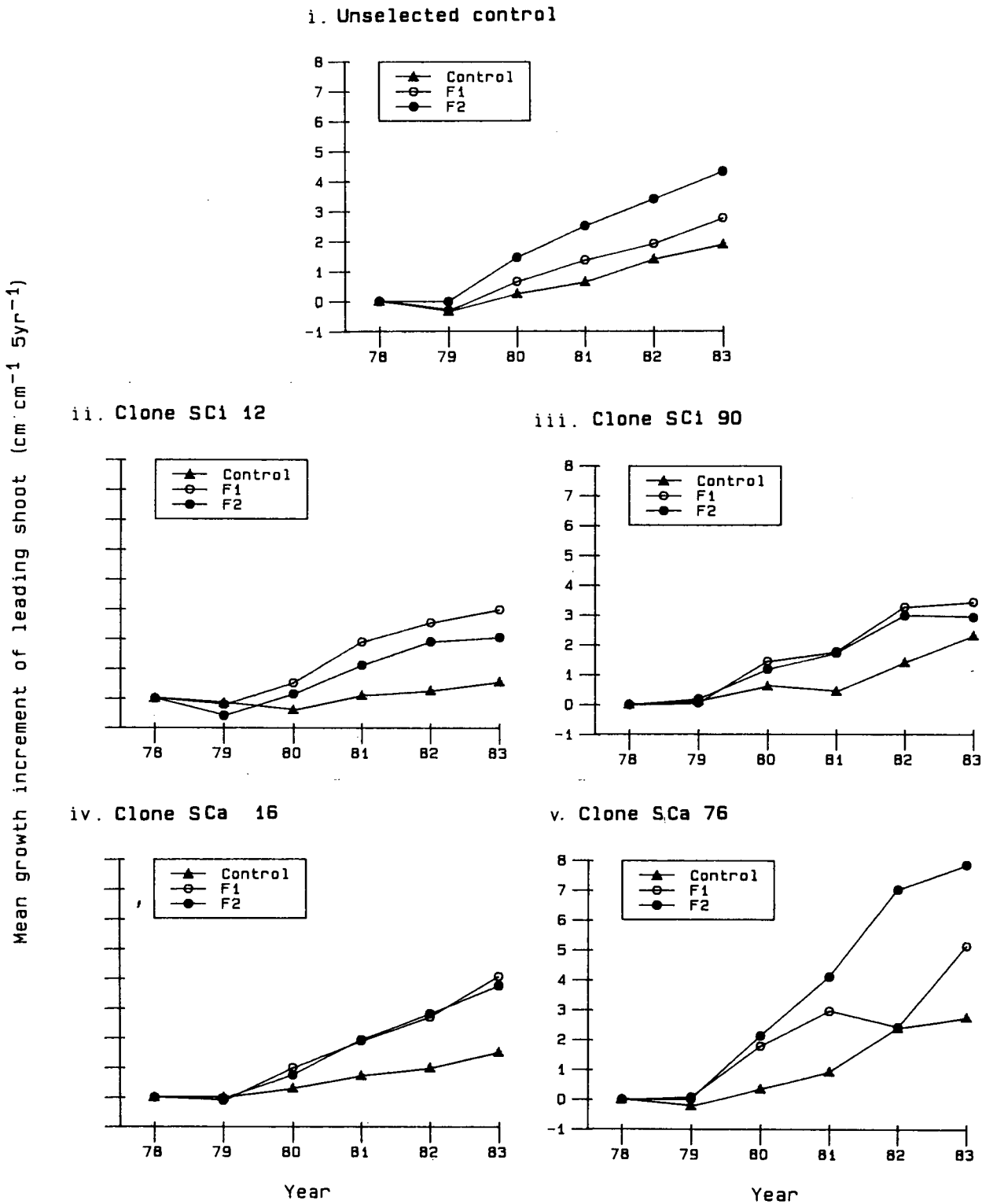
*Figure 23   Mean growth increment of the leading shoot of selected and unselected clones of willow, when treated with different levels of nitrogen:phosphorus fertilizer in the trial at the Tir-y-Gof site*

$F_1 = 20$ kg ha$^{-1}$ N + 88 kg ha$^{-1}$ P
$F_2 = 60$ kg ha$^{-1}$ N + 264 kg ha$^{-1}$ P

in nutrient-deficient, or drought-prone, soils, enabling them to exploit more of the meagre resources available, but why has this strategy not been adopted in birch? The answers may be revealed by an experiment in which uptake of phosphorus by severed root systems of selected and unselected birch was compared. Birch roots took up significantly more P than those of willow.

It seems, therefore, as if birch is efficient at taking up and using nutrients from soils containing them in low levels, while willow compensates for its relative
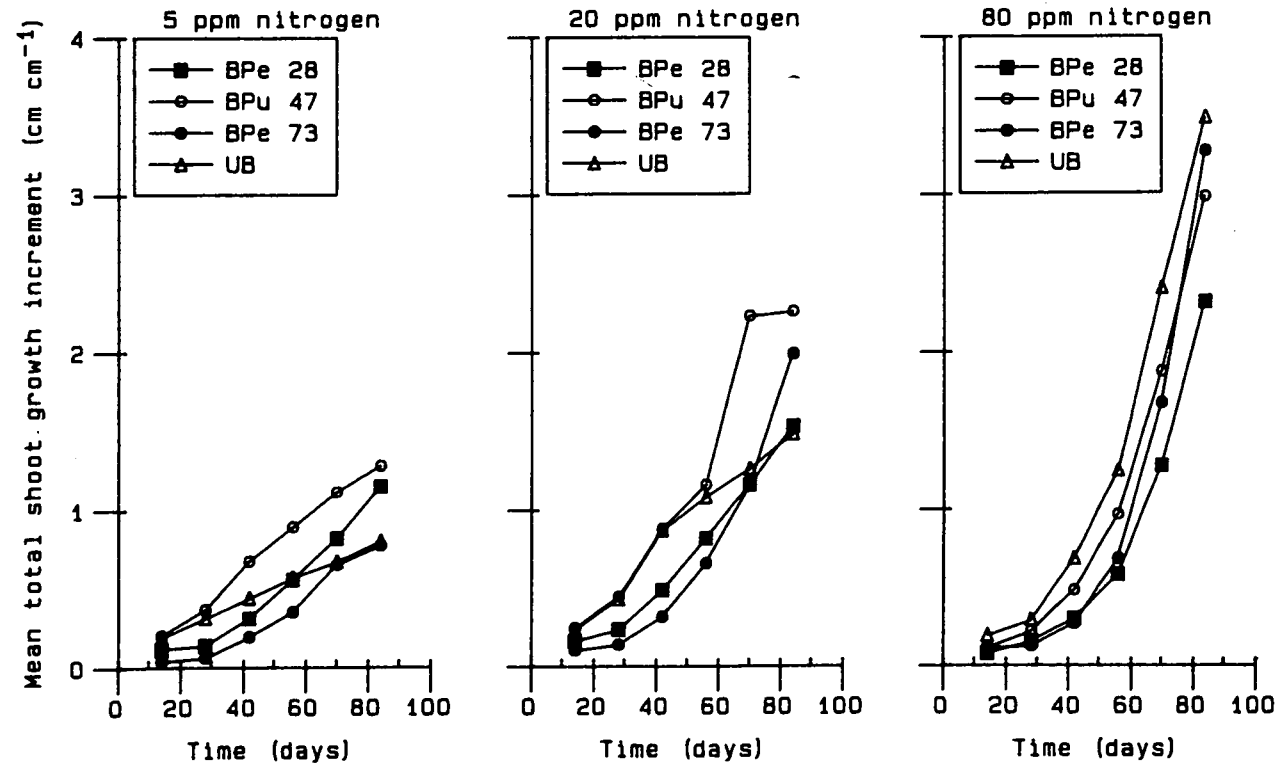
i. Willow
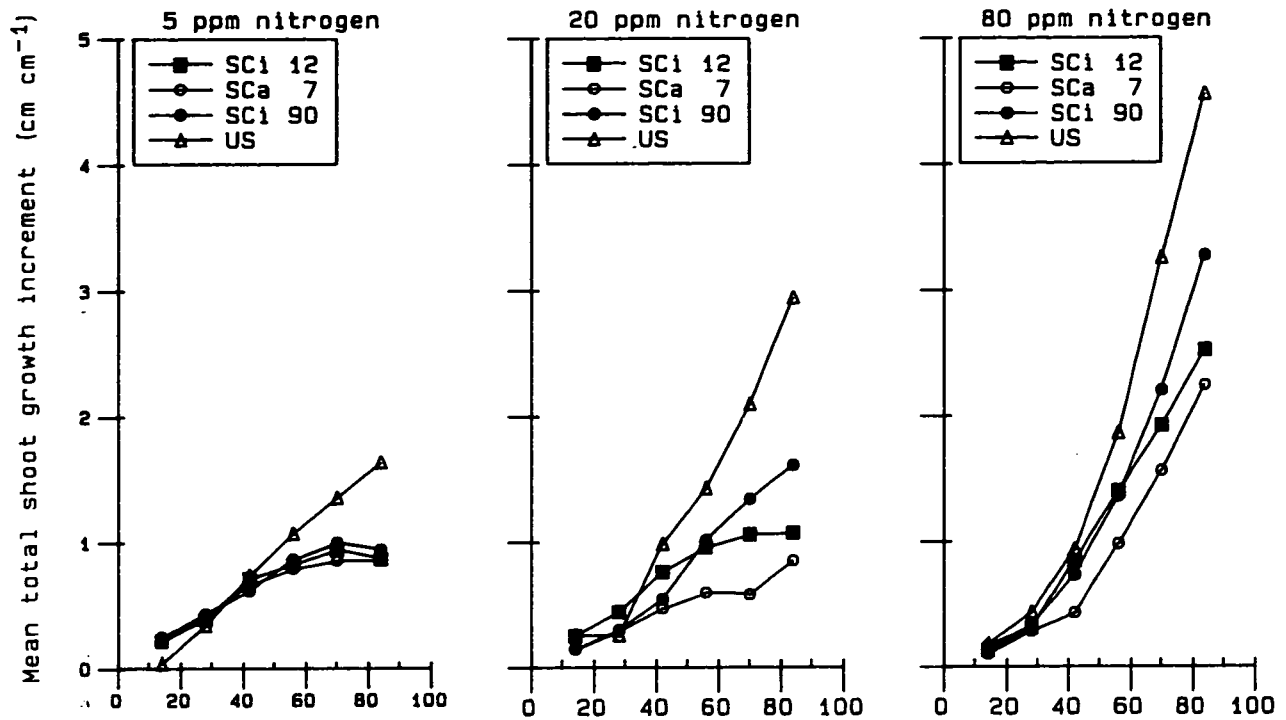


ii. Birch



Figure 24 *Mean total shoot growth increment (cm cm$^{-1}$) of selected and unselected clones of birch and willow grown at 3 different levels of nitrogen in solution culture*

inefficiency in this regard by developing a more extensive root system. Both strategies appear more or less equally effective in ensuring survival over a wide range of site types, as judged by their similar overall survival in the field trials (Table 9), but willow is able to grow faster, provided that the soil contains sufficient nutrients for exploitation by its more extensive root system.

In the mycorrhizal inoculation experiment, 2 clones of birch—one *Betula pendula,* the other *B. pubescens*—were successfully inoculated with a selected isolate of the fungus *Paxillus involutus,* obtained from the roots of a birch tree growing on coal waste. No successful inoculations were achieved with a second mycorrhizal fungus—*Lactarius pubescens*—of similar origin. The inoculations were carried out on rooted cuttings at various stages of their development, under non-aseptic, glasshouse propagation conditions. Successful mycorrhizal establishment was more common when established birch plants, rooted 56 days previously, were used, than when freshly rooted cuttings were inoculated.

The successfully inoculated plants, along with uninoculated controls, have been planted in a field trial on a hostile upland (230 m OD) site in south Wales, but it is too early yet to assess the effect of mycorrhizal inoculation on survival and growth. In a further pot experiment, selected birch and willow clones inoculated with a range of mycorrhizal fungi are being tested for phosphorus uptake, along with unselected controls. The aim of this and other current experiments on nutrition of the clones is to reveal the basis of their tolerance, and so to improve procedures for their future selection and testing.

*J E G Good and T G Williams*

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## RESTORING HEATHLANDS

The restoration, or re-establishment, of heathland vegetation can take 2 main forms. First, there is the direct restoration of areas, such as abandoned mineral workings, where the original heathland has been completely destroyed. Second, there is the rehabilitation of areas in which the composition of the vegetation has been changed. In this case, the former type of vegetation is encouraged to return, together with its associated animal communities; in a sense, this practice is similar to the management of areas for nature conservation. The latter type of area, needing rehabilitation, may have arisen through changes in the use of the land for agriculture, through excessive grazing, or through overburning, thereby enabling grasses such as wavy hair-grass (*Deschampsia flexuosa*), bristle bent (*Agrostis curtisii*) or purple moor-grass (*Molinia caerulea*) to dominate the vegetation.

Techniques for restoring heathland on derelict, or disturbed, land are now well established (Putwain 1983; Putwain *et al.* 1982). Experimental trials, reflecting both approaches, have been carried out recently on heathland in Dorset. In one of the earlier trials on ECC Ball Clay workings, a disused clay pit has been filled and its surface dressed with rotavated litter and topsoil from an adjacent piece of heathland, a procedure which ensures a good supply of propagules—mostly seed, but also roots—of heather (*Calluna vulgaris*), species of *Erica,* and other heathland plants. The trials on the restored heathland, the establishment of vegetation and soil chemical changes are being monitored in permanent plots. This trial is only in the early part of its second year, but there is already some regeneration of heathland plants, predominantly from seed; species so far noted include heather, cross-leaved heath (*Erica tetralix*), bristle bent, purple moor-grass, dwarf gorse (*Ulex minor*) and gorse (*Ulex europaeus*), together with a number of weed species.

*Table 11.* Seeds germinating in soil samples at different depths from 2 old fields which were formerly heathland

| | Depth 0-4 cm | Depth 4-12 cm | Depth 12-24 cm |
|---|---|---|---|
| Field A | *Agrostis capillaris*<br>*Deschampsia flexuosa*<br>*Holcus lanatus*<br>*Poa trivialis*<br>*Epilobium* spp.<br>*Cerastium fontanum* | *Agrostis capillaris*<br>*Poa annua*<br>*Epilobium* spp. | *Deschampsia flexuosa* |
| Field B | *Poa annua*<br>*Epilobium* spp.<br>*Spergula arvensis* | *Poa annua*<br>*Poa trivialis*<br>*Festuca rubra*<br>*Rumex acetosella*<br>*Stellaria media*<br>*Polygonum aviculare*<br>*Epilobium* spp.<br>*Cirsium* spp.<br>*Leontodon* spp. | *Poa annua* |

*Table 12.* Chemical analyses of field soils compared with heathland

|  | pH | LOI (%) | N | Na | K | Ca | Mg | P |
|---|---|---|---|---|---|---|---|---|
| Field A | 4·8 | 5·6 | 107·3 | 1·47 | 1·85 | 44·9 | 3·79 | 0·79 |
| Field B | 5·6 | 6·6 | 146·1 | 1·91 | 2·27 | 153·5 | 2·08 | 0·09 |
| Normal heathland | 4·0 | 12·0 | 173·0 | 4·62 | 3·50 | 20·4 | 6·32 | 1·40 |

An important aspect of this trial is the monitoring of the area from which the litter and topsoil used for dressing the restored site were taken. The procedure of stripping the litter and topsoil mimics turf-cutting, a practice which was widespread in former times on these heathlands. Thus, turf-cutting may have been more important than fire in maintaining open heathland, by preventing the regeneration of woodland and the accumulation of nutrients.

A second series of trials has been established in 2 abandoned fields that were formerly heathland. These fields now have a few scattered heather plants, which have grown up since cultivation was abandoned. A series of treatments has been devised which may encourage the heather to regenerate. The treatments are: rotavating the topsoil, turf-stripping, and the application of heather litter on topsoil with rotavating. The choice of these treatments was intended to provide tests of methods which could be applied on a large scale, with machinery if necessary. In undisturbed heathland, 90% of the heather seed is in the top 5 cm of soil (Putwain *et al.* 1982), and, in this trial, samples of soil were taken from 3 depths down to 24 cm. Seeds were allowed to germinate under glasshouse conditions, following heat treatment at 30°C. The majority of seed germinating (Table 11) was of grasses and agricultural weeds. Chemical analysis showed that, although the fields had been cultivated, they did not differ significantly from heathland, except in their content of organic matter, sodium and phosphorus (Table 12). In the first year, the results of this trial have been disappointing, because the capacity of the fields to regenerate as heathland seems small (no seedlings of heather having been reported in the samples), and the results seem to be contrary to those of Bakker (1978), who obtained successful heathland regeneration by turf-stripping. Further trials are contemplated, particularly for the rehabilitation of humid and wet heaths dominated by purple moor-grass. These treatments may yet offer alternatives to burning as a means of heathland management.

*N R Webb and A J Crane*

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## THE REINFORCEMENT OF GRASSED WATERWAYS

(This work was supported by Construction Industry Research and Information Association (CIRIA) funds)

The Reservoir Safety Act, 1975, brings in statutory requirements for some earth dams to be provided with extra spillway capacity to deal with extreme storm events. For such works, consideration can be given to the use of low cost grass spillways, because only occasionally are they used. Plain grass can withstand a water flow of up to 4 m s$^{-1}$ for several hours (Whitehead 1976). There is a wide choice of man-made materials for the reinforcement of grassed waterways to improve their ability to withstand occasional discharges at high velocities. These materials vary from plastic mesh to open concrete blocks tied together with cables. In all cases, the grass cover to the surface maintains an acceptable environmental appearance. With the lightweight products, the strength of the surface lies in the interaction of the plastic mesh and the grass root system, whereas the grass component is largely cosmetic in the heavy duty systems.

A trial site has been set up at Jackhouse Reservoir, near Blackburn (Plate 5), to test channels of different materials at water velocities of up to 8 m s$^{-1}$. A grass mixture was selected comprising 40% S23 perennial rye-grass, 30% Novarubra creeping red fescue, 20% Monopoly smooth-stalk meadow-grass and 10% Carmen creeping bent. This mixture of species with deep roots and with different systems of reinforcement: 4 types of plastic mesh, including one with bitumen-bound gravel filling, 3 cable-tied concrete blocks, one set of non-tied interlocking concrete blocks, and an open mesh-inforced concrete cast *in situ*. When the grass component is well established in 1986, water will be pumped to the top of the dam and allowed to run down each type of channel in turn, in a series of runs at increasing velocities, with a rest period to allow the grass component to recover between tests. When failure occurs, the role of the grass in relation to the cause of failure will be investigated and assessed.

A desk study is also being made of the choice of grass species and varieties for this type of work, including the use of special methods of establishing and maintaining a suitable grass cover. The results will appear in a revision of the *Guide to the use of grass in hydraulic engineering practice* (Whitehead 1976). It is already clear that at present most of the work by consulting engineers is *ad hoc*, and there is an obvious

research need to define more precisely the strengthening effect of grass root systems in the soil, and especially the interaction between the grass root system and synthetic methods of soil reinforcement.

*L A Boorman*

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## Programme 4
## MANAGEMENT OF NATURAL AND MAN-MADE HABITATS

### GRAZING AND SAND DUNE MANAGEMENT

Along the north and west coasts of Scotland, crofters depend upon the nutritional value of duneland grazings (machair). In north and south Uist and Barra, the narrow coastal strips of machair, rich in shell fragments, amount to 6100 ha of a total land area of 63 200 ha. Numbers of animals allowed to graze the machair are fixed by the Scottish Land Courts (Kerr 1954), but, in reality, the winter optimum of about 4 to 5 sheep ha$^{-1}$ is usually greatly exceeded, to as much as 10-20 sheep ha$^{-1}$ (Knox 1974), with consequent losses attributable to starvation.

Elsewhere in Britain, the grazing value of duneland systems is less widely recognized, but, nevertheless, can be significant in some locations. On the common (measuring 240 ha) of Northam Burrows, north Devon, 451 local residents claimed grazing rights, under the Commons Registration Act 1965, for 16 672 sheep, 1337 horses and ponies, 607 cattle, 9 pigs, 44 donkeys, 483 geese and poultry (Dartington Amenity Research Trust 1970). In Wales, some villagers of Aberffraw and Llangadwaldr on the Isle of Anglesey exercise commoners' rights on the Aberffraw dune system of about 290 ha. On occasions, something like 200 cattle and 300 sheep can be found. At both Northam Burrows and Aberffraw, like the machair in Scotland, grazing pressures can be intense and, as a result, these habitats can be at risk.

To gain a better appreciation of the sustained carrying capacity of duneland ecosystems, an experiment was initiated in 1979 on Newborough Warren National Nature Reserve, Isle of Anglesey, where the production of floristically rich swards is one of the management objectives. However, this area has attracted interest since Ranwell surveyed the vegetation in 1954. He recognized a series of assemblages ranging from 'semi-fixed dune vegetation' with marram (*Ammophila arenaria*) to 'closed dry slack associes' with red fescue (*Festuca rubra*) and common bent

(*Agrostis capillaris*) and 'closed wet slack associes' with marsh pennywort (*Hydrocotyle vulgaris*) and variegated horsetail (*Equisetum variegatum*). Within 10 years of the cessation of rabbit grazing in 1954, the occurrence of false oat-grass (*Arrhenatherum elatius*) and sweet vernal-grass (*Anthoxanthum odoratum*) had greatly increased (Chandapillai 1970), whereas the occurrence of species of bent had appreciably decreased.

Before starting the experiment, a vegetation survey was made, including species lists and estimates of 'cover' for lichens, bryophytes and vascular plants. As a result, 7 vegetation assemblages have been identified.

1. A fixed dune grassland with marram grass and false oat-grass.
2. A herb-rich short grassland, lacking marram grass but with many pasture herbs (forbs) including lady's bedstraw (*Galium verum*) and bird's-foot trefoil (*Lotus corniculatus*).
3. A herb-rich short grassland strongly invaded by false oat-grass.
4. An assemblage in wetter locations than those in which 1-3 occur, but drier than the sites occupied by 5-7. This assemblage includes red fescue, meadow-grass (*Poa pratensis*), creeping willow (*Salix repens*) and silverweed (*Potentilla anserina*).
5. A moist grassland with red fescue, meadow-grass, sheep's-fescue (*Festuca ovina*) and common tormentil (*Potentilla erecta*).
6. An assemblage with red fescue, creeping willow and some tall herbs including black bog-rush (*Schoenus nigricans*) and perennial sow-thistle (*Sonchus arvensis*).
7. As with 6, red fescue and creeping willow plus sedges (common sedge (*Carex nigra*); carnation sedge (*C. panicea*)) bird's-foot trefoil and water mint (*Mentha aquatica*).

Assemblages 5-7 were identified by Ranwell within his 'closed wet slack associes'.

In 1979, the experimental site was divided into a series of plots, each of 0·3 ha, to test the 16 factorial combinations of:

i. with or without grazing January-April;
ii. with or without grazing May-August;
iii. with or without grazing September-December;
iv. grazed by 1 or 2 sheep or their equivalents.

By 1982, there was a noticeable decrease of oat-grass from the more heavily and continuously grazed plots. It was also noticeable that changes were least in the wetter areas which the sheep attempt to avoid. Thus, bog-rush is only eaten in the most heavily grazed plots, and it is left untouched elsewhere. In the red fescue grassland, there has been a conspicuous ingress of Yorkshire-fog (*Holcus lanatus*) where grazing has been intense.

Although the experiment is only 5 years old, there are clear signs of change attributable to grazing. The observations already made highlight the dynamic nature of sand dune ecosystems and indicate that the intensity of grazing must be carefully managed—the sad lesson being learnt from the semi-arid regions of the tropics.

*D G Hewett*

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## SIZEWELL ECOLOGICAL SURVEY

The Central Electricity Generating Board (CEGB) is proposing to build a second nuclear power station at Sizewell, Suffolk. On 7 April 1983, the Board commissioned ITE to survey the vegetation in some 850 ha around the site, and to report within 9 months. The objectives of the survey were to (i) identify and map the different types of vegetation, (ii) locate plant communities and species populations of special interest, and (iii) provide as full a list as possible of the vascular plant and bryophyte species in the area.

From maps, aerial photographs and reconnaissance visits, it was evident that the survey area contained a complex of habitats, including shingle beach, dune, brackish and freshwater ditches, marsh, heath, arable and woodland, with, in some instances, long boundaries separating adjacent habitats. These boundaries were of potential significance, as rare species are often found by searching narrow zones on environmental gradients associated with vegetation boundaries. To maximize the possibilities of obtaining a complete inventory of the flora at Sizewell, emphasis was placed on surveying the vegetation boundaries, and also on the intensive examination of other areas so as not to overlook inconspicuous species.

Eighteen vegetation types were recognized, and 649 species of vascular plants (more than 20% of the British flora) were recorded. Twenty-five per cent of the known vascular plant species recorded in Suffolk were found in the survey area, which represents only 0·2% of the area of the county of Suffolk. Seventy-five of the species recorded are described by Simpson (1982) as scarce or decreasing in Suffolk. Some of the most abundant species are important food-plants for wildfowl. Only 5% of alien or introduced species were found. The natural diversity of habitats and the relatively slow rates of change in land use are responsible for the highly varied flora, with few 'introductions'.

In former times, cattle-poached ground was levelled after spring grazing with sand taken from nearby sand pits so as to improve soil aeration. This facet of the traditional pasture management of marshes foreshadowed the much larger infill operations carried out by CEGB on the proposed future power station sites at Sizewell. Within 14 years of dumping shelly sand on wet peat, a remarkable simulation of species-rich dune slack vegetation has appeared. The 164 species present include 8 scarce species found nowhere else in the original survey area, and populations of marsh orchids *(Dactylorhiza incarnata)* with densities as large as 60 plants m$^{-2}$ (Plate 25). These observations suggest that we should be (i) cautious when discussing the origins of the marsh flora at Sizewell—they may not be natural, and (ii) aware of the possibilities of creating species-rich communities by appropriate management—important considerations when implementing the development plan for the Sizewell site, which aims to minimize 'ecological damage' and mitigate it, where necessary, by habitat restoration. The preservation and conservation of stocks of scarce plant species are currently being considered.

*D S Ranwell*

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## FALKLAND ISLANDS AIRFIELD ECOLOGY

Before construction of the new Falkland Islands airfield and its associated port began, ITE and the Nature Conservancy Council were commissioned to advise

jointly on the likely ecological impact of their construction and subsequent operation. The main aims of the commission were:

i. to reconnoitre the 130 km² of 'camp' (countryside) likely to be affected;
ii. to identify sites and plant and animal species of particular nature conservation value, if any;
iii. to assess the impacts of the various activities involved during (a) construction (eg stripping and disposing of overburden, landscape regrading, stone quarrying, sand excavation, road building) and (b) subsequent operation (eg water extraction, sewage disposal, recreation by personnel);
iv. to recommend how deleterious impacts noted in (iii) might be minimized.

The airfield is sited south of Mt Pleasant in East Falkland, with the port a further 9 km south at East Cove (Figures 25 and 26). The climate is cool and windy, with a markedly small annual rainfall of 450-500 mm. The potential growing season of 6 months is limited by spring droughts. Except for the quartzite outcrop of Mt Pleasant, and the abrupt 30 m southern scarp of March Ridge, just south of the airfield, the development area is gently undulating moorland, dotted with large shallow lakes ('ponds'), commonly less than 1 m deep.

Two terrestrial plants predominate, diddle-dee (*Empetrum rubrum*) (Plate 19) on well-drained soils (20% of the area) and white-grass (*Cortaderia pilosa*) else-where. Most of the bedrock is overlain by a sheet of clay, which impedes drainage, and, coupled with the slow decomposition of organic matter in soils that are cold for much of the year, results in the widespread occurrence of peaty topsoils and of blanket peat. Most of the ponds have very turbid water, a result of the year-round winds which cause turbulence and disturb clay deposits. This turbidity, with the action of waves, prevents the growth of macrophytes in most ponds. In contrast, the streams draining the ponds are well vegetated and are important feeding grounds for waterfowl.

The 'camp' within the development area, lacking rare species and unusual habitats, was like thousands of hectares elsewhere in East Falkland. The only site of noteworthy nature conservation value is located at Bertha's Beach, to the east of East Cove; it was proposed to extract limited quantities of sand from this beach, which, with its immediate hinterland, has a good range of vegetation types and birdlife, including a small colony of gentoo penguins (*Pygoscelis papua*) (Plate 20). It will inevitably become more accessible for recreation when the planned new roads are completed, but there are many other beaches on the north and east coasts of East Falkland with far larger assemblages of wildlife. The designated development area has been used for sheep ranching for many years, with most of it having been repeatedly 'burnt over'. Much of the vegetation on drier ground has been damaged by excessive burning and trampling; soil erosion by wind is widespread (Plate 21).
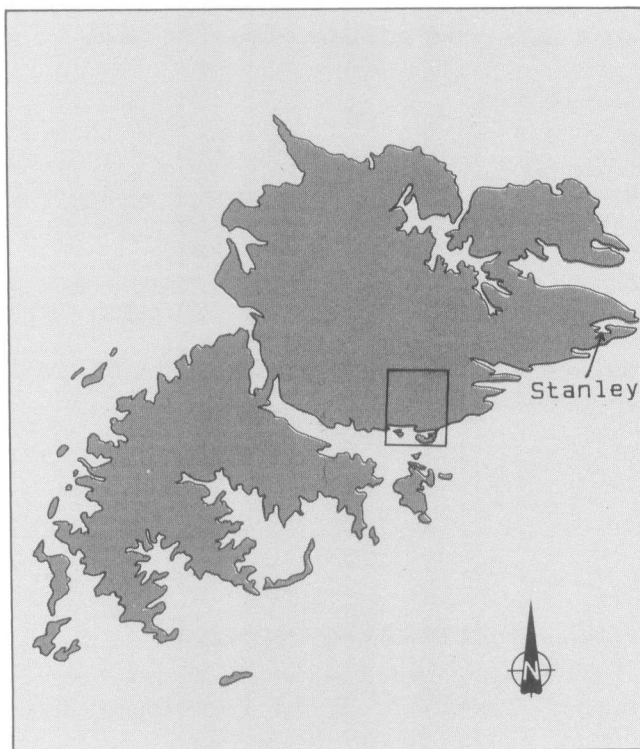


*Figure 25 East Falkland showing the location of the area surveyed. Scale approximately 1:1 800 000*
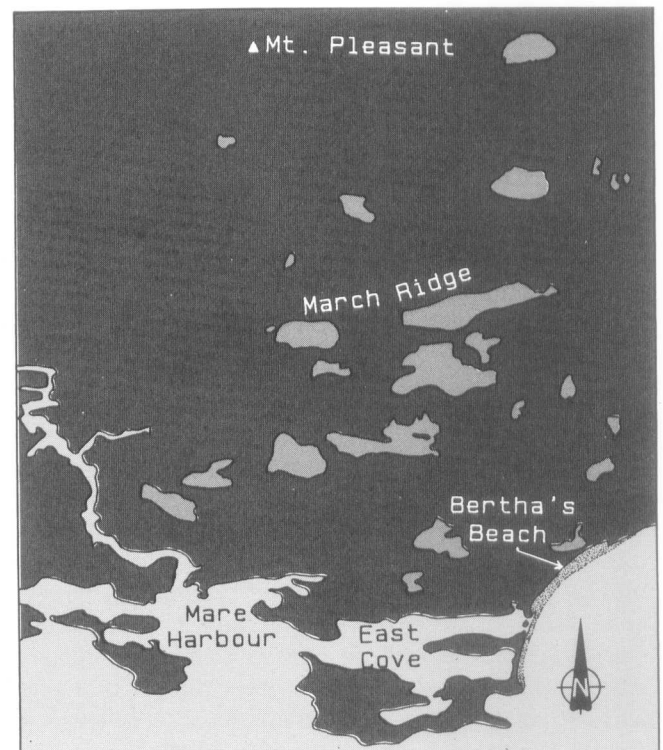


*Figure 26 Detailed map of the area of East Falkland surveyed in relation to the airfield under construction. Scale approximately 1:170 000*

It was concluded that, although the construction of the airfield and its ancilliaries would extensively disturb vegetation and alter the landscape, much of the damage attributable to (i) the movement of vehicles and mobile equipment, (ii) regrading, (iii) the disposal of overburden, (iv) the production of sewage effluent and food wastes, and (v) spillages of oil at East Cove could be either minimized or avoided by prudent management. Such management should include measures to:

i. confine movements of vehicles and heavy equipment to made-up roads and stances, thus reducing damage to vegetation (Plate 22);

ii. remove and store sods of topsoil when excavating, for later redistribution before reseeding, thus aiding revegetation;

iii. revegetate disturbed ground by conventional hydroseeding, with a bitumen or latex emulsion for temporary stabilization, thus minimizing soil erosion by wind;

iv. incinerate waste food to avoid attracting rats and gulls, recognizing that the latter pose a bird-strike hazard to aircraft;

v. prepare a code of practice to prevent oil pollution at the new port, and establish a capability to clean up oil spills;

vii. prevent excessive contamination of streams by peat when disposing of overburden;

viii. safeguard the wildlife interest of Bertha's Beach.

Implementation of these management recommendations should ensure that the effects of the airfield and associated developments on wildlife and nature conservation will be negligible. Interestingly, the major problem foreseen was a bird-strike hazard to aircraft by upland geese (*Chloephaga picta leucoptera*) (Plate 23). These birds are 'territorial' during the breeding season, with the gander defending the territory and thus limiting bird density on the ground. However, whereas densities are low on the white-grass/diddle-dee 'camp', they can be up to 100 or more times greater on reseeded grassland. Because large areas around the airport runways will have to be reseeded to prevent soil erosion by wind, and thus minimize the risk of damage to aircraft engines by the intake of sand and other soil particles, it is likely that numbers of upland geese will initially increase. To restrict this increase, it was concluded that the strategy for controlling numbers of geese should be aimed at making the airfield a poor habitat for geese, so discouraging breeding pairs. Shooting at Mt Pleasant would not be an effective method of control because, with about 500 000 upland geese on the islands, birds would quickly migrate into vacant niches. Indeed, removal of a breeding pair could result in a temporary influx of many more non-breeding, and thus non-territorial, birds. It was recommended that numbers of upland geese at the airfield should be controlled by:

i. forbidding the shooting of birds;

ii. sowing seeds of plants that are unpalatable to geese when seeding disturbed ground alongside the runways;

iii. allowing rank swards to develop within the airfield perimeter by minimizing mowing or burning;

iv. using, when necessary, conventional bird-scaring cartridges.

It was also recommended that the large clearwater pond in the angle between the main and lesser runways should be infilled, as it supported good growths of aquatic plants, and correspondingly held larger numbers of waterfowl which are likely to pose a bird-strike risk to aircraft.

*J Miles*

## ENVIRONMENTAL ADVICE TO WATER AUTHORITIES

Until relatively recently, a Water Authority wishing to promote a scheme for river improvement, for flood relief, or for drainage, would first make a feasibility study by engaging consultants of 2 types: (i) engineering, to produce a series of options for capital works and their associated costs; and (ii) financial, to estimate the benefits likely to be gained from each option. However, with increasing pressure from the environmental lobby (Friends of the Earth, RSPB, etc), and as increasing areas of land are drained, several Water Authorities have now found it advisable to seek the expertise of a third type of consultant, namely independent environmental assessors. The latter are expected to provide early warnings of likely environmental issues which might result from the different engineering and financial options, and, where possible, assessments of the validity of the environmental 'issues', and suggestions for ameliorating harmful impacts.

The introduction of environmental assessments has been hastened so as to comply with recent legislation. Section 48 of the Wildlife and Countryside Act amends Section 22 of the Water Act 1973, so that Water Authorities now have a duty 'to further conservation and the enhancement of natural beauty and the conservation of flora, fauna, and geological or physiological features of special interest'. Guidelines on the Act, issued to Water Authorities in October 1982 by the Department of the Environment, Ministry of Agriculture, Fisheries and Food and the Welsh Office, stress that special consultations should be held between the Water Authorities and the Nature Conservancy Council at an early stage when proposals for new works or improvements are being considered. However, any recommended expenditure to meet the needs of the Wildlife and Countryside Act must be consistent with the primary purpose of the works under the Land Drainage Act of 1976.

During the last 2 years, and in addition to assessments for the Nature Conservancy Council, ITE has been involved with engineering and financial consultants in bids for work relevant to 9 schemes. Five of these bids, involving 3 Water Authorities, were successful: 3 were concerned with schemes of river improvement, and 2 with studies of water resource development. In addition to the 6 members of staff intimately involved, the contracts have been supported by the entire range of expertise found within the Institute.

In every instance, the Water Authorities needed:

1. a list and map of statutory sites (NNRs, SSSIs, LNRs) within areas influenced by the different schemes;
2. a list of other sites of conservation interest within the 'areas';
3. predictions of damage likely to be inflicted by the different options;
4. suggestions for changing and/or modifying the different options so as to avoid damage;
5. an assessment of the strength of the conservation lobby in relation to the different sites.

The first requirement is fairly easy to satisfy from the Nature Conservation Review, SSSI lists and BRC files. The list of non-statutory sites of conservation interest is, however, somewhat open-ended and, to an extent, inevitably arbitrary. In predicting likely damage from drainage, ITE has become aware of the gaps in knowledge related to the role of soil moisture in controlling the composition and behaviour of plant and animal communities.

The main lesson learnt from ITE's collaboration with other consultants is the need for good communication. A contract requiring 5 man-days 'in the field' and 5 man-days 'in the office', preparing the interim and final reports, will need an equal number of days of discussion-meetings with local naturalists, the Nature Conservancy Council, collaborating engineering and financial consultants and, most importantly, the customer.

*M D Hooper*

## Programme 5
## SURVEY AND MONITORING

### TOWARDS A BIOLOGICAL MONITORING PROGRAMME

An appreciation of the changes that take place in the British landscape is of fundamental importance to ecologists. This statement is equally true at national,

regional and local scales, both as a context for commissioned and short-term research work, and as an information base for strategic research. A good deal of interest has been shown in the contribution that historical geography can make to an understanding of local landscape features and land use patterns. However, both nationally and regionally, the historical record is patchy and inconsistent, and generally inadequate as a baseline for the assessment of all but major changes.

Currently, therefore, much attention is being given to the need for a suitable baseline against which to monitor future changes in land cover and land use. At the national and regional scales, this effort is being directed towards a sampling approach, taking into account the potential roles of satellite and airborne sensors as major sources of data complementary to field survey (Barr *et al.*, see pp 133-135). Using a partial replacement sampling programme within an established framework of land classes, regular survey will give estimates of change in land use and cover types, both nationally and in major regions of Britain. Work on the development of such a land use monitoring programme within ITE is well advanced.

In the field of biological monitoring, the focus for national indications of change is the Biological Records Centre (BRC, see p 54). The publication of distribution maps showing records in different date classes has indicated the extent of change in the ranges of many species during this century. The maps are used to identify rarities, which can be recorded in more detail to establish reasons for their limited distribution, and possible needs for their conservation. For the majority of species covered in more than 60 BRC recording schemes, however, information on change, following the initial publication of an atlas, can only be determined by resurvey after a time span of 10-20 years. At the other end of the geographical scale, where monitoring is carried out in individual sample areas, the recording can be much more sensitive, dealing, for example, with phenological change or fluctuations in population sizes in relation to local ecological conditions (Hill & Radford, see pp 53-54). Certainly, such long-term monitoring projects have a continuing role in the Institute's strategic research, although it is important to consider the effective contribution of each to the overall research requirement.

It is at intermediate scales that there is most need for further developments in biological monitoring, drawing upon experience from some of the work already undertaken in specific habitats, notably fresh water. The general requirement is to monitor change in the distribution and abundance of a range of species, selected as indicators of important ecological conditions in the overall landscape pattern of Britain. In order to achieve realistic estimates of change, over periods in the order of years rather than decades, and, if possible, in relation to landscape features such as

cover types, an appropriate sampling strategy must be designed. To link this directly with the approach used for landscape monitoring is an attractive possibility, but research is necessary to demonstrate the feasibility. While this development work is taking place, there is an opportunity, in the shorter term, both to assess the potential contribution of repeating selected past surveys as a means of detecting change, and to consult with other organizations over areas of common interest and possibilities for co-operation. In view of the limited resources available for a potentially open-ended and expensive commitment to monitoring, shared access to relevant data sets and joint interests in research projects are of importance to ITE, to other NERC institutes, and to outside organizations.

In order to focus attention upon these issues, ITE has set up an Ecological Data Unit (EDU) based at Bangor Research Station, with the initial objective of developing a biological monitoring capability. The Unit is currently looking at the feasibility of different approaches to monitoring and is consulting within and outside ITE on sampling strategy, survey methodology, the value of repeating past surveys, and the existence and availability of relevant data sets as an information background for monitoring. This feasibility study will end in 1985, when recommendations for an operational EDU will be considered.

*G L Radford*

Ideally, there should be a national register of permanent vegetation plots, which would provide a picture for the whole of the United Kingdom. As a step in this direction, ITE has compiled a register of the permanent plots for which it is responsible, or for which it has assumed responsibility. The register is now (December 1984) in an advanced stage of preparation, and can be used to obtain an impression of the geographical and ecological spread of ITE's plots.

Arbitrarily, we have defined a recording programme as permanent if it has run, or is planned to run, for at least 10 years. On this basis, ITE has 60 recording programmes, comprising 2484 plots, covering a total area of 76 ha. Some of these plots were initiated by the former Nature Conservancy (set up in 1949), from which ITE was formed. However, no permanent plots survive from the first 5 years and only 9 recording programmes date from before 1965 (Figure 27).

Except for the fact that they include no sites in Scotland, the 9 early recording programmes are broadly representative of those developed later. Four of the programmes are based on plots located in upland grassland and moorland (Snowdonia and the Pennines). One series of plots is in an upland forest plantation (Gisburn Forest, Lancashire); another is in an acid oakwood (Ffestiniog, north Wales). In the lowlands, the 3 earliest programmes are on coastal shingle (Dungeness), a lowland heath (Hartland Moor, Dorset) and chalk grassland (Knocking Hoe, Bedfordshire).
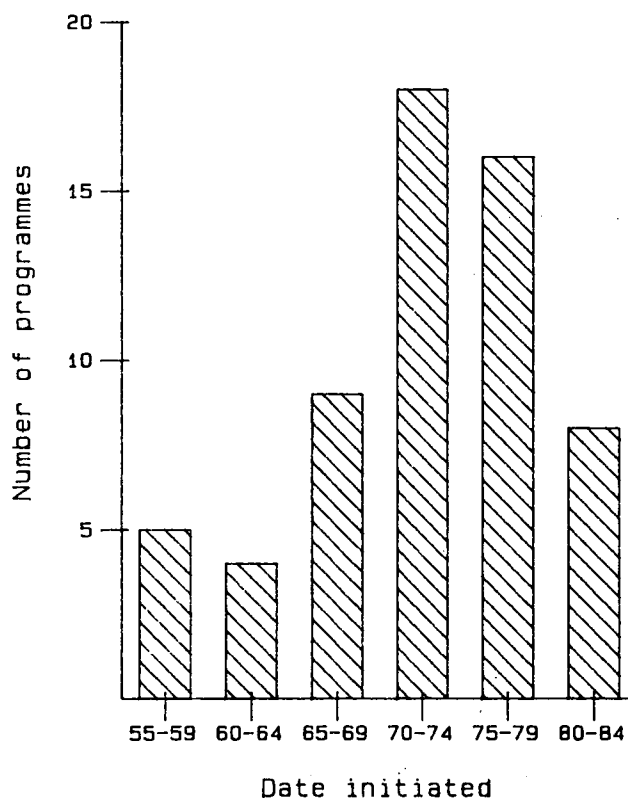
## REGISTER OF PERMANENT VEGETATION PLOTS

At the landscape scale, ecological change is slow. Only after a major disturbance such as fire, ploughing or windthrow is change normally fast. Even then, it slows down after one or 2 decades. Slowness of change does not imply that it is unimportant, but slow change is difficult to observe and even more difficult to measure. The standard method of studying the problem is to set up permanent plots and to observe or measure them at intervals.

Historically, the majority of permanent plots were established as a result of the research interest of an individual botanist, or group of botanists, and were not part of a designed programme of vegetation monitoring. This state of affairs is unsatisfactory, particularly as resources to maintain recording programmes are limited. For example, it is highly desirable that some plots should be maintained beyond the working life-time of the scientists who set them up, and that a wide geographic and ecological spread be achieved. Only through an awareness of the national picture can we hope to achieve a good overall selection of long-term plots.



*Figure 27  Initiation of vegetation recording programmes with permanent plots*

The early plots, like those established later, are mostly located in National Nature Reserves, reflecting the fact that ITE was formed from the Research Branch of the former Nature Conservancy, and that, since its establishment as a separate institute, ITE has continued to undertake contract research for the Nature Conservancy Council. There is also a measure of security of tenure which might be lacking elsewhere. The other major feature of ITE's permanent plots is that none is in arable land or improved pasture, and that the majority (34 out of the 60 programmes) are in the uplands.

*M O Hill and G L Radford*

## THE USE OF BIOLOGICAL RECORDS CENTRE DATA IN RESEARCH

(The work of BRC is partly supported by Nature Conservancy Council funds)

Since the Biological Records Centre (BRC) was set up in 1964, output from its data bank, in the form of species distribution maps, has been widely used in research papers and other publications to provide background information. Data recording the occurrence of species in the 10 km squares of the British and Irish National Grids, within various periods of years, have been analysed by several authors. For example, Strong (1974) and Kennedy and Southwood (1984) described the relationship between the current (and past) distribution of species of trees in Britain, and the species richness of their insect fauna.

More comprehensive data, in the form described for butterflies by Harding and Greene (1984), are now available for several taxonomic groups (eg rare vascular plants, marine algae, butterflies, dragonflies, grasshoppers, crickets, woodlice and some mammals). Although these data are still essentially records of the distribution of species, the extra information extends their usefulness. Data, such as these, which include early records from collections, herbaria and published sources, can be used in broad-based monitoring of changes in species distribution. Heath *et al.* (1984) demonstrated, using butterfly data, how a valuable insight can be gained into changing patterns of distribution. Further analyses of data on butterflies are being made, in conjunction with BRC, by Dr R H L Dennis.

BRC is collaborating with Dr N T H Holmes, the author of a proposed handbook on the taxonomically difficult plant genus, *Potamogeton*. The BRC computer files are based on records of specimens which have been identified by experts and have full details, including habitat coding and precise herbarium or literature sources. These files are the baseline for assessing the present occurrence of species, and for future monitoring. Some species have become rarer in recent years; the data should allow for the examination of possible correlations between the habitat preference of a species and the extent of its decline.

Information on habitats, collected with distribution records, for centipedes, millipedes and woodlice has been analysed in a collaborative project with Dr C P Fairhurst (Salford University) (Fairhurst *et al.* 1978; Harding & Sutton 1985). Data on habitats and island distributions of all 3 groups were analysed by Atkins (1979), as a postgraduate project.

Data on Orthoptera (10 000 records) were used by Milligan (1983) to compare and contrast a variety of analytical methods and statistical techniques, when applied to geographical distributions and habitats.

The use of BRC data in research is clearly secondary to the prime function of the Centre—to document the occurrences of species in the British Isles. It is, however, a use which ITE wishes to develop itself and to encourage.

*P T Harding, Dorothy M Greene, H R Arnold, C D Preston and B C Eversham*

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## BUTTERFLY MONITORING SCHEME: EFFECTS OF WEATHER ON ABUNDANCE

(This work was partly supported by Nature Conservancy Council funds)

The Butterfly Monitoring Scheme provides regular information on annual changes in butterfly abundance. The Scheme has now operated since 1976 (with earlier records from some sites) and receives data from over 80 sites in Britain. We have now begun to

consider assessing the role of weather in determining fluctuations of butterfly numbers.

There are good reasons for supposing that weather is an important factor. Many life table studies of Lepidoptera have shown key factors related to weather conditions, such as hours of sunshine during the oviposition period. Further evidence of the likely importance of weather comes from the data from the monitoring scheme; it is very obvious that in most species similar fluctuations are observed over wide areas. One such example is shown in Figure 28, where the fluctuations in abundance of the hedge brown butterfly (*Pyronia tithonus*) at Monks Wood can be seen to follow closely the fluctuations in data for this species from the other sites in the monitoring scheme. The hedge brown is a common and widespread butterfly in the southern half of Britain, and the national picture is based on counts at about 50 sites each year.

It is argued here that the degree of synchrony observed for the hedge brown, which occurs in discrete, fairly sedentary, local populations, indicates an important role for weather in determining fluctuations. Further, it suggests that the effects of weather are not subtle, dependent on precise timing of good or bad weather in relation to the life cycle, but may be related to such factors as mean winter temperatures, or spring rainfall, which may be expected to be similar over a large part of the country.

For a given species, the index of abundance in a given year is likely to be functionally related to the index of abundance in the previous year and to recent weather conditions. We have used the standard multiple regression models to study the relationship of the current index of abundance $(Y_i)$ (the dependent variable) to the previous index of abundance $(Y_{i-1})$ and to weather factors (independent variables). Initially, monthly averages of temperature, rainfall and hours of sunshine were used for each of the 14 months preceding and including the current flight period, giving 42 simple models of the type:

$$\log Y_1 = \alpha + B_0 \log Y_{i-1} + B_1 W_i + error$$

where the weather variable $W_i$ was successively taken to be $T_{ki}$, $R_{ki}$ and $S_{ki}$ (temperature, rainfall and sunshine, $k = 1, 2, \ldots, 14$).

Results for the hedge brown at Monks Wood (1973-84), using mean temperature data for the 14 months preceding the current flight period, are illustrated in Figure 29. Those using sunshine hours and rainfall did
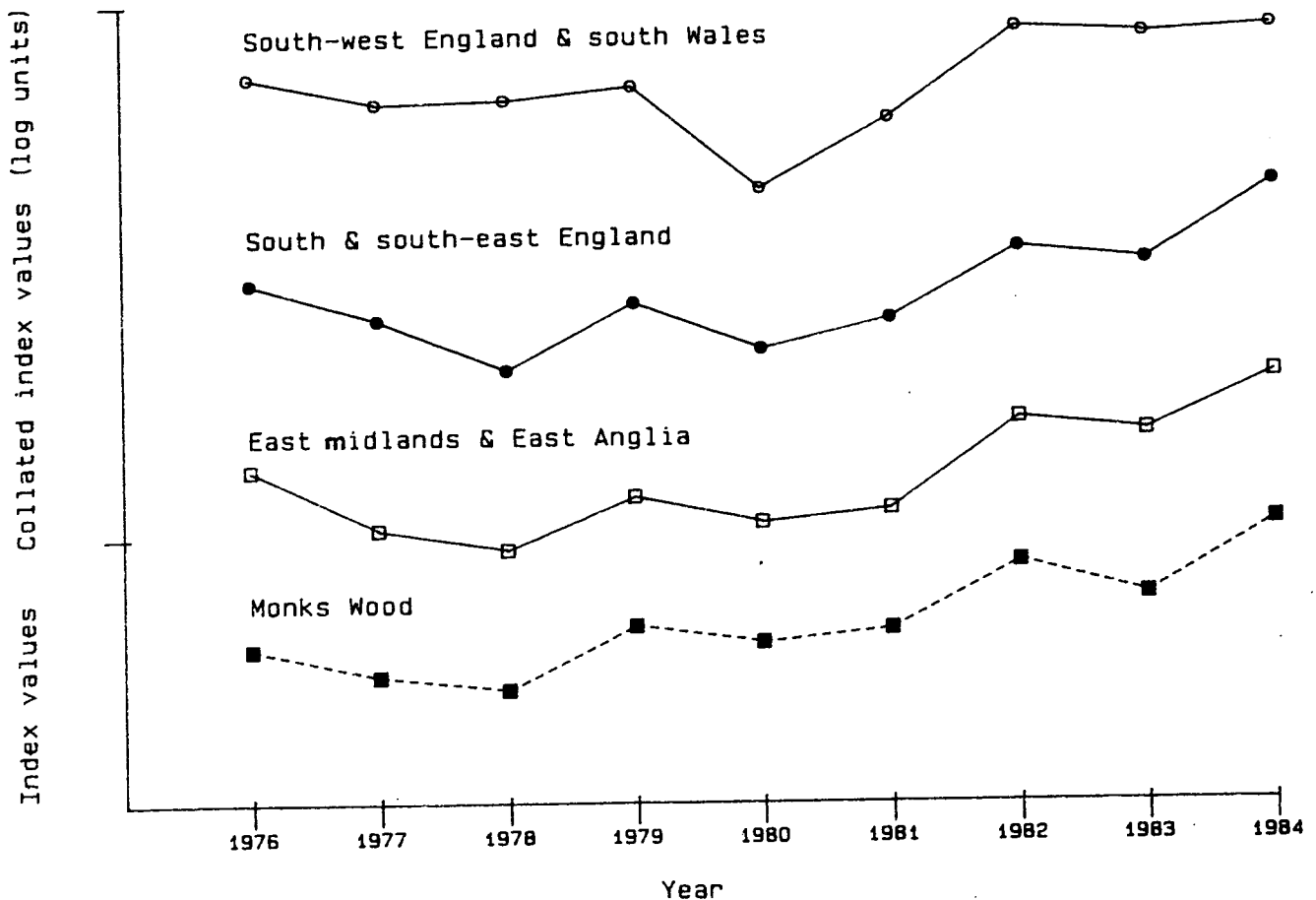


*Figure 28  Changes in abundance of the hedge brown butterfly in 3 areas of southern Britain and at Monks Wood NNR. Monks Wood data are also included in the east midlands and East Anglia collated index, but comprise <10% of the regional data*

not show such clear patterns. The results suggest that high temperatures during the previous autumn and current summer were associated with increased abundance, but high winter temperatures were associated with reduced abundance, although none of these equations individually gives a significant value for $R^2$ (% variability accounted for). Pooling the weather variables for groups of months and using the multiple regression 'build up' technique (Draper & Smith 1966) led to the model:

$$\log_{10} Y_i = -4 \cdot 94 + 0 \cdot 46 \log_{10} Y_{i-1} + 0 \cdot 17T_A + 0 \cdot 32T_S$$

where $T_A$ and $T_S$ are previous autumn and current summer mean monthly temperatures. The value of $R^2$ is 70% (significant at $P<0 \cdot 05$), and is not improved further by including winter temperatures in the regression model.

The approach provides no more than a guide to potentially important factors; in particular, given the shortness of the series of abundance data and the large number of choices available in selecting vari-

ables, the significance level attached to $R^2$ is of limited interest. However, the results are encouraging in that they make biological sense. Warm weather during the previous flight period may be expected to increase oviposition, and perhaps enhance survival of young larvae; cold winter has frequently been said to improve survival over winter; and warm weather during late larval and pupal stages is known to improve survival in the white admiral (*Ladoga camilla*) (Pollard 1979). It seems likely that, when many more species have been examined in the same way, patterns will emerge which add to our understanding of the impact of weather on butterflies.

*E Pollard and K H Lakhani*

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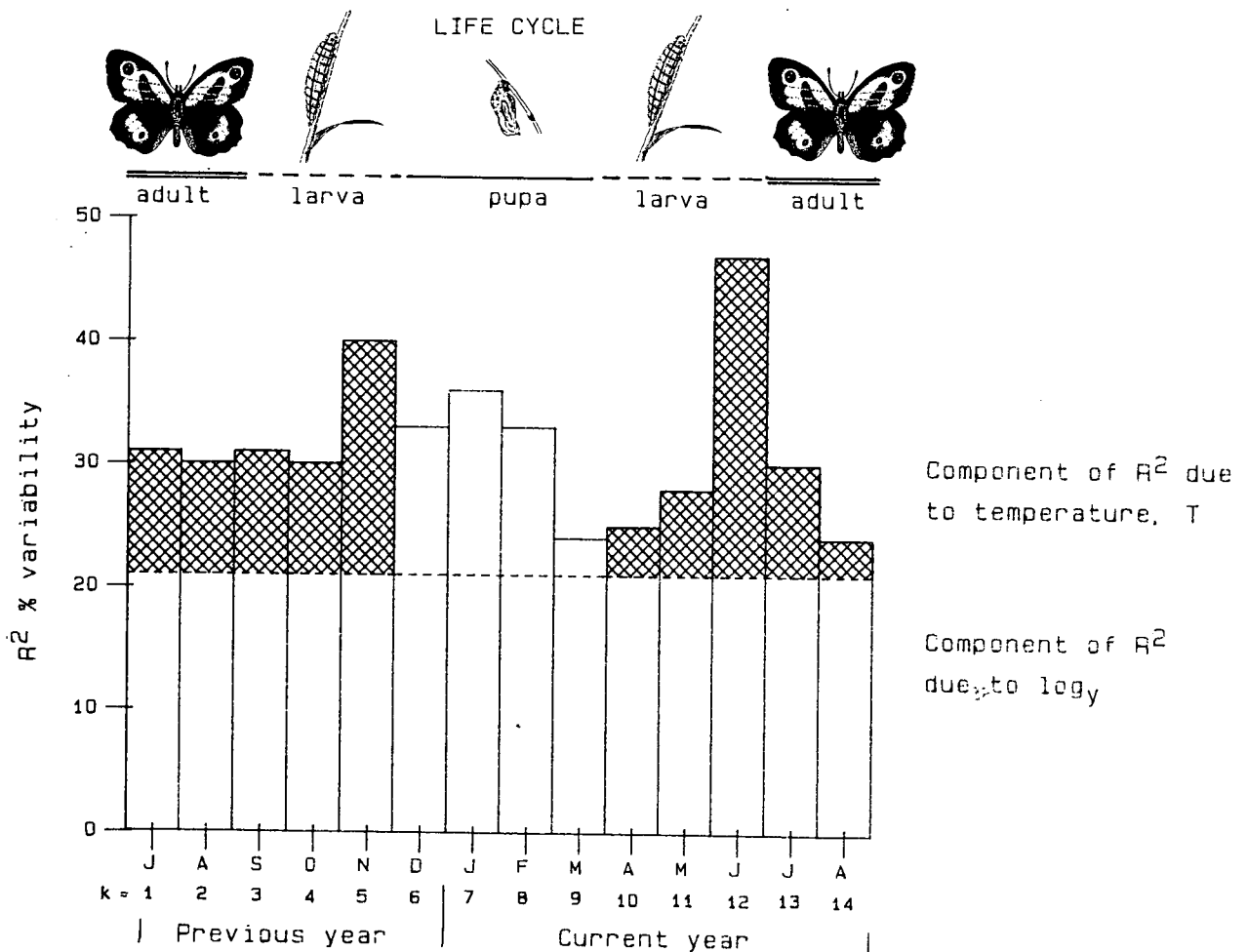
*Figure 29 Data for the hedge brown butterfly at Monks Wood (1973-84). Partitioning of $R^2$ (% variability accounted for) due to variation in the abundance in the previous generation and additionally due to the variation in the monthly mean temperature in each of 14 multiple regression equations, using the model:*

$$logY_i = \alpha + B_0\ logY_{i-1} + B_1\ T_{ki} + error\ (see\ text)$$

*Shaded areas show positive values of the coefficient of $T_{ki}$ (high temperatures associated with increased abundance); corresponding open areas show the negative coefficient of $T_{ki}$*

## Programme 6
## AIRBORNE POLLUTANTS, INCLUDING RADIONUCLIDES

### TREE HEALTH, THE DIRECT AND INDIRECT EFFECTS OF FLUORINE

Fluorine occurs naturally in some minerals, rocks and unweathered soils, but, despite concentrations ranging from 10-1000 $\mu g\ g^{-1}$, it is only released slowly in a soluble form that can be absorbed by plants (5-15 $\mu g$ fluorine $g^{-1}$ dry weight). Additionally, fluorine is emitted by a number of industrial processes as hydrofluoric acid (HF), a gas, or in particulate form combined with elements such as aluminium, sodium, calcium or silicon. While the brick and aluminium industries are the sources of fluoride ($F^-$) pollutants, they are emitted by other users of coal. For a number of years, members of ITE have been concerned in north Wales with the fate and effects of the gaseous and particulate fluorides emitted as a result of the electrolytic reduction of alumina, dissolved in sodium fluoride and aluminium fluoride. These emissions are directly deposited on to vegetation and soil (dry deposition) or carried from the atmosphere in rain (wet deposition) (Figure 30). The deposits on leaves which are not directly absorbed may be washed off and accumulated subsequently in soil, so adding to the amounts directly deposited on soil, whether by wet or dry deposition. Similarly, fluorides retained by leaves are ultimately transferred to soil as moribund foliage decomposes. The soil then acts as a natural 'sink' for airborne pollutants, but the contamination of some acid soils by pollutant fluorides is important because fluorides can be taken up by plants through their roots (Perkins *et al.* 1983). Thus, accumulations in soil depend upon leaf and root decomposition, in addition to rates of wet and dry deposition, these inputs being offset by the movement of fluorides through soil profiles. The amounts of fluoride available for plant uptake are additionally dependent upon soil chemistry, which fluoride, itself, may influence.

### Effects of fluoride emission on trees
Fluorides can be phytotoxic, adversely affecting many metabolic processes, with consequent effects on plant growth and production (Chang 1975). Guderian (1977) and Smith (1981) have reported damage to several species of coniferous and broadleaved trees growing near emission sources. In the present investigation, sycamores (*Acer pseudoplatanus*) near the aluminium works in north Wales developed marginal leaf necroses, dieback of shoots and premature defoliation. In severe instances, trees became stagheaded and died. Photographs taken on the ground and from the air (using infra-red (false colour) film) showed that damage was greatest downwind and on foliage facing the works; it decreased with increasing distance to form a gradient of effect from the works

outwards. In the area within 1 km of the works, there were sites where damage was greater, or less, than expected if distance was the only variable. To examine the inter-relationships of damage with (i) accumulations of emissions, (ii) edaphic factors and (iii) wind direction, observations were subjected to reciprocal averaging ordination (Hill 1973). These observations included assessments of damage derived from infra-red film, concentrations of fluoride, aluminium, calcium and phosphorus in leaves and 1:5 soil/water extracts, and the acidity of soil. The first axis of ordination arranged the sites in relation to changes in concentrations of fluoride and aluminium with distance from the works—the main environmental gradient.

### Foliar accumulations of fluorides
Total fluoride accumulations in sycamore leaves were negatively correlated with distance from the aluminium works ($r = 0.85$). To examine the inter-relationships with damage, accumulations were plotted against axis 1 of the ordination (Figure 31). Damage was most severe where foliar concentrations of fluorides were large. When leaves with 1000-2000 $\mu g$ $F^-\ g^{-1}$ of dry tissue were washed, it was found that 60% was retained; where leaves had 250 $\mu g\ g^{-1}$, 80% remained after washing. It is likely that the retained fluoride was accumulated as a result of direct foliar absorption and root uptake.

### Soil accumulations of fluoride
Fluoride has accumulated in soil in the vicinity of the aluminium works. While most is found near the surface, decreasing amounts have accumulated to a depth of at least 30 cm (Perkins *et al.* 1979). Additionally, much of the fluoride is water-soluble, and most of that accumulated since emissions commenced can be removed by successive water extractions (Perkins *et al.* 1983). Concentrations of water-soluble fluoride (1:5 soil/water mixture) were largest nearest the aluminium works, where most injury was recorded (Figure 32).

### Effects of fluorides on soils
Accumulations of fluorides in soils can result in:

i. a source of fluoride which, if in a water-soluble form, may be taken up by trees in possibly damaging concentrations, and
ii. change in soil chemistry causing the release of chemically bound and exchangeable forms of other elements, including aluminium.

The solubility of fluoride is associated with calcium, which is itself closely linked to soil acidity. In considering the effects of fluorides, both soil calcium and acidity must be considered. In laboratory experiments using plants grown in culture solutions, the inhibiting effects of fluoride were exacerbated by (i) low concentrations of calcium and (ii) greater acidity, these effects being most marked when the concentration ratio Ca/F was <2.
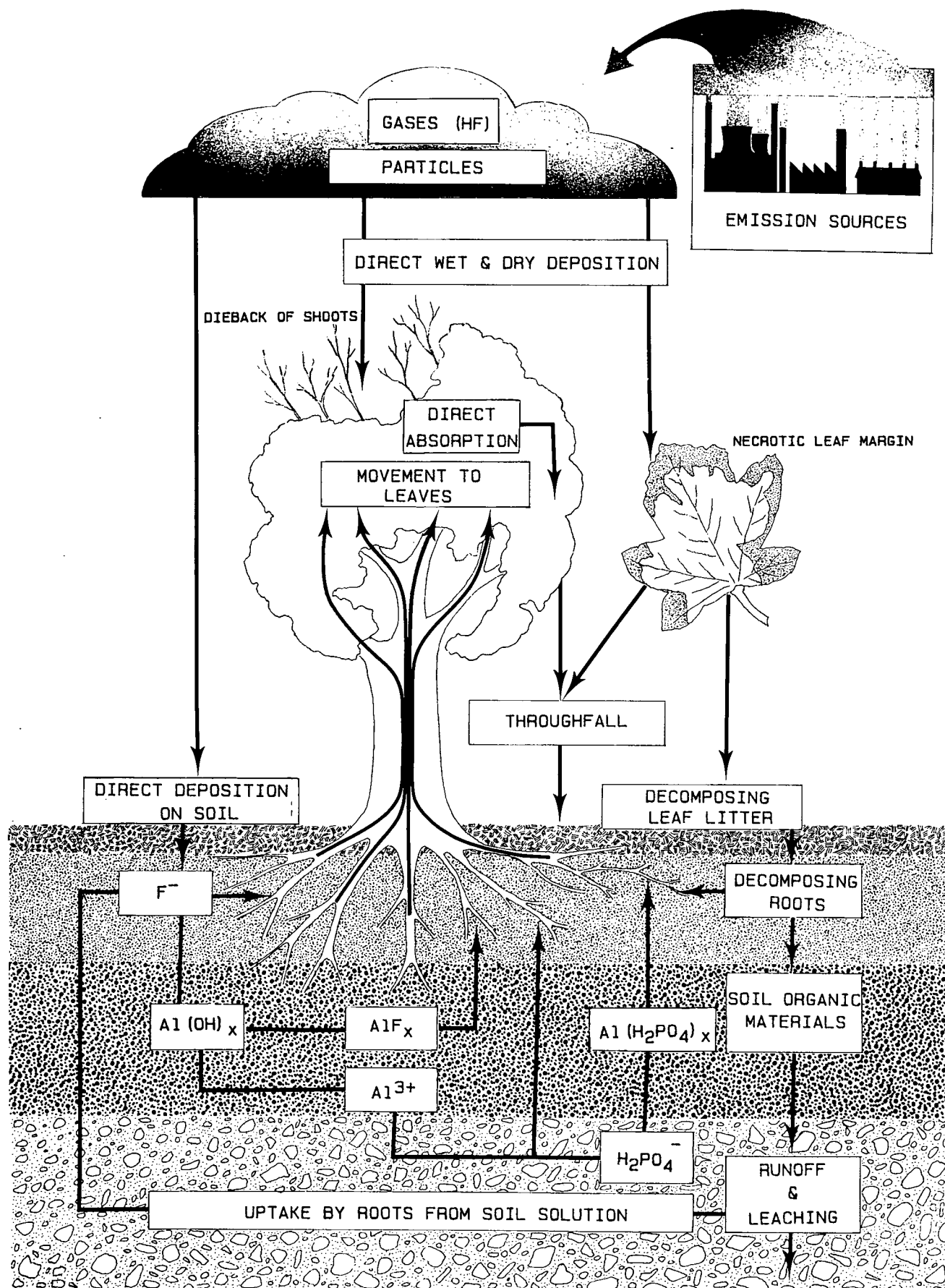
*Figure 30  The pathway and some of the processes involved in the direct and indirect effects of pollutant fluorides on trees*
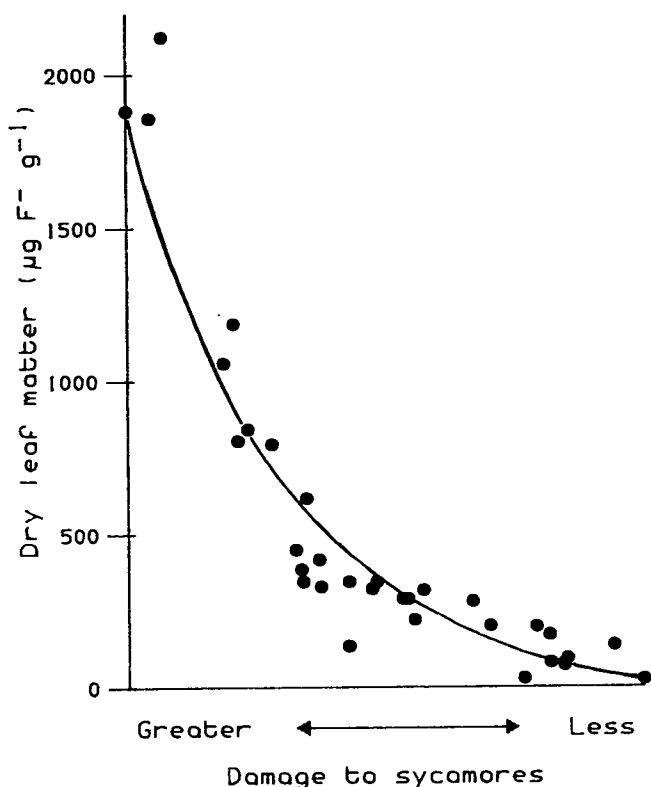
*Figure 31 Accumulations of fluoride (F⁻) in, and on, leaves of sycamores (growing at different distances and directions from an aluminium works) plotted against amounts of damage (the first axis of a reciprocal averaging ordination)*
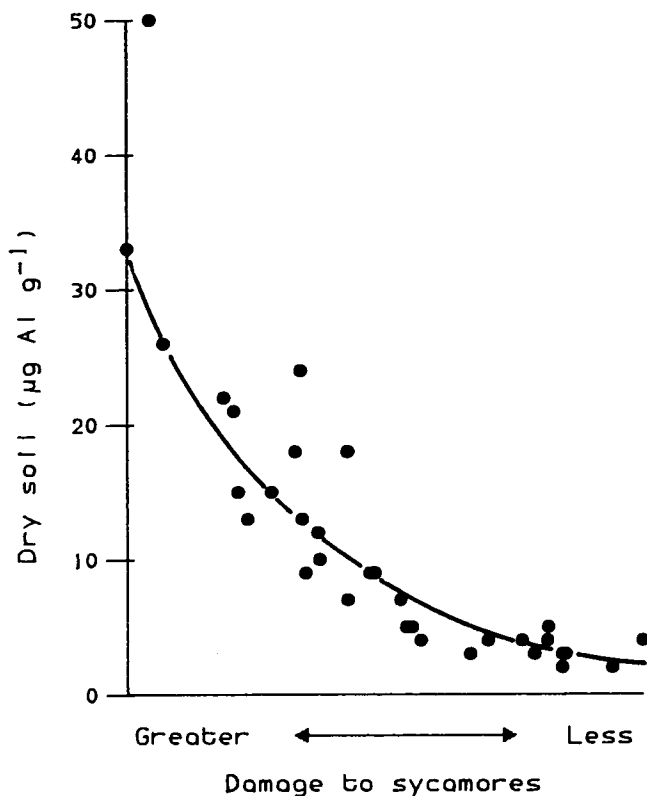


*Figure 33 Water-soluble aluminium in soils (1:5 soil/water extracts) from sites at different distances and directions from an aluminium works, plotted against the damage recorded on sycamores at the different sites (the first axis of a reciprocal averaging ordination)*

Additions of fluoride to soils increase the solubility of aluminium even at pHs at which it is normally mostly insoluble. Usually, alumino-hydroxides $(Al(OH)_x)$ are the predominant forms of aluminium. In the presence of fluoride, however, alumino-fluoride complexes of the form $AlF_x$ prevail. Soils at the experimental location contained large concentrations of water-extractable fluoride (up to 70 $\mu g\ g^{-1}$ dry soil), and aluminium (up to 50 $\mu g\ g^{-1}$), whereas similar but remote and uncontaminated soils contained between 0·6-8·0 $\mu g\ g^{-1}$ fluoride and 1-12 $\mu g\ g^{-1}$ aluminium. Amounts of sycamore damage were inversely associated with soil concentrations of water-soluble aluminium (Figure 33). Aluminium is regarded as being toxic to some plants, its toxicity being related to the combination of effects, the most obvious of which are inhibition of root growth, and decreased phosphorus uptake (Foy & Brown 1963, 1964). The concentration ratio, P/Al, is a useful indicator of likely inhibitory concentrations, ratios <2 being found to be detrimental to growth. Evidence for the toxic effect of aluminium ions on trees has also been put forward by Ulrich et al. (1980).



*Figure 32 Water-soluble fluoride in soils (1:5 soil/water extracts) at different distances and directions from an aluminium works, plotted against the damage recorded on sycamores at the different sites (the first axis of a reciprocal averaging ordination)*

When aluminium in soil is released, it forms alumino-complexes with fluoride and phosphate ions. Alumino-fluoride and alumino-phosphate complexes can both be absorbed by plant roots. When the former are absorbed, damage may not ensue, although fluoride

*Table 13.* The severity of 'fluoride' damage done to groups of sycamores at different distances from an aluminium works where soil pH and ratios of Ca/F and P/Al were markedly different

| Sycamore sites | Index of damage† | Mean distance of trees from aluminium works (m) | pH | Soil Ca/F | P/Al | (Ca + P)/ (F + Al) |
|---|---|---|---|---|---|---|
| A | 100 | 245 | 6·0 | 1·2 | 0·3 | 0·8 |
| B | 87 | 543 | 4·9 | 1·2 | 0·4 | 0·9 |
| C | 83 | 490 | 5·4 | 1·5 | 0·4 | 1·0 |
| D | 59 | 607 | 6·1 | 1·7 | 0·7 | 1·3 |
| E | 49 | 812 | 5·5 | 5·0 | 1·9 ' | 3·4 |
| F | 21 | 826 | 5·2 | 14·6 | 0·9 | 5·1 |
| G | 5 | 906 | 5·8 | 16·8 | 3·0 | 7·4 |

† Damage at sites in group A taken as 100%

($F^-$) and aluminium ($Al^{3+}$) ions might be damaging individually. Similarly, alumino-phosphate complexes can be absorbed by plant roots, but, although the total phosphorus taken may be increased, plants may be phosphate-deficient as they seem unable to utilize the phosphate complexes (Randall & Vose 1963).

In summary, changes in the chemistry of soil following additions of fluoride are complex, with the resultant chemical equilibrium dependent upon many factors, including the amounts of fluoride deposited, calcium and phosphate concentrations, and acidity of soil.

*Effects of fluoride and aluminium on sycamores*
While atmospheric fluorides are known to be phytotoxic, little attention has been given to their fates in, and effects on, soils. Near the aluminium works, trees were exposed simultaneously to aerial pollutants and changes in soil chemistry. Some indication of the relative importance of these direct and indirect influences was obtained from the 'ordinated' series of observations. Sycamore injury can be related, directly, to a gradient of leaf fluoride concentrations (Figure 31), accumulations of water-soluble fluoride and aluminium in soil (Figures 32 and 33), and also to soil acidity. Trees in site groups A, B and C, the groups closest to the aluminium works (245-543 m), were the most damaged, with damage indices of 100, 87 and 83 respectively; the least damaged group (G) was 906 m from the works (Table 13). The concentration ratios Ca/F and P/Al are closely and inversely related to the indices of damage, small ratios being associated with large amounts of damage, and *vice versa.* In glasshouse experiments with solution cultures, it has been possible to confirm that injury is greater when Ca/F and P/Al ratios are both low than when only one ratio is small. The ratio (Ca + P)/(F + Al) seems to be a good predictor of potential damage.

*Conclusions*
Accumulations of fluoride in the poorly buffered, acidic soils examined have had marked effects on the chemistry of the soil in which the sycamore trees were growing. It is likely that the damage sustained is due to a combination of both aerial deposition and soil-borne effects. The accumulations of fluorides occurred rapid-

ly, and the subsequent release of aluminium ions must be considered to be a factor causing the damage. Most of the fine roots of trees occur near the soil surface; they are the most likely to have been affected by changes in the ratios of Ca/F and P/Al. In the field, there is a rapid turnover of the biomass of fine roots, a large proportion of which need to be replaced annually. Laboratory experiments have indicated that root production is severely inhibited. Inhibition of root (i) production and (ii) replacement could lead to a considerable disruption of the uptake capability of both water and nutrients, and be the cause, indirectly, of much of the observed damage.

D F Perkins

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## PRODUCTION OF OXIDES OF NITROGEN DURING STRAWBURNING

The burning of cereal stubble and straw by farmers following harvest, practised throughout the UK for many years, has recently attracted considerable criticism. The concern arises largely from the quantities of black smoke and associated particulate material released (Bailey *et al*. 1983), and also because of damage to hedgerows and trees when inadequate safety precautions have been taken.

Large changes have taken place during the last 2 decades in the supply of, and demand for, straw. The ratios of straw to grain have increased slightly with the introduction of new cereal varieties: increases in grain yield from $7.7 \times 10^6$ tonnes in 1961 to $19.5 \times 10^6$ tonnes in 1981 have been matched by increases in straw to about $20 \times 10^6$ tonnes per year. On the demand side, the decreased numbers of livestock in the main cereal growing areas of eastern England have resulted in a decreased demand for straw for bedding. The increased adoption of 'minimum cultivation' techniques and the more widespread sowing of winter cereals have also both contributed to the increased practice of straw burning. Although not adequately documented, the total quantities of straw burnt which

vary between regions have been established (Bailey *et al*. 1983). In the main cereal growing districts of eastern England, about 70% of wheat straw and 60% of barley straw are burnt. The percentage becomes progressively smaller and is less accurately estimated with distance north and west—it is assumed that half of all the cereal straw in the UK is burnt, amounting to about $10^7$ tonnes annually.

Interest in the production of the oxides of nitrogen, NO and $NO_2$ (collectively known as $NO_x$), from straw burning is part of a larger interest in the sources and sinks for nitrogen oxides in the atmosphere. This concern has grown recently as it has been found that air concentrations of $NO_2$ are similar to those of $SO_2$ (Martin & Barber 1984; Fowler & Cape 1982). However, as industrial and vehicle emissions of $NO_x$ are only 40% of those of $SO_2$ (HMSO 1983), is it conceivable that the average residence times of oxides of nitrogen in the atmosphere are longer than those of $SO_2$, or are the estimates of $NO_x$ emissions too small?

The release of NO and $NO_2$ from strawburning was measured in a barley field after harvesting and baling the straw. From counts of numbers of bales and weights of 20 bales, it was possible to estimate the
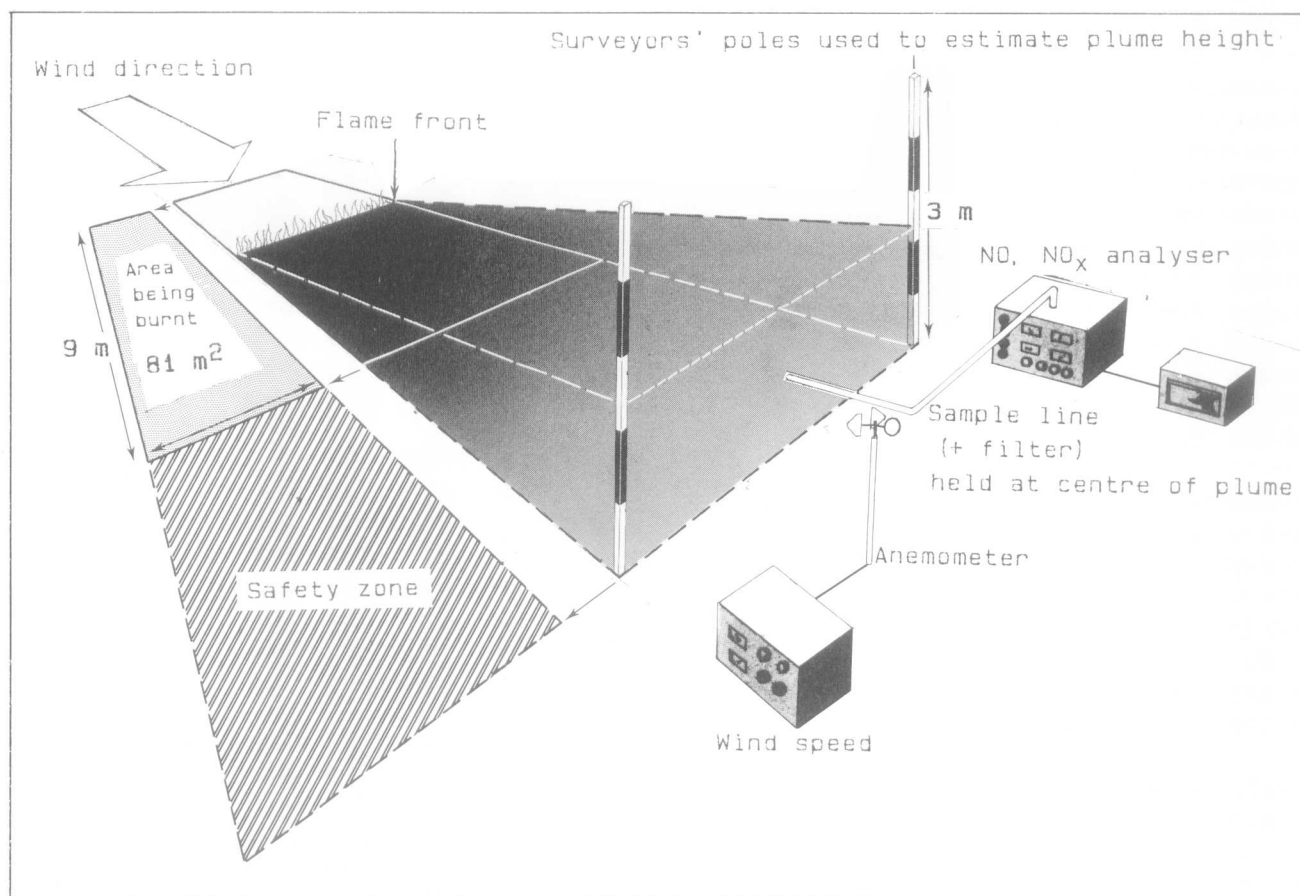


*Figure 34    Experimental layout for the measurement of oxides of nitrogen (NO_x) released during strawburning. Plots of different sizes with different amounts of straw were tested*

*Table 14.* Typical results of $NO_x$ release during strawburning (see Figure 34 for other site details)

| Date of burning | Amounts of straw burnt (kg) | Plume width (m) | Wind speed (m s$^{-1}$) | Total emissions (g) of NO | NO$_2$ | Specific emission of nitrogen oxides (g N kg$^{-1}$ straw) |
|---|---|---|---|---|---|---|
| 23.8.84 | 17·7 | 9 | 2·45 | 13·5 | 3·4 | 0·50 |
| 23.8.84 | 16·3 | 9 | 3·25 | 18·3 | 5·6 | 0·63 |
| 23.8.84 | 19·6 | 9 | 3·05 | 18·1 | 9·1 | 0·57 |
| 23.8.84 | 16·9 | 9 | 22·50 | 14·1 | 11·7 | 0·60 |
| 28.8.84 | 18·1 | 7 | 3·45 | 14·6 | 6·6 | 0·49 |
| 28.8.84 | 18·4 | 6·5 | 4·25 | 16·2 | 3·7 | 0·47 |
| 28.8.84 | 16·2 | 7·7 | 4·6 | 15·3 | 2·2 | 0·48 |
| $\bar{x}$ | | | 3·36 | | | 0·53 ±0·06 |

yield of straw per unit of land area. The straw was then redistributed at the 'harvest' density, and burnt; the experiments tested a range of wind speeds (1-6 m s$^{-1}$), plot sizes (20-100 m$^2$) and amounts of straw (5-40 kg). Instruments were placed downwind of the fire to measure wind velocity and air concentrations of NO and $NO_2$ in the plume (Figure 34). Estimates of plume height were made visually using surveyors' poles; plumes were assumed to be as wide as the experimental plots. Knowledge of the cross-sectional areas of the plumes, wind speeds, and duration of burn enabled the total yields of NO and $NO_2$ to be estimated.

Typically, the specific emission of nitrogen varied between 0·48 g and 0·63 g kg$^{-1}$ straw. In the experiments detailed in Table 14, the quantities of straw burnt were more or less equivalent to the density at harvest: in other experiments, with amounts of straw varying by factors of ± 40% of field density, there was no clearly defined relation with the specific release of nitrogen. Accepting a release of 0·5 g N kg$^{-1}$ straw, the yield of $NO_2$ from $10^7$ tonnes of straw burnt annually is 1·6 ×10$^4$ tonnes, that is about 1% of the $NO_x$ released from industries and vehicles in the UK (HMSO 1983).

This pilot study shows that the annual releases of $NO_x$ from strawburning are minor. However, they are of much greater significance during the 6-8 weeks of the year in which straw is burnt, when straw emissions may be 10% of the national emission total. Very locally, strawburning may lead to concentrations of the phytotoxic pollutant $NO_2$ reaching 200-300 ppbv, as in the plumes of straw fires.

*D N Fowler, S Mullock, I D Leith, J N Cape and M H Unsworth*

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## LAND USE AND THE DISTRIBUTION OF RADIO-NUCLIDES IN CUMBRIA

(This work is supported by Department of Environment funds)

A study has been started in west Cumbria to investigate the manner in which land use and agricultural practices affect the movement and distribution of radioactive substances. In so doing, it should enable better estimates to be calculated of the radioactivity to which inhabitants are exposed.

Within geographically defined areas, there will be inputs and losses of radioactivity as a result of natural processes, such as river run-off and the movement of agricultural products. At the same time, much of the radioactive material will be recycled and redistributed. As a result, concentrations of radionuclides can be either lessened or increased, in different parts, compartments, of the 'system'.

To assess the situation, it was decided to take advantage of sites in the vicinity of the Sellafield reprocessing plant where there is local concern about (i) possible accidental releases of radionuclides into the atmosphere, and (ii) the slightly enhanced concentrations of radioactivity occurring along the Cumbrian coast. The project is being focused on [137]Caesium and some of the isotopes of plutonium, notably [238]Pu and [239/240]Pu, and soil and vegetation are being analysed.

Because annual agricultural records are available from parishes in west Cumbria, the parish was chosen as the unit for an initial survey, 9 parishes near the Sellafield plant, extending from the Irish Sea coast to the watershed of the lakeland fells, being included. During 1984, a field-by-field ground survey was made of agricultural crops and natural vegetation which were categorized into 17 land use types.

The survey area is dominated by forms of grassland management for dairy produce, the production of meat and the exchange of live animals. Hay, silage, barley and root crops are grown for animal feed during winter, while the main arable crop, potatoes, is grown for human consumption. The fate of these products will be examined during the study in order to establish whether they remain within the study area or are exported elsewhere. For instance, how extensive is the movement of lambs from the area for fattening elsewhere?

Samples for radionuclide analysis are being collected at 15 locations, each 1 km², along 3 parallel transects, each 1 km wide (Figure 35). It is hoped to obtain 3

replicate samples of vegetation and soil for each land use type within each 1 km². Already there is evidence, as expected, that radionuclide concentrations are largest near the coast, falling off exponentially to landward.

The success of an exercise of this sort depends on the willingness of occupiers of land to provide information about management practices, and to allow samples to be collected. ITE acknowledges the co-operation of 50 farmers.
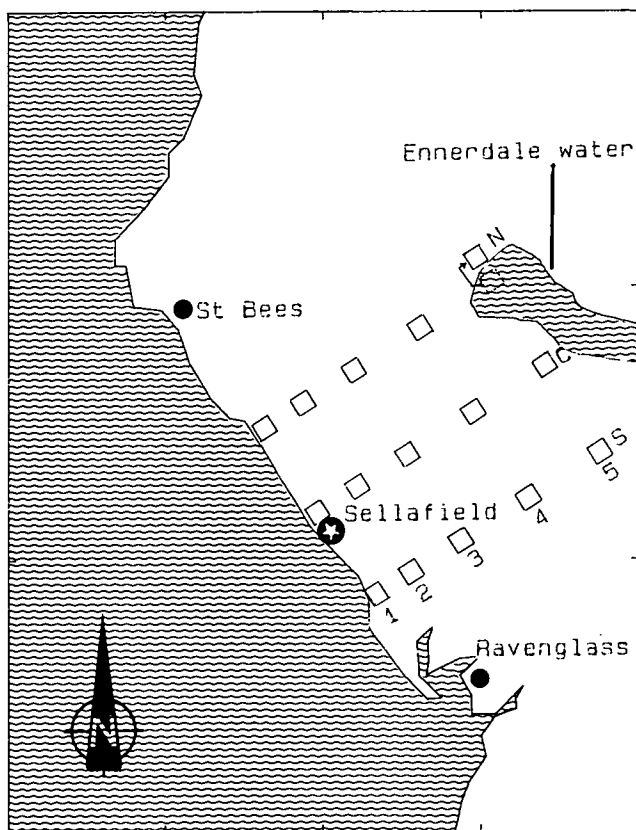
*A D Horrill, Brenda J Howard and N Beresford*



*Figure 35   Location of 15 1 km squares spaced along 3 transects in west Cumbria. Three replicate samples of each vegetation type and its associated soil are collected from each square*

## THE STATUS OF FISH IN SCOTTISH LOCHS VULNERABLE TO ACIDIFICATION

Although the topic has been discussed since the 1920s, it is only during the last 15 years or so that ecologists in the northern hemisphere have become increasingly concerned about the impact of acidic deposition on freshwater ecosystems. In Scandinavia (especially Sweden and Norway) and later in North America (both in Canada and the USA), numerous scientific studies have been initiated. Many other countries have recently contributed to the massive growth in the work on acid precipitation, but the input in Great Britain in the field of freshwater ecology has been relatively small.

Historically, one of the earliest and most important indicators of the acidification of fresh waters has been the disappearance of many formerly abundant species of fish—especially the salmonids (salmon, trout and char)—from rivers and lakes. For example, salmon have disappeared from many rivers in southern Scandinavia, and the number of lakes in those areas whose trout and char populations have completely disappeared has increased, especially over the last 15 years. Massive kills of salmon and trout have been observed during snowmelt and after heavy rain.

In October 1983, the Institute initiated a programme of research aimed at determining the status of fish populations in those Scottish lochs most likely to have been affected by acid deposition. This topic, although frequently referred to at meetings and in the press, is still one about which very little information is available. Many of the waters concerned, including some lochs in the Galloway area, have been examined in the past by the Institute, for other reasons.
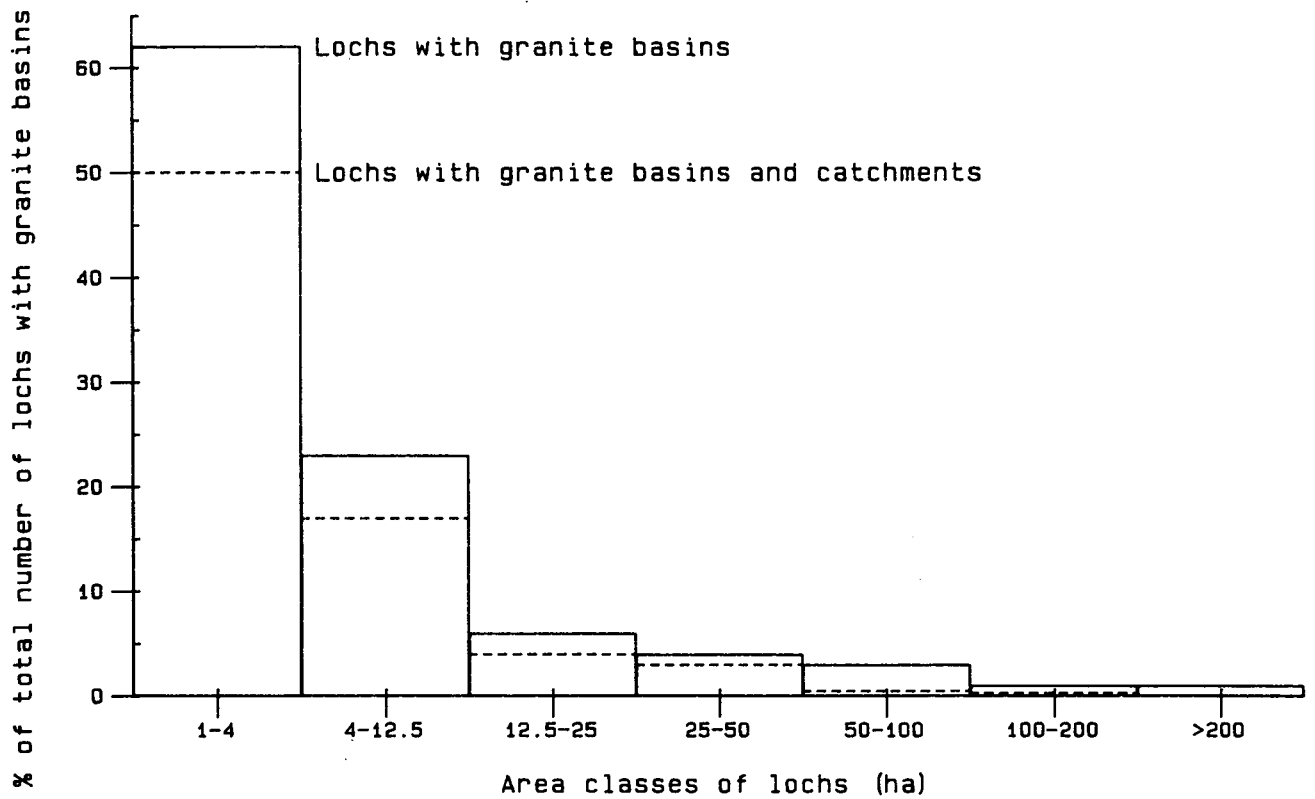
Figure 36  The size distribution (by area classes) of 2 types of loch in Scotland
  i.  those with granite basins and granite catchments
  ii.  those with granite basins but with catchments draining from other types of bedrock
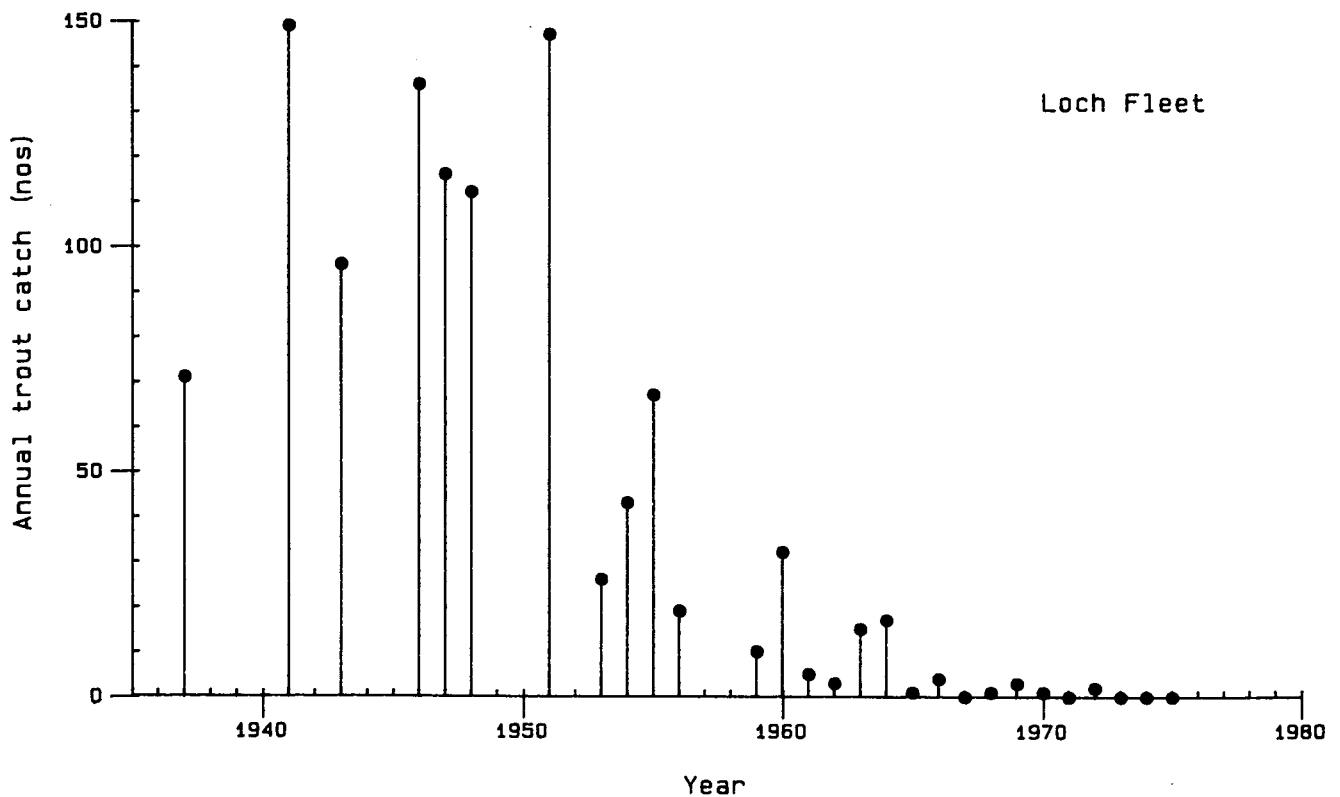


Figure 37  Annual catches of trout from Loch Fleet in Galloway (data by courtesy of Mrs Murray-Usher). Gill netting in the loch, and electro-fishing in inflow and outflow streams indicate that trout are no longer present in this system

The present project covers the whole of Scotland and deals primarily with lochs, although the outflows and major inflows have also been sampled at all sites investigated, because of their importance as nursery areas for salmonids. Attention has been centred on lochs whose basins and catchments lie on granite bedrock because much of the current evidence suggests that these are likely to be the most vulnerable. From a comprehensive study of 1:50 000 OS maps, many hundreds of potentially vulnerable lochs, of different sizes, were identified and enumerated (Figure 36). Lochs with granite basins but with other types (non-granite) of catchments were not included in the main series.

By modifying Anderson's (1939) block nomenclature system, it has been possible to devise a method for identifying the granite regions within the 5 major geological areas of Scotland. This information was transferred to OS 1:50 000 topographical maps, thus making it possible to identify and code each granite block individually within 5 regions of Scotland (northwest highlands, northern highlands, Grampian highlands, midland valley and southern uplands). Subsequently, the lochs and catchments within each granite block were counted and analysed.

From the main list of lochs, 120 have been identified as suitable for field study, but, in addition to these, 30 'control' lochs (whose catchments lie on rocks which are more base-rich than granite) have been included. The geographic position of these lochs is, of course, predetermined by the presence of granite. However, where possible, sites have been chosen which reflect the range of atmospheric acid inputs occurring in Scotland (Barrett et al. 1983). It is intended to investigate as many as possible of these 150 lochs during the next 2-3 years. During 1984, 32 lochs were sampled: fish in the lochs and associated streams have been assessed, observations of invertebrate benthos have been made, water samples are being analysed chemically and, in order to calculate water budgets, the bathymetry of the lochs (many of them previously unsurveyed) is being investigated by echo-sounding. The present-day records of fish are being augmented by historical information from the literature, estate records and individual anglers. Although this information varies in quality and quantity, there are certainly adequate data for some waters, including the general background information available from the Institute's own scheme (ITE project 124), which has been operating since 1966 (Maitland 1969). A detailed desk study of the catchment of each loch surveyed is also being undertaken in order to interpret chemical variation among the lochs.

The results to date have verified that many formerly important trout lochs in Galloway, eg Loch Fleet (Figure 37, Plate 24), now have pHs well below 5·0 and are fishless. Other lochs in this area have also become more acidic (eg Loch Grannoch) and trout stocks, though still present, are very much reduced. Most of the data are still being analysed, but the results from other parts of Scotland suggest that changes there have been less dramatic.

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## Programme 7
## PLANT PHYSIOLOGY AND GENETICS

### PROBABILITY OF FROST DAMAGE ON SITKA SPRUCE

Many of the fast-growing, non-indigenous forest trees grown in Britain are susceptible to frost damage, particularly when they are small (mainly because the coldest air occurs near the ground on calm nights). However, our knowledge of the probability of particular species and provenances being damaged by frosts has been obtained largely by trial and error — by planting different trees in different locations and years. A more rational approach is (i) to model the seasonal changes in frost hardiness or phenology of trees as functions of climatic variables, and (ii) to apply the models to past meteorological records at a range of sites, thereby estimating the long-term return times of potentially damaging frosts. Sitka spruce (*Picea sitchensis*) is susceptible to spring and autumn frost damage in Britain. The purpose of this research has been (i) to quantify the problem, (ii) to determine the potential for avoiding frost damage by genetic selection, and (iii) to predict the effects of future climatic change (this aspect will be reported later).

*Seasonal changes in frost hardiness*
Programmable freezing chambers, and experimental methods, were developed to enable the frost hardiness of detached tree shoots to be determined experimentally by subjecting them to simulated night frosts (Cannell & Sheppard 1982). The symptoms of frost damage, observed after 2 weeks on a mist propagation bench, were shown to resemble closely those observed in the field (Redfern & Cannell 1982).

The natural levels of frost hardiness of shoots of 4 provenances of Sitka spruce were monitored over 2 growing seasons (Figure 38). Six seasonal phases of
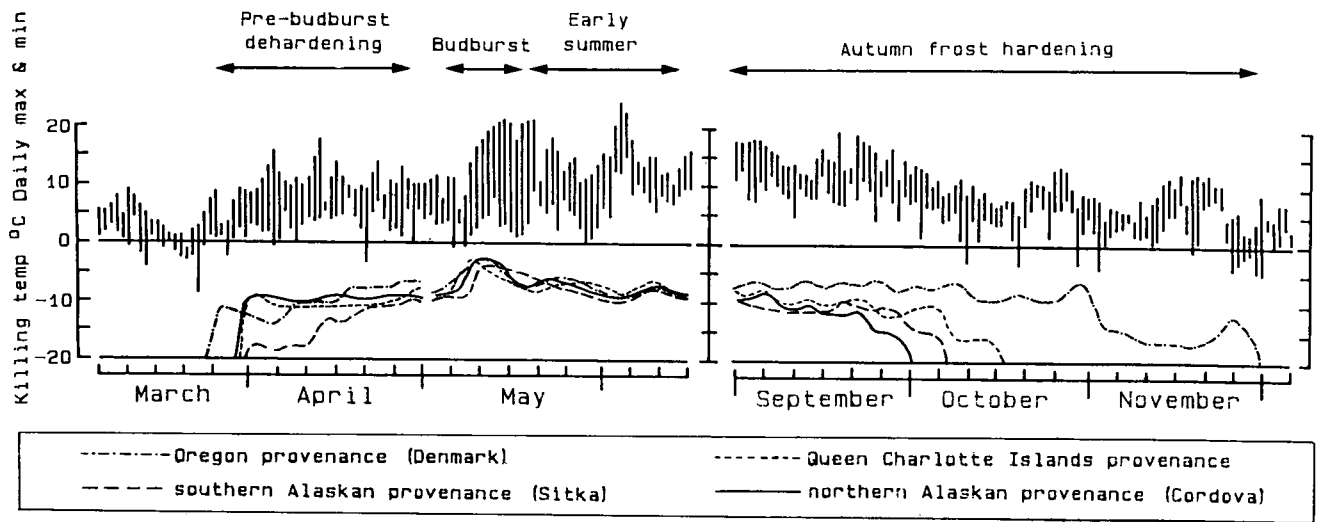
Figure 38    Seasonal changes during 1980 in the frost hardiness of shoots of Sitka spruce trees, 7-10 years old, growing at Bush Estate, near Edinburgh, determined using laboratory freezing tests. The killing temperature is the temperature at which half the seeds are killed: it was determined by fitting a line through 164 points per provenance (Cannell & Sheppard 1982)

frost hardiness were identified: (i) a period of autumn hardening, from September to November, when northern provenances hardened more rapidly than southern provenances; (ii) a winter period, when all provenances were hardy to below −20°C; (iii) a period of dehardening of the previous year's shoots in March-April, prior to budburst; (iv) the period of budburst, when the newly emerging shoots of all provenances were very susceptible to frost damage; (v) an early summer period, May-July, when the elongating shoots were moderately hardy, to between −5°C and −10°C; and (vi) occasionally, a period of later summer dehardening, usually in August (not shown in Figure 38).

Forest records show that frost damage has occurred mainly either at the time of budburst, or during the period of autumn hardening. Models were therefore constructed to estimate the frequency with which temperatures have fallen below predicted levels of frost hardiness at those times.

*Probability of frost damage at the time of budburst* Although trees within Sitka spruce provenances have different times of budburst, the average date of budburst for provenances from Oregon to southern Alaska is about the same in any year when they are grown together in Britain. Furthermore, the newly emerging shoots of all trees of all provenances are equally susceptible to frost damage. Consequently, the model needed to estimate the frequency of frost damage at budburst was not a model to predict frost hardiness, but instead a model to predict dates of budburst.

Using 14 records and observations of the dates of budburst on young trees of Sitka spruce growing near meteorological stations, it was possible to quantify the 'thermal time' (in day degrees >5°C) required to
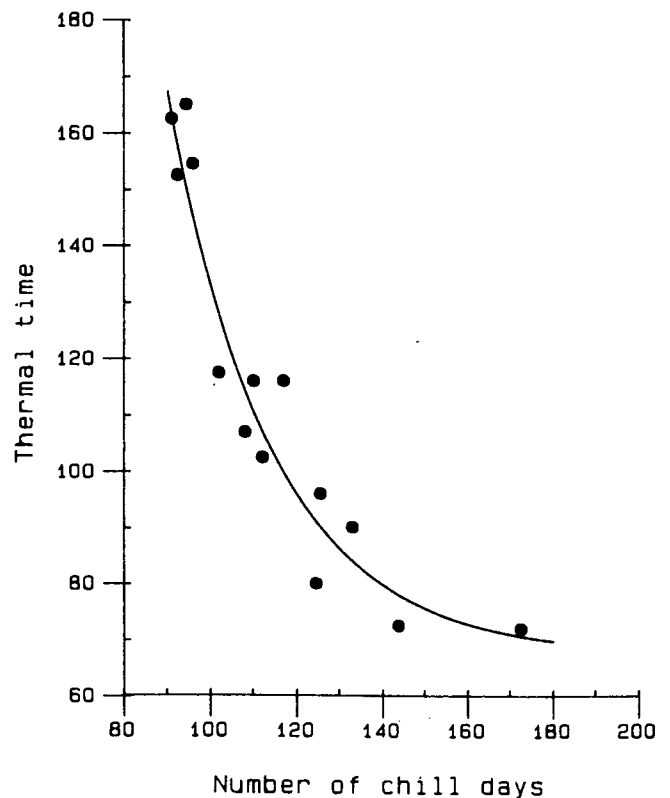


Figure 39    Model used to predict the date of budburst on the lateral shoots of young Sitka spruce in Britain. Each point represents a recorded date of budburst in Britain (at different sites, between 1960 and 1980). Thermal time is represented in day degrees >5°C from 1 February to the date of budburst. Number of chill days are those ≤5°C from 1 November to date of budburst
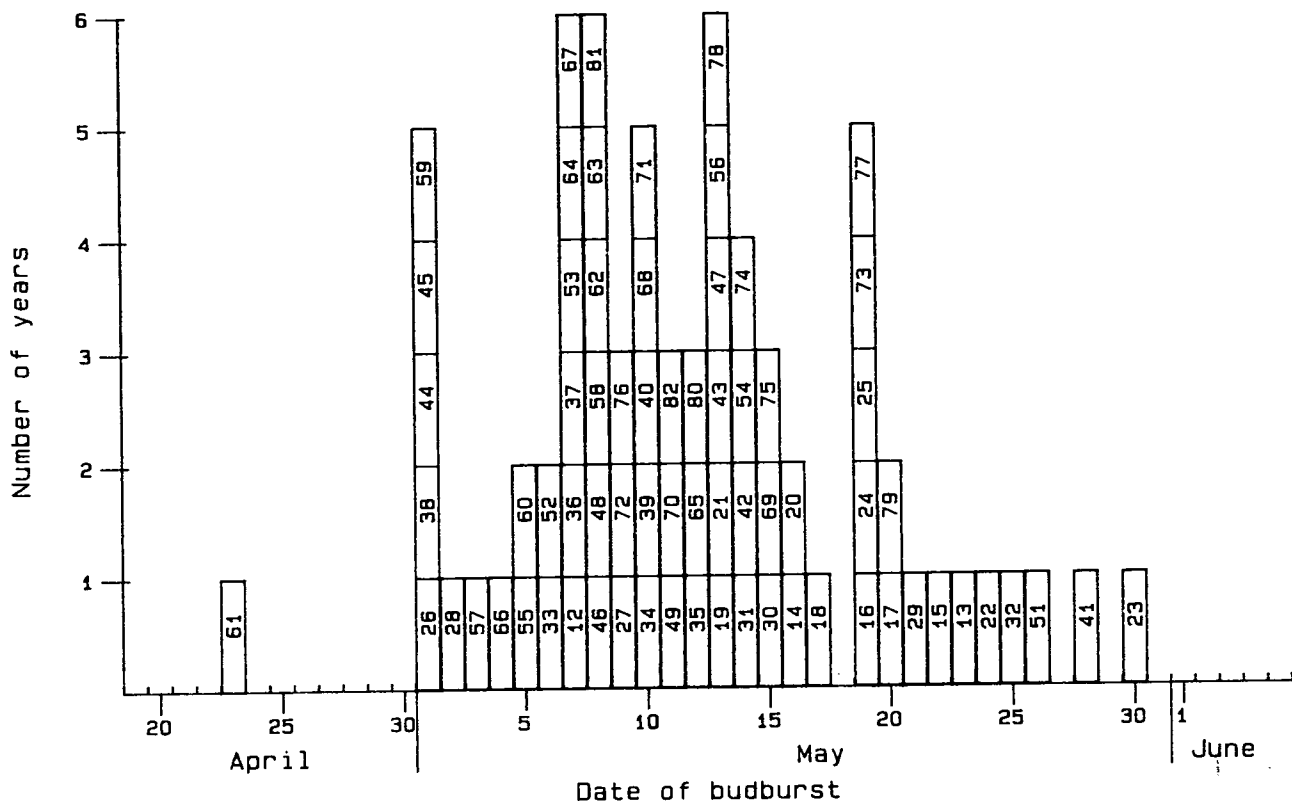
*Figure 40   Dates of budburst on young Sitka spruce at Eskdalemuir from 1898 to 1967, predicted using the model shown in Figure 39. The numbers refer to years, eg 61 = 1961*
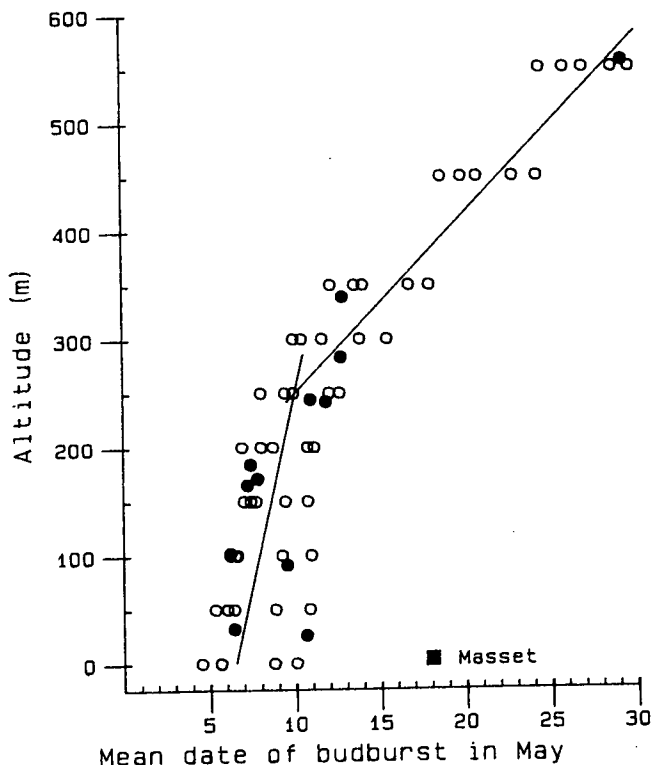


*Figure 41   Relationship between altitude and the mean predicted date of budburst on young Sitka spruce in northern Britain, and at Masset on the Queen Charlotte Islands*

● = *means based on actual temperatures at 12 sites,*

○ = *means based on lapse rates of 0·75°C and 0·55°C per 100 m altitude for daily maximum and minimum temperatures, respectively (Cannell & Smith 1984)*

induce budburst with different amounts of winter chilling. Different methods of calculating thermal time and chill units were tested; the following provided the best fitting model, accounting for 92% of the variation:

$$T = 67·4 + 4401·8 \ \exp(-0·042C)$$

where T is the day degrees >5°C from 1 February to the date of budburst, and C is the number of days ≤5°C counted from the previous 1 November (Figure 39). The assumptions of this model were examined experimentally, and with reference to the literature (Cannell & Smith 1983). The model suggested that the chilling 'requirement' of Sitka spruce is often not fully met in Britain.

Using this model, the dates of budburst of Sitka spruce were 'predicted' for the past 18 to 107 years at 12 sites in northern Britain, including all the upland sites with long meteorological records. The predicted dates of budburst varied between late April and early June, in different years, and were shown to be normally distributed (Figure 40). The effects of altitude on predicted dates of budburst were explored (for 66 to 107 years) with data for 5 meteorological stations, assuming a fixed linear temperature lapse rate with increase in altitude. The predictions confirmed observations that there is surprisingly little difference in the mean date of budburst within the altitude range 0-250 m (Figure 41). However, above 250 m, there was an average delay of 6·0 days in date of budburst for each 100 m increase in altitude.

Estimates were also made of the dates of budburst of Sitka spruce at Masset on the Queen Charlotte Islands in the years 1898-1967. (Most Sitka spruce seed has been imported from the Queen Charlotte Islands.) At Masset, the mean date of budburst was about 11 days later than at similar low altitude sites in Scotland (Figure 41).

A potentially damaging frost was considered to occur when screen air temperatures $\leq -2.5°C$ occurred between 7 days before the predicted date of budburst and 7 days after the date (based on analyses of grass and air minimum temperatures, observations on variation between trees, and the results of laboratory freezing tests). Frosts of this sort occurred about once
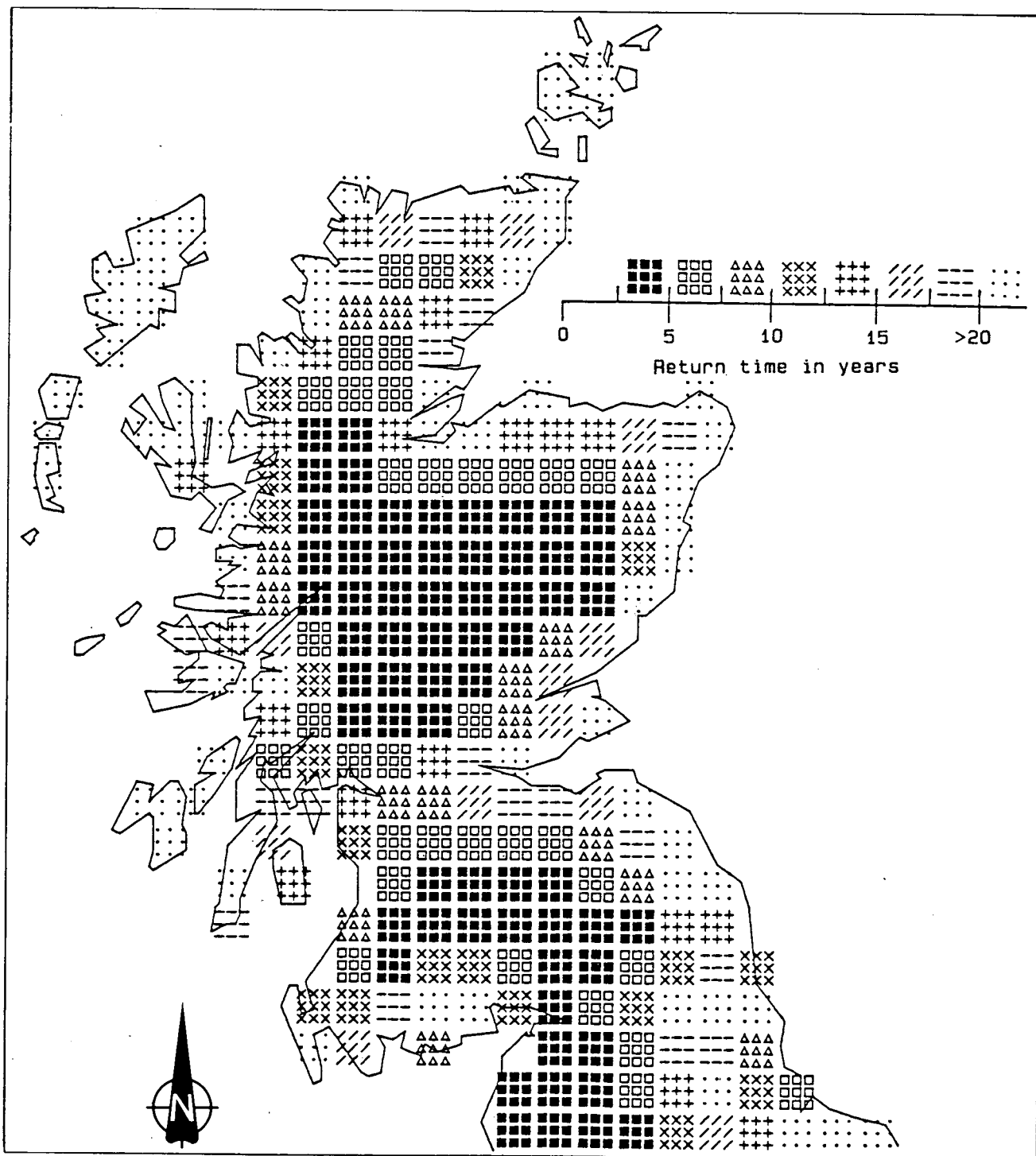


Figure 42    Return times (years) of potentially damaging frost occurring within 7 days of the date of budburst on young Sitka spruce in Scotland

every 3·0 years at Eskdalemuir (a typical upland planting site at 242 m altitude) and once every 8·8 years at Durham (102 m altitude). Only one such frost occurred at Masset in 68 years. The high incidence of potentially damaging frosts at upland sites in Britain could be attributed partly to relatively early budburst (owing to warm spring temperatures) and partly to a high incidence of late spring frosts. The probability of a −2·5°C air frost occurring at Eskdalemuir in mid-May is similar to that at Masset in mid-April (Cannell 1984). In fact, most Scottish upland plantation sites experience −2·5°C frosts later in the year than all coastal stations in the natural range of Sitka spruce south of Cordova, Alaska (60°31′N).

The 'return time' for frost damage at budburst was estimated for each 20 km × 20 km grid square in northern Britain using 4 parameters.

1. The mean date of budburst was estimated as a function of altitude, using the relationships shown in Figure 41.
2. The date of budburst was assumed to be normally distributed, with a mean variance of 83 days.
3. The mean dates of the last frosts were estimated as functions of altitude, distance from the sea, and latitude, which together accounted for 80% of the variation among 42 meteorological stations in northern Britain (Cannell 1984).
4. The variances of the dates of the last frosts (−2·5°C) could be estimated as a function of altitude; distributions were shown to be normal (Cannell 1984).

The predicted dates of budburst and dates of last frosts were independently distributed, so it was possible to estimate, for each 20 km × 20 km square, the probability that the date of budburst (± 7 days) in any year would precede the date of the last −2·5°C frost. This procedure showed that potentially damaging frosts have occurred once every 2·5 to 5·0 years at a wide range of upland sites in northern Britain, including most of the areas where Sitka spruce has, or could be, planted (Figure 42).

How could this high incidence of frost damage at budburst be lessened by selecting clones within provenances with inherently later dates of budburst? To answer that question, 12 clones were subjected to different degrees of chilling and warming, and temperature integrators were used to determine the extent and nature of clonal variation in the equation given earlier:

$$T = A + B \exp(-rC)$$

The clones differed in values of A and B, but not in r. The model was then run to predict dates of budburst using different values of A and B, corresponding to the likely behaviour of different clones. The results show that the present mean date of budburst of 12 May at Eskdalemuir would have to be delayed about 13 days

(by selecting the late budbursting clones) in order to increase the return time of damaging frosts from about once every 3 years to once every 6 years (Figure 43).

## Probability of autumn frost damage

To predict the probability of autumn frost damage, a model was needed to predict the temporal changes in frost hardiness of shoots of different provenances, as illustrated in Figure 38. Using observations of (i) natural changes in frost hardiness, monitored over 3 years on 4 provenances, and (ii) effects of long days (provided by lights in the field), warm temperatures (in a glasshouse) and frosts (in a growth room), an iterative computer model was constructed of the form:

$$\Delta T_k = a + b \, (T_{min} - T_k)$$

where $\Delta T_k$ is the daily change in the killing temperature, $T_k$ (as shown in Figure 38), and $T_{min}$ is the air minimum temperatures on the previous day. $T_k$ was assumed to begin at −5°C on 15 August and was calculated until the end of December. Observed
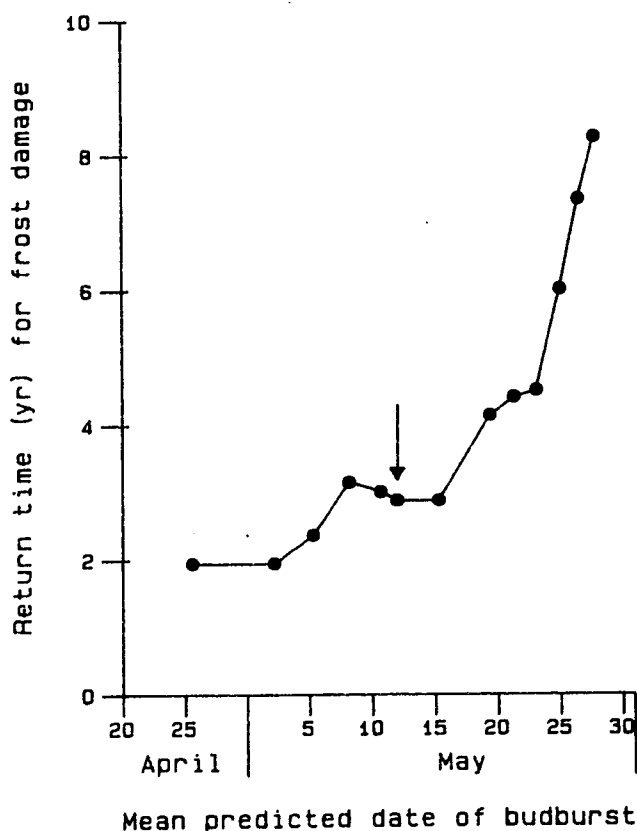


Mean predicted date of budburst

*Figure 43   Return time of potentially damaging frosts occurring within 7 days of the date of budburst on young Sitka spruce clones with different thermal time/chill day requirements, giving different mean dates of budburst, at Eskdalemuir. The arrow marks the value predicted using the function in Figure 39 which applies to current Queen Charlotte Island populations in Britain*

changes in $T_k$ could be simulated by assuming that $b = 0.05$, and that $a$ had a different starting value for different provenances, and decreased daily after experiencing either a frost or a critical short daylength. Parameter values were chosen for each provenance which produced changes in autumn hardening (and dehardening) which most closely matched observed changes in frost hardiness. The model was in agreement with an extensive literature on the effects of temperature and daylength on frost hardening in trees.

Because the inputs to the model were only daily minimum air temperatures, and daylengths, the model could be used to identify those occasions in past years when frosts occurred that would have been below $T_k$.

Figure 44 shows the predicted changes in hardiness of 3 provenances at one site in 6 years, identifying 1971 as a year when a damaging frost occurred. The estimated 'return time' for autumn frost damage at Eskdalemuir was 8·3 years for an Oregon provenance, but over 10 years for a Masset provenance. Most damaging frosts occurred in October, but frosts like that in October 1971 (Figure 44), which followed warm weather and caused widespread damage in Scotland (Redfern & Cannell 1982), were shown to be quite rare (Cannell *et al.* 1985).

The 'return times' for autumn frost damage on even an Oregon provenance were over twice the return times for damaging frosts at budbursts. QCl and Alaskan
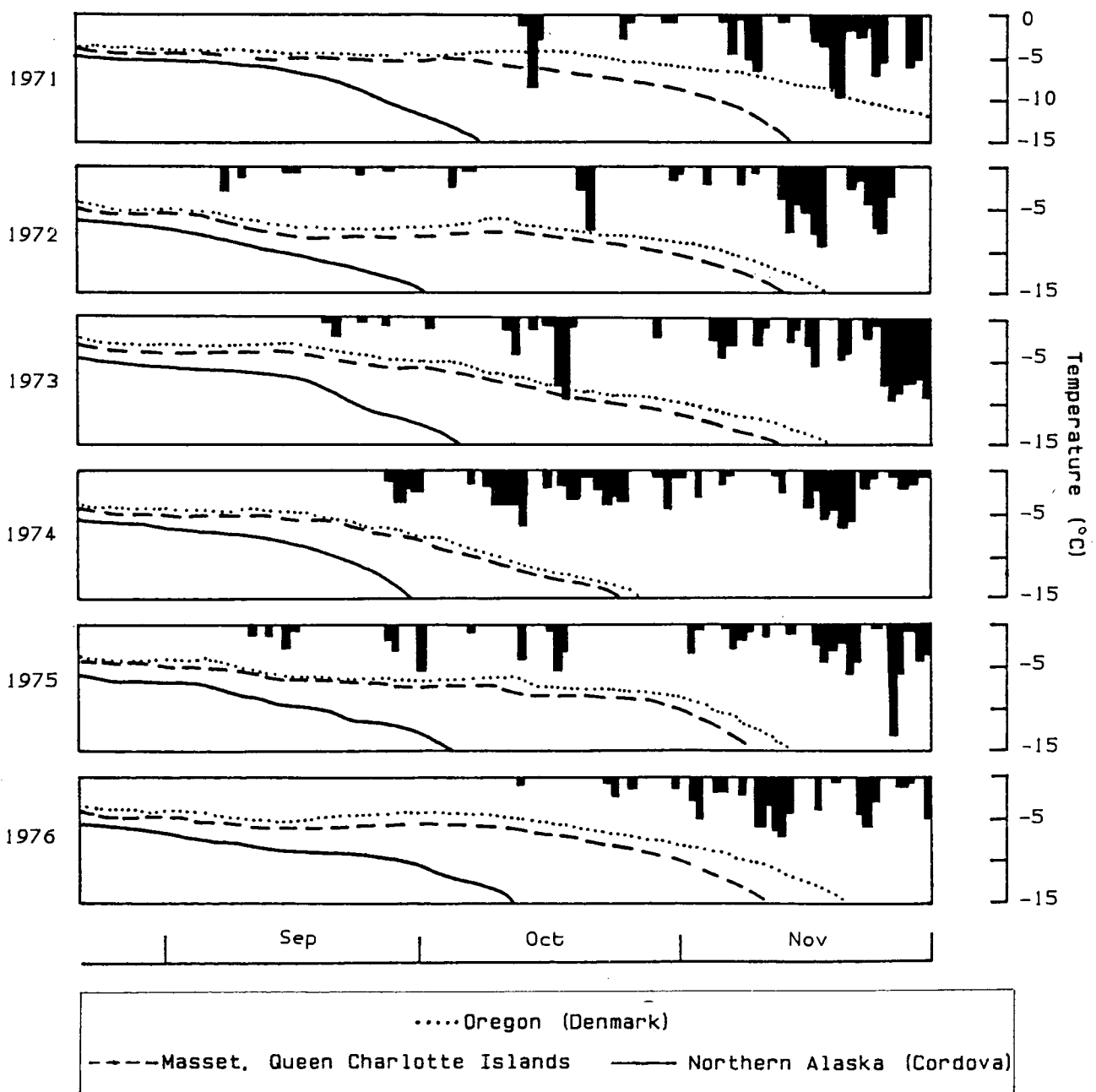


Figure 44   Predicted autumn frost hardening of 3 provenances of Sitka spruce in 6 years at Kirroughtree, Scotland (54°57'N, 8 m altitude). The lines mark killing temperatures, as in Figure 38; the black histograms are 'grass' minimum temperatures, which are likely to be close to needle tissue temperatures

provenances escape autumn frost damage in Britain, even though, at upland sites, −2·5°C and −4·5°C frosts occur about 4 weeks earlier than at Masset (Cannell 1985). The main reason for their frost avoidance is that rapid hardening is induced by shortening daylengths in September-October, even in warm weather.

Autumn frost damage on QCI provenances of Sitka spruce seems to be a problem only at very exposed or high altitude sites. At those sites, hybrids between Sitka spruce and white pine (*Picea glauca*) perform better than Sitka spruce. The hybrids have been shown, over 2 seasons, to be consistently 2°C more frost hardy than Sitka spruce from July to October (Sheppard & Cannell 1985).

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## NUTRIENT USE EFFICIENCY IN CONIFERS

Tree growth rates in nutrient-poor forest soils might be increased cheaply by planting genotypes which have inherently low demands for nutrients per unit of stemwood or total dry matter produced. Genotypes of this sort could be said to have high nutrient use efficiencies, and they would be especially valuable before canopy closure, when forest trees make the greatest demands on soil nutrients. Trees could differ in the amount of dry matter they produced per unit weight of absorbed nutrients if they had different tissue nutrient concentrations, or if there were differences in the proportions of dry matter allocated to stemwood (which has a low concentration) as opposed to branches and foliage (which have high nutrient concentrations).

Clonal differences in nutrient use efficiency were determined in Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) by estimating the total N, P, K, Ca and Mg contents of the litterfall and above-ground parts of trees, 8 years old, growing in a fertile loam near Edinburgh (Cannell *et al.* 1983; Sheppard & Cannell 1985). Three trees were analysed for each of 7 clones per species; additional analyses were done on the foliage of the same clones growing in a peaty-gley soil about 30 km south of the other site.

Integrated over the 8 years since planting, the specimens of Sitka spruce had absorbed a similar weight of N per unit dry weight increment to lodgepole pine, but Sitka spruce had taken up proportionately more P, K and Ca; that is, Sitka spruce had a relatively low nutrient use efficiency for P, K, and Ca.

Within both species, there were significant differences between clones in the weight of dry matter produced per unit of nutrient element, the most efficient clones producing up to 30% more dry matter per unit of nutrient absorbed (Figure 45). Among Sitka spruce clones, the efficient use of one of the physiologically active nutrients (N, P, K or Mg) was usually accompanied by the efficient use of others. Thus, clones C and F produced more dry matter per unit of N, P, K and Mg than clones D and E. In contrast, among lodgepole pine clones, the efficient use of one nutrient rarely implied the efficient use of others. Thus, clone L produced more dry matter per unit of N than the others, whereas it was the least productive with potash (K). These differences between clones in nutrient use efficiency were related to 3 characteristics.

1. In both species, there were clones which had unusually small concentrations of nutrients in their needles, of all ages, at both sites. Because needles had over 50% of most of the nutrients absorbed by the trees, over the 8-year period, these clones had high nutrient use efficiencies (Table 15).

2. The N, P and K requirement for a unit increment in stem dry weight was usually less than half of that
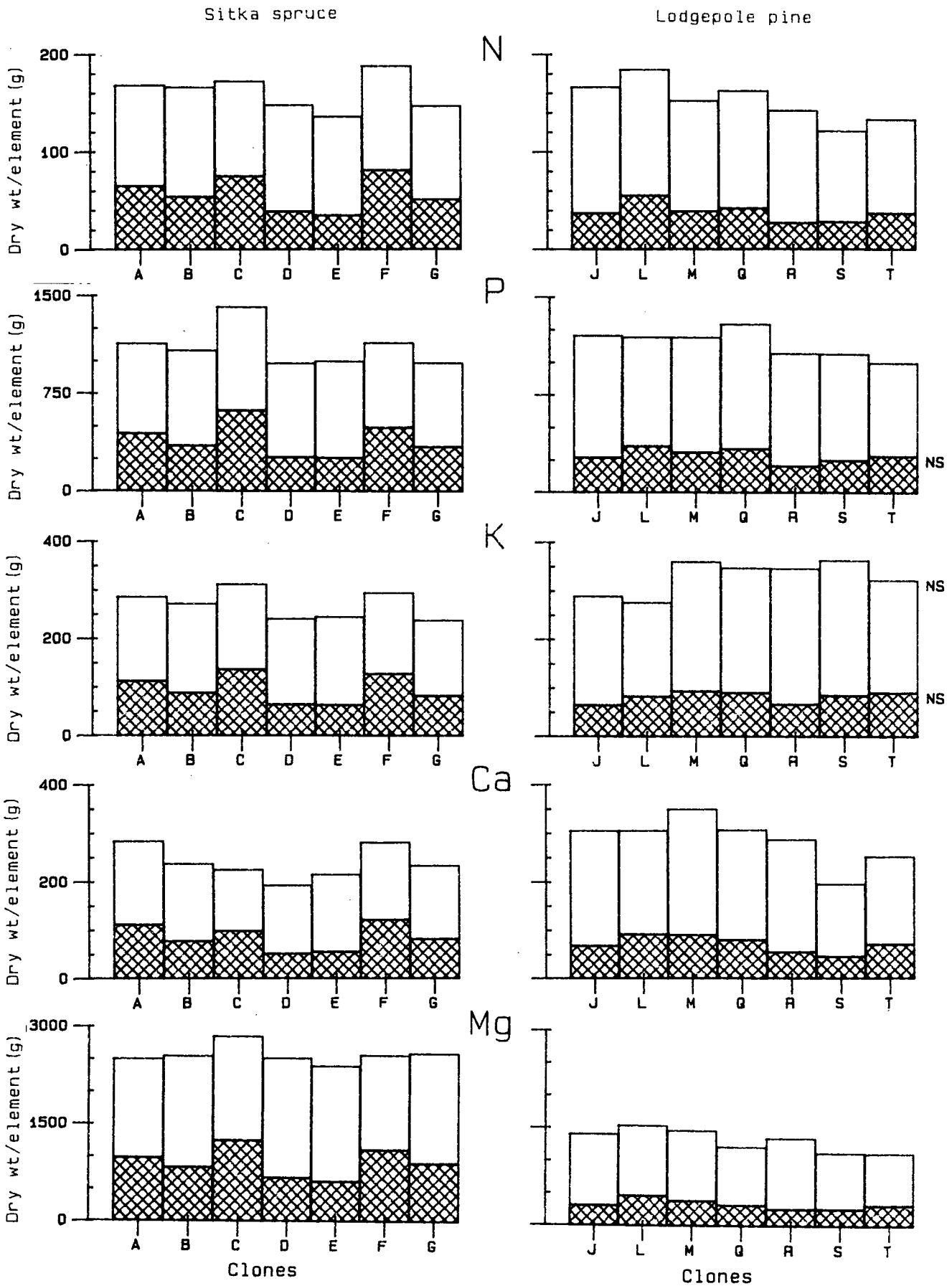
Figure 45   The 'nutrient use efficiencies' of 7 clones of Sitka spruce and lodgepole pine, ie the mean weights of dry matter produced to age 8 per unit weight of nutrient element taken up, including estimates of the weights and nutrient contents of fallen needles, but excluding roots. Values are given for (i) total dry weight produced/nutrient absorbed (shaded plus unshaded) and (ii) stem dry weight produced/nutrient absorbed (shaded only). Significant differences among clones existed at P<0·01 for both (i) and (ii) unless marked NS

STONE CHEST - PLAN

Sitka spruce
Japanese larch
Hybrid larch
Western hemlock
Lodgepole pine
Survey plot

Improved land
Road
Hedgerow
Mature tree
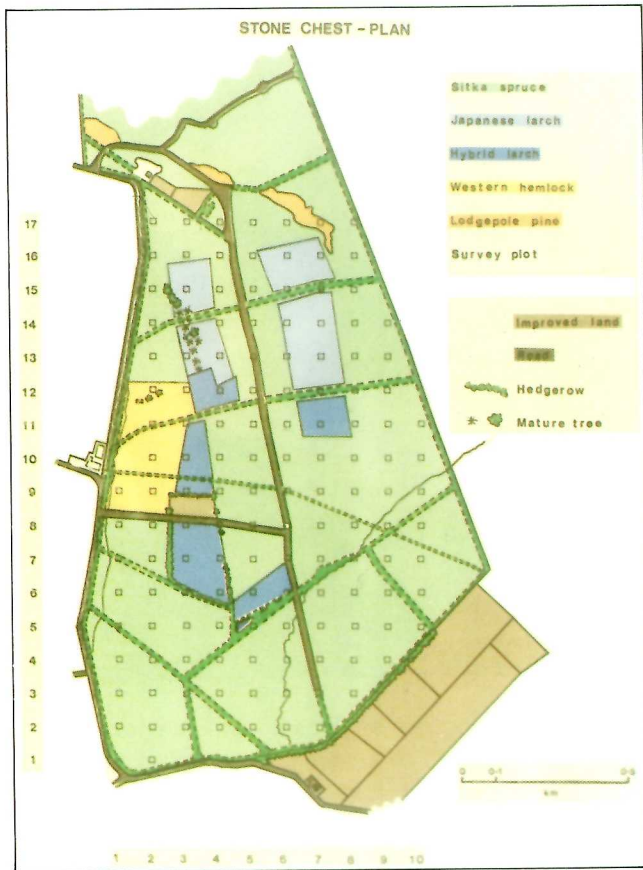
Plate 2  Stone Chest site plan, showing planting pattern and distribution of sample plots
(Photograph D R Briggs)



Plate 3  Chicks of the short-eared owl, a predator of small mammals during the first 8 years of a coniferous plantation at Stone Chest
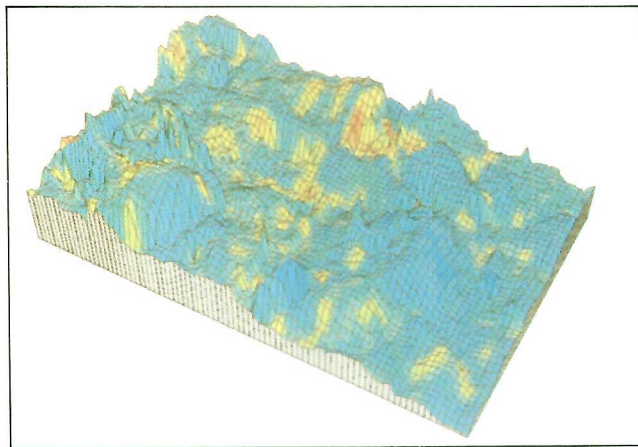(Photograph V P W Lowe)



Plate 4  Small-scale variations in topography and soil depth in a natural habitat of the clubmoss Lycopodium annotinum
(Photograph Brita Svensson, University of Lund, Sweden)

ABOVE    45
40  -  45
35  -  40
30  -  35
25  -  30
20  -  25
15  -  20
10  -  15
 5  -  10
 0  -   5
BELOW     0

Plate 5  General view of trial site at Jackhouse Reservoir, near Manchester. When the vegetation has matured, water will be run down each of the channels at increasing velocities to test the ability of the reinforcement to withstand water flow. From left to right, the channels are:

1. Lotrak (fabric)
2. Dycel (concrete blocks)
3. Netlon (net )
4. Enkamat 7220 (fabric)
5. Plain grass
6. Petraflex (concrete blocks)
7. Armorflex (concrete blocks)
8. Enkamat A (fabric with gravel filling)
9. Dymex (concrete blocks)  10.  Grasscrete (concrete)



(Photograph L A Boorman)

Plate 6 Section through the top 50 cm of restored 'soil' at the Tir-y-Gof site, south Wales. Topsoil and subsoil were unavailable and the restored material consisted of nitrogen- and phosphorus-deficient shale and sandstone of coarse texture
(Photograph J E Good)



Plate 7 Compaction of topsoil and subsoil during restoration can lead to severe waterlogging problems on restored opencast sites. Careful soil handling, and the use of subsoiling machinery to alleviate compaction, can largely prevent this problem
(Photograph J E Good)



Plate 8 This fine silver birch, of good form and bark colour, was the result of natural seeding on to pure lignite coal at an opencast mine near Cologne, West Germany. Cuttings were taken, and the resultant plants are being tested on restored opencast sites throughout Britain
(Photograph J E Good)



Plate 9 Selected clones of birch and willow, 5 years after planting at the Ty Cerrig restored opencast coal site, north Wales
(Photograph J E Good)

for a unit increment of branch dry weight, and only 5-15% of that for a unit increment of needle dry weight. Consequently, the sparsely branched Sitka spruce clones, which partitioned a large proportion of their dry matter to stems, had relatively high nutrient use efficiencies (Table 15).

*Table 15.* Correlation coefficients (r) between 'nutrient use efficiency' and other characteristics among 7 clones of each of Sitka spruce and lodgepole pine. Nutrient use efficiency is defined as the total net dry matter increment above ground over 8 years including fallen needles divided by the weight of nutrient taken up over the same period

| | | Stem/total dry weight at age 8 | Mean nutrient concentration in all needles† | Mean nutrient concentration in needles 1&2 years old | Percentage of needles >2 years old |
|---|---|---|---|---|---|
| *Pinus contorta* | N | 0·76* | −0·68 | −0·52 | 0·72 |
| | P | 0·81* | −0·21 | 0·45 | 0·77* |
| | K | 0·82* | −0·67 | 0·27 | 0·82* |
| | Ca | 0·57 | −0·68 | −0·64 | 0·36 |
| | Mg | 0·80* | −0·60 | 0·32 | 0·55 |
| *Picea sitchensis* | N | −0·12 | −0·76* | −0·89* | 0·91* |
| | P | −0·36 | −0·24 | −0·47 | 0·90* |
| | K | 0·37 | −0·75* | −0·48 | −0·78* |
| | Ca | −0·34 | −0·84* | −0·81* | 0·75 |
| | Mg | −0·30 | −0·80* | −0·66 | 0·68 |

† Taking into account the different weights of needles of different ages
* Significant at P<0·05

3. In both species, clones that retained needles longest tended to produce most dry matter per unit of nutrient taken up (Table 15), possibly because these clones produced more photosynthate per unit of nutrient invested in the needles.

These 3 characteristics, which might be said to form the 'ideotype' for high nutrient efficiency, were also found to be associated with a high stemwood production per unit of foliage (Cannell *et al.* 1983); their selection could be readily incorporated into tree improvement programmes.

*Lucy J Sheppard and M G R Cannell*

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## BUD DIFFERENTIATION AND CONE DEVELOPMENT IN LODGEPOLE PINE

(A CASE studentship project)

Owens and Molder (1975) studied cone initiation in specimens of lodgepole pine (*Pinus contorta*) growing in their native habitat in British Columbia, but, as far as is known, comparable surveys have not been made in Britain where this species is used in upland forests. Because afforestation depends upon reliable supplies of seed, it is desirable to be able to manipulate the formation and subsequent development of cones in a predictable manner.

Attempts have been made to manipulate coning in the Pinaceae, but with less success than has been achieved in the Cupressaceae and the Taxodiaceae, where coning can be induced by applying gibberellic acid ($GA_3$). However, coning has been induced in some spruces (*Picea* spp.) by applying a mixture of gibberellins A4 and A7; in lodgepole pine, coning, and especially the formation of female cones, has been stimulated, to some extent, by altering the daily photoperiods.

To establish the time course of cone initiation and differentiation in buds of lodgepole pine in natural conditions, buds were sampled at intervals from an experimental plantation at the Bush Estate, near Edinburgh. They were fixed, dissected and examined with a scanning electron microscope. The first microscopic stages of bud development were found in April to mid-May, when the apical domes of buds enlarge with the initiation of sterile primary cataphylls (protective bud scales without axillary buds). From mid-May onwards, bud scales with axillary buds (fertile primary cataphylls) were found, with secondary cataphylls developing around the axillary buds (Stage 1 of Figure 46).

These early stages of development in buds that are destined to produce male or female cones are morphologically indistinguishable from those in buds destined to produce foliage with short shoots (needles) and long shoots (branches). Female cone initiation begins in mid-July, 2 to 3 weeks before that of male cones. Both male and female cones can be initiated until late September depending on the clone and the position of the cones within buds. Male cones differentiate acropetally (from below upwards) from axillary buds at the base of the main bud. The secondary cataphylls surrounding the male cones increase in length from about 500 μm to 800 μm, while the diameter of the apex of the axillary bud increases from 100 μm to 200 μm: the apex of the axillary bud becomes rounded (Stage 2 of Figure 46). When the axillary bud is more than 200 μm in diameter, microsporophylls (the initials of sporangia destined to produce pollen) begin to be initiated from the base of the bud meristem upwards. Microsporophyll primordia are smaller than those of secondary cataphylls (Stage 3 of
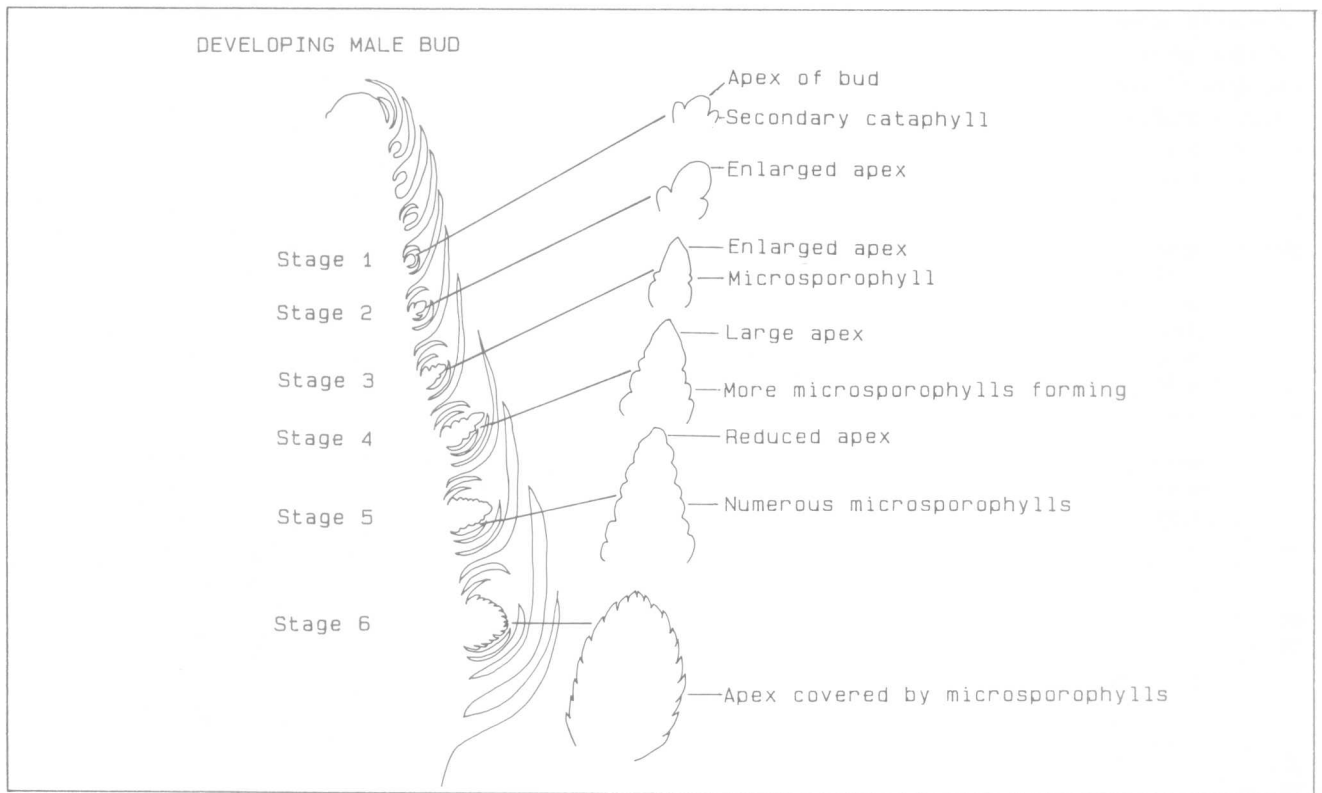
Figure 46 Longitudinal section of male cone development in a bud of lodgepole pine
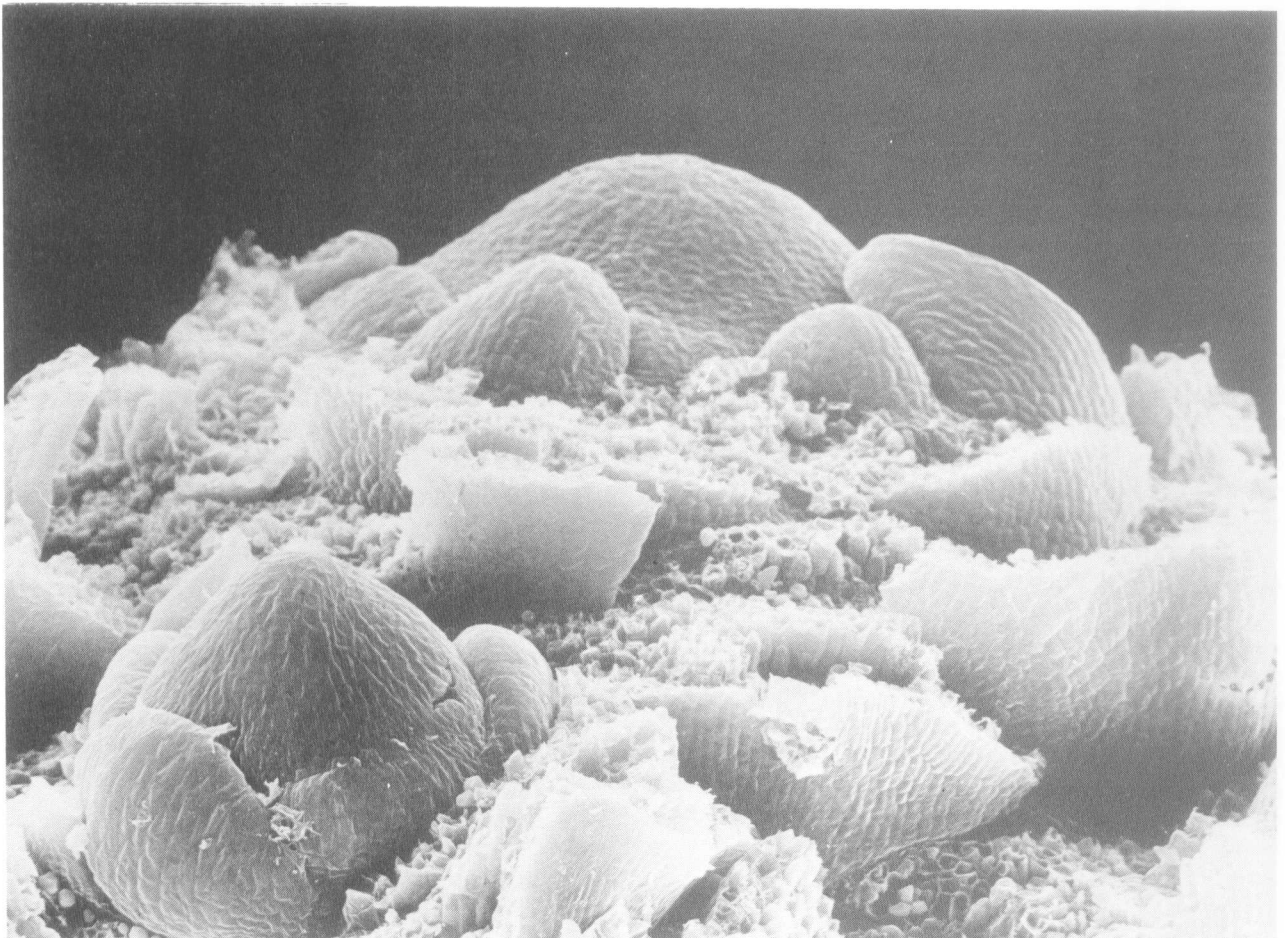


Plate 10 Scanning electron micrograph of the apical region of a lodgepole pine bud with an early stage female cone (left foreground) (diameter of the cone about 300 μm: apex of the main bud (background) is initiating sterile primary cataphylls)
(Photograph C J Couper)

Figure 46): they are arranged spirally in an 8:13 phyllotaxis in contrast to the 2:3 ratio arrangement of cataphylls. As the diameter of the apex of male cones increases to about 300 μm, rates of microsporophyll initiation also increase (Stage 4 of Figure 46). Initially, the microsporophylls are smooth and raised, but, as male cones develop, they become flatter with strongly divided edges, pressed tightly to the sides of the cones. The microsporophyll primordia progressively occupy more of the apical dome until the apex is completely occupied (Stages 5 and 6 of Figure 46). The cone continues to increase in size until the onset of dormancy in the autumn. The final stages of differentiation and the production of pollen take place in the following spring.

In contrast to male cones, the first female cone normally develops from an axillary bud near the top of a main bud: it increases in size until its apex is noticeably larger than those of lower, undifferentiated axillary buds. As the first cone develops, up to 6 other female cones may start differentiating while the apices of terminal buds start to initiate sterile primary cataphylls (Plate 10). As each one increases in size, additional, tightly adpressed, secondary cataphylls are produced. When the apical dome of the cone is about 400 μm in diameter and surrounded by about 30 cataphylls, bract primordia are initiated from the base of the cone (Plate 11). During the autumn, bract initiation continues until cones are about two-thirds covered. The cone then becomes dormant, until the spring of the following year, by which time bract scales completely cover the apices of cones when ovuliferous scales are initiated. Thereafter, ovules develop and pollination occurs.

In supporting experiments in controlled environments, linear correlations were obtained between shoot lengths and needle numbers on the one hand, and between bud length and the breadth and numbers of primary cataphylls within buds, on the other. Evidence suggested that the growth of buds is, to a large extent, buffered from environmental effects, with temperature and differences in photoperiod having relatively minor short-term effects on rates of increase in bud length, breadth and number of cataphylls initiated. In high temperature/short day environments, growth rates of axillary buds are faster than those at lower temperatures in long days. In short days, sterile cataphylls are initiated at the apex, while the internodal lengths between newly formed primordia are decreased, suggesting that the apex is entering dorman-



*Plate 11  Scanning electron micrograph of female cones of lodgepole pine in the late autumn of their first year of development (3 cones, with their secondary cataphylls removed, surround the terminal apex of the bud; bract scales occupy about three-quarters of the surface of the cones) (Photograph C J Couper)*

cy. However, in buds on vigorous shoots, a second batch of axillary buds may be formed, possibly reflecting rapid rates of shoot growth. In short days, female cones are often initiated while, in long days, there is some evidence that male cone formation may be promoted. The types of cones initiated can also apparently be changed by altering the temperature regime. At high temperatures, branch differentiation is stimulated.

In summary, it is apparent that bud differentiation in natural conditions is environmentally controlled by interactions between different temperatures and photoperiods, with buds on different clones responding differently to temperature and photoperiod. It now remains to quantify these inter-relations so as to be able to predict the course of events.

C J Couper

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## THE RESPONSE OF PLANTS, NOTABLY CLUBMOSSES, TO ENVIRONMENTAL STRESS IN NORTHERN LATITUDES

(This work has been largely supported by Swedish Royal Academy of Sciences funds)

Many of the current ideas about processes controlling plant populations and communities have been formulated from a biased sample of vegetation from temperate latitudes. In severe environments, such as deserts and tundra, it can be argued that population processes and selection pressures differ from those in temperate regions (Callaghan & Emanuelsson 1985), but the evidence tends to be anecdotal. Consequently, a research programme has been developed to investigate plant growth strategies and population processes in the tundra in northern Sweden in order to formulate and test general hypotheses. By combining physiological and demographic studies (Callaghan 1984), it has been possible to interpret short-term physiological processes in the context of long-term population trends.

Research has been focused on the clubmoss *Lycopodium annotinum*, colonies of which grew slowly with (i) indefinitely spreading horizontal branches and (ii) vertical photosynthetic branches with finite periods of growth (Callaghan 1980). Svensson and Callaghan are relating the demography of *L. annotinum*, in terms of survival, reproduction, growth and direction of spread, to micro-environmental features such as micro-

topography and soil depth (Plate 4), and concentrations of soil nutrients, plant associations at the 'micro' level, and climate.

Preliminary results suggest that the extension growth of clubmoss colonies is controlled by temperatures during June and July, whereas the survival of 'growing points' is related to the ability of plants to produce roots. The formation and release of new branches (vegetative reproduction) to form new colonies reflect the release of suppressed growing points from apical dominance ('correlative inhibition'), following the death of primary growing points. The distribution and direction of travel of horizontal branches appear to be controlled by the slope and absolute height of ground undulations: horizontal branches are not generally found in the valleys or on the tops of hummocks.

Demographic studies have emphasized the importance of the indefinitely growing horizontal branches in the conservation of nutrients and their transport over rocks and tracks. Headley *et al.* (1985) argue that plants could overcome poor soil conditions by (i) increasing root/shoot ratios, (ii) economizing on the use of nutrients and carbon by having tissues that function for relatively long periods, (iii) using small concentrations of nutrients efficiently, (iv) recycling nutrients from senescing structures to young growing points, and (v) having roots that take up nutrients very efficiently from soils with as little as 26 $\mu$g P g$^{-1}$ soil.
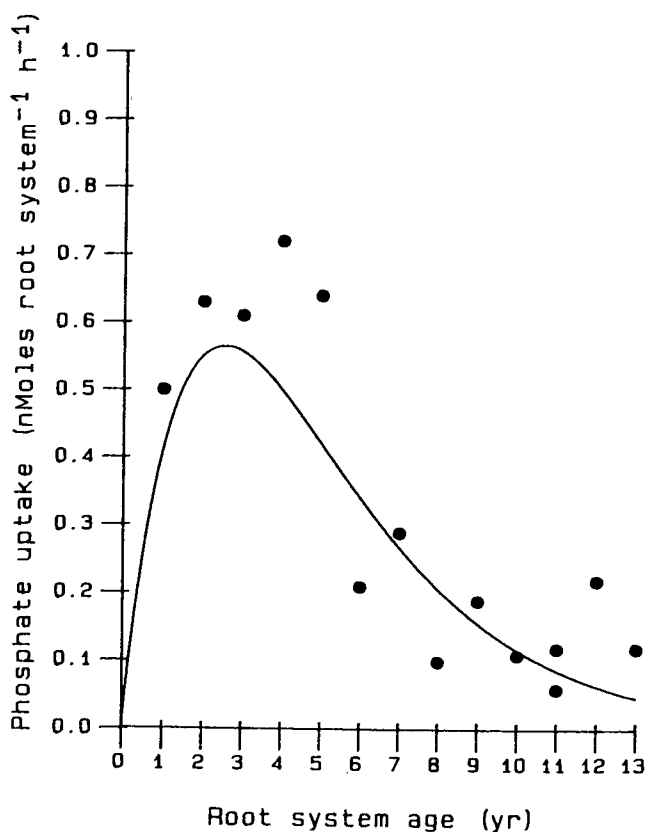


Figure 47 The changing rates (y) of phosphate uptake by ageing (x) root systems of Lycopodium annotinum $y = 0.606x \ exp(-0.395x)$

However, atypically, Lycopodium annotinum has a very small root biomass (4-5% of total biomass), although individual roots are functional for up to 13 years, with significant phosphate uptake over a 4-5 year period (Figure 47). Rates of phosphate uptake in the field (53 nM $g^{-1}$ dry weight $h^{-1}$) are very small (Headley et al. 1985), but, within the species L. selago and between 5 Lycopodium species, rates of phosphate uptake increase as phosphate concentrations in the soil decrease (Figure 48). The transport of phosphate into above-ground parts of plants is very slow (5% to 20% over 30 hours), and initial distribution patterns appear to depend upon water potential gradients and evapotranspiration streams.

Phosphorus is used economically by Lycopodium spp. Tissue concentrations are small, with an overall efficiency of phosphorus utilization of 1·25 mg P $g^{-1}$ dry weight attributable to (i) the protracted longevity of tissues (over 20 years) and (ii) the recycling of about 75% of the phosphorus that leaves senescing tissues. The phosphorus requirement, estimated from tissue longevity and phosphorus concentrations, is approximately 670 µg per horizontal branch system per year, equivalent to a demand of 0·69 mg P $g^{-1}$ root $yr^{-1}$, after making allowances for recycled phosphorus. The observed rates of phosphate uptake in the field are sufficient to satisfy this demand within the short growing season of northern Sweden.
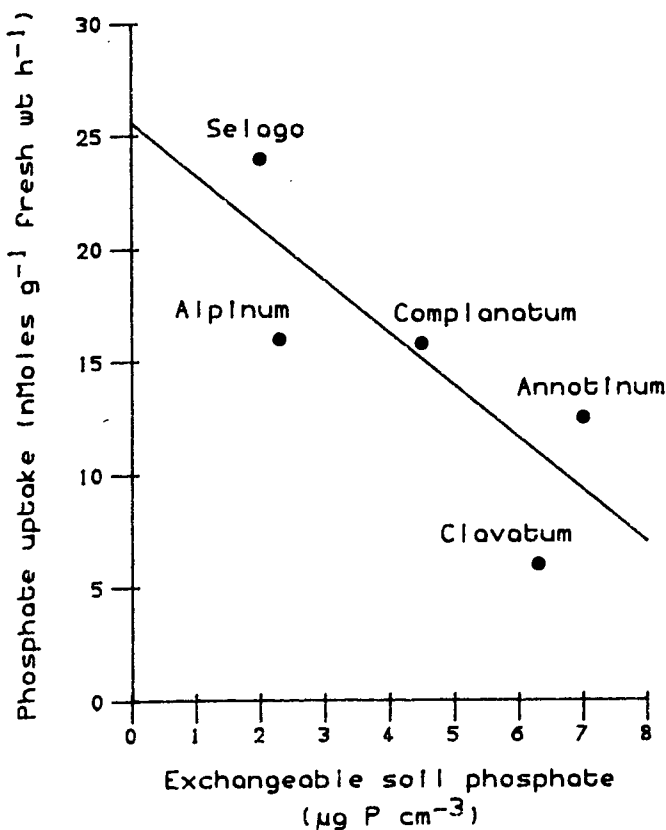
Its physiological strategies and patterns of distribution enable L. annotinum to survive indefinitely in severe conditions by continually 'moving around' its environment: it can forage for nutrients. When obstacles are met, active growing points may die, but many more growing points elsewhere on the plant may become active as they are released from dormancy. The young growing points increase the potential area of substrate that may be exploited, and, in doing so, will increase the probability of finding favourable niches. These strategies also allow plants of L. annotinum to minimize competition with themselves and other species.

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## APPLYING SCANNING ELECTRON MICROSCOPY TO FUNGAL TAXONOMY

Fruitbodies (toadstools) of Laccaria species, members of the white-spored Tricholomataceae, occur in a diverse array of forests in many parts of the world, with Laccaria laccata being the species most frequently recorded. In an intensive study of the fruitbodies associated with a young plantation of silver birch (Betula pendula) and downy birch (B. pubescens) in Scotland, L. laccata was rarely found (Mason et al. 1982). Instead, most of the fruitbodies appeared to be the closely related 4-spored species, Laccaria proxima, or a previously rarely recorded 2-spored species, Laccaria tortilis. At about the same time, 2- and 4-spored species of Laccaria were identified in association with trees in southern India (Natarajan 1977). These findings caused some concern, as Laccaria species are leading candidates for controlled inoculations of trees (Molina 1982; Mason et al. 1983), and,



Figure 48    Rates of phosphate uptake by 5 species of Lycopodium growing at 'natural' sites with different concentrations of soil phosphorus

for this reason, correct species identification is obviously highly desirable. As a result, it was decided to 're-investigate' the identification of forms of *Laccaria* found in the field.

Samples of mature *Laccaria* fruitbodies were collected at 9 sites in northern Britain, their macroscopic features being recorded in detail. By their macroscopic features, the fruitbodies appeared to belong to 3 species – *L. proxima*, *L. tortilis* and *L. laccata*. In

collections made in association with Mexican pine (*Pinus patula*) and *Eucalyptus* spp. growing at 2 locations in Tamil Nadu, southern India, 2 species, *L. proxima* and *L. ohiensis*, were tentatively identified.

*L. tortilis* was readily identified by its very small stature and *L. ohiensis* by its thick stipe (stalk) (Table 16). There was, however, greater uncertainty in separating *L. proxima* from *L. laccata*, primarily because their pileus (cap) and stipe dimensions overlap. After careful
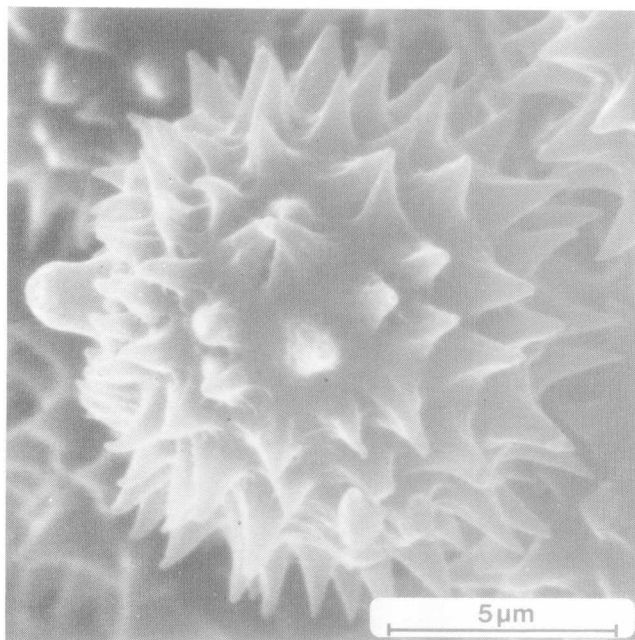


Plate 12   Basidiospore of Laccaria tortilis—*Q value of 1.06, 4.2 spines 9 μm$^{-2}$ and average height of spines 1.9 μm*
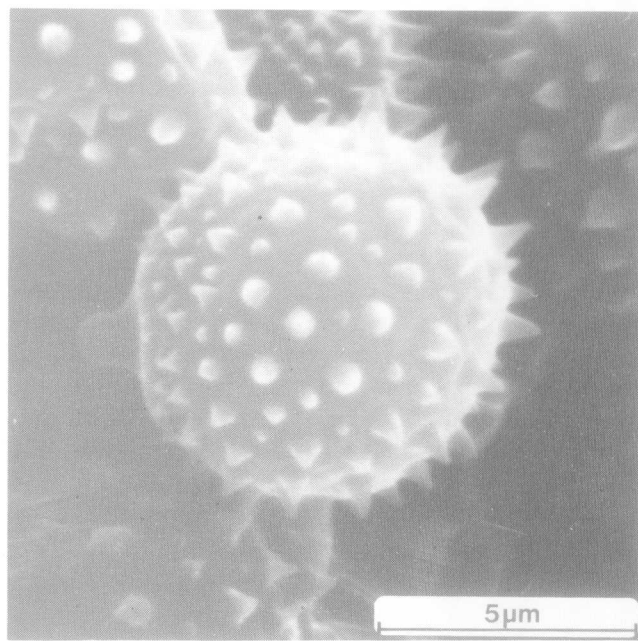(Photograph A D Crossley)



Plate 13   Basidiospore of Laccaria ohiensis—*Q value of 1.05, 11.3 spines 9 μm$^{-2}$ and average height of spines 0.9 μm*
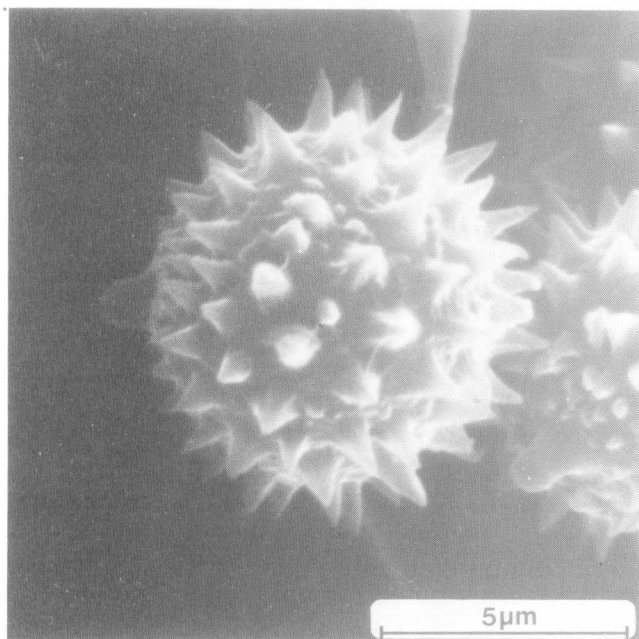(Photograph A D Crossley)



Plate 14   Basidiospore of Laccaria laccata—*Q value of 1.01, 8.6 spines 9 μm$^{-2}$ and average height of spines 1.0 μm*
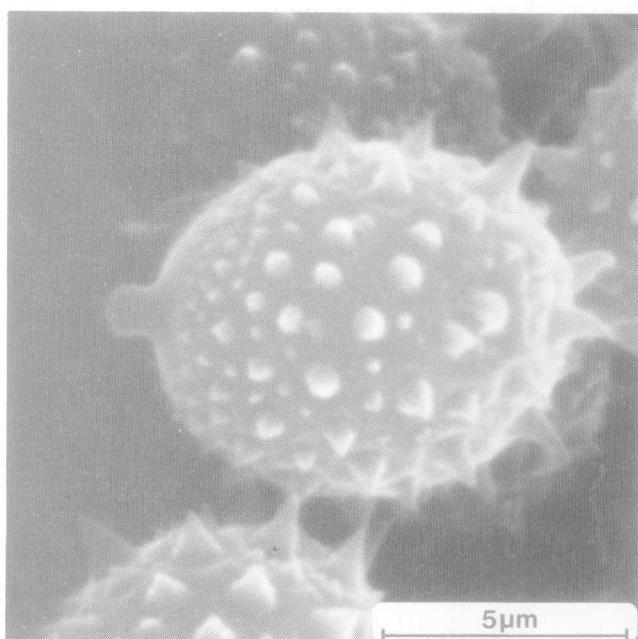(Photograph A D Crossley)



Plate 15   Basidiospore of Laccaria proxima—*Q value of 1.20, 16.3 spines 9 μm$^{-2}$ and average height of spines 0.7 μm*
(Photograph A D Crossley)

Table 16. Fruitbody (toadstool) characteristics of 4 types of Laccaria found in association with trees in Scotland and/or southern India

| | 'L. proxima' | 'L. laccata' | 'L. tortilis' | 'L. ohiensis' |
|---|---|---|---|---|
| **Pileus (cap)** | | | | |
| Diameter (mean) | 6-47 (20) mm | 5-33 (14) mm | 2-28 (10) mm | 20-30 mm |
| Texture | Dark scales prominent in centre of maturing cap | Smoother than 'L. proxima' Flesh pink-brown when fresh | Slight scurf of surface | Central depression |
| **Stipe (stalk)** | | | | |
| Length (mean) | 16-110 (40) mm | 12-50 (34) mm | 2-18 (7) mm | Up to 45 mm |
| Width (mean) | 1·5-10 (5) mm | 2-5 (3) mm | 0·5-2 (1) mm | c 5 mm |
| Texture | Fibrillose with prominent axial fibres | Slightly fibrous but generally smoother than 'L. proxima' | Slightly fibrous | Smooth to fibrillose |

examination, however, L. proxima could be recognized by its (i) darker scales in the centre of the cap, and (ii) more fibrillose stipe.

In addition to macroscopic features, the separation of Laccaria species is dependent upon microscopic details. Gill fragments of air-dried specimens were rehydrated in 10% ammonia so that comparative measurements of critical basidiospore characteristics could be made with a light microscope. Other air-dried specimens were rehydrated in 10% ammonia so that comparative measurements of critical basidiospore characteristics could be made with a light microscope. Other air-dried fragments were prepared for examination with a scanning electron microscope (SEM).

The species identified by fruitbody characteristics as L. tortilis and L. ohiensis were found to have basidia that form 2 spores (basidiospores), whereas L. proxima and L. laccata had 4-spored basidia (Table 17). Spore measurements (always exclusive of ornamentation) made under a light microscope were extremely variable with wide and overlapping ranges. However, the spores of L. proxima were consistently subglobose-ellipsoidal, whereas those of the others were globose-subglobose.

The air-dried spores examined with the SEM were usually 20% smaller than fresh spores, but their shapes remained unaltered. The ellipsoidal spores of L. proxima had Q values around 1·20, compared with 1·00-1·06 range for the globose forms (Q value = spore length, through its apiculus, divided by spore width). Details of spore ornamentation could only be resolved satisfactorily with the SEM – the spines of L. tortilis (Plate 12) were large and robust

Table 17. Basidiospore characteristics of 4 types of Laccaria found in association with trees in Scotland and/or southern India

| | 'L. proxima' | 'L. laccata' | 'L. tortilis' | 'L. ohiensis' |
|---|---|---|---|---|
| **LIGHT MICROSCOPE OBSERVATIONS** | | | | |
| Number of basidiospores per basidium | 4 | 4 | 2 | 2 |
| Shape of basidiospores | Elliptical | Globose to subglobose | Globose to subglobose | Globose to subglobose |
| Size of basidiospores (Length × width excluding spines) | 6·8-11·1 × 6·1-9·5 μm | 7·4-10·0 × 7·0-10·5 μm | 10·3-15·2 μm diam | 7·0-10·9 × 7·0-10·1 μm |
| **SCANNING ELECTRON MICROSCOPE OBSERVATIONS** | | | | |
| Basidiospore Size (length × width excluding spines) | 6·5-7·7 × 5·4-6·9 μm (7·1) (6·0) | 5·7-7·1 × 5·3-7·3 μm (6·3) (6·3) | 9·0-12·0 × 7·9-10·9 μm (10·1) (9·6) | 6·5-8·3 × 6·3-7·8 μm (7·1) (6·8) |
| Q values† | 1·09-1·33 (1·20) | 0·92-1·11 (1·01) | 1·00-1·14 (1·06) | 1·00-1·16 (1·05) |
| Spines Height (mean) | 0·3-1·2 (0·7) μm | 0·4-1·6 (1·0) μm | 1·4-2·4 (1·9) μm | 0·5-1·4 (0·9) μm |
| Numbers 9 μm$^{-2}$ | 16·3 | 8·6 | 4·2 | 11·3 |

† Q value = length of spore, through its apiculus, divided by its width (measurements were exclusive of ornamentation and apiculus)

compared with those of *L. laccata, L. proxima* and *L. ohiensis*. Of the 4-spored forms, *L. proxima* had twice as many spores per unit area (Plate 15) as *L. laccata* (Plate 14). Although spine densities of *L. ohiensis* (Plate 13) and *L. laccata* were similar, the former were 2-spored in contrast to the 4 spores of *L. laccata*.

The first detailed spore descriptions of *L. proxima* (Boudier 1881) and *L. laccata* (Rea 1922) clearly indicated that *L. proxima* produced oval, finely echinulate spores, whereas those of *L. laccata* were globose and echinulate. Subsequent reinterpretations of the original concepts of the different *Laccaria* species, with an emphasis on spore size, have introduced uncertainties and the possible mixing of *L. laccata* and *L. proxima*. However, by returning to the original densities, it seems that *L. proxima* can be separated from *L. laccata*.

The ability of the SEM to separate 2 contentious species when applied to basidiospore characterization has important implications for the future role of SEM photographs in fungal taxonomy.

*A Crossley*

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## THE BIOCHEMISTRY OF FREEZING INJURY IN SACCHAROMYCES CEREVISIAE

The maintenance of micro-organisms in culture collections requires methods that ensure long-term viability and stability. To minimize the many problems, including genetical instability, that occur when cultures are maintained by conventional subculturing, other methods of preservation have been developed; those most commonly employed are storage in a frozen stage (usually under liquid nitrogen) or lyophilization (freeze-drying). While strain stability may be improved

substantially by using these newer techniques, there is increasing evidence that selection or mutation may still sometimes occur.

To study the selective effects of freezing, studies were made of the cellular responses of the yeast *Saccharomyces cerevisiae* (National Collection of Yeast Cultures strain NCYC 914) to freezing and thawing stresses. *S. cerevisiae* was selected for these studies, which form part of a long-term examination of the effects of preservation on the viability and stability of micro-organisms, because it has been reported to be unstable following some methods of preservation.

### The cell wall and freezing injury
At slow rates of cooling, it is generally assumed that cells are damaged by stresses associated with the removal of water, as ice, and consequent exposure to concentrated solutions. It was therefore decided to investigate whether the responses of *S. cerevisiae* to osmotic shrinkage and rehydration, at a constant temperature, provided an appropriate model system for determining the mechanism of freezing injury. Following short-term (15 min) exposures at 20°C to non-penetrating compounds such as sodium chloride and glycerol, the cellular viability upon rehydration was found to be dependent upon the external osmolality, decreasing as the osmolality increased within the range 1000-5000 mOsm (Figure 49). In contrast, with
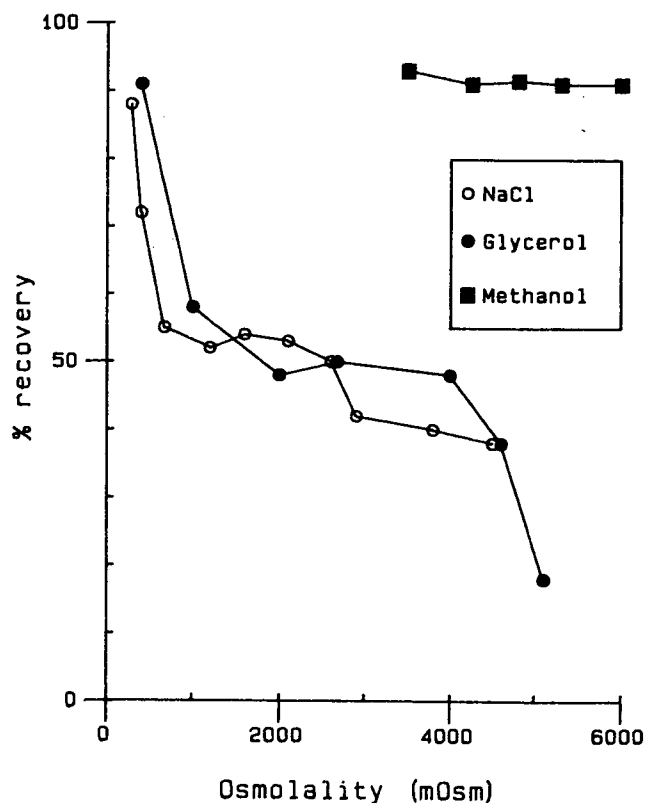


*Figure 49 Effects on subsequent recovery of exposing cells of* Saccharomyces cereviseae *NCYC 914 for 15 minutes to different concentrations of NaCl, glycerol and methanol*
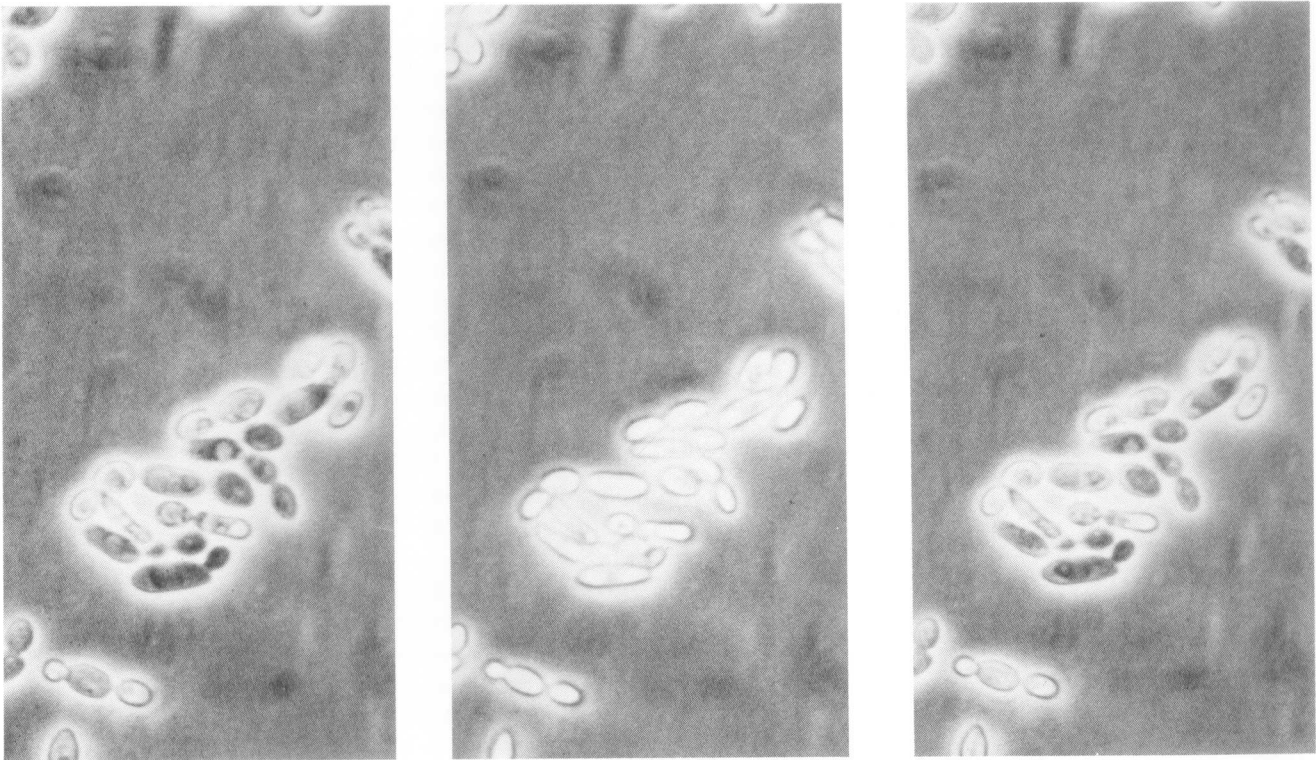
*Plate 16* *Effects of non-penetrating sodium chloride on suspensions of* Saccharomyces cerevisiae *NCYC 914*
  i.   *Cells in isotonic solution, the control*
  ii.  *Cells after exposure to 1.0 M NaCl for 100 seconds*
  iii. *The same cells resuspended in an isotonic medium for 60 seconds (light microscope × 1200)*
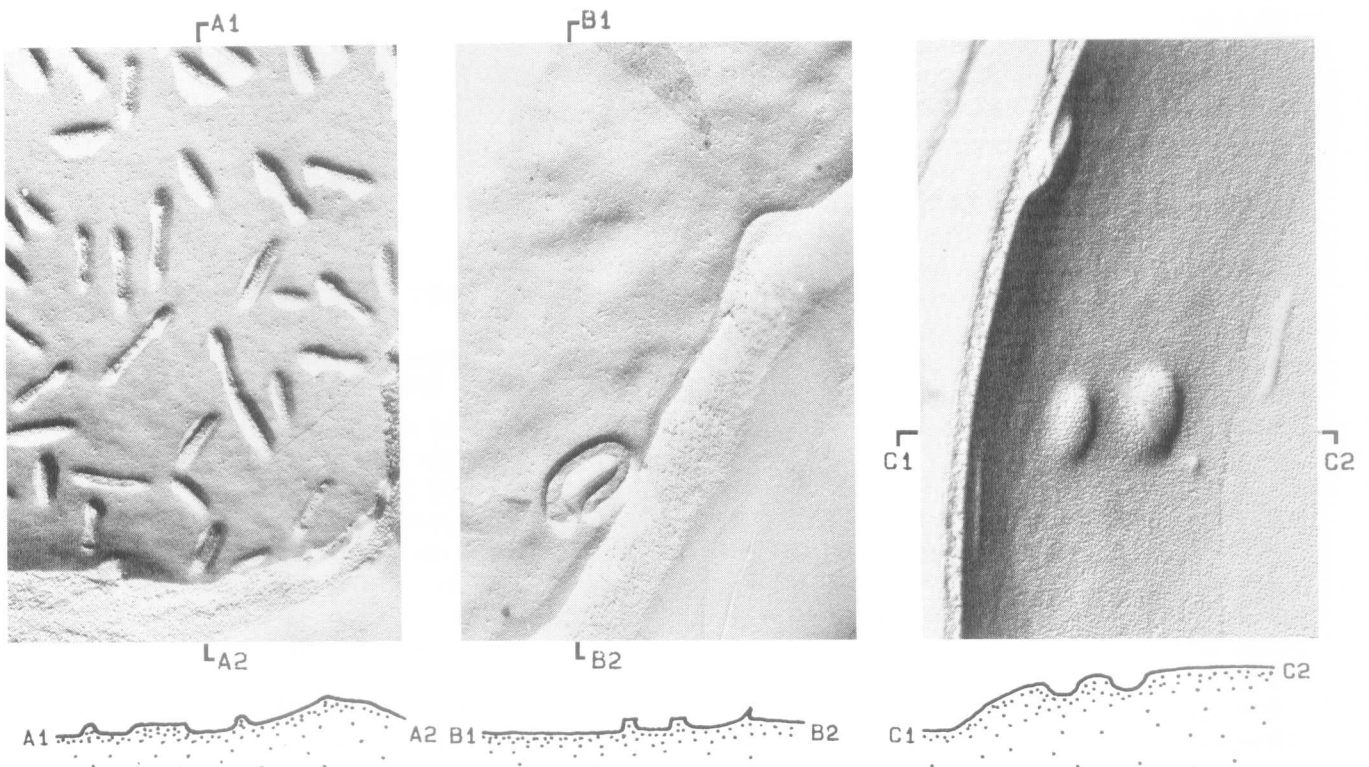*(Photograph Glynis E Coulson)*



*Plate 17 Freeze fracture electron micrographs of the effects of non-penetrating sodium chloride on* suspensions of Saccharomyces cerevisiae *NCYC 914*
  i.   *Cells in isotonic solution, the control*
  ii.  *Cells after exposure to 2.5 M NaCl*
  iii. *The same cells resuspended in isotonic medium*
*Schematic profiles shown below each micrograph (magnification ×40 000)*
*(Photograph K J Clarke)*

the rapidly permeating methanol, cellular damage was not observed even at osmolalities of 6000 mOsm. These results suggest, therefore, that osmotic shrinkage and rehydration, rather than increased osmolality *per se,* determine cellular viability.

When suspensions of *S. cerevisiae* were prepared in non-permeating additives (sodium chloride and glycerol), it was found, when using light and electron microscopes, that there was limited plasmolysis (separation of the protoplast from the cell wall) in addition to cell wall shrinkage (Plate 16). Using a specially constructed light microscope stage, enabling volume and surface area changes to be determined accurately, it has been found that cellular shrinkage occurred in hypertonic solutions of sodium salts ($Cl^-$, $I^-$, $Br^-$, $NO^{2-}$ acetate), chlorides ($Na^+$, $CS^+$, $Li^+$, $Rb^+$, $NH_4^+$, $K^+$, $Ca^{2+}$, $Mg^{2+}$, $Mn^{2+}$, choline) and non-ionic solutes (proline, glycerol, glucose, glycine-betaine). Thirteen strains of *S. cerevisiae,* and 14 of other species of yeasts responded similarly. In contrast, other cells with walls (eg plant tissue cultures and algae) plasmolyzed when exposed to hypertonic solutions at 20°C. Because this plasmolysis did not happen to *S. cerevisiae,* it seems that plasmalemma and cell walls are closely inter-linked: a possibly important determinant of cellular injury during freezing and thawing.

Using freeze-fracture electron microscopy of shrunken cells, it has been possible to identify major alterations in the organization of plasmalemma and cell walls with the appearance of novel structures which may have been formed by localized plasmolysis or by the projections of cell wall tissue into cytoplasm (Plate 17). These structural alterations were observed following exposure at 20°C or 0°C to solutions of either sodium chloride or glycerol, more concentrated than 2500 mOsm: they did not occur in hypertonic solutions at less than 2000 mOsm. Upon rehydration, these novel changes in cellular ultrastructure disappeared – they are reversible. They were not seen when rapidly permeating compounds (eg methanol) were used, even at concentrations of 5000 mOsm.

It is generally assumed that the primary site of cellular injury, induced by osmotic shrinkage and rehydration, is the cell membrane; the cell wall is not considered significant in determining cellular responses to osmotic and rehydration stresses. However, in *S. cerevisiae,* changes in cell walls were evident following shrinkage and rehydration either at constant temperatures or following freezing and thawing. Enzymic treatments which break down the cell walls of control, untreated, cells are ineffective against cells which have been through a shrinkage and rehydration cycle. The precise biochemical nature of the implied change in cell wall structure is currently being investigated. Is the change a primary cause of freezing or a secondary pathological effect?

*Selective effects of freezing*

Growth conditions before freezing may modify resistance to freezing injury; it has already been established that cells of *S. cerevisiae* maintained at both sub- and supra-optimal temperatures were more resistant to freezing injury than cells from cultures kept at the optimum temperatures for growth (24°C). Light microscope examination of the resistant cells cultured at 42°C (supra-optimal temperature) showed that they were morphologically distinct from those in cultures maintained at 24°C; they were smaller, and without mitochondria (when stained with specific histochemical stains). This absence was substantiated when the triphenyltetrazolium chloride overlay assay confirmed that more than 95% of cells grown at 42°C were respiratory-deficient mutants; at lower temperatures, there were fewer than 0·1% of these mutants.

As yet, factors conferring resistance to freezing injury on the respiratory-deficient mutants have not been determined. However, our observations demonstrate that, if there is a reduction in viability following cryopreservation, there is likely to be an enrichment of the population with pre-existing, freezing-resistant, respiratory-deficient mutants. While this enrichment might not be important – mutants would be rapidly outgrown by wild types — this system provides a useful model to investigate selection following cryopreservation and other methods of maintenance.

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**Programme 8**
## ECOPHYSIOLOGY AND POLLUTION IN ANIMALS

### FACTORS ASSOCIATED WITH THE VARIATION IN THICKNESS OF GREY HERON EGGSHELLS

The thickness of eggshells of the grey heron (*Ardea cinerea*) has been inversely correlated with the concentration of DDT metabolites (mainly DDE) in the egg contents, and measuring shell thickness has been suggested as a rapid and economical bioassay of DDE levels (Cooke *et al.* 1976). Marquiss (1983) collected eggshells in 1981-82 from 32 Scottish heronries, and demonstrated not only variation in the thickness of hatched eggshells between regions and habitats (presumed to be associated with varying DDE levels), but also variation associated with embryonic development and whether or not eggs were successfully incubated. With a sample of 88 heron eggs, with no embryonic development, the relationship between the thickness of an egg's shell and the DDE concentration of its contents is highly variable (Figure 50). Some of this variation is due to the variation in shell thickness within clutches, but this is of little help in assessing