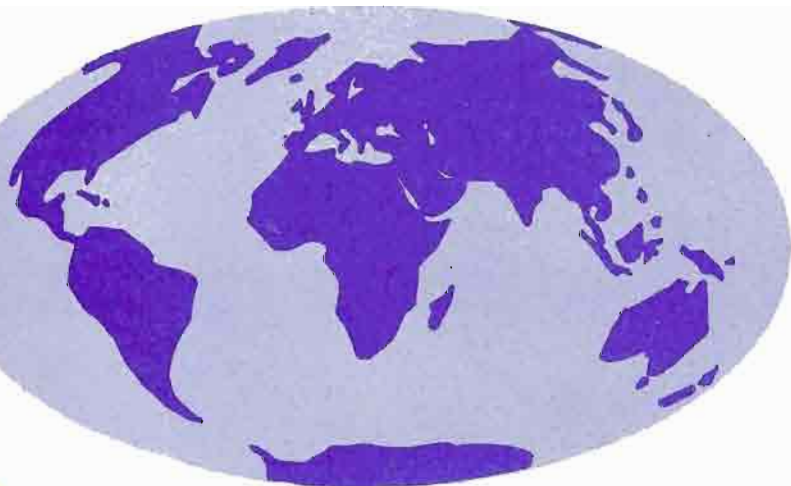


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EDITORIAL

Biology in 1919, when the International Union of Biological Sciences was founded, was very different from its present day descendant. Like the organisms with which it deals, biology itself has evolved. One can indeed argue that its evolutionary progress in the 70 year lifetime of the IUBS has been at least as great as in the 60 years that separate the founding of IUBS from the publication of Darwin's "Origin of Species". Before 1858 all branches were still exploiting the legacy of Linnaeus, and were confined by the shackles of his premise of immutability. It was Darwin who loosened them. His concepts brought biology to life as an entity, with the recognition that there was a theme common to all organisms; they inspired research throughout all its branches, from the study of the fossil record to that of embryos, and have continued to do so, from virology to primatology. It remained for the science of genetics to appear on the scene, to provide the mechanisms by which Darwinian evolution could be understood. This understanding was just in the 20 years between the discovery of Mendel and the founding of the IUBS.

In the early years of IUBS then, biology though still essentially taxonomic was beginning to profit from the combination of Mendel and Darwin-how successfully is shown in Huxley's "Evolution, the modern synthesis" of 1942. Emphasis began to shift away from the individual and the type to population and variability. By midcentury it was accepted that the evolution entity was the population, its predecessors and successors. Evolution was the change that occurred over generations. Variation was no longer seen as an awkward incidental but as the key to evolution and, as the new genetic work showed, the evolutionary mechanism was in gene frequencies. This new emphasis in turn led to awareness of the interrelationships and interactions of populations with each other and with their environment, to ecological viewpoint and the concepts of checks and balances. Today "ecology" and "the ecosystem" have entered popular (and even political) parlance. In the present phase the biological hierarchy, cells, tissues, organs, organisms, populations, ecosystems, is seen as complex at all levels, the rules that apply to one do not necessarily apply to the other, and the processes that create complexity at one level are not necessarily those relevant to another. Evolution is seen as the outcome of optimisation processes acting on ordered as well as random events. Biological complexity is the successor to the simpler ecological concepts.

At each stage in this historical sequence, IUBS has made a noted contribution. In the early days it was important to organize congresses to stimulate dissemination of the new knowledge and this was an obvious

role. Then the great conception of the International Biological Programme pointed the way forward in international collaborative work and proved highly successful in stimulating research throughout the world. With its experience in this, the IUBS initiated its research programmes of the last few years, e.g. the Bioindicators and the Decade of the Tropics programmes with their ecological orientations, and these are proving similarly successful. The newly developing programmes on biological complexity and biological diversity are promising well.

While population-oriented biology was emerging, another sequence was also progressing, that of the determinants of individual variation, explored in terms of developmental processes, biochemistry and the molecular basis of biochemical and genetic variation, again linking together all living things and all branches of biology. This was the sequence that gave rise to the massive research effort described in the following pages, the human genome project. Once again IUBS has a contribution to make, and is already doing so in its Decade of the Tropics programme, which incorporates the exploration of genetic variability in tropical man, with a view to understanding the human genome as well as describing it.

Thus IUBS, its interests and influence, have evolved *pari passu* with the evolution of biology itself, and may well hope to continue to do so. Indeed its viewpoint, which is as wide as biology itself, may enable it not only to parallel but to encourage further new developments in science and also to put them into perspective.

*D. F. Roberts
Department of Human Genetics
The University
Newcastle upon Tyne, U.K.*

THE HUMAN GENOME INITIATIVE AND THE IUBS

by

D.F. Roberts

Department of Human Genetics

The University, Newcastle upon Tyne, U.K.

The human genome initiative is an ambitious project, probably the most ambitious in the whole history of biological science. It aims to map man's genes, to lay bare that infinite complexity of biological information that makes him human. It is the outcome of decades of progress in the knowledge of human genetics, the Cinderella of the sciences who has so recently emerged transformed in all her richness. It is only conceivable now because of that progress.

How little was known of the location of human genes by contrast with those of experimental animals such as drosophila or the mouse had been obvious for decades, then in the early 1970s came some critical technical discoveries. The first, in human cytogenetics, was that human chromosomes take up stain differentially, giving rise to characteristic banding patterns for each chromosome, and so providing as it were map references by which to specify the location of genes on it. Secondly, in somatic cell genetics, came the technique of interspecific cell fusion, by which nuclei are formed that contain chromosomes from parents of different species, from which in subsequent cultures random chromosomal loss allows the identification of the chromosome or part of the chromosome that carries the gene of interest.

At the same time the remarkable progress that was being made in bio-chemical genetics was bearing fruit. Theory had advanced from the «one gene one enzyme» concept of Beadle and Tatum to «one gene one polypeptide chain», and indeed beyond. It became clear that information in genes is sufficiently discrete to specify individual amino acids, that extensive biological ramifications may be brought about through different modifications of only a single amino acid, that an enormous variety of such modifications may occur to give the variations found in a single protein in different individuals. Even so, genes could only be identified by the effects they produce in the phenotype, the outwardly observable or testable characters that derive from the genes responsible, interacting with the developmental milieu.

In parallel, knowledge was accumulating that made it possible to understand the fundamental nature of this genetic diversity and trace it to its molecular source. The first critical item was the identification of DNA in the chromosomes as the chemical substance that carries the genetic information that is transmitted from parent to child, so that genes could be seen as sections of DNA. The molecular architecture of DNA as described by Watson and Crick - easily thought of as a miniature spiral staircase, of which the railings are the phosphate/sugar backbones of the molecule and the treads holding them together are the bonds between the base pairs - explained gene specificity, gene replication and gene mutation. Once the four bases in the pairs were seen as the letters of the genetic alphabet, the genetic code was soon broken, with groups of three bases (DNA codons) making the genetic words to specify particular amino acids, and the sequence of codons (the gene) making the sentence, specifying the sequence of amino acids to be strung together to form the protein required.

With the recognition that the function of DNA in cells is to dictate the structure and govern the synthesis of enzymes and other proteins, and the discovery of how it is processed through transcription to RNA, the oversimplicity of the one gene one polypeptide chain concept was seen. For molecular analysis soon showed that a protein was not simply the product of a gene; different parts or different stages in the making of a protein may be under the control of different genes, possibly on different chromosomes. Inserted into the DNA sequence specifying the polypeptide structure may be sequences of base pairs that are apparently meaningless. Thus in the base pair sequence specifying the 146 amino acids of the beta chain of human haemoglobin are inserted two intervening sequences, one between the codons for amino acids 30-31 and the other between codons 104-105. The first of these intervening sequences is 122-138 base pairs, and the second 850-904 base pairs, in length. So that these intervening sequences are in fact longer than the structural sequence into which they are inserted. These «irrelevant» sequences are excised and spliced in processing messenger RNA from the DNA, ready for transfer from the nucleus into the cytoplasm where the messenger instructions are acted on.

Recombinant DNA techniques

At the same time remarkable progress was being made in another area. The discovery in 1970 of restriction endonucleases to cut DNA into fragments led to the development of recombinant DNA technology in the mid-70s. Restriction enzymes recognise specific base sequences. For example *HaeIII* recognises the sequence (5'-GGCC-3'), cleaving the molecule between the G and C bases. Once pieces of DNA are cut out, they can be introduced into a bacterium and in that way cloned, to produce as much DNA as is required. When a large DNA molecule is cut into many fragments, these can be separated by size, by agarose gel electrophoresis, so that as the DNA fragments migrate towards the anode because of their negative charge, smaller fragments move through the gel more quickly than larger ones, producing a gradient of DNA fragment size along the gel. Once separation has

been achieved, the DNA is denatured to form single strands and transferred from the gel on to a nylon filter by Southern blotting. The bases on the strand form a template, to which DNA containing the complementary base sequences will anneal (hybridisation). Thus pieces of DNA from a specific chromosome location can be identified by radioactively labelled DNA probes containing a given sequence. By a series of overlapping steps, isolating a new clone which begins with the fragments from the end of a previous one (the process known as chromosome walking) maps of long stretches of DNA can be built up, and a modification of the process (chromosomal jumping) uses sequences from the ends of large DNA fragments. To overcome the limitations of the standard DNA gel electrophoresis in respect of large DNA molecules, their migration being independent of their molecular weight, pulsed field gradient gel electrophoresis or field inversion gel electrophoresis may be used. Numerous other techniques have been developed. With the discovery of the polymerase chain reaction, it became possible to amplify small amounts of DNA so that direct scanning could be carried out. This allows identification of point mutations, and has been highly useful in characterizing the variation in the hypervariable region of the DRB chain of the major histocompatibility complex on man's chromosome 6. Besides the DNA sequences obtained from overlapping cloned segments, additional information comes from restriction fragment length polymorphisms, that is to say DNA fragments of different sizes (morphs) which result from cutting with known restriction enzymes, and which occur at different frequencies.

These molecular techniques again have emphasised that not all human DNA is informative. Part of it specifies proteins, but the function of a great deal of it, possibly 98%, is unknown, and so it is often termed «junk DNA»; though it may of course be functional in some as yet undiscovered way. The amount of this junk that characterises man and other higher organisms, and distinguishes them from bacteria and yeasts, poses a major problem for evolutionary thought.

With the many new techniques that have been developed, in the past few years it has come to be generally thought that the complete specification of the human genome (the mapping of loci and establishing the full DNA sequence) is feasible, and could be completed by the end of the century. The United States Government committed itself to such a programme with promised support of \$200,000,000 per year. Other governments have already begun or are preparing to support similar programmes. In the last three years the United States' effort in the human genome initiative has been formalised by human genome programmes in the National Institutes of Health and in the Department of Energy. An international organisation, the Human Genome Organisation (HUGO) has been incorporated. The human gene mapping workshops that have been held at intervals since 1973 have been re-organised, and workshops are planned in England in 1991 and Japan 1993.

Difficulties

The size of the task should not be underestimated. In man there are thought to be some 4,000,000,000 base pairs, making up perhaps 100,000 genes, the remainder (a great deal) being of unknown function. The genes vary in size, from relatively small genes e.g., for the alpha chain (141 amino acids, 429 base pairs) or beta chain (146 amino acids, 444 base pairs) of the human haemoglobins, to the cystic fibrosis gene of some 200,000 and to the muscular dystrophy gene of some 2 million base pairs. The handling of the sheer amount of data has necessitated the development of ever more sophisticated computer skills and facilities. The final difficulty is the representation of the information when it is obtained. An indication of the extent of this difficulty comes from the experience with mitochondrial DNA. The mitochondrial DNA is a fairly small circular molecule of 16.5 kilobases. It was completely sequenced by Anderson et al (1981) and the sequence filled three closely printed pages of *Nature*. The haploid nuclear genome is about 200,000 times as large, so to print it would require about 600,000 pages of *Nature* or their equivalent.

Yet progress is already remarkable. When the first international human gene mapping workshop was held in Newhaven at Yale University in 1973, the outcome was a table summarising the 25 genes that had then been mapped in man. At least two of those locations were wrong. At these workshops a common nomenclature is followed and data from individual laboratories are compared and combined to provide an up-to-date and accurate account of the human gene map. The data include three types of markers, functional genes, DNA segments of unknown function known only by their sequence, and inherited chromosomal markers. At the tenth workshop in 1989 in Newhaven the number of mapped functional genes, i.e., named genes identified by their effects, that can be assigned to a definite chromosomal locus had risen to 1631. This is a remarkable figure when one remembers that it was only in 1968 that the first gene in man was assigned to a chromosome, the Duffy blood group locus to chromosome number 1.

It is the junk DNA that is now a source of controversy in the genome project. Should it be avoided? One way of attacking the genome is to start at the telomere of the p arm of chromosome 1, work steadily through each of the chromosomes down to the most distal point on the q arm of the X or Y chromosome. An alternative is to take a leaf out of nature's book, for she trims out junk and passes on the message of even a very large gene in a very much smaller form. Brenner (1990) suggested that instead of cloning DNA, perhaps what should be done is to clone messenger RNA. It would be more economical to concentrate on the known genes in the first instance, locate and sequence them and the DNA in their immediate vicinity, and so filter out the most important part of the human genome. That will identify gene location on the map, and is likely to provide some return for the money spent, for the application of this knowledge is already proving to be of value in diagnostic and preventive medicine. But for a gene to be known by its effects, there must be alternatives, that is to say, it must have one or more alleles. Large though the number of known genes is in man, there are very many that are not yet known, particularly those that relate to continuously varying

homozygotes occur at very high frequencies. For this led to experimental investigations of the role of this polymorphism in relation to another malarial species, *Plasmodium vivax*.

The problem of the future

The search for the function of the genomic variants already discovered has barely started - not surprisingly, in view of the concentration of activity in extending the knowledge of the genome itself and relating the discoveries to medical applications. But this will be the next major research area that will need attention as the genome map nears completion. It was recognised as one of the objects of the human genetic section of the IUBS Decade of the Tropics programme (Roberts and de Stefano, 1986) - *«To gain an understanding of the true extent of genetic variability within and between human populations in the Tropics; of the biological significance of that variation; of the factors responsible for its origin and maintenance»*. For though with the many new techniques that have recently become available, there has been vast expansion of human genetic knowledge, this mostly relates to temperate populations, and the tropical have been virtually ignored. Many tropical environments are intrinsically hostile to man, and the genetic mechanisms evolved to combat this hostility represent major evolutionary triumphs, and there must be still others awaiting discovery. Exploration of the vast reservoir of genetic heterogeneity that exists amongst tropical populations is particularly urgent in many instances, not only to establish its extent, but also to understand and learn its function before the populations disintegrate or become extinct and it will then be too late.

To attain the objects of the programme, it was hoped to encourage units already in existence and working with the new techniques to divert some of their time and expertise to dealing with material from tropical samples. Since the participating units are autonomous and already have their own research programmes, this seemed the most appropriate procedure, though it meant that there could be no overall directed attack on one particular type of genetic variation. Thus

some units are concentrating on exploring the better-known serological polymorphisms in hitherto undescribed populations (e.g., blood groups, red cell enzymes, serum proteins, HLA types). Others are incorporating the newer molecular variants, identified as restriction fragment length polymorphisms or DNA sequences. As a result, there is a considerable amount of activity in genetic exploration of tropical material, both by those who have registered their projects with the Decade of the Tropics programme, and by others who have not yet done so.

The present state of the programme

At present, genetic studies are under way in the tropical regions of each continental area - the Americas, Africa, India and South East Asia, Australasia, and the Pacific area. To illustrate the productivity, Table 1 lists the published contributions during the course of the programme, from one particular unit coordinated by Dr. Salzano working on populations in Brazil, and Table 2 publications on the work coordinated by Dr. Papiha. Of the work concentrating on molecular variation, globin-associated restriction fragment length polymorphisms have perhaps been the most widely studied, and many polymorphic restriction sites are known both in the α and β gene clusters (Collins and Weissman, 1984). Fewer combinations of restriction sites are found than would be predicted, and many combinations are characteristic of specific populations (Summers, 1987). In southern Africa, the β globin genes in the Bantu populations in the vicinity of the Cunene, Kavango and Limpopo rivers studied in Dr. Jenkins' unit show the same mutation that is present in the Central African Republic. Arbitrary DNA probes identifying over 23 polymorphic restriction enzyme sites on chromosomes 1, 4, 7, 8, 11 and 17 are being applied to establish morph frequencies in Bantu and Bushmen. RFLP alleles on the X chromosome identified by probes 754, XJ1.1, pERT 87.8 and DXS7 show different frequencies in a Zaria sample (Nigeria) from those in South India and Europe (Papiha et al, 1988; 1989), and others identified by probes RC8, L1.28, FX (TaqI) and DX13 show that New Guinea, Thai

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and Aborigine population frequencies are different from each other and from Indian and European (Summers, 1987; Wadhwa et al, 1989). Dr. Serjeantson and colleagues in Canberra are using RFLPs identified by TaqI and BamHI respectively in the DQ α and β regions, that are associated with the serological specificities at the DQ locus, in Oceania to extend the work done on the serological testing of the HLA A, B, C and DR loci; recombination between the DR β ' and DQ β and DQ α loci is extremely rare, and the Pacific populations show DR.DQ haplotypes that are not found in Europe or the Far East (Serjeantson, 1989). Apart from nuclear DNA, mitochondrial DNA variation is being studied by Dr. Stoneking and colleagues, in New Guinea and Australian aboriginal populations, using a large number of restriction sites (averaging 370 per individual genome) to allow them to distinguish between closely related mtDNA types. A small sample of aborigines from different parts of Australia showed that their mtDNA types were not shared between regions and there was very little geographic clustering. A larger sample of individuals in New Guinea showed greater mtDNA variation in highland and coastal populations, no differences among coastal populations, but differences among highland and between highland and coastal groups. Australia and New Guinea show no clear phylogenetic relationship, but both appear to be close to Asia, both in the distribution of restriction site mtDNA polymorphisms, and from the evidence of length mutations (Stoneking and Wilson, 1989).

These molecular studies show that there is greater diversity between groups than would have been predicted from serological studies alone. The numbers of subjects, and the numbers of

populations studied, are as yet small. But certainly some polymorphisms and some morphs occur exclusively in particular populations and of the latter many show appreciable variation in frequency. Of particular interest are the comparisons of the results of DNA studies with those of serological phenotypes, for these enhance understanding of both. It is already apparent that some DNA polymorphisms predate the divergence of populations into racial groups, while others strongly suggest the effects of selective pressures maintaining similarities and increasing diversities. For those polymorphisms where there is no suggestion of any functional advantage attaching to particular variants, the data will provide a valuable control in assessing hypotheses of population migration and origins.

The examples of activities given above do not indicate the number of participating units, or the real international nature of the contribution. For example, in tropical America, besides the work of Dr. Salzano's unit, contributions are being made in Brazil by Dr. Guerreiro in Para; on populations of Ecuador by Dr. Bernal of Bogota, Dr. Papiha from Newcastle, and Dr. de Stefano from Rome and their colleagues; in Central America by Dr. Lefèvre-Witier and colleagues from Toulouse, in Nicaragua and Costa Rica by Dr. de Stefano and colleagues, and in Yucatan by Dr. Ferrell and colleagues from Pittsburgh; and in Cuba by Dr. Hidalgo.

What is required now is the encouragement of further units to register their work with the Decade of the Tropics programme, so that a true appraisal can be made of the extent of the activity, gaps identified, and steps taken to fill them.

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THE IUBS DECADE OF THE TROPICS PROGRAMME AND IGBP

THE ROLE OF TROPICAL SOIL BIOLOGY AND FERTILITY STUDIES IN IGBP

By M.J. SWIFT

IITA, Oyo Rd., PMB 5320, Ibadan, Nigeria

Soil is the largest terrestrial pool of carbon, nitrogen and sulphur, and is intimately involved in the main terrestrial fluxes of these important greenhouse elements. Soil is also the fundamental resource on which human populations are dependent for food, fuel and fibre. Land use shifts and their sustainability are an important part of Global Change, and it is through the response of the plant-soil system that climate change will have its main impact on humankind. Furthermore, it is in the tropics that the demands of developing human populations are tightly linked to climate and soil-determined limits. Paradoxically, it is in these regions and topics that our scientific knowledge is weakest.

The Tropical Soil Biology and Fertility Programme (TSBF) was initiated in 1984 by the International Union of Biological Sciences and the UNESCO Man and Biosphere Programme in order to stimulate research in the tropics, and in particular on the poorly-understood topic of the role of biological processes in the maintenance of soil fertility. The TSBF strategy includes focus on the paths of carbon, nitrogen and water through the soil-plant-atmosphere system, and the key factors which regulate them. The immediate targets are to synchronise plant demand with nutrient and water availability, and to manipulate/conservate soil organic matter pools. The tools with which this can be achieved are the management of the quantity, quality and timing of organic

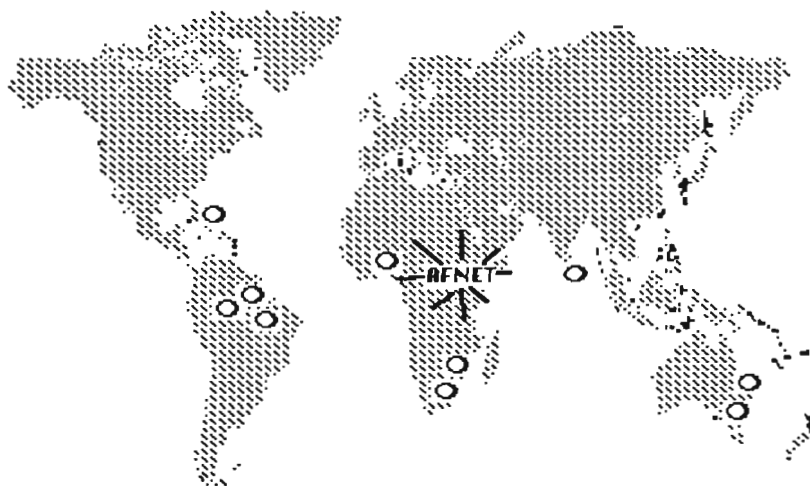


Figure 1 - The network of TSBF Programme Centres

inputs, and the control of soil organisms. A key tactic is the comparison of managed systems with the natural ecosystems from which they were derived. These concepts are being developed by a network of researchers at 16 sites spread throughout the wet and dry tropics (Figure 1).

The International Geosphere/Biosphere Programme aims to describe and understand the interactive physical, chemical and biological processes that regulate the total Earth system, the changes that are occurring in this system, and the manner in which they are influenced by human activities. Process-orientated research, modelling and the monitoring and documentation of environmental change are the central elements of the proposed programme. The IGBP planning process has highlighted the fragmented and geographically uneven distribution of the ecological research community; the inadequacy of the databases for predictive purposes; the limited understanding of soil processes in element fluxes; and the lack of coordination in this type of study. The TSBF programme is able to offer its experience, data, site network, models and conceptual framework towards the solution of these problems.

The key elements of the TSBF programme of direct relevance to the IGBP are:

The TSBF Programme is a detailed study of the pool sizes, fluxes and controlling factors of carbon and nitrogen in tropical ecosystems. The main 'greenhouse' gases - CO₂, CH₄, and NO_x - are all generated and consumed as part of the transformations of these elements in the soil-plant system. Sulphur has not been considered by TSBF, but would be relatively easy to include since it is controlled by similar processes. Soil contains the largest terrestrial biosphere carbon pool, and is susceptible to major changes through management and climate shifts at the time-scale of decades to centuries. It therefore has substantial potential to act as either a source or a sink of atmospheric carbon.

The controlling effect of climate on soil biological processes has been explicitly considered by TSBF. In conjunction with the process-oriented and model-based research philosophy, this forms a basis for the prediction of the consequences of climate change on carbon and nitrogen compound fluxes to and from both natural and derived tropical terrestrial ecosystems. The influence of feedback effects controlled by soil biological processes, and lags induced by the range of turnover times in soil carbon pools, will be especially critical in assessing the net consequences of climate change.

The CENTURY terrestrial ecosystem model has been the main tool for conceptual formalisation, data synthesis and extrapolation within the TSBF programme. This model has been identified by the SCOPE terrestrial ecosystem modelling group as a contender for interfacing with GCM's in the IGBP programme. The process of parameterisation of the CENTURY model for the TSBF research sites has contributed to its current structure and validation in tropical ecosystems.

The TSBF programme is located in the tropics, where scientific knowledge, expertise and data are least available. The programme has an established network of sites which have been characterised in detail, and a core of experienced personnel (Figure 2).

The TSBF programme has designed and implemented a minimum data set for studying terrestrial ecosystem carbon and nitrogen fluxes. Site characterisation and calibration has been completed at the ten major programme centres. The documentation and testing of a standardised set of methods, parameters and units has been a key activity. These tried-and-tested techniques are disseminated in the form of a methods handbook.

One of the major potential effects of Global Change on human societies is through its impact on agriculture, and in particular in those areas of the world where the population is heavily dependent on local food production, and frequently exists close to the limits which the environment can support with currently available technologies. The TSBF is targeted at the development of sustainable tropical agriculture.

The TSBF programme has had experience of the difficulties inherent in interaction with social scientists which could help the IGBP efforts in this respect.

The spectrum of TSBF sites spans the wet and dry tropics, and the transition between them. Some of the sites are located in the marginal lands near the tropical-temperate transition. This is particularly important, since it is near the climatically-determined margins that Global Change has, and will continue to have, its greatest impact.

The possession of soil and vegetation information, such as maps and computer databases, is not by itself sufficient for the prediction and extrapolation of the consequences of Global Change at a regional scale. However, in conjunction with the understanding of dynamics

and the modelling capability provided by TSBF, they provide a rigorous foundation for large-scale prediction.

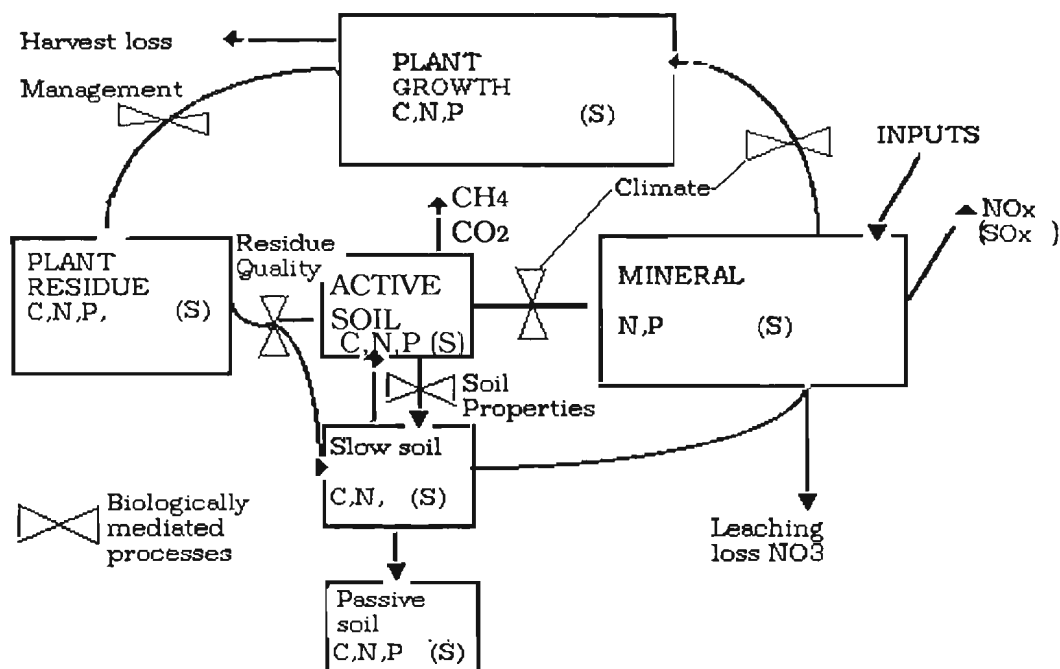


Figure 2 - Simplified TSBF conceptual model in relation to climate and fluxes of greenhouse gases

Recommendations

There is considerable communality between the objectives and research programme of the IGBP and TSBF. The potential for further interaction should be directed towards three areas:

The application of TSBF knowledge, expertise and experience in tropical soils to the development of the IGBP core programmes on land-atmosphere interactions and impact of Global Change on terrestrial ecosystems. In particular, the experience in site characterisation gained by TSBF should be applied in any calibration of terrestrial research and monitoring sites. TSBF can offer methods and technique training for this purpose.

The IGBP should initiate a detailed study of the consequences of climate change on soil biological processes, carbon and water fluxes in the tropics, using the TSBF calibrated sites and concepts, as captured in the CENTURY model. In particular, the model should be used to explore the possibility of ameliorating the CO₂ rise by sequestering carbon in tropical soils and biomass.

The IGBP should assist in incorporating studies of sulphur dynamics and denitrification into the TSBF programme.

The IGBP should consider the development of selected TSBF intensive study sites as part of their network of global research and monitoring stations.

SAVANNAS AND GLOBAL CHANGE

by O. T. Solbrig

Bussey Professor of Biology
Department of Organismic and Evolutionary Biology
Harvard University, 22 Divinity Avenue, Cambridge, Mass. USA

Current trends in degradation of tropical savannas around the world, involving changes in composition and productivity, are adversely affecting their capacity to support humans and their domesticated animals. These changes are part of a wider concern with impending global environmental changes that include such issues as ozone depletion, global warming, waste disposal, deforestation, and species extinctions. Almost one fifth of the world's population live in savannas, many of them in rural societies that depend on subsistence agriculture. Per capita food production in these communities is usually low, the result of environmental, social and economic constraints.

Compounding the effects of these changes is the dual nature of land use in many savanna regions. The most productive lands are often set aside for cash crops while the poorer lands are used for local food production or extensive cattle grazing. This, combined with the continuing rapid growth of the human population in the tropics, is placing increasing pressure on marginal lands, resulting in many cases in degraded environments, reduced productivity and low carrying capacity. There is therefore an urgent need to find alternative models of development designed to increase the satisfaction of human needs without causing a decline in long term productivity and resilience.

In order to arrest or reverse these changes we need to acquire a better understanding of savanna dynamics under prevailing and projected patterns of land use. As part of the programme «Responses of Savannas to Stress and Disturbance», of the «Decade of the Tropics», of IUBS and MAB Unesco, a workshop on «Savannas and Global Change» will take place at the Harvard Forest in Petersham, Mass., USA, 14-19 October, 1990, sponsored jointly with the IGBP (International Geosphere Biosphere Programme) of ICSU.

Dynamics of Savanna Resources and Ecosystems Processes

Any modelling effort must begin from a consideration of water and nutrient distribution. Water is the key climatic variable in savannas. Soil moisture regimes in turn are affected by (1) the total amount and seasonal distribution of annual rainfall and the proportion of this waters that enters the soil; (2) by the water holding capacity of the soil, which is largely a function of soil texture and depth; and (3) by the amount of evapotranspiration, which is related in complex ways to climate, soil texture, soil surface characteristics, and the type of vegetation at a site.

In order to understand the essential role of water it is necessary to emphasize that savannas are seasonal systems; that is, their fundamental ecological processes develop in two contrasting rythms during each annual cycle, passing from a period of intense and diversified activity to one of more or less prolonged low activity of the vegetation. Excepting in areas lying near or within the subtropics, that is, where temperature has a pronounced seasonality, there is true dormancy among grass species. Mean annual rainfall in savannas ranges from about 300 mm to 1600 mm and normally does not exceed potential evapotranspiration, though it may do so seasonally. The Amercian savannas in contrast to African and Australian ones are exclusively humid (precipitation mostly above 1000 mm), tropical ecosystems (Sarmiento and Monasterio, 1975).

This intrinsic seasonality is clearly expressed in the structural and functional changes of the

ecosystem throughout the year, with all the complexity of the successive or simultaneous development of different phenophases that characterize the evolutionary strategy adopted by each group of species of similar phenological behaviour. In a similar manner, these changes constitute an essential part of the rhythmicity shown by the productive processes (Sarmiento, 1984).

The soil-water dynamics in savannas appears highly correlated with community structure and composition along moisture gradients (Silva, 1972 and Sarmiento, 1976 a,b). The effects of variation in rainfall are compounded by differences between soils in permeability and moisture retention properties. Savanna soils vary widely in texture, structure, profile and depth, reflecting at one scale the interaction of geology, geomorphology and climate, and at another the influence of topography, relic features of past landforms, the kind and extension of vegetation cover, and animal activity (Young, 1976; Montgomery and Askew, 1983).

A distinctive feature of savannas is the coexistence of herbaceous and woody plants in a characteristic pattern where the woody species grow dispersed in a matrix of a more or less continuous layer of herbs, mostly C4 grasses. This coexistence has been hypothesized (Walter, 1971; Walker, 1985; Frost et al. 1986) to be the result of a partition of the soil substrate into two horizons: a superficial one dominated by the roots of herbaceous plants, and a deep one controlled by the roots of trees. According to this theory, the importance of trees diminishes when water table is very deep, or when soils become shallow, be it on account of a well developed lateritic hard pan (Santamaria, 1965; Santamaria & Bonazzi, 1964), or plintite layer. In areas with low precipitation, or very good drainage, trees are absent or restricted to depressions where water accumulates (Sarmiento & Monasterio, 1971) while in wet areas with poor drainage trees are found only on elevations. That is, the dynamics of water in the landscape controls the structure of the community at the first physiognomic level.

Many American and African savannas are found

on soils that are extremely poor in nutrients and which show characteristics derived from the high temperature and moisture regime. Three other factors may also have played an important differentiating role in pedogenesis: topography, parent material, and age. Most of the American savannas occupy plains of relatively flat or slightly undulating topography. The principal influences that relief has over the ecosystem is on the regulation of the drainage conditions, and ultimately over the water balance. This influence in turn translates into important consequences regarding the chemical and nutritional characteristics of the soils. The factors that produce the relief, through their action on pedogenesis, have indirectly determined the physico-chemical characteristics of the soils (Sarmiento, 1984).

A poorly known aspect is the nutrient dynamics in savannas. Medina (1982 b) and Sarmiento (1984) have summarized existing knowledge regarding nutrient partition between various compartments in American savannas and have proposed preliminary models for the nitrogen cycle and other elements. The principal conclusion of these studies is that fire represents the principal source of nutrient loss from the system, that internal cycling accounts for the greatest proportion of nutrient fluxes, and that the most important compartment is the organic matter in the soil. The deficit in nitrogen must be covered through rainfall input and free nitrogen fixation.

An accurate appraisal of tropical savanna productivity is essential for our understanding of the input of organic material into the ecosystem and the amount of material available for producers and decomposers including those in the soil. Such knowledge is also necessary to understand the potential effect of removal of vegetation as a result of fire and grazing. An accurate assessment of tropical savanna productivity is also indispensable to establish a baseline against which the effects of future changes in global CO₂ levels may be assessed.

Management of savannas is concerned principally with manipulating the two principal limiting

factors to which seasonal savannas are subjected: water and nutrients. Water shortages are seasonal: a long season without available soil water for the herbaceous vegetation with more or less shallow roots. This environmental constraint and the corresponding drought stress it induces on savanna grasses are very hard to correct, since if there are possibilities for irrigation, it cannot be justified economically to maintain a natural grassland, since irrigation offers more lucrative alternatives: improved grasslands or artificial crops.

Nutrient availability can however be modified combining low levels of fertilization combined with simple and not too expensive management techniques, such as the regulation of fire and grazing, that can improve the nutrient status of the soil through an acceleration of natural nutrient cycles, an increase in the nutrient stock, and a reduction of nutrient losses.

Seasonal savannas can be managed at least at three contrasting levels of technology and production. The first is that of the traditional extensive livestock grazing that does not employ inputs of any kind (fertilizers, pesticides, energy, machinery, improved varieties, etc.). This is the most primitive way of utilizing the savanna, the least costly, and the least productive. The other extreme is represented by the replacement of savanna grasses by introduced grasses (or other crops). Without irrigation only one annual crop (corn, sorghum, cotton, etc.) can be obtained in the seasonal savanna, and only through the use of species that are resistant to drought (such as *Panicum maximum* or *Hyparrhenia rufa*) and not too demanding regarding nutrients can a permanent artificial grassland be maintained. In both cases the investment is relatively high, as is the resultant primary and secondary productivity. Between these two extremes we have systems of medium intensity management such as the one we propose to study, that involve simple technologies (burning, differential grazing), low levels of inputs (fertilization, some energy), that lead to a notable increase of productivity in comparison with the extensive system.

Our basic working hypothesis is then as follows:

Wet, oligotrophic, seasonal savannas are characterised by climatic seasonality (Sarmiento, 1984), and the rhythm of the wet and dry seasons regulates the rhythm of growth and reproduction of the herbaceous and woody vegetation. But wet and dry seasons are not sharply defined, internally homogeneous, intervals of time (not even in terms of rainfall), but are rather yearly oscillations in PAM (Plant Available Moisture) and PAN (Plant available Nutrients) that in turn regulate the growth rate of the vegetation, that then will affect the light regime within the canopy, and the amount of standing live and dead biomass, that in turn affects the probability of fire. The onset of the rainy season is characterized by a period of increasing frequency of rainfall, that slowly saturates the upper profiles of the soil. Consequently, any species that is active early in the season will be faced with occasional water stresses. On the other hand, the ashes rich in nutrients resulting from the fires that have taken place during the dry season, as well as relatively large dead underground biomass, mean a relatively good soil nutrient environment. Because the PAM and PAN status is more favorable in the under layers of the soil, early growing species are expected to have primarily superficial roots. Furthermore, at the beginning of the wet season, following the fires the ground is very open and the light environment very favorable. Consequently we expect early species to be of low stature, and globose, i.e. of a typical bunch grass shape. By blooming prematurely, seeds of early species can germinate immediately and successful seedlings attain a sufficiently large aerial and underground biomass by the end of the growing season to withstand the ensuing drought.

As the season progresses, the PAM in the soil becomes more favorable, but the PAN less so, as more nutrients are removed by growing vegetation. As more biomass accumulates, the light environment within the canopy also becomes less favorable. Roots of later growing species will therefore grow deeper into the soil profile, and aerial biomass higher. Finally toward the end of the growing season, PAM again deteriorates, but the accumulation of both the aerial and underground dead biomass means that PAN either

stabilizes or improves. Light environment within the canopy is now very poor as the canopy has attained its maximum size. We expect late species to be more shade tolerant, and to rely extensively on runners as a means of vegetative propagation during the late growing season. If they reproduce by seeds, these have dormancy to withstand the dry season, since any seedling that germinates late in the season will not attain the minimum size to withstand the dry season before the end of the rainy period.

In other words, our basic hypothesis is that the changing status of PAM, PAN, and light, circumscribe different niche spaces that are utilized by species with different morphologies, physiologies, and life histories. The objective of the proposed modelling effort is to test this hypothesis rigorously, by modelling aspects of the nutrient, water, and carbon economy of representative species of each of the major phenological types of savanna grasses and trees.

Questions

We are basically dealing with the general question of what are the response mechanisms of savanna communities to stress and disturbance. Our hypothesis is that mechanisms are determined to a large extent by the dynamics of communities and the physiology and life history characteristics of component species. Therefore, we would like to dissect this general question into a number of more specific questions and apply them to each group of species.

(a) What is the effect of disturbance upon recruitment? To what extent does disturbance affect annual seed crop, germination, seedling survivorship, and individual reproduction? What physiological and life history mechanisms are involved in these effects?

(b) What is the effect of disturbance upon plant survival? In particular, how does individual plant size affect survivorship?

(c) If an individual of a given species gives up space, either by outright mortality, or by reduction of its biomass, What type of species takes over?

Is the space taken over by a species with a different life-history? Is the space taken over by species already in the community, or by outside invaders?

(d) Is the space opened by a disturbance occupied by seedlings or by runners of nearest neighbor species or by specialized colonizers? What determines whether sexual or asexual propagules prevail?

(e) Given the heterogeneity of savannas and the fact that fires are spatially irregular, what is the role of spatial variations in fires on maintaining high diversity in these communities? Is there anything like the seed effect in the sense of Wittaker and Levin? What are the implications of this effect on the management of savannas through fires?

(f) How do coexisting grass species with different life histories, form and phenology, react to experimental changes in the prevailing regimes of fire, grazing, water, and nutrient supply?

For further information on the workshop contact: Professor Otto T. Solbrig; Department of Organismic and Evolutionary Biology; Harvard University; 22 Divinity Ave.; Cambridge Mass. 02138, USA. Tel (617) 495-4302; or Dr. Talal Younés, IUBS, 51 Bld de Montmorency, 75016 Paris, France. Tel (1) 45.25.00.09, Fax (1) 42.88.94.31

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IUBS FINANCIAL STATEMENT FOR THE YEAR 1989

STATEMENT 1. Balance sheet at December 31, 1989 (Expressed in US\$)

ASSETS: *Cash and Banks*

Crédit Lyonnais, Paris

in US\$	135.169	
in FF	(16.930)	
in US\$		
(Deposit Account)	200.000	318.239
Merrill Lynch, New York (in US\$)	459.919	459.919

Other Assets

Other receivables	23.000	23.000
		801.158

LESS: *Liabilities*

Sundry creditors	16.667	16.667
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Excess of assets over liabilities **784.491**

Represente by accumulated fund **784.491**

STATEMENT 2. Income and Expenditure for the year ended December 31, 1989 (Expressed in US\$)

1. INCOME

ICSU Subventions	15.660
Special Subventions from International Organisations	435.022
Contributions from national members	211.386
Interests and dividends	44.165
Gain on Exchange	790
Other Income	30.222

2. EXPENDITURE

Business Meetings

Executive Committee Meetings	21.156	
Officers meetings and travels	3.021	24.177

Publications

	13.526	13.526
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Scientific Programmes and Activities

Grants to IUBS Scientific Programmes	252.791	
Representation at scientific meetings	6.838	
Contribution to other Organisations	6.056	
Scientific Activities of IUBS Scientific Members	20.417	286.102

Administrative Expenses

Salaries	62.039	
Related charges	54.680	
General office expenses	45.990	162.709

Other

Bank charges & loss over exchange	5.025	
Audit fees	4.136	9.136

TOTAL EXPENDITURE **495.675**

TOTAL INCOME **737.245**

Excess/Loss of Income over Expenditure **241.570**

Accumulated balance carried forward **784.491**

PUBLICATIONS REVIEW

BIOTIC DIVERSITY AND GERMPLASM PRESERVATION, GLOBAL IMPERATIVES

Edited by L. Knutson and A. K. Stoner. Published by Kluwer Academic Publishers, 1989, (530 pages).

This volume consists of the invited papers at a symposium held May 9-11, 1988, at the Beltsville Agricultural Research Center, Beltsville, MD, USA. It includes 5 sections dealing with vital concerns of biotic diversity and germplasm preservation from diverse perspectives, especially basic research and germplasm status, frontiers in germplasm utilization, and germplasm collection and data management.

This book provides concrete recommendations for action, and call attention to areas of research that must be pursued with intensity.

CONSERVING THE WORLD'S BIOLOGICAL DIVERSITY

Edited by J.A. McNeely, K.R. Miller, W.V. Reid, R.A. Mittermeir & T.B. Werner. Co-published by the World Bank, WRI, IUCN, Conservation International & WWF, 1990, (174 pages).

This book explains what biological diversity is and why it is important to the future of all countries. The authors describe how biological diversity can contribute to development and be integrated into policies for resource use. Appendixes include the World Charter for Nature, a summary of international legislation supporting biological diversity conservation, the Bali Action Plan on protected areas, and a description of the World Bank's wildlands policy.

AMAZONIAN RAIN FOREST

Edited by C.F. Jordan. Published by Unesco- & Parthenon Publishing, 1989, (176 pages).

This book addresses the role and importance of nutrients in a tropical rain forest, and in slash-and-burn agriculture derived from rain forest. The experimental results are specific to a study area at San Carlos de Rio Negro in the Amazon Territory of Venezuela, but the Study site is compared with forests in other tropical regions to indicate the extent to which the results can be generalized.

THE CONTROL OF EUTROPHICATION OF LAKES AND RESERVOIRS

Edited by S.-O. Ryding and W. Rast, Published by Unesco- & Parthenon Publishing, 1989, (314 pages).

This volume of the Unesco MAB Series summarizes research in many different countries on the practical control of eutrophication. It has been written by experts from all over the world, but it is intended for those who have to manage lakes and reservoirs and for the interested non-scientist who would like to understand eutrophication and what can be done to combat its effects.

The book should have a wide appeal to all those who are concerned with environmental issues. It deals with the effects of agriculture and forestry, as well as with aquaculture and fisheries enhancement. It also presents the minimum requirements for the monitoring of lakes and reservoirs.

EXPLOITING THE TROPICAL RAIN FOREST

Edited by D. Lamb, Published by Unesco- & Parthenon Publishing, 1990, (229 pages).

This book describes a large pulpwood logging operation in the lowland rainforests of Papua New Guinea. It examines the events leading up to the decision to commence pulpwood logging and some of the consequences the projects has had on the forests and people of Papua New Guinea.

DROUGHT RESISTANCE IN CEREALS

Edited by F.G. W. Baker. Published by C.A.B. International, on behalf of ICSU Press, 1989 (222 pages)

This book includes papers based on a symposium held in Cairo, Egypt, in Nov., 1988, organised by CASAFA (ICSU) and the Australian Council of International Agricultural Research. Topics covered include limits to production in drought conditions, breeding for drought resistance and evaluation of dehydration avoidance and water efficiency traits in cereals. Focus is on four major cereal crops of rice, wheat, maize and sorghum.

TREES OF NIGERIA

By R. W. J. Keay. Published by Oxford Science Publications (Clarendon Press Oxford), 1989 (476 pages)

This book is a revised version (in one volume) of 'Nigerian Trees' (1960, 1964) by R.W.J. Keay, C.F.A. Onochie and D.P. Stanfield. This volume fills the need for a textbook on the Nigerian flora providing information on Nigerian native plants, their identification, their scientific and vernacular names, description, distribution and known uses.

SUBSISTENCE AGRICULTURE IN AFRICA: PROBLEMS AND PROSPECTS

Edited by B. Amoako-Atta. Published by the ICSU/Unesco African Biosciences Network (ABN), 1987 (271 pages).

This book comprises the presentations made at the 6th African Association of Insect Scientists (AAIS) conference held in Monrovia, Liberia, from 24 to 26 March, 1986. It includes a review of the status of subsistence agriculture in Africa; an overview of technical crisis and socio-economic impacts on subsistence agriculture; and relevance of improved planting materials, low energy input mechanisation, and integrated pest management in subsistence agriculture in Africa.

THE ROLE OF BIOLOGY IN RESOLVING THE FOOD CRISIS IN AFRICA

Compiled by A.T. Bâ & M. Ndoye.

This document reflects the main conclusions and recommendations of the International Symposium on the Role of Biology in Resolving the Food Crisis in Africa, organised in July, 1989 in Yamoussoukro, Côte d'Ivoire. This document will be followed by a second one: the symposium proceedings which will contain all communications and papers presented.

(For more information please contact Dr. Bâ, ABN Coordinator, Unesco-BREDA, BP 3511, Dakar, Sénégal).

MANAGEMENT OF TROPICAL RAINFORESTS

Edited by E.F. Bruenig & J. Pöker. Published by Nomos Verlagsgesellschaft- Baden Baden, 1989 (112 pages)

This is the proceedings of an international symposium "Management of Tropical Rainforests: Utopia or Chance of Survival?" held at the Food and Agriculture Development Centre of the German Foundation for International Development (DSE) in Feldafing, FRG, 15-21 January, 1989. It is based on the case studies and the compiled experiences of experts from relevant disciplines concerned with tropical rainforest management, its utilisation, and with the people living near, and depending upon them.

INVENTORY AND EVALUATION OF TROPICAL FOREST LAND: Guidelines for a Common Methodology

By L. Tauber, E.M.A. Smaling, W. Andriess & R.T.A. Hakkeling. Published by Tropenbos Foundation, 1989 (170 pages).

This issue 4 of the Tropenbos Technical Series, provides guidelines for comparative studies on tropical ecosystems, dealing with approaches to the inventory and evaluation of tropical forest lands. The study sets out the ingredients of a recommended methodology, taking up such aspects as basic concepts, environmental factors, survey procedures, and report and map preparation.

MAB DIGEST SERIES

The Unesco-MAB Digest Series was launched by Unesco in 1989. Three main types of publication are envisaged. First are distillations of the substantive findings of the Unesco-MAB Programme activities, second are overviews of recent, ongoing and planned activities within MAB in particular subject or problems areas, and third are proposals for new research activities.

Eutrophication Management Framework for the Policy-Maker

By W. Rast, M. Holland & S.-O. Ryding, 1989 (83 pages)

The purpose of this digest is to highlight those aspects of eutrophication control which are of primary importance to the policy-maker or 'decision-maker' (e.g. executive, legislator, senior administrator, director, etc.). More especially, the aim is to provide:

- Quantitative tools for assessing the state of eutrophication of lakes and reservoirs;
- A framework for developing cost-effective eutrophication management strategies;
- A basis upon which strategies can be tailored for each specific case; and
- Specific technical guidance and case studies regarding the effective management of eutrophication.

Contributing to Sustained Resource Use in the Humid and Sub-humid Tropics: Some Research Approaches and Insights

By M. Hadley & K. Schreckenberg, 1989 (59 pages)

This digest consists of an overview of recent and ongoing activities within the framework of MAB relating to the ecology of humid and sub-humid tropical ecosystems, principally forests and savannas.

Role of Land/Inland Water Ecotones in Landscape Management and Restoration: Proposals for Collaborative Research

Edited by R. Naiman, H. Décamps & F. Fournier, 1989 (93 pages)

This digest presents a research proposal on management, restoration and creation of ecotones, role of ecotones in monitoring changes or stability of landscape patches, role of ecotones in understanding landscape patterns and biological diversity and in monitoring global change, and nutrient cycling in ecotones.