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Number 2

The International Biological Programme Project at Moor House

O. W. Heal

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Contents

I.B.P. Moor House

O. W. Heal
The Nature Conservancy, Merlewood Research Station, Grange-over-Sands.

The International Biological Programme (I.B.P.) is concerned with "The Biological Basis of Productivity and Human Welfare". Within this, the PT Section (Productivity Terrestrial) is responsible for the study of biological production, both primary and secondary, of land communities.

The I.B.P. study at Moor House National Nature Reserve in the northern Pennines was largely developed by Dr. J. B. Cragg, while Director at Merlewood Research Station. The programme was described in some detail in the Royal Society publication 'The United Kingdom Contribution to the I.B.P.' published in February 1967. Since then Dr. Cragg has left Merlewood, and in 1967 I was appointed, in a part-time capacity, as co-ordinator of the project. The aims of the present paper are to outline the present state and suggest developments in this moorland community study.

1. Objectives

The objectives of I.B.P. (PT) are to assess the primary and secondary production in a variety of ecosystems and to understand the processes influencing them. The ultimate objective is to provide a better understanding of the functioning of ecosystems. From this it should be possible to improve management of the system to obtain maximum production to man without causing deterioration of the system.

Two kinds of projects are recognised in PT (I.B.P. News No. 9), Moor House coming into the first.

a) "A few major, really comprehensive, projects of which the aims are to estimate the primary and secondary production of a particular site, and to establish its overall energy flow and organic production.

b) A number of limited or supporting projects arriving at the evaluation of the organic production or energy flow of certain types of plant communities or of a given level of consumers".

The approach to these objectives is through intensive study of the circulation of dry matter, energy, carbon and nutrients. This requires whole ecosystem studies wherever possible and emphasises the abiotic factors influencing production and the quantitative relationships between organisms. Within each intensive site study some emphasis must be placed on examination of the variation in production under different conditions. However extensive between site comparisons will also provide information on factors influencing production. Such comparisons must be an important part of I.B.P. The study will provide an improved picture of the structure of the ecosystems and, by examination of this and comparison with other systems, will help to answer such questions as:

Does removal of one of the primary consumers alter primary production and effect other consumers?

Is the grazing component of the food chain larger or smaller than in other terrestrial sites and does it vary significantly under different bog conditions?

Can the system support larger quantities of herbivores or are the herbivores limited by other factors such as climate?

Does the rate of decomposition limit plant growth, and if so, how can rates of decomposition be increased?

Are the transfer efficiencies in this ecosystem greater than in other systems and if so why?

What is the relative importance of the factors influencing production on this blanket bog and are they different from other Tundra areas?

2. Moor House in international context

At an international level PT projects have been classified under five main habitats - grassland, woodlands, tundra or shrub communities, wetlands and deserts. Moor House has developed strong links with the Tundra group of which Dr. F. A. Pitelka (University of California, Berkeley, U.S.A.) is the convenor. The contact was established as a result of A. J. P. Gore's visit to U.S.A. in 1966-67. A preliminary tundra meeting was held at Moor House in November 1967 and will be followed by a second near Oslo (Norway) in September 1968. These meetings are to develop contact between tundra study groups to ensure comparability of data and to examine the use of systems analysis as a means of comparison. Reports of these meetings can be obtained through A. J. P. Gore or O. W. Heal. (Merlewood).

3. Moor House in national context

Within the United Kingdom 3 major habitats have been chosen for intensive study - woodlands, grasslands and moorlands. Moor House is the main moorland site and "supporting programmes" listed by the Royal Society 1967 are:-

1. Productivity of Calluna moorland ecosystem in Scotland - a study on primary production in relation to management, including studies on grouse (Lagopus scoticus).

2. Productivity of arctic-alpine vegetation, - quantitative and qualitative studies on productivity of dwarf shrub heaths in Scotland and Iceland, including studies on ptarmigan (Lagopus mutus).

3. Study of southern heath ecosystems - a quantitative study of Calluna dominated vegetation on base-poor mineral soils, including parts of the decomposer cycle.

These studies will allow limited comparison of production of Calluna dominated vegetation on different soils and under different climatic conditions. They will also provide more detailed information than will be obtained from the main site on certain aspects such as the production of grouse and ptarmigan and their relationship to their food supply. More contact is required between these moorland studies.

It is possible that available data on the restricted sheep-grazed grasslands at Moor House can be used to support the Main Site grassland programme in Snowdonia, Wales.

4. Moor House Site

The Moor House National Nature Reserve consists of 10,000 acres, about 80% of which is covered with blanket peat with an average depth of 6-9'. This peat carries vegetation dominated by Calluna, Eriophorum and Sphagnum and is typical of much of the northern Pennines. The area has been managed mainly for sheep and grouse which has involved burning and draining on the blanket bog. Limited areas of Juncus squarrosus, Nardus and Festuca-Agrostis grassland occur on peat or mineral soils, and these are the main areas of sheep grazing.

The altitudinal range on the Reserve is 1,000' to 2,780' and the climate is severe for the United Kingdom with a mean annual temperature of 5.1°C; 73.6" rain; 248 days on which rain occurs and 63 days of snow.

The main research effort is being concentrated on the blanket bog, initially at Bog End where much research has previously been carried out. This is an area of lightly grazed, moderately wet bog which is relatively poor in Sphagnum and intensive primary production studies are being made on Syke Hill. In the same area, Bog Hill provides an example of ungrazed, slightly wetter bog with more Sphagnum. The very wet, Sphagnum-rich bog on Burnt Hill is being used for intensive studies on Sphagnum production.

5. Measurements

For each of the main components in the blanket bog system it is hoped to estimate the biomass, rates of biomass change, the main factors influencing biomass change, and also the utilisation or transfer efficiencies between different components. Although initial measurements will usually be made in terms of wet or dry weights, it is essential that we also estimate:

energy, carbon, nitrogen and phosphorus

This will allow the construction of budgets and flow diagrams for all these components. These are the units which are generally accepted in PT studies.

Where facilities for chemical analyses are not readily available, arrangements may be made with the Chemical Service at Merlewood Research Station, Grange-over-Sands. It is also desirable that where independent analyses are being made, some duplicate samples should be analysed at Merlewood to ensure comparability.

The number of sites and treatments which need to be studied is debatable and is limited largely by manpower. Estimates of the primary production will be obtained from a number of sites but the effort required to estimate soil fauna or microflora production on the same sites is much greater. The main emphasis, because of limited resources, will be on the intensive study of two or three sites on relatively untreated bog, providing field data on 'natural' variation.

Apart from this, the main variables for potential study in the field are:

a) Management variation - particularly burning, draining, fertilising, sheep grazing and tree planting. A number of experimental plots, set up at various times since 1952, may be used for particular topics.

b) Climatic variation - particularly temperature variation related to altitude.

Within I.B.P., studies on such variation are few, e.g. studies on Rubus in relation to burning and grazing, or the effect of altitude on development of Tipulidae and Oscinella.

It is possible that after the present phase of I.B.P. (1967-1972) a more experimental approach will be desirable and the results will indicate some of the conditions which should be tested.

The above discussion has been concerned mainly with the examination of variables in the field. However, complimentary laboratory studies are examining the following variables.

Independent variables	Dependent variables
Radiation	Plant respiration and photosynthesis
Temperature	Plant respiration and photosynthesis
	Fauna growth and respiration
	Microflora growth and respiration
Soil moisture	Fauna activity
Nutrients	Microflora growth and respiration
Oxygen concentration	Microflora growth

6. Current Research programme

The Moor House project relies heavily on past research, and on current research which is not controlled by I.B.P. The effort must be guided into using non-I.B.P. information and to fill the main gaps to provide a total ecosystem study.

A list of publications concerning Moor House is given in Appendix 1. So far, the only major attempt to review parts of the work has been by Cragg (1961), but the Nature Conservancy hope to publish a comprehensive review research of Moor House in 1969.

The critical path network (Fig. 1) attempts to summarise the main relevant studies and their development in time; many of the cross links, e.g. with temperature, are omitted for simplicity. The apparent emphasis on soil fauna studies is the result of the studies carried out by Durham University students since 1952. This has provided considerable information available on species composition, distribution, life histories and numbers of many animal groups. I.B.P. is sponsoring a limited amount of research on those groups mainly to develop the population data into production estimates.

Short factual accounts of current research are produced each October in the Moor House Annual Progress Report. These are for limited circulation and enquiries should be made to O. W. Heal (Merlewood).

The current research relevant to I.B.P. is listed below, projects directly supported by I.B.P. being marked*:

6.1 Environmental recording

6.1.1. Standard meteorological records are available since 1952 and continuing (M. Rawes, Moor House).

*6.1.2. Radiation recording with a Lintronic integrating counter and solarimeter will start in 1968. This will replace the Kipp which is unsatisfactory for Moor House (O. W. Heal, Merlewood).

*6.1.3. A Grant temperature recorder is being used to obtain temperature profiles in and above blanket bog and Juncus squarrosus grassland (O. W. Heal, Merlewood).

*6.1.4 Vertical fluctuation in water table in connection with 6.2.2. (R. S. Clymo, Westfield College, London).

6.1.5. Movement of water at different depths (D. B. Smith, United Kingdom Atomic Energy Authority).

6.2 Primary production

*6.2.1. Field primary production above and below ground, including litter (G. I. Forrest, I.B.P. Moor House).

*6.2.2. Estimation of net and gross Sphagnum production (R. S. Clymo and J. Reddaway, Westfield College, London).

6.2.3. Photosynthesis and respiration of Calluna, Eriophorum and Sphagnum (H. Woolhouse and J. Grace, University of Sheffield).

6.2.4. A study of the biology of Rubus chamaemorus in relation to burning and grazing (K. Taylor, University College, London).

6.2.5. Production of blanket bog vegetation related to fertilizers and cropping (A. J. P. Gore, Merlewood).

6.2.6. Bog vegetation in relation to sheep grazing and burning (M. Rawes, Moor House).

6.2.7. Tree growth and nutrition on peat (A. H. F. Brown, Merlewood).

6.3 Secondary production : Herbivores

6.3.1. Invertebrate survey (J. M. Nelson, ex. Moor House).

6.3.2. Preliminary estimates of numbers of grouse and invertebrates (B. P. Springett, ex. Moor House).

6.3.3. Studies on sheep grazing, (M. Rawes, Moor House).

*6.3.4. Distribution and phenology of Oscinella frit (A. Ibbotson, Newcastle University).

6.3.5. Population dynamics of a homopteran, Neophilaenus lineatus (J. B. Whittaker, Lancaster University).

*6.3.6. Psyllid populations and their effects on primary production (J. B. Whittaker, Lancaster University).

6.4 Secondary production : Decomposers

*6.4.1. Rates of decomposition and respiration of decomposing vegetation (O. W. Heal, P. M. Latter, Merlewood).

*6.4.2. Nutrient availability in relation to microbial activity (A. J. Holding and N. Martin, Edinburgh University).

*6.4.3. Studies on anaerobic and facultative micro-organisms in peat (V. G. Collins and B. T. D'Sylva, Freshwater Biological Association).

*6.4.4. Population and production studies on Tipulidae (J. C. Coulson and J. Horobin, Durham University).

*6.4.5. Population, production and feeding studies on Enchytraeidae (V. Standen, J. A. Springett and P. M. Latter, Durham University, I.B.P. and Merlewood).

*6.4.6. Production studies on Collembola (W. G. Hale, Liverpool College of Technology).

*6.4.7. Feeding studies on a rhabditid nematode (W. B. Banage and O. W. Heal, Makerers University College, Uganda and Merlewood).

*6.4.8. Production and feeding studies on Acari (W. C. Block, Leicester University).

6.5 Secondary production : carnivores

6.5.1. Preliminary studies on gut contents of frogs and shrews (J. C. Coulson and K. Housten, Durham University).

6.5.2. Distribution and biology of Coleoptera (J. C. Coulson and K. Housten, Durham University).

6.6 Hydrology and output

6.6.1. Fish production and bottom fauna at Moor House and Teesdale (D. T. Crisp, Freshwater Biological Association).

6.7 Synthesis

6.7.1. Methods of assessment and computation of ecological models are being developed and will be used in I.B.P. Moor House (Systems Section, Merlewood).

7. Future research

It is hoped that most or all of the existing lines of research will be continued until 1972 to make full use of information being currently obtained. However, it is possible that financial restrictions may prevent some of the projects being extended beyond existing financial arrangements. It is therefore necessary to examine briefly the subjects in which research development is likely to help most in achieving the objectives of I.B.P.

7.1 Primary production. Estimation of primary production appears to be adequately covered although two important aspects are only marginally covered.

7.1.1. Production in relation to management. Nature Conservancy staff have carried out various experiments on the blanket bog, to study the composition of the flora in relation to burning, draining, grazing and fertilizing, and the relation of these to the general fertility. M. Rawes recently started a small field experiment on vegetation changes related to different intensities of sheep grazing on bog which has been burned or drained. A. J. P. Gore's work is dealing with cropping effects from which it will be possible to estimate some of the extreme consequences of burning and grazing. Results of fertilizer effects are also available

from this work. The current I.B.P. project allows only for limited examination of the effects of management and more emphasis needs to be placed here.

7.1.2. Nutrient uptake by plants. The primary studies will show the quantities of nutrients used by the vegetation. The relative importance of the various sources (rainwater, re-cycling from dead organic matter, mineral soil or internal translocation) are under study both directly and indirectly using systems models, but more direct measurements are required, specifically using tracer techniques.

7.2 Herbivores and carnivores. Available information (see p. 5 and Fig 3) suggests that herbivores are a minor component in the system. However, most of these studies have been superficial; a number of herbivores have not been investigated, e.g. voles, and the effects which herbivores have on the plants has not been assessed. Apart from studies on meadow pipits (Anthus pratensis) and spiders there are virtually no data on carnivores. Therefore to obtain a correct picture of the trophic structure of the blanket bog, more information is necessary on both herbivores and carnivores. This is urgently required for international comparisons (Table 1).

The indications that available food is less fully utilised by both herbivores (Fig. 3) and carnivores (Coulson 1956, Cherrett 1961) when compared with lowland sites, needs clarification. This may be important generalisation and studies on vertebrates could answer both the questions of trophic structure and efficiency.

7.3 Soil Fauna. As a result of earlier work data on species composition, distribution and numbers of soil fauna is relatively well advanced. The necessary development within I.B.P. is quite well covered by concentration on estimation of production in the main groups. However, studies are inadequate on the quality and quantity of food of some of the soil fauna required for understanding the trophic structure and energy flow in the ecosystem.

7.4 Microflora. By comparison with other I.B.P. areas, Moor House has been very fortunate to have close ties with microbiologists at three places, (Freshwater Biological Association, Edinburgh University and Merlewood) plus contact through I.B.P. with a fourth (Liverpool University). However the importance of the microbiological studies is real, it is shown later that about 78% of the decomposition of organic matter is carried out by the microflora, compared with about 6% by the soil fauna. These studies will provide very valuable information on the functional relationships of the major processes of decomposition and nutrient circulation.

A particular microbiological aspect which needs urgent coverage is that of nitrogen fixation. Estimates of quantities fixed are necessary for adequate interpretation of a nitrogen budget.

7.5 In summary therefore, it appears from the above discussion, and from considerations of improved international comparisons that:

7.5.1. High priority must be given to the development of microbiological studies, especially as those funded by I.B.P. end in 1969, while most of the plant and soil fauna studies are funded until 1970 or 1971.

7.5.2. The three main new projects which require development are on relevant aspects of:

Vertebrates, both herbivores and carnivores.
Nutrient uptake by plants.
Effects of management on primary production.

8. Synthesis

Individual research workers will use data obtained for publication in the normal scientific journals and will compare their own results with those from other areas. However, it is essential that all research workers should see their research in the context of the whole project and should be able to make full use of information being obtained by other workers and in previous studies. Efforts are being made to improve retrieval of past and present data by the development of a readily available inventory of subjects and sources of information. From this should develop a data bank, probably on punched paper tape which will be available for general use.

The data from individual projects must be synthesised to produce information on the whole ecosystem which can then be examined for use internally and for comparison with other I.B.P. areas. Comparisons between sites will probably be made using:

The estimates or primary and secondary production per unit area per year.

The transfer efficiencies calculated for different pathways in the system.

Static flow diagrams of energy and nutrient circulation.

Dynamic computer models using techniques of systems analysis.

For Moor House, all these methods of synthesis and comparison will be used and others may be developed. The first three are relatively straightforward and the available information allows a preliminary diagram to be drawn of the main pathways of energy flow. This is shown in Fig. 3 and it is stressed that it is a first approximation.

In the diagram the figures in boxes represent standing crop; arrows into a box represent assimilation; arrows out of boxes represent energy in net production (——), or in respiration (.....). All figures are in K calories/ m^2/yr.

Data are from the following sources: primary production from G. I. Forrest (personal communication) and Gore and Olson (1967); burning data from Allen (1964); herbivores from M. Rawes and B. P. Springett (pers. comm.); microflora from Latter and Cragg (1967), Latter, Cragg and Heal (1967); soil fauna from various papers including Cragg (1961) and Springett (1967); peat accumulation from Gore and Olsen (1967); output in streams from Crisp (1966). In many cases data have been freely extrapolated and I take full responsibility for the use and misuse of the results.

This crude synthesis indicates a number of features of this blanket bog ecosystem and points to aspects which need clarification.

8.1. Assuming that primary production below ground is equal to that above ground, giving total net primary production of about 3150 K cals/m^2, then

herbivores assimilate<1% of the primary production
soil fauna assimilate 6% of the primary production
microflora assimilate 78% of the primary production
15% accumulates as peat.

8.2. The above ground primary production is about twice that on grasslands at Moor House probably associated with the higher standing crop.

8.3. Consumption by herbivores is very low and invertebrates appear to assimilate more of the primary production than vertebrates.

8.4. Consumption of above ground production by herbivores is much less (1%) than on grasslands at Moor House where about 8% is consumed by sheep alone.

8.5. The great dominance of decomposers in this ecosystem is emphasised, their importance being greater than in most ecosystems, including those in which the detritus food chain is dominant.

8.6. Loss of minerals in sheep crop and fauna loss in streams are small compared with losses in burning. Losses of peat from erosion areas are much greater as shown by Crisp (1966).

8.7. The data are least accurate for the group responsible for most of the utilisation of primary production - the microflora. The estimate of energy passing through this group has been obtained by subtraction of all other groups from the total primary production.

8.8. Information on carnivors is lacking.

8.9. Comparisons with other sites can be made using various ratios of ecological efficiency. From the present information the only generally applicable ratios which can be calculated are for primary production and herbivores. Some examples are given and compared with mean ratios from five natural communities (Kozlovsky 1968).

i) Trophic level productivity efficiency

$$\frac{\text{Net productivity, herbivores}}{\text{Net productivity, plants}} = 0.1\% \text{ cf. } 10\%$$

ii) Utilization efficiency

$$\left\{\frac{\text{Assimilation, herbivores}}{\text{Net productivity, plants}}\right\} = 0.5\% \text{ cf. } 20\%$$

iii) Tissue growth efficiency

$$\frac{\text{Net production, herbivores}}{\text{Assimilation, herbivores}} = 24\% \text{ cf. } 40\%$$

These ratios show that, compared with other sites the herbivores at Moor House use very little of the available primary production (i, ii). However, they are reasonably efficient in production of tissue from assimilated food (iii), two of the communities reviewed by Kozlovsky (1968) having tissue growth efficiencies of 20-25%.

8.10. The efficiency ratios used in most published papers have not applied to the decomposer food chain, and it is necessary to formulate new efficiency ratios for comparison of this major part of many ecosystems (Kozlovsky 1968).

8.11. The flow diagram (Fig. 3) shows the energy transferred in a year, but the dry weight losses from litter are of the order of 5-25% per year and 80% decomposition is probably not reached until periods of about 10-20 years. However, the calorific value of matter processed each year is about equivalent to the annual primary production, although it is obtained from matter of varying ages. It should be possible to incorporate this 'rate' into the model.

These static models although valuable, do not readily allow expression of the ways in which individual components vary under given circumstances, nor of the functional relationships between components. Such features can be incorporated using mathematical equations to express the relationships and from this, dynamic models can be developed. These models improve analysis of the system, and allow prediction of the way in which the system would alter under particular stresses.

The development of computer based mathematical models for Moor House is a direct result of the work of A. J. P. Gore. He has

applied systems models to his data from experiments on cropping and nutrient circulation by blanket bog flora. This work has been published (Gore and Olsen 1967) and it is hoped that further developments will allow incorporation of more data and the use of such models by those involved in Moor House I.B.P.

Under the Director, Mr. J. N. R. Jeffers, a Systems Section has been set up at Merlewood, headed by A. J. P. Gore, and it will be concerned with the development and use of mathematical models of ecosystems. Limited computer facilities, plus discussion and advice on systems analysis, will be freely available at Merlewood, to those involved in I.B.P. Moor House.

The Tundra meeting at Moor House in November 1967 was aimed at improving synthesis of data and comparisons between sites. A simple flow diagram which defined the main pathways of energy and nutrient flow in tundra ecosystems was produced (Fig. 2). Using this an inventory of the tundra studies is being compiled to indicate the main pathways for comparison. The current inventory (Table 1) will be enlarged at the meeting in Norway in September 1968. This contact and information has already caused the modification of some I.B.P. projects to achieve greater comparability. However, much more needs to be done by direct contact between workers from different sites and by use of common methods of analysis and synthesis. It is hoped that a number of centres, such as Merlewood, will provide facilities which will encourage research workers and teams to process their I.B.P. data in common forms.

9. Acknowledgements

I am very grateful to many people associated with I.B.P. and the Nature Conservancy for valuable discussion. However, I take responsibility for the views expressed and would welcome comments on them.

10. References

References not included in the Moor House reference list (Appendix 1) are:

Anon (1967). The United Kingdom Contribution to the International Biological Programme. The Royal Society, London, 94 pp.

Anon (1967). I.B.P. News No. 9, pp. 68.

Kozlovsky, D. G. (1968). A critical evaluation of the trophic level concept. 1. Ecological efficiences. Ecology, 49, 48-60.

Summary of pathway inventory at 30/8/68

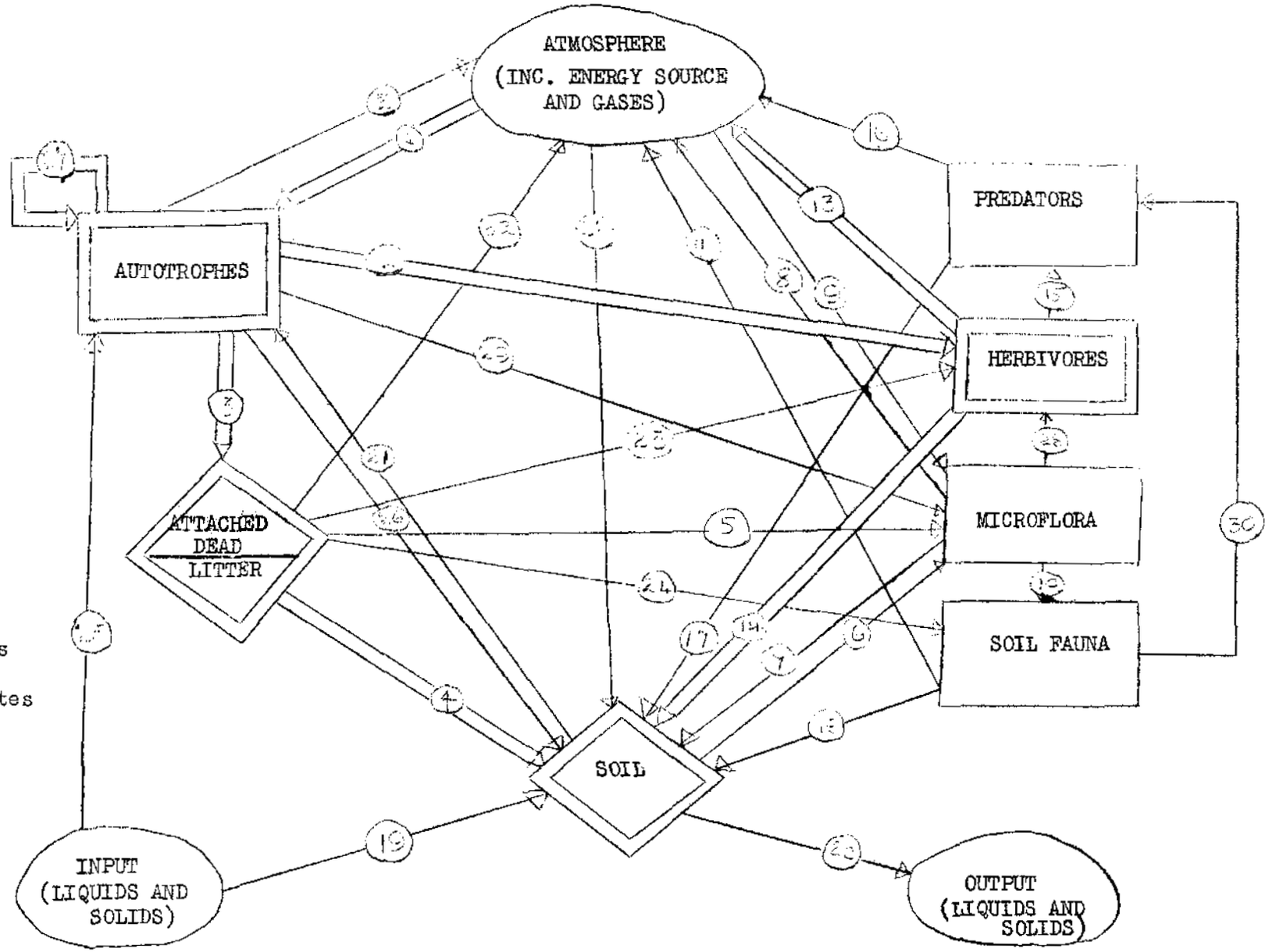
Notes and Abbreviations:- 1. Measurements made daily (D) monthly (M) or annually (Y). 2. Possible dependent variables:- E = Energy, DM = Dry Matter, W = Water, C = Carbon, N = Nitrogen, P = Phosphorus and /or other non-gaseous nutrient elements. Noting (i) that where E passes back into "atmosphere" it is irreversible unlike C which may be recycled. (ii) An entry of D, M, or Y indicates that one or more of these dependent variables is being measured. 3. [ ] = Approximate estimates only. 4. * = At present difficult to distinguish Decomposers from Microbivores among the Soil Fauna. 5. The Predator box will have to be sub-divided into primary or secondary Predators where necessary.

Pathway	Possible Dependent Variables	Disco (Greenland)	Hardangervidda (Norway)	Kevo (Finland)	Moor House (U. K.)	Mt. Washington (U.S.A.)	Point Barrow (Alaska)
1. Energy or Atmospheric Gases to live plants (including Sphagna)	All ex P	D (Lab.) M, Y. (field)		D, M, Y	D (Lab.) M, Y (Field)	D, M	?
2. Live Plants to Atmosphere	All ex P	D (Lab.)		D, M, Y	D (Lab.) 3 main spp. M,Y,(Field)	D for 2 species (W, C) D for 8 species (C only)	
3. Live Plants to Standing Dead	All ex P	Y		Y	M, Y	Y	M, Y
4. Standing Dead to Soil	All	-		-	M, Y	Y	Y
5. Standing Dead to Microflora	All	-		-	Y	-	?
6. Soil to Microflora	All	-		-	[D, Y]	-	[Y]
7. Microflora to Soil	All	-		-	[D, Y]	-	[Y]
8. Microflora to Atmosphere	All ex P	-		[D, Y]	[D, Y]	-	[D]
9. Atmosphere to Microflora	All ex P	-		-	-	-	-
10. Microflora to Soil Fauna *	All	-		-	[Y]	-	-
11. Soil Fauna to Atmosphere	All ex P	-		[D, Y]	D, M, Y	-	-
12. Live Plants to Herbivores	All	-		[Y]	D (for sheep), Y	Very minor	D, Y

Pathway	Possible Dependent Variables	Disco (Greenland)	Hardangervidda (Norway)	Kevo (Finland)	Moor House (U. K.)	Mt. Washington (U.S.A.)	Point Barrow (Alaska)
13. Herbivores to Atmosphere	All ex P	-		-	[M, Y]	-	[M, Y]
14. Herbivores to Soil	All	-		-	[M, Y]	-	Y
15. Herbivores to Predators	All	-		-	[Y]	-	Y
16. Predators to Atmosphere	All ex P	-		-	[Y]	-	[Y]
17. Predators to Soil	All	-		-	-	-	[4Y]
18. Soil Fauna to Soil	All	-		-	[Y]	-	-
19. Input (Solids and Liquids) into Soil principally	All	M (Rain) ?		-	M, Y (Rain) Y (Sheep immigration)	D, M (Precip.)	[Y]
20. Output (Solids and Liquids)	All	-		-	M, Y, Y (Sheep emmigration)	Very minor	M, Y
21. Soil to Live plants	W, N, P	-		[Y]	-	D (W in 2 species) M, Y (P in several species)	M
22. Atmosphere to Soil	C, W, N	-		-	-	-	-
23. Standing Dead to Herbivores	All	-		-	M (for sheep) Y	minor	M
24. Standing Dead to Soil Fauna *	-	-		-	-	-	?
25. Input (Solids and Liquids) to live plants	C, W, N, P	-		-	-	-	?

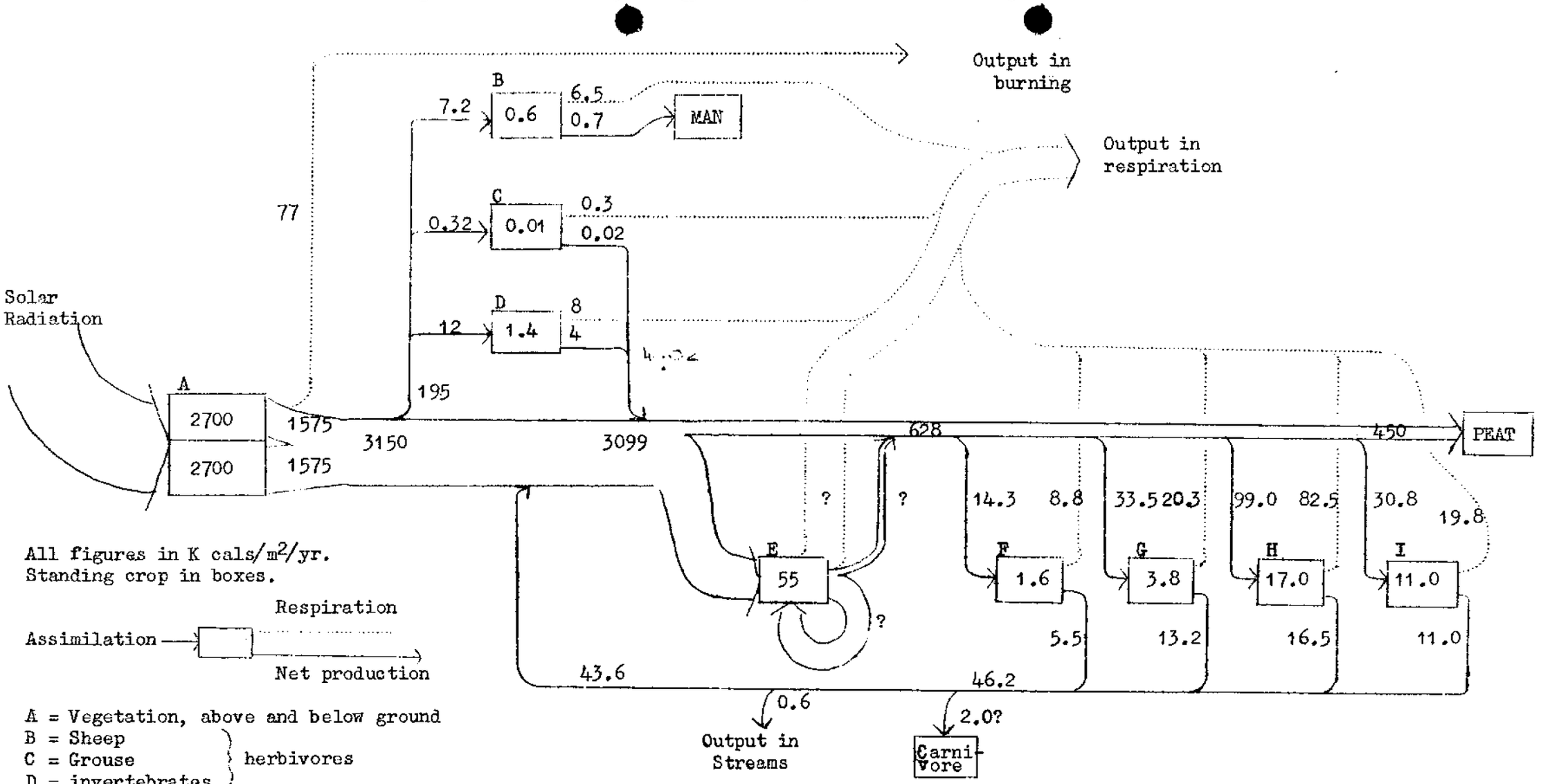
Pathway	Possible Dependent Variables	Disco (Greenland)	Hardangervidda (Norway)	Kevo (Finland)	Moor House (U.K.)	Mt. Washington (U.S.A.)	Point Barrow (Alaska)
26. Live Plants to Soil (i.e. roots etc.)	All	-		[Y]	M, Y	[Y]	Y
27. Translocation within live plants	All	M, Y		-	M, Y	M, Y 1 species	M
28. Microflora (lichens) to herbivores (reindeer)	All	-		[Y]	-	minor	-
29. Live Plants to Microflora	All	-		[Y]	-	-	-
30. Soil Fauna to Predators	All	-		-	[Y]	-	[Y]
31. No Pathway on revised scheme	-	-		-	-	-	-
32. Standing Dead to Atmosphere	C, W, N	-		-	Y	-	[Y]

Fig. 2. Flow diagram for energy and nutrients in Tundra ecosystems



Compartments and pathways agreed for common basic studies by at least 4 sites (Norway September 1968)

Fig. 3. Preliminary energy flow diagram for blanket bog at Moor House



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