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Institute of
Terrestrial
Ecology

**Ecology of blaeberry
and
its management
in
British moorlands**



Natural Environment Research Council

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SUMMARY

Review of existing knowledge

Blaeberry (*Vaccinium myrtillus*) is a long-lived rhizomatous dwarf shrub, usually 10–60 cm high. The stems are photosynthesising and stay green for several years; they gradually develop into thick woody axes and become prostrate. The plants mature slowly, the rhizome not forming till seedlings are three years old at the earliest.

Aerial growth starts relatively early in March–April in British moorlands, several weeks sooner than in other ericoid species growing there. Flowering occurs in May–June and berries develop by July–August; the yield of berries is affected by frost in the previous winter and during flowering.

Berries normally contain viable seeds and are eaten by birds and mammals. However, dispersal by transmission through animals seems to be infrequent, and seedlings are rare. Some workers have reported that the seeds remain viable in the soil for many years; others believe that viability quickly declines.

Blaeberry prefers well-drained acid soils, but is tolerant of shading and snow cover. Hence it grows in woodlands as well as moorlands, and ranges across Europe from Spain to Iceland and northern Norway. Ecotypic differentiation has been demonstrated in Britain and Finland, but no subspecies have been recognised.

Blaeberry responds only modestly to fertilizers, but suffers from trampling and cutting. It can survive fire and moderately heavy grazing but flourishes best when grazing is light and taller-growing species have not had time to become dominant.

The chemical composition of blaeberry and its availability in spring, due to growth starting early, and in winter, due to its green stems, make it a valuable food. In some nutrients blaeberry is of higher feeding value than heather, in others of lower value, but the differences vary seasonally. Studies have been made on aspects of the use of blaeberry by many different herbivores, including deer, grouse, lemmings (*Lemmus lemmus*), lepidopteran caterpillars, ptarmigan (*Lagopus mutus*), sheep and voles.

Studies on reproduction and establishment

Searches at and near blaeberry stands showed that seedlings occurred very rarely in Scottish moorlands.

The seed bank was examined from a moorland site that had blaeberry and heather (*Calluna vulgaris*) co-dominant. Despite regular and prolific fruiting, only two seedlings of blaeberry germinated in a glasshouse in 40 125-ml samples of surface soil; in comparison, hundreds of heather seedlings germinated. Further samples obtained in the following year yielded only one blaeberry seedling, and other moorland sites had negligible germination of blaeberry.

Seeds obtained by squashing berries had very high viability. Most germination occurred 10–20 days after sowing at a temperature of 20°C in bright light, but germination was slower in an unheated glasshouse. Less germination was obtained when seeds were sown on turves with lawn grass, mat-grass (*Nardus stricta*), or blaeberry dominant than on bare peat.

Seeds obtained from squashed berries were buried in autumn at two sites at 300 m and 710 m. There was little fall in viability to the next April, but then a rapid reduction in the following two years. Decline was sharper in the litter layer than the soil H layer, several samples buried in this latter horizon still having most seeds viable two-and-a-half years after burial. Some seeds were found to have germinated and then died in the litter layer, this presumably occurring in summer, despite the lack of light, due to high temperatures.

Few berries were found to be taken from the bushes, most falling to the ground. Observations on fallen berries showed that many disappeared within ten days, and some got opened and the seeds were removed. Voles and mice are believed responsible; captive voles quickly ate berries. It is suggested that the seeds are damaged in the digestive tract of the rodents, hence the small size of the seed bank.

Studies on impact and performance

Utilisation by herbivores at moorland sites in NE Scotland was greater in autumn and winter than in spring and summer. Blaeberry here grew amongst heather, and the herbivores showed on average a slight preference for heather; this was more marked when the blaeberry bushes were shorter than the heather. Cattle, mountain hares (*Lepus timidus*), rabbits (*Oryctolagus cuniculus*), red deer (*Cervus elaphus*) and sheep all grazed blaeberry substantially, shoot utilisation exceeding 45% at sites where these species were alone the principal grazers.

Effects of sheep grazing on two blaeberry-dominant swards were measured in the Peak District. Fencing was erected in 1990 so that year-round grazing could be compared with summer protection, winter protection and total protection. At one site heather was virtually absent, at the other it occurred in scattered patches with c 25% mean cover. Sheep occupance, as measured by pellet group counts, peaked in autumn at both sites; the sheep showed a relative preference for the pure blaeberry site from April to September, and for the heather/blaeberry site from October to March. When seasonally protected plots were reopened they attracted greater use than the continuously grazed plots; this difference persisted for several months in winter at the heather/blaeberry site.

Utilisation of blaeberry at these Peak District sites paralleled sheep occupance, occurring mostly between August and January. Utilisation also increased in April, especially in the newly opened winter-protected plots, the sheep biting into the previous year's shoots when taking new growth. The final end-of-winter levels of shoot utilisation averaged about 70%, the ungrazed shoots mostly occurring below the top canopy. Changes in botanical composition between 1990 and 1993 were small at the pure blaeberry site, but at the heather/blaeberry site the heather bushes both spread and grew taller, causing a significant decrease in blaeberry cover. Seasonal protection did not benefit blaeberry compared to year-round grazing, but total protection from grazing led to a fall in blaeberry cover; although blaeberry height increased significantly in these protected plots, there was a spread of grass and heather.

Long-term trends in blaeberry cover at moorland sites in NE Scotland have been monitored since 1969; blaeberry is here usually a minor species with cover less than 20%. Blaeberry was unreactive under many different grazing treatments, its only significant decrease occurring at a site where the heather exceeded 25 cm in height and gained in cover. At several sites where heather was much reduced by heavy grazing, blaeberry either gained cover slightly or was unchanged. At one site with negligible occupance from large herbivores, blaeberry has co-existed with heather and wavy hair-grass (*Deschampsia flexuosa*) for 24 years, blaeberry cover fluctuating between 35 and 40%. Only after a severe frost in 1975 was cover temporarily reduced to 25%.

Effects of muirburn were assessed at two sites in NE Scotland, and cutting treatments were imposed in the ungrazed control plots at the Snake Pass sites. Blaeberry increased significantly in cover over one cycle of muirburn at one of the Scottish sites; the cutting treatment caused more branching, giving a shoot density similar to the grazed stands.

Studies on palatability and value to herbivores

Blaeberry and heather shoots were presented to captive red grouse (*Lagopus lagopus scoticus*), black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao urogallus*) in replicated trials in summer 1991; before the trials the birds had been fed on pellets and fresh heather. Red grouse preferred heather, capercaillie selected for blaeberry, and black grouse showed no preference. Cocks of all three species took relatively more heather than hens.

In similar tests on chicks of red and black grouse, the food given immediately before the trials was varied, either heather or pellets being omitted. In both grouse species heather was preferred, but preference was greater when heather had not been available in the 24 hours before the trials. Preference for heather over blaeberry declined during the trials.

In four-day digestibility trials with cock grouse in summer, it was found that the blaeberry eaten was 6% less digestible than the heather eaten (ranges 73–75% cf 72–81%). The total daily intake of dry matter increased as digestibility of diets containing blaeberry declined, but the rate of increase was not significant. Birds lost weight on diets of pure blaeberry or heather, despite eating large amounts.

At the Snake Pass sites, red grouse ate considerable quantities of blaeberry, both stem and leaf fragments being found in the faecal droppings. Heather was eaten in greater proportion than its extent on the sites. At a moorland site in NE Scotland with blaeberry occurring sparsely as an understorey within the heather bushes, more blaeberry was eaten by sheep than by red deer, judging from epidermal fragments in their dung.

Studies on propagation

The survival of cuttings planted out into a peat/sand compost was not affected by treatment with hormone rooting powders. Survival was also unaffected by cutting length. Fertilizer applied at 12.5 kg ha⁻¹ gave a modest increase in total dry weight after 12 months, but higher rates of application showed no extra benefit.

Six propagation techniques were compared at a grassland site at 300 m. Turf plugs taken from nearby moorland proved a total failure, and no germinations were recorded from seed sowing. The most successful technique was transplanting rooted cuttings, followed in declining order by transplanting rooted stems newly dug from nearby moorland, transplanting year-old seedlings in paper pots, and smearing berries. For all four of these techniques

there was greater success in ground pre-treated with herbicide.

At another site, seed sowing gave no establishments, whilst in a short grass turf smearing berries gave some germinations but the seedlings quickly died. Transplanting bare-root cuttings met with 23% survival at 1000 m on Cairngorm, and 20% survival at 640 m on the Lecht; turf plugs were very successful here with 80% survival after a year.

General discussion

The distinctive characters of blaeberry are outlined, and reasons why blaeberry has apparently less competitive ability than heather are put forward. It is considered that blaeberry-dominant moorland in Britain has resulted either from the occurrence of regular muirburn or from the loss of tree cover in ground once woodland. The conservation of blaeberry moorland is urged, stands being relatively scarce and supporting distinctive invertebrates, besides being valuable for game-birds and livestock.

INTRODUCTION

Blaeberry (*Vaccinium myrtillus*) has widespread occurrence in British moorlands and sometimes is the dominant species. More usually, however, blaeberry is subsidiary to heather (*Calluna vulgaris*), occurring as an understorey species or where heather dominance has been checked, eg along paths, on steep slopes or by rock outcrops.

Ecological studies on moorland species have tended to focus on the main dominants, ie heather and grasses, or the rare plants, and blaeberry has been comparatively neglected. Nevertheless, a considerable body of knowledge on blaeberry has been built up in western and northern Europe, which will be reviewed in the next section; well over 100 references have been examined.

This present study has been financed by the Joseph Nickerson Heather Improvement Foundation. It was motivated by the known value of blaeberry as a food for red grouse (*Lagopus lagopus scoticus*), and by the apparent greater tolerance of blaeberry than heather to heavy grazing pressures; in some districts where heather has declined, grouse populations seemed to be feeding largely on blaeberry. It was envisaged that blaeberry could have a role in making degraded 'white' moorland become valuable for red grouse. There was also concern that existing moorland dominated by blaeberry should not degenerate because of injudicious management. In order to manage blaeberry effectively in these varying situations, greater knowledge on its performance, establishment and propagation was required.

REVIEW OF EXISTING KNOWLEDGE

Many basic facts about blaeberry are contained in the *Biological Flora* account (Ritchie 1956), and Flower-Ellis (1971) provides detailed information on the structure and growth dynamics of its bushes. The plant has several other English names – bilberry, whinberry and whortleberry are the most well known.

Blaeberry is a deciduous, rhizomatous, dwarf shrub with aerial shoots normally between 10 cm and 60 cm in height; a top height of 100 cm is given by Stace (1991). The aerial shoots are of two types: long vegetative shoots which persist to form the framework of the bushes, and short axillary flowering shoots which normally fall after fruiting. The long shoots arise from the rhizomes, either from side branches or from the main rhizome turning upwards; other side branches then continue the underground growth. Both sorts of shoots have photosynthesising stems, which stay green in persisting shoots for several years and develop into thick woody axes. These axes last for up to 30 years (Flower-Ellis 1971), gradually becoming prostrate.

In seedlings the rhizome does not develop till the third year at the earliest (Sylvén 1906). The rhizomes then branch and grow into the surrounding area, producing roughly circular groups of shoots. Patches several metres in diameter have been shown to be a single clone, and Flower-Ellis quotes workers who have excavated rhizomes up to 8 m long. Annual outward growth of 40 cm by the rhizomes has been recorded, but probably the average extension is considerably less. Moreover, the expansion of the patch diameter is unlikely to be double this figure, as the alignment of the outermost rhizomes will not be exactly radial. Although the rhizomes decay when old, the vacated space appears to be reoccupied by other rhizomes, so that circular patches lacking shoots in the centre have not been reported. Anderson (1961), studying upland stands in north Wales, found that the portion of rhizome actively producing aerial shoots was usually younger than 15 years and less than 90 cm long.

Aerial growth starts relatively early in March–April (Ritchie 1956; Woolhouse & Kwolek 1981). Flowering occurs in May–June and berries develop by July–August. There is often a second period of flowering: this is reported as occurring in early summer by Ritchie, but Yalden (1983), in detailed studies on the availability of flowers for moorland bumblebees (Hymenoptera: Apidae), recorded flowering in late August and September in the Peak District. Ritchie (1956) lists many insects as pollinators but also observed self-pollination;

because the insects tend to visit nearby flowers, Ritchie considered blaeberry an habitual inbreeder.

Fruiting and the factors affecting fruit yields have been much studied in north-eastern Europe (Kuchko 1988; Raatikainen & Vänninen 1988), the berries being harvested as a crop in some areas. Frosts during flowering, and severe frosts in the previous winter greatly reduce yields, and there are also relationships with the extent of shading in forests and the depth of snow cover, snow giving protection from frosts.

The berries normally contain viable seeds; Ritchie (1956) reported a mean of 18 fully mature seeds per berry, and germination percentages ranging from 35% to 64%. Grime *et al.* (1981), studying plants from Yorkshire, found that mean seed weight was 0.26 mg, that freshly collected seeds gave a germination percentage of 95%, and that the time for 50% germination was 20 days. The berries are eaten by many birds including grouse, partridge (*Perdix perdix*), pheasants (*Phasianus colchicus*) and ptarmigan (Ritchie 1956) and also by mammals (Heintze 1915). However, it is not known how many seeds are dispersed in this way; Welch (1985) did not find any blaeberry seedlings germinating in the dung of cattle, deer, red grouse, hares (*Lepus spp.*), rabbits (*Oryctolagus cuniculus*) and sheep deposited on moorland, although heather seedlings were numerous.

Many workers consider that the seedlings of blaeberry are rare in natural habitats and that reproduction is largely vegetative (Kujala 1926; Södergård 1934; Perttula 1941; Ritchie 1956; Flower-Ellis 1971). Death during transmission by frugivores, rapid decline in viability in soil or litter, specific germination requirements and lack of niches are likely explanations for seedling rarity, but it is unclear which is the principal cause. Thus, Granström (1982) found many viable seeds of blaeberry in the seed banks of Swedish coniferous forests, and in five-year burial experiments viability remained high (Granström 1987); on the other hand, Hill and Stevens (1981), studying Welsh conifer plantations in which blaeberry formerly or currently had high cover in the ground vegetation, found very few viable seeds. Their interpretation was that the seeds die quickly, and they suggested that viable blaeberry seeds in the litter of a site lacking a field layer had entered recently in bird droppings.

Blaeberry has a wide distribution in Europe and North Asia, extending to Iceland, northern Norway, Spain and the Caucasus. It prefers well-drained and acid soils (Ritchie 1956), and requires a stable, well-

aerated humus layer (Sjors 1989). It is tolerant of shading and snow cover, which helps explain its distribution pattern. Thus, blaeberry is abundant in some woodland types, particularly birch (*Betula* spp.) and pine (*Pinus* spp.), and can withstand shading better than heather (Hester, Miles & Gimingham 1991a, b). In alpine and subarctic regions, blaeberry is limited both by a lack of snow protection and also by too much snow accumulating, which causes the growing season to be too short (Sjors 1989); phytosociological descriptions of European subalpine communities dominated by blaeberry are given by Schaminée, Hennekens and Thébaud (1993). In Britain, blaeberry is scarce in the lowlands due to the lack of moorland and woodland habitats. In the uplands it has little cover in blanket bogs and where heather is strongly dominant, but is more prominent when heather is checked by grazing pressures or altitude. However, it seems to thrive best in heaths with moist soils (H12 in the classification of British moorland communities by Rodwell 1992), and tends to be replaced by bell heather (*Erica cinerea*) in drier, warmer districts (H10 heaths).

Considerable knowledge now exists on the growth and performance of blaeberry, and the effects of fertilizer treatments and other impacts. Ecotypic differentiation has been demonstrated within Britain (Butler 1985; Woodward 1986) and within Finland (Vanninen, Laakso & Raatikainen 1988), so caution is necessary in extrapolating from studies on single populations. In Britain, seeds from Sussex and six Scottish sites with altitude ranging from 120 m to 1000 m were germinated in controlled experiments (Butler 1985); the Sussex population had the greatest seed weight, fastest germination and fastest growth rate, and the Cairngorms high-altitude populations, though having the slowest growth rates, performed better at 15°C than 22°C. Differences in height between plants collected at 200 m, 610 m and 1100 m on Ben More in Argyll persisted in cultivation (Woodward 1986); the higher-altitude plants had shorter and thinner stems, and their leaves bore more stomata. Photosynthetic rate was found to be directly related to altitude. In Finland, transplanting turves to a single site showed that plants from the north had significantly lower annual growth increment than plants from the south (Vanninen *et al.* 1988); this was considered to be a response to lower winter temperatures and the need for shoots to be covered by snow for protection. Latitudinal differences in heat and cold resistance are also known (Bannister 1970; Havas 1971). Despite the known geographical and ecotypic variations in morphology, only one form (*f. pygmaea*) has been thought sufficiently distinct to be given recognition (Ritchie 1956).

Blaeberry has been found to respond only modestly to increased nutrient levels. Hester *et al.* (1991a), giving fertilizer treatments to *in situ* vegetation in moorlands and birch woods in NE Scotland, observed both losses and gains in blaeberry cover and concluded that competition from heather and wavy hair-grass (*Deschampsia flexuosa*) was controlling blaeberry performance, and that the response of the latter species to fertilizers and shading determined the reaction of blaeberry. In pot trials with rooted shoots of blaeberry, the same fertilizer treatment raised shoot weights by 49% and height by 13 cm over a two-year period, but these increases were negligible when wavy hair-grass was growing in the pots; these authors suspected that blaeberry performance was being impaired by restrictions to the root system in the 4435 ml volume pots. Summers (1978) also gave fertilizer treatments to *in situ* vegetation, on a site at 990 m in the Cairngorms. Wavy hair-grass, stiff sedge (*Carex bigelowii*) and three-leaved rush (*Juncus trifidus*) increased in cover in the fertilized plots at the expense of blaeberry, despite improved growth in individual shoots of the blaeberry; shoot length was raised from 4.1 cm to 4.7 cm by the full fertilizer treatment, and leaf area from 80 mm² to 114 mm². In culture experiments with seedlings from a Swedish forest source, Ingestad (1973) found that, as nitrogen concentrations increased, there was first a slight increase in growth rate and then a sharp decline, high concentrations being lethal.

Trampling and cutting impacts on blaeberry have been studied by Anderson (1961), Watson (1985) and Hester *et al.* (1991a). Anderson imposed cutting treatments to ground level and stamping with a hammer on 1 m² plots of grassy *Vaccinietum* in north Wales. Both treatments lowered standing crops in the following summer, and lowered the leaf/stem ratio; Anderson believed that reduced aeration in compacted soil caused the poorer performance. Watson (1985) observed that transects affected by skiing and trampling at about 1000 m on Cairngorm had negligible cover of blaeberry, whereas nearby undisturbed transects had cover of 3–5%. Clipping to a height of 5 cm was imposed on *in situ* vegetation at the Scottish moorland and birch wood sites previously quoted (Hester *et al.* 1991a); all green material from the current and previous years' growth was removed initially, then new growth was removed in two further cuts, clipping twice a year. After 18 months, blaeberry cover was significantly reduced but grasses were unaffected. Conversely, the removal of grazing in a south Pennine oak (*Quercus* spp.)/birch wood with a short turf dominated by wavy hair-grass in 1955 led to rapid recovery of blaeberry (Pigott 1983); shoot height reached 7–15 cm by 1959 and 25–40 cm by 1961, and cover increased from 1% in 1956 to over 50% in 1965.

Fire is a major biotic factor affecting blaeberry. Ritchie (1956) believed that burning seldom destroyed more than the aerial shoots, and that rapid colonisation of burnt moorland often occurred from the surviving rhizomes. A subseral blaeberry stage following heather burning has been described by Adamson (1918) and Elliott (1953).

Although blaeberry is usually viewed as a subsidiary species controlled by other stronger-growing plants, there is a suggestion that it can influence vegetation composition by producing toxic substances (Andre *et al.* 1987).

The chemical composition of blaeberry and its ready availability throughout the year make it a valuable food for herbivores. Thomas and Trinder (1947) showed that both leaves and stems were rich in calcium (Ca), and that the phosphorus (P) content was greater than in most other British moorland plants. Trinder (1975) considered that the new shoots were of higher feeding value than young heather shoots, but that in autumn and winter the leaves had similar value to heather. Powell and Malcolm (1974) sampled seasonally the aerial standing crops of several communities in the Pentland Hills, and found that blaeberry stands peaked earlier in nitrogen (N), P and potassium (K) than heather, and had higher Ca and N levels but a lower level of K. Stewart and Bannister (1973) showed that carbohydrate levels in aerial shoots of blaeberry peaked in August and stayed high during autumn and winter. Pakonen *et al.* (1991) reported that glucose, fructose and sucrose concentrations peaked in November, the glucose and fructose occurring mainly in the shoots and the sucrose in the underground stems. Further information on blaeberry nutrient content is contained in papers by Karlsson (1987), Pakonen *et al.* (1988) and Pulliainen and Tunkkari (1991).

Recent workers have made detailed investigations of the nitrogen and organic chemistry of blaeberry, these studies being in part attempts to explain the cycling of vole and lemming populations in Scandinavia. The nitrogen of blaeberry is held mainly in proteins, part being stored as amino-acids in autumn and winter (Lähdesmäki *et al.* 1990a, b); heavy grazing does not raise phenol concentrations (Laine & Henttonen 1987; Oksanen & Ericson 1987), so blaeberry is thought unlikely to be a causal factor in microtine cycling. Other comparisons are attempts to explain food selection in particular environments; for example, Tschager *et al.* (1982) found blaeberry at 2000 m in an alpine heath to have lower lipid contents than bearberry (*Arctostaphylos uva-ursi*), heather, crowberry (*Empetrum nigrum*), trailing azalea (*Loiseleuria procumbens*) and cowberry (*Vaccinium vitis-idaea*).

Studies on the palatability of blaeberry to herbivores have been few. Using captive ptarmigan, Summers (1971) found that in two trials heather was preferred to blaeberry, and in a third trial preference was equal, but he suspected that pre-trial feeding influenced the results. Judging from rumen samples, Hudson *et al.* (1975) considered blaeberry was eaten more by red deer than by sheep in the east Grampians, but heather and grasses were the main foods for both herbivores.

Blaeberry is known to support considerable populations of invertebrates, particularly Lepidoptera whose larvae feed on the leaves. Moreover, blaeberry flowers provide a valuable source of pollen for some bees (Yalden 1983, 1984). Ritchie (1956) lists 20 lepidoteran feeders and also some aphids, scale insects and saw-flies (Hymenoptera: Symphyta). Fielding (1992) found from the literature that the larvae of 57 macrolepidopteran species and 23 microlepidopteran species were known to use blaeberry, and in her own observations at sites ranging from 290 m to 650 m in Co Durham saw 15 macrolepidopteran species feeding on blaeberry. In Swedish spruce forests the most numerous taxa using the blaeberry-dominant field layer were geometrids, tortricids and pyralids (all Lepidoptera), and saw-flies (Atlegrim 1992).

Lepidopteran and saw-fly larvae are important foods for the chicks of capercaillie (*Tetrao urogallus*), black grouse (Picozzi 1986; Baines 1991, 1993) and red grouse, and in Scottish pinewoods the numbers of larvae are directly correlated with the size of the blaeberry standing crop (Baines & Sage 1992). In comparisons of nearby blaeberry and heather stands at the Co Durham moorland sites (Fielding 1992), densities of lepidopteran larvae were found to be greater on blaeberry in the May–June period; this probably results from the earlier onset of growth in blaeberry. It is in spring that the game-bird chicks need insect food, so the presence of stands of blaeberry within heather moorland could lead to better survival of chicks. Fielding (1992) also studied the development rates of three larval species common on blaeberry and heather – July highflyer (*Hydriomena furcata*), northern spinach (*Eulithis populata*) and the chevron (*Eulithis testata*); development appeared to be faster on blaeberry than heather.

Finally, we comment on *Vaccinium intermedium*, the hybrid between blaeberry and cowberry. This has a puzzling range, occurring on several moors in Derbyshire, Staffordshire and south Yorkshire and also sporadically in north Germany, Poland and NW Russia (Ritchie 1955), yet it has never been recorded in many regions where the parents grow together. Ritchie suggested that the flowering of the two parents coincided more closely at certain

latitudes and altitudes, and that there was greater abundance of blaeberry and cowberry in the south-east Pennines because these areas experienced more irregular burning regimes than other British moorlands (Elliott 1953). *Vaccinium intermedium* reproduces largely vegetatively; although berries are produced, they contain few seeds and the seeds have low germination rates (Ritchie 1955).

STUDIES ON REPRODUCTION AND ESTABLISHMENT

In these studies we sought to confirm the reported rarity of establishment from seedlings, and to explain this anomaly in a plant that fruits prolifically.

Seedling occurrence

Moorland containing blaeberry was closely searched each summer in NE Scotland, Argyll and Derbyshire, with 15-minute inspections of likely niches near fruiting stands, eg paths, mole-hills, rabbit holes, and other ground lacking a field layer. At most sites no blaeberry seedlings were found but other dicotyledonous seedlings were noticed, eg heather, harebell (*Campanula rotundifolia*), heath bedstraw (*Galium saxatile*), tormentil (*Potentilla erecta*) and chickweed wintergreen (*Trientalis europaea*). At three sites there were seedlings of blaeberry, all in disturbed areas: Rothiemurchus, Inverness-shire, NH 9--0--, on bare mineral soil in a small quarry; Hill of Kirkney, Aberdeenshire, NJ 49-31-, at 400 m, on an old stony track with many fruiting bushes on the banks; Clash Hill, Aberdeenshire, NJ 59-06-, at 300 m, on trampled ground within two grouse butts. The total number of blaeberry seedlings observed was only 20, confirming their rarity.

Viable seed bank

The Clash Hill site at which blaeberry was known to have fruited regularly throughout the previous 20 years was chosen for study. Patches of blaeberry

and heather co-existed, but in places one species was replacing the other. The surface soil was sampled in April 1990 and April 1991, cores being taken to a depth of 5 cm after loose litter had been cleared. In 1990, 40 samples were obtained for four vegetation history types judged on 20 years of observations (heather-dominant throughout, blaeberry-dominant throughout, blaeberry replacing heather, heather replacing blaeberry), and a nearby grassy moorland was also examined. In 1991, six further samples were obtained at positions where blaeberry had been dominant for 20 years. Each sample was made up of eight 2 cm diameter cores and totalled approximately 125 ml. The samples were spread out in trays in a glasshouse, and germinations were counted at fortnightly intervals until their rate of occurrence became negligible after about four months.

Very few blaeberry seedlings germinated: only one in each of the vegetation types dominated by blaeberry in the 1990 trials, and only one in the 1991 trial (Table 1). The great majority of germinations were of heather, and numbers were greater in samples from the positions where heather was currently dominant. The grassland site yielded many grass germinations, as expected; these were mostly of common bent (*Agrostis capillaris*) and wavy hair-grass.

In other determinations of the seed bank of moorland sites in NE Scotland (Miller & Cummins 1985; G R Miller & J Miles, pers. comm.),

Table 1. Mean number of seedlings germinating from 125 ml samples of moorland soil obtained from 0-5 cm cores from different vegetation types at a site in NE Scotland

Vegetation type	Collected April 1990			Collected April 1991		
	Heather	Heather formerly blaeberry*	Blaeberry formerly heather*	Blaeberry	Grassland	Blaeberry
SPECIES						
Blaeberry			0.1	0.1		0.2
Heather	58	64	43	29	5	14
Bell heather	1			2	1	
Tormentil		0.2		0.7		0.3
Other dicotyledonous plants					1	0.8
Graminoids (= grasses, sedges and rushes)	1	1	0.4	5	40	5

*Average time since vegetation change = 10 years

blaeberry germinations were zero or negligible. But at these sites blaeberry, if present, was not known to have fruited regularly, unlike the Clash Hill site reported here.

Viability of seed from collected berries

Berries were collected in July–August 1990 from Eredine (NM 01-13-, 250 m), Hill of Kirkney (NJ 49-31-, 400 m), Bin of Cullen (NJ 47-63-, 230 m), Clash Hill (NJ 59-06-, 300 m) and Bennachie (NJ 69-24-, 250 m), and in August 1991 from Glen Dye (NO 64-84-, 230 m). The berries were squashed through fine sieves which retained the seeds, and the residues of seeds and pulp were air-dried; the dried residues consisted mainly of seeds and were kept at room temperatures. Seeds were later counted out individually for experimental use. Germination trials were conducted above a water bath kept at 20°C and given continuous bright light; the seeds were placed on rockwool discs in Petri dishes.

The 1990 seeds were found to have a germination percentage of 87% in a test on 150 seeds, started in November 1990. Seeds from this source were used in the burial test of longevity, and 990 seeds buried from September 1990 to April 1991 gave a mean germination percentage of 89% in May 1991 (210 seeds in seven buried bags that had high decay were omitted in this calculation). The 1991 seeds gave a germination percentage of 94% in a test on 150 seeds started in November 1991.

It is evident that blaeberry at moderate altitudes in Scotland normally produces a high percentage of viable seed. Although the five sites sampled in 1990 were not tested individually, there were so few non-viable seeds in the bulked material that at no site could viability have been less than 50%. Similar high viability of seeds is reported from Yorkshire (Grime *et al.* 1981, see literature review).

Seed longevity

Longevity was tested by burying seeds in the litter and surface soil at two Scottish sites. At Clash Hill three habitat types were examined at 300 m, respectively grassy, blaeberry-dominant and heather-dominant, and another blaeberry-dominant sward was used at Cairnwell at 710 m (NO 14-77-). Seeds were counted out in batches of 30 and placed in 5 cm x 5 cm polyester bags. The bags were buried in September 1990 in shallow scrapes at the top of the soil humus layer and within the litter layer above this, the litter being carefully replaced. For each habitat type there were five replicate positions and at each position three bags were buried in both layers; after the litter had been replaced, wire mesh

was positioned above and anchored down to prevent disturbance by animals. Bags were removed from the sites in April 1991, April 1992 and April 1993, one bag being taken from each layer at each position on each occasion. Other bags lying in the litter and soil were disturbed as little as possible in the 1991 and 1992 collections, and the litter was put back as it had been before the sampling. The exhumed bags were carefully opened and the seeds were placed on rockwool discs to measure percentage germination. Similar conditions were imposed as in the initial viability test described above.

A rapid decline in seed viability occurred in both litter and soil in all habitats (Table 2a), the difference between 1991 and the two later years being highly significant ($P < 0.001$). Decline was sharpest in the litter layer: nearly half the bags recovered in 1993 contained no viable seeds (Table 2b). But in the soil H horizon viability was little reduced in some bags, three bags in 1993 having 24–28 seeds still viable out of the 30 buried. Longevity was affected by habitat type, especially in the H horizon, differences there between types being significant ($P < 0.05$) in 1991 and 1992; viability fell more rapidly in the grass and heather-dominant habitats than in the blaeberry swards.

Seeds could have died from decay, or because they germinated *in situ* in the field, or because small invertebrates penetrated the bags and ate or removed the seeds. This last cause was unimportant because nearly all the buried seeds were recovered, but a considerable number of dead germinated seedlings were found in the bags, particularly those placed in the litter layer. In checks in September 1991 on six bags at three positions at Clash Hill with blaeberry dominant, six living seedlings whose green cotyledons had broken through the polyester material were observed. It seems likely then that for the litter layer premature germination brought about by high temperature is the main cause of loss, whereas for the H horizon decay caused by fungi or micro-organisms is important; this decay is no doubt related to small-scale patterns in soil conditions, so that in the same habitat some bags had negligible losses but others nearby had no or very few viable seeds.

Berry dispersal

Berries are ripe by August and fall from the bushes later in the month (Table 3). Ritchie (1956) implied that dispersal was mostly by birds eating the berries, but this was not true at the sites observed. Many berries were seen on the ground below bushes in late August, and bushes had fractured pedicels rather than bitten ones. Moreover, the red

Table 2. Decline in viability of seeds placed in litter and soil in contrasting habitats
a. Mean germination percentages

Site and altitude	Vegetation dominant	% germination					
		Litter layer			H horizon		
		1991	1992	1993	1991	1992	1993
Clash Hill (300 m)	Grass	64 ^a	14 ^a	4 ^{ab}	51 ^a	14 ^a	28 ^a
Clash Hill (300 m)	Heather	74 ^a	11 ^a	3 ^a	61 ^{ab}	44 ^a	12 ^a
Clash Hill (300 m)	Blaeberry	92 ^a	12 ^a	2 ^a	94 ^b	69 ^b	53 ^a
Cairnwell (710 m)	Blaeberry	88 ^a	16 ^a	9 ^b	95 ^b	22 ^a	33 ^a

Within years, means with different superscript letters differ significantly ($P < 0.05$)

b. Number of sample bags in viability classes

		Number of bags					
		Litter layer			H horizon		
		1991	1992	1993	1991	1992	1993
Bags with percentage germination at the four sites	0	0	2	9	0	2	2
	1-25%	1	16	10	3	9	6
	26-75%	3	2	0	4	7	6
	76-100%	16	0	0	13	2	3
Total bags collected		20	20	19	20	20	17

and black grouse population was too small in the years of study to remove a significant part of the berry crop, whilst partridge and pheasant were absent and ptarmigan occurred only at the Cairnwell site. Smaller frugivorous birds such as mistle thrushes (*Turdus viscivorus*) were also infrequent on the moors, and fieldfares (*Turdus pilaris*) and redwings (*Turdus iliacus*) arrive only after the berries have fallen.

The fallen berries soon disappeared at the study sites (Table 3) and by late September few were visible on the ground. The berries are probably

eaten; small mammals, insects, or molluscs are likely to be responsible. In 1990 the position of ten newly fallen berries was recorded on 23 August at the Bennachie site; by the next visit on 11 September, seven berries had gone and the three remaining were shrivelled up. Further observations were made in 1991 (Table 4). Over half the berries positioned were lost within ten days, and in the two later trials most of the berries remaining had been opened and the seeds removed (Figure 1). Only animals with small mouths and a capability of grasping the berries could do this, and we believe mice or voles are responsible. A 'mouse' hole

Table 3. Observations on berry ripening and dispersal

Site	Altitude (m)	Berries ripe but not falling	Berries both on bushes and ground below	Berries very few on bushes and on ground below
Eredine	250	25 July 1990		
Bin of Cullen	230	1 August 1990		
Hill of Kirkney	400	9 August 1990		
Bennachie	250		23 August 1990	11 September 1990
Glen Dye	230	15 August 1991 21 August 1991	27 August 1991	13 September 1991 ¹ 21 September 1991 ¹
Tillypronie	380		15 September 1993	
Buck of Cabrach	450			11 September 1993
Clash Hill	300			15 September 1993
Glen Clunie - Cairnwell	450-680			16 September 1990 ²

¹ c10% of crop still on bushes on 13 September, c2% still on bushes on 21 September

² Berries only found on bushes above 600 m, and here more were lying on ground than present on bushes

Table 4. Observations on the disappearance of fallen berries at Glen Dye in 1991

Trial 1	Number of berries							
	Trial 2		Trial 3		Position			
	Position 1	Position 2	Position 1	Position 2	Position 1	Position 2		
27 August	26	24	10 September	16	11	20 September	20	20
28 August	20	20	12 September	15	9	23 September	8 ^e	10 ^e
2 September	9	13	13 September	15	9	28 September	8 ^e	10 ^e
10 September	3	2	20 September	2 ^e	3 ^e	1 October	7 ^e	6 ^e

^eIndicates that some or all the berries counted had seeds eaten *in situ*

appeared near position 1 in the first 1991 trial, and tiny rodent droppings were found at the end of trial 2 (Table 4). Also, berries given to captive field voles (*Microtus agrestis*) were eaten within two hours, with no traces left.

Berries are known to be an important food for small rodents. Boström and Hansson (1981) reported that *Vaccinium* berries had been eaten by 100% of the bank voles (*Clethrionomys glareolus*) trapped in a Swedish forest in September 1977, and by 52% of the voles in a nearby mire. In that forest *Vaccinium* berries contributed 75% of the diet of bank voles in September and presumably blaeberry was the main species; in the mires bog bilberry (*V. uliginosum*) also occurred. *Vaccinium* berries were also present in small amounts in the diet of field voles (*Microtus agrestis*) at the same sites. In feeding trials in Poland, Drozd (1966) observed that bank voles readily ate berries of blaeberry, but yellow-necked field mice (*Apodemus flavicolis*) took smaller quantities. In trapping studies at reafforestation sites in northern Sweden, *Vaccinium* berries made up 50% of the diet of bank voles in July, and c10% of the diet of field voles (Hansson & Larsson 1978). The comments by Corbet and Southern (1977) also point to voles or mice being responsible for the opened fruits found in the present study – wood mice (*Apodemus sylvaticus*) and bank voles are reported as opening hazel nuts

by making a hole, and wood mice take the carpels of rose hips but discard the flesh. In a study on fruit dispersion in guelder-rose (*Viburnum opulus*) in central Sweden (Englund 1993), bank voles and yellow-necked field mice were found to take 26% of the fruits. These rodents and bullfinches (*Pyrrhula pyrrhula*) were considered seed predators eating and destroying the seeds, whereas waxwings (*Bombygilla carrulus*) and thrushes were judged seed dispersers; only 1% of the fruits were dispersed by the seed dispersers in the study years.

Effects of surface vegetation on germination

Seeds from the 1990 berry collection were divided into 36 aliquots, the average seed number being estimated from two counts which gave 448 and 453 seeds. Turves were placed in plant pots with six replicates for mat-grass-dominant turf, six replicates for blaeberry-dominant turf, and 12 replicates of a mossy lawn turf; a further 12 replicates with unvegetated peat humus were used as controls. In early 1991 the seed aliquots were scattered over the 24 turves. Six of these controls and six lawn turf replicates were placed above a water bath kept at

Table 5. Effect of surface vegetation on percentage germination observed in a glasshouse and a growth chamber

	Mean % germination	No. samples with <50% germination (out of 6)
Bare peat		
Growth chamber	73	0
Glasshouse	64	1
Mossy lawn turf		
Growth chamber	23	6
Glasshouse	Trace	6
Blaeberry turf		
Glasshouse	1	6
Mat-grass turf		
Glasshouse	9	6

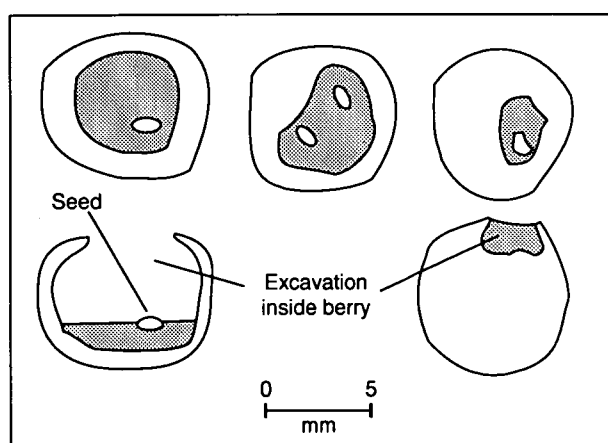


Figure 1. Top views, cross-section and side view of berries from which pulp and seeds have been removed

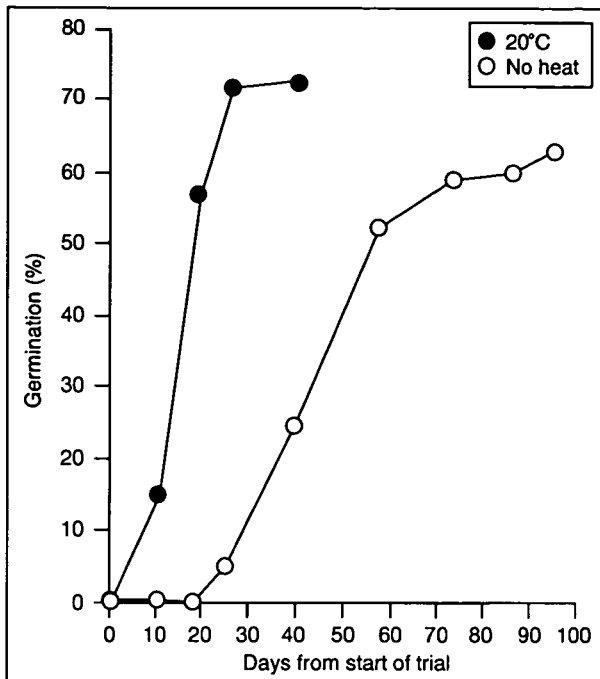


Figure 2. The onset of germination in a growth chamber kept at 20°C and in an unheated glasshouse in February–May

20°C and given continuous bright light as in the germination trials (p12). The remaining 24 replicates were placed in a glasshouse given heat only to prevent frosting.

Germination was much affected by surface type (Table 5). Even on bare peat, percentage germination was lower than the potential average of 87% measured in the trials on rockwool discs, this difference being significant in *t* tests ($P < 0.05$). On the peat, seeds could have fallen into cracks, could have decayed, or could have been eaten by soil invertebrates. In the glasshouse there was a slower onset to germination due to the lower temperature (Figure 2), and this gave more time for losses to occur. On turf types that blaeberry berries could reach in the wild, germination was at most 23%. For the lawn turf, the difference in germination between the glasshouse and growth chamber doubtless resulted from the dense growth of grass and moss (*Rhizidiadelphus squarrosus*) which developed in the glasshouse before germinations could have been expected. The mat-grass turves had the least moss layer, and gave rise to the highest germination in the glasshouse on turves, albeit only 9%.

DISCUSSION

The tests of germination on different substrates are consistent with the field observations that germination occurs mainly on bare ground. But some germinations did take place on the blaeberry turves, and seedlings became established, whereas in the wild no seedlings were found in prolonged

searches in blaeberry swards, despite the large berry production there.

That the berries contain large numbers of viable seeds has been established beyond doubt, but we do not know if these seeds ever become free from the berries; the germination percentages of c90% were obtained by squashing berries and sieving off the seeds. The burial experiment showed that seed longevity is sufficient in soil and litter for plenty of germinations to occur given the right conditions and normal berry production, and the conclusion must be that the seeds are damaged in some way once the berries fall, and that they do not become incorporated into the litter and soil.

The fact that the berries disappear from the ground below blaeberry bushes within a few days of falling clearly points to them being eaten, and research on small rodents has shown that *Vaccinium* berries are an important food in August and September. We believe that the seeds are damaged during feeding or digestion, but to prove this hypothesis under field conditions requires another series of observations involving catching rodents, recording gut contents and collecting droppings.

STUDIES ON IMPACTS AND PERFORMANCE

In these studies we tried to estimate the intensity and timing of herbivore browsing on blaeberry, and to assess the reaction of blaeberry to these and other impacts.

Levels of utilisation on moorland in NE Scotland

Bushes within 1 m² permanent areas were examined for bitten shoots at nine sites during 1990–93 in conjunction with observations on heather utilisation. Recording took place in September and April. At each site there were 16 1 m² areas and percentage utilisation was recorded on an index scale (0–9%, 10–39%, 40–89%, 90+% shoots bitten); site means were obtained using arbitrary values of 5%, 25%, 65% and 95% respectively for these utilisation bands. Only the current year's shoots were judged, so by April they were nearly one year old and it was thought that utilisation would have peaked. Additional September observations made during 1969–74 were available for three of the nine sites, together with three extra ones. In all observations, herbivore occupancy was assessed on a six-point index scale from the standing crop of dung.

Much greater utilisation occurred in autumn and winter than spring and summer (Table 6). This was

Table 6. Mean % utilisation of blaeberry main shoots at nine moorland sites in NE Scotland with altitude 300–720 m

Month of observation	Blaeberry height	
	Equal or taller than heather	Less than heather
April 1990	47	27
September 1990	11	8
April 1991	49	26
September 1991	14	10
April 1992	55	28
September 1992	20	14
April 1993	49	38
September 1993	20	13
Mean for September	18	11
Mean for April	50	30
April mean for grazing	{ heavy 60 { moderate 50 { light 35	{ heavy 35 { moderate 34 { light 12

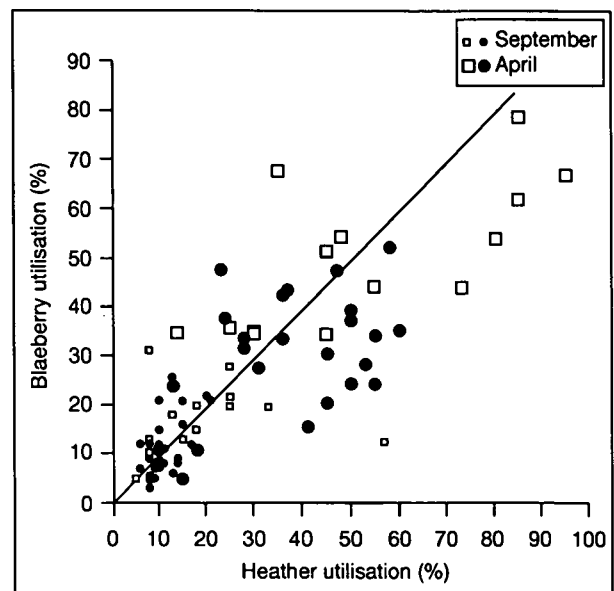


Figure 3. Ratios of blaeberry to heather utilisation at individual sites in September and April, classified by relative height (open symbols for blaeberry \geq heather height; closed symbols \leq heather height). The solid line marks equal utilisation of the two species

true both for sites where blaeberry equalled or was taller than the heather, and for sites where it was overtopped. There was less utilisation at these latter sites, the difference between site groups being significant both in September ($P < 0.05$) and April ($P < 0.001$). At sites with heavier grazing, mean percentage utilisation was greater, as could be expected (Table 6), and all the main herbivores (cattle, mountain hares, rabbits, red deer and sheep) grazed blaeberry substantially. Mean utilisation exceeded 45% at sites where all these species were alone the principal grazers.

In comparison to heather, there was a slightly lower level of utilisation on blaeberry. For April the mean ratio of blaeberry to heather utilisation was 0.81 at sites where blaeberry was overtopped, and 0.93 at sites where blaeberry equalled or surpassed heather. For September the difference between blaeberry and heather was negligible, the ratio of use averaging 0.92 for all sites combined. The additional data collected in 1969–74 gave a mean of 1.14 for the ratio of blaeberry to heather utilisation up to September. However, at individual sites the ratios of utilisation varied considerably (Figure 3); the ratios were doubtless affected by the total availability of food plants in the herbivores' ranges, by the condition of the main food species, and by the timing of peak grazing. Heather, by retaining leaves during the winter, is likely to be preferred then, but sometimes in severe weather its green shoots become browned.

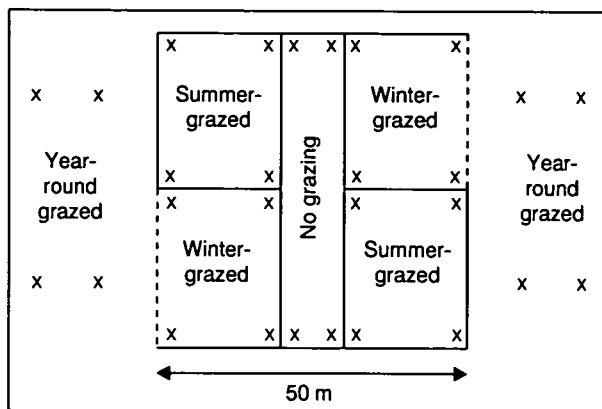


Figure 4. Layout of an enclosure and its control plots grazed year-round at the Snake Pass. The corners of the point quadrat grids are shown; two dung plots crossed each grazed area

Seasonal trends in utilisation observed in a grazing experiment in the Peak District

Enclosures were built at two adjacent sites in the Ashop Valley near the Snake Pass, so that the effects of year-round grazing could be compared with seasonal and full protection. Both enclosures were of similar design (Figure 4), with a central 50 m x 10 m area that was never grazed, and four 25 m x 20 m sections that were protected from grazing either in winter or summer. The side fences could be moved around the mid-distance posts, so that either the upper or lower sections were open to grazing; sheep readily crossed the 25 m long gaps. The enclosures were first closed on 1 October 1990, since when the fence placing has been changed in early April and early October each year. Control areas receiving year-round grazing were positioned alongside each enclosure (Figure 4). At one of the

sites heather was virtually absent, but at the other it occurred in scattered patches with an overall mean cover of 25%; blaeberry initially had 60–70% cover at both sites.

The sites lay at 310 m on the lower slopes of a large tract of unenclosed moorland extending to the summit of Kinder Scout. This 1600 ha area carried roughly 1000 ewes and followers of Swaledale and assorted moorland breeds year-round, but grazing pressures were undoubtedly heavier on the lower ground. Here heather is rather more extensive than blaeberry and there are areas of bracken (*Pteridium aquilinum*), but grassland has little extent. Both sites have well-drained soils.

Utilisation of blaeberry and heather was recorded four times yearly. Stands of 2 m² were examined in permanent positions, utilisation being assessed on a seven-point index scale (0, 1–9%, 10–29%, 30–49%, 50–69%, 70–89%, 90+% shoots bitten). Sheep were the main herbivores, and their occupancy was estimated by pellet group counts on permanent dung plots; two of these crossed each grazed plot at each site. Initially all dung was cleared, then accumulations were counted and cleared six or seven times each year. The visits were more frequent in summer to avoid pellet groups being lost by decay before they could be counted.

Utilisation of blaeberry occurred mainly between August and January (Table 7), at which time sheep usage was much greater than in the rest of the year (Figure 5). The final levels of utilisation observed in April differed little between plots grazed year-round or plots protected for six-month periods. When protected plots were re-opened to grazing, they attracted greater sheep usage than the continuously open plots (Figure 5); in spring 1992 and 1993 this

Table 7. Accumulated utilisation on blaeberry (Vm) and heather (Call) in successive years at the two Snake Pass sites

Grazing treatment	Plant	% Shoots grazed											
		Oct 1990	Apr 1991	Aug 1991	Oct 1992	Jan 1992	Apr 1992	Aug 1992	Oct 1992	Jan 1993	Apr 1993	Aug 1993	Oct 1993
Blaeberry site													
Year-round	Vm	60	75	13	30	60	70	4	40	60	80	5	45
Summer	Vm	45	(50)	0	30	(–)	50	1	21	(–)	50	4	40
Winter	Vm	55	75	(0)	(–)	65	75	(0)	(–)	50	70	(–)	(–)
Heather/blaeberry site													
Year-round	Vm	35	60	10	30	65	65	4	21	41	65	8	50
	Call	13	45	4	17	55	55	6	21	55	65	3	40
Summer	Vm	40	(45)	11	40	(–)	70	4	35	(–)	65	18	60
	Call	30	(40)	3	20	(–)	45	9	21	(–)	55	8	26
Winter	Vm	45	65	(0)	(–)	60	75	(0)	(–)	50	80	(–)	(–)
	Call	30	55	(0)	(–)	50	65	(1)	(–)	50	60	(–)	(–)

– = no observation

Parentheses show periods when plots were protected from sheep grazing

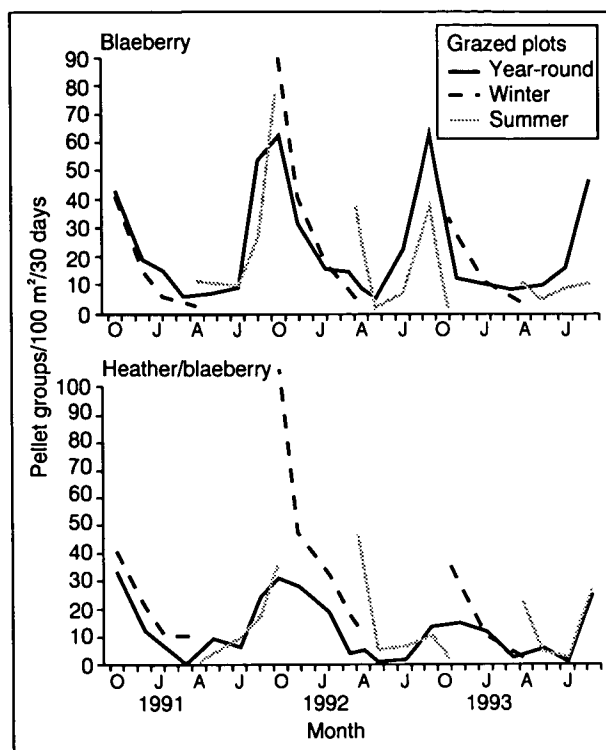


Figure 5. Sheep occupancy at the two Snake Pass sites

led to utilisation levels on both blaeberry and heather being much higher in April than the previous October, despite grazing occurring just in the final three weeks of this period. The appearance of new shoots on the blaeberry bushes in April probably helped to attract greater usage, and in taking the new growth the sheep often bit into the previous year's shoots.

Heather and blaeberry received broadly similar levels of utilisation at the two sites, although the final mean rates were often slightly greater in blaeberry (Table 7). In summer and autumn blaeberry tended to be the more heavily utilised species, but during winter the difference narrowed, presumably because the sheep then preferred the heather's green foliage. From the ratio of pellet group counts at the two sites (Table 8), the sheep each year showed increasing preference for the heather site in winter. Although the heather bushes were generally

Table 8. Preference of sheep for the blaeberry site compared to the heather/blaeberry site at the Snake Pass, expressed by the ratio of pellet groups deposited on the seasonally grazed and year-round grazed plots at the two sites

	Ratio of pellet group counts on blaeberry: heather/blaeberry plots			
	1990	1991	1992	1993
Jan-Mar		0.92	0.67	1.11
Apr-Jun		1.27	0.84	1.03
Jul-Sep		1.79	1.80	1.19
Oct-Dec	1.03	0.95	0.86	0.84

taller than the blaeberry, the plants tended to grow separately so herbivores had equal access (*cf* the protection given by overtopping heather at the Scottish sites where the species were usually more intimately mixed). The final levels of utilisation observed in April averaged about 70%, and the ungrazed shoots mostly occurred below the top canopy of the swards. The length of shoot removed was not measured, but this intensity of defoliation was certainly sufficient to keep sward height checked.

Long-term trends in moorland in NE Scotland

Blaeberry was unreactive (Figure 6) at the moorland sites where botanical composition and herbivore usage have been monitored since 1969 (Welch 1984a; Welch & Scott 1995). Mostly it was a minor species with cover less than 20%, whereas heather cover was initially in the range 50–80% at the majority of sites. When heather cover was sharply reduced by heavy grazing, blaeberry generally survived in small quantity (Figure 6), and at site G2 under heavy grazing from cattle and sheep it increased slightly. None of the increases in blaeberry cover, however, were significant in Sign Tests (see Welch 1984a), even for selected periods within the full timespans monitored. The only significant decrease in blaeberry was at site 12; here, heather cover reached 95% and mean height exceeded 25 cm from at least the 15th year of observation. So, the observed changes in blaeberry appeared to be mostly fluctuations caused by observational error or year-to-year differences in performance.

At a site rarely grazed by large herbivores (Clash Hill), blaeberry and heather have co-existed since 1969 with neither taking control (Figure 7). This moorland was previously a pinewood, but was not replanted after the trees were felled in the 1940s, and has since been virtually unmanaged although some grouse shooting has taken place. Wavy hair-grass has had most cover, its tall inflorescences growing through the ericoid sward. The heather bushes are gradually 'moving' down the 5° slope, with building shoots and stems in their lower sectors and dead and dying parts at their upper edges. Blaeberry shoots grow into these dying areas, and besides the interstitial wavy hair-grass there is a thick bryophyte layer dominated by *Hylocomium splendens* and *Pleurozium schreberi*; bryophytes are lacking only inside the densest heather bushes. From 1984 to 1988 sheep grazed intermittently at a low density, and this perhaps caused the decline in heather cover to 40% observed in 1985 and 1988 (Figure 7). The main fluctuation of blaeberry occurred between 1975 and 1977, percentage cover being respectively 43.3% and 24.5% in these

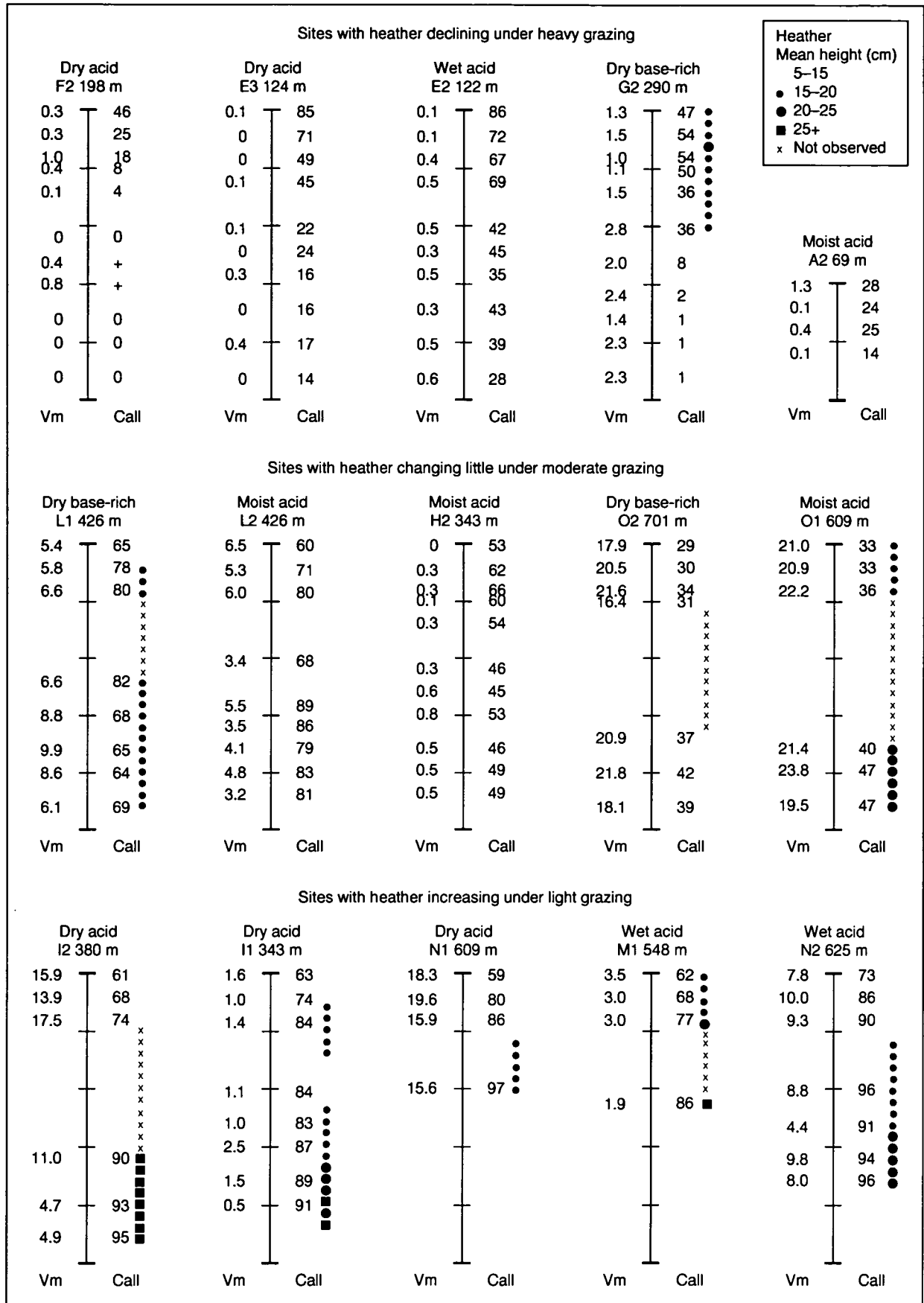


Figure 6. Trends in % cover of blaeberry and heather at moorland sites, classified by type of heather trend experienced. Cover was measured for up to 24 years, the vertical axes being marked in five-year intervals. Site types, codes (Welch & Scott 1995) and altitude (m) are given, and mean heather height class is shown next to the cover values

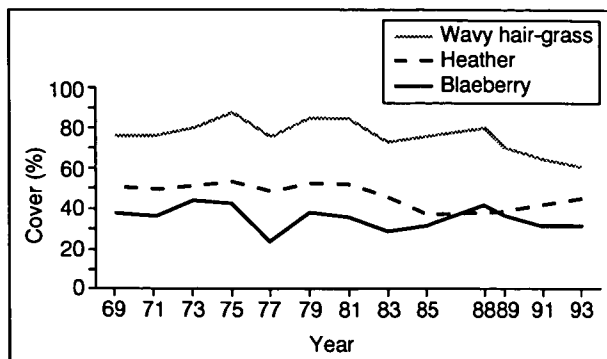


Figure 7. Trends in % cover of blaeberry, heather and wavy hair-grass at a dry moorland site virtually ungrazed by large herbivores

years. Browning of the leaves due to an air frost in June 1975 was noted in the July 1975 recording, and subsequently the shoots died back considerably.

Effects of muirburn on blaeberry cover

At one of the long-term monitoring sites in NE Scotland, blaeberry and three other heath plants gained significantly in cover during the muirburn cycle (Table 9). The current recovery phase is not exactly comparable to the previous one because sheep grazing is now less intensive, hence heather has grown taller (20 cm *cf* 8 cm) although its cover is less (32% *cf* 61%). However, blaeberry is now the species with most cover, and, having similar height to the heather, it is likely that much of this cover will be retained as the heather gradually spreads in the next few years. At the wetter M1 site the only heath plant to have benefitted is cross-leaved heath (*Erica tetralix*), the main increasers being grasses.

Table 9. Changes in ericoid % cover during one cycle of muirburn, from measurements made at approximately similar stages in the recovery phase at two Scottish sites

Year observed Time before or after fire (yr)	Site I2			Site M1		
	1970	1993	Sig	1970	1993	Sig
<i>Calluna vulgaris</i>	60.8	32.0	---	56.1	27.8	---
<i>Empetrum nigrum</i>	0.3	8.8	++			
<i>Erica cinerea</i>	2.5	6.8		1.2	0.7	
<i>E. tetralix</i>	2.5	10.0	+	3.5	5.0	
<i>Vaccinium myrtillus</i>	20.2	39.5	++	3.5	3.5	
<i>V. vitis-idaea</i>	10.0	27.8	+++	0.3	0	
Mean height of <i>Calluna</i> (cm)	7.8	20.2	+++	15.2	10.3	---

Significance of changes was given by Sign Tests on the number of pins (out of 10 in a 1 m frame) that contacted the species in 40 permanent positions (60 at M1), and by *t* tests on 160 spot measures for heather height

Comparison of the effects of winter, summer and year-round grazing by sheep in the Peak District

Vegetation trends were assessed using grids of point quadrats in all plots at the Snake Pass sites (Welch 1993): the corner positions of the grids are marked on Figure 4. Every point was checked for contacts to determine the main plants and plant groups present, and the heights of the uppermost contacts of *Vaccinium* and heather were recorded.

Sheep usage peaked in autumn as described in the section on utilisation (pp17-18). The seasonally protected plots showed a similar pattern of usage to year-round-grazed plots (Figure 5), but when newly opened after being protected they were grazed more heavily than the year-round controls. At the heather/blaeberry site this preference lasted for several months on the winter-grazed plots, causing the total usage on these plots to be almost as great as accumulated in the whole year on the control areas. At the blaeberry site, and at the heather/blaeberry site for the summer-grazed plots, the seasonal plots received roughly half the usage estimated for the year-round plots.

Changes in composition between 1990 and 1993 have been relatively minor at the blaeberry site, few being significant in *t* tests using data from the individual rows of the sampling grid (Table 10). Grasses gained cover most in the summer-protected plots, as could be expected, but did not have a big increase in the ungrazed strip. Here heather plants began to invade, ten separate ones being encountered in the 200 points and others being visible. Blaeberry and mat-grass both generally decreased, and dead plants of mat-grass were seen in the ungrazed plot, crowded out by the dense tall growth. Blaeberry showed a greater decline between 1990 and 1992 (Welch 1993), perhaps being damaged by frost in 1991, but regained cover between 1992 and 1993 in the grazed plots.

The height of blaeberry increased markedly between 1990 and 1993 in the ungrazed plot, and there were also significant increases in the seasonally grazed plots (Table 11). The sampling of height change was more adequate than that of compositional change for blaeberry, with about 200 measures available each year in each plot for the *t* tests; hence, quite small differences proved to be significant. However, the effects of seasonal grazing and year-round grazing were not found to be differentiated.

At the heather/blaeberry site there were significant declines in blaeberry cover under all treatments (Table 10). With heather increasing significantly in

Table 10. Effects of grazing treatment on the composition of blaeberry swards at the two Snake Pass sites

	Initial % cover in 1990				Trends in % cover in 1990-93			
	Vm	Call	Ns	Gr	Vm	Call	Ns	Gr
Blaeberry site								
Year-round	73	0	16	77	-1.3	+0.3	-0.7	+4.7
Summer-grazed	73	1	23	81	-5.7	0	-3.7	+6.3
Winter-grazed	73	1	15	75	-2.0	+0.4	-4.0	+13.0 ***
Ungrazed	53	2	31	81	-5.5	+3.5*	-6.0	+3.0
Heather/blaeberry site								
Year-round	73	28	12	61	-25.5*	+9.0	+0.5	+5.5
Summer-grazed	70	20	16	55	-21.3***	+5.0	-6.0*	+22.7***
Winter-grazed	69	20	13	56	-14.3*	+4.0	-3.4	+21.0
Ungrazed	61	28	13	55	-31.0***	+10.0	-5.5	+7.5

Vm = *Vaccinium myrtillus* (blaeberry); Call = *Calluna vulgaris* (heather); Ns = *Nardus stricta* (mat-grass); Gr = Other grasses
*P<0.05>0.01; **P<0.01; ***P<0.001

height (Table 11) and its cover also increasing, it is evident that its bushes were shading out blaeberry; heather height averaged about 30 cm but blaeberry height only 15 cm. The greatest decline of blaeberry and the greatest increase of heather, for both cover and height, occurred in the ungrazed plot. Grasses generally increased at this site, the main species involved being wavy hair-grass. This grass is able to survive inside the heather sward, sending out tall inflorescences above the heather canopy, but the smaller gain of grass in the ungrazed than the seasonally grazed plots does suggest that the density of the vegetation there was checking grass growth. Mat-grass suffered least decline under year-round grazing, as at the blaeberry site.

The steady progression of the change from blaeberry to heather is shown in Table 12. Possibly the weather in the study period has been unusually

Table 11. Effects of grazing treatment on the mean height of blaeberry and heather at the two Snake Pass sites

	Mean height (cm) 1990		Trends in height (cm) 1990-1993	
	Vm	Call	Vm	Call
Blaeberry site				
Year-round	13.2	-	+0.3	-
Summer-grazed	13.1	15.1	+0.9***	+4.0
Winter-grazed	13.2	14.0	+1.0***	+2.6
Ungrazed	12.5	19.0	+4.2***	+7.2*
Heather/blaeberry site				
Year-round	15.7	26.4	+0.3	+5.2***
Summer-grazed	15.8	24.7	-1.1	+5.0***
Winter-grazed	15.3	27.6	-0.4	+2.8*
Ungrazed	16.0	24.7	+0.9	+7.2***

Significance levels as in Table 10

favourable to heather, the winters being relatively snowless. Now that the heather exceeds 30 cm in mean height, it will tend to protrude above the snow in most storms, making it available for heavy utilisation. Also, as the bushes mature, their growth rate will fall, so it is unlikely that the succession to heather will continue at its present rapid pace. It is very desirable that these observations continue; such changes are hard to detect from inspections on single occasions, but it has generally been thought that blaeberry does not succeed to heather under moderate grazing.

Effects of cutting shoot tips

A treatment intended to simulate grazing was imposed on blaeberry swards at the virtually ungrazed Clash Hill site, and also in the ungrazed area at one of the Snake Pass sites. Shoot tips were removed by hand in six 40 cm x 60 cm quadrats, approximately 2 cm lengths being taken. This was done in December-January in half of each quadrat, and in June-July in the other half. On each occasion, 40 shoots were cut, this being 50-70% of the shoots

Table 12. Progressive change at the Snake Pass heather/blaeberry site in blaeberry cover and heather height

	1990	1991	1992	1993
Blaeberry % cover				
Year-round grazing	72.5	61.0	62.0	47.0
Summer grazing	70.3	66.0	53.3	49.0
Winter grazing	69.0	63.3	52.3	54.7
Ungrazed	61.4	58.0	47.5	30.5
Heather height (cm)				
Year-round grazing	26.4	27.9	30.0	31.6
Summer grazing	24.7	26.0	28.8	29.7
Winter grazing	27.6	27.4	31.2	30.4
Ungrazed	24.7	26.4	31.3	31.9

present in the 40 cm x 30 cm areas. The treatments began in December 1990 and June 1991.

By June 1993 sward structure was clearly different in the quadrats compared to the ungrazed stands around. The density of shoots was greater in the cut areas, the main shoots having more branches in their upper parts that reached to the sward canopy, but there were no differences detectable by eye between the winter-cut and summer-cut plots. In another study of simulated grazing (Tolvanen *et al.* 1992), clipping the current year's branches had a less damaging effect than removing leaves, probably because only the former treatment caused new branches to develop.

DISCUSSION

Blaeberry is eaten by all the main herbivores present on British moorlands, and, unless protected by being overtopped by heather, the bushes will experience substantial loss of shoot tips each year. The clipping treatment in ungrazed stands showed that this defoliation leads to greater branching; doubtless the carpet-like swards of blaeberry with dense shoots and mean height 10–15 cm that are widespread in the Peak District are being maintained by quite heavy grazing pressures.

The sharp autumn peak in sheep usage at the Snake Pass sites (Figure 5) was unexpected, especially as it straddles the period when the leaves fall. However, carbohydrate contents rise in autumn (see p9), and stems were grazed as readily as leaves. This was shown from the food items present in the Derbyshire grouse droppings (see p27) and from the amount of utilisation that accumulated at the Scottish sites between the September and April observations (Table 6). Therefore, the probable explanation for the Snake Pass autumn peak is the changing palatability of alternative food plants and vegetation types. Thus in spring and summer the sheep seek out graminoids, but when these senesce in autumn they turn instead to dwarf shrubs which have stayed photosynthetic. Both heather and blaeberry are then heavily utilised, but in the early part of winter blaeberry seems slightly preferred whilst later the heather is more favoured (Table 8). A possible cause for this shift in preference is the inability of sheep to avoid consuming previously bitten shoots in stands where the shoots are densely packed and utilisation has been heavy; in blaeberry a hard callus forms at the tip of bitten shoots, whereas in heather with narrower stems there is less scar tissue.

The stocking rate of sheep at the Snake Pass plots can be readily calculated using conversion factors. At 17 pellet groups deposited per day (Welch 1982), the density on the year-round plots averaged

2.2 and 1.4 sheep ha⁻¹ respectively for the blaeberry and heather/blaeberry sites. Occupance was rather less on the seasonally grazed plots, as shown by Figure 5. At the heather/blaeberry site this stocking was evidently insufficient to stop the heather increasing in cover and height (Tables 10 & 11). This result agrees with the Scottish finding (Welch 1984b) that the stocking above which heather declines is 2.7 sheep ha⁻¹, given average heather performance.

In the long-term observations on blaeberry cover at the lightly grazed Clash Hill sites, the main change was a sharp decrease which followed frosting damage in June 1975 (Figure 7). Some browning of blaeberry leaves, suspected as being caused by frost, was noted at the Snake Pass blaeberry site in June 1991, particularly in the winter-protected plots, and this may have contributed to blaeberry's decline there (Table 10). Although the decline was quite small over three years, blaeberry average cover was less in August 1991 and 1992 than in April 1993. In contrast, at the heather/blaeberry site there was a progressive fall in blaeberry cover (Table 12), the rate somewhat increasing in 1992–93 compared to the previous years. Doubtless the associated rise in heather cover and height has led to the blaeberry being shaded out, fitting with the conclusion of Hester *et al.* (1991a) that competition from heather controls blaeberry performance.

It is generally accepted that blaeberry can withstand moderately heavy grazing better than heather, as reported by Anderson and Yalden (1981) for the Peak District. The observations over 24 years at the Scottish moorland sites support this view (Figure 6): blaeberry cover remained at around 0.5–2.0% at three sites with heather declines from 85% to 14%, 86% to 28% and 47% to 1% caused by heavy cattle and sheep grazing. Only at a site where heather was reduced from 46% to 0% in ten years was blaeberry made extinct. A likely explanation for blaeberry's better survival than heather under severe defoliation is its growth form, the stems staying photosynthetic for several years and the below-ground rhizomes providing a protected store of assimilates from which new aerial shoots can arise.

Spread of blaeberry in moorland where heather is checked or declining could be expected, but occurred only to a minor extent at the Scottish study sites (Figure 6). In the absence of fire, the biggest increase was just 4.5% bringing cover to 9.9% at site L1, and even here there was a subsequent fall to 6.1% cover. Only at a moorland site burnt in 1987 did blaeberry gain substantially, having 40% cover in 1993 compared to 16% in 1986 and 20% in 1970. Similarly, in mid-Wales, Edgell (1971) reported that at Cader Idris blaeberry heaths had developed

from burnt Callunetum subsequently subjected to grazing. Whether the gain in blaeberry cover during a burning cycle under favourable grazing pressures, and the frequency of occurrence of burning are sufficient to produce stands of blaeberry with 70–90% cover, such as occur in the Peak District and Wales, is rather doubtful. Many sites of this type were probably once wooded, shading being known to favour blaeberry at the expense of heather (Hester *et al.* 1991a). Having become well established in woodland, blaeberry could then have persisted with considerable cover long after the trees were lost.

STUDIES ON PALATABILITY AND VALUE TO HERBIVORES

These studies aimed to provide understanding for the observed patterns in utilisation of blaeberry by herbivores. Having comparative knowledge on the value of different plants at different seasons helps decide which types of vegetation should be encouraged. Because heather is often abundant in the home ranges of the herbivores feeding on blaeberry, and is much eaten, we use it as a yardstick in assessing the palatability and digestibility of blaeberry.

We did feeding trials with captive red grouse, black grouse and capercaillie and made supplementary observations on dietary preference in wild red grouse from counts of epidermal fragments in faeces. For ruminants we report on consumption of blaeberry by red and roe deer (*Capreolus capreolus*) living in conifer plantations newly established on moorland, and by sheep and red deer grazing heather moorland in 2.5 ha paddocks.

BLAEBERRY AND HEATHER AS FOODS FOR GROUSE

The willow ptarmigan (*Lagopus lagopus*) has a circumpolar range and many populations eat *Vaccinium* species, including blaeberry, in both summer and winter (Dement'ev & Gladkov 1952; Cramp & Simmons 1980). Although the main food of red grouse is heather, they also eat blaeberry when it is available; a summer peak in blaeberry consumption was found by Savory (1974) examining the crops of birds shot monthly from one moor over a 12-month period (Table 13). It is not clear from Savory's data whether heather or blaeberry is the preferred grouse food; heather

Table 13. Dry weight of heather and blaeberry as a percentage of total food in the crops of red grouse shot on one moor (adapted from Savory 1974)

	Mean % dry weight	
	Heather	Blaeberry
January	99.3	0.0
February	98.0	0.4
March	94.1	0.7
April	91.3	0.6
May	90.9	0.8
June	68.3	20.5
July	70.2	14.6
August	74.6	0.0
September	94.5	0.0
October	97.1	0.9
November	95.7	0.3
December	93.8	5.9

may predominate in the diet of red grouse simply because it is far more abundant than blaeberry on most grouse moors. To see whether more blaeberry is eaten at sites where it is more abundant, we examined grouse droppings collected from the Snake Pass sites (p17).

Protein and phosphorus are probably the main limiting nutrients in the diet of grouse (Moss 1967) and blaeberry contains more of both than does heather. This suggests that blaeberry should be a better food than heather. On the other hand, food quality is not simply a matter of nutrient content. Animals adapted to a food may thrive better on it than on a food to which they are not adapted, even though the latter is richer in nutrients (Moss 1975). Different species with the same foods available may choose different diets (Moss & Hanssen 1980). Thus, in summer capercaillie eat more blaeberry than black grouse, and black grouse more than red grouse (Dement'ev & Gladkov 1952; Cramp & Simmons 1980). One might therefore expect that, if preferences in captivity reflect diets in the wild, red grouse should prefer heather and capercaillie blaeberry, with black grouse intermediate. This expectation was tested in the present studies; the work was done by three students – George Nikolakopoulos (1990), Simon Luke Elliott (1991) and Audrey Brynes (unpublished).

Preference tests

Methods

Relative consumption of blaeberry and heather by chicks of red grouse and black grouse, and by adult red grouse, black grouse and capercaillie, was measured in July–August 1991. The birds (Table 14) had been reared in captivity, and fresh heather had regularly supplemented the artificial pellets which formed the main bulk of their food.

Table 14. Preferences of red grouse, black grouse and capercaillie hens and cocks for heather and blaeberry: values >1.0=preference, <1.0=avoidance

	Heather	Blaeberry	Probability
Red grouse	1.23	0.74	4.058
Black grouse	1.10	0.94	NS
Capercaillie	0.58	1.43	<0.01

Note: Preference is the mean proportion eaten divided by the proportion expected if bundles were eaten at random. An analysis of covariance showed that plant species ($F_{1,18}=8.79$, $P=0.0083$), bird species ($F_{4,18}=3.98$, $P=0.0174$) and sex ($F_{2,18}=5.27$, $P=0.0083$) each affected preferences. Bird species and sex were entered into the model as plant/bird and plant/sex interactions respectively. Cocks of all species took more heather and less blaeberry than hens

There was a total of 14 replicated trials: nine with chicks, three with adult hens and two with adult cocks. For two weeks before the trials, and between trials, fresh blaeberry and heather were both provided. These were cut twice a week and kept in damp hessian sacks.

Bundles of heather and blaeberry were prepared for the trials. They were bound with rubber bands, the stalks being cut to about the same length; they were of similar weight and each was individually labelled. All were kept overnight in two black plastic bags, one for each species, so that they tended to have a similar moisture content. Four bundles of each species were then weighed and oven-dried to provide a conversion factor for calculating the starting dry weight of every bundle used in the trials. For each trial, eight bundles – four of each species – were clamped upright in random order between two wooden splints (Moss, Miller & Allen 1972) and put into the cage. When one of the eight had had most of its greenery removed, all the bundles were taken out, dried and weighed.

For each bundle, its species, row position and dry and wet weights before and after the trial were recorded. Preference was estimated as the weight removed from each bundle divided by the total weight removed from all eight bundles in that replicate. The calculation was done for both dry and wet weights but both methods led to identical conclusions and so only the data on dry weights are used here. If the total weight removed was less than 10% of the weight offered, the results were excluded (Moss *et al.* 1972).

Trials with both chicks and adults lasted approximately six hours but were carried out over a period of three weeks, with sufficient replication between weeks to assess whether preference changed with time.

To see whether preferences were affected by details of how the food was presented, background treatment was varied in trials with chicks.

Treatment 1: No green food for 24 hours immediately before the trial, with pellets *ad lib* during it.

Treatment 2: Green food before the trial with pellets *ad lib* during it. This was also the treatment used for all trials with adults.

Treatment 3: Green food before the trial, with the pellets removed during it.

Results

Adults

The analysis (Table 14) showed that:

- hens of the three grouse species differed in their preferences – red grouse preferred heather,

capercaillie preferred blaeberry, and black grouse showed no clear preference;

- cocks of all three species preferred heather more than did hens;
- there were no changes in preferences with time.

Chicks

An analysis of covariance showed that:

- chicks of both red and black grouse preferred heather (preference indices, defined as in Table 14, were 1.38 and 0.53 respectively, $P=0.0001$);
- the two species showed no difference in preference;
- the preference for heather over blaeberry decreased with time ($P=0.0001$);
- the background treatment affected preference: heather was most preferred in treatment 1 and least preferred in treatment 2 ($P=0.002$).

Discussion

A difficulty when interpreting preferences for heather and blaeberry was that the birds had previously been accustomed to a supplement of heather in their diet, but not blaeberry. It was possible that preferences might change as the birds became more accustomed to blaeberry. To check this possibility, the trials were conducted over a period of three weeks. If preferences were changing, this would be detected by a change in the relative consumption of the two foods over the three weeks.

In fact, the chicks' preference for heather over blaeberry did decrease over the three-week period. Therefore, the results on the chicks' preferences are difficult to interpret. The work with chicks also showed that the details of how the foods were presented affected preferences. Heather was most preferred when the chicks had had no natural food for the 24 hours before the trial and least preferred when natural food and pellets were both available in the 24 hours before the trial.

The adults' preferences did not change with time and so were easier to interpret. Red grouse hens preferred heather, capercaillie hens preferred blaeberry, and black grouse hens showed no clear preference. This confirmed that preferences in captivity reflected diets in the wild. The observation that cocks preferred heather more than did hens was unexpected and deserves further study.

Digestibility trials

There are problems with using captive birds to study the digestion of natural foods. Captives are adapted to a rich artificial diet, have smaller guts, and digest natural foods less well than wild birds, and so may lose weight on a diet of entirely natural

food (Moss & Hanssen 1980). As well as measuring the digestibility of heather and blaeberry to captives, the present work contrasted the effects of fresh heather and blaeberry on the digestion and intake of diets consisting partly of artificial pellets and partly of heather or blaeberry.

Eight cock grouse were used in the work, which was carried out between May and August 1990. Four were assigned at random to be given blaeberry as a natural food, the remaining four getting heather. They were given fresh natural food and pellets *ad lib* for 12 days before measurements of digestibility began. Fresh water and grit were freely available throughout.

The first digestibility trial started on 4 June and lasted four days. Pellets and bundles of natural food were provided *ad lib* and daily dry matter intake was measured. Droppings were collected from trays under the wire-floored cages to measure daily dry matter output. Digestibility for each bird was the difference between its intake and output, divided by its intake. In the second trial, which started on 12 June, the amount of pellets given daily was reduced to half the average amount eaten by each bird in the previous five days. This caused them to eat more natural food, which was provided *ad lib*. In the third trial, starting on 19 June, the two groups of birds were given 100% natural food *ad lib*. They lost weight rapidly and two birds were removed from the trial to avoid excessive weight loss. Hence, calculations for this trial were done on three birds per group. In a fourth trial, starting on 9 August, the digestibility of pellets – with no natural food – was measured.

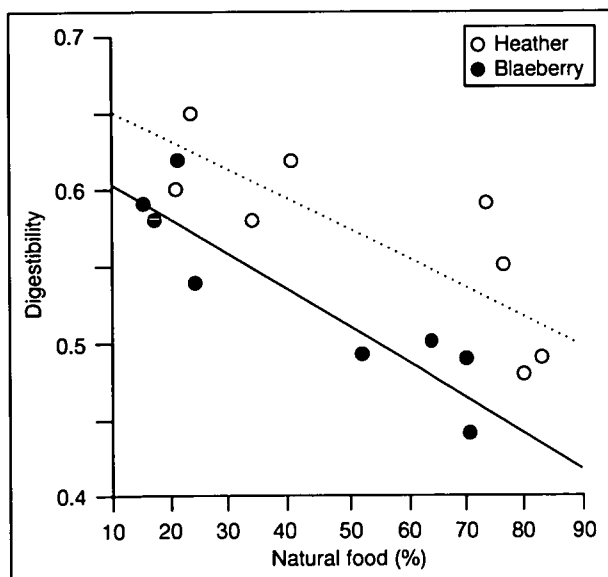


Figure 8. The digestibility of mixed diets comprising artificial pellets and natural food: heather (open circles) and blaeberry (solid). Data with natural food less than 50% are from trial 1, otherwise trial 2. The lines are from regression equations

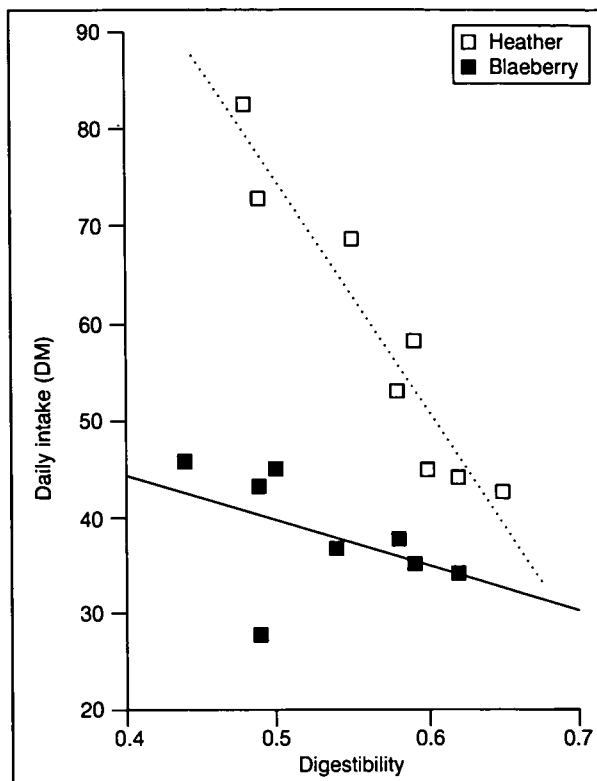


Figure 9. Daily intake of mixed diets of artificial pellets and fresh foods: heather (open squares) and blaeberry (solid) respectively. The lines are from regression equations

The digestibility of the diets comprising a mixture of pellets and natural food declined between trials 1 and 2, as the proportion of natural food increased (Figure 8, legend). The rate of this decline in digestibility was -0.2% for each 1% increase in the proportion of natural food ($F_{1,13}=36.97$, $P=0.0001$ by an analysis of covariance, $R^2=0.77$), irrespective of whether it was heather or blaeberry. Diets containing blaeberry were about 6% less digestible ($F_{1,13}=14.40$, $P=0.0022$) than diets containing the same percentage of heather.

The total daily intake of dry matter increased as the digestibility of diets containing heather declined (Figure 9), at a rate of 2.36 g for each percentage unit decrease in digestibility ($F_{1,12}=37.70$, $P=0.0001$ by an analysis of covariance, $R^2=0.91$). The rate of increase was slower for diets containing blaeberry ($F_{1,12}=26.93$, $P=0.0002$) and not significantly different from zero.

The digestibility of pure heather ranged from 0.72 to 0.81 ($n=3$, median 0.80), of blaeberry from 0.73 to 0.75 ($n=3$, median 0.74), and of pellets 0.47 – 0.55 ($n=8$, median 0.52). Birds lost weight on diets of pure heather or blaeberry, even though they ate very large amounts (150 – 196 g dry matter per day for heather, 84 – 114 for blaeberry).

The results are puzzling. Both heather and blaeberry were highly digestible when eaten alone

(0.80 and 0.75 respectively) and more digestible than pellets alone (0.52). Therefore, one might expect that the digestibility of a mixed diet of pellets and natural food would increase as the proportion of natural food increased. In fact (Figure 8), it declined at a similar rate for both heather and blaeberry; but the blaeberry/pellet diet was about 6% less digestible than the heather/pellet diet, irrespective of the percentage of natural food in the diet. Also (Figure 9), daily intake of the heather/pellet diet was greater than intake of the blaeberry/pellet diet, and intake of the former increased relative to the latter as digestibility of the mixed diet declined. In short, both blaeberry and heather depressed digestibility of the mixed diets relative to expectations from the digestibility of their two components. This effect was greatest for the blaeberry/pellet diet, and intake of the blaeberry/pellet diet was less than intake of the heather/pellet diet. This result suggests that blaeberry was a poorer food than heather for red grouse.

The digestibilities of unadulterated heather and blaeberry recorded here are very much higher than found in previous work (Moss & Hanssen 1980). This is probably because the present study was done in June, when both plants have soft, young leaves and shoots. Previous work was done with material from later in the year, when tissues would have been much harder and less digestible. In a Swedish study using rumen liquor collected from roe deer and moose (*Alces alces*), the digestibility of blaeberry collected in June and July was twice as great as blaeberry collected in October, November and December (Cederlund & Nyström 1981).

Although the red grouse digested heather and blaeberry well and ate more than the 70 g of heather per day typically eaten by wild birds (Moss & Hanssen 1980), they lost weight rapidly when given entirely natural food. This shows that fresh heather and blaeberry were both poor foods for captive grouse, particularly when they formed a large proportion of the diet. Perhaps the fresh foods contained secondary compounds which caused

weight losses when eaten alone, which inhibited digestion of mixed diets, and to which the captives were poorly adapted.

The diet of red grouse at the Snake Pass sites

These sites had abundant blaeberry (mean cover 68% at both), but differed in the extent of heather (mean cover 1% and 24%); diet was assessed from faecal deposits. Samples were obtained in April, August, September and October, by collecting singly about 20 droppings at each site. In the spring sampling on 22 April, older droppings deposited in February and March were separated from fresh droppings deposited in the previous fortnight. To prepare the material for analysis, subsamples from every pellet were bulked together for each collection, then fragmented using a scalpel, and mixed. The resulting paste was examined under a dissecting microscope, cover values being estimated by eye for ten 'fields'. Fragments of different food plants could be recognised from epidermal features and other attributes.

The proportion of main plant species in the droppings differed considerably between the two sites (Table 15), despite their nearest plots being separated by only about 200 m. Much more blaeberry occurred in the droppings from the site where it was the sole dominant, but at both sites the droppings contained proportionally more heather than was present on the ground; either the birds were feeding on swards of different composition around the sites or they were selecting for heather. Other foods were found only in August; many berries of crowberry (*Empetrum nigrum*) were then available, this species being little grazed by sheep.

Similarly, Eastman and Jenkins (1970) showed that droppings collected over a 14-month period from a Scottish moor contained 65% heather fragments and 2% blaeberry fragments compared with, respectively, 51% and 18% cover for these plants on

Table 15. Seasonal variation in the content of food items in grouse droppings deposited at the Snake Pass sites

Period of deposition	Site	% Fragments in dung				
		Blaeberry stem	Blaeberry leaf	Heather leaf	Crowberry seeds	Grass seed-heads
February–March	{blaeberry	80	0	20	0	0
	{heather/blaeberry	35	0	65	0	0
April	{blaeberry	85	0	15	0	0
	{heather/blaeberry	60	0	40	0	0
Late July–early August	{blaeberry	0	70	Trace	10	20
	{heather/blaeberry	0	0	80	20	0
September	{blaeberry	0	60	40	0	0
	{heather/blaeberry	0	15	85	0	0
October	heather/blaeberry	10	0	90	0	0

the ground. However, in both studies the two measures (ground cover and proportion in droppings) were not certainly comparable and so one cannot definitely conclude that red grouse preferred heather to blaeberry.

BLAEBERRY AND HEATHER AS FOOD FOR RUMINANTS

Selection by red deer and sheep for blaeberry when grazing heather moorland

Red deer and sheep were grazed for ten-day periods in six 2.5 ha paddocks containing heather moorland at the Glensaugh Experimental Farm, Kincardineshire (Clarke, Welch & Gordon 1995). In each paddock, 20% of the area had been sown with grass, either in one large patch, four medium-sized patches, or 12 small patches; the two replicates for each sowing treatment were used to compare deer and sheep and the species assigned to paddocks alternated in succeeding trials. Small patches of blaeberry occurred in the heather swards in all paddocks, mainly as an understorey and always with total cover less than 10%. After each grazing period, three dung samples were collected from each paddock, and epidermal fragments were later counted (Cuartas, unpublished). Although there are problems in this technique caused by differential digestion, eg between grasses and ericoids, it was thought unlikely that between-herbivore differences would be so great as to obscure any pattern in blaeberry intake.

Blaeberry was found to contribute about 2% of the epidermal fragments counted (Table 16), heather and grasses comprising virtually all the remaining fragments. More blaeberry fragments occurred in the dung of sheep than the dung of deer, but there was variation between trials and patch treatments. Part of this variability doubtless resulted from the small number of faecal depositions that could be examined with this time-consuming technique, but part was related to differences between paddocks in

blaeberry cover. More blaeberry fragments were found in the dung when the animals grazed in paddocks with higher cover of blaeberry, eg the paddocks used by sheep in Trials 1 and 3 and deer in Trial 2 in the one-patch treatment. Using the estimated availability in each paddock, a mean index of selection was calculated for each herbivore in each patch type (Table 16). Sheep selection of blaeberry, as estimated by this index, was greater than deer selection except in the one-patch paddocks; here, sheep spent considerably less time than the deer grazing heather moorland (Clarke *et al.* 1995). In the four-patch and 12-patch paddocks, the sheep and deer utilised the heather about equally, and it appears that the sheep, having smaller mouths, were more able than the deer to select for blaeberry within the heather sward.

Selection by red deer and roe deer in conifer plantations

This work formed part of a PhD study carried out from 1989–93 by J Latham; greater details are given in Latham (1993). Rumens were obtained from red and roe deer shot in four Scottish forests as part of the regular cull controlling numbers. Each forest contained a mixture of stand ages and included some open ground bearing remnants of the former moorland vegetation. The deer were shot in summer (May–August: 21 red deer, 58 roe deer) and winter (November–February: 24 red deer, 44 roe deer). Material from each rumen was examined in trays and the volume of identifiable fragments estimated by the line intercept method.

It was found that in summer red and roe deer ate little heather and blaeberry (Table 17), the main foods being grasses in red deer (c40% of rumen volume) and forbs in roe deer (c70% of rumen volume). In winter much heather was eaten by both species, but, whereas roe deer ate more blaeberry than in summer, red deer ate less. Analysis of variance indicated that this difference between red and roe deer in the consumption of blaeberry in winter was significant ($P=0.023$). As the ground

Table 16. Differences in the intake of blaeberry by red deer and sheep grazing moorland in experimental paddocks, measured by the number of blaeberry fragments in the dung, expressed as a percentage of all epidermal fragments

Paddock type	% Blaeberry fragments in dung						Estimated index of selection for blaeberry*	
	Trial 1		Trial 2		Trial 3		Deer	Sheep
	Deer	Sheep	Deer	Sheep	Deer	Sheep		
One-patch	0	3.8	4.0	0	0	2.5	22	20
Four-patch	0	5.8	0.2	0	1.4	1.4	6	23
12-patch	1.6	1.4	2.1	5.2	1.0	3.1	19	29
Mean for all types	0.5	3.7	2.1	1.7	0.8	2.3	16	24

*Calculated for the three trials from the estimated cover in each of the paddocks grazed

Table 17. Mean percentage volume contributed by blaeberry and heather in rumens of deer shot in four Scottish forests

	Red deer		Roe deer	
	Blaeberry	Heather	Blaeberry	Heather
Summer	4.2	7.6	2.7	2.2
Winter	1.5	41.8	7.3	17.0

vegetation in the four forests contained more heather than blaeberry (mean cover respectively 12% and 2.5% observed in summer), the results are interpreted by Latham as showing that red deer tended to eat plants in proportion to their availability, but that roe deer were more selective. Because of leaf fall, the cover of blaeberry is considerably diminished in winter.

In Scandinavian feeding trials (Holland & Staaland 1992), roe deer fed blaeberry stems *ad lib* in winter achieved 54% DM digestibility, retention time increasing and intake amounts decreasing compared to a concentrate diet; *in vitro* digestibility of the blaeberry forage was only 36%.

DISCUSSION

No consistent differences in herbivore preferences between blaeberry and heather have been found in the studies reported. Herbivore species, the availability and positioning of the food plants, and diet immediately prior to the observations all affected preference. The digestibility trials suggested that blaeberry was a slightly poorer food than heather for captive red grouse in summer.

Comparisons of the growth rates of larger herbivores fed on blaeberry and heather are not available, but development has been compared in lepidopteran larvae living on pure stands of blaeberry and heather. Development rates were little differentiated, although one species had more rapid growth on blaeberry in spring (Fielding 1992).

With differences between blaeberry and heather in the timing of growth and decay, it is likely that in the wild herbivore preferences between these species will fluctuate both seasonally and spatially, but that the two species will often complement each other in their diet in comparison to other types of food such as grasses and forbs. Therefore, on present evidence, manipulation of moorland to encourage either blaeberry or heather to oust each other does not seem worthwhile, but their co-existence should be encouraged, giving greater choice to all herbivores.

STUDIES ON PROPAGATION

This work was aimed at finding practical ways of creating blaeberry stands in farmland or grassy moorland that currently lacks blaeberry. With some marginal farmland being abandoned, with the enforced set-aside of parts of arable farms, and with an increasing area of 'white' moorland devoid of heath plants, there is now considerable scope for developing moorlands suitable for red grouse.

Propagation methods

Blaeberry can be propagated from seed or from cuttings, bare-root transplants, turves or cores of rooted material. All methods can be successful under suitable horticultural conditions. However, such conditions are rarely realised in field situations, so that in practice the range of techniques for field use is generally more restricted. Only the more robust techniques such as transplanting well-rooted plants seem to result in high survival rates. But seeds or cuttings may provide a satisfactory source of material if used to produce well-established plants for subsequent transplanting.

Experimental propagation of cuttings

Experiments were set up to examine the possible benefits of (i) stem slitting and hormone treatment, (ii) cutting length, and (iii) fertilizer treatment, on survival and subsequent growth of cuttings. In each experiment cuttings were grown in 50:50 peat/sand compost in 10 cm x 10 cm square pots, five cuttings to a pot. There were five replicates of all treatments, arranged in fully randomised blocks in a cool greenhouse (range 8–25°C) with automatic spray irrigation.

In the first experiment, 10 cm cuttings were dipped in one of two proprietary hormone rooting powders, Seradix (4-(3 indolyl)-butyric acid) and Murphy (Captan and 1-naphthylenic acid), or left untreated. Half the stems were slit to 2 cm with a razor blade prior to being planted. The survival of control cuttings was better than that of either slit or hormone treatments, which appeared to confer no obvious benefits (Table 18).

Table 18. Effects of rooting hormones and stem slitting on % survival after nine months of 10 cm blaeberry cuttings (*P<0.05; NS=not significant)

	% Survival			Analysis of variance
	Controls	Murphy	Seradix	
Uncut stems	72	28	44	*
Slit stems	56	48	48	NS

Table 19. Comparisons of % survival and mean numbers of new shoots produced after nine months by short (10 cm) medium (15 cm) and long (20 cm) shoots of blaeberry. All shoots were planted to expose 5 cm of aerial shoot (NS=not significant)

	Cutting length (cm)			Analysis of variance
	10	15	20	
% survival	88	76	80	NS
Mean no. new shoots	5.2	4.2	5.5	NS

A second experiment compared the establishment of cuttings differing in length but having the same length of exposed shoot. The three lengths used were 10 cm, 15 cm and 20 cm, cut from the same source, and planted in the same size of pots. There were no significant differences in either percentage survival or mean numbers of new shoots produced after nine months (Table 19), so that cutting length appeared to have no pronounced influence on survival.

The final experiment examined the effects of fertilizer additions in the range 0–200 kg ha⁻¹ of NPK applied as 7:7:7 slow-release Sustanams fertilizer. Survival tended to decline with increasing fertilizer rate but the effects on shoots/plant showed no obvious trend after nine months. Total dry weights of roots and shoots after twelve months were greatest at the lowest fertilizer addition (12.5 kg ha⁻¹) but showed no benefit of any other level of addition (Table 20).

Overall, it appears that the use of slitting, hormone powders, and different lengths of cutting have little or no beneficial effect on survival or growth, and fertilizer had only small benefits at very low levels of application.

Field trial of different propagation techniques

This trial was undertaken to compare the establishment of blaeberry in permanent grassland, using plant material ranging from seeds to turf plugs. The site at Clash Hill (300 m) was upland grassland dominated by cock's-foot (*Dactylis glomerata*). The site had not been fertilized or subjected to agricultural grazing for several years, but grazing by rabbits was heavy. The soil was freely drained sandy loam and the ground had been reclaimed from dry heather moor at some time in the past.

The part of the site used for the trial was fenced to exclude rabbits. Strips of ground were treated with paraquat in September 1991 to reduce the

Table 20. Effects of fertilizer additions on survival and numbers of shoots/plant after nine months and dry weight after 12 months. Analysis of variance: * P<0.05; NS=not significant

	Fertilizer level (kg ha ⁻¹)						Analysis of variance
	0	12.5	5	50	100	200	
Survival (%)	84	68	72	72	56	56	*
Shoots/plant	6.1	6.0	4.7	3.8	5.2	4.9	NS
Dry weight (g)	4.0	7.0	4.1	4.3	4.3	4.0	*

competition from grasses, whilst other strips were left untreated. Then six different types of material of blaeberry were planted into both weedkiller-treated and untreated ground, with six replicates of each treatment and propagation combination arranged in randomised blocks. The six types of propagation material were:

- i. dried seeds separated from berries collected August 1991 (see p12);
- ii. berries smeared on to bare soil (these berries came from the stock that yielded the dried seeds (i); the seeds had 94% viability (p12));
- iii. one-year-old seedlings in paper pots;
- iv. pot-grown rooted cuttings 18-months-old, averaging 8–10 cm tall;
- v. bare-root transplants from adjacent moorland, averaging 10 cm tall;
- vi. turf plugs from adjacent moorland of 10 cm diameter.

Individual plots were 0.5 m x 0.5 m, planted with four plants, plugs or aliquots of seeds. At approximately four-month intervals the survival of the blaeberry material was monitored, the plots being clipped at mid-summer in the second and third years to reduce competition from grasses.

The best survival resulted from rooted cuttings followed by transplanted bare-root cuttings (Table 21). The turf plugs were a failure, perhaps because of a tendency to dry out soon after planting. Transplanted seedlings and smeared berries had a small number of survivors at both analyses, but no establishments from dried seeds were recorded. The weedkiller substantially improved plant survival and is probably essential to reduce competition from vigorous grass growth at a site such as this. Possibly in more open grassland such treatment might be less necessary, but this was not investigated.

Height increment in the cuttings and transplants has been modest. Dieback of the main shoots occurred in the first ten months in many plants, after which growth was continued either by side shoots or new stems emerging from below ground. The height of the tallest shoot in summer 1993 was only 18 cm, this plant being a cutting.

Seedlings have remained distinct from the plants developed from cuttings and transplants, in having tiny leaves and stems less than 1 mm wide. In the cool glasshouse, seedlings of the same origin as those planted developed stronger shoots in their third summer of growth (Figure 10), and it is likely that the surviving seedlings at Clash Hill will grow more vigorously in future years.

Taking into account the relatively large amount of effort required to produce rooted plants from cuttings, the most cost-effective way of establishing blaeberry at this site appeared to be by using rooted stems from adjacent moorland.

Other trials of propagation techniques

Transplanting was attempted at two high-altitude sites at Cairn Gorm and the Lecht (McGowan & Bayfield 1992). At Cairn Gorm, bare-root cuttings transplanted in a freely drained gravel soil at 1000 m had 23% survival after 12 months. The use of hydrophilic gel powder to improve moisture retention was of no benefit. At the Lecht at 640 m, turf plugs and bare-root transplants were compared. Turf plugs had 80% survival after a year compared with 20% for bare-root transplants. This result suggests that site conditions and the state and size

Table 21. Success of different propagation techniques at a permanent grassland site

Surface treatment	% plants surviving after			
	10 months		20 months	
	W	O	W	O
Transplanting rooted stems from moorland	74	25	52	8
Transplanting rooted stems grown in pots	83	58	70	17
Transplanting turf plugs	0	0	0	0
Transplanting one-year-old seedlings in pots	39	29	17	0
Smeared berries	33	0	19	0
Sowing seeds*	0	0	0	0

*No germinations were observed in 7 subsequent visits, but we do not know if any viable seeds remain
W=weed killed, O=unsprayed

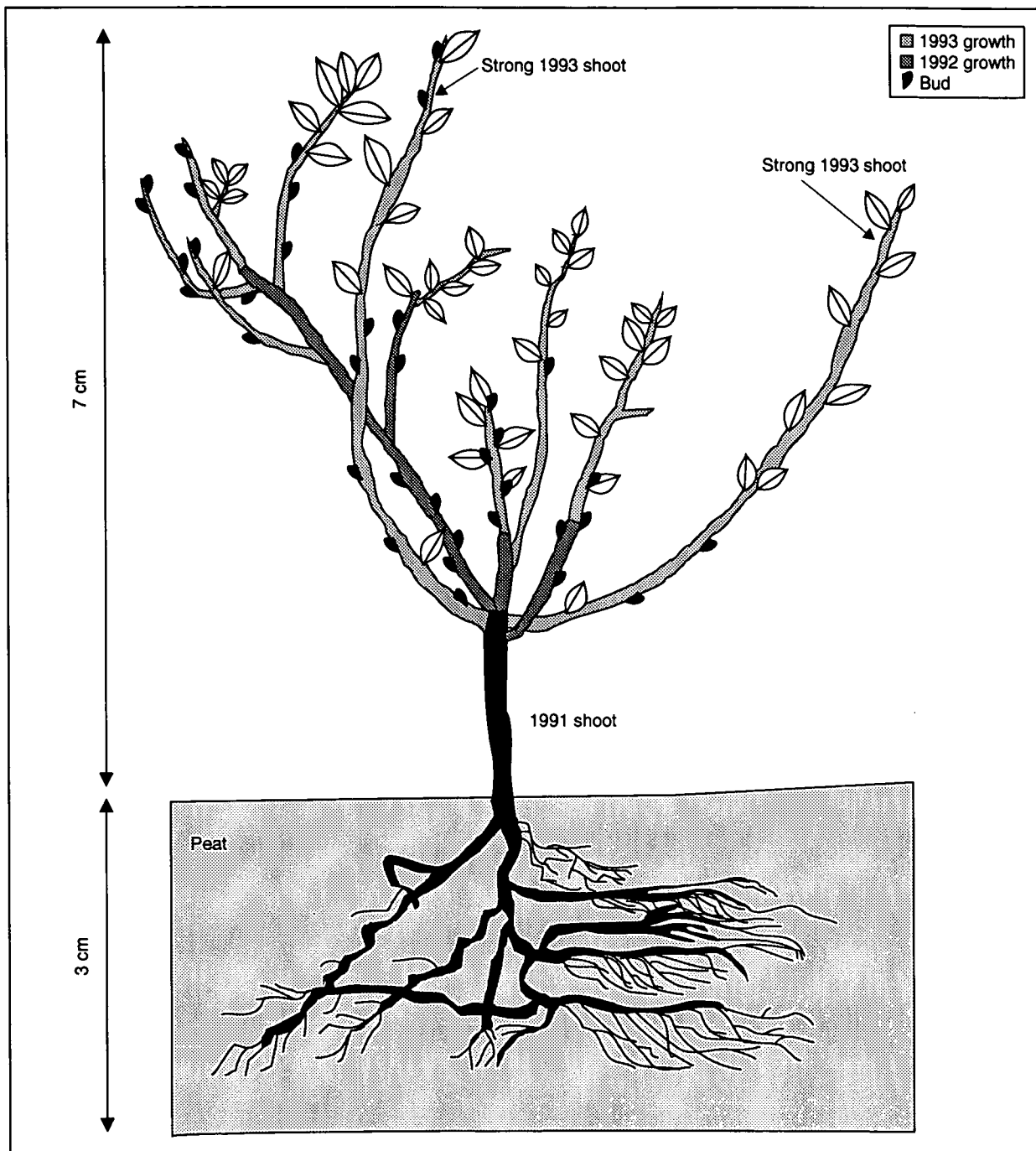


Figure 10. A seedling after three years' growth in a glasshouse, but stressed by competition from c25 other seedlings in a 14 cm x 12 cm tray. Two strong shoots with angled stems have arisen in 1993 from the 1991 stem: this is now woody

of the plants being introduced much influence success; perhaps turf plugs had better survival at the Lecht than at Clash Hill because the plants were smaller, which meant that a greater proportion of their root system was retained in the soil plug. More trials at a range of sites, using plugs, bare-root and rooted-cutting material are needed to give a proper evaluation of these techniques.

Further attempts to establish blaeberry from seeds and squashed berries were made respectively at Tillyfour (NJ 598093, 305 m) and Garrol Hill (NO 719912, 198 m) in NE Scotland. At Tillyfour, gorse

(*Ulex europaeus*) scrub invading heather moorland had been cleared by bulldozer, leaving a bare peat soil. About 1000 seeds were scattered over a marked 1 m² in December 1991; the same stock of seeds was used as in the 1991 viability test (p12), which gave 94% germination. Checks for germination and establishment were made during 1992 and 1993, but the only seedlings found were of gorse, heath bedstraw and heather. At Garrol Hill, a dense grass sward dominated by crested dog's-tail (*Cynosurus cristatus*) and Yorkshire fog (*Holcus lanatus*) had developed from heather moorland under heavy grazing (Welch & Scott 1995). Aliquots

of squashed berries were smeared in ten permanently marked 20 cm x 20 cm areas, approximately 30 berries contributing to each aliquot. The berries were obtained in August 1991 from Glen Dye (p12) and the smearing was done in September 1991. In July 1992, three blaeberry seedlings were found growing singly in three of the marked areas, but they had disappeared by the time of the next observation six weeks later. Further checks in 1993 showed that no seedlings became established, the dense grass turf evidently being unsuitable for tiny slow-growing seedlings, despite its height averaging only 5-8 cm.

GENERAL DISCUSSION

Blaeberry has unusual characteristics for a British moorland species, which influence its competitive ability. The early start to growth, the leaves appearing in April, suggests that blaeberry is adapted to deciduous woodland; field layer species in this habitat normally develop early because photosynthesis is limited by shading in summer. But the availability of new growth when only old shoots are present on other dwarf shrubs makes blaeberry attractive to herbivores. And even when growth begins in heather and other heaths (*Erica cinerea*, *E. tetralix*), the greater mass of new tissue available from blaeberry makes it a better host for relatively immobile animals, such as moth larvae, which cannot search widely for favoured food, compared with hares and ungulates.

Early growth means that blaeberry is vulnerable to frost damage, and a clear reduction in cover was observed at a Scottish site following a late-spring frost (Figure 7). The effects of frosts on fruit yields have been quantified in Scandinavia, but for shoot growth neither the immediate nor the long-term losses due to frosts have been measured.

Compared to heather, blaeberry is obviously less competitive when growing in open moorland, but the reasons for this are unclear. Selective grazing may sometimes be a contributing factor, but annual utilisation rates were found to differ little between heather and blaeberry; at some sites there was a switch in herbivore preference from blaeberry in summer to heather in winter. When protected from grazing, blaeberry bushes had smaller increases in height than had heather bushes, and blaeberry seedlings grew much more slowly than heather seedlings in a glasshouse; we believe that blaeberry is simply a slower-growing and less productive species than heather. As a next step in studying blaeberry, the development of a model for biomass production, offtake and losses, akin to the Macaulay Land Use Research Institute heather model (Armstrong 1990), would be desirable. We suggest that attributes like the ability of the stems to photosynthesise for several years give blaeberry stress tolerance (Grime 1979) at the expense of efficient production. Also, there is a considerable loss of assimilates annually in berry tissue, greater than the expenditure on seed production by heather.

The feeding value of blaeberry to birds and mammals is roughly similar to heather. With differences in the timing of growth and the longevity of the leaves, seasonal variation in relative palatability and digestibility is inevitable, and weather sequences may also have different effects

on the two species. Red grouse, black grouse and capercaillie were found to differ in their relative preference for blaeberry compared to heather when fed a common diet, and evidently preference is affected by what foods the herbivores are used to eating. We now know that both heather and blaeberry are valuable, and that, because they to some extent complement each other as food for grouse and livestock, it is desirable to have both species growing on moorland.

The origins of blaeberry-dominant moorland in Britain are uncertain, and short-term studies can only produce ideas which need testing with long-term observation. At high altitudes blaeberry dominance is associated with prolonged snow-lie, but in lower moorlands we believe that either muirburn or tree cover has been involved in the development of most blaeberry-dominant swards. Under moderate levels of grazing, blaeberry declined at sites in Derbyshire, and at sites in NE Scotland it was unreactive, with very few increases in cover either over 2–3 year periods or cumulatively in 20-year periods. The only substantial increase in blaeberry cover that we recorded was at a Scottish site which was burnt. On moorland that was not burnt, blaeberry was sometimes replaced by heather and sometimes by grasses, and it seems that there is only a narrow range of grazing pressures that permit blaeberry spread but check heather.

The slow attainment of mature bush size and the difficulties of transplanting make blaeberry unsuitable for use as a main species in schemes to recreate moorland; heather is easier to establish, either from transplants or from seeding. The best methods by which blaeberry swards can be established at moderate cost are rooting cuttings in a glasshouse and then transplanting, and moving cores from shallow-rooted stands. The effort involved in picking and squashing berries, and then distributing the pulp on to ground intended to become moorland, with only a chance that some bushes will have developed in ten years' time, means this method cannot be recommended.

It is odd that a plant which fruits so prolifically should give rise to so few seedlings. Perhaps the plant became adapted for its seeds to be dispersed by birds, but the bird species involved do not now live on moorlands, or have become scarce, or have turned to other foods. Black grouse are likely candidates as once-important dispersal agents, being known to eat the berries and having declined sharply in numbers (Baines 1993); a study of the droppings of black grouse would be useful to find

out if blaeberry seedlings germinate and become established on them in field conditions. Dispersal by birds, even when outweighed by rodent consumption, may have advantages to the plant, in that propagules are taken considerable distances to environments where the plant is absent. Similarly, Englund (1993) concluded from his study on dispersion in guelder-rose that the species has 'a very costly bet-hedging seed-dispersal strategy'; only 1% of the seeds were dispersed (by waxwings and thrushes), the rest being destroyed by rodents. An example of how slow blaeberry is to colonise newly available suitable habitat is given by Dzwonko (1993). Deciduous woods were planted around an ancient Polish woodland with blaeberry abundant in the field layer, but after 70 years very few blaeberry plants have become established in the planted woods.

Although the current study was motivated by the value of blaeberry to game-birds and to the shooting industry, there are several other reasons for maintaining or spreading stands of blaeberry in British moorlands. Blaeberry provides livestock with useful feeding at times in the year when grasses are unpalatable or unavailable, and blaeberry moorland has considerable conservation value both in its own right as a scarce type of vegetation, and as habitat for animals. Several invertebrate species appear to depend on blaeberry, including the attractive bumblebee *Bombus monticola* (Yalden 1983), and more are likely to be found when invertebrate life cycles are better researched.

Blaeberry moorland could be affected by measures now being introduced to reduce grazing pressures on heather moorland in the interests of conservation, perhaps having to carry some of the displaced livestock. This is particularly likely in Environmentally Sensitive Areas (ESAs), such as the North Peak, where payments are being given for cutting rates of stocking on heather; it would be a pity if blaeberry were to decline as heather spreads.

In order to maintain existing blaeberry moorland, we need better knowledge about herbivore impacts and trends in composition. Modelling blaeberry production and impacts is clearly necessary but will be a considerable task; because the stems stay green and relatively non-woody for 2–3 years, losses will have to be monitored for more than a 12-month cycle, and the timing of defoliation within this period may be important. Muirburn effects are inconvenient to study being necessarily long term when the cycle length between fires in British moorland is often 25 years. However, we judge that these research topics are more important for practical management than studying the decline of

seed viability in the soil and the reasons why blaeberry is sometimes preferred by herbivores to other moorland food plants.

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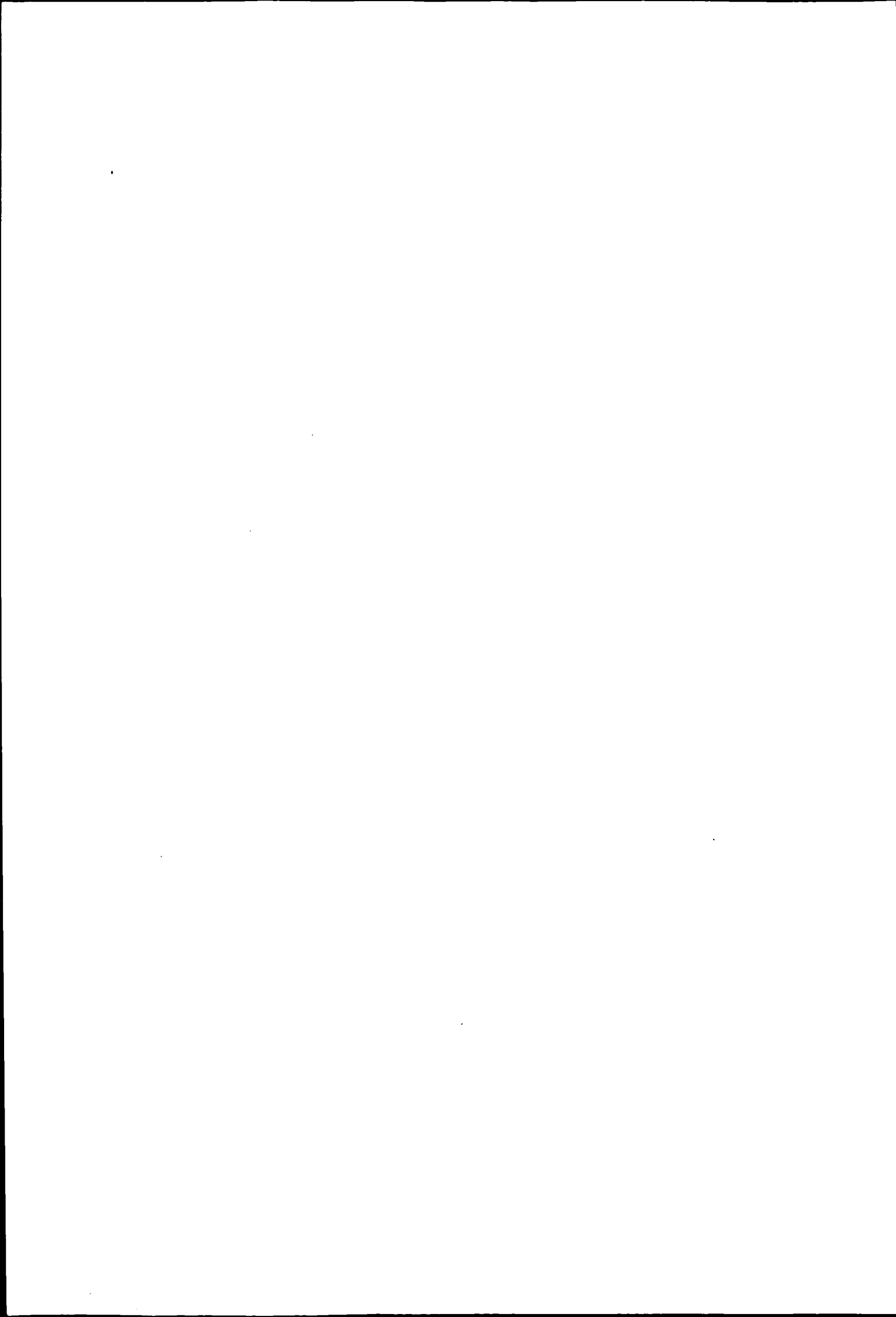
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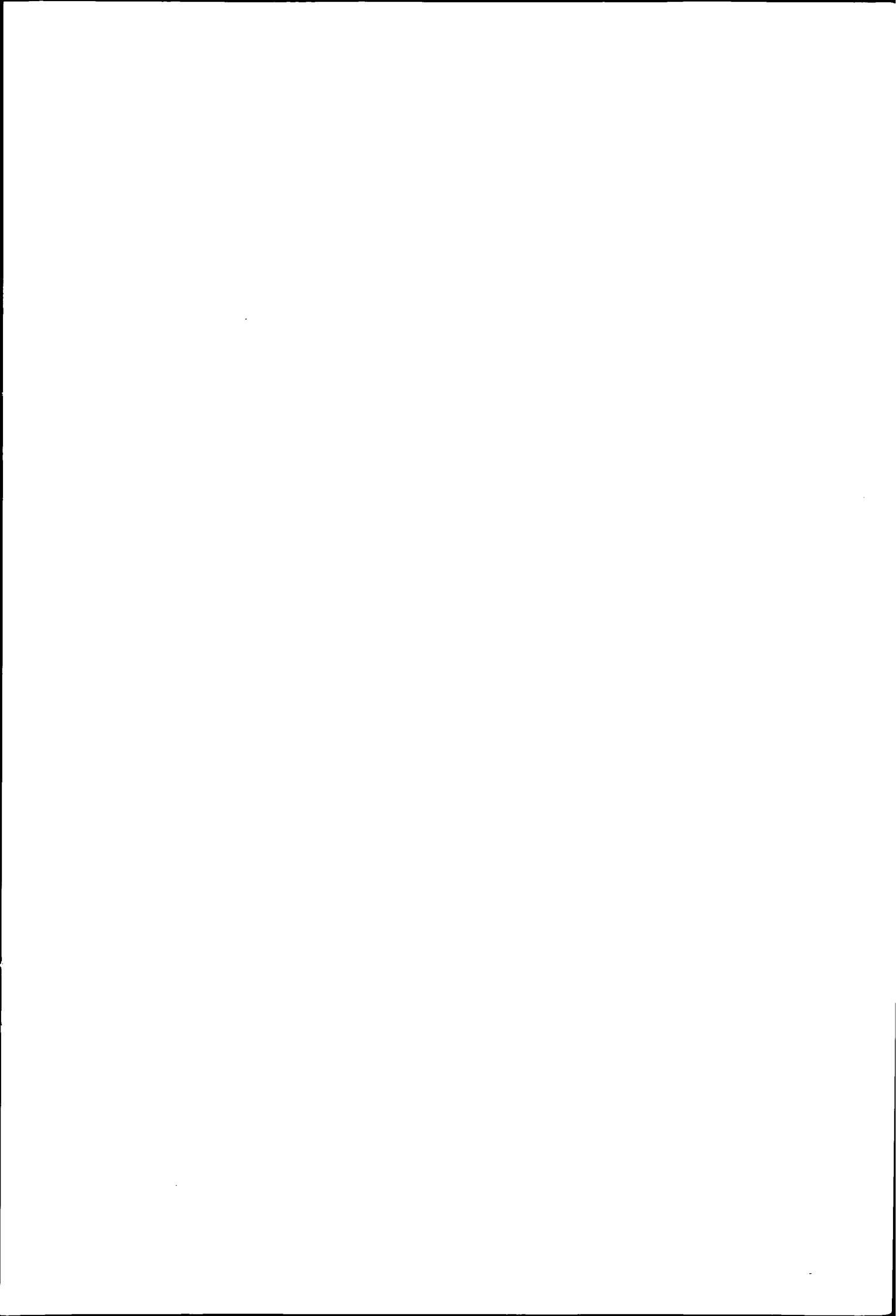
REFERENCES

- Adamson, R.S.** 1918. On the relationships of some associations of the southern Pennines. *Journal of Ecology*, **6**, 97–109.
- Anderson, D.J.** 1961. The structure of some upland plant communities in Caernarvonshire. II. The pattern shown by *Vaccinium myrtillus* and *Calluna vulgaris*. *Journal of Ecology*, **49**, 731–738.
- Anderson, P. & Yalden, D.W.** 1981. Increased sheep numbers and loss of heather moorland in the Peak District, England. *Biological Conservation*, **20**, 195–213.
- Andre, J., Gensac, P., Pellissier, F. & Trosset, L.** 1987. Regeneration of spruce populations at high altitudes, preliminary research into the role of allelopathy and mycorrhization in the final stages of development. *Revue d'Ecologie et de Biologie du Sol*, **24**, 301–310.
- Armstrong, H.** 1990. Modelling the effects of vertebrate herbivore populations on heather moorland vegetation. In: *Modelling heather management: a workshop report*, edited by M. Whitby & S. Grant, 56–67. Newcastle-upon-Tyne: Department of Agricultural Economics and Food Marketing, University of Newcastle-upon-Tyne.
- Atlegrim, O.** 1992. Mechanisms regulating bird predation on a herbivorous larva guild in boreal coniferous forests. *Ecography*, **15**, 19–24.
- Baines, D.** 1991. Factors contributing to local and regional variation in black grouse breeding success in northern Britain. *Ornis Scandinavica*, **22**, 264–269.
- Baines, D.** 1993. *The black grouse report*. Fordingbridge: Game Conservancy Trust.
- Baines, D. & Sage, R.** 1992. Capercaillie decline and caterpillar abundance in Highland pinewoods. *Game Conservancy Review of 1991*, 104–105.
- Bannister, P.** 1970. The annual course of drought and heat resistance in heath plants from an oceanic environment. *Flora (Jena)*, **159**, 105–123.
- Boström, U. & Hansson, L.** 1981. Small rodent communities on mires: implications for population performance in other habitats. *Oikos*, **37**, 216–224.
- Butler, P.** 1985. *The ecology of dwarf shrub species from diverse altitudes and latitudes*. PhD thesis, Cambridge University.
- Cederlund, G. & Nyström, A.** 1981. Seasonal differences between moose and roe deer in ability to digest browse. *Holarctic Ecology*, **6**, 59–65.
- Clarke, J.L., Welch, D. & Gordon, I.J.** 1995. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics. *Journal of Applied Ecology*, **32**. In press.
- Corbet, G.B. & Southern, H.N.** 1977. *The handbook of British mammals*. 2nd ed. Oxford: Blackwell Scientific.
- Cramp, S. & Simmons, K.E.L.**, eds. 1980. *The birds of the western Palearctic*. Vol. II. Oxford: Oxford University Press.
- Dement'ev, G.P. & Gladkov, N.A.** 1952. *Birds of the Soviet Union*. Vol. IV. First published Moscow. Translated into English (1967) by Israel Program for Scientific Translations.
- Drozdz, A.** 1966. Food habits and food supply of rodents in the beech forest. *Acta Theriologica*, **11**, 363–384.
- Dzwonko, Z.** 1993. Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. *Journal of Vegetation Science*, **4**, 693–698.
- Eastman, D.S. & Jenkins, D.** 1970. Comparative food habits of red grouse in northeast Scotland, using fecal analysis. *Journal of Wildlife Management*, **34**, 612–620.
- Edgell, M.C.R.** 1971. A preliminary study of some environmental variables in an upland ecosystem: Cader Idris, Merionethshire. *Journal of Ecology*, **59**, 189–201.
- Elliott, R.J.** 1953. *The effects of burning on heather moors of the south Pennines*. PhD thesis, Sheffield University.
- Elliott, S.L.** 1991. *Feeding preferences of captive grouse using heather (Calluna vulgaris) and blaeberry (Vaccinium myrtillus)*. BSc thesis, University of Southampton.
- Englund, R.** 1993. Fruit removal in *Viburnum opulus*: copious seed predation and sporadic massive seed dispersal in a temperate shrub. *Oikos*, **67**, 503–510.
- Fielding C.** 1992. *Aspects of the ecology of the Lepidoptera associated with heather Calluna vulgaris*. PhD thesis, University of Durham.
- Flower-Ellis, J.G.K.** 1971. Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.). *Research Notes of the Royal College of Forestry, Stockholm*, no. 9, 108pp.
- Granström, A.** 1982. Seed banks in five boreal forest stands originating between 1810 and 1963. *Canadian Journal of Botany*, **60**, 1815–1821.
- Granström, A.** 1987. Seed viability of fourteen species during five years of storage in a forest soil. *Journal of Ecology*, **75**, 321–331.
- Grime, J.P.** 1979. *Plant strategies and vegetation processes*. Chichester: Wiley.
- Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. & Shaw, S.** 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**, 1017–1059.
- Hansson, L. & Larsson, T-B.** 1978. Vole diet on experimentally managed reforestation areas in northern Sweden. *Holarctic Ecology*, **1**, 16–26.

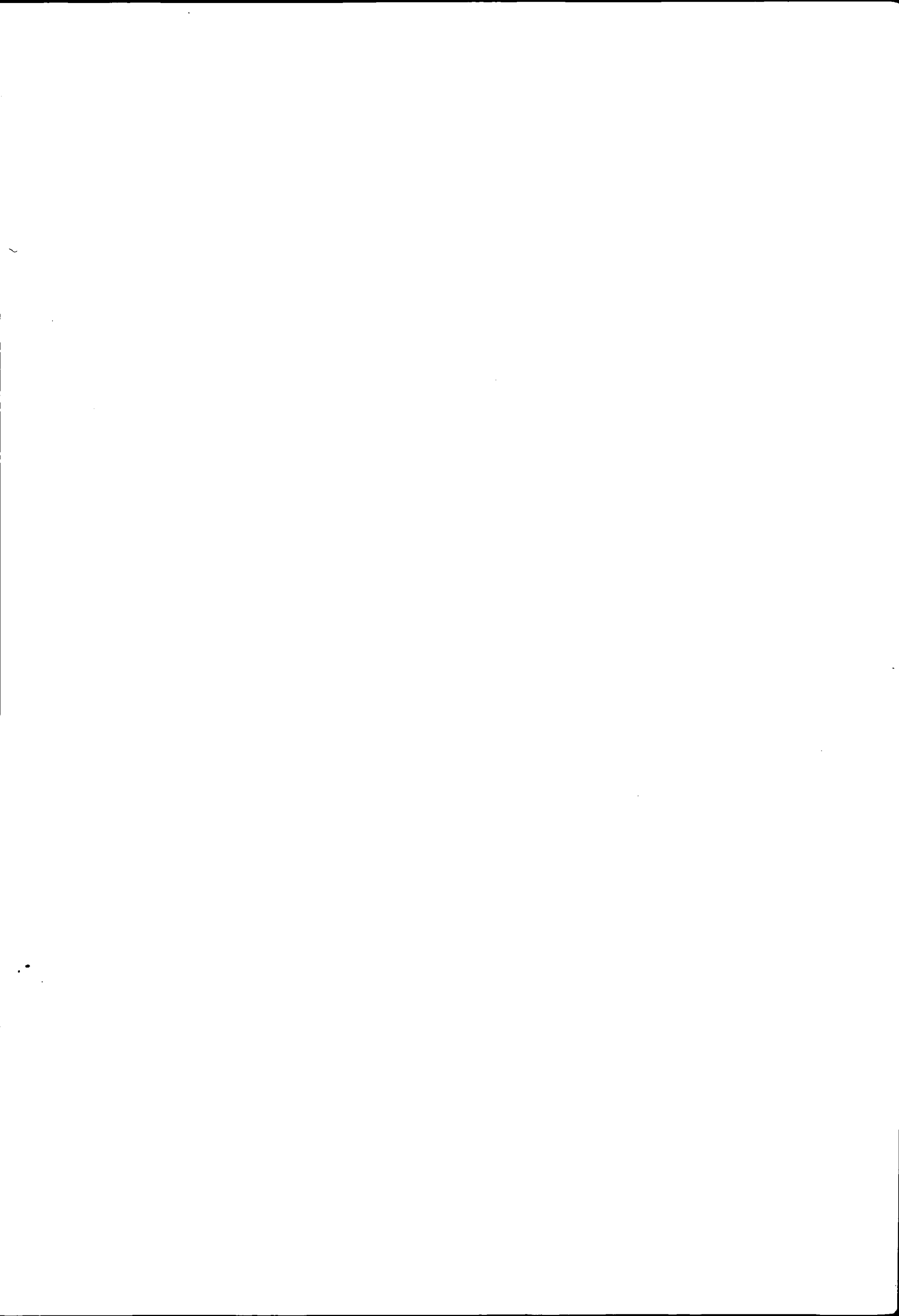
- Havas, P.** 1971. The water economy of the bilberry (*Vaccinium myrtillus*) under winter conditions. Report Kevo Subarctic Research Station, **8**, 41–52.
- Heintze, A.** 1915. Om endozoisk fröspridning genom skandinaviska däggdjur. *Botaniska Notiser*, 251–291.
- Hester, A.J., Miles, J. & Gimingham, C.H.** 1991a. Succession from heather moorland to birch woodland. I. Experimental alteration of specific environmental conditions in the field. *Journal of Ecology*, **79**, 303–315.
- Hester, A.J., Miles, J. & Gimingham, C.H.** 1991b. Succession from heather moorland to birch woodland. II Growth and competition between *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Agrostis capillaris*. *Journal of Ecology*, **79**, 317–328.
- Hill, M.O. & Stevens, P.A.** 1981. The density of viable seed in soils of forest plantations in upland Britain. *Journal of Ecology*, **69**, 693–709.
- Holland, O. & Staaland, H.** 1992. Nutritional strategies and winter survival of European roe deer in Norway. In: *The biology of deer*, edited by R.D. Brown, 423–428. New York & Berlin: Springer.
- Hudson, P.N., Mann, S.O., Summers, R. & Staines, B.W.** 1975. Rumen function in red deer, hill sheep and reindeer in the Scottish Highlands. *Proceedings of the Royal Society of Edinburgh B*, **75**, 181–198.
- Ingestad, T.** 1973. Mineral nutrient requirements of *Vaccinium vitis idaea* and *V. myrtillus*. *Physiologia Plantarum*, **29**, 239–246.
- Karlsson, P.S.** 1987. Micro-site performance of evergreen and deciduous dwarf shrubs in a subarctic heath in relation to nitrogen status. *Holarctic Ecology*, **10**, 114–119.
- Kuchko, A.A.** 1988. Bilberry and cowberry yields and the factors controlling them in the forests of Karelia, USSR. *Acta Botanica Fennica*, **136**, 23–25.
- Kujala, V.** 1926. Untersuchungen über die Waldvegetation in Süd- und Mittelfinland. I. *Communicationes ex Instituto Quaestionum Forestalium Finlandiae*, no. 10.
- Lähdesmäki, P., Pakonen, T., Saari, E., Laine, K. & Havas, P.** 1990a. Environmental factors affecting basic nitrogen metabolism and seasonal levels of various nitrogen fractions in tissues of bilberry *Vaccinium myrtillus*. *Holarctic Ecology*, **13**, 19–30.
- Lähdesmäki, P., Pakonen, T., Saari, E., Laine, K., Tasanen, L. & Havas, P.** 1990b. Changes in total nitrogen, protein, amino acids and NH_4 in tissues of bilberry, *Vaccinium myrtillus*, during the growing season. *Holarctic Ecology*, **13**, 31–38.
- Laine, K.M. & Henttonen, H.** 1987. Phenolics/nitrogen ratios in the blueberry *Vaccinium myrtillus* in relation to temperature and microtine density in Finnish Lapland. *Oikos*, **50**, 389–395.
- Latham, J.** 1993. *Factors affecting the relative densities of red and roe deer in Scottish forests*. PhD thesis, University of Aberdeen.
- McGowan, G.M. & Bayfield, N.G.** 1992. *Monitoring of upland revegetation trials 1992*. (NERC contract report no. 7 to Scottish Natural Heritage.) Banchory: Institute of Terrestrial Ecology.
- Miller, G.R. & Cummins, R.** 1985. How important are banks of buried seeds in the Cairngorm Mountains? *Annual Report of the Institute of Terrestrial Ecology 1984*, 101–104.
- Moss, R.** 1967. Probable limiting nutrients in the main food of red grouse (*Lagopus lagopus scoticus*). In: *Secondary productivity of terrestrial ecosystems*, vol. I, edited by K. Petruszewicz, 369–379. Warszawa and Krakow: Institute of Ecology, Polish Academy of Sciences.
- Moss, R.** 1975. Different roles of nutrition in wild and domestic game birds and other animals. *Proceedings of the Nutrition Society*, **34**, 95–100.
- Moss, R. & Hanssen, I.** 1980. Grouse nutrition. *Nutrition Abstracts and Reviews B*, **50**, 555–567.
- Moss, R., Miller, G.R. & Allen, S.E.** 1972. Selection of heather by captive red grouse in relation to the age of the plant. *Journal of Applied Ecology*, **9**, 771–781.
- Nikolakopoulos, G.** 1990. *The digestion of heather and bilberry by captive red grouse during the summer season*. MSc thesis, University of Aberdeen.
- Oksanen, L. & Ericson, L.** 1987. The role of phenol-based inducible defense in the interaction between tundra populations of the vole *Clethrionomys rufocanus* and the dwarf shrub *Vaccinium myrtillus*. *Oikos*, **50**, 371–380.
- Pakonen, T., Laine, K., Havas, P. & Saari, E.** 1988. Effects of berry production and deblossoming on growth, carbohydrates and nitrogen compounds in *Vaccinium myrtillus* in north Finland. *Acta Botanica Fennica*, **136**, 37–42.
- Pakonen, T., Saari, E., Laine, K., Havas, P. & Lähdesmäki, P.** 1991. How do seasonal changes in carbohydrate concentrations in tissues of bilberry (*Vaccinium myrtillus* L.) reflect carbon resource allocation patterns? *Acta Oecologica*, **12**, 249–259.
- Perttula, U.** 1941. Untersuchungen über die generative und vegetative Vermehrung der Blütenpflanzen in der Wald. *Annales Academiae Scientiarum Fennicae Series A*, **58** (1).
- Picozzi, N.** 1986. *Black grouse research in NE Scotland*. (NERC contract report to World Pheasant Association.) Banchory: Institute of Terrestrial Ecology.
- Pigott, C.D.** 1983. Regeneration of oak-birch woodland following exclusion by sheep. *Journal of Ecology*, **71**, 629–646.
- Powell, C.F. & Malcolm, D.C.** 1974. Seasonal and spatial variation in the mineral content of some upland vegetation types in Scotland. *Journal of Applied Ecology*, **11**, 1173–1184.

- Pullianen, E. & Tunkkari, P.S.** 1991. Responses by capercaillie *Tetrao urogallus*, and the willow grouse *Lagopus lagopus*, to the green matter available in early spring. *Holarctic Ecology*, **14**, 156–160.
- Raatikainen, M. & Vänninen, I.** 1988. The effects of the 1984–1985 cold winter on the bilberry and lingonberry yield in Finland. *Acta Botanica Fennica*, **136**, 43–47.
- Ritchie, J.C.** 1955. A natural hybrid in *Vaccinium*. I. The structure, performance and chorology of the cross *Vaccinium intermedium* Ruthe. *New Phytologist*, **54**, 49–67.
- Ritchie, J.C.** 1956. *Vaccinium myrtillus*. (Biological flora of the British Isles.) *Journal of Ecology*, **44**, 291–299.
- Rodwell, J.S., ed.** 1992. *Moorlands and mire communities*. (British plant communities. Vol. 2.) Cambridge: Cambridge University Press.
- Savory, C. J.** 1974. *The feeding ecology of red grouse in NE Scotland*. PhD thesis, University of Aberdeen.
- Schaminée, J.H.J., Hennekens, S.M. & Thébaud, G.** 1993. A syntaxonomical study of subalpine heathland communities in West European low mountain ranges. *Journal of Vegetation Science*, **4**, 125–134.
- Sjors, H.** 1989. Blåbär, *Vaccinium myrtillus* – ett växtporträtt. *Svensk Botanisk Tidskrift*, **83**, 411–428.
- Södergård, A.** 1934. Über das Vorkommen von Keimpflanzen bei: *Vaccinium vitis idaea*, *V. myrtillus* und *Linnaea borealis*. *Memoranda Societas pro Fauna et Flora Fennica*, **11**, 48–51.
- Stace, C.** 1991. *New Flora of the British Isles*. Cambridge: Cambridge University Press.
- Stewart, W.S. & Bannister, P.** 1973. Seasonal changes in carbohydrate content of three *Vaccinium* spp. with particular reference to *V. uliginosum* L. and its distribution in the British Isles. *Flora*, **162**, 134–155.
- Summers, C.F.** 1971. Food preference experiments with captive ptarmigan. *Transactions of the Botanical Society of Edinburgh*, **41**, 227–230.
- Summers, C.F.** 1978. Production in montane dwarf shrub communities. In: *Production ecology of British moors and montane grasslands*, edited by O.W. Heal & D.F. Perkins, 263–276. Berlin: Springer.
- Sylvén, N.** 1906. Om de svenska dikotyledonernas första förstärknings stadium eller utveckling från frö till blomning. *Handlingar Kungliga Svenska Vetenskapsakademien*, **40** (2).
- Thomas, B. & Trinder, N.** 1947. The ash components of some moorland plants. *Empire Journal of Experimental Agriculture*, **15**, 237–248.
- Tolvanen, A., Laine, K., Pakonen, T., Saari, E. & Havas, P.** 1992. Compensatory responses of a deciduous dwarf shrub, the bilberry (*Vaccinium myrtillus* L.) to simulated herbivory – some comparisons with the evergreen lingonberry (*Vaccinium vitis-idaea* L.). *Acta Oecologica*, **13**, 607–615.
- Trinder, N.** 1975. The feeding value of moorland plants. *ADAS Science Service*, 176–187.
- Tschager, A., Hilscher, H., Franz, S., Kull, U. & Larcher, W.** 1982. Seasonal dynamics of lipid storage in *Loiseleuria procumbens* and other *Ericaceae* of the alpine dwarf shrub heath. *Acta Oecologica–Oecologica Plantarum*, **3**, 119–134.
- Vänninen, I., Laakso, S. & Raatikainen, M.** 1988. Geographical variation in the phenology and morphology of bilberry in Finland. *Acta Botanica Fennica*, **136**, 49–59.
- Watson, A.** 1985. Soil erosion and vegetation damage near ski lifts at Cairn Gorm, Scotland. *Biological Conservation*, **33**, 363–381.
- Welch, D.** 1982. Dung properties and defecation characteristics in some Scottish herbivores, with an evaluation of the dung–volume method of assessing occupance. *Acta Theriologica*, **27**, 189–210.
- Welch, D.** 1984a. Studies in the grazing of heather moorland in north–east Scotland. III. Floristics. *Journal of Applied Ecology*, **21**, 209–225.
- Welch, D.** 1984b. Studies in the grazing of heather moorland in north–east Scotland. II. Response of heather. *Journal of Applied Ecology*, **21**, 197–207.
- Welch, D.** 1985. Studies in the grazing of heather moorland in north–east Scotland. IV. Seed dispersal and plant establishment in dung. *Journal of Applied Ecology*, **22**, 461–472.
- Welch, D.** 1993. Blaeberry research, a Derbyshire grazing experiment. *9th Annual Report of the Joseph Nickerson Reconciliation Project*, 33–37.
- Welch, D. & Scott, D.** 1995. Studies in the grazing of heather moorland in north–east Scotland. VI. 20–year trends in botanical composition. *Journal of Applied Ecology*. In press.
- Woodward, F.I.** 1986. Ecophysiological studies on the shrub *Vaccinium myrtillus* L. taken from a wide altitudinal range. *Oecologia*, **70**, 580–586.
- Woolhouse, H.W. & Kwolek, A.V.A.** 1981. Seasonal growth and flowering rhythms in European heathlands. In: *Heathlands and related shrublands*, edited by R.L. Specht, 29–37. (Ecosystems of the World, Vol. 9B.) Amsterdam: Elsevier.
- Yalden, P.E.** 1983. Foraging population size and distribution of *Bombus monticola* in the Peak District, England. *Naturalist*, **108**, 139–147.
- Yalden, P.E.** 1984. Flower visits by *Bombus monticola* Smith (Hymenoptera: Apidae) in the Peak District, England. *Entomological Gazette*, **35**, 235–242.









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