NUTRIENT CYCLING

IN

INDIGENOUS FOREST ECOSYSTEMS

Papers presented at a Symposium organized jointly by W.A. Forests Department and CSIRO Division of Land Resources Management.

Institute of Forest Research and Protection, Hayman Rd., Como, W.A.

May 9th and 10th, 1977.

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PREFACE

Present and potential problems associated with the use of forested lands for water catchments, mining operations, pine afforestation and woodchipping are causes for concern in view of limited resources. The aim of this symposium was to review our knowledge of the functioning of Australian forest ecosystems, particularly in relation to nutrient cycling, and to identify the data and processes most relevant to practical problems and the formulation of management options for forested lands.

The organizing committee wishes to express its appreciation to Mr B.J. Beggs (Conservator of Forests) and officers of the Forests Department, Western Australia, for provision of conference facilities and for their co-operation in arranging field excursions to the Donnybrook Sunklands, the Karri Forest near Pemberton, and the Northern Jarrah Forest near Dwellingup.

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CONTENTS

INTRODUCTION TO THE ECOSYSTEM CONCEPT

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It is useful to start with definitions of ecological systems or ecosystems and the following are found in recent texts:

> *"Any unit including all of the organisms (i.e., the 'community') in a given area interacting with physical environment so that a flow of energy leads to a clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and non-living parts) within the system."*
>
> Odum (1972)

> *"The complex self-sustaining natural systems of which living organisms are part. An ecosystem includes not only organisms but also the several non-living components of the environment within which the organisms are found. Most importantly, perhaps, it includes all the interactions that bind the living and non-living components together into a stable system. These interactions include those between organisms and the physical environment, and the interactions of various phases of the non-living environment which mold its own change."*
>
> Clapham (1973)

These two definitions are about similar in their expression of the ecosystem concept. The study of the ecosystem becomes the elucidation of extremely complex processes and their interactions, and the way they contribute to the maintenance of stability within a unit of vegetation that is self-sustaining in the long term. While the "ecosystem concept" may be defined to most peoples' satisfaction, there may be differences in the approach to the study of the ecosystem. Odum (1972) quotes Hutchinson (1964) in defining two such approaches:

(I) The holological or holistic approach in which the whole ecosystem is treated as a "black box" (i.e., a unit whose function may be evaluated without specifying the internal contents) with emphasis on inputs and outputs. A watershed study of the Hubbard Brook type would be in this category.

(II) The merological approach in which "we discourse on parts of the system and try to build up the whole from them". Under this approach there must be a mechanism for synthesizing the observations and experiments from the parts of the ecosystem into a single context so that the unity and dynamic nature of the ecosystem become clear.

Whatever approach is used, ecosystem research may provide much quantitative data on dynamic processes within a forest community. However, these data alone may not provide a satisfying interpretation of the processes measured, and the relationships between structure and function within that community. Any one community is but part of a whole complex of communities aligned along a series of environmental gradients. Thus, to be effective ecosystem research should not be divorced from that aimed at providing a broader appreciation of the way species composition, stand structure and dynamic processes vary with environmental factors and with time. If this is done, the ecosystem researcher is more likely to ask the most relevant questions of his ecosystem and to be more effective in appreciating the likely significance of the information he obtains.

This introduction to the ecosystem concept will be in two parts, the first illustrating the dynamic processes within a self sustaining ecosystem, and the second focussing on aspects of the ecosystem in a broader ecological perspective.

DYNAMICS OF ECOSYSTEMS

Dynamic processes within ecosystems can be described in terms of the fixation of light energy, the flow of this energy through the system, the cycling of nutrients within the system, and inputs to and outputs from the system. Because these may be dealt with in some detail in other contributions to this symposium, they will be examined here only in outline.

Fixation of Light Energy: Gross and Net Primary Production

Energy for growth is supplied by solar energy captured by green plants through the power of photosynthesis. The conversion of solar to chemical energy is not a highly efficient process; photosynthesis utilizes only those wave lengths of light absorbed by chlorophyll, the process of photosynthesis operates theoretically at an efficiency of about 20 percent, and there is a limit to the amount of chlorophyll which can be effectively distributed over a surface.

Some part of this fixed energy (gross primary production) is immediately used in the catabolic processes of the plant, leading to loss of energy from the plant. This is conventionally termed respiration in ecological literature. The net rate of storage of products of photosynthesis is termed net productivity, and the total amount of storage over the growing season, including that dying and eaten during this period, is the net primary production.

Estimates of gross and net primary production for world ecosystems show that forests use a considerably greater part of gross photosynthesis for maintenance than other ecosystems (Golley 1972). For tropical and temperate region forests, net primary production is only about 30 percent of gross production, while for grassland and tropical savannas, net production represents 60 percent of the gross production.

The net primary production of forest is dependent on environmental factors; it will be strongly influenced by environmental factors such as temperature, moisture, and available nutrients. While maximum daily rates of production may be similar in all types of vegetation, annual rates, reflecting differences in environment, vary greatly. In his summary of primary production in various ecosystem types Golley (1972) shows a net production of 2000 $g/m^2/yr$ for tropical forest, 1300 $g/m^2/yr$ for temperate forest, and 800 $g/m^2/yr$ for boreal forest. These all surpass the net productions for other communities including tropical savanna (700 $g/m^2/yr$) grassland (300 $g/m^2/yr$) and cultivated land (650 $g/m^2/yr$). These data are stated to be "rounded median estimates for all conditions within a specified ecosystem type".

Energy Flow

The energy stored in net primary production by green plants is available to the array of species populations in the ecosystem which are unable to derive energy from other sources. Thus from the energy or trophic standpoint an ecosystem has two components,

(I) an autotrophic component in which fixation of light energy, use of simple organic substances and build up of complex substances predominate, and

(II) an heterotrophic component in which utilization, rearrangement and decomposition of complex substances predominate. The heterotrophs may be subdivided into, (a) phagotrophs or macro-consumers; organisms (largely animals) which are living plant feeders (herbivores) or which ingest other organisms (carnivores) or particulate organic matter, and (b) saprotrophs or micro-consumers; chiefly bacteria, fungi and some protozoa that breakdown complex compounds, absorb some of the decomposition products, and release inorganic substances usable by the autotrophs together with organic residues which may provide energy sources, or which may be inhibitory, stimulatory or regulatory to other biotic components of the ecosystem.

The proportion of the net primary production of forest naturally consumed by living plant feeders (herbivores) has been estimated to range from 1.5 to 40 percent. This is a very wide variation, and would be a function of the proportion of net production oriented to stems, branches, etc., the relative ability of vegetation to resist grazing, and the characteristics of the herbivores themselves, for example the existence of grazing in tree tops.

The energy flowing to the decomposer organisms is used in the work of breaking-down the complicated biological structure built through the production process. The extent and amount of materials released to the substrate and available for uptake vary with the environment and the refractiveness of plant species populations within the ecosystem. The rate of energy flow to decomposer organisms will also influence microbial populations and processes, and through this the balance between simulatory and antagonistic factors affecting plant growth.

Energy also flows to the decomposer portion of the ecosystem from the herbivore food web as organisms die and are decomposed, and from excretory wastes and secretions. Not all organic material dying in systems may be decomposed. Dead organic matter may be moved by wind and water with the result that dependent ecosystems such as some streams and rivers, obtain most of their energy as import of organic material.

Available energy declines with each step in the flow process or food chain. Thus a system can support more herbivores than carnivores. The transfer of energy between herbivores, carnivores and decomposers is poorly understood in detail. Golley (1972) suggests that if we were to organise the populations into abstract categories such as herbivores, carnivores, top carnivores, etc., then probably 10 percent or less of the energy is transferred to the next level.

Nutrient Cycling, Inputs and Losses

Within an ecosystem,cations, anions and molecules are continually withdrawn from the abiotic portion, circulated through the biotic portion, and returned in one form or another to the abiotic reservoir. Just what constitutes the abiotic reservoir may vary with species, and will be considered further later in the paper.

Within the ecosystem the nutrients may be thought of as occurring in any one of four basic compartments (Likens and Bormann 1972).

(i) the atmosphere, including all elements in gaseous form both above and below ground,
(ii) living and dead organic matter,
(iii) available nutrients, i.e. ions absorbed in the clay-humus complex or dissolved in the soil solution; and
(iv) primary and secondary minerals comprising the inorganic soil and rock portions of the ecosystem.

The biogeochemical flux of elements involves an exchange between the various components of the ecosystem. Available nutrients and gaseous nutrients may be taken up and assimilated by the vegetation and microorganisms, some passed on to heterotrophic consumers and then made available again through respiration, biological decomposition, and/or leaching from living and dead organic matter. Insoluble primary and secondary minerals may be converted to soluble available nutrients through the general process of weathering; and soluble nutrients may be redeposited as secondary minerals.

In studying the nutrient cycle, information may be sought on the distribution of all available nutrients within the ecosystem (the soil, components of the living biomass and the dead biomass), the rate of flux between the components, and the way these parameters will vary with stage of stand development. Normally the greater the flux rate the higher the productivity is likely to be, or the smaller the amount of nutrient needed to be withdrawn from the abiotic reservoir.

Nutrients not only circulate within the ecosystem but there may also be continuing flow in and out of the system in a number of ways. Meterologic inputs and outputs consist of nutrients as wind-borne particulate matter, dissolved substances in rain and snow, or gases; geologic nutrient flux includes dissolved and particulate matter transported by surface and subsurface drainage and the mass movement of colloidal materials; and biological flux results when nutrients gathered by animals in one ecosystem are deposited in another.

DIVERSITY IN SPACE AND TIME

In this section, ecosystem studies will be considered in a broader ecological perspective. It will be highly desirable to design any ecosystem study against a background appreciation of the selection pressures which may have played a role in the evolution of species, communities and processes, and community relationships within vegetation and environmental gradients. This may give some lead to the more important environmental factors influencing a particular community's composition, structure and productivity, and the dynamic processes most likely to contribute to a realistic interpretation of relations between structure and function within that community. It will also be highly desirable to appreciate the position of the community in time, that is the successional status of the community and its development towards a steady state condition. In elaborating upon these themes, we can usefully focus upon species - environmental relationships and successional concepts within the eucalypt forest.

Diversity in Space; the Evolution of Pattern in Vegetation

Eucalyptus is unique in world vegetation in the way it dominates all but the most arid parts of the continent, and even here it is widely distributed within the more favourable environmental niches. The reasons for this must be sought in the evolutionary history of the Australian flora and any unusual environmental stresses to which the flora has been exposed. It is reasonable to suggest that *Eucalyptus* may represent a remarkable evolutionary response to strong and widespread selection pressures on the flora, a response which other taxa were unable to make, at least to the same degree.

Concepts and consequences of continental drift now seem to provide a fairly stable basis for understanding the changes which have taken place in the Australian environment (Walker 1972). It is envisaged that the continent began to drift northwards after parting from Antarctica about 45 million years ago, that is, during the early to mid Tertiary. It carried with it a vegetation which is presumed to have been similar to cool temperature rainforest of today, and which was subjected to powerful selection pressures as environmental factors changed. Just what were these environmental changes?

In most discussions of the evolutionary development of the Australian flora, emphasis is almost invariably placed on the selection pressure of changing climate. However, as long ago as 1913 Andrews suggested *Eucalyptus* was primarily a response of some ancestral Myrtaceous stock to poor soils and only secondarily after a long lapse to a drying climate. Little attention was directed to this theme until Beadle (1966) developed the thesis that early evolutionary directions within the Australian flora were established by soil rather than by climatic change. Soil changes include the widespread erosion leading to the peneplanation of the continent by the mid-Tertiary, and the subsequent recurrent and widespread phases of soil laterization. Both processes would have occurred under a tropical climate and at least, seasonably heavy rainfall regimes.

If this concept is valid, it should be possible to identify in the xeromorphic and sclerophyllous vegetation, characteristics which enhance survival and growth on low nutrient, and particularly, phosphorus deficient soils. While adaptation of woody shrub and herb vegetation to low nutrient and dry sites may not be unusual, the growth of large-boled, long-lived evergreen trees under both low nutrient and xeric conditions may be unique in world vegetation. The following parameters may contribute to these adaptations:

(I) Relative to comparable forests in the northern hemisphere the eucalypt forest gets by on a remarkably small amount of phosphorus within the biomass (Attiwill 1962). Attiwill suggests the eucalypt forest is quite unique among the broad-leaved evergreen forests of the world in the way it uses and conserves phosphorus.

(II) McColl (1969) and McColl and Humphreys (1967) suggest there are gradients in the ability of eucalypt species to take up and utilize phosphorus from "old" soils on the south coast of NSW, that is, soils with low total phosphorus, low calcium and high aluminium. Mulette et al. (1974) demonstrate the quite remarkable ability of one eucalypt (*E. corymbosa*) to grow well on only 1ppm of insoluble aluminium phosphate in a nutrient medium.

(III) Despite its outstanding productivity on coastal dune sands with very low phosphorus concentrations, *Pinus radiata* has a record of failure (without nutrient amendment) on many acid clay and lateritic soils in Australia. These same soils may have carried moderately productive eucalypt forests of commercial quality.

(IV) Elements of the original flora other than *Eucalyptus* may also have evolved specialised abilities to handle low phosphorus soils. An example is the growth of *Araucaria* species (normally a component of rainforest), without phosphorus fertilization, on soils where *Pinus* spp. have responded markedly to phosphorus addition (Richards and Bevege 1967).

(V) Polyphenolic compounds of leaves of some eucalypts may play important roles in mobilizing phosphorus present in iron complexes (Hingston 1963). This may be a more pronounced attribute of species growing on poor sites (Ellis 1967).

(VI) There has been little thought, let alone research, directed to the uniquely dynamic crown of the mature eucalypt. Continuing branch extension - dieback - epicormic replacement may be the basic mechanism for highly efficient use and conservation of phosphorus and other nutrients within the limited biomass "pool", leading to the characteristic development of large-boled trees even on very poor sites.

(VII) Finally, the role of the lignotuber in the regeneration of harsh environment sites is well recognized, but again, little thought has been given the selection pressures which created it and its function in the ecosystem. Under harsh environmental conditions, the tree seedling may need a root:shoot ratio of great proportions to permit it to "trigger" very rapid growth through the sapling and into the pole stage, and to form the ultimate tree bole. The lignotuber may in fact be the basic mechanism for achieving this under otherwise limiting conditions.

The existing pattern of distribution of eucalypts within the different subgeneric groups in southern Australia suggests it was *Monocalyptus* and *Corymbia* which bore the brunt of evolutionary adaption to declining fertility, particularly that involving immobilization of phosphorus.

Soil fertility changes have not of course provided the only selection pressure on *Eucalyptus*. Declining fertility would have been closely followed by increasing aridity. It is probable many of the adaptations for tree growth on low fertility soils would have contributed to survival and continuing evolutionary change as rainfall declined and temperatures increased. Undoubtedly fire frequency increased with the climatic change. This would have been yet another stress superimposed upon the evolutionary directions already well established within *Eucalyptus*, and acting to further enhance its adaption to a wide range of harsh environments.

Thus in any studies of the eucalypt ecosystem we might be conscious of the complex evolutionary background of Eucalyptus and the questions which might flow from this about tree and stand processes contributing to site adaptation, and the sensitivity of species and species associations to variations in environmental factors.

Diversity in Time

In looking at diversity in time in the eucalypt forest we might be concerned with the growth, interaction and death of individual organisms as they pass through their growth phases or life cycles, and the interrelationships between organisms at different stages of stand development. Before tackling this, we might ask whether the assemblage of species in a forest stand has evolved as a community, with the possibility of complex relationships between components, or more simply represents species which can compete successfully for space within a particular habitat. Goodall pursues this question.

> *"What part has evolution played in the development of the mixed community as we see it today - To what extent will the species of the community have undergone a process of mutual evolution - On* a priori *grounds we would expect mutual evolution to have been involved in the development of a community complex in space and time, even though the prospect for demonstrating it seems negligible."*
>
> Goodall (1966)

Despite general theoretical acceptance of the concept embodied in the above quotation, there has been little evaluation of the eucalypt forest in these terms, i.e., the possible relationships between understorey and tree components in the functioning of the forest ecosystem, and the way these relationships change with time. Indeed the literature seems to be far more concerned with the negative values of the lower storey of the eucalypt forest, particularly the way it can be a barrier to tree regeneration. Perhaps in many cases we emphasise the negative values of understorey because particularly in wet sclerophyll forest we are not seeing "normal" stages in development of ecosystems. Rather, we may be seeing ecosystems in which overwood and understorey components are distinctively out of phase with each other. Thus in studying the eucalypt ecosystem we might seek to establish a rationale for the mutual evolution of overwood and understorey in the system, and the "normal" successional development of a community complex in space and time.

Eucalypt regeneration commonly develops following a perturbation such as fire or some mechanical disturbance of the surface soil. This dependence is particularly notable in tall open or wet sclerophyll forest. However, the eucalypt is not the only component of the forest which may be disturbance dependent. Much of the understorey in both tall open and open forest will also regenerate prolifically after a hot fire, both vegetatively, and from seed which accumulates in soil and germinates in response to heat. Following the fire, the diversity, abundance and vigor of the understorey may decline with time, that is, where there is adequate overwood competition. In the absence of further disturbance there may be only limited replacement by other species, so that "succession" may move towards a more open forest, and in some situations a grassy forest floor. Park (1975) postulates this pattern for *E. pauciflora* and *E. delegatensis* forests, with rapid breakdown of the understorey taking place some 40 years after the fire. More detailed study of understorey dynamics is needed to support this, and to determine the extent to which it may generally apply in the eucalypt forests. It probably does not apply, for example, where an understorey rainforest tree stratum would have an extended life span (e.g. *Nothofagus* in Tasmania).

In ecosystem research, quantifying components and processes will provide valuable information on important basic characteristics of the ecosystem. However, the condition and the structure of the overwood and the composition and density of the understorey may reflect unusual or atypical sequences of past events, for example, high fire frequency. It may not be possible to determine just what these events were, let alone quantify their effects on the ecosystem components or processes. Thus in developing ecosystem studies the research net must be cast very wide. We might start by accepting fire as a factor which has greatly influenced nearly all the eucalypt forests, and might profitably be used in continuing ecosystem management. However, fire should be seen as influencing the whole ecosystem, not simply as a mechanism for obtaining regeneration. In the absence of fire, and with the long-term incorporation of large amounts of low N-high C organic matter (including up to 50% woody material), changes in soil organisms, soil biological processes and rates of nutrient mineralization may adversely affect the potential for plant growth (e.g. Florence and Crocker 1962). A hot fire may provide some immediate amelioration of the soil conditions, but it may be the concurrent regeneration and growth of *Acacia* and other legumes, *Casuarina*, and a wide range of other species which help ameliorate soil conditions for the longer term. But how frequent should fire be? - Obviously some balance is necessary between too frequent fire events which will deflect "normal" succession and life cycles too far, and too infrequent fire events which will lead to depression of productivity through biological, structural and species changes. It should be one role of ecosystem research to try to determine what that balance might be, and how the optimum frequency and intensity of fire might vary with stand and site conditions.

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BIOMASS AND NUTRIENT DISTRIBUTION IN INDIGENOUS FOREST ECOSYSTEMS.

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SUMMARY

Over sixty biomass and nutrient cycling studies, published and unpublished, covering a wide range of native woody vegetation formations are reviewed synoptically in the following broad categories: rain forest, sclerophyll forest and semi-arid to arid woodlands and shrublands. Levels of productivity and nutrient content are listed where data are available. Most studies are fragmentary or concentrate on litter fall and accumulation, as the gate through which the externally-cycled nutrients must pass. Less than ten percent of studies examined root systems and about the same proportion studied the soil subsystem.

Some of the conceptual problems associated with ecosystem studies are discussed; the need to investigate spatial variation in such parameters as litter fall and breakdown and soil nutrients caused by non-random distribution of individuals in the vegetation and the influence of species mixtures is highlighted. These aspects not only raise formidable sampling problems but also have as yet little-defined influence on ecosystem function. Ideally, studies aimed at determining average values for ecosystem pool sizes and fluxes should be complemented by investigation of spatial heterogeneity in order to strengthen the conclusions drawn. Mensurational and statistical aspects of analysis of mixed species, all-aged native vegetation are fields of research requiring further study if maximum effectiveness is to be gained from the considerable physical inputs required in this type of research.

INTRODUCTION

The forest ecosystems of Australia occur under an extremely wide range of edaphic - climatic conditions, resulting in diverse formations varying from tropical lowland rainforest to temperate rainforest, from wet sclerophyll forest to semi-arid mulga woodland. It is not surprising therefore, given the comparatively recent upsurge in interest in ecosystem dynamics, that studies of biomass and nutrient cycling have to date been restricted to comparatively few forest formations. These have generally been those with some forestry value, or which may have been subject to more indirect economic pressures such as surface-mining or agro-pastoral development.

Most studies have tended to concentrate on accumulation, decomposition and mineral composition of litter (e.g. Hatch 1955); often such studies were made in association with wider programmes concerned with, for example, controlled burning (e.g. Peet 1971). Concentration on litter, for whatever reason (not the least being the relative ease of measuring this compartment), is however a valid starting point in ecosystem analysis. As Olson (1963) points out, "a substantial fraction of the energy and carbon annually fixed in forests is contributed to the forest floor as litter - and because litter fall is generally related to the quantity of photosynthetic machinery in the system, it is an interesting index of ecosystem productivity." e.g. under Australian conditions, highly productive rainforests may have an annual litter fall of 10 t/ha/an (Brasell *et al.* 1977), whereas poorly productive saltbush shrubland can be as low as 1 kg/ha/an (Charley 1972). Charley (1972) extends Olson's rationale, and builds a strong case of concentrating on the dynamics of litter fall and mineralization as the key to overall ecosystem productivity. He argues that "an understanding of mineral regulation (of ecosystem production) is more likely to emerge from enquiry into activity patterns in the physiological milieu of the soil than it will from even the most exhaustive analysis of the above ground compartment of the system", i.e. the standing crop. Cooper's (1969) experience with ecosystem modelling lends support to this proposition when he says "systems are far more sensitive to changes in the organizational structure of relations between components than to changes in the values of the components themselves."

Charley however does not negate the value of determining biomass and mineral distribution in the ecosystem; although these parameters give us but a cameo at a particular point in time in the continual development of a system (see Florence, this symposium), and neither offer any information on the functional role of nutrients in the system, detailed analysis of the structure of various pools will give indications of the organization of the system; hence size and distribution of nutrient pools provide a datum for the study of cycling processes (see also: Richards and Charley, this symposium; Loneragan, this symposium).

Systems analysis offers one, and probably the most logical way out of this apparent impasse between the "quantitative" and "functional" approaches to ecosystem studies (see Reichle 1971). The system can be divided into any number of compartments or pools depending on the complexity desired. Pool sizes and energy and nutrient fluxes between them can be measured, the rates of change of pool size being represented by a series of differential equations. Jordan and Kline (1972), in their study of Puerto Rican rainforests, used annual average pool sizes and nutrient fluxes so that their equations could take linear form, thus simplifying the computations required. One outcome of the systems approach, at least as far as tropical rainforest is concerned, is the interesting and valuable finding from a management viewpoint, that large storage pools such as the woody component of trees, buffer the nutrient cycle against perturbations in the physical environment, i.e. "the presence of large components in an ecosystem may generally diminish the effects of large variations in the physical environment or of irregularities in the cycles and flows themselves. The converse of this principle may also be true. Lack of large compartments in an ecosystem may result in high sensitivity of the system to changes and variations" (Jordan and Kline 1972). We might for example consider the basic stability and buffering capacity of tropical rainforest in comparison with the lower buffering capacity of saltbush shrubland or heath, from this viewpoint of compartment size.

What then should our approach be? Smith (in Jordan and Kline 1972) suggests adoption of the following steps:

(1) definition of the components of the system and the links between them

(2) examination of the processes that influence transfer rates between pools

(3) measurement of the actual quantities of the various components.

For the remainder of this paper, I will discuss the available information for Australian forest ecosystems with regard to point (3) above and consider some of the sampling and analytical difficulties associated with biomass and nutrient estimation in native forests. (Aspects of points (1) and (2) are dealt with by Florence, and Richards & Charley respectively, elsewhere in this symposium).

BIOMASS AND NUTRIENT CONTENT OF ECOSYSTEMS

Rainforests

Structurally, rainforests are the most complex of communities and accumulate the highest levels of organic matter. Bazilevic and Rodin (1966) estimated total biomass of lowland moist tropical forests to be 600 t/ha, that of montane evergreen tropical forests in Brazil to be even higher - up to 1700 t/ha. Such high organic production is generally accompanied by high mineral accumulation in the standing crop and rapid rates of mineral turnover via the litter cycle. Unfortunately there have been no complete biomass studies conducted in Australian rainforests, but about 20 sites from N. Queensland to Victoria have been or are currently under investigation (see Appendix 1 and Feller, this symposium). Available data from some of these studies are presented in Table 1, and compared with Nye's study (1961) from Ghana. Total standing litter biomass and nutrient content are quite similar for the tropical and subtropical forests independently of their location; the submontane and temperate forests have somewhat lower levels of productivity paralleled by lower nutrient content. Nitrogen and calcium comprise the largest proportions of litter nutrients in all formations. Of note is the relatively high level of aluminium in litter of the submontane forest (*Ceratopetalum apetalum* type) relative to other minerals. Aluminium accumulation is not uncommon in the Australian rainforest flora (families Proteaceae, Cunoniaceae, Rubiaceae, Monimiaceae, Symplocaceae, Escalloniaceae) and as Webb (1954) has indicated, a high level of litter aluminium in certain ecosystems dominated by accumulators may be an important ecological and pedogenic factor.

A number of studies have examined or are examining various components of rainforest ecosystems; none of these permits a picture to be developed of the distribution of biomass and nutrients throughout the system such as in the detailed presentation of Duvigneaud and Denaeyer-de Smet (1973) for Belgian mixed-oak forest but these local studies do form a useful data base for making first approximations in developing theoretical models of rainforest ecosystems. Appendix 1 summarizes the data, albeit fragmentary, available for various east coast rainforests. The Papuan studies of Turvey (1974) on nutrient flows associated with the hydrological cycle are included because of their relevance to tropical rainforests in N. Queensland, and because they represent a most comprehensive study of this aspect of ecosystem dynamics in tropical forests. Certainly the techniques used could be adopted in other forest ecosystems of Australia.

TABLE 1. BIOMASS AND NUTRIENT CONTENT OF RAINFOREST LITTER FALL.

FORMATION	LOCATION	LATITUDE	RAINFALL mm	SOIL/P.M.		BIOMASS	ANNUAL LITTER FALL (kg/ha/an)								REFERENCE
							N	P	K	Ca	Mg	Na	Al	NPKCa	
MOIST TROPICAL FOREST	KADE Ghana	6°N	1650	latosol-sedimentary rocks	a	10530	200	7.3	68	210	45	-	-	486	(1)
					b	6720	141	5.8	67	136	36	-	-	350	
TROPICAL RAINFOREST	GADGARRA Qld.	17°S	2490	latosol-basalt	a	10300	117	9.3	46	145	31	4.9	-	318	(2)
"	WONGABEL Qld.	17°S	1680	latosol-basalt	a	9000	136	13.5	77	229	28	2.2	-	456	(2)
SUBTROPICAL RAINFOREST	COOLOOLA Qld.	25°S	1500	sand	b	8400									(3)
"	WHIAN WHIAN NSW	28°S	2280	latosol-basalt	b	5934	98	4.6	30	86	-	-	7.8	219	(4)
SUBMONTANE RAINFOREST	WHIAN WHIAN NSW	28°S	2280	basalt enriched rhyolite	b	3440	30	1.3	7.3	31	-	-	18	69	(4)
COOL TEMPERATE RAINFOREST	NEW ENGLAND NSW	32°S	1520	basalt tuff	a	5100	50	2.5	11	20				84	(5)
"	MT. DONNA BUANG Vic.	38°S	2410	latosol-dacite	a	6500									(6)
					b	2700									

a - total litter, b - leaf litter

vegetation formations after Wood & Williams 1960

(1) Nye 1961
(2) Brasell et al 1977
(3) Fergus & Reeve (pers.comm.)
(4) Webb et al 1969
(5) Richards & Charley 1977
(6) Howard 1973

Sclerophyll Forests of the High Rainfall Zone

These forests are the most studied to date, with records available from partial biomass investigations on at least 40 sites with a wide range of species, concentrated on the east coast from Fraser Island to Victoria, with a few in south-west Australia (see Appendix 2 and Feller, this symposium).

Only three studies have attempted to measure biomass and nutrient content of the living vegetation. Attiwill (1972) studied *Eucalyptus obliqua* foothill forest in Victoria, and reported on biomass and nutrient distribution (P, Ca, K) in various components of the tree stratum, litter and soil, with estimates of nutrient return in litter and rainfall. Rogers and Westman (1977) and Westman and Rogers (1977) studied a mixed sclerophyll forest on the sand dunes of Stradbroke Island, involving nine species in the tree stratum; they collected data on biomass and nutrients (N, P, K, Ca, Mg, Na, Fe, Cu, Zn, Mn, Cl) for various tree components (including roots), the understorey vegetation, litter and soil. Seasonal litter fall and its nutrient content have also been examined. To my knowledge this is the most comprehensive biomass study undertaken in high forest to date. Turton (this symposium) estimated above ground tree biomass and nutrient content in the wet sclerophyll karri forests (*E. diversicolor*) in the Pemberton area.

The compartment most studied in other investigations has been litter, both "standing crop" and annual accession. Table 2 compares the available data from these studies. Extreme variation in standing litter biomass and accession rate is apparent; this probably reflects the lack of steady state conditions in these forests, in many of which fire plays a major role. For example, the data for *E. marginata* and *E. diversicolor* reflect variable periods since burning, while the litter biomass from the Stradbroke Island study represents seven years accumulation since the last wildfire. The variability is also reflected in the values of k (decomposition constants) and half-lives (after Olson 1963); the latter vary from only 0.8 years for *E. saligna* wet sclerophyll forest in New England (Richards and Charley, pers. comm.) to 6.8 years for mixed *E. piperita* - *A. costata* dry sclerophyll forest on the Hawkesbury sandstone (derived from Hannon 1958).

These data suggest that it is important in biomass studies to define, or at least attempt to describe, the seral status of the community, particularly with regard to fire; they also demonstrate the need to recognize the essentially dynamic nature of these communities and that steady state conditions rarely apply (see also Florence, this symposium); a consequence of this is that interpretation of decay constant (k) data requires considerable caution and background knowledge of the system under study, and may not even be relevant under many forest conditions characterized by rapid recovery following major perturbation, e.g. fire, logging, insect attack.

Semi-Arid Woodlands

Data on these extensive woodlands are meagre, reflecting the surprising lack of interest by ecologists in these communities. Available information from 18 studies is summarized in Appendix 3 (see also Feller, this symposium). The most detailed published* biomass study has been

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* The unpublished thesis work of Burrows (1976) on mulga and mallee systems probably represents the most comprehensive studies to date.

TABLE 2. BIOMASS AND NUTRIENT CONTENT OF EUCALYPT FOREST LITTER.

LOCATION	DOMINANT SPECIES	STANDING LITTER (kg/ha)						ANNUAL LITTER FALL (kg/ha/an)						LITTER DECOMPOSITION		REFERENCE
		BIOMASS	N	P	K	Ca	Mg	BIOMASS	N	P	K	Ca	Mg	k	Halflife (yrs)	
Eume Pl. Vic.	OBLIQUA	18000		5	16	64		3600		1.0	5.5	20.7		.20	3.5	(1)
	REGNANS							6600	43.5	1.3	4.6	39.5	(pole stand)			(2)
								7760	57.6	1.9	7.5	48.8	(mature stand)			
Brindabella ACT	FASTIGATA	27000	216	19.3	105	212	59									(3)
	"	18100	109	10.7	74	125	38									
"	ROBERTSONI	9200	55	5.2	52	87	33									(3)
"	DELEGATENSIS	17800	125	14.3	95	195	73									(3)
WA	DIVERSICOLOR	18800	(50% canopy, 7 yrs since previous fire)													(4)
	MARGINATA	7275	(50% canopy, 5 yrs since previous fire)													(4)
Dwellingup WA	"	8780	(50% canopy, 5 yrs since previous fire)					2370	10.3	0.5	5.6	18.3	6.5	.26	2.7	(5)
New England NSW	SALIGNA	18000														(6)
"	"	12370	92	4	8	102	3	10010	77	7.5	24	74		.81	0.8	(7)
"	VIMINALIS	4520	28	2.0	3	24	1.5	3850	33.5	2.5	7	23		.85	0.8	(7)
Sydney NSW	PIPERITA	6270	12					640						.10	6.8	(8)
Stradbroke Is. Qld.	SIGNATA	27000	195	6.8	22	142	34	6430	39.6	2.1	6.0	36.4	11.2	.24	2.9	(9)
Cooloola Qld.	"							4200								(10)
"	PILULARIS							6700								(10)
Whian Whian NSW	"							6500	44.0	1.4	8.5	24.6				(11)
Sydney NSW	"							450								(8)
Taree NSW	"							7520	21.2	1.1	(pole stand)					(12)
								6970	23.6	1.0	(mature regrowth)					
								7180	21.2	1.0	(overmature virgin stand)					
"	"	17320	(25 year old pole stand)					4320						.25	2.8	(13)
			(39 year old pole stand)					5580								

TABLE 2 CONT.

LOCATION	DOMINANT SPECIES	STANDING LITTER (kg/ha)						ANNUAL LITTERFALL (kg/ha/an)						LITTER DECOMPOSITION		REFERENCE
		BIO-MASS	N	P	K	Ca	Mg	BIO-MASS	N	P	K	Ca	Mg	k	Halflife (yrs)	
Fraser Is. Qld.	PILULARIS	15020	87	1.9	6.8	89	23		(overmature virgin stand)							(14)
		15270	105	1.3	12.4	67	19		(46 year old regrowth)							
Benandra NSW	MACULATA							3600	(sapling stand)							(15)
								6800	(mature stand)							

(1) Attiwill 1972
(2) Ashton 1975
(3) Meakins 1966
(4) Peet 1971
(5) Hatch 1955
(6) Smith 1974
(7) Richards & Charley 1977
(8) Hannon 1958
(9) Rogers & Westman 1977
(10) Fergus & Reeve (pers. comm.)
(11) Webb et al 1969
(12) Florence 1961
(13) Van Loon 1969
(14) Richards & Charley (pers. comm.)
(15) McColl 1966

that of Moore *et al*. (1967) on the brigalow (*Acacia harpophylla*) ecosystem. Of note was the high biomass and nutrient content of the forest, and the high proportion of dead biomass; total biomass was 293 t/ha, of which 46% was litter and standing dead material. Contrast this with the extremely high turnover rate for the *Atriplex* shrubland studied by Charley and Cowling (1968), in which standing litter was only 4.5% of biomass and annual litter fall exceeded litter biomass by seven times; the differences lie in the relatively low amount of woody material in *Atriplex* litter (4.5%) compared to brigalow (75%). These data emphasise the slow rate of organic matter turnover and subsequent nutrient release in the semi-arid woodland systems; Table 3 compares the litter biomass and nitrogen content of woodlands, shrublands and heaths of the semi-arid zone - brigalow (*Acacia harpophylla*), cypress pine (*Callitris glauca,* syn.: *C. columellaris glauca*), mallee (*Eucalyptus* spp.), mulga (*Acacia aneura*), saltbush (*Atriplex* spp.) etc. The brigalow ecosystem has a far greater litter biomass and nitrogen content than any other arid zone community; compared to the rainforests, annual litter fall in semi-arid woodlands is also very low, but standing litter is very high as a consequence of the slow decay of woody material in this dry environment. The role of termites as primary decomposers and re-distributors of nutrients in such systems is worthy of greater study.

SPATIAL VARIATION IN BIOMASS AND NUTRIENT DISTRIBUTION: PROBLEMS OF RECOGNITION AND SAMPLING

Trees are not randomly distributed through the forest, but essentially are clumped, due to regeneration patterns, soil physical conditions and moisture status, fire, browsing and logging history, competition between developing individuals and common influence of gregarious species. Sayn-Wittgenstein (1970) has indicated how "many patterns of spatial variation in forests are influenced by the combined effect of competition and common influence". Added to this, the reciprocal influence of trees on soil is reflected in spatial variation in soil nutrient levels, pH, organic matter content, radially from stem to canopy edge. Overlapping zones of influence of adjacent trees further confuse the pattern and the position is exacerbated by species differences in mixed forests due to different seasonal patterns of litter fall and variable nutrient retention in litter by different species, e.g. leaf litter of *E. umbra* is somewhat higher in nitrogen and sulphur than that of *E. signata* on the same site; potassium, sodium, iron and manganese are somewhat lower (Rogers and Westman 1977). Variation in green leaf nutrient levels are probably reflected in litter levels also; several workers record large differences in nutrient content of foliage of different species growing on the same site (see Table 4); such variation can lead to different rates of incorporation of litter depending on the species mix involved, e.g. high nitrogen *Acacia* litter can improve the rate of incorporation of admixed *Eucalyptus* litter.

Spatial variation from trunk to canopy edge in litter fall and the nutrient content of throughfall have been recorded for *E. signata* and *Banksia aemula* (pers. comm.) by Fergus and Reeve. Curtis (1975) studied cypress pine woodlands in the Pilliga Scrub of NSW and found significant variation in nitrogen, phosphorus, organic matter and pH with three different species (*Eucalyptus crebra*, *Callitris columellaris* and *Casuarina luehmanni*), in going from trunk to outer canopy to the open. Other local studies demonstrating the significance of this source of spatial variation due to the influence of individual trees are those of Ebersohn and Lucas (1965) - *E. populnea* woodlands in S.W. Queensland;

TABLE 3. BIOMASS AND NUTRIENT CONTENT OF STANDING CROP AND LITTER FALL IN SEMIARID WOODLANDS AND SHRUBLANDS.

FORMATION	LOCATION	DOMINANT SPECIES		STANDING CROP (kg/ha)			ANNUAL LITTER FALL (kg/ha/an)			LITTER DECOMPOSITION		REFERENCE
				BIO-MASS	N	P	BIO-MASS	N	P	k	Half-life	
SHRUB STEPPE (SALTBUSH)	FOWLERS GAP NSW	Atriplex vesicaria	A•	2228	24	0.94						Charley & Cowling 1968
			R^{45}	910	6	0.32						
			L	148	<1	0.05	1094	8.9	0.65	7.4	.09	
ARID SCRUB (TURKEY BUSH)	CHARLEVILLE Q	Eremophila gilesii	A	2370	38	1.95						Burrows 1971, 1972
			R^{r}	776	6	0.31						
			L	794	16	0.87	500	10.0	0.55	.63	1.1	
ARID SCRUB (MULGA)	CHARLEVILLE Q	Acacia aneura	A	70256	422	14.3						Burrows 1976
			R^{100}	25442	224	6.2						
		E. populnea	L	13892	110	3.2	2263	35.7	1.14	.16	4.2	
"	WILUNA WA	Acacia aneura	L				260					Wilcox 1960
SEMIARID MALLEE	RANKINS SPR. NSW	E. socialis	A	40164	88	5.0						Burrows 1976
		E. dumosa	R^{100}	28533	104	6.7						
			L	11372	54	3.1	3160	16.0	0.77	.28	2.5	
"	RANKINS SPR. NSW	E. socialis	A	19553	75	5.8						Burrows 1976
		E. gracilis	R^{100}	20501	47	3.8						
		E. foecunda	L	7547	41	2.1	1495	7.9	0.47	.20	3.5	
"	MT. HOPE NSW	E. dumosa E. oleosa	A	20114			(60 yrs after fire)					Holland 1969
"	WYPERFIELD VIC	E. incrassata	A	8864			(20 yrs after disturbance)					Holland 1969
SCLEROPHYLL MALLEE	KEITH SA	E. incrassata	A	9150			(12 yrs after fire)					Specht 1966
		Mel. uncinata	A	7000	31	1.2	(6 yrs after fire)					
HEATH (BANKSIA)	KEITH SA	B. ornata	A	10800	48	2.3	(25 yrs after fire)					Specht et al 1958
		X. australis	R^{75}	33000	223	8.9						
		Cas. pusilla	L	3000	17	0.47						
LAYERED SCRUB (BRIGALOW)	MEANDARRA Q	Acacia harpophylla	A	176800	874	22						Moore et al 1967
			R^{90}	40700	360	6						
			L	75500	368	10						
	MEANDARRA Q	Acacia harpophylla	L				(same stand concurrent studies) 1110			.02	46	Tunstall 1973
MIXED WOODLAND (CYPRESS PINE)	PILLIGA NSW	Callitris columellaris	R$^{7.5}$	11350	83	3.7						Curtis 1975
			L	7300	70							
MIXED WOODLAND (CYPRESS PINE)	YULEBA Q	Callitris columellaris	L				1260 1800 (stand fertilised with N)					Johnston & Bevege (unpubl.)
"	YULEBA Q	C. columellaris	L				1366 (unburnt)					Hawkins 1966
		E. dealbata	L				1960 (moderately burnt)					
		Cas. luehmanii	L				1144 (severely burnt)					

• A - above ground R - roots below ground to depth (cm) indicated L - litter layer
L - litter layer r - estimated from previous work

vegetation formations after Wood and Williams 1960

TABLE 4. VARIATION IN FOLIAGE AND LEAF LITTER MINERAL CONCENTRATIONS OF DIFFERENT SPECIES ON THE SAME SITE.

FORMATION	LOCATION	SPECIES		CONCENTRATION OF MINERAL (ppm)													REFERENCE
				N	P	K	Ca	Mg	Na	S	Al	Mn	Zn	Cu	Fe	B	
WET SCLEROPHYLL FOREST	WALLABY CREEK VIC.	Eucalyptus regnans	F	15200	1170	11300	2300	2500									(1)
			L	3300	350	2900	5600	2000									
		Pomaderris aspera	F	23800	1800	11300	14200	3200									
			L	11200	460	4000	14200	3600									
		Clearia argophylla	F	15300	1540	17800	5300	1800									
			L	5000	770	10200	7200	2100									
"	BRINDABELLA ACT	Eucalyptus fastigata	F	15000	960	1300	10000	4200									(2)
			L	8000	710	3900	7900	2200									
		Pomaderris apetala	F	20000	1250	1000	10200	2900									
			L	18000	730	4000	16300	2900									
		Acacia dealbata	F	24000	860	1200	2500	1900									
			L	26000	710	7700	7200	2300									
"	BRINDABELLA ACT	Eucalyptus delegatensis	F	14000	1020	1200	8000	4900									(2)
			L	7000	800	5300	10900	4100									
		Acacia melanoxylon	F	28000	2080	8900	3700	1500									
			L	19000	780	3300	18900	2700									
"	PEMBERTON WA	E. diversicolor	F	11000	610	6200	9100	2600	2200	1120		189	4.5	1.1			(3)
		E. calophylla	F	10700	540	8700	6500	3300	2400	1220		60	9.4	1.1			
	WA	E. diversicolor	F	11000	600	7400	10400	2400		1000		506	5.8	4.6			(4)
		Bossiaea aquifolium	F	27300	400	7000	8700	2000		2000		81	8.8	7.7			
DRY SCLEROPHYLL FOREST	WA	E. marginata	F	8400	400	5700	5800	4300		1000		177	5.6	2.9			(4)
		Acacia pulchella	F	21500	400	8600	11900	2400		2900		47	8.0	4.5			
"	DWELLINGUP WA	Eucalyptus marginata	F	10300	910	3700	4400	3400				170					(5)
			L	4700	220	2500	7700	2400				220					
"	HUME PLAT. VIC	Eucalyptus obliqua	F		710	4200	3200										(6)
			L		180	860	5100	2000	760								(7)
"	BRINDABELLA ACT	Eucalyptus robertsonii	F	14000	1040	1200	4200	3800									(2)
			L	6000	560	5700	9500	3600									
		Bedfordia salicina	F	19000	2680	800	9200	2000									
			L	12000	1080	5100	11500	6300									
"	STRADBROKE ISLAND Q	Eucalyptus signata	F	12000	500	4000	5500	2800	3400	880^{S}		95	12	29	146		(8)
			L	6100	200	1500	4400	1500	1900	580^{S}		160	7	11	110		
		Eucalyptus umbra	F	11100	500	4000	5400	2400	3900	780^{S}		57	13	28	192		
			L	7000	200	1000	4200	1800	700	650^{S}		104	11	11	88		

TABLE 4 CONT.

				CONCENTRATION OF MINERAL (ppm)														
FORMATION	LOCATION	SPECIES		N	P	K	Ca	Mg	Na	S	Al	Mn	Zn	Cu	Fe	B		Reference
DRY SCLEROPHYLL FOREST	BENANDRA NSW	E. maculata	F		730	9400	5800	2500	2300		82	362	41					(9)
		E. paniculata	F		790	4600	8500	3100	3000		110	764	13					
		E. maculata	F		520	9400	7500	2200	2200		182	450	35					
		E. pilularis	F		600	3700	3000	3300	2000		134	136	16					
"	SYDNEY NSW	E. pilularis	F	9600														(10)
		E. qummifera	F	9000														
		Ac. discolor	F	16500														
		Cas. torulosa	F	11700														
"	SYDNEY NSW	E. qummifera	F	6200														(10)
		E. haemastoma	F	5700														
		Cas. distyla	F	7200														
		Bossiaea*	F	8800													* for species see reference	
		Dillwynia*	F	11000														
		Gompholobium*	F	10900														
		Pultenaea*	F	10000														
MIXED WOODLAND (CYPRESS PINE)	MILLMERRAN Q	Callitris glauca	F	10500	820	3900	8400	1900	200	540^S								(11)
		Casuarina leuhmanii	F	9000	670	3300	2500	1100	980	480^S								
		E. bancroftii	F	13100	640	6200	2900	1500	50	650^S								
LAYERED SCRUB (BRIGALOW)	MEANDARRA Q	Acacia harpophylla	F	16600	620	7450	7400	1930	160		3000	920	14	9	230	140		(12)
		Geijera parviflora	F	16400	790	13460	8500	1620	210		3500	850	51	21	170	26		
SEMI-ARID SCRUB (MULGA)	CHARLEVILLE Q	Acacia aneura	F	20900	1010													(13)
			L	18900	740													
		Eucalyptus populnea	F	16000	830													
			L	15500	410													
		grasses*	F	10700	460												* for species see reference	
SEMI-ARID MALLEE	RANKINS SPR. NSW	Eucalyptus spp.*	F	9900	680												* E. socialis, E. dumosa	(13)
		Mel. lanceolata	F	7300	350													
		Euc. & Mel.	L	6300	390													
		Shrubs*	F	11400	700												* for species see reference	
			L	8300	830													
"	RANKINS SPR. NSW	Eucalyptus*	F	10000	690												* E. foecunda, E. gracilis, E. socialis	(13)
			L	7900	480													
		Shrubs*	F	10200	480												* for species see reference	
			L	3900	650													
		Triodia	F	600	130													

Vegetation formations after Wood & Williams 1960.

(1) Ashton 1975
(2) Meakins 1966
(3) Turton 1977
(4) Malajczuk & Grove 1977
(5) Hatch 1955
(6) Attiwill 1972
(7) Attiwill 1968
(8) Rogers & Westman 1977
(9) McColl 1969
(10) Hannon 1956
(11) Bevege & Johnston (unpublished)
(12) Moore et al 1967
(13) Burrows 1976

S SO_4-S. Other analyses are Total S

Smith (1974) - N-mineralization patterns in bark halos of *E. saligna* in wet sclerophyll forest of N. NSW; and Meakins (1966) who studied the effects of understorey species on soil properties in montane eucalypt forests of the ACT. Spain (1973) demonstrated that non-randomness of litter fall could even be measured in pine plantations and he is currently examining this question in relation to litter fall and resulting faunal activity in N. Queensland rainforests (Spain, pers. comm.). Burrows (1976) presents a most useful and up-to-date exposition on the problems of estimating litter fall in natural communities. Zinke (1962) discusses the problems associated with conifer forests of the USA; as he points out, the zones of influence of individual trees tend to merge as forests become more dense, but probably intensify as trees age; the classic example is of course the development of "egg-cup podzols" under kauri pine (*Agathis australis*) in New Zealand. We could therefore expect greatest differences due to these effects in sclerophyll forests dominated by large, overmature, widely spaced trees - a not uncommon condition in many eucalypt forests and woodlands.

Consideration of these patterns is essential in biomass studies in natural vegetation; ideally, sampling for litter fall, precipitation throughfall, standing litter, mineralization and soil nutrient status should be efficient enough to account for this variation by using sufficiently intensive sampling schemes. Logistically however this is virtually impossible, but I concur with Charley and West (1975) in suggesting that such sampling deficiencies can be partially overcome by including in nutrient cycling studies, adequate investigations of spatial variation about individual trees.

SAMPLING AND ANALYTICAL PROCEDURES

It is apparent that existing studies on native forest ecosystems are fragmentary in terms of components examined, with a dearth of information, not only on distribution of biomass and nutrients within the systems, but also of the processes and pathways involved in nutrient cycling and energy flow. It would appear essential that some consideration be given to delineating those forest systems where information is most lacking, and defining those aspects which are deserving of critical study within a framework of relevance to forest management in the broadest sense. Feller (this symposium) has listed a number of forest types which he feels are in need of study because of current utilization pressures likely to result in considerable change to the forest ecosystem.

It is desirable also that consideration be given to the sampling problems involved in ecosystem studies. Of the work cited in the Tables and Appendices, Moore *et al*. (1967), Richards and Charley (this symposium) and Burrows (1976) are the only local workers whose studies attempted to estimate sampling errors associated with ecosystem investigations.

Traditional forest mensuration techniques were developed essentially for even-aged stands and the establishment of appropriate methodology for measuring and sampling biomass of uneven-aged, mixed stands of broad-leaved and needle-leaved species demands further attention. The application of mean tree and regression approaches to biomass estimation (Madgwick 1963, 1970; Baskerville 1965, 1972), and the determination of allometric relationships between tree components (e.g. Attiwill 1962; Holland 1969; Pressland 1975) are the more obvious bases from which suitable methodology can be developed. IUFRO has produced two methodological studies (IUFRO 1971, 1973) which consist essentially of compendia of techniques; these provide useful approaches for estimating biomass and other stand components.

Root studies in particular have virtually been neglected to date; e.g. only 10 percent of studies examined for this review made any attempt at estimating root biomass and nutrient content. Annual shedding of roots and their contribution to subsurface litter is a problem that has not been satisfactorily resolved anywhere.

Some agreement would also seem desirable on the analytical procedures used to determine nutrients in certain components; this applies in particular to litter studies where samples in various degrees of degradation and soil mixing can give variable results, at least in my experience, depending on whether they are analysed as plant or soil material. Attention also needs to be given to preparation of soil samples (grinding, sieving, removal of particulate organic matter, fine roots etc.) if analyses are to be used to calculate nutrient weight unit area/soil volume, as distinct from their more conventional use as empirical indices within certain silvicultural or agronomic contexts.

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APPENDIX 1. ECOSYSTEM STUDIES IN AUSTRALIAN RAINFORESTS

FORMATION	COMPARTMENTS STUDIED	LOCATION	REFERENCE
TROPICAL RAINFOREST	litter fall - biomass and nutrient content	ATHERTON TLD QLD.	Brasell et al 1977
"	litter fall - biomass, site and seasonal variation	ATHERTON TLD, INNISFAIL, QLD.	Bailey 1976 a, 1976 b
"	litter fall - biomass, nutrient content, faunal decomposition	"	Spain et al current study CSIRO
"	nutrient flows via hydrological cycle	Papua	Turvey 1974
SUBTROPICAL RAINFOREST	mineral content of wood	QLD.	Swain 1928
"	mineral distribution in trunks of trees	Gibraltar/Styx NSW	Beadle & White 1968
"	soil profile nutrient analysis	Fraser Is. QLD.	Florence et al 1964
"	soil profile nutrient analysis	"	Webb 1969
"	litter fall and standing litter - biomass, nutrient content, decomposition, soil profile nutrient analysis, N and S mineralisation	"	Richards & Charley current study UNE
"	soil profile nutrient analyses, atmospheric accession, litter fall - biomass and nutrient content	Cooloola QLD.	Fergus & Reeve current study CSIRO
"	soil profile nutrient analyses, stand tables for dominant species	"	Webb & Tracey 1975
"	litter fall and standing litter - biomass, nutrient content, decomposition, soil profile nutrient analyses	Imbil and Yarraman QLD.	Bevege et al current study Qld. Dept. For.
"	litter fall - biomass and nutrient content	Whian Whian NSW	Webb et al 1969
SUBMONTANE RAINFOREST	litter fall - biomass and nutrient content	"	Webb et al 1969
COOL TEMPERATE RAINFOREST	litter fall - biomass and decomposition	Donna Buang VIC.	Howard 1973
"	litter fall - biomass and decomposition	Kinglake VIC.	Gill 1964 in Howard 1973
"	soil nitrogen mineralisation	New England NSW	Smith 1974
"	litter fall andstanding litter - biomass, nutrient content, decomposition and N mineralisation	"	Richards & Charley 1977 Charley & Richards 1974

APPENDIX 2. ECOSYSTEM STUDIES IN EUCALYPTUS (SCLEROPHYLL) FORESTS

DOMINANT SPECIES	COMPARTMENT STUDIED	LOCATION	REFERENCE
OBLIQUA	standing crop and litter fall biomass and nutrient distribution, litter decomposition, rainfall accession, soil nutrients.	Hume Flat. VIC	Attiwill 1962, 1966, 1968, 1972
a OBLIQUA b REGNANS	standing crop and litter fall biomass and nutrient distribution, stem flow and throughfall, soil leachate composition.	Maroondah VIC	Feller current study Univ. Melb.
REGNANS	litter fall - biomass and nutrient content, nutrients in foliage, senescence withdrawal.	Wallaby Ck. VIC	Ashton 1975
REGNANS	nutrient loss following slash burning.	Florentine Vy. TAS	Harwood and Jackson 1975
a REGNANS b OBLIQUA c SIEBERIANA d RADIATA	rock weathering to release P and K.	Gembrook VIC	Ellis 1969
RADIATA BICOSTATA	nutrient loss from soil and litter with burning.	Stanley VIC	Rowe and Hagel 1974
a FASTIGATA b ROBERTSONI c DELEGATENSIS	nutrient content of foliage, biomass and nutrients in standing litter, spatial variation in soil properties.	Brindabella ACT	Meakins 1966
a DELEGATENSIS b PAUCIFLORA	litter fall - biomass and nutrient content, decomposition and influence of management practices.	Snowy Mts. ACT	Park 1975
PAUCIFLORA	litter fall - biomass, nutrient (N and P) content, decomposition and fungal activity.	Snowy Mts. ACT	Macauley current study ANU
a FASTIGATA b SALIGNA	litter fall - biomass, nutrient content, decomposition and mineralisation.	New England NSW	Charley and Richards 1974 Richards and Charley 1977
SALIGNA	litter distribution and N-mineralisation.	"	Smith 1974
a SALIGNA b MACULATA PANICULATA c MACULATA PILULARIS d GUMMIFERA	litter fall - biomass and decomposition, foliage and bark nutrient status soil chemical properties.	Benandra NSW	McColl 1966, 1969 McColl and Hymphreys 1967
a PIPERITA b PUNCTATA HAEMASTOMA GUMMIFERA c PILULARIS	biomass andnitrogen distribution in standing crop and soil.	Sydney NSW	Hannon 1956, 1958

APPENDIX 2. CONT.

DOMINANT SPECIES	COMPARTMENTS STUDIED	LOCATION	REFERENCE
PILULARIS	litter fall and standing litter biomass.	Taree NSW	Van Loon 1969
PILULARIS	litter fall - biomass, N and P content.	"	Florence 1961
PILULARIS	litter fall and standing litter - biomass and nutrient content, N-mineralisation, soil nutrients and effect of leaching.	Fraser Is. QLD	Richards and Charley current study UNE
PILULARIS	litter fall - biomass and nutrient content.	Whian Whian NSW	Webb et al 1969
MACULATA	standinglitter and soil - biomass and nutrient content, foliage nutrients, N-mineralisation and effect of burning.	Maryborough QLD	Bevege et al current study Qld. Dept. For.
SIGNATA	litter fall - biomass, nutrient content and decomposition, soil nutrients and atmospheric accession.	Cooloola QLD	Fergus and Reeve current study CSIRO
SIGNATA UMBRA	standing crop and litter fall - biomass and nutrient content.	Stradbroke Is. QLD	Rogers and Westman 1977 Westman and Rogers 1977
ROSSII MACULOSA	throughfall and stem flow.	Lidsdale NSW	Smith 1974
DIVERSICOLOR CALOPHYLLA	standing crop, litter fall, throughfall - biomass and nutrient content.	Pemberton WA	Hingston et al current study CSIRO
DIVERSICOLOR	soil properties and management.	"	Valentine 1976
a DIVERSICOLOR b MARGINATA	standing litter - biomass and effect of fire.	WA	Peet 1971
MARGINATA	standing litter and litter fall - biomass nutrient content and decomposition.	Dwellingup WA	Hatch 1955
SIEBERIANA	biomass and nutrient content of crop; soil nutrient status and management effects.	Eden NSW	Turner and Lambert current study NSWFC

APPENDIX 3. ECOSYSTEM STUDIES IN SEMIARID WOODLANDS AND SHRUBLANDS

FORMATION	COMPARTMENTS STUDIED	DOMINANTS	LOCATION	REFERENCE
SHRUB STEPPE	standing crop and litter fall - biomass, N and P content, nutrient status of soils.	ATRIPLEX	Fowlers Gap NSW	Charley and Cowling 1968 Charley 1972
ARID SCRUB	standing crop and litter fall - biomass and nutrient status.	EREMOPHILA	Charleville Qld.	Burrows 1971, 1972
"	allometric relationships in trees.	ACACIA ANEURA	Charleville Qld.	Pressland 1975
"	allometric relationships canopy/bole, root biomass and distribution.	"	"	Burrows and Beale 1970
"	standing crop and litter fall - biomass and nutrient distribution, decomposition and fungal succession, soil nutrients.	"	"	Burrows 1976
"	seasonal litterfall biomass.	"	Wiluna WA	Wilcox 1960
SEMIARID MALLEE	standing crop and litter fall - biomass and nutrient distribution, decomposition, soil nutrients.	(a) E. SOCIALIS E. DUMOSA	Rankins Spr. NSW	Burrows 1976
"		(b) E. SOCIALIS E. FOECUNDA E. GRACILIS		
"	allometric relationships in trees, biomass of standing crop.	(a) E. DUMOSA E. OLEOSA	Mt. Hope NSW	Holland 1969
		(b) E. INCRASSATA	Wyperfield Vic.	
SCLEROPHYLL MALLEE	standing crop and nutrient content - development following fire.	E. INCRASSATA MEL. UNCINATA	Keith SA	Specht 1966
HEATH	standing crop and nutrient content.	BANKSIA ORNATA	Keith SA	Specht et al 1958
LAYERED SCRUB	standing crop biomass and nutrient content, soil nutrient status.	ACACIA HARPOPHYLLA	Meandarra Qld.	Moore et al 1967
"	seasonal litter fall - biomass stem flow and through fall soil pH and salinity.	"	"	Tunstall 1973
MIXED WOODLAND	surface roots and litter - biomass nutrient content, spatial variation in soil nutrients, nitrogen mineralisation.	CALLITRIS COLUMELLARIS	Pilliga NSW	Curtis 1975
"	seasonal litter and seed fall, effect of burning.	"	Yuleba Qld.	Hawkins 1966
"	litter fall and nutrient content, nutrient levels in canopy.	"	"	Johnston and Bevege (unpubl.)
"	litter biomass and nutrient content, N mineralisation, nutrient levels in tree canopy.	C. COLUMELLARIS CAS. LUEHMANII	Millmerran Qld.	Bevege and Johnston current study Qld. Dept. For.

NUTRIENTS IN EUCALYPTS

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Trees from two sites in the karri forest near Pemberton in South-Western Australia were sampled and analysed during 1976.

The House Brook Road site carried only karri (*E. diversicolor*) and trees of 20, 25 and 33cm D.B.H. were selected from a 0.16ha plot with 444 stems per hectare.

The Grays Road site carried karri and marri (*E. calophylla*) and a 0.16ha plot contained 148 karri and 290 marri per hectare. For this plot, trees of 18, 30 and 38cm D.B.H. for karri and 23, 30 and 36cm D.B.H. for marri were selected.

After the whole trees (above ground) had been sampled, understorey, litter and soils were examined but results will not be detailed here.

METHOD

The trees were divided into trunks (wood and bark) to the crown break, branches and leaves. Branches were divided into bottom, middle and top depending upon their position in the crown and weighed separately as were the corresponding leaves plucked therefrom. Representative samples of all tree parts including dead wood, bark and fruit if any were taken for drying and analysis. For branchwood samples (bark not separated), one average branch from each of the bottom, middle and top categories was cut into small pieces and a subsample taken. All the leaves from each branch category were well mixed before subsampling.

Samples of about 1kg (dried at 70°C) were ground in a 20cm"Christy and Norris"mill with a 2mm screen. Subsamples were finely ground for the chemical analysis for nitrogen and for XRF analyses of the other elements.

Estimated dryweights of the karris at House Brook Road are 224 tonnes/ha and of the karris and marris at Grays Road 217 and 67 tonnes/ha respectively.

Results of the tree analyses are summarized in three tables.

Table 1 shows the proportions of tree biomass in the various component parts.

Table 2 shows the mean concentrations of elements in the various parts of the trees.

Table 3 gives an approximation of the total amounts of elements on an area basis in the whole trees and trunks for the two sites.

TABLE 1

Distribution of Tree Biomass between Parts

Tree Identity[+]	1	2	3	4	5	6	7	8	9
Basal Area cm^2	325	537	883	263	742	1140	401	730	965
Total dry weight kg	178	460	870	172	588	1157	193	412	466*
Tree parts	Proportions of biomass in each part (%)								
Wood	75.7	86.2	83.2	72.2	77.0	70.7	73.8	74.1	70.9
Bark	8.1	9.0	9.5	12.5	11.0	11.1	17.8	16.4	13.6
Trunk	83.8	95.2	92.7	84.7	88.0	81.8	91.6	90.6	84.6
Leaves	2.9	1.2	1.8	4.5	3.5	2.5	1.8	2.0	1.9
Branches	11.4	3.6	4.7	10.8	8.5	15.7	6.6	7.4	11.6
Dead wood	1.9	-	0.7	-	-	-	-	-	-

[+] Trees 1, 2, 3 *Eucalyptus diversicolor* (40 yr old Karri stand) - House Brook Rd, Pemberton
Trees 4, 5, 6 *Eucalyptus diversicolor* (mixed Karri-Marri stand) - Grays Rd, Pemberton
Trees 7, 8, 9 *Eucalyptus calophylla* (mixed Karri-Marri stand) - Grays Rd, Pemberton

* 0.8% fruit in biomass.

TABLE 2

Mean Concentrations of Elements in Parts of Trees

Element	Karri at House Brook Road Mean B. A. (3 trees) 581cm^2						Karri at Grays Road Mean B. A. (3 trees) 715cm^2						Marri at Grays Road Mean B. A. (3 trees) 699cm^2						Legend
	W.	B.	Tr.	L.	Br.	Tree	W.	B.	Tr.	L.	Br.	Tree	W.	B.	Tr.	L.	Br.	Tree	
N %	.037	.17	.05	1.07	.21	.077	.055	.17	.071	1.10	.15	.112	.069	.17	.084	1.07	.22	.116	W. Wood
P %	.004	.019	.005	.061	.025	.007	.005	.013	.006	.061	.015	.009	.002	.008	.003	.054	.016	.006	B. Bark
K %	.032	.42	.071	.71	.30	.093	.054	.30	.087	.62	.22	.12	.081	.32	.12	.87	.28	.16	Tr. Trunk
Ca %	.063	2.13	.27	.95	.63	.30	.073	2.03	.33	.91	.47	.37	.14	.47	.20	.65	.83	.26	L. Leaves
Mg %	.028	.24	.049	.22	.19	.060	.049	.28	.079	.26	.20	.10	.10	.14	.11	.33	.24	.13	Br. Branches
S %	.002	.022	.004	.082	.023	.006	.005	.021	.007	.112	.018	.011	.007	.022	.010	.122	.027	.014	Tree Whole tree
Na %	.007	.11	.017	.20	.066	.023	.010	.092	.021	.22	.052	.031	.035	.13	.051	.24	.065	.061	
Cl %	.034	.47	.078	.44	.17	.088	.045	.45	.100	.35	.16	.115	.15	.61	.23	.57	.30	.24	
Cu ppm	<1	3	1	5	7	1	1	1	1	3	3	1	1	2	1	3	2	1	
Zn ppm	<1	2	<1	7	3	<1	<1	2	<1	6	3	1	<1	2	1	12	5	1	
Mn ppm	18	488	65	542	299	86	11	340	55	227	113	67	3	15	5	72	54	11	

TABLE 3

Nutrients in Trees on Karri and Karri-Marri Sites

Nutrient	Karri Site B.A. 26.0 m^2 ha^{-1}		Karri-Marri Site B.A. Karri 24.3 m^2 ha^{-1}		B.A. Marri 13.2 m^2 ha^{-1}		Total 37.4m^2 ha^{-1}	
	Karri		Karri		Marri		Total trees	
	Whole tree	Trunk	Whole tree	Trunk	Whole tree	Trunk	Whole tree	Trunk
N kg ha^{-1}	172	104	243	129	78	50	321	179
P "	15.7	10.4	19.5	10.9	4.0	1.8	23.5	12.7
K "	206	147	260	159	107	71	367	230
Ca "	672	559	803	601	174	118	977	719
Mg "	134	101	217	144	87	65	304	209
S "	13.4	8.3	23.9	12.8	9.4	5.9	33.3	18.7
Na "	52	35	67	38	41	30	108	68
Cl "	197	162	249	182	161	136	410	318
Cu "	0.29	0.19	0.24	0.15	0.07	0.05	0.31	0.20
Zn "	0.11	0.05	0.19	0.06	0.09	0.04	0.28	0.10
Mn "	19.3	13.4	14.6	10.1	0.7	0.3	15.4	10.4

LEGUME UNDERSTOREY BIOMASS, NUTRIENT CONTENT AND NITROGEN FIXATION IN EUCALYPT FORESTS OF SOUTH-WESTERN AUSTRALIA

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INTRODUCTION

Understorey vegetation can have an important role in nutrient cycling in forest stands because (a) it increases the total litterfall annually, (b) it is often richer in nutrients, and (c) it often decomposes more readily allowing for rapid recycling of nutrients (Ovington 1959). Nitrogen—fixing understorey plants are especially important since nitrogen seems to be a limiting factor in the productivity of many forest ecosystems (e.g. Gessel *et al.* 1973).

Manipulation of forest ecosystems through practices such as prescribed burning, logging and clearfelling result in losses of nitrogen. Under favourable conditions these losses may be replenished by nitrogen fixation by understorey legumes. Thus where management practices affect the growth of understorey legumes overall forest health and productivity may be affected.

Some preliminary results are presented here for biomass, nutrient content and rates of nitrogen fixation for understorey legumes in the jarrah (*Eucalyptus marginata* Donn ex Sm.) and karri (*E. diversicolor* F.Muell), dry and wet sclerophyll forest respectively, which develop following intense fire.

PLANT DENSITY AND BIOMASS

The density and biomass of the most abundant legumes, in each experimental forest site six months after burning are given in Table 1.

TABLE 1

Numbers and Biomass of Legume Species from the Wet and Dry Sclerophyll Forests of South-West Australia six months after burning.

	Plant density No/ha	Above-ground biomass kg/ha
Wet sclerophyll (karri)		
Bossiaea laidlawiana	241.0×10^3	8.77
Acacia urophylla	71.0×10^3	8.10
Dry sclerophyll (jarrah)		
Acacia pulchella	6.6×10^3	1.94
*Kennedia coccinea**	8.4×10^3	3.96
*Kennedia prostrata**	41.0×10^3	22.38

* Ground cover species

Ground cover legumes contributed significantly to the biomass and density of legumes in the jarrah forest. They were totally absent from the karri forest. Although the karri forest had six times the number of legume species than in the jarrah forest they represent only two-thirds the total biomass.

Plant density and biomass of older understorey legumes in the karri forest are presented in Table 2. The variation in density and biomass is partly explained by a variable proportion of non-legume component in the understorey. There is a general trend of decreasing plant density and increasing biomass with time since burning. In 36-years

TABLE 2

Numbers and Biomass of Bossiaea laidlawiana *in Stands of Different Ages.*

Age of regrowth (years)	Years since burning	Plant density No/ha	Above-ground biomass kg/ha
4	4	122×10^3	6405
7	7	47×10^3	9334
Mature	12	62×10^3	29328

old karri regrowth, biomass of the understorey represents five per cent of the total above-ground biomass (Turton and Hingston, personal communication).

NUTRIENT CONTENT

Green leaves of the understorey legumes had twice the nitrogen concentration of eucalypt leaves for both forest types. Other elements were also higher (Table 3).

TABLE 3

Nutrient Concentrations in Green Leaves of Overstorey and Legume Understorey Species in the Wet and Dry Sclerophyll Forests of South-western Australia

	Nutrient Element Concentration								
	N	P	K	Ca	Mg	S	Cu	Zn	Mn
				%				$\mu g\ g^{-1}$	
Wet Sclerophyll (7 years after burning									
Overstorey (Karri)	1.10	0.06	0.74	1.04	0.24	0.10	2.6	5.8	506
Understorey (*Bossiaea*)	2.73	0.04	0.70	0.87	0.20	0.20	7.7	8.8	81
Dry Sclerophyll (6 years after burning)									
Overstorey (Jarrah)	0.84	0.04	0.57	0.58	0.43	0.10	2.9	5.6	177
Understorey (*Acacia*)	2.15	0.04	0.86	1.19	0.24	0.29	4.5	8.0	47

NITROGEN FIXATION

Nitrogen fixation by legumes in the jarrah and karri forests represented rates of approximately 3 kg nitrogen per ha per annum for all species examined (Table 4).

TABLE 4

Rates of Nitrogen fixed by Legumes in the Wet and Dry Sclerophyll Forests of South-West Australia (kg/ha/annum)

	Age 6 months	Age 4-15 years
Wet sclerophyll (karri)		
Bossiaea laidlawiana	2.8	8.6
Dry sclerophyll (jarrah)		
Acacia pulchella	3.0	-

For sites of different aged legume understorey in the karri forest, an average rate of fixation was 9 kg nitrogen per ha per annum. The oldest site (age 15 years) had a rate of 15 kg nitrogen per ha per annum.

CONCLUSIONS

The present study indicates that intense fire is important for the regeneration of a legume understorey in both the wet and dry sclerophyll forests of Western Australia. In both forests types leguminous plants represent a significant component in the understorey. This component however varies in both species composition and density between and within the two regions, and with overstorey and understorey development. The ability of leguminous plants to fix and store atmospheric nitrogen, as well as many other essential elements suggests that they are an important compartment in the cycling of nutrients in the eucalypt forests. It has been shown by Springett (1976) that the nitrogen-rich litter from understorey legumes decomposes more readily than *Eucalyptus* litter. Higher nitrogen concentrations in litter have been recorded in the jarrah forest beneath *Acacia pulchella* than in stands without it. Presumably the productivity of the forest stand is enhanced through association with legumes. We see the parallel with the use of legumes to maintain agricultural soil productivity. Experiments are being initiated to examine for this eucalypt tree response to legume understorey.

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SOURCES OF, AND SINKS FOR, NUTRIENTS IN FOREST ECOSYSTEMS

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Major sources of nutrients in forest ecosystems are the atmosphere, soil and basement rocks, and major sinks are the atmosphere, soil and drainage water. In managed forests additional inputs are in fertilizers and nutrients are removed in harvested products.

The aim here is to review the methods for estimating inputs and outputs and some of the limitations of these methods.

THE ATMOSPHERE AS A SOURCE

The quantities of Na, K, Ca, Mg, S and N in rainfall and in dry fallout collected in continuously open funnels and in rainfall collected in funnels which are only open during rainfall events, have frequently been used as an estimate of inputs to forest ecosystems. The data to about 1973 are tabulated by Steinhardt (1973). These nutrients originate from oceanic spray, volcanic emissions and terrestrial aerosols, and pollution from industrial emissions is also an important source in many parts of the world, particularly in the northern hemisphere. In Australia oceanic spray appears to be the major source for forested lands situated as they are towards the coastal fringe of the continent. The concentration of salts collected in rainfall decreases with distance from the coast in this region (Hutton and Leslie 1958, Hingston and Gailitis 1976, Hutton 1976). Attempts have been made to assess the relative contributions from oceanic and terrestrial sources and although the results are not clear-cut, local terrestrial sources are reflected in the composition of salts in rainfall (Hingston and Gailitis 1976). An example is provided by the variation in "excess" sulphate over the calculated oceanic component in Western Australia (Table 1).

Thus there are considerable regional differences and sometimes quite local differences in the concentration and composition of salts in rainfall.

The ranges of inputs of elements in rain for Europe and Australia are similar for many elements (Table 2), but on a broad scale both in Europe and in North America values for SO_4-S, NO_3-N and NH_4-N are commonly higher than in Australia.

Although estimates made in this way for inputs from the atmosphere have often been used for nutrient balances in catchment studies, there has been considerable speculation about the input due to aerosol impaction on vegetation. This appears to be of particular relevance to forested areas. The problem is to make a reliable estimate of this salt trapped by the forest canopy. An indication of the magnitude of this input is provided by measurements of "throughfall" collected under the forest canopy (Attiwill 1966; Carlisle, Brown and White 1967; White and Turner 1970; Eaton, Likens and Bormann 1973; Miller, Cooper and Miller 1976). Estimates of salts in throughfall pose sampling problems because of the variability of the canopy which are not encountered in sampling rainfall in the open. Further, the additional nutrients in throughfall are derived from two sources, aerosol impaction, i.e., an input, and leaching of nutrients from cracks in leaf cuticle and epidermal cells (Watson 1942), i.e., recycling within the ecosystem.

TABLE 1

Selection of Centres with Excess Sulphate Precipitation (1973)

Centre	Excess sulphate* (kg ha^{-1})	Probable reasons for excess
Yanchep	0.7	Low value-centre in National Park
Floreat (metro area)	11.9	
Perth (city)	24.3	Urban and industrial pollution (pop. ≃ 650,000)
Bunbury (outside city centre)	5.7	Urban and industrial (pop.≃ 18,000)
Kalgoorlie (Airport)	9.7	Mining centre
Norseman	9.1	Mining and salt lakes
Wiluna	47.9	Salt lakes

* Excess over sea-salt contribution.

Gosz et al. (1975) have made one of the few attempts to assess the relative contributions of aerosol impaction and crown leaching to throughfall in their study of maple, birch and beech trees. They conclude that the relative amounts of elements released by leaching was K greater than Mg, Ca and N and least leached was Na. The older leaves released elements faster and more completely than younger leaves.

Miller et al. (1977) have made an assessment of amounts of elements contributed by aerosol entrapment and by leaf leaching. They used a regression technique, where the amounts of elements in rainfall collected in the open over weekly periods was regressed against the amounts collected in throughfall for the same periods. The results for Corsican pine (Pinus nigra var. maritima) in the Laigh of Moray Forest (Scotland) are shown in Table 3.

For comparison the mean values for elements in rainfall and throughfall estimated for two sets of catchments in the Collie area, south west of Western Australia, and some values for Hubbard Brook (Eaton et al. 1973) are shown in Table 4.

Eaton et al. (1973) consider that their results do not indicate that aerosol impaction is an important factor for the majority of elements (Ca, Mg, K, P and N) and it is possible that large amounts of S in throughfall may be the result of direct absorption of SO_2 or impaction of small particles of SO_4 on the leaves. In their situation the values obtained for salts in rainfall collected in the open are most appropriate as inputs. Similar conclusions were reached by Attiwill (1966) for Eucalyptus obliqua forest in Victoria.

The results of throughfall studies to date suggest that the variations due to forest types and locations could be considerable. The estimation of inputs of nutrients through trapping of aerosols on vegetation appears to present a difficult problem, which needs solution if total inputs to catchments are to be estimated accurately.

TABLE 2

Accessions of Elements in Rainfall

Element	Ranges of values reported (kg ha^{-1} yr^{-1})	
	Europe[1]	Australia[2]
Na	1 - 155	2 - 111
K	.7 - 10	.3 - 14
Mg	.4 - 17	.3 - 15
Ca	2 - 40	.8 - 35
Cl	1 - 345	2 - 180
SO_4 - S	2 - 300	.7 - 19
NH_4 - N	.4 - 4	.7 - 2
NO_3 - N	.3 - 6	.3 - 1
P	.1 - .7	.1 - .3

Note: 1. Abstracted from Steinhardt (1973)

2. Compiled from Drover & Barrett-Lennard (1956)
Hutton & Leslie (1958)
Hingston & Gailitis (1976)
Probert (1976)

TABLE 3

Mean Values for Elements in Throughfall Contributed in Gross Rainfall, Crown Leaching and Aerosols Trapped in the Canopy of Corsican Pine (Pinus nigra var. maritima)

Source	Elements in Throughfall					
	N	P	K	Ca	Mg	Na
			(kg ha^{-1} yr^{-1})			
Gross Rainfall	4.8	.04	2.8	2.9	2.6	25.2
Crown Leaching	-.4	.04	6.0	1.5	3.0	19.9
Trapped Aerosols			6.9	3.5	2.1	15.2

From Miller, Cooper and Miller (1976).

GASEOUS INPUTS FROM THE ATMOSPHERE

Nitrogen

The ultimate souce of most organic nitrogen in forest ecosystems is through fixation from the atmosphere, either through micro-organism-plant symbiosis or through free living micro-organisms. Especially in the early stages of forest successions, when the density of nitrogen fixing plants is often high, inputs of nitrogen can equal the highest rates achieved in agricultural systems. Thickets of alder for example, are thought to fix around 50 to 100 kg N ha^{-1} yr^{-1} (e.g., Daly 1966, Voigt and Steucek 1969). Lower but none-the-less important inputs are made as nitrogen-fixing plants become less dominant. In Western Australia, for example, acacias, bossiaeas, kennedias, casuarinas and macrozamias are common understorey plants capable of fixing nitrogen. In recent studies Halliday and Pate (1976) estimated that about 19 kg N ha^{-1} yr^{-1} is fixed by macrozamias on sandy soils of the Swan Coastal Plain. Acacia pulchella on lateritic soils in the jarrah forest east of Dwellingup has been estimated to fix about 10 kg N ha^{-1} yr^{-1} over a two year period on a burnt site at a density of 5 plants m^{-1}. In more sparse understorey the amount of nitrogen fixed would be lower, but it would probably be higher than the input of <1 kg N ha^{-1} yr^{-1} estimated for precipitation. Nitrogen inputs through fixation are being studied at present by Grove and Malajczuk (personal communication) in the jarrah forest and in the denser bossiaea and acacia understorey of the karri (E. diversicolor) forests of the south west of Western Australia.

Rates of non-symbiotic fixation of nitrogen in forest soils are usually considered to be low, however with improvements of techniques more reliable estimates may show that this means of N fixation is more important than hitherto supposed. Jorgensen (1975) reported 1 kg N ha^{-1} yr^{-1} fixed in upland soils on the South Carolina Coastal Plain and 10 kg N ha^{-1} yr^{-1} in swamp soils in the same area. Todd et al. (1975), estimate that 5 to 14 kg N ha^{-1} yr^{-1} is fixed in the floor of the deciduous hardwood forest in North Carolina.

Non-symbiotic fixation of nitrogen does not appear to have been studied extensively for Australian forests and possibly deserves greater attention in the future.

TABLE 4

Mean Values for Amounts of Elements in

Throughfall and Rainfall

Catchment		Elements in throughfall and rainfall					
		Na	K	Ca	Mg	Cl	SO_4-S
				(kg ha^{-1})			
Wights & Salmon							
Proportion of cover ≃.7							
Rainfall 845 mm	Throughfall	34	9.5	4.2	5.8	73	4.8
October 1973 to	Rainfall	24	1.7	2.6	3.2	48	3.3
July 1974	Difference	10	7.8	1.6	2.6	25	1.5
Dons, Ernies & Lemon							
Proportion of cover ≃.5	Throughfall	10.4	2.3	1.6	1.8	21.9	1.7
Rainfall 437 mm	Rainfall	7.7	1.3	1.3	1.1	15.4	1.4
October 1973 to	Difference	2.7	1.0	.3	.7	6.5	.3
July 1974							
Northern Hardwood*							
New Hampshire	Throughfall	.6	26.9	7.0	2.0	6.6	24.2
1 June 1969 to	Rainfall	.4	.4	.9	.2	2.5	5.1
28 October 1969	Difference	.2	26.5	6.1	1.8	4.1	19.1
Rainfall 556 mm							

* Eaton, Likens and Bormann (1973).

INPUTS OF ELEMENTS BY ABSORPTION OF GASES

In locations where the gaseous pollutants SO_2 and NO_2 occur the amounts of these gases absorbed by forest vegetation and soils can be large. Calculations based on uptake of SO_2 by vegetation indicate that 1 kg SO_2 ha^{-1} day^{-1} can be absorbed in the forest situation and the soil can absorb a further 0.3 kg SO_2 ha^{-1} day^{-1} (Hill 1971, Moss 1976). This amounts to about 500 kg SO_2 absorbed in a year. Around some industrial areas problems have arisen due to toxicity from large amounts of pollutants. The acid rain phenomenon of Scandanavia (Wright and Gjessing 1976) and North America which affects forest and fresh water lakes in these regions, has been attributed to continuing inputs of pollutants from industry.

PARTICULATE INPUTS FROM THE ATMOSPHERE

Dust is a usual component of the material collected in continuously open rainfall collectors and the range of values obtained in Western Australia was from 8 to 319 kg ha^{-1} yr^{-1} (mean 78 kg ha^{-1}). The elemental composition of this dust was not determined but recent studies near large industrial centres show that inputs of some elements can be considerable. Studies of trace element inputs have been made at a relatively unpolluted site near Lake Windermere (Westmoreland) by Cawse and Peirson (1972) and at the Walker Branch Watershed, Oak Ridge, Tennessee U.S.A., where there were local contributions from coal fired steam plants and automotive emissions (Table 5).

TABLE 5

Inputs of Trace Elements in Rain

Location of Sampling Sites	Inputs of Elements (kg ha^{-1} yr^{-1})							
	Cd	Cr	Cu	Hg	Mn	Ni	Pb	Zn
32 stations in U.S. (average values)	-	-	.20	-	-	.04	.30	.89
8 stations in Delaware Watersheds	.08	-	.04	.001	-	-	.06	-
Lake Windermere North West England	<.25	.04	.33	<.003	.12	<.09	<.20	1.21
Walker Branch Watershed, Tennessee	.15	.04	.23	.003	.25	.09	.25	.50

Accumulation of toxic elements such as Pb may affect the functioning of forest ecosystems, directly through toxic effects on tree nutrition, or more indirectly through decreasing the rate of litter decomposition, and hence nutrient cycling (Dixon, Luxmoore and Begovich 1976).

The dispersal of lead emissions from a smelter in Port Pirie in South Australia (Tiller, Merry, Cartwright and Bartlett 1975) shows that the area affected by industrial emissions can be large. Such pollution would need to be taken into account for forests adjoining industrial plants.

THE ATMOSPHERE AS A SINK FOR NUTRIENTS

Although there have been many studies of inputs of nutrients from the atmosphere, outputs to the atmosphere from forest ecosystems have received less attention. Outputs possibly occur through wildfires, prescribed burning, denitrification, reduction of sulphur compounds to H_2S, and erosion by water and wind.

The effects of fire have been studied for many forest conditions. Ashing of litter releases nitrogen to the atmosphere largely as N_2, but products such as NH_3 and NO_x (NO and NO_2) have been detected. Lewis (1975) reports unexpectedly high concentrations of NO_2^- in a water extract of gases from experimental burning pine litter. Elements other than nitrogen remain in the ash and fine particles may be transported by wind or convection into the atmosphere. Most field studies do not show significant losses of cations, phosphate or sulphate directly attributable to fire. However after an intense wildfire in a coniferous ecosystem at Entiat Experimental Forest, Washington, Grier (1975) reported losses through volatilization and ash convection of 855 kg ha^{-1} N, 75 kg ha^{-1} Ca, 33 kg ha^{-1} Mg, 282 kg ha^{-1} K and 698 kg ha^{-1} Na.

Generally losses of nitrogen from forest ecosystems due to denitrification have not been quantified because convenient methods for estimation have not been developed. Todd, Waide and Cornaby (1975) recently estimated potential denitrification in a deciduous forest ecosystem at 18 kg N ha^{-1} yr^{-1} using the N_2O incubation method (Barbaree and Payne 1967). If this potential is approached in the field, denitrification could result in outputs of nitrogen to the atmosphere that are significant in relation to the inputs resulting from biological fixation.

SOILS AND ROCKS AS SOURCES OF NUTRIENTS

Soils function both as stores in nutrient cycling and as sources of inputs from weathering. The largest quantities of nutrients are released at the soil/rock weathering interface. An estimate of the amounts of elements contributed from this source can be calculated if the rate of rock weathering is known. Barth (1961) estimates that on a world scale the rate of rock weathering is about 270 kg ha^{-1} yr^{-1} and although rates are particularly difficult to estimate with confidence, values of the same order have been found by other workers. Accepting this world rate for the granites weathered to laterite in Western Australia, and the weathered zone and rock analyses given by Gilkes et al. (1973) the following amounts of nutrients would be released annually (Table 6).

The amounts of elements that have accumulated in a 40 year period in the karri forest in the southwest of Western Australia are shown in Table 7 for comparison with inputs to the ecosystem in rainfall and possible inputs from weathering.

Ovington (1968) estimates that well grown forest plantations in temperate regions have mean annual accumulation rates, over a 50 year period of about 12 kg N ha^{-1}, 6 kg K ha^{-1}, 7 kg Ca ha^{-1} and 1 kg P ha^{-1}. These rates are similar to those in Table 7.

TABLE 6

Elements Released by Weathering Granite

Element	Amount released annually (kg ha^{-1})
Na	9
K	9
Ca	6
Mg	2
Mn	.11
P	.07
Zn	.03
Cu	.003
SO_4-S	.004+
Cl	.06+

* Based on a weathering rate of 270 kg rock ha^{-1} yr^{-1}.

\+ Sulphate sulphur concentration was higher in weathered material - release estimated from concentration in rock. Chlorine released was estimated from average concentration in a set of 30 granite samples from Belka, W.A. (Bettenay, Blackmore and Hingston, 1964).

THE SOIL AS A NUTRIENT SINK

Nutrients such as phosphate, molybdate and minor elements undergo reactions in soils which lead to their "fixation" in very stable minerals. The elements may become associated with iron oxides, form minerals such as the goercexites, (Norrish 1968) or become associated with manganese oxides (McKenzie and Taylor 1968). Elements are also bound in litter and soil organic matter which may be considered as temporary sinks.

DRAINAGE WATER AS A NUTRIENT SINK

Possibly the most significant sink for nutrients is the drainage flowing from forested catchments. This has been recognised in the classic studies of nutrient balances by Bormann, Likens and their co-workers. These studies have been particularly successful in integrating inputs and outputs for forests occupying small catchments. However the applicability of catchment balance studies is limited by the accuracy with which inputs and outputs can be estimated and the problem of possible concealed leakage from the catchments. Large changes in forest management have produced clear changes in composition of drainage water, thus providing a valuable large scale monitoring system (Likens et al. 1970, Peck and Hurle 1973). However for smaller changes effects are more difficult to assess because of wide fluctuations in input-output balances resulting from fluctuations in climate.

Balances for forested catchments in New Zealand and in New Hampshire U.S.A. are compared with those for eight catchments in the Darling Range in Table 8.

TABLE 7

Annual Accumulation of Elements in Karri Forest

South West of Western Australia

Element	Mean Accumulation over 40 years ($kg\ ha^{-1}\ yr^{-1}$) Trees	Understorey	Litter	Total
Na	1	.1	N.D.	>1.1
K	5	1	.6	6.6
Ca	15	1	9	25
Mg	3	.2	1.5	4.7
Mn	.4	.01	.3	.7
P	.4	.04	.2	.6
Zn	.002	.0008	.01	.01
Cu	.006	.001	.01	.02
S	.3	.15	.65	1.1
Cl	4	.6	N.D.	>4.6
N	4	1.5	2	7.5

The Western Australian catchments appear to be more out of balance for chloride than either of the other two areas. This may be the result of a small proportion of clearing (up to about 5%) or spread of jarrah-dieback in the Western Australian catchments. Based on previous records, Peck and Hurle (1973) estimated that the ratio of saltflow to saltfall was about 1.1 to 1.6 for these catchments, compared with ratios of 3 to 21 for catchments with 30 to 70% of the land cleared. For catchments that are out of balance an alternative way of considering the data is to calculate the net output from the difference between the output and a past input estimated from the Cl output and the proportion of ions in rainwater. This calculation is intended to indicate the relative losses and gains of nutrients to the catchment over a longer period than was sampled. It is based on the assumption that Cl is not significantly removed from the cycle

TABLE 8

Studies of Nutrient Balance for Forested Catchments

Taita - New Zealand, Area = 4.36 ha

Element	Input	Output	Input-Output	
			Δ = Net Input (kg ha^{-1})	$\Delta Cl = 0$
Na	17.1	22.7	-5.6	-6.9
Mg	2.3	1.5	0.8	0.6
Ca	2.8	2.3	0.5	0.3
K	2.3	1.8	0.5	0.3
Cl	34.2	31.6	2.6	*

Hubbard Brook W6, Area = ≃ 30 ha

Element	Input	Output	Input-Output	
			Δ = Net Input	$\Delta Cl = 0$
1966-67				
Na	1.3	6.8	-5.5	-5.9
Mg	0.4	2.9	-2.5	-2.6
Ca	2.4	10.7	-8.3	-9.1
K	0.6	1.7	-1.1	-1.3
Cl	6.9	4.6	+2.3	*
SO_4-S	14.4	17.1	-2.7	-7.5
1967-68				
Na	1.8	8.8	-7.0	-7.0
Mg	0.8	3.4	-2.6	-2.6
Ca	3.0	12.2	-9.2	-9.1
K	0.8	2.4	-1.6	-1.6
Cl	5.2	5.3	-0.1	*
SO_4-S	16.0	19.3	-3.3	-3.0

Table 8 cont.../

Catchments in south west of Western Australia (8) Mean area = 10,900 ha

Element	Input	Output	Input-Output Δ = Net Input	 ΔCl = 0
1972				
Na	24	47	-23	0.0
Mg	3.0	6.6	-3.6	-0.7
Ca	2.3	3.6	-1.3	+0.9
K	1.9	1.8	+0.1	+1.9
Cl	45	88	-43	*
SO_4-S	2.9	2.8	+0.1	+2.9
1973				
Na	40	73	-33	-7.9
Mg	4.9	9.7	-4.6	-1.7
Ca	3.8	4.4	-0.6	+1.8
K	3.2	2.9	+0.3	+2.3
Cl	75	122	-47	*
SO_4-S	4.9	4.6	+0.3	+3.4

TABLE 9

Ratios of Elements to Chloride in Eucalyptus diversicolor *and* E. calophylla

	Ratios of Elements to Chloride Na	 K	 Ca	 Mg	 S
E. diversicolor	.27	1.05	3.29	.77	.084
E. calophylla	.25	.64	1.09	.52	.056
Rainwater	.56	.021	.020	.067	.047

in vegetation or by fixation in the soil and that rainwater composition is similar from year to year. An interesting indication from the calculation is that sulphate, potassium and calcium appear to be accumulating in the forested catchments of the Darling Range. Six cleared catchments in the Darling Range which appear to be more seriously out of balance, losing much more as output than received as input, give results (Net Input for ΔCl = 0, + 18 kg Na ha^{-1}, -10 kg Mg ha^{-1}, + 2 kg Ca ha^{-1}, + 12 kg K ha^{-1} and + 14 kg S ha^{-1}) indicating past accumulation of sulphur, sodium, potassium and perhaps calcium in the catchments.

Analysis of cores to 30 m depth in some Darling Range laterites shows that the amount of adsorbed sulphate stored in the profile is much greater than would be accounted for by its proportion in rainwater salts or by the concentration of sulphur in granites sampled nearby. It seems possible therefore that some of the net gain of S to the catchments could be due to adsorption in the deep lateritic sediments. Loss of sulphur by reduction to H_2S and gaseous loss may occur from swampy areas.

Calcium and potassium and to a less extent magnesium and sulphur are taken up in biomass in larger relative proportion to chloride than occurs in rainfall (Table 9). Therefore these elements will be cycled close to the soil surface and deeper drainage water will be relatively depleted. Some evidence of this relative depletion is given in the proportions of exchangeable and soluble potassium and calcium in the pallid zones of laterites.

Contributions to streamwater from weathering, aerosol salt trapped by vegetation, and losses from the catchments in dust (soil and organic debris) are among the factors not taken into account in the simplified analysis given here. The errors introduced by these omissions could substantially alter interpretations of nutrient balances for the catchments. As an example consider the data from the Western Australian catchments if throughfall (Table 4) represents increased inputs due to trapping of aerosol salts. Recalculation of the data on this basis would indicate a closer balance of chloride inputs and outputs. Net inputs of K^+ would be greater, Mg^{2+} would be slightly greater, Ca^{2+} would be little affected, SO_4^{2-} would be slightly less and Na^+ would be considerably less. However if the change in composition of throughfall passing through the canopy is due to leaching of some ions from leaves, branches etc, i.e. is not a net input to the catchments, the results in Table 8 are more appropriate. There are similar uncertainties concerning the effects of inputs from weathering on the ionic composition of streamwater. Thus estimates of net nutrient contributions to, or losses from, relatively undisturbed forest systems made from catchment studies alone seem unlikely to be reliable. Studies of paired catchments or comparisons of catchments prior to and after a large amount of disturbance appear to offer better prospects for qualitative assessments of changes in nutrient balances; however even for these the situation is complex (see O'Loughlin "Hydrologic aspects of nutrient transport" in this symposium).

CONCLUSION

While the sources and sinks for nutrients in forest ecosystems can be readily identified, accurate estimates of the amounts of nutrients involved are clouded by some uncertainty.

Review of the available data suggests that the differences between inputs and outputs are probably small for undisturbed forests. In forests disturbed through harvesting (including clear-felling) or fire, or mining for example, significant increases in outputs of particular nutrients have sometimes been found. Estimates of annual inputs of nutrients from the atmosphere, and possible inputs from weathering, are of the same order of magnitude as the quantities of elements accumulating in the biomass of young forest stands (up to 40 years old). However since inputs cannot be considered in isolation from outputs, it cannot be deduced that the nutrient requirements of the forest can be made up solely from these sources.

It can be argued that the soil has a relatively large store of nutrients which can be drawn upon. While this is true for the total amounts of elements, their availability to plants is extremely low in many forest soils. Thus the possibility remains that fertilizer may need to be applied after forest disturbance even for conservative management of forest ecosystems.

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SOME PROBLEMS OF MEASUREMENT IN NUTRIENT CYCLING STUDIES

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The distribution of nutrients in indigenous open forest ecosystems is notoriously variable, and an accurate measure of any part of the nutrient cycle is a major exercise in sampling technique. This note comments on three common problems of measurement, using illustrations from the Cooloola area of south-east Queensland.

Nutrient cycling studies at Cooloola, which is typical of the coastal sand-masses of the area, are one facet of a program of multidisciplinary research on processes involved in landscape stability. The vegetation of the different ecosystems present ranges from low shrubby forms near the coast, through open eucalypt forests dominated by either scribbly gum or blackbutt, patches of rain-forest, and then depauperate woodland and heath further inland. Nutritional characterization has involved measurement of atmospheric accession, throughfall and litterfall, ground litter and nutrients in the soil compartment and drainage waters. The initial aim was to obtain a broad picture of nutrient status. The following problems appear of particular importance:

(1) What proportion of nutrients is in the biomass? This seems indeterminate without enormous labour input, though mensuration techniques at least offer an approximation. For some studies, nutrient fluxes will characterize ecosystem activity adequately. But in areas such as Cooloola where the soil store of nutrients is small, the size of the biomass compartment becomes a more significant factor in ecosystem stability.

(2) What is the size of the soil compartment? Even though the majority of roots are in the upper horizons, small but significant nutrient supplies may be available at depth, in either B or C horizons, and given adequate water and oxygen supply should favour root proliferation. This may be the situation at Cooloola, where the soils are podzols, some with B horizons at considerable depth[+].

(3) Lateral variability at the forest floor. This is clearly large, but at least part can be allocated to specific features - such as tree density, species, and size. It might be feasible then to separate these features, and describe the ecosystem in terms of "selected positions," rather than to seek a mean value for the entire system. This can be illustrated by the throughfall data in Table 1.

In this example it is of value to know how the "selected positions" differ from one another, and certain of them could be used as characteristics of the ecosystem. It is desirable to have a measure of the proportion of ground surface covered by the selected positions - perhaps with the help of photogrammetry.

An analagous problem arises with agricultural crops, where two types of experiment can be recognized: (a) <u>agronomic</u>, for which an average value for a field is desired. Replication is used to reduce error, and variability is only of interest in its effect on precision; (b) edaphic, where studies are confined to small areas for which variability is low. Comparisons are made between several such areas, with the object of recognizing the reasons for variability between them. A similar concept may be useful in ecosystem studies.

TABLE 1

Throughfall Analyses for "Selected Positions" under the Canopy of two Tree Species and in the Open (9-month period)*

Species	Position under canopy	Ca	Mg	Na	K
			(kg/ha)		
Scribbly Gum	Base	11.8	22.1	105.6	22.4
	Half Canopy	7.0	15.3	83.6	11.8
	Canopy Edge	6.4	16.2	79.1	12.9
Banskia	Base	6.3	12.8	82.1	9.9
	Half Canopy	8.0	14.9	69.5	13.1
	"Open"	3.8	7.8	45.9	6.9

* Tri-acid digest

+ Thompson, C.H. (1975). Proc. R. Soc. Qld. 86: 109-20.

SYMBIOTIC NITROGEN FIXATION BY CORALLOID ROOTS OF THE CYCAD *MACROZAMIA RIEDLEI*: PHYSIOLOGICAL CHARACTERISTICS AND ECOLOGICAL SIGNIFICANCE.

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Abstract

'Coralloid' roots containing blue-green algae occur commonly on the upper root stocks of *M. riedlei* in natural habitat in Western Australia. Each coralloid mass persists for several seasons; replacement sets form at irregular intervals, especially after fire.

$^{15}N_2$ and acetylene reduction assays demonstrate that coralloid roots fix nitrogen at physiologically significant rates.

C_2H_2 reduction rates by coralloid roots are higher in winter than in summer. Performance is positively correlated with rainfall; soil temperature appears to be of lesser importance. Diurnal fluctuations in nitrogenase activity occur.

Calibration using $^{15}N_2$ gives a molar ratio of C_2H_2 reduced: N_2 fixed of 5.8:1. The seasonal average of C_2H_2 reduction of 14.8 nmol per g fresh wt coralloid root per min is then equivalent to 37.6 g N per kg fresh wt per year, a fixation rate potentially capable of doubling coralloid root nitrogen once in every 8 weeks, and whole plant nitrogen every 8-11 years.

Returns of fixed nitrogen in two natural populations of *Macrozamia* are estimated by compounding measurements of biomass of host and symbiotic organs with the seasonal average for coralloid fixation rate. The values obtained (18.8 and 18.6 kg N ha^{-1} $year^{-1}$) indicate that *Macrozamia* contributes significantly to the nitrogen economy of its ecosystem.

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NITROGEN FIXATION RATE OF *Albizia lophantha*

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INTRODUCTION

Albizia lophantha (Willd) Benth. rapidly colonizes moist jarrah forest sites in South Western Australia following fire (Dell 1970). It also establishes rapidly when seeded onto rehabilitated bauxite mined sites, which occur within the jarrah forest, and as such may have value as a pioneer cover crop.

Several shrub species native to the jarrah forest fix nitrogen at physiologically significant rates (Halliday and Pate 1976; Shea and Kitt 1976) and this investigation extends observations to the legume *Albizia lophantha*. The quantity of actual nitrogen fixed by seedlings is compared to that predicted from rates determined by the acetylene reduction technique (Dilworth 1966) and the quantitative relationship between acetylene reduced and nitrogen fixed determined.

MATERIALS AND METHODS

Five germinating *A. lophantha* seeds were sown into each of 48 15 x 15 x 10cm plastic pots of sterile white sand in a glasshouse maintained at 22°C. Each pot was inoculated with 200ml of freshly pulped nodule suspension obtained from four month old *A. lophantha* seedlings. All pots were supplied with 200ml of full strength, minus nitrogen, nutrient solution (Halliday 1975) twice a week for six weeks then one third strength once a week. Pots were brought up to field capacity daily and thinned to four plants each at week four.

Four weeks after sowing shoots were severed, roots shaken free of sand and all root plus nodule material from each of eight replicate pots incubated. Standard assay consisted of incubating roots plus nodules for 60 minutes in a 750ml vessel containing a 90:10 air-acetylene mixture. Incubation proceeded in the light at 22°C. Following incubation, gas chromatography for detection of ethylene produced was carried out using the technique of Halliday and Pate (1976). Further assays were similarly conducted until the eighth week after sowing. Actual nitrogen per whole plant was recovered as ammonia by steam distillation of Kjeldahl digests.

RESULTS

Specific activity, expressed as nmole acetylene reduced per mg fresh weight of nodules per minute, was plotted for each sampling occasion (Fig. 1). The resulting curve was simply integrated by assuming the indicated mid-week fixation rate was maintained for the whole week. Nodule fresh weight data were also interpolated mid-week (Fig. 2). Actual nitrogen per plant values were corrected by subtraction of an average seed nitrogen content of 0.184 mg and are plotted in Figure 3.

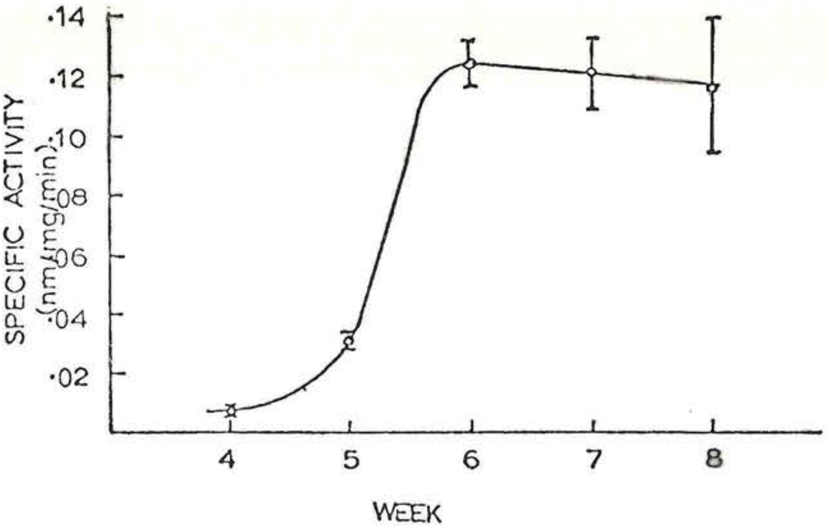

Figure 1. Specific activities measured by acetylene reduction assay.

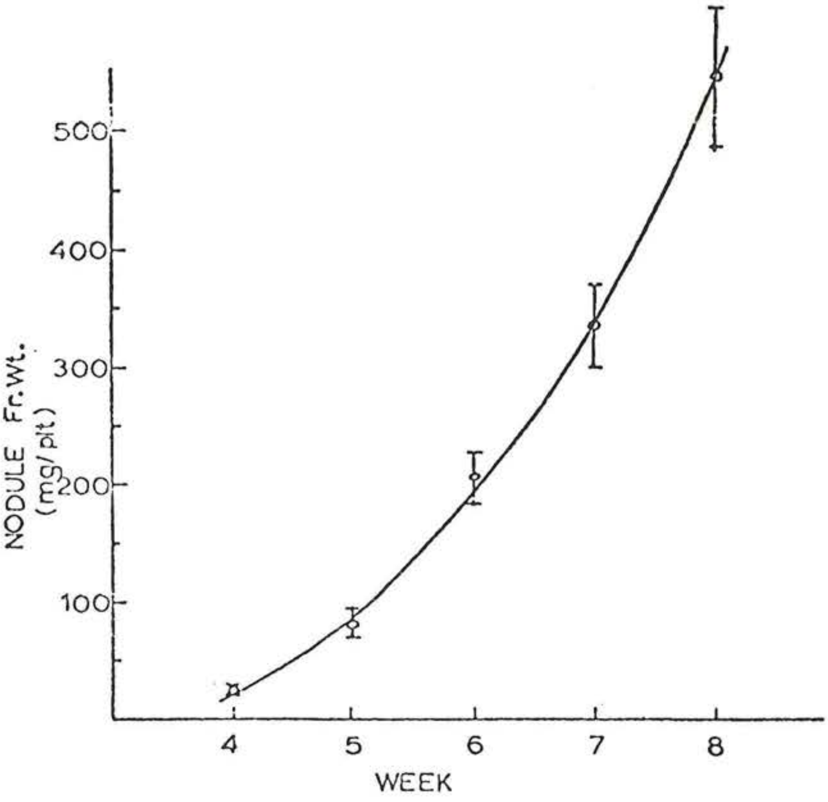

Figure 2. Nodule fresh weights of plants used in acetylene reduction assay.

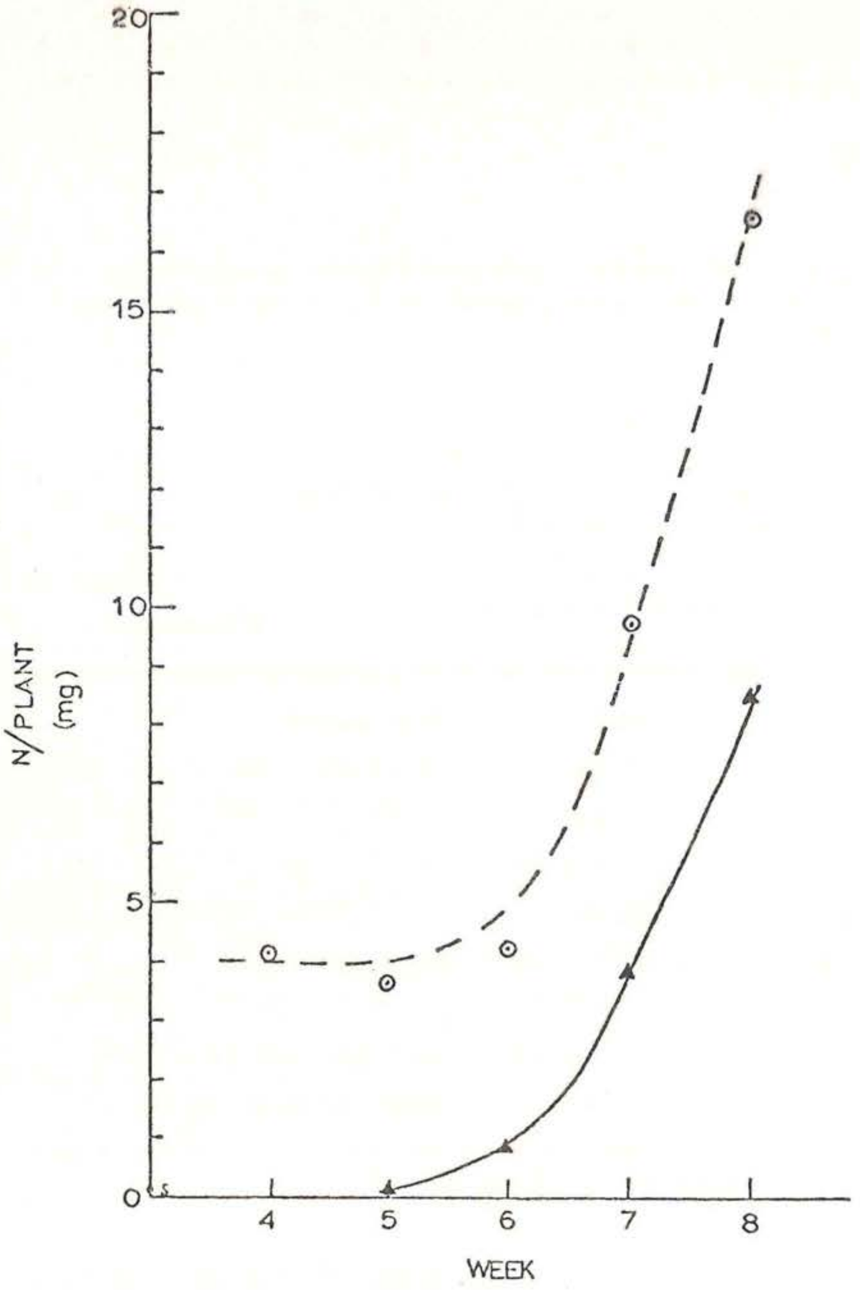

Figure 3. Plots of actual --⊙-- and predicted —▲— rate of N accumulation by Albizia lophantha

S = Seed nitrogen.

Assuming an acetylene reduced to nitrogen fixed ratio of 3:1 and molecular weight of nitrogen equivalent to 28.02 $gmol^{-1}$, predicted nitrogen content is less than actual nitrogen per plant (Fig. 3). A conversion ratio of 2.04:1 is indicated under the conditions of this experiment.

DISCUSSION

Specific activity of *A. lophantha* eight weeks after germination, compares quite favourably with rates reported for a variety of agricultural legumes (Table 1).

TABLE 1

Specific Acetylene-reducing Activities of Some Nitrogen Fixing Plants

Species	Specific Activity $nmol\ mg^{-1}\ min^{-1}$	Reference
*Albizia lophantha**	0.12	This paper
Glycine max	0.15	Cited in Hardy *et al.* 1973
Medicago sativa	0.11	" " "
Pisum sativum	0.11 - 0.22	" " "
Trifolium pratense	0.35	" " "
Lupinus angustifolius	0.10 - 0.25	Halliday 1975
Vigna sinensis	0.20 - 0.60	" "
*Macrozamia riedlei**	0.005 - 0.032	Halliday and Pate 1976
*Acacia pulchella**	0.064	Shea and Kitt 1976

* Species occurring naturally in jarrah forest.

These data indicate that *A. lophantha*, in terms of nitrogen fixing ability, is as suitable for minesite revegetation as alternative agricultural species. It is interesting to note that *A. lophantha* displays higher acetylene reduction activity than *Acacia pulchella*, which showed the greatest activity of four jarrah forest legumes examined by Shea and Kitt (1976). It is possible, however, that sub-optimal nodulation or activity in their experiment may account for this difference.

Fixation rate varies diurnally, in a species dependent manner. Minchin and Pate (1974) have shown that *Pisum sativum* cv. Meteor displays peak fixation during the photoperiod whereas Halliday (1975) found that *Vigna sinensis* showed maximum fixation at night. Since *Albizia* is essentially a sub-tropical genus (Fosberg 1965), as is *V. sinensis*, it may also reach peak fixation at night. Assays here conducted during the day may therefore have underestimated fixation potential, thus explaining the disparity between predicted and actual nitrogen fixed. Diurnal fixation data for *A. lophantha* are needed to clarify this point.

Aspects of technique which may have suppressed fixation include decapitation (Oghoghorie 1971; Hardy *et al.* 1973) and dessication (Hardy *et al.* ibid.). Competition by nitrogen due to failure to replace air with an inert gas is reported to reduce acetylene reduction by soybean nodules by 10 to 20% (Hardy *et al.* 1968). *Macrozamia riedlei* however, showed no change in fixation rate in an argon-oxygen atmosphere (Halliday and Pate 1976). It is possible that disruption of xylem and phloem continuity may have occurred when shaking roots to dislodge sand, thus interfering with the supply of metabolites to the nodules during assay.

No data exist on the nodule density achievable by *A. lophantha* in the field nor on rates of leakage and return of nitrogen to the soil. However, *A. lophantha* is known to achieve high plant densities naturally (Dell 1970) and when seeded on minesites. This combined with its short life span (Loneragan *pers. comm.*) indicates that the species may be capable of contributing ecologically significant quantities of nitrogen in both cases.

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CARBON AND NITROGEN FLUX THROUGH NATIVE FOREST FLOORS

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The forest floor, which is defined for the purpose of this symposium as the surface litter layer together with the underlying humus-enriched mineral soil, is the site of mineralization processes which release nutrients previously immobilized in the plant biomass. Decomposition is mediated through the interaction of soil animals and microorganisms which receive a continual supply of food and energy in the form of litter fall. Thus it is on the forest floor that the two major functional processes of energy flow and nutrient cycling interact. A knowledge of energy and nutrient flux through the forest floor should therefore lead to a greater understanding of the factors that regulate the productivity of the whole system, and perhaps serve as a basis for predicting the ecological effects of forest management practices.

It is not practicable to review all the literature relevant to our brief, viz. that dealing with 'flows of energy, water, carbon and nutrients, including litter decomposition and mineralization processes'. Instead, we will briefly outline some background ecological theory, and then describe our experience in studying forest floor metabolism. Some of the results achieved and the difficulties encountered will be discussed.

BASIC PREMISES AND PROCESSES

We accept the conventional graphic model of an ecosystem as a series of storages and compartments linked by flows of energy and materials; and we further accept the need to identify and measure as many of the individual flows and storages as possible. But given that our resources for undertaking such studies are limited, which ones and how many should we attempt to identify, and how do we go about measuring them? What is the best way of finding out how the system works?

There are three broad physiological processes basic to ecosystem function, viz: photosynthesis, respiration and nutrient absorption. Except in special circumstances, the solar energy captured by photosynthesis (gross primary production) is the total amount of energy available for all the energy-requiring reactions of the system. These include biosynthesis, growth, nutrient uptake and transport, and the energy needed for these purposes is provided by the conversion of photosynthate in the process of respiration. Thus nutrient fluxes are mediated by energy transformations, and hence the key to understanding nutrient cycling lies in the partitioning of energy flow through respiration. This may be achieved through a knowledge of the basic production equations (Table 1).

TABLE 1

Ecosystem Production Equations

Net primary production:	$NPP=GP^{\dagger}-R_a$	(1)*
Net community production:	$NEP=GP-R_e$	(2)*
Total community respiration:	$R_e=R_a^{\dagger}+R_h$	(3)*
Heterotroph respiration:	$R_h=R_c^{\dagger}+R_d$	(4)*
Net community production: (by substitution)	$NEP=NPP-R_h$	(5)*
Decomposer respiration:	$R_d=R_z^{\dagger}+R_m$	(6)
Microbial respiration:	$R_m=R_f^{\dagger}+R_b^{\dagger}+\ldots$	(7)

* Adapted form Woodwell & Botkin (1970)

† GP = gross production; R_a = autotroph (producer) respiration; R_c = consumer (herbivore and carnivore) respiration; R_z, R_f, R_b = respiration of soil and litter fauna, fungi and bacteria respectively.

'It is a first objective in study of the function of terrestrial ecosystems to solve these equations' (Woodwell & Botkin 1970). Our initial concern, in studying energy and nutrient flux on the forest floor, is to determine R_d, decomposer respiration. Ultimately we may need to partition R_d into its several components, i.e. solve equations (6) and (7), but the first step in understanding forest floor metabolism is to measure R_d, i.e. the rate of release of carbon and energy in the soil-litter subsystem, and the concomitant fluxes of major plant nutrients.

MEASURING FOREST FLOOR METABOLISM

Forest floor metabolism reflects the energy and nutrient demands of the soil and litter biota. Three approaches to its measurement seem most useful, viz. through litter fall, litter decomposition, and soil respiration. These will be described in turn.

1) Litter Fall Method

In a mature forest, approximating a steady state system, the annual input of litter and the amount which is decomposed each year should be equal, i.e. $L=R_d$. The amount of litter that accumulates on the forest floor at equilibrium depends on the rate of litter fall relative to that of litter breakdown. Forest ecosystems differ considerably in these respects (Table 2).

TABLE 2

Litter Fall, Energy Input and Surface Litter Accumulation in Three New England Forests

Forest	Litter Fall* $t\ ha^{-1}\ yr^{-1}$	Energy Input $kJ\ m^{-2}\ yr^{-1}\ x10^{3}$	Surface Litter† $t\ ha^{-1}$
Grassy forest	3.85	7.94	4.52
Layered forest	10.01	20.28	12.37
Mossy forest	5.10	10.35	8.11

* Means of 3 years' observations, 1972-75

† Means of 4 samplings spread over a 54 week period, 1973-74

Olson (1963) has examined the relationship between production and decomposition of organic matter on the forest floor. If X represents the accumulated surface litter, and L the annual input in litter fall, then $dX/dt = L-kX$, where k is the 'decomposition constant'. At steady state, X does not change hence $L=kx$ and $k=L/X$. The decomposition constant may therefore be estimated by measuring L and X, provided steady state conditions prevail.

While this method provides a very simple and direct measure of forest floor metabolism, estimates of L and X frequently lack precision. Apart from the question of design of litter traps there are considerable sampling problems, and replication must be adequate to cope with temporal and spatial variations in litter fall. A minimum of 25-30 traps per hectare has been recommended (Medwecka-Kornaś 1971), but the number needed for any given level of confidence will depend on the variance of the sample and hence its mean value, and so the requirements for major litter fractions such as leaves will differ from those for relatively minor ones such as branches. This is illustrated by our studies in three New England forests, where a sampling intensity of 30 traps (0.45 m^2) per hectare was used.

In these studies[1], litter was collected at 4-weekly intervals (13 collection periods p.a.) and partitioned into six components, viz. leaves, barks, twigs, branches, flowers and fruits, and miscellaneous. Mean daily inputs per

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[1] The forests are described, the project aims stated, and some findings reported in Charley & Richards 1974; Richards *et al.* in prep.)

4-week period were calculated for each fraction. Except for leaves (and for bark and twigs in one community) these litter samples had coefficients of variation in excess of 10% in all periods during three years of observation. The number of periods in any one year in which the coefficient of variation in leaf fall (the major litter fraction) was less than 10% ranged from 2 to 12 depending on forest type. Thus if one is interested in monthly fluxes of various litter components, then 30 traps per hectare provide an inadequate sample in these communities. Temporal variability is reduced when total litter fall (all fractions combined) is considered, but at periods of minimum input variability still falls outside acceptable limits (Table 3). This table shows however, that if the major concern is the total annual litter fall, then the sampling intensity used was adequate. It is also apparent that variability is greatest in the community with the most discontinuous canopy, viz. Grassy Forest; this is no doubt due to greater spatial variation in litter fall at this site. All sites however showed considerable spatial heterogeneity, as evidenced by the fact that there were highly significant 'trap' effects each year, i.e. mean annual litter input differed significantly among traps.

In the final analysis, the time available to collect and process the litter samples will greatly influence the sampling intensity chosen. While no practicable sampling procedure will give adequate precision for all litter fractions over monthly intervals at all times of the year, 30 traps per hectare is clearly sufficient to estimate total annual litter fall in the three test communities with a high level of precision.

TABLE 3

Coefficients of Variation (%) in Periodic and Annual Litter Fall*

Year	Community†	Period of Max Input	Period of Min Input	Annual Input
1972-73	GF	10.6	100.6	7.0
	LF	4.0	58.0	2.8
	MF	10.0	53.2	5.7
1973-74	GF	9.0	170.3	5.5
	LF	4.1	25.6	1.9
	MF	7.3	63.8	3.6
1974-75	GF	7.9	59.6	4.8
	LF	3.9	20.6	1.9
	MF	5.8	26.4	3.8

* Each period is of 4 week's duration, i.e. 13 periods p.a.

† GF = Grassy Forest; LF = Layered Forest; MF = Mossy Forest

Seasonal and spatial variation must also be taken into account in sampling the standing crop of litter on the forest floor. The three New England forests differed in the amount of litter accumulated on the soil surface. Means of 4 samplings (10 replicate, 0.5 m^2 quadrats per sample) over a 58-week period are given in Table 2. The corresponding coefficients of variation were: GF, 33.2%; LF, 32.8%; MF, 11.1%. Placement of quadrats in these samples was to some degree subjective in that logs were avoided, as too were obvious accumulations of bark around the bases of gum-barked eucalypts. The 'bark halo' effect around *Eucalyptus saligna* in the Layered Forest was investigated by Smith (1974). He found a significantly greater ($p<0.01$) accumulation of bark downslope from these trees than along transects directed upslope or along contours; however immediately adjacent to the base of most trees there was a narrow zone (*c.* 25 cm wide) where less bark had accumulated, possibly as a result of stem-flow run-off during rainstorms. The halo effect extended for at least 1 m from the base of the trees, and significantly higher levels of bark ($p<0.01$) were found within 1 m of the trunk than at distances greater than 1.25 m. Other species of plants undoubtedly show similar effects, for example even casual observation suggests an accumulation of fronds around the bases of tree ferns in the Layered Forest. Such spatial variation in surface litter may not however be always so apparent.

TABLE 4

Decomposition Constants and Litter Half-Lives

Forest	Based on Surface Litter Only		Based on Surface + Incorporated Litter	
	k*	$t_{\frac{1}{2}}$ (wks)	k	$t_{\frac{1}{2}}$ (wks)
Layered forest	0.96	37.5	0.75	48.0
Mossy forest	0.60	60.1	0.44	81.9

* Values of X used for calculating k are means of 3 samplings and therefore differ slightly from weights of surface litter shown in Table 2.

Calculation of Litter Half-Life. The decomposition constant ($k=L/X$) may be used to estimate the rate of decay of litter once it reaches the forest floor, assuming no further input of litter occurs. This is a special case of the general equation $dx/dt = L-kX$ in which L is zero and thus $dx/dt = -kX$. In other words, the decomposition rate is proportional to the amount of litter present and decay is exponential.

We may therefore calculate a theoretical 'litter half-life', analogous to the half-life of a radionuclide, which is given by the expression, $t_{\frac{1}{2}} = \ln 0.5/k$. Decomposition constants, and thus half-lives, will differ according to forest type, and will be different for differing litter fractions within any one forest type. But there is a further source of variability, due to the fact that a substantial proportion of litter is incorporated in the topsoil (buried by animal activity?) and can be recovered as recognizable components by wet sieving. This is another cause of spatial heterogeneity in forest floor litter, in addition to those already discussed, and adds to the sampling problems involved in estimating litter standing crop. The inclusion of this material, which is undecomposed but incorporated in the topsoil markedly affects the calculation of the decomposition constant and hence litter half-life (Table 4).

2) Litter Decomposition Method

Of several variants of this technique, the most common involves placing weighed quantities of air-dry leaves in nylon or fibre glass mesh bags and fixing them in or on the litter mat in the field. Replicate bags are taken up, the contents cleaned, dried and weighed at predetermined intervals, and decay rates (weight lost per unit time) calculated directly. It is imperative that the leaves to be used be collected as they fall from the canopy in the weeks immediately preceding the commencement of the exercise, so that they approximate the energy and nutrient status of leaf fall at the time the bags are set out. The method does not seem well suited to other litter components but is particularly useful for studying the effects of soil fauna on leaf comminution and subsequent decomposition. For example, particular kinds of soil animals may be excluded from the bags by appropriate choice of mesh size, so that some idea of the relative contribution of various taxonomic groups, and their interaction with microorganisms, can be obtained (e.g. Edwards & Heath 1963). Confining litter in mesh bags creates somewhat artificial conditions however, and may result in reduced decay rates (Witkamp & Olson 1963). Furthermore, leaf fragments may be lost during recovery of the bags, and foreign material may enter the bags, so that the variability of the estimate of weight lost increases greatly as time progresses.

Decay curves approximate exponential functions, with a period of rapid initial weight loss followed by protracted breakdown of more refractory plant products. Superimposed on this pattern of exponential decay are seasonal variations due to changes in temperature and moisture (Olson & Crossley 1961). In the New England forests no significant seasonal effects were observed. Overall leaf decay rates, based on 1 cm mesh nylon bags, are given by the following equations (W = percentage of initial weight in grams after T days):

LF $\ln W = 2.2594 - 0.00136T \qquad R^2 = 0.566$

MF $\ln W = 2.3114 - 0.00161T \qquad R^2 = 0.753$

Neither the regression coefficients nor intercepts in the two equations differ significantly, indicating that leaf decomposition proceeds at about the same rate in both forests. This does not accord with the results obtained from the litter fall method (Tables 4, 5).

TABLE 5

Half-Life of Leaf Litter as Determined by Different Methods

Forest	Method		
	Leaf Fall		Mesh Bag
	k	($t_{\frac{1}{2}}$ (wks)	$t_{\frac{1}{2}}$ (wks)
Layered forest	2.89	12.5	72.8
Mossy forest	1.51	23.9	61.4

3) Soil Respiration Method

Soil respiration, as an index of microbial activity in soils under controlled conditions in the laboratory, has been used by many workers. Useful as this approach is for comparative purposes, it cannot give an estimate of respiration rates in the field. This is especially so if the soil samples are mixed, air-dried and re-wetted before testing: in the New England forest soils, disturbed samples respired at more than four times the rate of undisturbed soil cores (Watson 1977).

As a measure of forest floor metabolism, soil respiration must provide a means of estimating the annual CO_2 output from decomposer organisms. Ideally, this could be achieved by monitoring CO_2 evolution in the field with an infrared gas analyser, provided that appropriate adjustment could be made to account for root respiration. This is not practicable in remote field locations where the only means of access is by 4-wheel drive vehicle, which is the situation confronting many forest research workers in Australia. In the absence of facilities for continuous monitoring in the field, a method is required which at least takes account of the major field determinants of soil respiration rates, viz. soil temperature and water potential. Woodwell & Botkin (1970) have described how gas exchange techniques can be used to study the metabolism of terrestrial ecosystems, and we are adapting their approach in building soil respiration models for two New England forests. A preliminary model, based on temperature as the environmental variable, was developed by Wise (1976) for the Layered Forest, using unpublished data of G.J. White, R.J. Hartigan and G.W. Watson (Watson 1977; White & Hartigan, in prep.). The essential steps are as follows:

(a) Establish the relationship between CO_2 output and soil temperature in the laboratory, measuring the respiration of large (23 cm diam.) litter/soil cores in a water bath, using an IR gas analyser. The regression equation was:

$$R_d = -2701.0 + 490.1T \qquad R^2 = 0.99$$

R_d is the decomposer respiration in cc CO_2 m^{-2} day^{-1}. The relationship holds for soil at 'optimum' moisture constant, i.e. *c.* pF 2.5 or 73% WHC, over the temperature range 13-22°C. (The negative intercept is unrealistic but not statistically significant, and an exponential model gave essentially the same end result.)

(b) Determine the annual soil temperature curve in the field, by monitoring temperature at 3-hourly intervals throughout the year. (The data used actually covered only 1-2 days per week for a period of five months, but was extended to cover the whole year by regression analysis based on soil temperature records from the CSIRO Pasture Research Station at Chiswick, near Armidale.)

(c) Use the regression of CO_2 on temperature to compute the annual soil respiration. This is a graph of the daily CO_2 output throughout the year (Fig. 1).

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(d) Obtain the area under the soil respiration curve, i.e. the annual CO_2 output, by integration. This provides an estimate of 1721 l CO_2 m^{-2} yr^{-1} as the respiration from the forest floor in the Layered Forest during 1975. It may be taken as a maximum value if soil water potential were maintained at a level optimum for microbial activity year-round.

The model could be refined if soil water potential were monitored in the field, but we have only a crude measure of the water regime in 1975 based on gravimetric determinations of moisture content at monthly intervals. Using this information, together with regressions of CO_2 production on soil water status derived from laboratory and field studies (Watson 1977), soil respiration in the Layered Forest is believed to be between 64 and 85% of that predicted by the model, i.e. 1101-1463 l CO_2 m^{-2} yr^{-1} or 589-783 g C m^{-2} yr^{-1}. This may be compared to a value of 430 g C m^{-2} yr^{-1} (1001 g litter m^{-2} yr^{-1}) derived by the litter fall method for the same year.

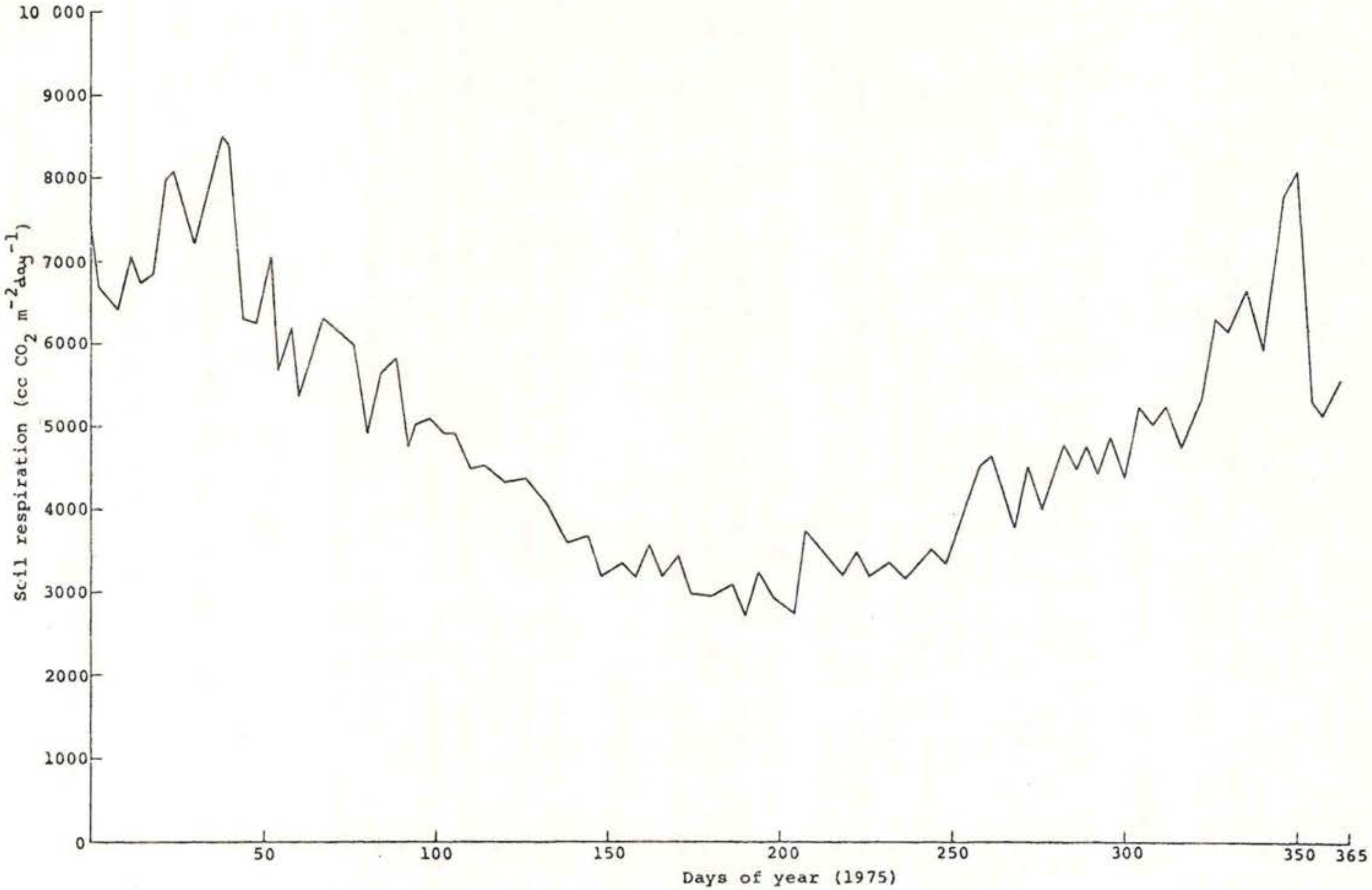

Figure 1. Annual Curve of Soil Respiration - Layered Forest (after Wise 1976)

Our estimate of forest floor metabolism based on the annual soil respiration curve utilizes CO_2/temperature regressions established in the laboratory. Soil respiration in the field is likely to be higher because it contains a component of root respiration (part of R_a) as well as decomposer respiration (R_d). At another site (Mossy Forest) field respiration was found to be 1.5 times laboratory respiration when both were measured on the same cores by alkali absorption (White & Hartigan, unpub. data). As a first approximation we have assumed that CO_2 output from intact cores, as measured by an IR gas analyser, represents decomposer respiration only, though the cores undoubtedly contain some severed root segments.

NITROGEN TURNOVER AND THROUGHPUT

Nowhere is the interaction of energy and nutrient pathways more apparent than in the nitrogen cycle, and discussion of nutrient fluxes will be confined to this element for that reason. With no primary mineral source of nitrogen available for plant nutrition, mineralization-immobilization reactions of the soil microflora play a key role in determining ecosystem productivity. The energy needed to drive these reactions is that released during the oxidation of soil organic matter, the supply of which is maintained through the processes of litter fall and decomposition on the forest floor.

A first step in studying the dynamics of nitrogen in the soil-litter subsystem is to identify major pools of the element and the transfer rates between them. Some of the problems encountered in doing so are illustrated below, by reference to studies in New England forests.

1) *Nitrogen Storages*

Surface Litter Layer. The standing crop of nitrogen in the litter layer may be determined by summation of the nitrogen contents (o.d. weights x % N) of individual litter components (Table 6). Problems of spatial heterogeneity in surface litter, and the degree to which undecomposed fragments are incorporated in the upper mineral soil are exacerbated by the variation in N concentration among litter components. Basing standing crop estimates on a composite sample of the litter layer may therefore lead to inaccuracies.

TABLE 6

Nitrogen Storages on the Forest Floor (g m^{-2})

Forest	Litter	Soil	
		Total N (0-15 cm)	Mineral N (0-7.5 cm)
Grassy forest	3.35	1004	0.307
Layered forest	9.19	450	0.269
Mossy forest	11.01	457	0.410

Soil Organic Matter. Only the nitrogen capital of the upper mineral horizon has been determined. This underestimates the total store of soil nitrogen but probably represents the most active zone so far as turnover of nitrogen is concerned. Detailed grid sampling revealed considerable spatial variability in total N concentration at all sites.

Mineral Nitrogen. Ammonium and nitrate levels were determined on eight occasions over a period of one year. Despite substantial within-site variability, significant community effects in mean standing crop of mineral N (NH_4 + NO_3) were discerned (Table 6). The greater store of mineral N in Mossy Forest was due to higher ammonium levels, viz. 324.1 mg N m^{-2} compared to 230.4 in Grassy Forest and 175.2 in Layered Forest. In all three communities, the concentration of mineral N was lowest in autumn and winter (2-8 ppm), rising rapidly in spring and remaining high throughout summer (15-20 ppm in GF and MF, 5-8 ppm in LF). These seasonal and spatial changes emphasise the need for careful design of sampling procedures if valid estimates of mineral N pools are to be obtained.

2) Nitrogen Fluxes

Litter Input. Nitrogen input to the forest floor varied appreciably among communities both in terms of total deposition and in the relative contributions of various litter components. Seasonal trends can be observed also, and normal patterns of accession may be distorted by chance events such as windstorms. Superimposed on these sources of variability were temporal changes in N concentration within individual litter fractions. To obtain accurate estimates of nutrient input it is essential to distinguish between litter falling at different seasons, to fractionate the litter samples, and to analyse the components separately. Preliminary estimates thus obtained for the annual accession of nitrogen in the Layered Forest are: leaves 5.65, bark 0.61, twigs 0.65, branches 0.17, total litter 8.25 g N m^{-2}. Leaves were the major vehicle of litter N input in Grassy Forest and Mossy Forest also, amounting to 65 and 60% of the totals (2.95 and 5.50 g N m^{-2} respectively).

Litter Decomposition. Chemical analyses of leaves from nylon bag experiments provide direct evidence of nitrogen release from decomposing litter. As an example, decay curves for Layered Forest are shown in Fig. 2. The rate of loss of nitrogen from leaves closely parallels dry weight loss in this community.

Decomposition constants for leaf nitrogen can also be calculated from the formula $k = L/X$, as for organic matter. The values determined were 2.92 for Layered Forest and 1.52 for Mossy Forest; corresponding half-lives for nitrogen are 12.3 and 23.7 weeks. This method is not really applicable to the Grassy Forest where ground vegetation makes a substantial contribution to energy and nutrient input to the forest floor.

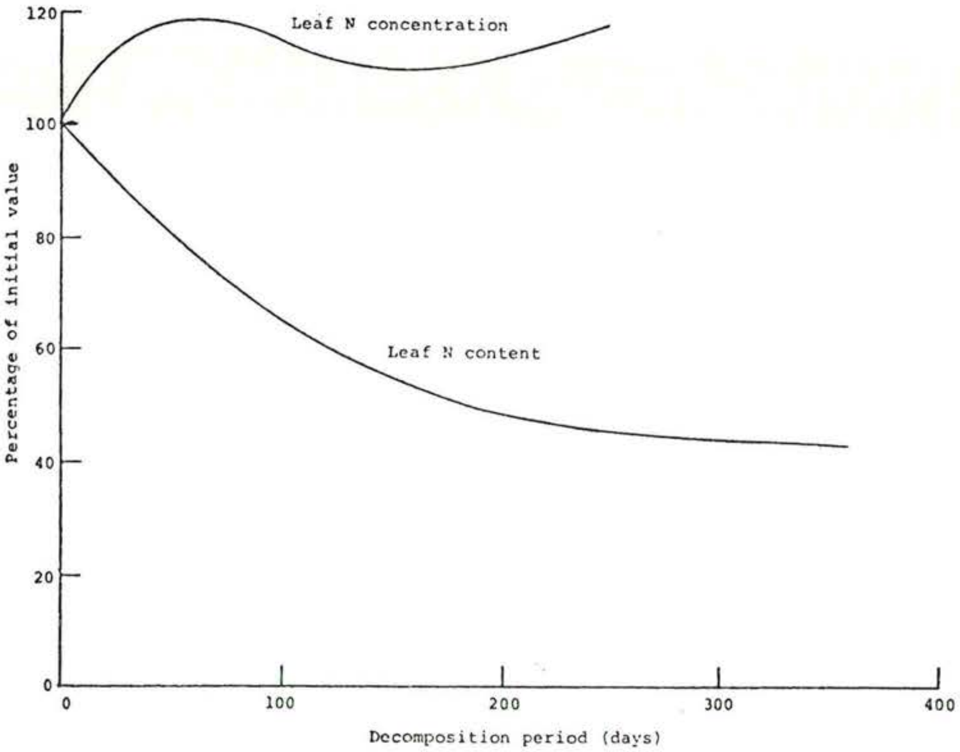

Figure 2. Decay Curves for Leaf Nitrogen Concentration and Content - Layered Forest

Mineralization Rates. Incubation of soil samples for 2 weeks in the laboratory released over 90% of the organic N immediately available for oxidation. Rates of mineralization were determined as the difference in mineral N of field-moist, paired soil cores before and after incubation at 33°C. The seasonal pattern of ammonification potential was similar at all three sites but the Layered Forest soil showed much greater capacity to nitrify and more variability in nitrification potential throughout the year than did the other two soils. Despite this temporal variability, the mean values of eight samplings throughout the year (Table 7) revealed highly significant differences in the capacity of the three forest soils to mineralize organic nitrogen.

TABLE 7

Nitrogen Mineralized in Intact Soil Cores

($g\ m^{-2}\ 2\ wks^{-1}$)

Forest	NH_4-N	NO_3-N	Total Mineral N
Grassy forest	3.73	0.024	3.75
Layered forest	2.15	0.437	2.59
Mossy forest	6.29	0.090	6.38

Significant within-site variation in ammonium and nitrate production was evident in each forest. In a further study of mineralization rates using Bremner's (1965) technique, (Bale 1974) showed that sites with a southern aspect had a greater capacity to mineralize nitrogen than those with a northern aspect: mineralization coefficients, i.e. mineral N produced during 2 weeks' incubation expressed a percentage of total N) averaged 2.76% in the former, 1.67% in the latter. There was in addition a significant site x aspect interaction which may be related to changes in vegetation type with changing aspect.

Laboratory incubation studies, even with intact soil cores, may not be a satisfactory guide to mineralization rates in the field, and this makes the estimation of mineral N fluxes very difficult. For one thing, mineralization rates can be affected by the presence of plants (Cornish & Raison 1977), and the rhizosphere effect on mineralization-immobilization relationships can be extremely complex (Bartholomew & Clark 1950). Incubation of disturbed samples is normally carried out with the fine soil fraction after sieving to remove root fragments and other extraneous material. This may give quite unrealistic results if there is a large quantity of roots in the soil. Thus net mineralization in cypress pine soils was reduced when roots sieved from the soil were replaced before incubation (Curtis 1975).

A more useful approach than laboratory trials might be to incubate soil cores *in situ* where they would be subject to prevailing weather conditions. Such studies, in conjunction with some form of field lysimetry, may offer the best solution to the problem of determining nutrient fluxes. In the meantime we must make use of whatever data is available. While there is little doubt that field mineralization rates fall well below the rates recorded in the laboratory, it is possible to make an estimate of the former from a knowledge of temperature/mineralization response curves and a knowledge of the soil temperature regime in the field. Smith (1974) developed multiple regression equations relating ammonium and nitrate production to temperature, using air-dried and sieved soil samples in the laboratory. The relationships for Layered Forest soil are shown in Fig. 3. The optimum temperature for nitrification of about 25°C is well above those found at 5 cm depth in the field for all but a few weeks of the year. The two temperature optima for ammonification are thought to be real for there is evidence from microbiological studies that a range of ammonifying populations is present each with its own distinctive temperature optimum. Ammonification is feasible at temperatures well in excess of any likely to be experienced in the field, and this seems to be related to the presence of thermophilic bacilli. Soil respiration is also possible at these very high temperatures (Watson 1977).

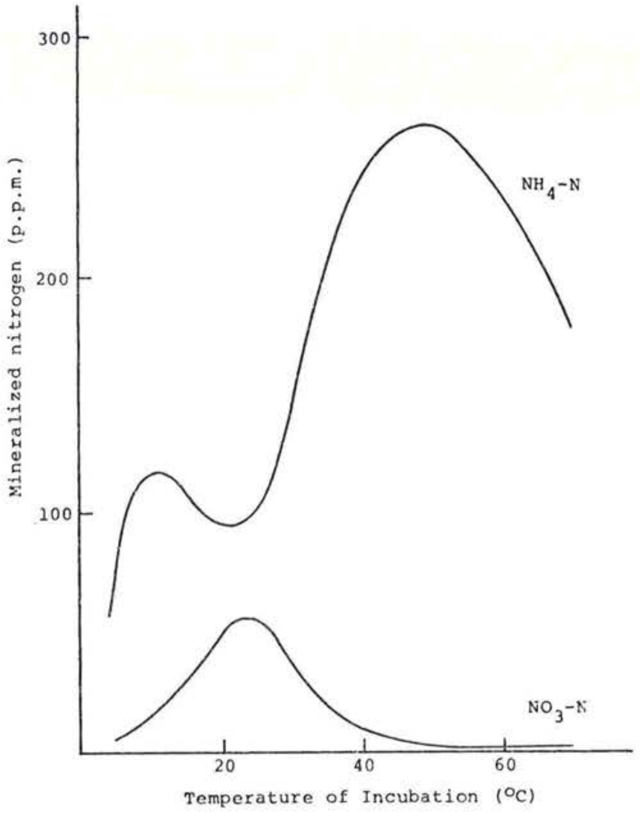

Figure 3. The Effect of Incubation Temperature on Production of Inorganic Nitrogen - Layered Forest (after Smith 1974)

The modelling approach used by Wise (1976) for predicting the annual CO_2 output could be used to estimate annual net mineralization, though the problem is more complex due to the absence of information on plant uptake rates and the effect that withdrawal of labile nitrogen by roots has on subsequent mineralization-immobilization reactions. For the present, we have made a rough estimate for the Layered Forest site as follows:

(a) Calculate N mineralized in disturbed samples per 13-week period from temperature/mineralization regressions, using mean seasonal soil temperatures for the four seasons. (Soil temperatures at 5 cm were estimated from air temperatures by regression equations based on measurements made at the site.) Sum these to determine annual production.

(b) Calculate the N mineralized per year if incubation of disturbed samples had been carried out at 33°C (the temperature used for incubating intact cores). Express the annual production as determined in (a) as a percentage of this value.

(c) Calculate the N mineralized per year from intact cores incubated at field moisture content, and reduce these values by the proportions indicated in (b).

Using this procedure, estimated field production is 33.5 g m^{-2} yr^{-1} of NH_4-N, and 11.4 g m^{-2} yr^{-1} of NO_3-N.

Model of Forest Floor Nitrogen

Fig. 4 is a model showing the major storages and fluxes of nitrogen on the forest floor. It is apparent that nitrogen in surface litter turns over very quickly, the standing crop being about the same size as the annual flux. In contrast the soil organic matter pool is very large, about an order of magnitude larger than the amount of mineral N flowing through it. Turnover in the ammonium and nitrate pools is extremely rapid, standing crop of each being two orders of magnitude less than the annual throughput.

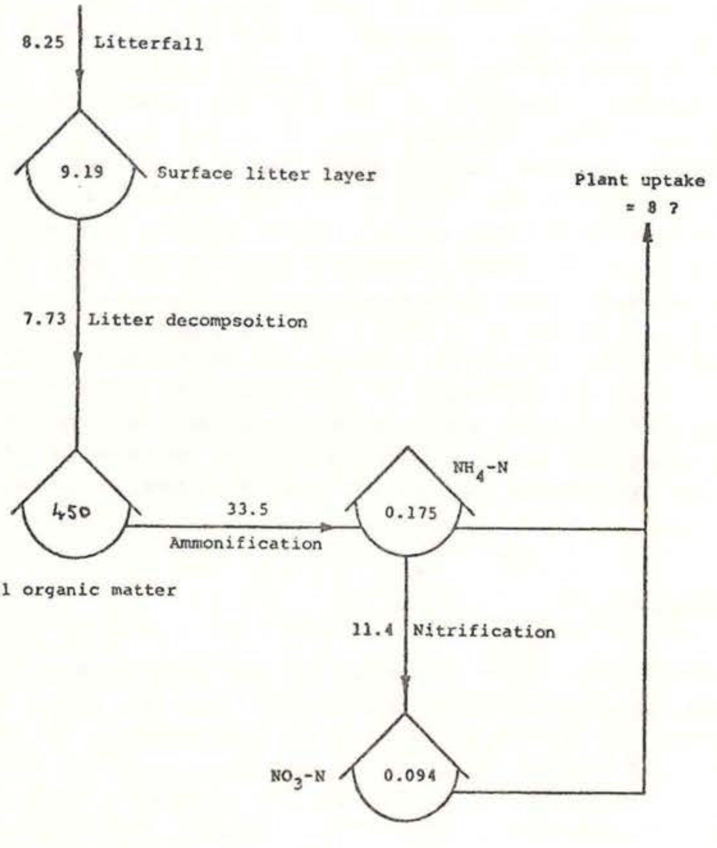

Figure 4. Storage (g m^{-2}) and Annual Flux (g m^{-2} yr^{-1}) of Nitrogen - Layered Forest

The model is admittedly very crude, in that inputs and outputs do not all balance. This is partly because not all pathways of nitrogen transfer between pools have been shown. Furthermore, many aspects of the cycle including denitrification, nitrogen fixation and microbial immobilization have been omitted altogether. Nevertheless it gives some understanding of how the system functions and has potential as a means of predicting the effects of management practices. For example, surface litter is a relatively small pool that releases nitrogen to the soil quite rapidly. Return of the litter layer to steady state after partial or complete destruction should also be quite rapid, a prediction borne out by empirical observation of the build-up of fuel following prescribed burning. In fact the effects of low intensity fires may be quite trivial as only minor withdrawal from the large soil organic matter storage should be sufficient to reconstitute the litter layer and restore equilibrium. Management practices such as clearfelling are more difficult to assess as they result in greater depletion of the nitrogen reserves on the site, and a longer period of dependence on the soil nitrogen pool before steady state conditions apply once more.

SUMMARY AND CONCLUSIONS

Forest floors are fundamental components of forest ecosystems where the interrelated processes of organic matter decomposition and nutrient mineralization have a regulatory function in determining community productivity. Since nutrient fluxes through the forest floor are mediated by respiratory energy release during litter breakdown, the partitioning of energy flow through respiration is a first step towards understanding nutrient cycling. In particular it is necessary to obtain a measure of overall decomposer respiration as an index of forest floor metabolism. This may be done directly by estimating carbon dioxide output from the soil-litter subsystem, or indirectly by the litter fall or litter decomposition methods. Advantages and disadvantages of all three approaches were discussed, and examples given. Nitrogen storages and fluxes were described, and models of forest floor respiration and nitrogen throughput presented. These models could serve as a basis for mathematical simulation studies by which the long-term effects of management practices might be predicted. Such an approach is desirable as intensive silvicultural techniques associated with even-aged management become more widespread in indigenous forests, since the alternative method of monitoring productivity by comparing yields through successive rotations is not practicable.

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NUTRIENT ABSORPTION AND ITS RELATION TO THE NUTRIENT COMPOSITION OF PLANTS

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Nutrient absorption is a key factor determining the nutrient composition of plants. However, its impact is modified by the distribution of nutrients within the plant, the loss of nutrients from the plant, and by the rates at which these processes operate in relation to the rate of plant growth and development.

This paper briefly reviews the nature of the processes involved and their interaction in determining the nutrient composition of forest crops.

ABSORPTION

Plant roots absorb nutrients only in a restricted region near their tips. A region at the root tip which has no mature xylem elements comprises the root cap, the meristematic cells, and the region of cell elongation. The cells, especially those of the meristem, have an unusually high capacity to absorb ions. They pass few of the absorbed ions to the xylem since they have a very high growth rate and since they can only transport ions to the xylem over relatively long distances in the symplasm.

Towards the base of the root, cells in the endodermis, pericycle, or the cortex may become heavily thickened and suberized; in advanced stages, they form a thick periderm of suberized cells which appear impermeable to water and minerals.

Most of the ions which reach plant leaves are absorbed and transported to the xylem in the region of the root lying between its heavily suberized base and its immature tip. In this region a central stele is clearly delineated. It contains fully differentiated dead xylem cells which provide a direct and uninterrupted connection with xylem vessels of the leaves.

Ions moving from the environment to the xylem must cross a permeability barrier at the endodermis. Most ions appear to do this by absorption into the cytoplasm of cortex cells and movement within the cytoplasm to the xylem parenchyma where they are excreted into the sap. The behaviour of calcium suggests that it may pass to the xylem sap by another as yet undefined route.

Absorption of ions from solution responds strongly to the concentration of the absorbed and other ions in solution. At the concentrations usually present in soil solutions absorption of ions into the xylem sap is metabolically controlled and hence is sensitive to oxygen concentration and temperature of the root environment.

Most results suggest that mineral accumulation ceases under anaerobic conditions and responds to increasing oxygen tensions to about 10%. Temperature coefficients vary from 2 at temperatures above 10°C to 6 or more at lower temperatures. Climatic factors influencing transpiration sometimes also influence both the rate of movement of minerals to the root surface and the rate of mineral accumulation in the xylem.

In soils the roots of many forest trees form ectotrophic mycorrhiza in association with soil fungi. Endotrophic mycorrhiza are now also known to occur in many plants. Both types of mycorrhizae appear important in absorption of phosphate, enhancing it markedly under conditions of low phosphorus supply. Some recent work with endotrophic mycorrhizae suggests that some strains may be much more effective than others in enhancing phosphorus absorption so offering a potential mechanism for improving phosphorus nutrition.

LEACHING

Nutrients which have accumulated in plant organs to concentrations in excess of their metabolic requirements appear to leach easily from leaves and stems in rain, fog, or dew. Consequently nutrients leach rapidly from plants given an excessively high supply and from organs at maturity. The nature of the nutrient seems less important since leaching can remove large amounts of both phloem-mobile and phloem-immobile elements. For example, leaching has removed up to 80% of both potassium and boron from leaves and more than 50% of calcium. Much of the loss may occur in guttation fluid which is subsequently washed from leaves. However, nutrients may also be washed out of the leaves themselves.

Potassium also leaches from leaves which do not contain excessively high concentrations. Thus leaves of rye grass containing around 1% potassium on a dry weight basis lost 2% of their potassium content in a single day of light, simulated rain; this rate of loss approximated the rate of potassium absorption.

MOVEMENT OF NUTRIENTS IN PHLOEM

The ability of plants to remobilise nutrients from leaves and transport them in the phloem to other organs is an extremely important property in the relationship between nutrient supply and the development of nutrient deficiency and in the relationship between nutrient concentrations in plants and plant growth.

Mobile Nutrients

A number of nutrients such as N, P, and K move readily to other plant organs from leaves in which they have accumulated. Indeed, their movement to young growing organs may continue to the detriment of the old leaves in which their concentrations may fall to deficient levels.

Several consequences flow from the rapid mobility of these nutrients. Plants which have accumulated excess concentrations in their leaves may continue to grow unchecked even when they have no external supply of these nutrients. Moreover, deficiencies do not develop until the total amount of nutrient in the plant as a whole becomes inadequate. For these mobile nutrients the concentration of nutrient in the plant as a whole gives a reasonable indication of the nutrient status of the plant. The concentration of nutrient in old leaves also gives a good indication of nutrient status and an early indication of deficiency. By contrast, the concentration of a mobile nutrient in young growing organs generally gives a poor guide to nutrient status since it remains high even when the plant is deficient.

Immobile Nutrients

These characteristics of nutrient deficiency for mobile nutrients stand in direct contrast with those for immobile nutrients such as Ca. Once deposited in plant leaves, Ca becomes virtually immobile. As a result, plant organs can only grow if they receive a continuous supply of Ca from the external medium or from the transpiration stream. The development of Ca-deficiency is thus largely independent of the total amount of Ca in the plant since it develops as soon as the external supply of nutrient becomes inadequate regardless of how much excess nutrient may be stored in older leaves. For example, plants transferred from high-Ca to low-Ca solutions developed severe symptoms of Ca-deficiency even though they contained up to five times more Ca than healthy plants given a low but continual supply of Ca: the oldest leaves of the deficient plants retained an excess of Ca in their leaves while apices and young leaves on the same plant developed symptoms of severe Ca-deficiency. Similar observations have been made for B, which is generally considered to be immobile in phloem.

Clearly, the contrasting behaviour of mobile and immobile nutrients must be taken into account when devising procedures for deficiency diagnosis. Concentrations of immobile nutrients in old leaves and whole plants, unlike those of mobile nutrients, may be quite misleading in assessing the nutrient status of plants. On the other hand, their concentrations in young tissues give a good indication of nutrient status.

NUTRIENTS OF INTERMEDIATE OR VARIABLE MOBILITY

Studies with radioactively labelled nutrients applied to leaves have led to the proposal that some nutrients (Fe, Mn, Zn, Cu, Mo) have a mobility from leaves intermediate between the freely mobile and the highly immobile nutrients. The degree of mobility of some of these nutrients may be highly variable depending upon environmental conditions and upon the stage of plant growth: under some conditions they behave as if highly mobile and under other conditions they behave as if immobile.

In the case of three nutrients for which data are available, mobility varies strongly with the adequacy of supply of the nutrient itself: mobility is highest at luxury concentrations and lowest at deficient. Such behaviour may lead to some peculiar anomalies in the relationships among nutrient supply, nutrient concentration in plants, and yield. In addition, experiments on retranslocation in plants given a luxury supply of nutrient may be quite misleading if extrapolated to interpret the behaviour of plants during the development of deficiency of the same nutrient. When given luxury supplies of Zn, several plant species have been shown to mobilise appreciable quantities of Zn from old leaves to developing inflorescence and grain but under conditions of Zn-deficiency the same species mobilise little if any Zn from old leaves even when they are senescing from Zn-deficiency.

Sulphur too is highly mobile when present at luxury levels. Apparently excess sulphur is present in leaves as sulphate and this moves readily out of leaves in phloem. By contrast, old leaves lose none of their protein - S or soluble organic-S even when S deficiency develops until they senesce.

Copper seems to behave in a manner similar to sulphur being highly mobile when adequate for plant growth and immobile from old leaves when deficient. Like sulphur but unlike zinc, copper moves out of old copper deficient leaves when they senesce.

The variable mobility of these elements influences the usefulness of analytical data for deficiency diagnosis. In the case of copper, the youngest leaves of plants given an excellent guide to the copper status of the plants whereas the old leaves may be positively misleading.

GROWTH AND ITS EFFECTS ON NUTRIENT COMPOSITION

The processes already discussed determine the content and distribution of nutrients in plants. Their effects on the concentrations of nutrients in plants depend upon the rates at which they change nutrient contents relative to the rate of change in the amount and distribution of plant matter, i.e. growth and development.

NUTRIENT MOBILITY AND LEACHING IN FOREST SOILS

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INTRODUCTION

There is a considerable literature on nutrient movement and interactions in soils, possibly commencing with a paper by Way (1950): 'On the Power of Soil to Retain Manure.'

Much of the literature concerns agricultural soils and it is useful to commence by examining differences from forest soils. Forest soils usually have an A_o organic layer at the surface. Additionally the nature of organic matter in soils is somewhat different to that in agricultural or grassland soils and the humus may be dominantly of fulvic acid type in soils developed under sclerophyll forests (Kononova 1961). Also Australian forest soils developed in association with eucalypts and over long periods without rejuvenation of the land surfaces are different to soils developed under conifers or deciduous hardwoods.

Much of forest soil science has however developed from studies of conifer or deciduous hardwood forests and relatively little is known of the dynamic mechanisms of nutrient movement in Australian forest soils. The text book classification of 'mull' and 'mor' is often not applicable to Australian forest soils and the L (litter), F (fermentation), and H (humic) layers in the A_o horizons are often indistinguishable. The A_o horizon may often be dispersed into the mineral soil by insects and, although mineralization is mediated by microorganisms, an overall view of mineral cycling in most Australian ecosystems would have to include mineralization by periodic fire.

Sources of nutrients can be classified as sedimentary or atmospheric (Odum 1971), and specific nutrients may enter or leave the forest ecosystem by either pathway. Once absorbed into the forest ecosystem nutrients are cycled at different rates by different pathways and mechanisms, both internally within the vegetation and externally via litterfall, stemflow and throughfall. The interface between litter and mineral soil where nutrients cycled in organic form are mineralized, and nutrients cycled in ionic form enter the soil system, is a convenient entry point at which to examine mechanisms of leaching.

Nutrient movement in soils can occur by mass flow or diffusion in saturated or unsaturated conditions. The gravitational (downward) flow of water through the forest ecosystem and into groundwater is a major interactant in most processes and for the purpose of examining leaching is a more convenient framework than one using energy flow through the ecosystem. It should also be remembered that absorption into the vegetation occurs not only by movement of nutrients to the rhizosphere of roots, but also by movement of roots to strongly fixed nutrients such as phosphorus.

NUTRIENT MOBILITY

Nye and Greenland (1960) developed the concept that movement and mobilization of cations in soils were dependent on the concomitant movement of anions. As electrical neutrality is necessary for the movement of dissolved salts in the soil solution, H^+ ions can be exchanged for cations held on the negative exchange sites of the soil. Nitrate, carbonate and sulphate ions can form in the soil by nitrification and soil respiration respectively. The incidence of both nitrate and sulphate in precipitation (acid rain) is now common in a number of forest ecosystems in Europe and North America as a product of industrial effluents in the atmosphere. The efficiency of anions as exchangers is a function of their bonding energies in a specific soil. Generally nitrate and sulphate ions are more efficient than carbonate ions.

The concept of an anion input (carbonates and nitrates) generated *within* the terrestrial ecosystem is however of particular interest because this has potential to explain one of the necessary cybernetic feedback mechanisms in which mobilization from fixed sources of nutrients could match nutrient uptake and why the retention of nutrients within terrestrial boundaries appears to be so efficient in face of the necessary mobilization for uptake.

LEACHING

Carbonic Acid Leaching. McColl (1972) working in Douglas fir forest in the Pacific Northwest of the USA developed a model of leaching based on carbonate ions. The source of carbonic acid is carbon dioxide associated with soil respiration. Bicarbonate and carbonate ions are formed in solution, bicarbonate being the dominant ion in most forest soils.

$$CO_2 \xrightleftharpoons{\text{pH } 4.5} HCO_3^- \xrightleftharpoons{\text{pH } 8.2} CO_3^=$$

McColl found that the partial pressure of CO_2 increased in the soil during periods between rains. Temperature was a major factor affecting decomposition and hence temperature integrated over time between rains was correlated with bicarbonate ion activity. A long dry period of high temperature could thus result in a considerable mobilization of nutrients in association with the first rainfall.

The general form of McColl's model is

$$I = a + bx + cy + dz$$

where I = total ions transported from the forest floor
x = total flow of solution
y = mean temperature of the dry period preceding flow
z = duration of the dry periods.

The effect of fire on soils also results in the formation of mobile ions at the soil surface. Initially the dominant anions may be OH^-. Equilibration with soil and atmospheric CO_2 and moisture results in carbonates, and cations in the ash and soil are again mobilized in the soil by the addition of mobile anions (Grier 1975).

Similarly, fertilizer applied to the surface of a forest floor can result in mobilization of both fertilizer ions, and native cations in the soil. Nitrate and sulphate fertilizers are relatively mobile in forest soils. Urea which hydrolyses to ammonium carbonates is not as mobile in the soil as the sulphate and nitrate salts of ammonia (Cole and Gessel 1965). Crane (1972) found that following decomposition of urea fertilizer, potassium, calcium and magnesium ions were mobilized in association with the bicarbonate ion.

However, urea fertilization and the resulting hydrolysis to ammonium bicarbonate resulted also in a mobilization of organic matter. This phenomenon also occurs with the addition of sodium or ammonium polyphosphates to organic rich soils.

Organic Acid Leaching. The phenomenon of mobilization of nutrients in association with the addition of some substance with dispersing or complexing properties introduces a second mechanism of leaching: that which can be labelled as 'organic acid.'

It has long been suggested (Cameron 1911; Wiklander 1958) that organic acids could play a major role in mobilizing nutrients in soils. Leaching of this type is obviously fairly common in most soils, and particularly so in most sclerophyll forest soils, where podzolization is the natural soil-forming process associated with organic acid leaching (Ponomareva 1964). The role of organic matter in mobilizing metals (nutrients) in respect to uptake by plants (rather than in relation to soil formation) has not been so readily accepted, possibly because the mechanisms of uptake of nutrients complexed with organic matter are not as fully studied or understood (Epstein 1972).

The mechanism of organic acid leaching should not be taken singularly, as the phenomenon embraces a wide range of organic physico-chemistry. Additionally it should be stated that organic matter in forest soils is being studied increasingly and our present understanding of its nature is changing rapidly. Forest humic material is polymeric, weakly acidic and polyanionic. Molecular weights range from several hundred to over 100,000 (Flaig 1971; van Dijk 1963) and the nature of organo-metallic bonding is complex and at present poorly understood (Jacks 1963; Greenland 1965; Zunino and Martin 1977). The latter workers have proposed multiple mechanisms and energies of bonding. Few workers would, however, disagree with the concept that mobilization of nutrients (particularly micronutrients) by organic matter is a major component of most mineral cycling processes in terrestrial ecosystems (Allison 1973).

Organic acid leaching is different to purely ionic leaching only in that organics are involved. Dissociated organic acids can act purely as electropositive or negative (usually anionic) exchange ions, so that cations may mobilize electrically neutral salts of organic acids in similarity to carbonic acid leaching.

However, organic matter can also act as mobile exchange ligands in which metal ions are complexed (Geering and Hodgson 1969). The mobilization of nutrient ions, which could not exist in solution form at the pH levels normally found in soils, is dependent on such a complexing relationship.

Johnson (1975) studying various forest ecosystems from tropical through temperate to alpine, found that organic acid leaching could comprise the dominant mechanism in some forest ecosystems, and carbonic acid leaching the dominant mechanism in others. Both were operative in temperate ecosystems, the relative proportion of each varying with many factors, particularly decomposition. In ecosystems where decomposition of litter was slow due to colder temperature, wide C/N ratios, etc., organic acid leaching was operative. Where decomposition was faster and more complete, such as in some tropical ecosystems, carbonic acid leaching of the type proposed by McColl (1972) appeared to predominate.

CONCLUSION

Few studies have been made on nutrient leaching in Australian forest ecosystems. Ellis (1971) has shown that eucalypt litters have varying (but generally considerable) abilities to complex heavy metals. Organic acid leaching is likely to be a considerable component of nutrient movement in many Australian forest ecosystems in relation to the complexing nature of the organic matter, wide C/N ratios of litter and, in many temperate ecosystems, relatively low rates of decomposition. Additionally the role of insects in the incorporation of litter into soils and decomposition may result in a considerable insect frass component of litter and consequently a specific organic chemistry which to date has not been qualified.

The decomposition/respiration rates shown by Richards and Charley (this symposium) must also be reflected in a carbonate equilibrium following the release of CO_2 into the upper soil horizons, so that carbonic acid leaching is also likely to be a component of leaching in Australian native forests. The role of fire also has considerable significance in changing the chemistry and mobility of nutrients in

Australian forest soils (Humphreys and Lambert 1965), and in view of its natural occurrence and increasing use as a part of management, the influence of fire on nutrient mobility is one of the first perturbations which should be studied.

Work in this area of research, concerning the mechanisms of nutrient mobility and leaching in Australian forest ecosystems appears to be necessary to answer many of the nutritional and environmental questions which are currently facing those managing Australian forests.

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HYDROLOGIC ASPECTS OF NUTRIENT TRANSPORT

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In earlier decades, the major impetus to the development of hydrology was its uses as an engineering design tool, with applications mainly in computing peak flood flows and reservoir storage requirements. In applications to agriculture, we have seen the development of soil-water physics in relation to the availability of soil water for plant use and the behaviour of saline soils. But the use of the known hydrological techniques in nutrient budget problems such as those becoming obvious on forest catchments, shows that much of the past emphasis is not relevant to the questions we are trying to answer. In the forest context those parts of the hydrological cycle useful for describing and understanding nutrient transport are those relevant to the flux of water between the times rainfall penetrates the forest canopy and when the same water appears at the catchment outlet - perhaps many years later; and the changes in solute chemistry need to be understood as water fluxes through each domain. It is the uncertainty of the water path and the residence time in each domain which makes the nutrient transport problem so poorly understood. Superimposing on these uncertainties a very sketchy understanding of the physico-chemical and biological processes which regulate the mobility of nutrient ions relegates the problem to one which takes it far beyond traditional hydrologic expertise, one which needs to be tackled with basic principles.

Water provides the medium by which most of the nutrients leave a catchment (gaseous transport and physical removal of biomass must, of course, be included in the budget arithmetic, but these are not considered here). To appreciate the quantity of nutrient materials which can be carried away with streamflow, it is worth reviewing the case history of the well documented Hubbard Brook watersheds. Part of that investigation involved comparing nutrient fluxes from two neighbouring and hydrologically similar coniferous catchments, one of which was clear-felled and treated with herbicides to inhibit all vegetative growth for three seasons. All biomass was left in situ. Johnson *et al.* (1969) published data on the chemical composition of the streamflow in the undisturbed catchments, and attempted to rationalise the observed variations in water chemistry in terms of dilution, ion exchange, and biological phenomena. The following table summarizes the observed relationships:

TABLE 1

General Behaviour of Major Ions in Stream Water of Hubbard Brook Catchments (Johnson et al., 1969)

	Dilutes with Stream Discharge	Concentrates with Stream Discharge	Chemically Buffered (Limited Extremes)	Response to Biologic Activity
Na	**	-	*	-
SiO_2	**	-	*	-
Mg	*	-	**	-
SO_4	*	-	**	-
Cl	-	-	*	-
Ca	*	*	*	-
Al	-	**	*	-
H	-	*	*	-
NO_3	0	**	*	**
K	-	*	*	**

** consistent occurrence
* irregular occurrence
- not manifested

Some ions behaved as though their original concentrations in the soil water became diluted as they were flushed out of the soil matrix by the percolating water. Others showed the reverse behaviour, becoming more concentrated in the stream as flow increased. Empirical relationships were derived to systematise the observations, but these seem less than satisfactory in explaining the reasons for the observed measurements. But in general terms, the study did at least identify some of the physical, chemical and biologic processes which gave credence to the variations in ion concentrations. The changes in stream chemistry and flow which occurred after the clear operations on one catchment have been reported by Likens *et al.* (1970), and by Bormann *et al.* (1974). As in the case of the earlier papers describing the Hubbard Brook experiments, the authors concentrated on stating the gross changes in flow and ionic concentrations, and produced credible but generally unsubstantiated arguments for the processes which could explain the changes. Table 2 lists some of the important changes which were observed in the years following deforestation.

Almost every ion showed a dramatic change in its behaviour. Nitrate reached levels in the effluent stream which were injurious to health; it has been stated that the stream water changed from a dilute sulphuric acid solution to a more concentrated nitric acid after the forest was cleared.

The Hubbard Brook work has suggested some processes which, when perturbed, grossly influence the nutrient transport on the catchment scale (the catchment scale is used here to distinguish from smaller scale and reversible processes which likewise affect local fluxes of nutrients, but which do not always lead to their loss from the catchment). One of the most dramatic relates to the nitrifying bacteria, whose numbers were observed to increase up to thirty-four fold; ammonia which would normally be taken up by living vegetation, was apparently oxidised to nitrate by the microflora of the deforested watershed, producing an abundance of nitrate ions which could rapidly be flushed through the soil. Hydrogen ions appear as a 'byproduct' in the nitrification process; H^+ ion concentration increased fivefold; these in turn became available to participate in ion exchange reactions in the mineral soil, mobilising in the process the metallic cations Na^+, Ca^{++} and Mg^{++}. While it is open to doubt that the pH change due to nitrification would still occur if natural re-vegetation had been permitted, it nevertheless focusses attention on the interdependence of biological and chemical or thermo-dynamic processes, and the critical sensitivity of catchment chemical balance to this kind of disturbance.

TABLE 2

Behaviour of Major Ions and Streamflow in Hubbard Brook Catchment Before and After Clearing (Likens et al., 1970).

	Concentration in Rainfall (mg/l)	Concentration in Runoff (mg/l) 1965/66	1966/67
Ca	0.22	1.81	6.45
Mg	0.03	0.37	1.35
K	0.05	0.19	1.92
Na	0.13	0.87	1.51
Al	0.1	0.22	1.5
NH_4	0.19	0.14	0.07
NO_3	1.45	0.94	38.4
SO_4	3.2	6.8	3.8
Cl	0.35	0.54	0.89
HCO_3	0	0.8	0.1
Evapotranspiration - cm		44.7	12.2
Runoff - cm		79.9	119.9
pH	4 - 7	5.1	4.3

We do not question the possibility that changes and effects similar to the Hubbard Brook experience can occur here. But we would be better placed to judge the likelihood of similar occurrences if we knew the properties of the physico-chemical environment at Hubbard Brook and if we knew whether the critical reactions (biological and chemical) could be transposed elsewhere. Particularly important should be the moisture content and water flux through the forest floor; these probably establish the in situ conditions in the top metre of soil, where most of the significant changes in soil-water chemistry occur. The subsequent history of water with its solutes is primarily a question of soil-water physics.

The point of the preceding discussion was to establish that knowledge of water movement into the forest soil is a pre-requisite to understanding solute transport. And the Hubbard Brook experiment has been cited to illustrate that soil "buffering" effects can be quite unstable, and not up to the task of preventing massive nutrient outflows given the right sort of perturbation.

What are the conditions which determine the moisture content changes in a soil mass and the water flux through it? Some of the important variables can be readily identified:

(i) the soil properties: its moisture content, hydraulic conductivity (dependent on moisture content and structural properties; variable with depth)

(ii) net water inputs: precipitation intensity and duration, evapotranspiration, groundwater fluxes;

(iii) topography: slope geometry, soil volume, water table geometry, etc.

Given knowledge of these conditions, we can at least empirically describe water movement in the soil and iteratively predict the changes in moisture content which occur. Analytical prediction of these changes is not yet at the 'elegant' exact stage, because nonlinearities intrude, but an intensive effort is currently directed at solving the water entry problem for the boundary conditions appropriate to rainfall, rather than for ponding of free water at the soil surface, for which the Philip infiltration theory is valid.

It is inappropriate here to discuss the status of infiltration theory under rainfall conditions, but it is worth considering the demonstrated relevance of the soil hydraulic conductivity, a property of the soil/soil water matrix. Knowledge of its variation with time (by in-situ tensiometer measurements) and with depth allows us to make inferences about the path followed by percolating water (i.e. vertical, or downslope?) and the chemical environments traversed by the moving water. If comparable knowledge on adsorption/desorption isotherms is available, then we can calculate the progressive changes in ion concentration which might occur. Again in this instance it is unlikely that analytical solutions for concentration changes are feasible or even desired, but the point is that powerful analytical methods exist for interpreting experimental observations within a coherent framework of physical chemistry. Hypothetical statements explaining ion concentration changes can thereby be validated or dismissed.

To the writer's knowledge, no study has been carried out on a natural surface slope where sufficient data have been collected to describe both water and solute fluxes in two dimension. It would seem that studies of this kind, in natural and 'disturbed' conditions, need to be made to supplement the Hubbard Brook type of gross catchment observation. Harr (1977) has calculated the rate of water movement along measured potential gradients in unsaturated slopes to demonstrate the importance of downslope movement of water, in a manner analogous to the elusive "interflow" discharge, long accepted by hydrologists. Harr's work is likely to be supported by supplementary experimental and analytical work which should allow the stream hydrograph characteristics to be related to measurable catchment properties notably hydraulic conductivity and geometry. A "spinoff" from Harr's work relevant to nutrient transport will be the knowledge of the pathways traversed by the moving water, and therefore the ion exchange conditions likely to be encountered.

Much attention has been given to the role of 'variable source areas' for generating overland flow during recent years. It should be demonstrable that rainfall striking one of these source areas will not have the opportunity of participating in ion exchange reactions or mobilising nutrients from within the soil mantle. It will instead be more prone to transport surface particulate matter, potentially rich in carbon and adsorbed phosphorus. It would be reasonable, therefore, to seek at least empirical relationships between particulate loads (if these are judged to be important) and the extent of these source areas. Such areas are most likely to occur at the toe of a concave slope, where the water table intersects the ground surface; their extent should be easily measured by observing piezometer levels close to the stream in relation to fixed topography. Steady state groundwater hydraulics suggests relationship between the saturated hydraulic conductivity (easily measured in the field), streamflow, slope, and the width of the saturated zone at the toe of the slope. The relationship has yet to be verified, but it is surprising that simple principles have apparently not been applied to the variable source area problem. In quite a contrasting analysis, Freeze (1972) has solved the complete set of equations for this situation, but the complexity of his analysis (necessarily numerical) makes it almost useless for exploratory nutrient transport work.

So opportunity exists to at least observe the occurrence of these variable source areas; it would seem logical to tie together the arithmetic of calculating the runoff produced from these overland flow areas, and their expected low dissolved solute loads and high particulate loads. As an aside, the occurrence of such source areas should be highly relevant to the type of forest floor disturbance which could be tolerated during forest operations; burning and loosening of the surface soil could have immediate and obvious consequences if carried out in an area which contributes to surface runoff.

In conclusion, some aspects of hydrologic processes in relation to nutrient transport deserve to be emphasised. The first deals with the fate of rainfall when it strikes the forest floor; will it infiltrate, or will some of it runoff? The different pathways infer that solute and particulate transport will differ markedly in the two cases. Resolution of this problem depends on analytical developments in infiltration theory for rainfall conditions, and verification of the relevance of variable source areas for surface runoff generation. The second aspect concerns development of satisfactory methods for sampling soil water for chemical analysis. Streamwater samples reflect catchment chemistry determined at times which are unlikely to be known, because many streamflow events can occur during the time required to transport solutes from their point of origin to the stream boundary. If suction lysimetry techniques are developed to the point where they can be used in the heavier forest soils, then the essential nutrient flux observations can be made in the domains where most of the significant changes take place, and the observations can be directly associated with known rainfall and runoff events.

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WHY CATCHMENT ECOSYSTEMS?

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The impetus given to nutrient cycling studies in forest ecosystems by the Hubbard Brook experiments (Bormann and Likens 1967, 1970) changed the direction of research towards studies of catchment ecosystems and increased the awareness of water as an important medium of nutrient transport. Ecosystem delimitation is an artifact of the researcher's objectives and because the boundaries of a rectangular prism (plot) placed over a unit of forest present no physical barrier to lateral movement, the catchment ecosystem concept has been considered to be a more self-contained integrative unit of study. Plot based studies however exploit the very large vertical component of nutrient movement in forests. The choice of approach lies in the degree of dissection of the structural, dynamic, and strategic attributes of forest ecosystems.

TABLE 1

Attributes of forest ecosystems (after Reichle 1975)

Structural	Dynamic	Strategic
Components	Homeostasis	Optimisation
Organisation	Circulation	Efficiency
Diversity	Stability	Adaption
Connectivity	Sensitivity	Perpetuation

Broadly, plot studies investigate structural aspects such as components and connectivity in more detail, with dynamic aspects being applicable at different scales to both approaches. Homeostasis and stability however, can be inferred from a less-sensitive catchment ecosystem approach.

Plot ecosystem studies may nestle within catchment ecosystems but the base of the rectangular prism is generally somewhere below, but within easy reach of, the soil surface. It is the intervening soil system that makes the water and nutrient dynamics of the above-ground forest ecosystem spatially, temporally, chemically, and conceptually distant from the stream water chemistry elucidated from a catchment study. Water passing through the forest canopy and litter layer becomes "nutrient charged", but the water chemistry changes very rapidly through only a short depth of soil (for example, Riekerk and Gessel 1965, McColl 1973a, 1973b).

In elucidating catchment response to forest ecosystems the distinction must be made between fluctuations in ecosystem functioning and larger perturbations of an external nature and the ability of the ecosystem to absorb change. Overall it appears that for mature, stable, forested catchments fluctuations in the internal cycling of nutrients, productivity, and biomass (apart from marked seasonality) are not reflected in stream water quality. Catchment ecosystems then represent the product of weathering under forest cover and as such are geochemical units (Bricker et al. 1968, Johnson et al. 1968).

Drastic surficial changes such as compartmental or total ecosystem removal are reflected clearly in stream water chemistry as demonstrated by the clear-falling experiments at Hubbard Brook (Bormann et al. 1974). There is, however, some consensus that the conditions prevailing after this deforestation were extreme and did not represent normal operations (Sopper 1975, Tamm et al. 1974). The buffering capacity of the soil is exceeded by clear falling, but this is not necessarily so for other edaphic traumas such as fertilisation and fire. The levels of fertilisation used in normal forestry operations are absorbed in most soils but can lead to differential leaching (Cole and Gessel 1965, Tamm et al. 1974). The effects of fire on stream water quality depend on the intensity of the fire but most material released at the surface is retained in the upper soil horizons (Severson et al. 1975, Grier and Cole 1971).

On the results of the deforestation experiments of Hubbard Brook, Gersmehl (1976 p.225) states:

".....in a striking commentary on the state of mid-twentieth century ecology, the news was hailed as revolutionary. Ten years of hindsight make the conclusions of those studies appear almost too obvious. In retrospect, the Hubbard Brook experiments seem more significant as outlook-changing stimuli than as knowledge-augmenting research."

How far does "the local context" justify duplicating catchment deforestation?

If one is after geochemical base data or the effects of large ecosystem manipulations it would be preferable to have at least paired catchments, but the constraints of homogeneity of treatments, vegetation, soils, slope, aspect, climate, and the need for an impermeable bedrock, which are imposed by the catchment ecosystem approach are such as to make experimental catchments unrepresentative or even untenable.

The catchment ecosystem, whilst being a powerful synthesising tool having the attributes of a more entire physical and conceptual framework, is a round-about, long-term, and expensive way of assessing changes and differences in nutrient cycling in forest ecosystems.

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SOME EFFECTS OF EXTERNAL FACTORS ON NUTRIENT CYCLING IN THE JARRAH FOREST ECOSYSTEM

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SUMMARY

The effects of three factors, viz

1. prescribed burning
2. jarrah dieback disease
3. bauxite mining

on the nutrient cycle in the jarrah forest ecosystem are briefly discussed.

Prescribed burning does not appear to have had any marked effect on the nutrient cycle, whereas jarrah dieback disease and mining operations can completely disrupt the process.

INTRODUCTION

Natural forest ecosystems which have persisted in an area over a long period of time tend towards equilibrium with their environment and under these conditions the movement of nutrients within the ecosystem is essentially cyclic in nature. Any disturbance of this system can have serious effects on the nutrient cycle and site deterioration has been reported where losses from this cycle are not balanced by the accession of nutrients (for example, Tamm 1932).

This paper outlines the results of some preliminary studies covering the effects of three different perturbations on the jarrah forest ecosystem in Western Australia, that is:

1. prescribed burning
2. the occurrence of *Phytophthora cinnamomi* Rands (Jarrah Dieback Disease)
3. bauxite mining

PRESCRIBED BURNING

The jarrah forest zone in the south-western corner of Western Australia experiences a typical Mediterranean climate with cool wet winters and hot dry summers and fire protection of the forest has always been a major forestry operation. The role of fire in the jarrah forest environment has been discussed in detail by Wallace (1966). In the early fire protection of the jarrah forest (1930-1953) regular burning of firebreaks alongside main roads, railway lines and other places of high fire risk were carried out and every effort was made to completely protect the forest country adjacent to the breaks. After 1953 the forest policy was altered so that regular prescribed burning on a 5-year cycle was carried out throughout the whole of the forest.

A comparison of the surface soils of the firebreaks and the unburnt compartments showed that no significant soil deterioration occurred as a result of the regular burning (Hatch 1959; Table 1). The most pronounced difference between the two sets of soils was the absence of the thick A_o horizon in the firebreaks whereas in the long protected compartments a litter accumulation of 25 tonnes per hectare has been observed.

TABLE 1

Analytical Data for Surface Soils (0-9 cm) from Protected Compartments and Regularly Burnt Firebreaks

		Compartment	Firebreak
		Mean Values	
pH		6.27	6.38
Total soluble salts %		0.016	0.015
Organic carbon %		2.96	3.00
Nitrogen %		0.125	0.128
Exchangeable cations			
Calcium	m.equiv./100g (%)	3.92 (67)	4.23 (69)
Magnesium	" " "	1.35 (24)	1.42 (23)
Potassium	" " "	0.11 (2)	0.10 (2)
Sodium	" " "	0.35 (7)	0.34 (6)
Exchangeable Hydrogen (pH 8.4)	" " "	12.00	10.97
Cation exchange capacity	" " "	17.73	17.06
Metal ion saturation %		32.1	35.5

Notes: (a) The data are the means of three composite samples each of which was made up of 27 individual constant volume subsamples.

(b) Differences were not statistically significant (P=0.05)

Additional data are available from Amphion 6, 19 km east of Dwellingup. This compartment has been protected from fire since 1932, and the firebreak has been regularly burnt on a 3-year rotation. Surface soil (0-10 cm) nitrogen values are available for two sampling periods, for which the results are shown below (Table 2).

TABLE 2

Amphion 6: Surface Soil Nitrogen Values

	Nitrogen (%)	
	1953	1977
Compartment	0.120	0.128
Firebreak	0.132	0.135

Note: (a) Differences in N levels are not significant (P = 0.05)

Preliminary experiments have shown that the nitrogen fractions in these two sets of soils are similar. For instance, there were no significant differences in the amount of nitrogen extracted by the standard sodium pyrophosphate-sodium hydroxide reagent (Kononova 1966). Similarly the nitrogen fractions released by hydrolysis of the soil organic matter with 6N hydrochloric acid (ammonium, hexosamine, serine, threonine and amino-acid nitrogen) were not significantly different, and finally the infra-red spectra of the two sets of humic acids showed no marked differences.

The burning of the forest floor releases nutrients from the litter and probably the most important loss from the system is that of nitrogen. Experimental work has shown that the bulk of the nitrogen is probably lost as gaseous nitrogen (Vines *et al.* 1971), as only a slight increase in nitrogen oxides was detected and no ammonium was present in the smoke. Similarly, some of the ash formed by the burn has been detected in the smoke; however, over a range of prescribed burns this amounted to only 4 per cent of the total ash.

In considering the effects of the prescribed burns on the jarrah forest soils there are several factors which appear to be related to the lack of differences below the two soil treatments:

Firstly, the temperature of the burn is not high and in some experiments at Dwellingup, it was observed that temperatures of the burns were of the order of 320-450° in three year-old litter. Secondly, the litter on the fire break consists mainly of leaves and fine twigs and thus burns rapidly. Therefore, the soil is not exposed to prolonged high temperatures in the prescribed burn. In addition the burns are carried out during the spring months and the maximum litter fall occurs during January, February and March (Hatch 1964). This fresh litter is exposed to several winters' rains between burns and experimental evidence has shown that jarrah litter loses one third of its oven-dry weight during the first winter. This loss in weight includes the majority of the inorganic cations as well as a considerable amount of readily soluble organic constituents.

Another factor which helps to maintain the nitrogen status of the forest is the role played by the native legumes and *Macrozamia* sp. in nitrogen fixation. Foliar analyses of a range of native species show a wide range of nitrogen values (Table 3), and it is evident that the legumes and *Macrozamia* have higher foliar nitrogen levels than the other jarrah forest species on the same sites. These higher nitrogen levels are believed to be due to the fixation of nitrogen by these plants which are therefore adding nitrogen to the ecosystem. This factor is probably of major importance in replacing any losses of nitrogen caused by prescribed burning.

Another aspect of the role of fire in the ecosystem is that the intensity of the fire can markedly influence the volume and composition of the understorey vegetation. The normal prescribed burn tends to produce a sparse understorey of shrubs but recent work by Shea and his colleagues at Dwellingup has shown that it is possible to increase the legume component of the vegetation by the use of high intensity burns. The rapid increase in native legumes afterwards will replace any nitrogen lost during the hot fires.

TABLE 3

Foliar Nitrogen Values, Dwellingup

Species	Nitrogen (%)
* *Acacia pulchella*	1.38
* *Acacia extensa*	1.42
Banksia grandis	0.75
* *Bossiaea aquifolium*	1.47
* *Bossiaea ornata*	1.36
Casuarina fraserana	0.93
Eucalyptus calophylla	0.94
Eucalyptus marginata	0.84
Hibbertia montana	1.04
Lasiopetalum floribundum	1.22
Leucopogon verticillatus	1.05
Lomandra sonderii	0.96
* *Macrozamia riedlei*	1.43
* *Mirbelia dilatata*	1.39
Persoonia longifolia	0.96
Phyllanthus calycinus	1.00
Pteridium esculentum	1.03
Xanthorrhoea gracilis	0.75
Xanthorrhoea preissii	0.77

* Nitrogen-fixing species.

JARRAH DIEBACK

The jarrah forest ecosystem is threatened by a serious disease known as dieback, caused by the soil-borne fungus *Phytophthora cinnamomi* Rands (Pc). The first sign of the disease is normally observed in the understorey strata where *Banksia grandis, Xanthorrhoea preissii* and *Macrozamia riedlei* yellow and die. The jarrah overstorey is affected later, often after most of the understorey has died. A typical symptom is a thinning-out of the leaves leading to twig and branch dieback followed by the eventual death of the tree (Batini 1973).

This disease has a drastic effect on the nutrient cycle in the jarrah forest. With the reduction in crown cover there is a marked decline in the annual litter return to the forest floor. It has been shown that the average annual litter return in the jarrah forest is of the order of 3.5 tonnes ha^{-1}, whereas in several areas affected by Pc the annual litter fall varied between 0.3 and 1.5 tonnes ha^{-1}, with the very low litter falls being recorded in the severely affected areas.

Chemical analysis of normal jarrah forest litter indicates that this material is a valuable nutrient sink and average annual returns of 13 kg nitrogen, 1 kg phosphorus, 7 kg potassium, 24 kg calcium and 7 kg magnesium per hectare to the forest floor have been recorded.

This recycling of nutrients via the litter is severely reduced in the diseased areas and in addition the loss of tree canopy causes a marked deterioration in the chemical properties of the surface horizon, with organic carbon and nitrogen levels showing a marked decline (Table 4).

TABLE 4

Organic Matter Levels in Healthy and Diseased Jarrah Forest Surface Soils

	Healthy Areas	Diseased Areas
Organic Carbon (%)	3.44	1.52
Nitrogen (%)	0.097	0.042

In the coarse textured lateritic gravelly soils the cation exchange capacity of the soil is largely dependent on the organic matter level of the soil and in some of the older dieback areas there has been a decline in cation exchange capacity (pH 7) from 8.2 to 3.9 m.equiv/100g soil. Associated with this decline in CEC there has been a reduction in the exchangeable cations, although the proportions of the cations do not vary between the diseased and healthy soils (Ca 69%; Mg 23%; K 2%; Na 6%). It is interesting to note that the reduction in these soil parameters has not affected the pH of the surface soils which is generally mildly acid with a mean pH value of 6.40 ± 0.32.

BAUXITE MINING OPERATIONS

Over the areas where bauxite mining is carried out there is complete destruction of the jarrah forest ecosystem.

Firstly, the upper soil horizons are removed from the site and stockpiled, then the bauxite horizons are mined leaving a heavy compact kaolinitic clay subsoil. Finally, the upper soil horizons are replaced, the mined site ripped mechanically and the revegetation process commenced.

Considerable changes in the chemical properties of the soils are caused by the removal and mixing of the upper soil horizons. In the original profile there is a pronounced accumulation of organic matter and nutrients in the surface horizon, with organic carbon and nitrogen values of 3 and 0.1% being recorded. In the replaced gravel these horizons have been thoroughly mixed and the corresponding levels of organic carbon and nitrogen are 0.67 and 0.034 per cent. In addition the gravelly horizons are generally much shallower following mining due to uneven distribution of the replaced overburden.

In addition the subsoils in the mined areas are generally an unsatisfactory medium for root growth as they consist of heavy compact kaolinitic clays, which are acid in reaction with pH values ranging from 4 to 5. These horizons are also devoid of organic matter and only very low levels of plant nutrients have been observed. The exchangeable cations are predominantly magnesium and sodium and only minor amounts of exchangeable calcium and potassium are present.

The revegetation of the mined sites is the subject of a very vigorous research programme and extensive trials have been established with native legumes, clovers and tree crops. Considerable success has been achieved to date but the majority of the experiments have not been established for a sufficiently long period to ascertain the fate of the new generation of tree species. Under present conditions it will take many years before we can expect the normal nutrient cycle observed in natural forest ecosystems to operate successfully in the mined areas.

Another aspect of bauxite mining that is becoming increasingly important is the effect of the mining on the hydrology of the area. Due to the lack of vegetation there is an enormous increase in surface runoff water which because of its turbid nature cannot be fed directly into the Water Supply dams. In addition, beneath the mined areas there has been a marked rise in the water table, with rises of up to 6 metres being recorded. In areas currently being mined this does not pose any serious problems because the subsoil water is very low in soluble salts. However, in the jarrah forest country to the east of Dwellingup high concentrations of salt have been discovered in the deep soil profiles. Mining in these areas, with the subsequent rise in the soil water table will flush this salt out of the profile into the adjacent streams and cause a marked deterioration of the water draining into the South Dandalup Dam.

CONCLUSIONS

The data presented show that prescribed burning has had little effect on the nutrient cycle in the jarrah forest ecosystem. This conclusion is supported by the fact that no soil deterioration can be detected in the burnt breaks. Parallel studies also show that there is no decline in tree growth rates on the firebreaks.

Jarrah dieback, which causes a marked decline in the crown cover on a jarrah site has a profound effect on the nutrient cycle due to the breakdown of the litter cycling processes.

Finally, mining operations destroy the jarrah forest ecosystem on the mined areas and the most urgent problem is to restore a permanent cover to these areas and thus recommence the nutrient cycling processes.

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RESTORATION OF NUTRIENT CAPITAL AFTER BAUXITE MINING

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Nutrient capital depletion occurs during bauxite mining due to:

(1) Salvage logging and wood cutting.

(2) Heaping and burning of all remaining vegetation including stumps.

(3) Stockpiling of topsoil (including ash from burns). These stockpiles are generally exposed during a winter when degradation and leaching of nutrients would be active.

(4) Some root material is removed in the 4-5m of bauxite.

An obvious rehabilitation strategy is to offset this loss by fertilization and fostering of leguminous species.

Agricultural legumes have been investigated as a means to rapidly rebuild a nutrient bank. Table 1 shows the yields and nutrient returns obtained from a rate of phosphate trial on clover (*Trifolium subterraneum*, cultivar Seaton Park).

TABLE 1

Yield and total nutrient returns from subterranean clover for varying levels of applied P.

Applied P kg/ha	Herbage Yield kg/ha	Total O.M* kg/ha	Total N* kg/ha	Total P* kg/ha
0	0	0	0	0
30	2300	3450	86.2	6.9
61	3800	5700	142.5	11.4
91	4300	6450	161.0	12.9

* Calculated using a tops/roots ratio of 2:1, and average values of 2.5% for total N and 0.2% for total P.

This performance in the first growing season after rehabilitation is unlikely to be matched by native legumes. Clover has the additional advantage of bringing about rapid soil stabilization as a complete ground cover is attained within 6 weeks after germination.

Since mining areas are in State Forest and the final objective of rehabilitation is to establish a cover of native vegetation, it must be demonstrated that natives could later be successfully established in clover stands before its widespread use could be sanctioned.

Present mining areas are in the high rainfall water catchment western zone of the Northern Jarrah Forest. To promote water yield it is appropriate to have a fertility constraint on the vigour of replantings and so rapid restoration of site fertility is not an objective. However, clover may have a significant role to play in rehabilitation after bauxite mining in saline areas and in the revegetation of raw coal mine spoils at Collie.

THE EFFECT OF CROWN SCORCH ON NUTRIENT CYCLING IN LITTER OF THE JARRAH FOREST.

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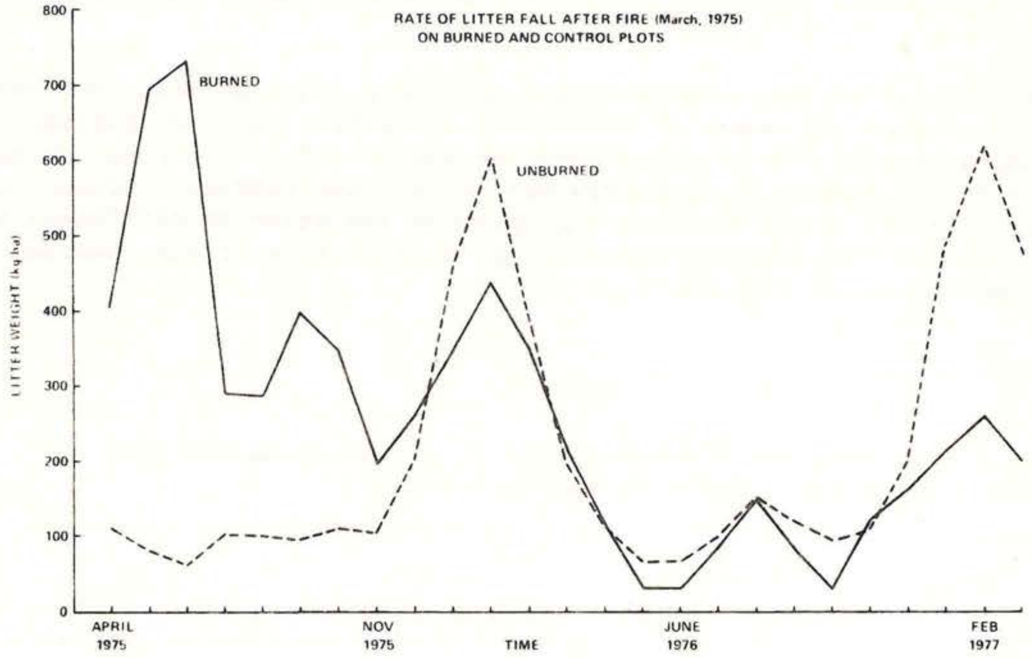
Intense prescribed burns, which have been proposed as a management practice designed to stimulate growth of a leguminous understorey in the jarrah forest may result in crown scorch of the overstorey species. This paper reports the results of litter fall measurements made following an intense experimental fire in re-growth jarrah near Dwellingup, W.A., in March 1975.

Thirty five litter trays each 1.5 m^2 were located on 7 sites within the burnt area and 20 trays were placed in an adjacent unburnt area. Litter was collected monthly over a two year period following the fire and its nutrient content was determined.

Extensive crown scorching resulted from the fire causing changes in the pattern of litter fall, the annual amounts of litter falling in the two years following the fire and in the chemical composition of the litter.



In the autumn and winter of 1975 almost 5 times as much litter fell on the burnt sites as on the unburnt control area. Crown regeneration commenced in late 1975 with considerable epicormic growth along the tree boles. The depletion of crowns due to the loss of scorched leaves and twigs resulted in a depressed summer leaf fall peak on the burnt sites in the 1975-76 summer. The normal winter pattern was re-established during 1976 with similar amounts of litter falling both on the control and on burnt sites in the months May to November. In the second summer following the fire, however, the litter falling on the burnt site amounted to only about half that on the unburnt controls.

TABLE 1

Annual Litter Accessions (kg/ha) on Burned and Control Sites for 2 years following Burning.

Year	Litter weight (kg/ha)		Significance
	Burned	Control	
1	5147	2634	***
2	1678	2847	***

The annual litter accession to the forest floor on the burnt site in the first year following the fire was almost twice that on the unburnt controls. This was due largely to the accessions from scorched crowns in the winter following burning. In the second year the litter falling on the burnt site amounted to only 60% of the litter on the controls, due to the relatively small amounts of litter accession in the summer leaf fall period.

Withdrawal of some elements into the trees prior to leaf senescence is an important means of internally re-cycling plant nutrients. Approximately 80% of the phosphorus and 60% of the nitrogen contained in jarrah leaves is conserved within the tree biomass. Crown scorch effectively short-circuits this process and prevents withdrawal of nutrients thus causing considerable modification to the chemical composition of the post-fire litter.

TABLE 2

Mean Annual Nutrient Concentrations in Litter on Burned and Control Sites for 2 years following Burning.

Year	% P		% N		% Ca	
	Burned	Control	Burned	Control	Burned	Control
1	.031	.014	.66	.36	.67	.62
2	.019	.012	.39	.36	.72	.69

In the first year following the fire the concentrations of nitrogen and phosphorus in the scorched litter were approximately double those found in the litter from the unburnt controls. Calcium, a relatively immobile element in plant tissue, was at similar concentrations in the litter from the burnt and unburnt plots.

In the second year after burning differences between the sites persisted for phosphorus, however nitrogen concentrations had returned to their previous levels.

TABLE 3

Nutrient Accessions (kg/ha) in Litter on Burned and Control Sites for 2 years following Burning.

Year	P (kg/ha) Burned	P (kg/ha) Control	N (kg/ha) Burned	N (kg/ha) Control	Ca (kg/ha) Burned	Ca (kg/ha) Control
1	1.59	0.38	34.2	9.5	34.4	16.4
2	0.31	0.36	6.6	10.4	12.0	20.0

Differences from the normal pattern in the amount and composition of the litter during the first year after the fire results in corresponding large differences between the burnt and control sites in the weight of nutrients returned to the forest floor. The litter from the scorched crowns contains approximately 4 times the normal amount of phosphorus and nitrogen and twice the amount of calcium. In the second year after burning the amounts of nutrients in litter falling on the burnt site are all less than on the control area, reflecting the decreased weight of litter falling on the burnt site during the second year.

Relatively high element concentrations in the post fire leaf **fall**, particularly nitrogen, could be important to the subsequent rate of litter decomposition and thus the cycling of nutrients. A question to be posed is to what extent regular scorching of the tree crowns, which prevents withdrawal of nutrients prior to litter fall, affects the nutrient pool of the above ground biomass in the long term? This may be important for phosphorus which normally tends to be retained within the tree and which is also relatively slowly mineralised from the litter layer of the jarrah forest.

EFFECTS OF FIRE ON CONCENTRATIONS OF PHOSPHORUS AND POTASSIUM IN JARRAH (*Eucalyptus marginata*) FOREST SOILS.

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Prescribed burning of forests causes immediate changes in concentrations of nutrients at the soil surface. The extent of these changes will depend in part on the intensity of the fire. Increasing attention is being focused on the use of more intense fires in the jarrah (*Eucalyptus marginata* Donn ex Sm.) forest to increase the growth of native legumes. This paper reports some results from a study of the effects of an intense fire on jarrah forest soils.

Two experimental sites were selected on yellow sandy gravels, the dominant soil type of the northern jarrah forest. The soils were sampled at three depths (0-3cm, 3-10cm and 10-20) from nine plots on each site before, immediately after, and one year after an intense autumn burn. The fine earth fractions (<2mm) were analysed for phosphorus (Bray No.1 extractant), and potassium (leaching with M NH_4NO_3).

Concentrations of extractable phosphorus at 0-3cm increased two to three-fold over preburn levels immediately after burning at both sites (Table 1). After one year the concentration of phosphorus at site A was still significantly higher at 0-3cm. At 3-10cm the concentration was significantly lower than the preburn level. Similar changes in extractable phosphorus following burning have been reported elsewhere and may result largely from the precipitation of phosphorus in acid-insoluble forms (Smith 1970).

TABLE 1

Concentrations of Extractable Phosphorus in Yellow Gravelly Soils (<2mm fraction) Before and After Burning.

Depth (cm)	Time	Site A		Site B	
		Mean (ppm)	Significance	Mean (ppm)	Significance
0 - 3	Preburn	11.2		15.0	
	Postburn	29.0	***	34.6	***
	1 year	15.7	**	17.5	n.s.
3 - 10	Preburn	6.1		6.7	
	1 year	4.8	***	6.1	n.s.
10 - 20	Preburn	3.4		3.5	
	1 year	3.1	n.s.	3.1	n.s.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Significance levels apply to differences in concentration before and after burning.

Microbial immobilization and uptake of phosphorus by new plant roots may also be important. At site B concentrations of extractable phosphorus after one year were not significantly different to preburn levels at any depth.

Concentrations of extractable potassium at 0-3cm approximately doubled at each site immediately after the fire (Table 2). After one year concentrations were not significantly different to preburn levels. At the lower depths chemical analyses of bulked soil samples from site B indicate that the concentration of extractable potassium may increase in the year after the fire. Leaching of potassium from the soil surface may be important following burning.

TABLE 2

Concentrations of Extractable Potassium in Yellow Gravelly Soils (<2mm fraction) Before and After Burning.

Depth (cm)	Time	Site A Mean (ppm)	Site A Significance	Site B Mean (ppm)	Site B Significance
0-3	Preburn	92		128	
	Postburn	196	***	202	*
	1 year	105	n.s.	133	n.s.
3-10	Preburn	41		46	
	1 year †	44		52	
10-20	Preburn	27		21	
	1 year †	29		31	

*** $P < 0.001$, * $P < 0.05$. Significance levels apply to differences in concentration before and after burning.

† Concentrations in bulked samples.

A large proportion of the increase in concentration of phosphorus and potassium in the top 3cm of soil immediately after the fire is probably caused by a repartitioning of these nutrients from litter to soil. Gains in the amount of extractable phosphorus and potassium in the soil are more than double the loss of these elements from surface litter (Table 3). Other factors which may be important in increasing the concentrations of these elements are the burning of vegetation, destruction of soil organic matter, and heat effects on other soil properties. The increase in concentration may be partly offset by losses from volatilization, removal of ash, or fixation in insoluble forms.

Other studies have shown the importance of temperature and the type of burn to changes in concentrations of soil nutrients (e.g. White *et al.* 1973; Tarrant 1956). Further experiments are planned to investigate the effect of duration and temperature of heating on the nutrient content of litter residue and on the concentrations of extractable nutrients in jarrah forest soils.

TABLE 3

Phosphorus and Potassium Weights in Litter and Soil (0-3cm) Before and Immediately After Burning. Means of Site A and Site B.

	Preburn (kg/ha)	Postburn (kg/ha)	Difference (Postburn-Preburn)
Phosphorus			
Litter (total P)	2.2	0.7	-1.5
Soil (extractable P)	2.0	5.3	3.3
Potassium			
Litter (total K)	11	5	-6
Soil (extractable K)	16	32	16

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NUTRIENT CYCLING IN TASMANIAN OLIGOTROPHIC ENVIRONMENTS

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It has been previously argued (Jackson 1968) that fire exerts a major control over the distribution of plant communities in Tasmania. This control is effective because of the low inherent fertility of most soils and because the high rainfall and steep topography result in high losses of nutrients in run-off and leaching following fires. This argument has been supported by the results of a simulation model (Henderson and Wilkins 1975) which is general and can be applied to other situations. Aspects of the Tasmanian syndrome are present in many Australian environments, such as the wet tropics and sub tropics and in drier climates because of widespread low inherent soil fertility.

One source of nutrient loss which has not been sufficiently investigated is the direct loss by vaporisation. This loss has been determined for a regeneration burn in mixed Eucalypt-Rainforest in Tasmania by Harwood and Jackson (1975). Differences in the biomass immediately before and after the fire showed a loss to the atmosphere of 18% P, 17% K, 12% Ca and 29% Mg, the losses being expressed as a percentage of the resource of that element in the biomass consumed.

The percentage loss of individual elements was proportional to their sublimation temperatures and was not related to their relative proportions in the biomass consumed in the fire. Hence in this case it can be assumed that vaporisation of the salts was the principal cause of loss and not transport by particulate matter, such as smoke. The results show that the flame temperatures in a cool fire are sufficient to cause losses of about 1/6th of important elements like phosphorus. The combined losses due to vaporisation, particle convection, deflation, run-off and leaching will vary with the intensity of the fire, the slope and the rainfall, but can be expected to lie between 60% and 80% of the fuel consumed under average Tasmanian conditions.

Work has begun to determine the driving forces in the selection of plants in oligotrophic conditions, so that the ecological drift due to fire can be explained. Measurements of nutrient cycling have commenced near the Boyd River, South-West Tasmania, (Harwood, 1972) in the three major vegetation types: *Nothofagus cunninghamii* - *Atherosperma* tall closed rainforest, *Eucalyptus nitida* open wet sclerophyll forest and *Gymnoschoenus sphaerocephalus* - *Sprengelia incarnata* wet hummock sedgeland. The preliminary results (Spring months) (Table 1) show: (1) slightly less than average levels of nutrients in leaves relative to similar communities in Australia and New Zealand; (2) very large (to 95% in *Gymnoschoenus*) resorbtion or recretion values for phosphorus and potassium; (3) a low rate of litter production in all communities about one half to one quarter of similar communities in Australia and New Zealand. As a consequence, the return of nutrients by litter fall is correspondingly reduced.

TABLE 1

Return of Nutrients in Litter Falls (Spring)
(kg of oven-dry weight of litter/hectare/month)

Source	P	K	Ca	Mg	Total litter
Tasmania *N. cunninghamii* Rainforest	.07	.25	.52	.14	124
*New Zealand *N. truncata* Rainforest	.17	.49	5.2	.75	453

* data from Miller (1961). *N.Z. J. Sci.* 6, 388-413.

The relative levels of nutrients in the foliage of the communities reflects their position in the ecological drift to oligotrophic conditions except for an apparent anomalous relation between *Atherosperma* and *Nothofagus*: *Atherosperma* 2 > *Nothofagus* 2 > *Eucalyptus* 2 > *Gymnoschoenus*. The high rates of resorbtion (and/or recretion) of P and K indicate an adaption to oligotrophic conditions and the importance of these elements in limiting processes. The release of P by chemical weathering processes is probably less than 0.1 kg/hectare/year on precambrian quartzites and the input by cyclic salt is of the order of 0.5 kg/hectare/year. Thus the total input is of the order of 0.6 kg/hectare/year, mainly from cyclic salt. Accurate run-off and P data for small watersheds are not available, but the P loss would appear to be less than .4 kg/hectare/year in unburnt watersheds.

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THE RESPONSE OF FOREST ECOSYSTEMS TO DISTURBANCE: REGENERATION OF FOREST STANDS THROUGH VEGETATION SUCCESSIONS FOLLOWING DISTURBANCE

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Succession in classic plant community studies implies the development of plant communities with time. A number of trends or progressive developments underline most successional processes (Whittaker 1970):

i) there is usually progressive development of the soil;

ii) the height, massiveness and differentiation into strata of the plant community increase;

iii) productivity (rate of formation of organic matter per unit area) increases with increasing development of the soil and community structure, and with increasing utilization of environmental resources;

iv) as height and density of aboveground plant cover increase, the microclimate within the community is increasingly determined by the community itself;

v) species diversity increases from the simple communities of early succession to the richer communities of late succession;

vi) populations rise and fall and replace one another along a time gradient;

vii) relative stability of the communities consequently increases.

These trends are more obviously seen in primary succession situations where the community is developing on some new or extensively disturbed ground.

Rather than concentrating on structural changes in the community, the strategies of nutrient conservation and cycling following disturbance may be of more interest in many situations. Disturbance can potentially change the quantity and availability of nutrients and these factors alone can cause succession patterns to move along the different paths and/or to end with different species compositions. Hence this paper emphasises general species attributes in relation to nutrients and reviews nutrient changes following disturbance and how these can determine vegetation successions.

NUTRIENT CYCLING CHARACTERISTICS

Most of the progressive developments outlined above represent structural and productivity characteristics of the ecosystem. However factors influencing the nutrient cycle may be different and can include:

i) the role of nutrient conserving species immediately after disturbance;

ii) species which affect nutrient availability - specifically N fixers but also species with selective mycorrhizae;

iii) changes in species or successional patterns as a result of changes in availability or loss of nutrients.

To understand the overall effect, the type, severity and frequency of disturbance has to be considered. The effect can be more easily seen by example.

DISTURBANCE DUE TO FIRE

The following are effects of fire on the nutritional regime:

i) conversion of many nutrients to a more readily available form;

ii) potential (actual) decrease in total nutrients in the system by volatilization or particulate updraft (especially nitrogen and sulphur);

iii) removal of direct competition;

iv) destruction of organic compounds such as allelopathic substances (Mount 1969; Florence and Crocker 1962).

In the case of a *light burn* or *controlled burn* situation (as studied by Van Loon in N.S.W.) there are comparatively low temperatures for short durations with relatively low "removals" of litter and understorey. Data from Floyd (1966) illustrate temperatures reached under three differing fuel types:

> *Light fuel* - branchlets and dried leaves loosely heaped to a height of 1.2 m. The fuel produced the hottest surface temperature (510°C) but only maintained a temperature above 100°C for 15 min. The maximum temperature at 2.5 cm depth was 44°C, whilst at greater depths the temperature rise was insignificant.
>
> *Medium fuel* - branches and stems up to 20 cm diameter with some leafy branchlets to a height of 1.8 m. The fuel only reached a maximum surface temperature of 386°C, but maintained a temperature above 100°C for 113 min. Heating was more pronounced at subsurface levels, rising to 85°C at 2.5 cm, 67°C at 5 cm and 48°C at 10 cm.

Heavy fuel - large logs up to 120 cm diameter with some lighter material up to 1.6 m high. The temperature of the soil surface under the heavy fuel rose more slowly to a maximum of 370°C and remained above 100°C for approximately 800 min. At a depth of 2.5 cm it rose and fell more slowly than in the other fuel types, reaching a maximum of 76°C, with 68°C at 5 cm and 57°C at 10 cm.

After the fire, regrowth can be from several sources, two of these being:

i) resprouting from existing plants (probably utilizing existing nutrient reserves within the plant (Siddiqi *et al.* 1976);

ii) growth of seeds stimulated by the fire (e.g. *Acacia, Banksia, Dodonea, Kennedia*). The intensity and duration of the fire (as previously discussed) will determine to a large extent the species composition of the regeneration, as minimal germination will occur without burning. The type of fire will thus partly affect the species composition explained in part by the effect of temperature on seed germination (Table 1).

TABLE 1

Temperature Requirements for Germination of Species in a Moist Hardwood Forest Type (Floyd 1974)

Species	Optimum Temp. (°C)	Optimum Duration (min)	% Germination Heated	% Germination Unheated
Dodonea triquetra	90	10-100	100	0
Kennedia rubicunda	80	10-150	100	6
Seringia arborescens	-	10- 40	90	0
Acacia longifolia	70	10-200	100	5
Acacia myrtifolia	-	-	80	0
Acacia sylvestris	-	-	100	2
Acacia falcata	50	10-400	85	40
Phytolacca octandra	40	20- 60	55	10

Apart from stimulation of seed germination by fire, the species coming in immediately after a fire often can efficiently utilize the flush of freely available nutrients. An estimate of potential nutrient release from the burning of a forest floor is shown in Table 2. While nitrogen can be volatilized, there is however an increase in ammonium -N concentration in the soil as a result of heating for four hours as shown in Table 3.

TABLE 2

Nutrients Contained in the Forest Floor of a Eucalyptus pilularis Stand (Marcia J. Lambert, unpubl. data).

Component	Organic Matter	N	P	K	Ca	Mg	Mn	Zn
	(kg/ha)							
Twigs (under 2.5 cm diameter)	4000	10	0.66	2.6	23.4	5.8	0.9	0.08
Bark	2000	7	0.42	1.3	7.7	2.5	0.4	0.04
Leaves	5000	45	1.85	3.8	28.3	10.5	1.9	0.13
Fines*	7000	56	4.76	23.1	52.9	15.1	2.4	0.25
Total	18000	118	7.69	30.8	112.3	33.9	5.6	0.50

* Fines include miscellaneous decomposing material difficult to define as to source.

TABLE 3

Effect of Temperature on Soil Ammonium Nitrogen Concentrations (Humphreys 1969)

Temperature (°C)	Ammonium-N (ppm)
0	46
100	55
200	215
300	235
400	38
500	25
600	15

The nutrient contents of selected species at different stages after a fire are shown in Table 4. These species have been selected to illustrate that species invading a site immediately after a fire can have the role of being nutrient conservers, an aspect which may be less critical in more stable systems. The concentration of available potassium in the ash is relatively high and is reflected in the potassium concentrations in the *Amaranthus* and *Bidens* spp. while the high nitrogen concentrations in these species are probably a function of the increased ammonium-N soil concentration immediately after the fire.

TABLE 4

Nutrient Concentrations in Foliage from Selected Understorey Species grouped according to Relative Predominance After Fire (J. Turner, unpubl. data)

Species	N	P	Ca	Mg	K	Na	Mn	Zn	Fe	Al
	(%)					(ppm)				
Species Present Within 3 Months After Fire										
Amaranthus hybridium	4.11	0.37	0.58	1.03	7.97	360	625	110	190	365
Bidens pilosa	3.09	0.29	0.74	0.32	4.55	2595	125	55	200	265
Species Present 1 Year After Fire										
Acacia longifolia	3.43	0.24	0.32	0.37	2.09	3340	280	55	420	165
Pteridium spp.	2.82	0.18	0.24	0.30	1.64	930	435	35	205	185
Species Present 5 Years Plus										
Persoonia linearis	1.12	0.18	0.26	0.27	0.58	3745	920	45	190	325
Casuarina spp.	1.31	0.11	0.69	0.16	0.60	1820	365	30	150	160
Species Present After Frequent Burns										
Imperata cylindrica	0.73	0.08	0.22	0.17	0.71	300	85	20	140	140

After a single burn, there is an influx of annuals and relatively short-lived perennials, followed by a trend back towards the pre-existing stable situation. There is a restoration of the store of buried seeds by which these species were able to regenerate the site.

If controlled burns are regular, such as every 2 to 4 years, the release of nutrients may not be so great (dependent upon the stability time for the forest floor), the seed sources may not be as readily replenished and it is possible that certain species will tend to be eliminated. Developing species are annuals or rapidly developing shrubs. N.S.W. north coast studies have shown there is lowered diversity (*Imperata* spp. dominated) while there was a tendency towards elimination of some species such as *Casuarina* spp. and *Acacia* spp. That is, potential nitrogen fixers are removed (A. Van Loon, *pers. comm.*).

Wildfire directly affects both overstorey and understorey and also causes a dramatic change in nutrient availability. Most of the effects are similar to lighter burns except at a greater intensity. However since the maximum temperatures are different, the species compositions will also be different.

The effects of a wildfire on species composition in an Eden, N.S.W. forest on Ordovician sediments have been studied by the N.S.W. Forestry Commission. In the 2 years immediately after the fire, there was a high number of species but this number decreased during the next 10 years after which the number of species increased (Table 5). The species coming in after 12 years were different from those immediately after disturbance.

TABLE 5

Changes in Selected Species after a Wildfire at Eden, N.S.W. All plots were on Ordovician sediments

Species	Years since wildfire			
	2	4	10	14
	(No. per hectare)			
Tree Species				
E. muelleriana	510	230	300	40
E. sieberi	1050	350	300	90
E. bridgesiana	-	-	-	42
Understorey Species				
Acacia spp.	2220	988	150	40
Casuarina spp.	-	-	50	150
Billardiera spp.	1250	413	99	80
Glycine spp.	240	500	550	700
Pteridium spp.	5550	380	200	184
Senecio spp.	1180	500	170	32
Total No. of Species	24	9	10	19

Van Loon (1974) in a study of a wildfire at Naghi S.F., N.S.W. reported an increase in the numbers of *Acacia* spp. from 1821 stems/ha before the fire to 8200 stems/ha after the fire. Regeneration was 50% higher on moderately burnt seedbeds than on those heavily burnt. This indicates some cause of spatial variation.

DISTURBANCE DUE TO CLEAR CUTTING

Clear cutting, among other effects, removes from the site various quantities of nutrients and redistributes a further amount. This quantity is variable depending on the type of stand and the species involved but our estimates for a typical stand at Eden N.S.W. are shown below (Table 6).

TABLE 6

Nutrients in a Mixed Eucalyptus Stand at Eden N.S.W. (E. muelleriana, E. cypellocarpa, E. obliqua).

Component	N	P	K	Ca	Mg	S
			(kg/ha)			
Foliage	83.2	4.1	34.4	48.3	16.8	8.3
Branches	62.8	2.2	19.3	12.7	5.6	12.0
Total crown	146.0	6.3	53.7	61.0	22.4	20.3
Bark removed	16.5	0.7	7.0	25.4	3.4	6.6
Sapwood removed	31.4	1.1	9.6	6.4	2.8	6.0
Heartwood removed	93.5	0.6	2.2	16.8	4.1	11.5
Wood & bark remaining	25.0	0.4	3.3	8.6	1.8	4.3
Total bole	166.4	2.8	22.1	57.2	12.1	28.4
Total tree	312.4	9.1	75.8	118.2	34.5	48.7
Litter	118.0	7.7	30.8	122.2	33.9	-

In a logging operation the bark, sapwood, and heartwood are usually removed from the site. The bark may not be removed to the mill but stripped off at the log dump (either being burned or left) but is nevertheless effectively removed from most of the site. There is a potential in this for significantly lowering some nutrients, especially sulphur and calcium, in the soil. However this potential does not necessarily tend to a lowering in productivity but a change in species composition in the initial stages of succession. At the end of a rotation, accessions may well have made up the loss but there may be reduced availability at the time of regeneration.

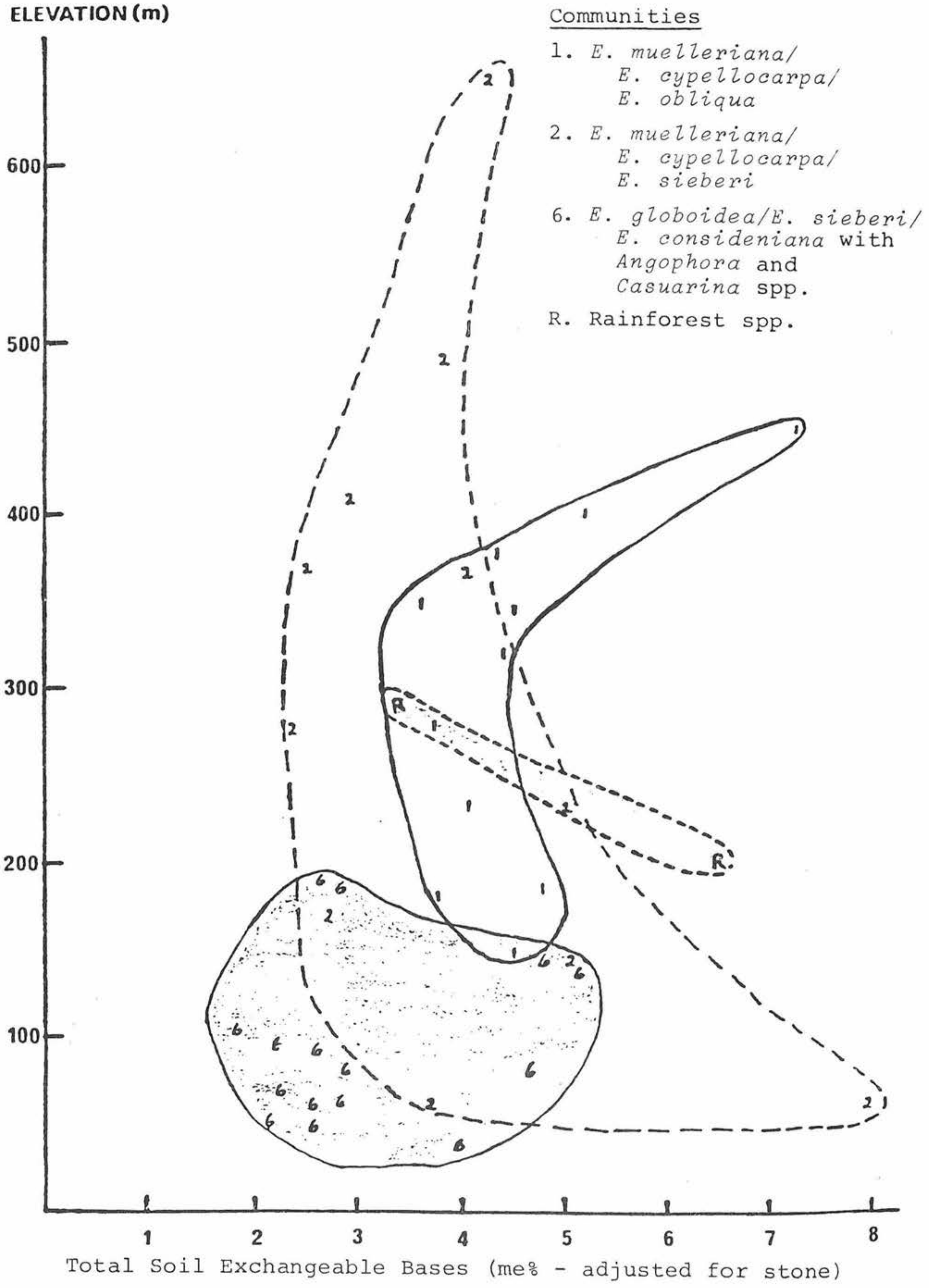

Figure 1. *Plot of Total Soil Exchangeable Bases Versus Elevation for Various Communities in Eden, N.S.W. Forests (J. Turner unpubl. data).*

It is difficult to predict the total effect of logging since the disturbance can lead to increased organic matter decomposition and hence increased nutrient availability. The developing species will probably be different to those in a fire situation due to varying effects on seed germination although the disturbance can cause cracking of seed coats as shown by Table 7 (Floyd 1974).

TABLE 7

Effect of Physical Disturbance on Germination (Floyd 1974)

Species	% Germination	
	Control	Seed Coat Ruptured
Acacia fimbriata	15	35
Dodonaea triquetra	0	40
Phytolacca octandra	15	77

The regeneration or development biomass after logging is lower and more poorly developed than after burning. Twelve months after clearing at Coffs Harbour (Floyd 1974), the cleared area biomass was 160 kg/ha while that in the burnt area was 390 kg/ha. In the unburnt area 78% of the mass were weak annuals, low growing ferns and grasses while on the burnt site 75% of the total mass were vigorous woody plants.

After some disturbance there is an influx of relatively short-lived species with specific nutrient requirements but there is evidence that the longer term tree portion of the community is related very closely to the longer term stable soil chemical characteristics, i.e. the fertility levels. In Fig. 1, various communities in Eden, N.S.W., forests are related to soil characteristics. Changes in soil fertility at disturbance due to nutrient loss or availability could change the subsequent species regrowth. A decline in phosphorus availability in the short term for example, could lead to *Eucalyptus obliqua* being replaced by *E. sieberi* in the *E. muelleriana/E. cypellocarpa/ E. obliqua* associations, or if calcium declined in the short term, *E. cypellocarpa* may disappear from the community. Any declines in nutrient availability as a result of logging would be short term as mineralization and accessions would replenish nutrient reserves in the longer term.

The relationship between species composition and soil fertility is a function of many variables including nutrient availability, species nutrient requirement and other factors. Species requirements (concentration patterns) differ greatly, as shown in Table 8, and in order to exist on a site the species has to be able initially to obtain the nutrients and then to efficiently utilize them. Thus it appears that some species can redistribute nutrients more effectively than others and some can accumulate specific nutrients hence affecting their distribution and especially if there is any decline in the availability of that nutrient. For example calcium levels in *E. cypellocarpa* are very

TABLE 8

Chemical Analyses of Foliage, Wood and Bark from Various Species in a Forest at Eden, N.S.W. (Marcia J. Lambert, unpubl. data).

Species	Component	P	Al	Ca	Mg	K	Na	Fe	Mn	Zn
					(ppm on O.D. (105°C) wt basis)					
E. obliqua	Foliage	1345	400	8090	2800	5150	1790	130	1115	50
(Messmate)	Bark	310	50	1680	620	1550	2565	160	35	20
	Sapwood	175	35	1060	490	1060	800	180	20	9
	Heartwood	8	37	400	18	60	60	110	2	8
E. cypellocarpa	Foliage	500	65	9770	1850	5450	2110	10	685	20
(Monkey gum)	Bark	90	25	14685	1550	2240	1370	45	480	10
	Sapwood	240	30	700	510	2110	450	140	60	11
	Heartwood	5	30	420	85	50	100	120	5	5
E. muelleriana	Foliage	625	40	5560	2510	4400	1925	20	340	10
(Yellow stringybark)	Bark	120	50	1390	150	990	1010	100	40	7
	Sapwood	100	10	1110	420	990	300	120	15	7
	Heartwood	12	30	380	20	60	45	110	3	4
E. sieberi	Foliage	400	10	3880	1750	4550	2220	10	205	15
(Silvertop Ash)	Bark	60	35	1015	310	690	320	40	15	5
	Sapwood	150	20	660	160	780	530	185	15	6
	Heartwood	30	35	640	(20)	120	130	100	4	4
E. globoidea	Foliage	315	40	2760	1230	3100	2220	50	250	15
(White stringybark)	Bark	45	115	2100	140	390	770	50	30	15
	Sapwood	130	25	475	150	810	420	80	25	9
	Heartwood	6	30	225	16	35	30	65	3	5

high and if this is related to the requirements of the species, a decline in soil calcium concentration could affect its distribution; similarly for phosphorus in *E. obliqua*. The redistribution of nutrients, especially phosphorus, from heartwood to sapwood is very evident and possibly represents a nutrient reserve which is utilizable in periods of decreased nutrient availability in the soil. Bamber (1976) has suggested that large scale resorption of some essential elements takes place when heartwood forms.

The successional patterns after disturbance depend upon the type and severity of the actual disturbance. Various disturbances alter the availabilities of certain nutrients and hence the types of species present are those which are more able to utilize the altered nutritional status.

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REGENERATION AND PLANT SUCCESSION IN THE KARRI FOREST

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SUMMARY

Pure karri forests largely exhibit two seral stages, the first composed largely of legumes, and the second, which appears at 10-12 years of age, composed largely of non-legumes. However karri/marri mixtures, although containing some of the plant species of the pure karri stands, also have a far greater species diversity and do not in the main exhibit recognizable seral succession phases beyond 1 or 2 years after burning.

INTRODUCTION

Karri (*Eucalyptus diversicolor* F.Muell.) is endemic to the lower South West of Western Australia between latitudes 34° and 35° South. The species ranges over approximately 140,000 hectares and is bounded in the east and north by the 45" (1140mm) rainfall isohyet. In fact past research on peat swamps suggests that the species previously occupied a far greater area, and that the major determinant of the species range is annual rainfall.

The soils of the area are basically derived from granite gneiss parent material, and in the area different soil types are largely recognizable by the vegetation type that they support. The pure karri stands occur on the well drained, relatively fertile red earth soils, but as the species composition changes to a marri/karri stand the underlying soil changes to shallower, less fertile podzolics which are usually located on slopes or ridges.

Fire is thought to be an integral part of the karri forest ecosystem as regeneration of the species requires conditions of almost full light and cleared seedbed. The species, unlike marri (*E. calophylla* R. Br.) does not develop satisfactorily under shade as it lacks the lignotuberous growth and coppicing abilities possessed to a large degree by marri.

Consequently, to achieve adequate restocking of a stand after logging, the area is first cleared of all remaining cull trees and is then burnt. This burning both relieves competition to the developing karri by removing aerial cover, and also develops the soil heating/ashbed effect that seems optimal for karri regeneration. After burning the area is regenerated naturally from seed trees, which are later removed, or it is regenerated artificially by either planting or seeding.

RECOGNIZABLE ECOTYPES

In the karri forest there are two broad forest type classifications, one being the pure karri stands which occur on the red earth soils, and the second being the karri-marri mixture which occur on the podzolic soils of the region.

The pure karri stands differ according to their geographic position in the species range. In the north west of the range pure karri stands tend to display 2 seral stages, the first being legume dominated, mainly by netic (*Bossiaea laidlawiana*) and the second being dominated both by netic and hazel (*Trymalium spathulatum*). In the species' central range (around Pemberton) once again a two seral stage is displayed, where the first is again legume dominated, in this instance by *Acacia* species and the second is a mixture of hazel, karri oak (*Casuarina decussata*) and *Chorilaena quercifolia*. These seral successions are to some extent being overridden by the prescribed burning operations to reduce litter build up in the karri forests. As these burns are carried out on a 6-8 year rotation, and the leguminous species of the first seral stage largely depend upon fire for germination they are being regenerated about 3 to 4 years before they would die out naturally and allow hazel and karri oak to dominate the understorey. While the hazel and karri oak persist under these controlled burning practices, they do not reach the stage where they dominate the stand's understorey.

In the southern karri forests however, only one distinct seral stage is seen, and this is dominated by the leguminous species, karri wattle (*A. pentadenia*).

The karri/marri mixtures, as opposed to these pure karri stands, tend to have a far more diverse species range contributing to the shrub layer, with legumes and non legumes fairly evenly represented, including most of the species found in pure karri forests. In these stands there is little successional change after 2 years following the fire.

POSSIBLE PLANT INTERACTIONS IN THE REGENERATING FOREST

Regeneration following logging disturbance usually occurs in the autumn following the burn, with the shrub species regenerating from seed stored in the soil and the karri from seedfall onto the burnt seedbed. Competition between the karri seedlings and the faster growing shrub species possibly commences in earnest in the second autumn after the burn, particularly in the denser shrub types of the pure karri stands such as the karri wattle areas. This is ameliorated to some degree by selective browsing by macropods who do not appear to browse karri. However in most cases by the age of 6 or 7 the karri stems have become dominant and form an emergent canopy over the shrubs, and the legumes in particular begin to die out.

This vigorous competition between shrubs and karri in the areas of denser scrub types could be very important as karri seems to be very much a light-stimulated species. It is hence possible that where the shrubby understorey is thickest, the karri seedlings are being favourably stimulated to increased growth, both because of competition for light and greater stores of soil nitrogen that are being fixed by the leguminous species.

In areas of very dense karri regeneration the shrub species may be overtopped very early by the karri, and in this case not only is an effect of light competition lost, but also a possible nutrient input which may have an inhibiting effect on stand development.

THE INFLUENCE OF PARASITES ON THE DENSITY OF THE JARRAH LEAF MINER

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The jarrah leaf miner, *Perthida glyphopa* Common (Lepidoptera:Incurvariidae), is a defoliator of jarrah (*Eucalyptus marginata* Donn ex Sm.) in the south-west of Western Australia. In 1975, the area of damaged jarrah in the forest and partly cleared land was approximately 14,500 km^2. The damage causes a loss of girth increment (Mazanec 1974), but the trees recover even after a heavy attack. In most areas, however, repeated attacks have caused permanent damage to the tree crowns.

Attempts at controlling the leaf miner with insecticides have been made, but the methods proved expensive (Wallace 1966). Considering an ecological approach to the problem, it is worth noting that outside the outbreak areas, where the leaf miner has existed at low population densities for a long time, outbreaks are being prevented naturally. Data collected from such situations indicate that low population densities of the leaf miner are maintained by a high mortality of feeding larvae in leaves, caused by parasites and predators. The parasites are 7 species of hymenopterous insects and the predators are locally-dwelling song birds. In some situations most of the feeding larvae of the leaf miner are killed by the parasites and the remainder is eaten by birds. In areas where parasites are absent, most of the leaf miners are eaten by birds, but these situations tend to deteriorate into outbreaks in the years favouring leaf miner oviposition.

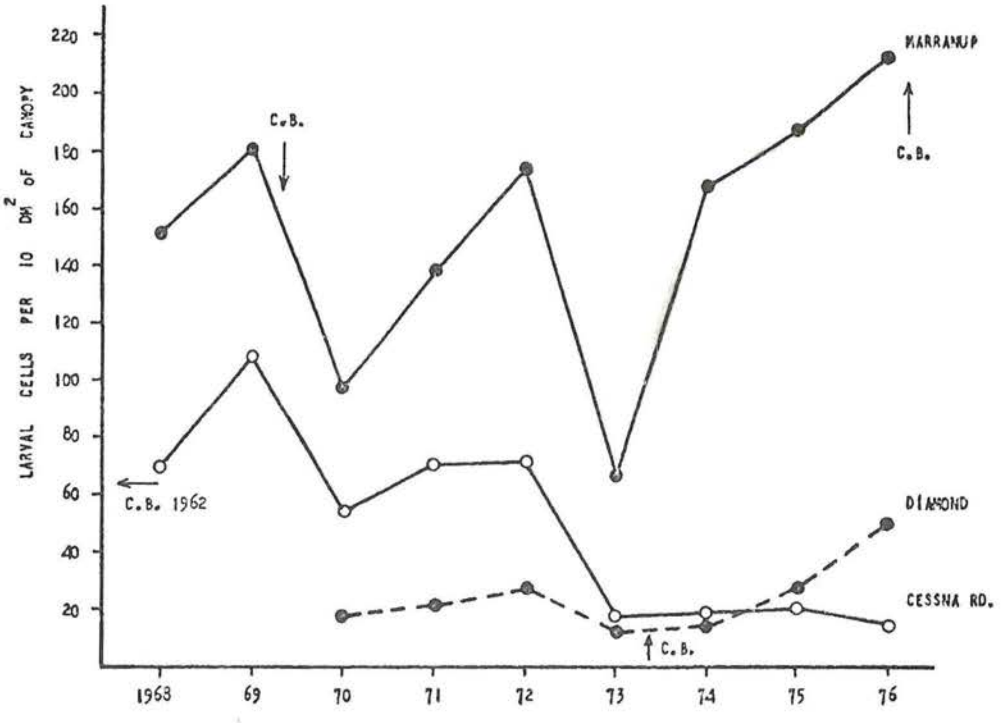

Figure 1. Trends of larval cell fall per 10 dm^2 of forest canopy at 3 sites. Each point is a mean of 20 readings. C.B. = controlled burn.

Figure 1 shows the population densities of the jarrah leaf miner estimated from the number of larval cells trapped under the forest canopy. At Marranup (2 km east of Manjimup) the leaf miner has persisted at high densities, except for the temporary decline in the years following droughts in 1969 and 1972. The second highest density at Cessna Rd. (4 km west of Tone River) declined in 1973 and has remained low, while the low density at Diamond (8 km south west of Manjimup) began to increase in that year. The figure also shows the incidence of controlled burning (C.B.) at the sites.

The above population densities related well to the degree of parasitism on the feeding larvae, particularly by the internal parasite *Neochrysocharis* sp. Parasitism has been low at Marranup and Diamond, but high at Cessna Rd. The low degree of parasitism by *Neochrysocharis* sp. at some sites appears to stem from the parasite's poor synchrony with its host. Table 1 shows that up to 95% of adults emerge before mid-June, but their eggs have not been found before late June, when hosts of adequate size become available. Adults emerging in April and May therefore either perish or must find food to survive till late June at least, to be effective as parasites.

TABLE 1

Pattern of Parasite (Neochrysocharis sp.) Emergence in the Manjimup Area, 1973

	April		May		June	
Numbers emerged	4	34	45	60	2	7
Cumulative percentage	3	25	55	94	95	100

In the laboratory *Neochrysocharis* sp. lived for up to 70 days when fed on a solution of honey and water. It is well known that hymenopterous parasites in general require carbohydrates for longevity and proteins and free amino acids, i.e. compounds of nitrogen, for continuous production of eggs. In the field these compounds are obtained by feeding on plant pollen, extrafloral nectaries, honeydew of sucking insects (Leius 1960, 1961a, 1961b, 1963; Baker and Baker 1973; Hagen 1974), and also by feeding on the host (Bartlett 1964). The natural food of parasites on the jarrah leaf miner, apart from feeding on the host is not known, but the view that they may obtain it from plants other than jarrah is reinforced by the work of Leius (1967), who showed that the presence of floral undergrowth in orchards influenced the parasitism of lepidopterous hosts. The decline of the leaf miner at Cessna Rd suggests that conditions for longevity and fecundity of parasites are favourable, while the upward trend at Diamond suggests the opposite. Under such circumstances, Marranup would represent a site where the leaf miner population escaped its natural enemies a long time ago and where no change is occurring now.

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CURRENT AND PLANNED STUDIES IN AUSTRALIAN INDIGENOUS FORESTS

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INTRODUCTION

The holding of this symposium shortly after a similar one-day seminar in Canberra and in addition to other recent nutrient cycling symposia indicates that the importance of nutrient cycling is finally being recognized in Australia. Important it truly is since nutrient cycling is fundamental to the structure of ecosystems and to the countless complex processes which occur within them. The productivity and "health" of ecosystems can be determined from nutrient cycling studies.

From the view point of one who has been trained in North America, it seems that in contrast to North America it is rather difficult to determine what research is actually taking place in Australia. Due to frequent travelling by research workers, numerous conferences, and strong pressures to publish, it is moderately easy to keep in touch with current research in North America. In Australia, on the other hand, research results often appear in obscure in-service publications, and there is not as much travelling or publishing of results as elsewhere. This is partly by way of apology to those whose work I have neglected in this paper, but to me it is a valid observation all the same.

There have been several recent developments in Australia which have tended to counter this research communications problem. One very important development has been the development of the Australian Forestry Council's Forest Research Working Groups. They may not have been established for this reason but they certainly provide an excellent forum for communication of research results and a cross fertilization of ideas. They tend, naturally, to be dominated by foresters, although in the multidisciplinary ecological fields, this is somewhat restrictive.

Another important development has been the annual publication of research news such as the CSIRO Forestry Research Newsletter. This is another excellent means of disseminating forestry research information. It has been very valuable in disseminating CSIRO research information but less valuable for other organizations although this has probably been the fault of those organizations in not sending off material to be included in the newsletter. This has been the case for my organization anyway. The Australian Water Resources Council's Inventory of Water Resources Research is also valuable in disseminating research information.

A third development which is not really new but appears to be growing in frequency is the holding of conferences or symposia on specific topics such as the present one on nutrient cycling. Those who attend such meetings must surely benefit, as well as the scientific community as a whole.

EXISTING KNOWLEDGE OF NUTRIENT CYCLING IN AUSTRALIAN FORESTS

In Australia, our knowledge of nutrient cycling in indigenous forests is minimal, to say the least. There has not been one comprehensive nutrient cycling study of an Australian forest published. Studies such as those of Cole and co-workers (Cole *et al.* 1967) in the U.S., or Ulrich, Mayer and co-workers (Ulrich *et al.* 1971) in Germany have simply not yet been carried out in Australia although I believe work done by the School of Natural Resources Forest Ecology Research Unit at the University of New England, CSIRO Division of Land Resources Management in Perth, the New South Wales Forestry Commission, Rogers *et al.* in the Botany Department, University of Queensland, and CSIRO Division of Forest Research in Canberra will soon help to overcome part of this deficiency.

To date the most comprehensive nutrient cycling study of an Australian forest has been that of *Eucalyptus obliqua* forests near Melbourne by Attiwill (1972). This study, however, neglected the important nutrient - nitrogen - and also all nutrient movement through the soil, a vitally important part of the ecosystem. There has been no other comparable study published although work about to be published by Rogers *et al.* will approach in detail that of Attiwill.

There have been several studies of individual components of the nutrient cycle, such as inputs in precipitation (Hutton 1968; Wetselaar and Hutton 1963), litterfall (Ashton 1975; Hannon 1958; Hatch 1955; Park 1975; Webb *et al.*1969), tree uptake (Cromer *et al.* 1975; Specht 1969), litter decomposition (Park 1975; Wood 1974) and geochemical weathering (Baker 1973; Ellis 1969). The effect of operations such as burning or clearfelling on individual components of the nutrient cycle have also been studied. Thus, the effects of fire (Humphreys 1969) or clearfelling and fire (Valentine 1976) on soil nutrient status, and nutrient loss to the atmosphere as a result of fire (Harwood and Jackson 1975) have been studied.

This list of published work is not comprehensive, but does indicate the types of study which have been carried out. Each study is valuable in itself. However, these studies of individual components of the nutrient cycle present us with a rather fragmented and spotty picture. Without all the fragments, our knowledge is imperfect and the conclusions that can be drawn from these various studies are somewhat limited.

In addition there have been numerous published and unpublished fertilizer studies carried out throughout Australia. These are valuable in that they provide quick answers to the problem of increasing forest productivity and to the question of which nutrient(s) is(are) limiting. They are of great value to the forest manager but of minimal value to the forest scientist who is seeking to answer the question - why? Fertilizer studies usually tell us very little about the way a system is functioning. In the field of soil nutrition, a holistic approach is needed to the study of fertilizers. Such an approach has been well discussed in Australia by Crane (1974). An understanding and study of the nutrient cycle, emphasising the soil, is the key to this approach.

What I am suggesting here is that perhaps rather than continuing a large number of rather *ad hoc* random fertilizer studies, the time has come for a more detailed holistic look at fertilizers. Plant response to fertilizers depends on many factors, not just properties of the fertilizer added. Soil properties are of utmost importance here so perhaps we should be correlating soil or ecosystem types with plant growth and fertilizer response. Such an approach to fertilizers has recently been carried out by Neilsen and Crane (1977). A similar approach is being adopted by Turvey for A.P.M. in Victoria.

CURRENT AND PLANNED NUTRIENT CYCLING STUDIES IN INDIGENOUS FORESTS

Here my knowledge may be lacking as explained above. I have used as many sources as possible to obtain this information but there will inevitably be sources which are not available to me. Annual reports, research reports, Forestry Research Newsletters, and personal contacts were my main sources.

Nutrient cycling research can be summarized as follows:

GOVERNMENT FOREST SERVICES

South Australia, Tasmania and Western Australia - no current studies. New South Wales, Victoria - nutrient content of soils and vegetation is being studied, primarily to determine nutrient losses as a result of woodchipping operations. In addition, nutrient budgets are being prepared for several catchments by looking at precipitation inputs and streamflow outputs.

Probably the most comprehensive nutrient cycling study in Australia has recently been established by the New South Wales Forestry Commission (J. Turner), at Lidsdale. Nutrient movement through a number of catchments together with movement within the catchments (litterfall, throughfall) and distribution between components (soils, litter, and vegetation) is being studied. The studies are aimed at determining the effects of conversion to pines, air pollution from a nearby power plant, and prescribed burning on forest nutrient cycling.

Queensland - nutrient inputs and outputs in a few catchments are being monitored.

CSIRO

The *Division of Forest Research,* Canberra, has been carrying out several nutrient cycling studies for some time. Catchment nutrient budgets (precipitation - streamflow) are being monitored, as are litterfall nutrient fluxes. Soil nutrient fluxes are currently under study, as is the role of fire in certain aspects of nutrient cycling. Unfortunately, these studies have tended to be isolated unrelated ones. This may be remedied soon, however, if plans to establish a comprehensive research program involving several people from different disciplines in the one detailed nutrient cycling study are realized.

The Queensland Regional Station (Stocker and Prazell) is carrying out litterfall and throughfall studies in rainforests.

The *Division of Land Resources Management* in Perth has various nutrient cycling studies. M. J. Trinick and N. Malajczuk are studying nitrogen fixation by understorey species, G. N. Harrington *et al.* are studying nutrient movement in poplar box woodlands, and F. J. Hingston and colleagues are studying nutrient return to the soil via throughfall, litterfall, and litter decomposition in several forest types, as well as nutrient composition of soils and vegetation. The aim of this study is to determine the effects of forestry practices, such as woodchipping and prescribed burning, on forest nutrient regimes.

The *Division of Soils,* Adelaide, has been involved in some fertilizer studies for a number of years. Litter decomposition is also being studied.

The *Division of Soils* in Queensland (I. Fergus) is studying nutrient movement in litterfall and throughfall and nutrient distribution in *Banksia*, eucalypt and rainforest ecosystems.

Universities

Australian National University, Department of Environmental Biology, Research School of Biological Sciences - Litterfall and litter decomposition is being studied by Macauley in both semi-arid and woodland ecosystems (Mallee), and higher elevation wet sclerophyll forest and sub-alpine snow gum ecosystems. Reports of this work have appeared in CSIRO Forestry Research Newsletters (No. 2, 1975 and No.3, 1976) and in Macauley (1975).

Australian National University, Department of Geology-Catchment nutrient budgets and soil loss are being determined in areas near Eden subjected to woodchipping operations. The project is being carried out for a Ph.D. thesis by D. Hough.

James Cook University of North Queensland, School of Biological Sciences - P.A.M. Crossland is studying nitrogen fixation in tropical ecosystems.

University of Melbourne, Department of Botany - P.M. Attiwill is studying nutrient cycling in mangrove ecosystems. One of his students, H. B. Guthrie, has recently determined nutrient (Na, K, Ca, Mg) balances for a *Eucalyptus obliqua* catchment near Melbourne. Another of his students will soon be studying nutrient cycling in Gippsland eucalypt forests which will be converted to pines.

University of Melbourne, Faculty of Agriculture and Forestry - I am studying nutrient cycling in mixed stringybark and *Eucalyptus regnans* forests near Melbourne. A brief description of this work appeared in CSIRO Forestry Research Newsletter No. 3, 1976.

University of New England, School of Natural Resources, Forest Ecology Research Unit - This has a high quality forest nutrient cycling study in progress. Working in northern New South Wales several workers led by B.N. Richards and J.L. Charley have been concentrating on a study of nutrient turnover on forest floors (litter + surface mineral soil). The Unit is also conducting research into the nutrient status of soils on Fraser Island, particularly as affected by management practices, such as burning. Reports of this work have appeared at the I.F.A. 7th Triennial Conference at Caloundra (Charley and Richards 1974), at the 3rd Australian Specialist Conference in Soil Biology at Glen Osmond in 1975, and in the CSIRO Forestry Research Newsletter No. 3, 1976.

University of New South Wales, School of Botany - Nutrition of various eucalypts and litter turnover in eucalypt forests are being studied.

University of Queensland, Department of Botany - Rogers *et al*. are studying the distribution of nutrients in soils and vegetation, as well as litterfall and litter nutrient dynamics in eucalypt forests on Stradbroke Island.

University of Tasmania, Department of Botany - W.D. Jackson is studying the effects of fire on nutrient cycling.

University of Western Australia, Department of Botany - J.S. Pate is studying nitrogen fixation in native species.

University of Western Australia, Department of Soil Science and Plant Nutrition - The processes by which soil organic nitrogen is converted to available inorganic nitrogen are being studied.

In addition to the above studies, there are numerous fertilizer trials, stream chemistry studies, and studies which are closely related to aspects of nutrient cycling; for example, studies of soil fauna, soil chemistry, and hydrologic studies. They have been omitted because they are not nutrient cycling studies *per se*.

PROBLEM AREAS IN AUSTRALIAN NUTRIENT CYCLING STUDIES

Forest Ecosystems Requiring Study

Forests which are being drastically and rapidly changed are those most in need of study - not only from the nutrient cycling viewpoint but from all viewpoints. We must have sufficient information about such forests to understand the effects of man-imposed changes on them. These changes include clearfelling, fuel reduction burning, and conversion to pines or different native species. The effects of these changes may not be immediately obvious or important, but they might be highly significant in the long term. Studies now may prevent costly mistakes and lessen the need for more costly future research. To be forewarned is to be forearmed. Forests which will not be drastically altered in the near future are not in need of urgent study since they will probably still be around for studies in the future.

With this in mind it can be seen that the forests most in need of study are the following -

1. Forests from Coffs Harbour to southeast Queensland (potential woodchipping operations).
2. Forests on the south coast of New South Wales (existing and expanding woodchipping operations).
3. Drier forests of New South Wales (existing and expanding pine conversion operations).
4. Drier forests of Victoria (existing and expanding pine conversion operations.
5. Forests of East Gippsland, Victoria (potential woodchipping and expanding clearfelling operations, spreading cinnamon fungus).
6. Mountain ash forests, Victoria (expanding clearfelling operations).
7. Most Tasmanian forests (existing and expanding woodchipping

and pine conversion operations).

8. Forests of southwestern Western Australia (existing and expanding woodchipping and bauxite mining operations, spreading cinnamon fungus).

Of these 8 general areas, those in which significant nutrient cycling studies are taking place include numbers 1, 2, 3, 6, 8, and possibly 4 and 5. The lack of nutrient cycling research in Tasmania's forests is probably the most serious in Australia, in view of the large scale commitment of these forests to wood and pulp production. Future work by the CSIRO Division of Forest Research Regional Station in Tasmania or the Tasmanian Forestry Commission may overcome part of this problem but in view of the diversity of forest ecosystems being altered it will be a large task indeed.

The drier Victorian forests are not being studied at all apart from limited catchment studies (merely precipitation inputs and streamflow outputs) by the Victorian Forests Commission. However, I am studying nutrient movement in some of the wetter of these forests and Attiwill's (1972) study may also be appropriate to at least some of them.

The Victorian East Gippsland forests are being studied to some extent by the Victorian Forests Commission. Their nutrient work, however, consists merely of determining the nutrient content of soils and vegetation and is, in effect, a study of a static state. Nutrient dynamics are not being studied, neither is nutrient flow into streams. Thus, the conclusions able to be drawn from this work will necessarily be limited. A possible complicating factor in East Gippsland is the cinnamon fungus which may interact with logging operations to have a significant effect on forest nutrient cycling.

Adequate nutrient cycling research is probably being carried out on - the forests around Coffs Harbour by workers at the University of New England and various workers in Queensland, the drier forests of New South Wales by workers in the New South Wales Forestry Commission and in the CSIRO Division of Forest Research in Canberra, the Victorian mountain ash forests by various workers in the Victorian Forests Commission and Melbourne University, and the forests of Western Australia by workers in CSIRO Division of Land Resources Management.

There are some nutrient cycling studies being carried out in the New South Wales south coast forests but these do not all appear to be interrelated. The New South Wales Forestry Commission studies are similar to their Victorian counterparts in East Gippsland except that in New South Wales nutrient loss in streams is also being measured.

The Soil as an Important Dynamic Entity in the Forest Ecosystem

The soil is one of the most important entities in a forest ecosystem for without soil there would be no such ecosystem. It is the soil which provides the vegetation with most of its water and nutrients, amongst other things. Nutrients taken up by plant roots come from 3 main sources - from decomposing organic matter, from mineral weathering, and from solution either from rain or throughfall. Nutrients such as K and sometimes Mg are returned to the soil mainly in solution (as throughfall) whereas nutrients such as Ca, N, and P are returned to the soil mainly in solid form (as litter). Mineral weathering inputs to the soil are likely to be less than release from decaying organic matter so the dynamics of litter decomposition and nutrient release to the soil becomes critically important from the nutrient viewpoint. As most plant roots and most nutrients occur in the surface layers of the mineral soil it is there where the action is happening. Studies of the nutrient dynamics of the litter and surface layers of the mineral soil would seem fundamental to any forest nutrient cycling study which is trying to assess the effects of forestry practices on forest nutrient status. This has been recognized by many workers in Australia. It apparently has not been recognized by all, however. In an effort to get quick answers one can avoid the more complicated, longer term, and more thorough studies of soil nutrient dynamics. But unless we can determine nutrient return to the soil we can say little conclusive about the significance of forestry practices on forest nutrient status.

Nutrient inputs to the soil from mineral weathering have yet to be adequately quantified anywhere in the world, let alone Australia. However, they must be considered in any complete nutrient cycling study. Such inputs in certain situations might be important in replacing nutrient losses from the system resulting from man's activity, although limited evidence suggests that weathering inputs are likely to be small. Anderson (1941) and Ellis (1969) have both done some work on nutrient release by mineral weathering in Australia. My own research includes the estimation of mineral weathering inputs by using catchment sodium budgets as has been done in the U.S. (Johnson *et al*. 1968). I understand that CSIRO Division of Forest Research in Canberra will also be looking at mineral weathering. Catchment sodium budgets are becoming increasingly available and may offer one means of estimating mineral weathering inputs to the soil although there are many problems in their use.

Soil Nutrient Availability

Whilst it is relatively simple to measure the total nutrient content of the soil it is not at all easy to determine the amount of nutrients available to plants. Of most significance in this case are the non-metallic nutrients N and P.

In the case of N, a number of biological and chemical methods of estimating N availability have been used with varying degrees of success. The biological methods are probably more accurate (Bremner 1965) but N availability in the soil is still a subject of debate. N is a particularly difficult nutrient to study because it may be added to forest ecosystems by N-fixation reactions and lost by N-volatization reactions, all of which are extremely difficult to quantify. It is, however, a very important nutrient and worthy of much greater study than at present, particularly in southeast Australia. Although it may not be the limiting nutrient in many Australian soils, positive growth responses to N fertilizers have been found (for example, Cromer 1972). Furthermore, much N may be entering the system through fixation, a substantial portion of which might come from plants with root nodules containing N-fixing bacteria. Such plants may be declining as a result of management practices; for example cool fuel reduction burns may decrease the abundance of legumes in an area (McCormick, quoted in Shea and Kitt 1976). Furthermore, most N in the soil comes from organic matter which is easily lost by burning. Fires may cause significant N losses from ecosystems (for example, Harwood and Jackson 1975; Grier 1975). Thus in certain areas, N might become a critical nutrient in the future due to changes imposed by man on forest ecosystems.

The problem of determining soil nutrient availability is probably greatest in the cast of P. The complexity of the problem and the current absence of a solution has been well discussed by Donnelly (1970). The determination of the amount of P in the soil available to Australian forest trees would be a most valuable field of research. Bioassay techniques using seedlings to exhaust the soil of its available P might be relevant here.

Streamwater Chemistry and Nutrient Cycling

Nutrients lost from forest soils often end up in streams. Consequently many research projects throughout Australia have been monitoring stream water chemistry, often with the aim of determining nutrient losses via stream water as a result of some forest management practice. It is indeed relatively easy to accurately measure nutrient fluxes in stream water although it must be borne in mind that nutrients move in streams not only in solution but also in solid particles. Cationic nutrients such as K, Na, Mg, Ca will probably exist mainly in dissolved form in stream water (Bormann *et al.* 1969) whereas in any stream which carries significant suspended sediment loads, nutrients such as N and P will be lost mainly in particulate form, particularly if much of the suspended sediment is organic (Fredriksen 1971; Hobbie and Likens 1973). Thus, in streams carrying significant amounts of organic solids, measurement only of dissolved nutrients may not yield very accurate nutrient fluxes. In an undisturbed state a stream may not carry much suspended sediment and measurement of dissolved nutrients only may yield accurate nutrient fluxes. If forestry operations disturb the stream and increase its suspended sediment load then measurement of nutrients both in dissolved and solid form may be necessary to accurately determine the effects of those operations on stream nutrient fluxes.

Measurement of accurate stream nutrient fluxes may not be completely straightforward but is still relatively easy. However, we must now ask - exactly what do these measurements mean? This crucial question has yet to be answered by any research project in Australia and is still only in the process of being answered overseas.

Firstly, it is necessary to monitor precipitation chemistry, as most, but not all, Australian studies are doing. This is necessary to determine whether or not changes in stream chemistry are due to changes in precipitation chemistry. Precipitation chemistry might undergo some fluctuations, but unless one is close to the sea or industry, these changes are unlikely to be very great. However, a lack of precipitation chemistry data may not be the most important problem simply due to the difficulties encountered in interpreting streamwater chemistry data.

The chemistry of a stream is extremely complicated and a result of many processes. Nutrients may be concentrated in a stream through surface runoff, throughfall, or litterfall inputs, evaporation, decay of organic matter within or at the edge of the stream, and release from adsorption sites on organic or inorganic materials. Nutrient concentrations in a stream may be diluted as a result of uptake by organisms, adsorption reactions, or inputs of low concentration waters in the form of lateral seepage, tributary streams, or direct precipitation. All these processes are contributing to stream chemistry. If we are studying the effects of forestry operations on stream chemistry then this chemistry can be influenced by changes in any of the processes mentioned above. If any process has a high buffering capacity to a chemical change then that chemical change may not be manifest in the stream. Forestry operations may indeed change the nutrient status of the soil but in some cases the changes may not be manifest by changes in stream chemistry. For example, clearfelling may increase the flow of nutrients from soil to stream. The increased nutrients in the stream may be adsorbed to solid particles with which the stream comes into contact, or they may be absorbed by aquatic organisms. In both cases the increased flow of nutrients from soil to stream will not be detected by simply monitoring stream chemistry. Clearfelling operations have indeed been found to increase the growth of aquatic organisms (Hansmann and Phinney 1973; Likens *et al.* 1970). In one study in New Zealand, N and P added to a stream were found to be rapidly removed from solution (McColl 1974). In a Canadian study nitrate was found to be lost from stream water, presumably due to denitrification (Kaushik and Robinson 1976). These studies indicate that we need to study stream processes before we can reliably interpret streamwater chemistry data.

In view of these comments we can see that if we are studying the effects of some forestry operation on nutrient loss in streams by merely monitoring stream and perhaps precipitation chemistry, and we find little or no change in streamwater nutrient fluxes following the operation, then we can make very few reliable conclusions. We cannot conclude that the operation had little or no effect on nutrient loss from the soil unless we have some knowledge of nutrient behaviour en route from the soil to the point of measurement in the stream.

Some workers overseas but not, to my knowledge, in Australia, have used the assumption that stream baseflow chemistry is identical to groundwater chemistry. If this were so then one might be able to determine nutrient fluxes through the soil merely by studying stream chemistry, thus avoiding complicated and exhausting soil water studies. Unfortunately however, stream baseflow chemistry does not appear to be identical to groundwater or soil solution chemistry. As discussed above there are many processes influencing streamwater chemistry so there is little reason why soil water and stream water should have identical chemistry. My work in Canada (Feller 1974) had indicated this.

Forest Management Practices and Nutrient Cycling

A forester is interested in nutrient cycling presumably because he wants to know how his various management practices affect the nutrient status of ecosystems. A decline in nutrient status can indicate a decline in productivity so serious declines in nutrient status are to be avoided.

As a basis for studying the effects of management practices on nutrient cycling we can consider Fig. 1, the ideas for which I am indebted to Dr. J.P. Kimmins of the Faculty of Forestry, University of British Columbia.

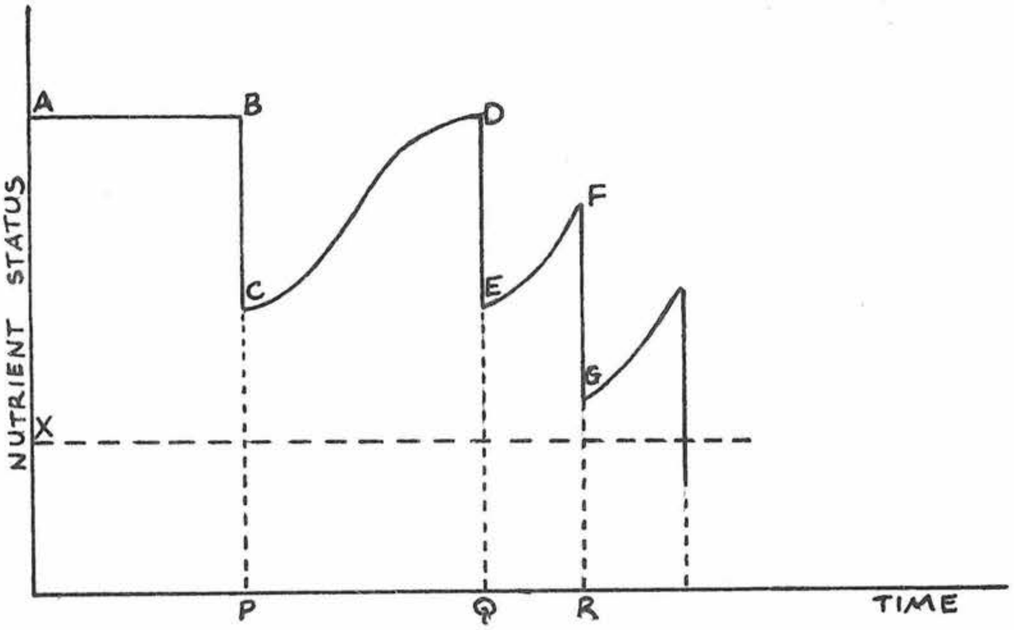

Fig. 1 Hypothetical nutrient status of an ecosystem. Details are explained in the text.

The figure depicts the hypothetical nutrient status of a forest ecosystem as affected by management practices. In an undisturbed state a relatively mature ecosystem will be in a state of dynamic equilibrium with a certain nutrient status (A in the figure). This status is maintained until a certain time (P) when the system undergoes a major perturbation (in the form of clearfelling, burning, etc.) which causes a decline in nutrient status from B to C. With time the system recovers and by time Q it has reverted back to its initial nutrient status. It may then undergo another similar perturbation at time Q causing a decline in nutrient status from D to E. If the time between perturbations (the rotation period) were to remain constant at PQ then the system might be capable of sustaining the perturbations indefinitely. If, however, the time between perturbations is decreased, to QR (QR<PQ), and the perturbation at time R causes a similar decline in nutrient status (FG) as that at time P or Q, then G will be less than E. Continued perturbations at frequent intervals (a time of QR between perturbations) might lead to a decline in nutrient status with each succeeding perturbation, as shown in Fig. 1. Ultimately the nutrient status of the system might drop to a certain critical level (X, say) below which productivity becomes greatly reduced.

Now this is all very hypothetical and may never happen in real life. However, the significance of the figure is that it indicates that if we wish to determine the effects of management practices on ecosystem nutrient status we must know the following:

i) initial nutrient status of the system

ii) nutrient loss caused by a perturbation
iii) recovery time from the perturbation
iv) critical nutrient levels
v) time interval (rotation length) between perturbations

Knowing these we can then predict the effects of various management practices (perturbations) on ecosystem nutrient status and can take any ameliorating measures necessary to maintain productivity.

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