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I.B.P. studies on montane grassland and moorlands

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The aim of the grassland and moorland studies was to measure primary and secondary production and to describe the main pathways of dry matter and nutrients within these ecosystems. The strategy was to make detailed studies on two main sites (Snowdonia and Moor House N.N.R. in the northern Pennines) with a limited number of supporting studies. The examination of the few sites in the U.K. must be seen as part of a series of sites within the International Grassland and Tundra Biomes. They are thus replicates and the series allows examination of trends in productivity related to environmental conditions. The Bi-Polar Botanical Project, with sites in Greenland and South Georgia, supported by the U.K., is part of the international series.

The Snowdonia project covered a range of sites but concentrated on a sheep-grazed *Agrostis-Festuca* sward at 460 m. At Moor House attention focused on blanket bog sites dominated by *Calluna*, *Eriophorum* and *Sphagnum* at about 600 m with supporting studies on dwarf shrub communities ranging from 1100 m in the Cairngorm Mountains to 60 m in Dorset.

Comparisons are made of three estimates of primary productivity, of herbivore consumption with production, and decomposer populations with process rates. These results are briefly reviewed in the context of the international range of sites; they allow us to distinguish broad patterns of ecosystem functioning.

Introduction

Studies on montane grasslands and moorland ecosystems in the I.B.P. concentrated at two sites, Llyn Llydaw within the Snowdon National Nature Reserve and Moor House N.N.R. in the northern Pennines. The programmes were initiated by R. E. Hughes and J. B. Cragg whose research and stimulus contributed greatly to our understanding of the ecology of the two areas. The I.B.P. research aimed at estimating primary and secondary production and quantifying the main pathways of energy and nutrient circulation within these ecosystems. Supporting studies on heathlands in Dorset, dwarf shrub communities in the Cairngorm mountains and grouse moors in eastern Scotland, although not financed by the I.B.P., provided results on particular aspects of productivity for comparison with the main sites (see table 1). Results are published in a variety of scientific papers and are being brought together in a single volume (Heal & Perkins 1976). The present paper summarizes the main results and adopts a comparative approach, although this was not a main objective of the U.K. programme. The concentration of effort into a few sites in the U.K. partly arose from the adoption of a comparative approach on an international scale, the Moor House and Snowdonia sites being linked with the Tundra and Grassland Biomes respectively.

The results presented here represent the efforts of a wide range of people and organizations. Their cooperation in the difficult subject of ecosystem analysis has been one of the strengths

of the I.B.P. Interpretation at the broad level of this paper obscures the effort which has gone into the detailed studies, but it does not minimize these efforts. We gratefully acknowledge the research detail on which this paper is based, and the efforts of the scientists who have collaborated in the synthesis and allowed reference to unpublished results.

PRIMARY PRODUCTION

The determination of standing crops (biomass) of vegetation and individual plant species and the assessment of net primary production were measurements common to most sites. These parameters were measured by harvest methods (Milner & Hughes 1968) at all sites while physiological methods, in the laboratory under controlled conditions (Grace & Woolhouse 1970, 1973 a, b; Marks 1974; Summers 1972), were used in a few studies. When noting similarities and differences the ecological interrelationships between grasslands, bogs and heaths should be considered. Grasslands are maintained in a semi-natural condition by grazing and would normally change to heath if grazing were removed. Heaths can be maintained in transitional stages towards mature heath by the practice of burning – this often being carried out in a regular cycle for purposes of management. Intermediate forms of grassland and heath can be found under different combinations of burning and grazing regimes and often contain different proportions of the species comprising the moorland and grassland habitats.
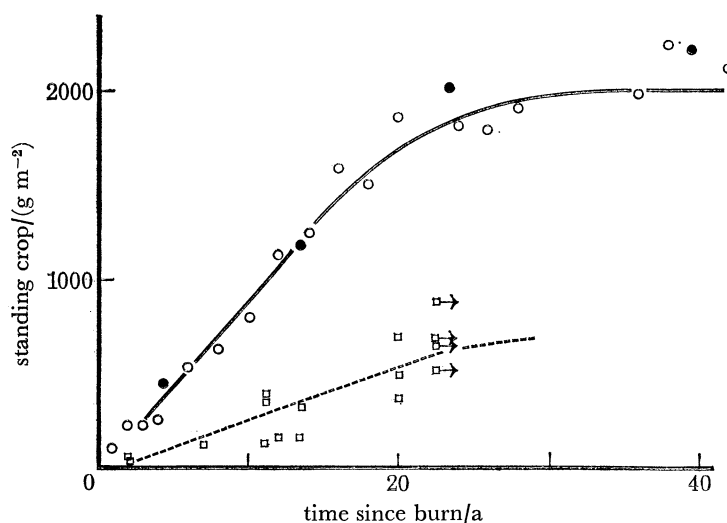

FIGURE 1. The development of above-ground standing crop of *Calluna* after burning. Dorset (○), Kerloch (●), Moor House (□; sites burnt more than 20 years before sampling □→). From Chapman, Hibble & Rafarel (1974 a), Miller & Watson (1976), and M. Rawes (personal communication). Curves are fitted by eye.

The principal vegetation types of the I.B.P. sites, indicated by dominant species in terms of biomass, together with the standing crop biomass at peak summer values, are given in table 2. There is much variation between and within the sites and this is due, in *Calluna*-dominated vegetation, mainly to the age of the stand and differences in climate; and in grasslands to differences in type of vegetation, soil type and climatic variations. The general trend of change in standing crop with age of the *Calluna* stands at Dorset, Kerloch and Moor House (figure 1) shows an increase in standing crop as the stand matures. There is evidence in some stands for

TABLE 1. GENERAL CHARACTERISTICS OF THE MAIN AND SUPPORTING SITES

site	altitude / m	plant community	soil type	mean annual temperature / °C	annual precipitation / mm
Snowdonia					
Llyn Llydaw	460	Herb-rich Agrostis-Festuca grassland / Festuca grassland	brown earth	7.4	3800
other sites	240–910	Nardus, Molinia, Juncus squarrosus grassland / Nardus, Festuca, Agrostis grassland	brown earth to peaty podzol	3.9–8.5	1500–5000
Pennines					
Moor House N.N.R.	550	Calluna, Eriophorum, Sphagnum blanket bog / Festuca, Agrostis grassland	peat / brown earth	5.1	1880
Dorset	60	Calluna heath	humus-iron podzols	10.7	800
Scotland					
Cairngorm	850–1000	various dwarf shrub heaths	skeletal to podzol	2.0	1020
Cairnwell	850–870			2.5	877
Beinn a'Bhuird	820–1100			2.0	1020
Kerloch	150	Calluna heath	peaty podzol	7.0	957

TABLE 2. COMPARATIVE STANDING CROP AND PRODUCTION DATA (ABOVE GROUND) FROM U.K. GRASSLAND AND MOORLAND SITES

(Data from Perkins, Jones, Millar & Neep (1976), Forrest (1971), Forrest & Smith (1975), Chapman, Hibble & Rafarel (1975a), Summers (1972), Miller & Watson (1976), Barclay-Estrup (1970).)

site	vegetation type	standing crop $\mathrm{g\,m^{-2}}$	growing season day	production $\mathrm{g\,m^{-2}\,a^{-1}}$	production $\mathrm{g\,m^{-2}\,d^{-1}}$
Snowdonia	Agrostis-Festuca (main site)	91 (220†)	210	270 (555–643‡)	1.35–(3.10‡)
	all types	70–430	200	12–600	0.06–3.0
Moor House	mixed aged Calluna-Eriophorum bog	1300	184	361±50	1.96
	Agrostis-Festuca	35–102	184	173 (202‡)	0.94–(1.1‡)
	all types	35–550	184	89–226 (264–202‡)	0.48–(1.43‡)
Dorset	Calluna dominated dry heath (6–42 years)	723–2453	250	320	1.28
Scotland					
Cairngorm	eroded Callunetum (14–24 years)	322	132	75	0.57
Kerloch	Calluna (2–42 years)	420–2200	204	240–270	1.17–1.32
Elsick	Bryophyte rich Calluna heath	889–2305	200	195–470	2.35

† Includes all living material above soil surface.
‡ Adjusted values allowing for losses from living to dead fractions during growing period.

a decrease in the rate of increase towards maturity and in the degenerate stage, attained between *ca.* 37 and 42 years, a decline was observed.

In contrast, the standing crop biomass of grasslands is much lower and ranges from *ca.* 35 to 550 g m^{-2} while heaths ranged from *ca.* 322 to 2453 g m^{-2}. Generally, those grasslands which are heavily grazed, e.g. the herb-rich *Agrostis-Festuca* types, tend to have lower standing crops. Those which are not heavily grazed, e.g. the types dominated by *Juncus*, *Nardus* and *Molinia*, together with the wetter *Eriophorum*-dominated bogs, tend to have standing crops approaching those found on heaths with *Calluna* in its early stages of regeneration. The larger figures in heaths reflect the increase in woody material as the *Calluna* develops. There is an accompanying increase in the quantities of mineral nutrients held in the standing crop from small amounts in heavily grazed grasslands to the highest levels in heaths.
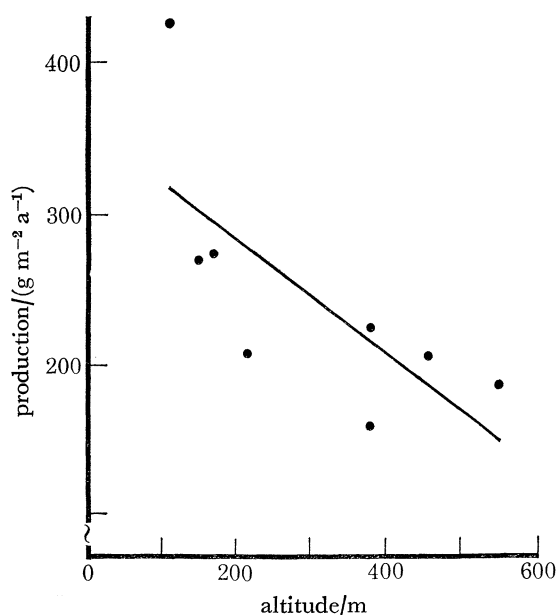

FIGURE 2. *Calluna* shoot production, corrected to 100% cover, in relation to altitude ($y = 356 - 0.37x$). (From Miller & Watson (1976).)

Table 2 also contains net primary production data from the U.K. sites and table 3 comparative data in the context of the Tundra Biome and the Grassland Biome (semi-natural pastures). Within heaths, the direct comparison of production is difficult where the percentage cover of *Calluna* varies greatly from site to site. Such a comparison, however, has been made by Miller & Watson (1976) by adjusting shoot yields to a hypothetical 100% *Calluna* cover, and a relation between annual production and altitude is apparent (figure 2). Some sites in Snowdonia, e.g. *Agrostis-Festuca* grasslands on brown earth soils, showed considerable variation, net primary production ranging from *ca.* 200 g m^{-2} a^{-1} at generally high altitude and rainfall to *ca.* 600 g m^{-2} a^{-1} at lower and drier sites. The range between major grassland types in the same area was from a mean of 366 g m^{-2} a^{-1} for *Agrostis-Festuca* types to a mean of 93 g m^{-2} a^{-1} for *Nardus*-dominated types on peaty podzols. At most sites, to reduce underestimation of production, attempts were made to adjust values for losses through death and transfer of material to the standing dead and litter components of the system.

TABLE 3. COMPARATIVE ABOVE-GROUND PRODUCTION DATA FROM GRAZED SEMI-NATURAL GRASSLANDS

site	vegetation type (dominant species)	altitude m	production† g m⁻² a⁻¹	source
Pin-au-Haras (France)	Poa-Lolium-Holcus	190	739‡ (1968–70)	Hedin (1973)
Pant-y-dŵr (Wales)	Festuca-Agrostis	302–344	220‡ (1968–69)	Munro, Davies & Morgan (1972)
	S 53 ryegrass	302–344	1060; 440 (1968–69)	
Snowdonia (Wales)	Agrostis-Festuca (main site)	488	270‡ (1966–70)	Perkins, Jones, Millar & Neep (1976)
	Agrostis-Festuca types	242–439	366‡ (1966)	Perkins & Milner (unpublished)
	Festuca types	379–909	203‡ (1966)	—
	Nardus-Molinia-Juncus types	379–424	217‡ (1966)	—
	Nardus-Festuca-Agrostis	242–424	93‡ (1966)	—
Moor House (England)	Festuca-Agrostis	550	173 (1966)	Rawes & Welch (1969)
	Nardus-Festuca-Agrostis		89 (1966)	—
	Juncus-Festuca-Deschampsia		226 (1966)	—
Pieniny Mts. (Poland)	Lolium-Cynosurus	600	200 (1970)	Traczyk & Piewczynska (unpublished)
Hardangervidda	Poa-Deschampsia-Carex	1200–1300	197‡ (1971–72)	Wielgolaski & Kjelvik (1973)

† Net primary harvestable above-ground material (unadjusted values), generally cut from vegetation protected from grazing (see Milner & Hughes 1968).

‡ Mean values, between or within stated years.

The length of the growing season was estimated as that period of the year over which significant measurable growth by harvest methods was recorded, thus allowing net primary production to be expressed as $g\,m^{-2}\,d^{-1}$. The greatest rates were at Elsick, where *Calluna* in the bryophyte heath attained a rate of $2.35\,g\,m^{-2}\,d^{-1}$, and the *Agrostis-Festuca* grassland at Llyn Llydaw which, although less productive than some other semi-natural grasslands in Snowdonia, attained a rate of between $1.35\,g\,m^{-2}\,d^{-1}$ (unadjusted value) and $3.1\,g\,m^{-2}\,d^{-}$ (adjusted value). The main species contributing to the production was *Agrostis tenuis* which had an overall adjusted seasonal value of $1.8\,g\,m^{-2}\,a^{-1}$, with a peak of $5.7\,g\,m^{-2}\,d^{-1}$, compared with *Festuca ovina* ($0.6\,g\,m^{-2}\,d^{-1}$ overall, $1.1\,g\,m^{-2}\,d^{-1}$ peak) and *Anthoxanthum odoratum* ($0.3\,g\,m^{-2}\,d^{-1}$, $0.7\,g\,m^{-2}\,d^{-1}$ peak). These values compare with maximum values for S53 ryegrass with added fertilizers at Pant-y-dŵr, Aberystwyth, of up to *ca.* $9.0\,g\,m^{-2}\,d^{-1}$ on an upland mineral soil and *ca.* $6.5\,g\,m^{-2}\,d^{-1}$ on a peaty soil (Munro, Davies & Morgan 1972), $4.97\,g\,m^{-2}\,d^{-1}$ in a *Deschampsia* wet meadow and $4.0\,g\,m^{-2}\,d^{-1}$ on a *Vaccinium* heath in the U.S.A. (Bliss 1966).

TABLE 4. MEAN ($\pm 95\,\%$ CONFIDENCE LIMITS) AERIAL BIOMASS AND ANNUAL PRODUCTION OF SHOOTS AND FLOWERS IN DIFFERENT GROWTH PHASES OF *CALLUNA* IN 1964–9

(Miller & Watson 1976.)

	growth phase of *Calluna*			
	pioneer	building	mature	degenerate
age/a	2–7	8–19	18–29	37–42
cover (%)	55	85	95	95
height/cm	17	33	41	40
aerial biomass/($g\,m^{-2}$)	420 ± 80	1180 ± 90	2000 ± 150	2200 ± 180
annual production/($g\,m^{-2}$) shoots	139 ± 9	177 ± 6	215 ± 9	193 ± 12
flowers	29 ± 4	33 ± 3	55 ± 5	45 ± 5
total	168 ± 13	210 ± 9	270 ± 12	239 ± 13

In heaths, the pattern of shrub development throughout the seral stages gives rise to variation in net primary production. Rates of production are greatest during the early stages of development, become relatively constant during mature stages and may decrease during degenerate stages (Chapman & Webb 1976; Chapman, Hibble & Rafarel 1975*a, b*). In the Dorset heath, net primary production above ground was estimated to be $320\,g\,m^{-2}\,a^{-1}$ for stands aged 15–40 years. At Kerloch the production of *Calluna* (table 4) was assessed in relation to that providing potential food for grouse (Miller & Watson 1976). Variations in shoot production were closely related to amounts of rainfall and sunshine in each year and also to the cover of *Calluna* in each stand examined. The annual shoot production of *Calluna* at a site at Cairnwell in the Cairngorms was $47–155\,g\,m^{-2}$ (Summers 1972, 1976), giving a daily production in the range $0.34–1.13\,g\,m^{-2}$. Much variation from year to year has been shown to be related to variations in climatic factors and also to inherent differences in specimens of *Calluna* grown from seed obtained from different sites (Summers 1972, 1976). *Calluna* seedlings from each site exhibit a continuum of growth form from erect to prostrate. All lowland plants were erect but upland plants varied widely in habit. Upland plants with an erect growth form had the highest maximum rate of net photosynthesis, as determined by I.R.G.A. under controlled conditions; erect and prostrate plants from high altitudes had higher respiration rates than lowland plants; upland plants with prostrate habit had the highest light compensation point; plants from

higher altitudes, particularly the erect forms, can photosynthesize over a wider range of temperature than lowland plants. These are all factors which are thought to bring about the high productivity at sites with the erect growth forms.

Where the location is too wet for heath or grassland, bog vegetation is developed with an increasing proportion of *Eriophorum vaginatum*. The blanket bog at Moor House, in the absence of burning and subject to very light grazing by large herbivores, is a *Calluna-Eriophorum* bog. There is a significant trend of decreasing production with increasing wetness (Forrest & Smith 1975). This is probably a result of decreasing contribution of *Calluna*, from 190 to 70 g m^{-2} a^{-1}, and *E. vaginatum*, from 195 to 84 g m^{-2} a^{-1}. This reduction is only partly replaced by increased *Sphagnum* production, from 92 to 213 g m^{-2} a^{-1}. Mosses form an important component of both the moorland and grassland ecosystems. They have a special role as components of the bog system and at Moor House there is an abundant cover of *Sphagnum* in the pool, lawn and hummock associations which comprise 39% of the area, and to a lesser extent in the general *Calluna-Eriophorum* bog which occupies 61% of the area (Clymo & Reddaway 1971). In the pool, lawn and hummock, four species of *Sphagnum* comprise the major component. Net productivity of *Sphagnum* in pools is about 4.4 g dm^{-2} a^{-1}, on lawns about 3.4 g dm^{-2} a^{-1}, and on hummocks about 1.8 g dm^{-2} a^{-1}. It is between three and six times more productive than either *Eriophorum* or *Calluna* on these micro-sites. On the *Calluna-Eriophorum* bog *Sphagnum* production is about 0.9 g dm^{-2} a^{-1}, much less than the production of the dominant species.
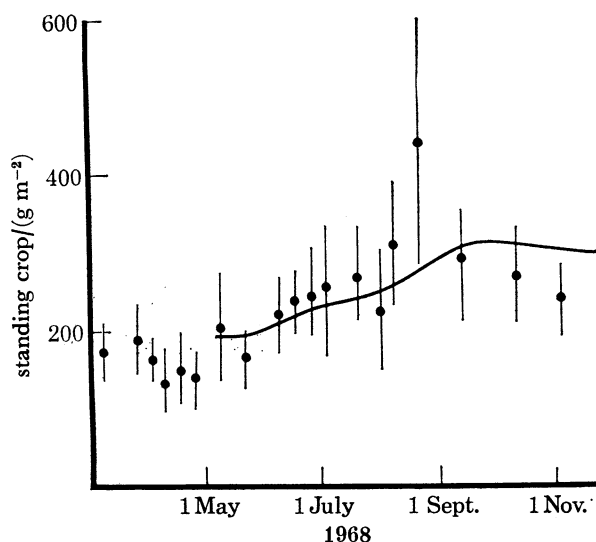

FIGURE 3. Standing crop of *Calluna* shoots at Moor House as measured by Forrest (1971) (● mean and 95% confidence limits) and as calculated from the *Calluna* growth model (——). (From Grace & Woolhouse 1974.)

Physiological studies to determine primary production were restricted to *Calluna vulgaris* and *Rubus chamaemorus* (Grace & Marks 1976). The highest rates were achieved by *Rubus* with 18 mg dm^{-2} h^{-1} at 12–18 °C, while rates for *Calluna* were only some 25% of this value. Analyses of the effects of variations in air temperature and light were used in conjunction with empirical models to predict growth of *Calluna* shoots. The predicted seasonal changes in standing crop showed good agreement with the field measurements of Forrest (1971) (figure 3, from Grace & Woolhouse 1974). From sensitivity analysis on the model, it was found that solar radiation had

relatively little effect on shoot increment but temperature increases, particularly in the second half of the growing season, led to marked increases in plant production. In contrast, *Rubus* responded only slightly to changes in air temperature but was sensitive to light intensity. In the presence of *Calluna* canopy and the consequent reduction in solar radiation available to *Rubus* leaves (40 % of full daylight), the assimilation of carbon per unit area of bog surface was reduced to one third of that where *Calluna* was absent, and overall the seasonal reduction was to 78 % of normal. This appears to be an important aspect of bog productivity, and to be related to the geographical distribution of the species. *Calluna* is centred on N.W. Europe (Gimingham 1960) and appears to thrive best under oceanic conditions, while *Rubus* is at the southern edge of its circumpolar distribution (Taylor 1971) and is further retarded by temperatures higher than those found at Moor House. This is probably due both to its inability to photosynthesize products sufficiently in excess of those utilized by respiration during the long southern growing season, and to a further loss of respirable material during higher winter temperatures.

Estimates of below-ground standing crops and production of roots have been made at Moor House, Snowdonia and Dorset. In the *Agrostis-Festuca* grassland at Llyn Llydaw (Perkins, Jones, Millar & Neep 1976) the standing crop of roots was estimated in 1969 to have a mean value of 612 g m^{-2} in the 0–30 cm soil horizon, and the production to be 288 g m^{-2} a^{-1}. Root turnover rates were calculated from differences in the standing crop measurements throughout the year. At Dorset root production (Chapman & Webb 1976) has been tentatively estimated to be a minimal 100 g m^{-2} a^{-1} while at Moor House on the blanket bog root production was 173–510 g m^{-2} a^{-1} (Forrest & Smith 1975).

The ratios of above-ground to below-ground standing crop biomass and net production for Moor House and Snowdonia indicate that there is a much larger proportion of plant biomass below the surface in grassland (1:3–1:9) than on bog (1:0.5). Despite the differences in distribution of standing crop the ratio of above-ground to below-ground production is similar (0.5–0.8) in grassland and bog. This conclusion must be tentative until more reliable methods are available for the measurement of production below the ground.

HERBIVORE CONSUMPTION AND PRODUCTION

A major difference between the sites is in the herbivore component with sheep as the main herbivore on the grasslands at Snowdonia and Moor House while on the dwarf shrub communities grouse and ptarmigan are dominant. However, the ecological importance of invertebrates is often overlooked and an attempt has been made to assess the relative importance of vertebrates and invertebrates.

In both Snowdonia and Moor House, sheep are unconstrained and range freely from April to September. Although their overall density is under the control of the farmer, the intensity of grazing on particular vegetation types is largely dependent on sward characteristics.

The density of sheep grazing different types of vegetation in Snowdonia was found to be inversely related to rainfall, acidity of soil parent material, altitude and the trend from species-rich to acid grasslands, moorland and heath (Dale & Hughes 1976; Hughes, Dale, Mountford & Ellis-Williams 1975). Within the *Agrostis-Festuca* site at Llyn Llydaw the number of grazing sheep varied from 11 to 14 ha^{-1} on preferred areas and from 5 to 7 ha^{-1} on less preferred areas; grazing occurred for about 200 days a year, from April to October. The sward preference was

reflected in differences in both botanical composition and net primary production which varied in one year under study from $155 \text{ g m}^{-2} \text{ a}^{-1}$ on the least preferred areas to $276 \text{ g m}^{-2} \text{ a}^{-1}$. Intake of herbage by sheep was on average 1 kg dry matter per sheep per day giving an estimated consumption of some $200 \text{ g m}^{-2} \text{ a}^{-1}$. Biomass and production were 10.6 g m^{-2} and $5.4 \text{ g m}^{-2} \text{ a}^{-1}$ respectively (Brasher & Perkins 1976; Perkins 1976).

At Moor House, sheep had an average density of 5.5 ha^{-1} on *Festuca-Agrostis* swards but were almost totally absent from the *Calluna-Eriophorum* bog (0.05 ha^{-1}) (Rawes & Welch 1969). Other types of vegetation, e.g. the *Nardus*, *Juncus squarrosus* and *Festuca* grasslands, supported intermediate numbers of animals. Intake of herbage on an *Agrostis-Festuca* site was recorded as 93 g m^{-2} for a season, lower than at Llyn Llydaw but in proportion to the lower net primary production and lower sheep numbers. Sheep production, measured as the net increase in mass of sheep over the season, for the whole Moor House Reserve was about $0.8 \text{ g m}^{-2} \text{ a}^{-1}$ from a biomass of 1.3 g m^{-2}. For the *Festuca-Agrostis* grassland, estimates of production $(3.8 \text{ g m}^{-2} \text{ a}^{-1})$ from a biomass of 6.8 g m^{-2} are similar to those from Snowdonia.

Grouse are restricted to *Calluna*-dominated moorland. At Kerloch, which is managed for grouse by burning, territory size was 2.09 ha over 1964–5, giving a density of about 1 adult per hectare. At Moor House, where the Reserve is not managed for grouse, population densities of 1.1–1.9 birds per hectare were recorded in 1971–2. This was a period of high populations associated with a series of mild winters and earlier estimates were of the order of 0.1–0.6 birds per hectare, indicating a slightly lower density than at the Scottish sites. Breeding success was also higher in 1971–2 at Moor House than in earlier years with an adult : young ratio in August of 1 : 3.3 compared with 1 : 0.3–1 : 2.0 in other years.

Dry matter production by grouse is estimated to be about $0.002 \text{ g m}^{-2} \text{ a}^{-1}$ in the poorest years and 0.060 in the best, i.e. a 30-fold range. Estimates of food consumption, based on daily consumption rates of 0.06–0.10 kg per bird per day, are of the order of $0.5\text{–}30 \text{ g m}^{-2} \text{ a}^{-1}$ at Kerloch and Moor House, depending on population density. This represents, at most, 12 % of the annual production of *Calluna* shoots and flowers, and about 5 % of the total primary production. Nutrient quality rather than quantity of the *Calluna* appears to determine consumption through behavioural mechanisms which control territory size. Despite the absence of burning at Moor House, grouse populations remain reasonably high in comparison with those on managed moors. This may result from the climax *Calluna* having a very mixed age structure with a high proportion of young age classes mixed with a few large, old plants. This age distribution provides a food supply of young shoots close to the ground and at the same time a canopy structure which affords cover. Such a combination with a large scale mosaic of *Calluna* of different uniform age classes, is usually produced by burning (Miller & Watson 1976; Taylor & Rawes 1974).

A preliminary survey of invertebrate herbivores in the *Calluna* canopy at Moor House, Kerloch, and in Dorset indicated considerable variation in dominant species – psyllids and possibly mites at Moor House; mites, thrips and psyllids at Kerloch (eastern Scotland); the heather beetle (*Lochmaea*), Lepidoptera larvae, thrips, mites and psyllids in Dorset (Whittaker, personal communication). Intensive studies on the psyllid *Strophingia ericae* at Moor House show that with a standing crop of 0.025 g m^{-2} and a two year life cycle, production is 0.02–0.13 $\text{g m}^{-2} \text{ a}^{-1}$ and consumption of *Calluna* phloem is $0.1\text{–}1.3 \text{ g m}^{-2} \text{ a}^{-1}$ – values at the low end of the range of the results for grouse. On the *Festuca-Agrostis* grasslands in Snowdonia, estimates for slug population are: standing crop 0.5 g m^{-2}, production $2.0 \text{ g m}^{-2} \text{ a}^{-1}$ and consumption

14.3 g m^{-2} a^{-1} (Lutman 1976). These results are higher than those for the psyllids on *Calluna*, but consumption is less than 10 % of the consumption by sheep on the grasslands. Little information exists on below-ground invertebrate herbivores on these sites, but results indicate that *Tipula subnodicornis* at Moor House is at least partly herbivorous and may make a significant contribution to production and consumption by this trophic level. Nematodes apparently play a minor role (Banage 1963) but the combined results for invertebrates indicate that although their consumption may be lower than that of vertebrate herbivores, their production is similar to or even higher than that of vertebrates (Coulson & Whittaker 1976).

<h3 style="text-align:center">Decomposition</h3>

Estimates of the rate of decomposition, by measurement of either mass loss or respiration, integrate the activity of the microflora and fauna. At Snowdonia rates of mass loss were 67–78 % per year for mixed *Agrostis* and *Festuca* litters. These rates were higher than for mixed litters (75 %), *Nardus* leaves (61 %) and mosses (51 %). By repeating measurements over periods of about 1–2 months during the year, seasonal trends and their relationship to temperature and moisture were examined. During the period of the year (May–November) when mean temperatures over the sample periods were 9–14 °C, losses were between 2 and 10 mg g^{-1} d^{-1} and were positively correlated with rainfall rather than temperature. Thus even in one of the highest rainfall areas of Britain, moisture conditions are often sub-optimal for decomposition during summer. During the winter period (November–April) rainfall is high but low temperatures reduce mass loss to less than 2 mg g^{-1} d^{-1}. On average, winter losses were about 25 % of summer losses (Perkins, Jones & Millar 1976).

The mass losses in Snowdonia are much higher than those on the Moor House blanket bog where *Nardus* litter, the only directly comparable material studied, lost 20–25 % per year. The difference probably results from soil rather than climatic differences, the Snowdon site being less acid, relatively nutrient-rich and better drained than the Moor House blanket peat. The soil conditions at Snowdon are more similar to those of the acid brown earths of the Moor House *Festuca-Agrostis* grasslands which, on the basis of studies on the decomposition of cotton strips, have a rate about 2–3 times higher than the adjacent bog. Rates of decomposition of *Calluna* litter on the Dorset heaths are more similar to those of the Moor House bog. Chapman & Webb (1976) estimated decay rates at less than 20 % per year for the litter layer, while at Moor House the initial rates of mass loss from *Calluna* shoots and stems are about 20 and 8 % respectively. This comparison suggests that although temperatures are higher at Dorset than at Moor House (mean 11 and 5 °C respectively), the lower rainfall (800 compared with 1900 mm a^{-1}) and better drainage of the sandy podzols compared with blanket peat cause decomposition to be inhibited by low moisture levels.

These results emphasize the importance of, and interactions between, two of the major factors controlling decomposition – climate and soil. A third factor, substrate quality, is emphasized by studies at Moor House where rates of mass loss of different litters on the blanket bog varied from less than 10 % per year on *Calluna* stems and *Eriophorum vaginatum* roots to nearly 50 % for leaves of *Narthecium ossifragum* (Heal & French 1974; Heal, Latter & Howson 1976). Attempts to define the major chemical characteristics related to decomposition have indicated the complexity of the subject, but suggest that the concentrations of soluble carbohydrate, phosphorus and calcium are positively correlated with decomposition, while lignin

and tannin concentrations show a negative correlation, a situation not unlike that in the digestibility of vegetation by ptarmigan (Moss, Gardarsson, Olafsson & Brown 1974).

Most of the I.B.P. studies concentrated on the initial stages of decomposition but it is the later stages which may have a more marked influence on the accumulation of organic matter within a site. Although a negative exponential curve often provides a reasonable fit to mass loss data, there is good theoretical evidence that decay rate declines as organic matter ages (Minderman 1968). This is supported by studies on the respiration rate of litters, which show a decline to about 50 % of the initial value by the time 50 % of the mass loss has occurred. This probably relates to the rapid breakdown and leaching of the soluble organic fraction, leaving the more resistant lignin fraction and its complexes. The degree of change with time will obviously vary with the different proportions of these fractions in the initial litter.

The change in rate with time is also dependent on the environmental conditions within the profile as the organic matter moves downwards. In the blanket peat at Moor House it is estimated that, within the surface 20 cm, the decay rate declines linearly by about 2–6 % per centimetre. The decrease is probably non-linear and results from the waterlogged, reducing conditions in the peat. It is this factor which is the major contributor to the total organic accumulation of about 70 kg m^{-2} on the bog compared with less than 10 kg on the grasslands at Moor House and Snowdonia and the heaths in Dorset.

MICROFLORA

Microbiological studies were concentrated on the Moor House blanket bog and aimed to examine the environmental control of microbial activity in a site where the rate of decomposition was obviously severely retarded. Detailed analysis of the distribution, composition and activities of the microflora (Collins, D'Sylva & Latter 1976; Martin 1971; Martin & Holding 1976) were therefore complementary with the broader measures of decomposition within the blanket bog. Limited information on the microbiology of grasslands at Moor House (Latter, Cragg & Heal 1967; Latter & Heal 1971) provides some points of comparison with the bog.

Population estimates of micro-organisms are always subject to problems of interpretation,

TABLE 5. ESTIMATED NUMBERS OF BACTERIA AND LENGTHS OF FUNGAL MYCELIUM WITHIN THE BLANKET BOG PROFILE AT MOOR HOUSE. FOUR 'HORIZONS' ARE RECOGNIZED BASED LARGELY ON COLOUR

(From Collins, D'Sylva & Latter 1976.)

		bacteria			fungal mycelium direct count	
		dilution plate				
	mean thickness	aerobic	anaerobic	direct count	stained	total
	cm	(10^5 g^{-1})	(10^5 g^{-1})	(10^9 g^{-1})	m g^{-1}	m g^{-1}
litter	3.8	260 ± 66	5.9	—	—	—
1–2 year	—	—	—	21	2760	6050
2–3 year	—	—	—	17	2190	9110
3 cm deep	—	—	—	18	2390	10050
black brown	6.0	110 ± 15	9.3	18	1030	9760
green brown	8.7	76 ± 19	6.3	26	750	4980
red brown	9.3	15 ± 4	0.5	12	200	790

especially in relation to viability or activity. The combination of a number of techniques, however, provides a general picture of declining populations of bacteria and fungi with increasing depth with about a 10-fold decrease from the litter to 20–30 cm in the peat (table 5). The direct counts are 10^3–10^4 times higher than the dilution counts, and stained mycelium constitutes about 20 % of the total mycelium, indicating that a high proportion of the microbial population is inactive, moribund or dead. This contrasts with the *Festuca-Agrostis* grassland where a higher proportion of the population is apparently viable with the direct count higher than dilution by a factor of 10^2–10^3 and about 50 % of the mycelium is stainable (Latter *et al.* 1967). Because of the difficulty in obtaining an absolute value for viable populations of bacteria and fungi the biomass estimates of 1 mg g^{-1} and 10 g m^{-2} to 20 cm, are very tentative. Fungal mycelium constitutes more than 95 % of this biomass, but in the maximum biomass (80 g m^{-2} to 20 cm), based on direct counts and total mycelium, the bacterial component rises to 30 %.

Microbial populations are restricted in numbers of taxa compared with adjacent grasslands. Gram-negative rods predominate in the litter layers, but are replaced by *Bacillus* spp. and *Clostridium* spp. with increasing depth, while among the fungi, species with segmented or sterile dark mycelium are most frequently isolated from washed particles.

Laboratory studies on isolated bacteria and fungi indicate that a combination of low concentrations of oxygen, available nutrients and carbon, plus low pH and temperature inhibits microbial activity, but it is not possible to assess the relative importance of these factors because they tend to interact with each other. Although many of the bacterial isolates were capable of growth over a wide range of oxygen concentrations when a substrate was readily available, restriction of the substrate decreased their ability to grow under limited oxygen. Low oxygen concentrations are probably responsible for the virtual absence of nitrifying bacteria and of nitrification, the low numbers of denitrifying bacteria probably being dependent on a supply of nitrate in rain. The reducing conditions however are associated with high numbers of sulphate reducers, particularly *Desulfovibrio desulphuricans*. Bacteria participating in the circulation of nitrogen are much more abundant on the grassland sites than on the bog.

The response of bacteria isolated from the bog to variation in pH in culture indicated that a very small proportion of the population was capable of growth below pH 5.0. This suggests that bacterial activity is restricted to pockets of relatively high pH within the peat which has a pH (H_2O) of 3.0–4.6 and that most of the decomposer activity is performed by fungi which are more tolerant of low pH than are the bacteria.

The activity of mixed populations within peat, in response to addition of a range of inorganic nutrients and carbon sources, has been measured in the laboratory and the field. Response in numbers and respiration was undetectable or very low with most nutrients and with glucose alone, the main response occurring when nitrogen and a readily available carbon source were supplied together. Some release of NH_4^+ from the native peat occurred when microbial activity was stimulated but there was additional immobilization of nitrogen and phosphorus within micro-organisms. Comparable information is not available from grassland sites, but the higher nutrients and lower lignin concentrations in the plant remains on grasslands indicate that the substrate composition, as well as the higher pH (4.6–5.6) and greater aeration, allow greater microbial activity.

Estimates of total microbial production and activity, on the same scale as plant and animal production, can only be obtained indirectly (Heal & MacLean 1975). Assimilation by fauna

represents about 5 % of the annual primary production and about 10 % is incorporated as peat below a depth of 20 cm. Therefore an estimated 85 % (about 550 g m^{-2} a^{-1}) of the input from primary production is decomposed by the microflora. Assuming that the efficiency of conversion of assimilated carbon to microbial production under partially anaerobic conditions is 0.2 for the total population, and that the production is recycled, annual production or turnover of microbial tissues is of the order of 125 g m^{-2}. Despite the errors attached to such an estimate, it is probable that microbial production is an order of magnitude greater than production by other heterotrophs.

Soil fauna

Comprehensive research on soil fauna at Moor House, before I.B.P. (Cragg 1961), indicated that the major animals on the blanket bog were the enchytraeid *Cognettia sphagnetorum* and the tipulid *Tipula subnodicornis*. Therefore intensive studies were maintained on these species (Standen 1973; Butterfield 1974), and on another tipulid *Molophilus ater* (Hadley 1969, 1971 *a, b*; Horobin 1971) which is abundant on peaty gleys and podzols under *Juncus squarrosus*. Results from all faunal work, summarized and reviewed in Coulson & Whittaker (1976) indicate that although there is a paucity of above-ground herbivores, both vertebrate and invertebrate, populations of soil and litter invertebrates are similar to those of lowland areas. This applies particularly to the *Festuca-Agrostis* and alluvial grasslands on acid brown earths where the standing crop is 45 g m^{-2} and annual production is about 40 g m^{-2} a^{-1}. Earthworms make a large contribution but their virtual absence on the peaty gleys under *Juncus squarrosus* reduces soil fauna standing crop and annual production to about 10 and 15 g m^{-2} while on the blanket peat sites comparable figures are 4 and 7 g m^{-2}. Under *Juncus* and on the blanket bog, fauna production is almost entirely by enchytraeids and tipulids.

The decrease in faunal production is associated with increasing acidity and waterlogging of the soil, and also with a decrease in the chemical 'quality' of the plant remains; lignin concentration increases and nutrient concentrations decrease. Despite the low nutrient concentrations in the vegetation on the blanket peat, the concentrations in the fauna are similar to those of fauna on the grasslands, indicating that there is a change in the mechanism of absorption and excretion of nutrients, possibly by selective feeding. The food of the fauna has not been defined but microbial cells may be important because of their high nutrient concentrations. The figures given above for standing crop and production are means, but population studies over a number of years have shown large fluctuations in numbers, often tenfold. These result in large variations in production but there is no evidence to suggest whether or not the population changes of different species are synchronized.

Of the two tipulid species, *Tipula subnodicornis* has shown wide fluctuation in numbers related to climate with very little evidence of density regulation, while *Molophilus ater* is relatively well regulated with mortality significantly related to egg density. Additional long-term data on two above-ground invertebrates, *Coleophora alticolella* and *Neophilaenus lineatus*, show little or no density-related mortality, populations varying with the vagaries of climate which, in the case of *Coleophora*, controls the supply of its food – the seed of *Juncus squarrosus*. These results, plus short-term studies on other species, suggest that species which are near the limit of their ecological range at Moor House show little or no population regulation compared with species which are living well within their range and show marked density-dependent mortality. A marked feature of the fauna populations, both vertebrate and invertebrate, at Moor House

compared with lowland populations, is the low level of parasitism and predation. This may result from the climatic conditions which can severely restrict the time available for the intensive searching required by many predators and parasites. Hymenoptera are particularly poorly represented at Moor House.

On the blanket bog at Moor House, Cryptostigmata dominate the mite populations and estimates of numbers, biomass and production are similar to those for oribatid mites in the acid *Calluna*-dominated heaths in Dorset (Chapman & Webb 1976). Litter consumption by oribatids in the Dorset heaths is approximately 2–10 g m^{-2} a^{-1} depending on the length of time since burning. This represents up to 10 % of the annual litter input, from which there is a mite production of 0.1–0.6 g m^{-2} a^{-1} (Chapman & Webb 1976). The results from Dorset and Moor House emphasize that soil fauna respire 5–10 % of the annual amount of carbon fixed by plants and whether expressed in terms of respiration, production or consumption, their activity is 5–30 × greater than that of herbivores.

Production estimates also provide a means of obtaining a first approximation of the contribution of fauna to nutrient circulation. Concentrations of nitrogen and phosphorus in animals are up to 10 × greater than those in the vegetation (Butterfield & Coulson 1975) and nutrients are also metabolized and eliminated from the animals. Therefore a much greater proportion of the nutrients in live plants and litter is assimilated by fauna than is indicated by simple energetic comparisons (Hodkinson 1973; Coulson & Whittaker 1976; Reichle 1971). An additional contribution by soil fauna to ecosystem function is through interaction with the decomposer microflora and it has been widely claimed that a major function of soil fauna is its stimulating effect upon microbial activity. Standen (1976, and in Whittaker 1974) showed that mass loss of litter in the presence of *Cognettia sphagnetorum* and *Tipula subnodicornis* at normal field densities, was about 1.35 × the rate when these animals were absent. The increase is only partially the direct contribution by the fauna, the main effect being through increased microbial activity.

Ecosystem

Although the concept of an ecosystem as a level of ecological organization distinct from that of a population or community has been recognized for a long time (Major 1969), our understanding of the characteristics and variations in ecosystem structure and function are in their infancy. Within the I.B.P. the term ecosystem has been used in the sense of Tansley (1935) of an area within which the processes of primary production, consumption, decomposition and recirculation are largely self-contained.

It is usually accepted that a recognizable vegetation–soil complex represents the ecosystem unit, but with the mobility of large herbivores and carnivores a range may also be considered as the basic unit or, because of the transport of nutrients by water and the interactions between terrestrial and aquatic habitats, a catchment may be a more logical unit. In the case of the range and the catchment, a number of vegetation–soil components usually occur within the area and evidence indicates (Rawes & Heal 1976) that the amounts of dry matter and nutrients transferred between these components is only a very small fraction of that circulating within them. Therefore we consider an ecosystem boundary to be defined by a major change in vegetation and/or soil type. It is assumed that an ecosystem consists of an interdependent set of organisms which are organized in a trophic as well as a physical structure. Ecosystem attributes of diversity and stability have received little study in the I.B.P. where effort has been concentrated

on attributes of the distribution, production and transfer of dry matter, energy and nutrients in an attempt to identify fundamental biological differences between ecosystems – assuming that such differences exist between terrestrial ecosystems.

Within the U.K. the number of ecosystems for which comprehensive information is available is too few to allow rigorous comparison and interpretation of characteristics – this will be difficult even at an international level – but some tentative, subjective interpretation can be attempted from a comparison of the sites at Moor House, Snowdonia, Dorset and Kerloch.
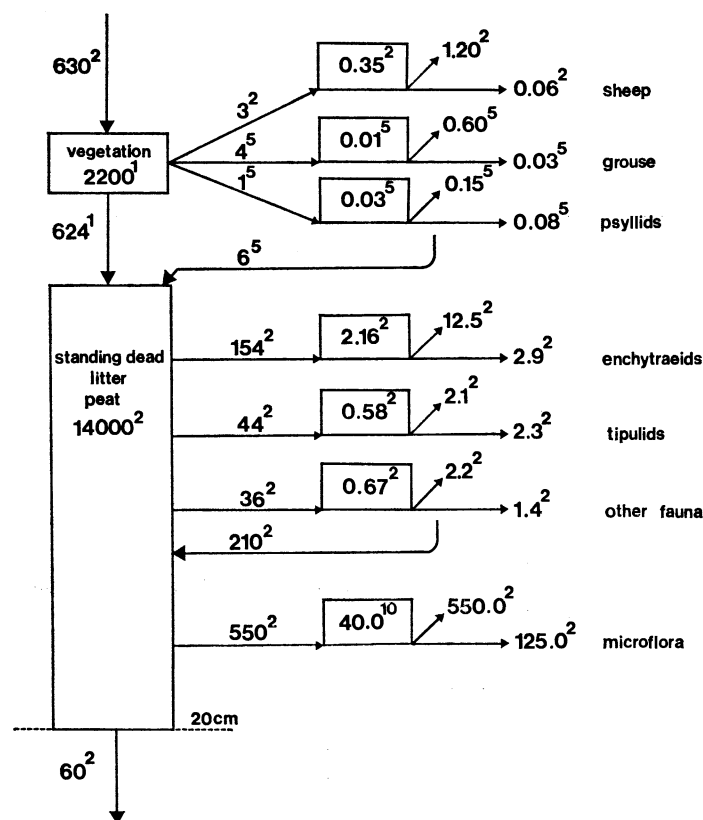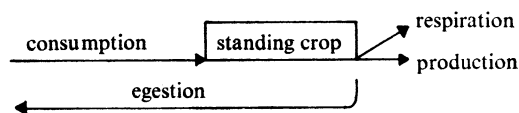

FIGURE 4. Estimated standing crops (g m^{-2}) and transfers (g m^{-2} a^{-1}) of organic matter in the surface 20 cm of blanket bog at Moor House. For fauna and microflora transfers are represented as:

Variability in estimated values, through sampling and systematic errors and between year and between site variation, are indicated by superscripts as: [1], 0.9–1.1 × mean; [2], 0.5–2.0 × mean; [5], 0.2–5.0 × mean; [10], 0.1–10.0 × mean.

There appear to be three types of system:

(i) steady-state, natural climax, e.g. blanket bog at Moor House;

(ii) steady-state, plagioclimax, e.g. grasslands at Snowdon and Moor House maintained by sheep grazing;

(iii) non-steady state, plagiocycle, e.g. dwarf shrub heaths in Dorset and Kerloch maintained by burning.

The pattern of distribution and annual transfer of dry matter in the top 20 cm of the Moor House blanket bog (figure 4) is used here as a basis for discussion of the other systems. It is important to recognize that the values given are means for a number of years and subsites, but include many assumptions in the estimation of respiration and production, and will vary with population size which ranges over an order of magnitude between years. The main features are that of the primary production a very low proportion ($< 1 \%$) is consumed by herbivores, the majority passing to decomposition where about 5% is assimilated by fauna, about 85% by microflora, and the remaining 10% is incorporated into peat below about 20 cm. The large majority of primary and fauna production is from five species: *Calluna vulgaris*, *Eriophorum vaginatum*, *Sphagnum rubellum*, *Cognettia sphagnetorum* and *Tipula subnodicornis*. Nutrient distribution and transfer on a gross scale can be estimated from the dry matter values, using relevant data on concentrations. The summary estimates for the blanket bog (table 6) show that over the series potassium–phosphorus–nitrogen there is an increase in the capital, and a decrease in the proportion of the capital which is contained in live organisms and in circulation, through

TABLE 6. A TENTATIVE NUTRIENT BUDGET FOR A MOOR HOUSE CATCHMENT DOMINATED
BY BLANKET BOG

(Inputs in rain and losses in streams (g m^{-2} a^{-1}) are for the catchment; input of nitrogen in fixation (g m^{-2} a^{-1}) is for the bog only; the amount (g m^{-2}) within the blanket bog system to a depth of 20 cm is subdivided into the percentage within the standing crop of organisms (plants, animals and microflora) and in circulation through annual production. Data from Crisp (1966), Gore (1968), Martin & Holding (1976).)

	N	P	K
input			
rain	0.82	0.02–0.03	0.23
fixation	0.91	—	—
in system	210	11	13
organisms	7%	12%	38%
circulation	4%	8%	23%
output			
solution	0.29	0.04	0.89
peat	1.46	0.04	0.21

plant, animal and microbial production. Estimated input in rain (Gore 1968) and by nitrogen fixation (Martin & Holding 1976), and output in solution and as peat in streams (based on Crisp 1966) have been added. The results indicate that potassium and phosphorus are potentially in short supply in absolute terms. The nitrogen capital is large but only a very small fraction is in an available form, and this largely as ammonium rather than nitrate. Losses in peat in run-off imply that the bog system has a net loss, particularly of nitrogen, but it is probable that the peat is derived largely from the small proportion of the bog which is eroding. It is thus irrelevant to the nutrient economy of the bog over anything but the longest time scale. From the limited information available, the dwarf shrub heaths of Dorset and Kerloch appear to be similar to the blanket bog in primary productivity, herbivore consumption and productivity, but with a more limited accumulation of organic matter. They have a higher nutrient capital, through proximity of the mineral soil, and although burning causes some loss of nutrients from the system, particularly nitrogen (Allen 1964), nutrients in ash are probably retained within the system (Allen, Evans & Grimshaw 1969) and are replenished through rain (Chapman & Webb 1976).

The grasslands at Snowdon and Moor House differ from the bog and heath systems particularly in having:

(i) a much greater proportion of the plant standing crop below-ground although total standing crop and production are similar to those for the bogs and heaths,

(ii) a higher consumption and production by herbivores,

(iii) a higher standing crop and production by soil fauna, with a major contribution by earthworms,

(iv) a higher rate of decomposition of plant litter and lower accumulation of organic matter,

(v) a higher nutrient capital and a smaller proportion of the capital in the organisms and in circulation, and

(vi) a greater diversity of flora, fauna and microflora in terms of numbers of species per unit area.

It appears that although the nutrient constraint which is present on the bog areas is reduced or removed on the grasslands, plant production is not increased. The main difference is in the chemical composition of the vegetation, with higher nutrient and lower lignin or fibre concentrations on the grasslands. This results in greater herbivore consumption and production, more rapid decomposition and reduced accumulation. Feedback mechanisms are therefore involved, the increased consumption and decomposition maintaining a readily available nutrient supply to the plants.

Such conclusions emphasize that the major difference in productivity between these highly contrasting ecosystems is in the quality, rather than the quantity, of production.

DISCUSSION

This paper has summarized some of the products of the I.B.P. research on moorlands and montane grasslands, but many of the scientifically interesting details have been omitted because of limited space, and the value of the research cannot be fully appraised until the international synthesis has been completed and the U.K. sites can be compared with others in the same biome.

Much of the research discussed in this paper adopted a descriptive approach – measuring production under a given field situation. However, some of the most valuable results on the regulation of growth and production have been obtained from a more experimental approach (e.g. Clymo 1973; Clymo & Reddaway 1971; Taylor & Marks 1971; Martin & Holding 1976), from physiological studies (Grace & Woolhouse 1970, 1973 a, b; Marks 1974), and from studies on succession (Chapman et al. 1975 a, b). Within the faunal research, the long-term population studies have provided information on population dynamics which is essential to the understanding of the regulation of production. It is the combination of physiological, population and production studies which provides most information, particularly when physiological experiments have defined functional relationships from which production under field conditions can be predicted and the predictions tested against field observations (Grace & Woolhouse 1974; figure 4). Thus an hypothesis derived from one set of data has been tested against an independent data set. In a similar way estimates of production, decomposition and compaction have been integrated in mathematical models to predict peat density, age and accumulation as a means of testing the validity of the estimates (Clymo 1976; Jones & Gore 1976).

One of the design features of the international programme was a comparative approach –

from production measurements on a series of sites, patterns, related to environmental gradients, could be interpreted. This requires definition of the population of sites being sampled and adequate replication; constraints which have not been fully overcome, partly because of the enormous effort in national and international cooperation required to achieve reasonable experimental design. The Royal Society has supported much of the U.K. contribution to the international synthetic study of all data from the Tundra Biome. A classification, based on principal component and cluster analyses of climatic and soil data, has been used to indicate some of the environmental relationships within the series of sites (French 1974). The classification has helped to distinguish patterns in microbial populations and rates of organic matter decomposition (Holding, Heal, MacLean & Flanagan 1974). The wide range of climatic regimes across the Tundra Biome is reflected in the length of growing season which varies from about 60 days at Devon Island in northern Canada, to almost the whole year at Glenamoy in Ireland and Macquarie Island in the subantarctic. This is probably the major cause of variation in primary production in tundra (Jones & Gore, in press), many sites having similar rates during the growing season. Comparison of total ecosystems is still at the exploratory phase, but some attempt has been made to translate general descriptions of their structure and function (Rosswall & Heal 1975) into more rigorous mathematical models (Bunnell & Scoullar 1975).

Although much valuable scientific information has been obtained, our understanding of ecosystem functioning would probably have been increased if greater emphasis had been placed on the interaction between components of the system: for example, the influence of herbivory on primary production, or of the fauna on the microflora, or of the micro-organisms on primary production. Such inter-disciplinary studies have been difficult to achieve. A final general point which has arisen is that to plan an integrated programme and to make full use of the results in synthesis, at national and international levels, requires much more effort than was originally envisaged. This must be a major consideration in future programmes such as 'Man and the Biosphere'.

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