PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Meathop Wood and the Pasoh Rainforest Projects

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The Meathop Wood and the Pasoh rainforest projects

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The Meathop Wood Project involved the study of a deciduous broad-leafed forest in Lancashire and an attempt has been made to obtain an energy balance for the community and to elucidate carbon and mineral cycling. Measurements have been made of radiation, rate of photosynthesis by the major components of the forest and their productivity. The rate of litter fall, sub-divided into the various components such as leaves, bracts, branches, etc., root productivity and the death of the roots and the addition of organic matter to the soil from this source were measured. The decomposition of the soil litter was followed, and the soil populations of the animals, fungi and bacteria were examined. The mineral uptake by various plant species was followed by monitoring the incoming rain, the through-fall in its passage through the leaf canopy, the trunk-flow and run-off and the leaching of the litter and soil. The processes involved have been summarized in a general energy flow diagram for the forest. Because of the detailed work undertaken by members of the Nature Conservancy staff, much of which was begun before the I.B.P. started, it was possible with the aid of additional workers from universities and the Liverpool Technical College to fill many of the gaps in the original work.

Similar but less complete studies were made jointly with the I.B.P. Committees of Japan and Malaysia on a virgin tropical lowland dipterocarp forest situated in Negri Sembilan in central Malaya.

At the outset the P.T. subcommittee decided that it would be wise to concentrate its efforts on a small number of major projects and therefore asked potential participants to choose their various contributions in a way which would combine with the major projects and thus gain the very considerable benefits from coordinated work. The three major projects in the United Kingdom were (1) the Meathop Wood Project, (2) the Moorhouse Moorlands Project, and (3) the Mountain Grassland Project at Snowdonia. In addition the P.T. subcommittee assisted in the development of the joint Malaysian, Japanese and United Kingdom Project in Pasoh forest in west Malaysia. In the present communication discussion is confined to the Meathop Wood and Pasoh forest projects; work associated with the other projects is reported separately.

Meathop Wood

Work on this woodland was begun by the Nature Conservancy, well before the I.B.P. began, as part of the on-going programme of the Merlewood research station. Although it was realized by the P.T. subcommittee that there were many disadvantages associated with the choice of that particular woodland there were, nevertheless, many advantages which more than compensated for the smallness and heterogeneity of the area available for study. In the first instance a great deal of the basic work had already been done in terms of general floristic, meteorological and soil surveys which provided a background that enabled the research workers joining the project to obtain the maximum value from the time spent. Moreover a number of productivity studies of the kind proposed for the I.B.P. had already been in progress for several years. In reporting on the I.B.P. contributions it is often difficult to dissociate specific I.B.P. work from that which had been or would have been undertaken by the staff of the Nature Conservancy even if there had been no I.B.P. but particularly because apart from anything else the cooperation between the different workers concerned was so close. In Appendixes I and II the names of the participants and their parent institutions are given and the major areas in which they contributed are shown but it must be reiterated that both in field work and in general discussions the contributions were often very difficult to allocate to any specific contributor.

Meathop Wood consists of an area of approximately 40 ha and is 3 km east of Grange-over-Sands in north Lancashire. It is approximately 50 m above sea-level and has a mean annual rainfall of 114 cm. Meathop Fell on which the woodland lies is an isolated area of Carboniferous Limestone overlying Upper Silurian deposits and surrounded by alluvial flats. It consists of a series of steps, with level terraces and steep outcrops. Glacial drift varies in depth from more than 2 m on the lower slopes to less than 0.5 m higher up. The drift material consists of fragments of slate and mudstones from the Bannisdale series to the north and northwest, and fragments of Carboniferous Limestone and grits.

The soil is a brown earth of high nutrient status with a humus of the mull type. Deep earthworm mulls occur in flushed areas and shallow arthropod mulls overlie the limestone outcrops but where these are exposed or near the surface the soil resembles a rendzina. A preliminary survey gave a pH range of 4.4–7.8, most readings being in the 5.5–7.0 range, the wide variation reflecting the local influences of the limestone.

The woodland consists of mixed *Quercus/Fraxinus/Betula* forest with patches of *Taxus baccata*. The dominant trees are 15–20 m high, and the composition is approximately 40 % *Quercus*, 30 % *Fraxinus*, 25 % *Betula* and 5 % species of *Tilia*, *Salix*, etc. The woodland includes young coppice, pole stage coppice and mature standards. The understorey varies but is generally well developed and locally dense. Understorey species include *Corylus*, *Fraxinus Crataegus*, *Euonymus*, *Rhamnus*. The ground flora is dominated by *Mercurialis perennis*, *Rubus fruticosus* and *Brachypodium sylvaticum*, with a wide range of herbs but few other grasses.

Because so much work had already been undertaken at Meathop it was considered possible to attempt a complete study of the biomass and dynamics of the forest. As the work proceeded it was reviewed periodically and as it became apparent that there were serious gaps in the programme other workers were invited to participate in order to try to provide the missing information.

Biomass

Estimates of the biomass of the above-ground tree vegetation were made by felling trees of all species and obtaining regression lines relating the trunk diameter to dry mass of the tree and its parts. Increment cores were used for estimates of periodic increments.

Estimates of root biomass were made partly by excavating whole root systems and partly from soil cores and trenches. Again allometric methods were used to extend detailed observations to more general estimations.

The measurement of the biomass of the ground vegetation presented special difficulties because of the short growing season of some species. It was found that the total biomass of this component rose to a peak in June and then declined. For the period 1962–7 the standing crop of the above-ground vegetation was estimated as approximately 106 tonnes/hectare and for 1967–72, 122 t/ha. The ground layer contributed only about 1 % of the total biomass. Root biomass in 1972 was estimated as 74 t/ha of which 85 % was in the top 20 cm of soil. About 20 % of the roots, by mass, were dead.

During the period 1962–7 the annual increment was approximately 3.9 t/ha but this fell to 3.2 t/ha in the period 1967–72.

Litter fall

Falling litter was collected in bins spaced throughout the area and removed for sorting and weighing at fortnightly intervals for a period of three years. The results for three successive years were surprisingly similar, the mass of total material collected being 5.2, 5.0 and 5.2 t/ha. Of this about 60 % was leaves of which over 80 % came from the three major tree species. Twigs and branches contributed 20–30 % and as might be expected showed the most variation in amounts. Fruits, bud scales, etc., contributed about 10 %.

Secondary production and decomposition

The concept of 'secondary production' has been greatly extended in recent years. Where large herbivores grazing on grass are being considered the concept is readily understood but as ecologists increasingly focused attention on the decomposition phases of the ecosystem the concept has gradually been widened to include all the organisms involved in the processes of decomposing and recycling the materials of the system. It is therefore much more difficult to dissociate biomass from activity with the secondary producers than it is with the primary producers.

Decomposition begins on the living plant and is most apparent in the activity of leaf-eating organisms. Populations of such organisms are notoriously variable. The dry mass of the larvae on the oak and hazel canopies varied from 1 to 4 kg/ha during the four years of observation.

In temperate conditions of managed or pre-climax forests most of the decomposition occurs on the ground or in the soil. Extensive studies were therefore undertaken to determine the numbers and relative activities of the soil and litter organisms. The more abundant soil animals were sampled periodically over a period of two years, but other groups less frequently, the estimates of molluscs for example being based on a single estimate. Despite the reservations that these sampling variations might produce it is felt that the estimate of 1.1 t/ha for the total biomass of the animals is reasonably accurate. Of this total, earthworms account for more than half.

The measurement of biomass for bacteria, actinomycetes and fungi presents special difficulties and it is generally agreed that the results give the order of magnitude of the amounts rather than accurate estimates. In estimating the biomass attempts have been made to distinguish as clearly as possible between the biomass of living material and of estimates made on visual counts. The living bacteria have been estimated at 37 kg/ha as opposed to an estimate of 9000 kg/ha based on direct visual counts. Similarly with the fungi the estimates of living mycelium give approximately 110 kg/ha, of which about 38 kg are in woody material. Again this contrasts with estimates of over 500 kg/ha based on estimates from visual measurements.

Hydrology and nutrient circulation

In an attempt to obtain as complete a picture as possible of the nutrient cycling detailed studies of the transport of essential nutrients by rain, throughfall, run-off and leaching were undertaken. These were then combined with information about the uptake by plants and the subsequent release on decomposition of the plant residues. The elements followed were nitrogen, phosphorus, potassium, sodium and magnesium.

The nitrogen budget may be taken as an example. The total mass of nitrogen in the system was estimated as 6.5 t/ha of which about 10% was in living material, most of the remainder being in the soil. Rainfall added about 6 kg/ha per year and biological fixation about 100 kg/ha per year.

Annual loss through the soil was estimated as 12 kg/ha leaving an annual gain of 78 kg/ha. Similar calculations showed that potassium and calcium were lost from the system but magnesium accumulated.

Overall balance of the system

Any attempt to give an overall picture of an ecosystem in quantitative terms is made difficult because choice of the method of expressing the individual quantities is determined by the aim of the writer. In the case of the cycling of an individual element the situation is simple as in the example of nitrogen given above.

With organic matter however it is more difficult and the most widely used measure, dry mass, while reasonably satisfactory for simple transformations and changes in amounts of plant material ceases to be so where conversions from plant to animal material or to microbial are involved. This has led zoologists to favour energy budgets as the best way to express the transformations taking place within the ecosystem. However concentration on energy levels can readily deflect attention from the importance of the cycling of crucial elements which may control the rates of many of the processes being studied. In the final detailed report on the Meathop project it is hoped to discuss these considerations further and to endeavour to provide a satisfactory overall model of the ecosystem.

So far as the energy relationships of Meathop are concerned the position may be summarized as follows. The energy stored in the system is 3.6×10^6 kJ/ha in the aerial biomass, 1.2×10^5 in the litter and 3.5×10^6 in the roots and soil.

The annual energy input to the system via photosynthesis is of the order of 4.7×10^4 kJ/ha and represents about 1% of the available solar energy. Of the energy fixed about half is lost in respiration by the photosynthesizing plants. About one quarter of the annual input is soon transferred to dead material via leaf and twig fall and is progressively released as decomposition proceeds. One eighth goes into living material above ground and one sixteenth into roots.

In Meathop the increase in both stored energy and biomass support the historical evidence that the forest is not yet in an equilibrium.

The Pasoh rainforest

The lowland dipterocarp forests of Malaysia have been of considerable interest to biologists for a very long time and are usually regarded as among the most complex of terrestrial ecosystems. The area chosen for study lies in the State of Negri Sembilan and it was through the good offices of the State Government that an area of approximately 2000 ha was set aside as a research forest in 1970. Subsequently a further 600 ha were added to the initial reserve in order to include the whole of the catchment area within the study region.

At the time the United Kingdom Subcommittee was negotiating with the Malaysian government it was learned that a team from Japan, under the direction of Professor Kira from the City University of Osaka, was also interested in setting up research projects in the Malaysian area. It was therefore agreed that we should if possible combine our resources and subsequently the United Kingdom and the Japanese entered into agreements with the Malaysian government to undertake research at Pasoh. With the aid of the research grant provided through the

Royal Society Dr J. Bullock, then of the University of Malaya, was invited to be the Honorary Director of the research project. He accepted the responsibility for coordinating the initial surveys, for the direction of the permanent staff and the general supervision of the research area. The team under Dr Bullock was also responsible for the maintenance of the regular meteorological records. Both the United Kingdom and Japanese groups arranged to have research stations built at the boundary of the forest area. When Dr Bullock returned to England Dr E. Soepadmo replaced him as Director.

Part of the forest had already been logged before the establishment of the reserve but this forms only a marginal portion and serves as a buffer area to the main study region which so far as can be determined has not suffered any serious interference by man. To the west and south of the study area a development scheme has been carried out involving the felling of the forest and planting with crops such as oil palm. The study of the forest therefore serves a most valuable reference for subsequent agricultural development. The forest was classified by Wyatt Smith (1961) as Meranti Keruing, the principal timber trees being *Dipterocarpus cornutus*, *D. sublamellatus*, *D. costulatus* and *D. crinitus*. In addition several species of *Shorea* are prominent, particularly *S. macroptera*, *S. leprosula* and *S. acuminata*.

Although the climate at Pasoh is described as continuously wet the rainfall is relatively low by Malaysian standards and averages about 1900 mm per year, with slight peaks in April and in July. The temperatures are fairly uniform both day and night with maxima at about 32 °C and minima round about 21 °C. The topography of the site is determined primarily by the drainage pattern which forms gently undulating areas although the general slope of the land is towards the west. To the east and north of the study area the land rises rapidly to form part of the central range. The soils which are derived partially from shale and partially from granitic rocks in the east are predominantly yellow or red latosols which vary somewhat according to their positions on the undulating surfaces. In some places they become more pronounced lateritic and have disk-like concretions at about 30 cm below the surface. In the new American nomenclature the most weathered soils would be termed oxisols or haplorthoxes whereas the less weathered soils would be classified as tropudults.

In many previous studies of tropical forests the comment has been made that there is little floristic differentiation between different areas of the forest and, except on a relatively large scale, that it is difficult to distinguish different plant communities and to correlate these either with soil differences or with topography. The detailed study of Pasoh undertaken by Dr P. S. Ashton however shows very clear correlations both between vegetation and differences in soil type and between the vegetation and the localized activity of native animals. The area was first surveyed by Wong Yew Kwan of the Forestry Research Institute, Kepong, in 1959. He labelled a number of trees and carried out measurements of interest to the foresters. In August and September 1970 a detailed survey of the area was carried out by Ashton. The ten one-acre plots (1 acre = 2.71 hectares) set up by Wong ten years earlier were readily located and most of the trees measured by him still bore their numbered tags. Five of the plots were selected for much more detailed study. In the areas intensively studied each tree was labelled with a small zinc tag, the trees mapped, leaves or live twigs collected for later identification where necessary and their girths recorded. In all 5907 were labelled, identified and their girth measured to the nearest centimetre. The 5907 trees included 473 species with trunks exceeding 10 cm in diameter. The very large number of species recorded in such a restricted area is indicative of the complexity and diversity of the lowland dipterocarp forest.

Structure

There is a fairly uniform closed canopy reaching a height of about 30–35 m above the ground. From this are a number of emergent species which may reach a height of 60 m. The crowns of the emergent species are usually well separated. Frequently species of *Shorea* or *Compassia* are the emergents with the main dipterocarp species forming the principal canopy. Between 30 and 10 m above the ground there is a fairly uniform distribution of leafy branches and there is a certain amount of disagreement as to the extent that this possesses any distinct layering. There is a pronounced shrub and ground vegetation which normally lies between 1 and 3 m. The relatively low rainfall of the Pasoh area is reflected in the relatively small number of epiphytes in comparison with the very large epiphyte populations in much wetter forests but lianes are relatively abundant.

It has been recognized for a very long time that light is one of the important factors involved both in the species distribution and in the development of individual plants within the rain forest. The mean relative light intensity at Pasoh was studied in detail by Yoda (1974). Taking the incoming incidence of energy as 100 % he showed that the light intensity was about 30 % below the canopy of an emergent tree, and then stayed more or less constant until the surface of the main canopy was reached. From there to approximately 3 m above the surface the light intensity fell off logarithmically and at the soil surface was only about 0.3 % of the incident intensity. Considerable lateral variation in light intensity occurs at any level but is most readily noticeable at the forest floor where the moving sun flecks form a very characteristic feature of tropical forests.

Biomass

Although there have been a number of investigations in temperate regions designed to estimate the total biomass of a forest system and to estimate the annual productivity there have been few comparable studies of tropical forests. Kira and his colleagues had previously carried out investigations in Southern Thailand and they adapted some of the methods which were undertaken by them there to the study in Pasoh. Certain areas were selected for clear felling and detailed measurement and weighing of the trunks, branches and leaves were made. From this work regression lines were obtained which enabled them to relate trunk diameter to total mass of the individual tree and its various parts. Comparisons of the biomass estimated by destructive sampling and by subsequent allometric calculations showed reasonable agreement but the allometric method underestimated the total biomass by about 7–8 %.

The clear-felled areas have subsequently provided interesting information in terms of the re-establishment of a forest on cleared areas. Growth of individual marked trees has been followed using the normal forestry techniques of girth measurement. Although initially attempts were made to excavate root systems and later to obtain some measure of root development by sample cores none of these studies have been sufficiently successful for the results obtained to be of any real value. They have simply emphasized the extreme difficulty of carrying out such work in a closed system like a tropical forest with closely interlocking root systems derived from so many different species. It is appreciated however that the absence of such measurements represents a serious gap in the present study. The detailed results of the biomass studies, undertaken by the Japanese team, will be published independently but their preliminary results indicate a value approximately 500 t/ha for the total biomass. Of this over 90 % was made up by the trees, lianes and shrubs making only a small contribution to the total biomass. Trunks

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account for approximately 75 %, leaves about 2–3 %. The biomass of the secondary producers is referred to later.

Litter fall

Estimates of litter fall were obtained in the conventional way by the use of traps catching the falling litter. The United Kingdom group used almost exclusively 1 m square trays set about 20 cm above ground level. The Japanese team used nets with circular openings about 1 m above the ground level. These were used because there was considerable evidence to indicate that the trays were disturbed from time to time by monkeys or other animals. Certain areas were selected for detailed measurement of fallen trunks and of fallen branches. One of the difficulties associated with the estimation of litter, branch and stem fall in tropical forests is the frequent occurrence of wind falls. These appear to be a normal feature and the wind fall may vary from a few trees to a substantial strip of forest sometimes 50 m wide and several hundred metres in length. Where a tree dies in the upright position decay of the smaller branches proceeds fairly rapidly and even the main branches are substantially decayed before the trunk falls so that when finally the trunk does fall because its crown has largely disintegrated it causes remarkably little disturbance to the surrounding vegetation. Where a living tree is blown down, even if only an individual is concerned, the falling of the very large crown causes considerable destruction particularly to the understorey vegetation and it provides a very different type of material at ground level for the organisms involved in the decay. The estimates of litter fall made by the two methods used were in very good agreement, giving a total litter fall of around 10 t/ha per year. Of this about 60 % fell as leaves and about 25 % as branches – the remainder being made of pieces of bark, flowers, fruit and seeds, budscales, etc. The value of 10 t/ha agrees very well with estimates made elsewhere in the tropics in wet evergreen forests.

In any consideration of the overall dynamics of the forest one needs to know, in addition to the litter fall, the loss from the system by the death and decay of large units such as trunks and branches which would not appear in the normal litter traps. Both the United Kingdom and the Japanese teams attempted estimates of this by somewhat different methods. Again the results were in reasonable agreement and showed that on average there is an increment to the surface organic matter on the death and fall of trees of approximately 4 t/ha per year. This includes trunks and large branches in various stages of decay although it seems as if 60–70 % of the material falls to the ground relatively undecayed.

Waterflow and nutrient cycling

As part of the study on nutrient cycling, arrangements were made to compare the direct rainfall with that which passed through the canopy and that which flowed along the branches and down the trunks. By using fairly well-established methods, the trunk flow, throughfall, and direct rainfall were collected at regular intervals over a period of several years. Subsequent analyses for the major constituents have given sufficient evidence to enable a provisional balance of nutrients in the system. The extent to which the canopy intercepts the falling rain varies with the intensity of the shower. With normal showers interception can be in excess of 40 %. About 50 % reaches the ground as through fall and about 10 % as trunk run off. The 40 % intercepted by the leaves and branches is presumably lost primarily by evaporation. In heavy and prolonged showers the proportion reaching the ground as through-fall increases considerably. The average of the measurements for several years gives a figure of slightly under 40 % for the amount intercepted by the canopy. The extent to which this causes surface wash and erosion has been studied by Dr Leigh. He has shown that despite the very dense vegetational cover and the relatively gentle slope of the undulating soil surface there is still considerable surface wash and erosion. Part of the soil moved is redeposited on the upper side of roots and fallen branches but substantial quantities are carried off as river sediment loads. Studies were also made by Leigh to determine the extent of passage of water downward through the soil and the accompanying chemical changes produced. Pits were dug and zinc plates 100 cm × 20 cm were inserted into carefully prepared slits on the upslope face of the pit. The water intercepted by these was collected in gutters and then piped into plastic containers for subsequent measurement and analysis. Samples were thus obtained from the surface 5 cm, 70–80 cm and 120–130 cm below the surface.

Soil meiofauna and insects

In an attempt to estimate the size and the distribution of the insect populations within the forest, extensive trapping, both by pitfall methods and by nets hung at different heights within the forest, has been carried out. The sorting and identification of the species collected has not yet been completed. Preliminary sorting and identification has shown however that of the insects caught in nets suspended from the tower, over 80 % were diptera and of these diptera close on 80 % were cecidomyiidae. Studies of the soil meiofauna were undertaken by Bullock and some of his colleagues from the University of Malaya, but as yet the data are still being examined. As might be expected Acari are abundant in the litter and particularly Oribatidii. Work undertaken by the Japanese team included the sampling of soil cores for mesofauna and the subsequent determination of respiration rates of some of the more abundant species under laboratory conditions in order to give the basic information which would enable calculations to be made of the possible carbon turnover rate, as influenced by these particular species.

As might be expected termites are a prominent feature of the Pasoh forest and extensive examinations both of the species and their populations were undertaken by the Japanese group. They made detailed estimates of the total number of nests of each species and from sampling studies of nests calculations of the numbers of individuals of each category determined. Again this was accompanied by laboratory work in order to obtain respiration rates and thus assist in the calculation of the probable carbon turnover by the termites.

Dynamics of the forest

In any ecosystem production, respiration losses and decomposition occur simultaneously. Where there is clear evidence of successional development one expects to find production exceeding the sum of the other two. In a stable climax community it has been assumed that these processes are in balance. It is of interest therefore to endeavour to obtain an overall estimate of the rates of the different processes.

Attempts have been made to estimate the productivity by three unrelated methods, one based on harvesting techniques and measurement of increase in biomass, another by estimating the photosynthetic activity of the leaves and the respiratory losses, and a third by measuring changes in carbon dioxide levels over continuous periods and comparing these with the energy balance.

Photosynthetic studies of two types have been made in the forest but as yet the results have not been analysed in detail. The work undertaken by the Japanese team involved the removal of branches, taking them back into the laboratory, and studying them under laboratory conditions. The work by Sunderland from the United Kingdom group was concerned with seedling plants in the forest and the rates were measured *in situ*. Similarly respiration studies undertaken by members of the Japanese group involved taking portions of branches or leaves into the laboratory and measuring the respiration there. Subsequent extrapolation based on the biomass estimates were then used to calculate total photosynthesis and respiration.

This work has not yet been correlated and one must therefore await the full published results. From the preliminary report however it would seem that the Pasoh forest produces somewhere about 80 t/ha of organic matter annually as gross production, of which somewhat under 70 % is consumed by respiration, leaving a net production of approximately 27 t/ha. Kira's estimate is that of this net production about three quarters is utilized in compensating for the losses caused by the death of leaves, flowers, fruits, etc., and only about 7 t/ha per year is available for the increment of longer-lived plant biomass. This is roughly equivalent to the mass of one big tree and from the general evidence obtained it would appear that on average the equivalent of one large tree per hectare falls per year. This would indicate that in terms of very rough approximations there is a reasonable equilibrium within the forest.

Assessment of the working of the International Biological Programme

Despite the opportunity to learn from other organized programmes such as the International Geophysical Year it was found difficult to transfer much of the experience from one organization to another which has very different needs, personnel and methods of working. It could be said in retrospect that there would have been many advantages in outlining the research programmes in much more detail in the initial stages and seeking specific research workers to carry out sections of the programme. It is, however, unrealistic to expect such a policy to be followed where the bulk of the people involved would be individuals drawn from a wide range of institutions and with commitments to the project essentially personal rather than imposed by their conditions of employment. There is no doubt at all in my mind that the policy of building on programmes already existing in the Nature Conservancy organization was a sound one both financially and scientifically. In contrast to the speed with which work was expanded and new aspects developed in Meathop and in the other two United Kingdom projects, the initiation from scratch of the Pasoh project involved much preparatory work in terms of choice of site, arranging agreements with the appropriate authorities, and then recruiting staff, and all this took far longer than was ever envisaged in the early days. This being so one has to contemplate a very different time-scale for projects of this kind.

Any large coordinated programme involving a substantial number of workers must inevitably involve large amounts of money being put into overheads and permanent equipment or organizations. If this is built on to some existing or proposed permanent organization then expansion could readily be justified. If one is starting from nothing then the long-term future of a project must always be kept in mind, and I would like to think that the Pasoh investigation will be continued far beyond the period covered by I.B.P. both for scientific and economic reasons.

The P.T. section organized from time to time meetings of its committee at the research sites where members met the individuals directly concerned in the research and had the opportunity to see the field arrangements and to discuss in the laboratory the progress of the work. These meetings had two very important functions. In the first place they gave a great deal of stimulus to the people involved in the work. In the second they strengthened the cooperative aspect of the programme and enabled an overall even though incomplete picture to be put together during the developmental stage. Such attempts at synthesis showed up gaps in the programme and provided opportunities to fill them. Moreover on a number of occasions they enabled ideas to be clarified and emphasis to be changed. In any future programme I would recommend very strongly that even more provision be made for meetings of the organizing committee jointly with the research workers involved. There is also need for workshop meetings restricted to scientific aspects of interest to small groups of specialists. Here again I think future programmes might well allocate more financial support but such meetings must be very strictly limited to people intimately involved in the project.

In preparing the above report I have drawn very heavily on unpublished work or on work which has been published only in abstract form. It is inevitable therefore that I have not done justice to the great amount of experimental work which still awaits detailed consideration. I hope that I have not misreported any of my many colleagues. For the Meathrop section I have relied primarily on the annual reports made available to me as Chairman of the P.T. Subcommittee and on the report of the British Ecological Society's Symposium in Liverpool 1973 (see *Bull. Br. Ecol. Soc.* IV, 3. 2–9). The report of the Pasoh work is based on the annual reports by Dr Soepadmo and on the I.B.P. Synthesis meeting held in Kuala Lumpur in 1974.

References (Burges)

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Appendix A. Contributors to the Meathop Wood I.B.P. Programme

(Numbers in parentheses indicate the parent organization as shown in Appendix B)

Community analysis and site description

History, physiography, soils, climate, vegetation, vertebrates, soil temperature and moisture:

J. E. Satchell (1); D. F. Ball (2); A. H. F. Brown (1); E. J. White (1); R. G. H. Bunce (1); V. P. W. Lowe (1); K. L. Bocock (1); D. A. Rose (3).

Population metabolism and function

Soil and litter invertebrates, bacteria, actinomycetes saprophytic fungi, mycorrhiza:

W. G. Hale (4); R. Stuttard (4); J. O. M. Thomas (4); J. B. Vincent (4); P. F. Newell (5); F. B. O'Connor (6); T. R. Piearce (7); I. N. Healey (8); A. Russell-Smith (8); T. R. G. Gray (9); S. T. Williams (9); H. L. Hatfield (9); R. Hisset (9); J. C. Frankland (1); M. Parry (4); B. Mosse (3); D. L. Hayman (3).

Primary production

Photosynthesis, trees and shrubs – above ground, trees and shrubs – below ground, *Rubus*, ground flora:

P. J. Mueller (10); R. G. Bunce (1); J. M. Sykes (1); J. K. Hibberd (1); K. Taylor (6); J. D. Grace (6).

Herbivory

Defoliating insects:

P. H. Smith (4).

Decomposition

Standing dead wood, leaves and branches in the litter layer, roots, soil and litter respiration:

O. W. Heal (1); A. D. Bailey (1); J. M. Sykes (1); J. K. Hibberd (1); M. J. Swift (11); M. E. Nesbitt (11); P. J. Howard (1); J. G. Jones (4); M. Spink (4).

Energy flow

F. B. O'Connor (6).

Phosphorus circulation

A. F. Harrison (1).

Circulation of other nutrients

E. J. White (1).

Hydrology

R. B. Painter (14); F. A. K. Farquharson (15).

Systems analysis and biometrics

R. V. O'Neill (12); D. Tait (13); D. K. Lindley (1).

Appendix B. Institutes

(1) Institute of Terrestrial Ecology (formerly Nature Conservancy) Merlewood.
(2) Institute of Terrestrial Ecology (formerly Nature Conservancy) Bangor.
(3) Rothamsted.
(4) Liverpool Regional College of Technology.
(5) Westfield College, University of London.
(6) University College London.
(7) University of Lancaster.
(8) King's College, University of London.
(9) University of Liverpool.
(10) Imperial College.
(11) Birbeck College
(12) Oak Ridge, U.S.A.
(13) University of British Columbia.
(14) Institute of Hydrology.
(15) Thames Conservancy.

Appendix C. Contributors to the Pasoh programme

T. Abe	University of the Ryukyus, Okinawa.
M. Aoiki	University of Osaka Prefecture, Japan.
P. S. Ashton	University of Aberdeen, United Kingdom.
J. A. Bullock	University of Leicester, United Kingdom.
N. A. Burges	New University of Ulster, United Kingdom.
L. S. Chia	University of Singapore.
S. Chiba	Hirosaki University, Japan.

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