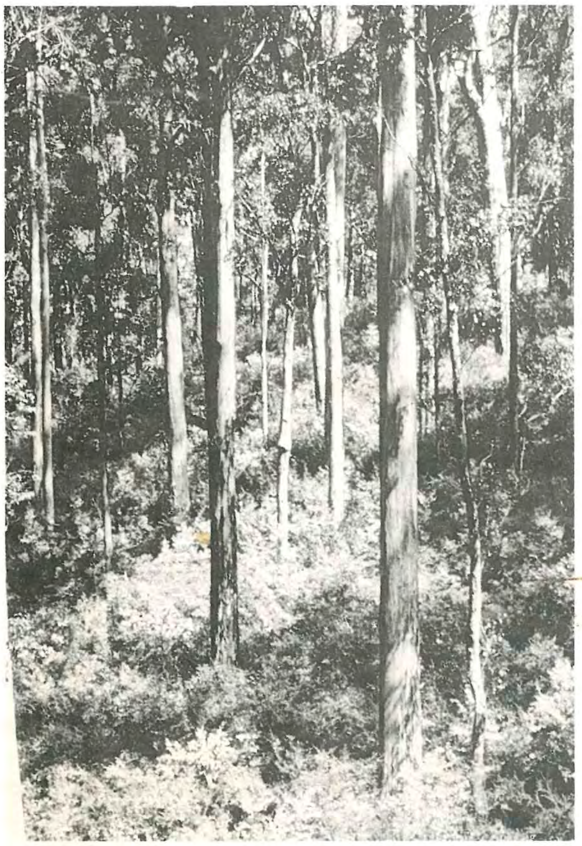
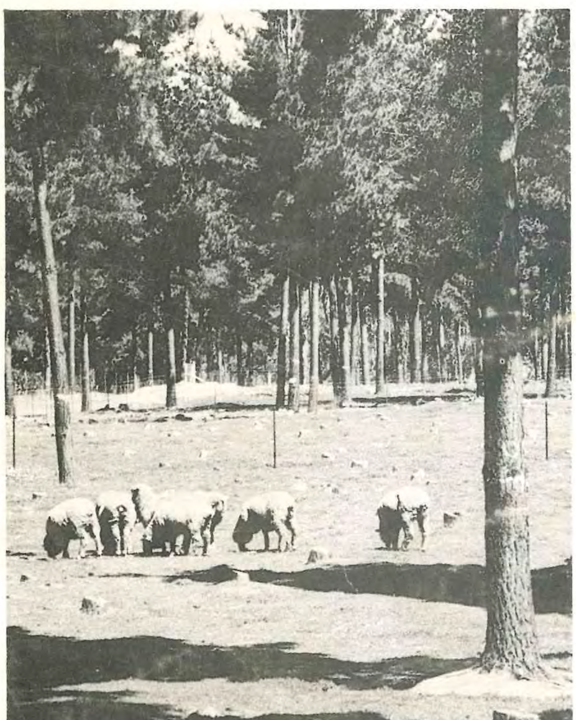
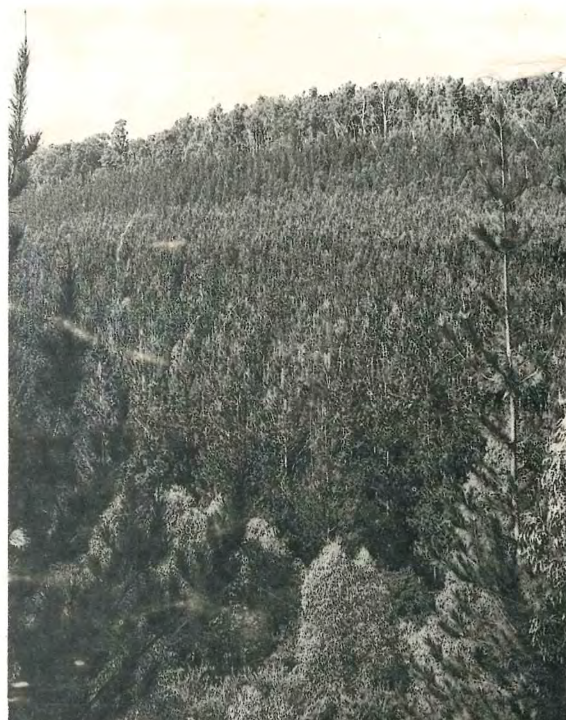


Managing Nitrogen Economies of Natural and Man Made Forest Ecosystems





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Managing Nitrogen Economies of Natural and Man Made Forest Ecosystems

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FOREWORD

This workshop was arranged by CSIRO, Division of Land Resources Management in collaboration with the Forests Department of Western Australia and with the assistance of Alcoa of Australia, Ltd.

Of the many interacting factors affecting the biological productivity of Australian forest ecosystems, nitrogen appears to be one of the nutrients of major importance. However there are many questions relating to the management of nitrogen in forest systems that need to be examined. For example, do forest scientists have enough understanding of the processes affecting the availability and cycling of this nutrient? Can the principles derived from agricultural research be directly applied to forests or are there problems peculiar to managing forests?

The objectives of this workshop were to address such questions so as to indicate the further research needed to solve practical problems for future management of forested lands, to enable a frank interchange of ideas on research priorities and to bring together a collection of papers dealing specifically with forest management problems relating to nitrogen cycling and availability.

We believe that the contributions, reflecting a wide range of opinions and points of view, go some way towards achieving those objectives. The proceedings should be useful to those concerned with understanding the interactions affecting nitrogen in relation to the management of native and plantation forests.

R.A. Rummery
F.J. Hingston
ORGANISING COMMITTEE

IN MEMORIAM

DR. GEORGE STANFORD (1917-1981)

A senior research scientist of international status, George Stanford had been on the USDA staff at the Agricultural Research Centre at Beltsville from 1965 until his retirement in November 1980. During this time he had brought together and led a group of research scientists doing work of major importance on the chemistry of nitrogen in soils, the effectiveness of nitrogen fertilizers in improving plant yields, and soil and fertilized nitrogen use efficiency in crops with modern conservation tillage systems.

George Stanford made major contributions to knowledge of plant nutrient availability in soils, improvement in fertilizer use and technology and, in recent years, to improvements in fertilizer usage in relation to environmental issues.

We were fortunate to have George Stanford as our visiting speaker at this workshop. His contributions to the proceedings and discussions, his enthusiasm and helpful friendly nature were very much appreciated by all participants. He will be kindly remembered in this part of the world for his courage and his dedication to science.

CONTENTS

SESSION 1.
Nitrogen in Australian Ecosystems

NATURAL INPUTS OF NITROGEN TO FOREST ECOSYSTEMS

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INTRODUCTION

In a study of the nutrient stocks in a Eucalyptus forest growing on a deep and particularly infertile sand podzol in south east Queensland, Westman and Rogers (1977) noted that nitrogen was one of the few elements in relative abundance. The observation is surprising for several reasons. Firstly, fires in the area are common and appreciable amounts of ecosystem nitrogen are probably lost when litter is burned. Secondly, the soil phosphorus levels at the site were particularly low, and Beadle (1953, 1962) has argued that nitrogen fixation is limited on such infertile soils.

Frequent fires and low phosphorus soils are common in most forested areas of Australia. None the less, large amounts of nitrogen have been recorded in the litter layer in various forests and several of these have weights in the order of 200 kg N ha^{-1} (Table 1). Assuming a fire frequency of about ten years, these ecosystems may periodically lose from fire alone the equivalent of about 20 kg N ha^{-1} $year^{-1}$. This estimate is obviously rather simplistic, yet it does serve to raise three basic questions concerning nitrogen inputs to these forest ecosystems.

Table 1. Nitrogen in forest floor litter layer.

N Wt kg N ha^{-1}	Forest Main Spp.	 Type	Time since fire	References
195	*E. signata*	Dry sclerophyll	7	Rogers & Westman 1977
50	*E. marginata*	Dry sclerophyll	6	O'Connell *et al*. 1979
220	*E. diversicolor*	Wet sclerophyll	6	O'Connell *et al*. 1979
92	*E. andrewsii* *E. saligna*	Wet sclerophyll	?	Richards & Charley 1977
33	*E. obliqua*	Dry sclerophyll	?	Richards & Charley 1977
109-216	*E. fastigata*	Wet sclerophyll	> 5	Meakins 1966
55	*E. robertsoni*	Dry sclerophyll	> 5	Meakins 1966
125	*E. delegatensis*	Wet sclerophyll	> 5	Meakins 1966
87-105	*E. pilularis*	Wet sclerophyll	?	Bevege 1978

(i) What are the nitrogen sources for Australian forest ecosystems?

(ii) Are these inputs constant or do they vary over time?

(iii) What factors influence the rates of nitrogen input and can these rates be affected by forest management practices?

DIRECT ATMOSPHERIC NITROGEN INPUTS

Many measurements have been made of nitrogen inputs in rainfall. Burns and Hardy (1975) quote studies from various parts of the world indicating a range of 7-9 kg N ha^{-1} $year^{-1}$. Most rainfall nitrogen measurements in Australia are less than this and vary between 0.3 and 3 kg N ha^{-1} $year^{-1}$ (Table 2). Rainwater nitrogen is usually in the ammonium form rather than the nitrate form, although Drover and Barrett-Lennard (1956) found the proportions varied widely from year to year and between sites. Flinn et al. (1979) were unable to detect any ammonium nitrogen in rainfall over Victoria.

Table 2. Nitrogen in rain water (kg N ha^{-1} yr^{-1})

Location	Total N	NH_4^+ N	NO_3^- N	References
World data	7-9	70%	30%	Burns & Hardy 1975
Australian data				
(a) Victoria	0.32	0	100%	Flinn *et al.* 1979
(b) N. Queensland	1.7	1.2	0.5	Probert 1976
	3.1	2.3	0.8	
(c) S.E. Queensland	60	?	0.17	Westman 1978
(d) Northern Territory	1.3	0.8	0.5	Wetselaar & Hutton 1963
(d) West Australia	0.6	* variable		Drover & Barret-Lennard 1956

* Proportion varies over 4 years of measurement and between the 6 sites - NH_4^+ generally dominant at inland sites while NO_3^- generally dominant at coast.

A very high value of 60 kg N ha^{-1} $year^{-1}$ has been recorded by Westman (1978) at a coastal site on Stradbroke Island in south east Queensland. Large amounts like this have been noted in the literature before, for example the 57 kg N ha^{-1} $year^{-1}$ measured in Nigeria by Jones (1960), and it has been suggested they are the result of an organic nitrogen input from microbial sources in the surface layer of the ocean (Wilson 1959). However there seems to be some doubt about this. Other measurements of rainwater nitrogen in south east Queensland at Cooloola are much lower than Westman's estimate; samples collected in a sequence ranging from 0.2 km to 25 km from the coast all contained nitrogen inputs of about 7 kg N ha^{-1} $year^{-1}$ (Reeve, pers. comm.). About half of this was in the form of organic nitrogen but there was no trend in this proportion with distance from the coast, which argues against it having an oceanic origin. These Cooloola data are more in keeping with the general worldwide estimates of rainfall nitrogen and suggest the higher values reported by Westman may result from microbial contamination of the collecting vessels.

The ecological significance of rainwater nitrogen is not easy to assess. In the first place, organic forms of nitrogen clearly do occur and yet these are not often measured. Reeve's data suggest they may equal the ionic nitrogen input and, over a normal forest rotation, these amounts might be quite significant. Secondly, rainwater nitrogen in the form of the positively charged ammonium ion is likely to be intercepted and retained in the topsoil but nitrogen in the form of the negatively charged nitrate ion will be more easily leached and may pass more quickly through the soil rooting zone and out of the ecosystem. Finally, some rainwater nitrogen may not represent a true addition to the ecosystem. This would be the case with the small amounts of nitrogen originating in bushfire smoke (Debell and Ralston 1970; Clayton 1976) and Wetselaar and Hutton (1963) have suggested, on the basis of ionic ratios, that much of the nutrient content of water at Katherine in the Northern Territory has a terrestrial rather than oceanic origin; that is, it is of local origin and is not a truly external input to the ecosystem. This pattern may be the same at other inland sites.

Besides nitrogen inputs in rainfall, several recent studies show gaseous ammonia in the atmosphere may be directly absorbed by plant leaves. One study used $^{15}N_2$ to show a direct transfer (Porter et al. 1972) while another monitored the disappearance of ammonia from an airstream flowing through a plant growth chamber

(Hutchinson *et al*. 1972). These experiments suggested plant leaves can absorb significant quantities of nitrogen - perhaps as much as 20 kg N ha^{-1} $year^{-1}$ at the naturally occurring levels of ammonia in the atmosphere and Hutchinson *et al*. (1972) believe direct absorption through plant leaves is a vastly underrated ecosystem nitrogen input. In contrast to these reports it should be noted that preliminary studies by Borman *et al*. (1977) showed only small amounts of direct ammonia uptake in tree species from the Hubbard Brook ecosystem study area.

BIOLOGICAL NITROGEN FIXATION

Biological fixation is carried out by non-symbiotic free-living autotrophs or heterotrophs, such as bacteria and blue green algae as well as by symbiotic associations. The latter may be a simple intermingling of the two partners of the symbiosis, such as the alga-fungal partnership in lichens or the association of alga and coralloid roots of cycads. Alternatively, there may be an association where the endophyte is intracellular and cannot exist separately from the host. The best known is the legume-*Rhizobium* association, but similar relationships are found in non-legumes such as *Casuarina*, *Alnus*, *Ceanothus*, *Myrica* and in some gymnosperm roots which bear a superficial resemblance to legume nodules.

There are a number of excellent recent reviews describing nitrogen fixation in various of these ecosystem components (e.g. Silvester 1977; Mague 1977; Knowles 1977; Mulder *et al*. 1977). Rather than repeat these, I would like to highlight some of the sources of biological nitrogen inputs more particularly relevant to Australian forest ecosystems. In some cases, data from Australian forests are already available. In other cases, studies in temperate and tropical forests overseas point towards possible nitrogen inputs in similar forest ecosystems in Australia.

In most forests the data should be treated as a first approximation. Direct measurements of ecosystem nitrogen inputs are difficult to make although fixation rates can be measured by ^{15}N

or the acetylene reduction technique. The problem is to extend these measurements sufficiently to cover the normal range of seasonal conditions. Perhaps the best measurements, at least at the ecosystem level, are still those made by indirect assessments of nett gains using an ecosystem nitrogen balance approach and calculating fixation as the difference between losses and the changes in the standing crop.

Nitrogen Fixation in Forest Legumes

While there are many measurements showing comparatively high foliar nitrogen concentrations in various leguminous species found in forest ecosystems (Table 3), there are comparatively few actual measurements of nitrogen fixation by these species. Most work has been carried out on species found in W.A. forests. Shea and Kitt (1976) measured N fixation by Acacia pulchella, A. extensa, A. strigosa, A. myrtifolia, Bossiaea aquifolium and Mirbelia dilatata growing in pots using the C_2H_2 reduction technique. All showed a capacity to fix nitrogen and the nitrogenase acivity of the root nodules of A. pulchella, the most widespread of the native legumes, compared favourably with rates measured in other leguminous species. In the field, these and other native legumes regenerating after fire are capable of fixing 3 kg N ha^{-1} $year^{-1}$ in jarrah (E. marginata) forest and 9 kg N ha^{-1} $year^{-1}$ in karri (E. diversicolor) forest (O'Connell et al. 1979).

Several estimates of nitrogen fixation by Acacia have been made in plantation ecosystems. A three year old plantation of A. pellita in the Northern Territory was estimated to have an annual fixation rate (C_2H_2 reduction) of 12 kg N ha^{-1} $year^{-1}$ when the planting density was 1110 trees ha^{-1} (Langkamp et al. 1979). This density is similar to that found in natural communities in the region where fire is excluded.

A particularly high estimate of fixation by Acacia has been recorded by Orchard and Darb (1956) for an A. mollissima plantation in South Africa. These workers found soil nitrogen had accumulated at the rate of 202 kg N ha^{-1} $year^{-1}$ over 3 ten-year rotations.

Table 3. Foliar nitrogen concentrations (%) of *Acacia* and *Casuarina* spp. in relation to other common forest species.

(a) Low scrub forest, Sydney (Hannon 1956)	
Casuarina distyla	0.72
C. littoralis	1.00
C. littoralis	1.29
Acacia discolor	1.26
A. suaveolens	1.53
A. suaveolens	1.86
Eucalyptus gummifera	0.62
E. haemostoma	0.57
E. pilularis	0.92
(b) Tall scrub forest, Sydney (Hannan 1956)	
C. torulosa	1.17
A. discolor	1.65
A. suaveolens	1.92
E. gummifera	0.92
E. pilularis	0.87
E. pilularis	0.96
(c) Cypress pine woodland, Millmerran Qld (Bevege 1978)	
Callitris glauca	1.05
Casuarina leuhmannii	0.90
Eucalyptus bancroftii	1.31
(d) Cypress pine woodland, Millmerran Qld (Johnston 1978)	
Casuarina leuhmannii	0.90
Callitris glauca	1.03-1.19
(e) Tall heath scrub Sydney (Maggs & Pearson 1977)	
Acacia	1.99
Casuarina	1.09
Banksia	0.63
Leptospermum	0.99
Melaleuca	1.17
Ceratopetalum	1.18
Lantana	1.99
Pteridium	1.96
Ricinocarpus	1.54

This rate may be an underestimate since it does not include nitrogen contained in the plantation biomass or nitrogen lost in the slash burns between rotations.

Casuarina

Sixteen of the 45 species in the genus Casuarina have been recorded as possessing root nodules (Bond 1974). These nodules contain the actinomycete Frankia (Silvester 1977). Evidence of nitrogen fixation has been found in C. equisetifolia, C. cunninghamiana, C. glauca, C. lepidophloia, C. torulosa, C. junghuhniana and Bond is of the opinion that nodules of the species not yet tested for fixation do, in fact, have that capacity under normal conditions.

Many species occur as pioneers on coastal areas or after volcanic eruptions, e.g. C. littoralis, C. cunninghamiana, C. equisetifolia and Silvester (1977) estimates C. littoralis is capable of fixing 218 kg N ha^{-1} $year^{-1}$. He quotes the data of Dommerques (1963) for a 12-year-old plantation of C. equisitifolia in which the annual accumulation of nitrogen in soil and trees was about 52 kg N ha^{-1} $year^{-1}$.

There appear to be no published estimates of nitrogen fixation by Casuarina communities in Australia. An approximate indication of fixation can perhaps be made, however, by examining foliar nitrogen concentrations in Casuarina and using these as indices of the amounts of fixed nitrogen likely to enter the ecosystem as litterfall. Such data suggest that Casuarina fixation rates may not be particularly high (Table 3). For example, Hannon (1956) recorded several species of Casuarina having foliar nitrogen concentrations larger than nearby Eucalyptus. However, the differences were not marked and the concentrations were much less than those in nearby Acacia. Similar results were reported by Maggs and Pearson (1977). Bevege and Johnston (quoted by Bevege 1978) actually measured lower foliar nitrogen concentrations in Casuarina leuhmanii than in Callitris and Eucalyptus in the same stand (Table 3). Further, Johnston (1978) was unable to find root nodules in this species despite extensive field sampling. An attempt to inoculate C. leuhmannii seedlings with nodules from C. glauca was unsuccessful and he concluded that C. leuhmannii does not produce nitrogen fixing root nodules in sufficient quantity to account for any major addition of nitrogen to these forests. Withers (1978) has also commented on the difficulty of locating nodules of C. littoralis and C. stricta in the field. In the cases of C. cunninghamiana, C. glauca and C. cristata optimal nodulation and fixation occur at pH 7 and 8; values greater or less than these cause nodulation and fixation to decline appreciably (Coyne 1973). Unsuitable soil pH levels may account for some of the observations noted above.

This limited amount of evidence suggests there are considerable differences in the nitrogen fixing capabilities of various Casuarina species and that their contribution to the forest nitrogen balance is less than that of Acacia.

Macrozamia

Eight of the nine cycad genera are known to have coralloid roots with blue-green algae (Silvester 1977). Macrozamia communis is a prominent understorey species in Eucalyptus maculata forests in N.S.W., and Bergersen et al. (1965) have shown it capable of fixing nitrogen. Halliday and Pate (1976) have also demonstrated a similar capacity for the Western Australian Macrozamia riedlei. Using the C_2H_2 reduction method, they estimated up to 19 kg N ha^{-1} $year^{-1}$ could be fixed in communities with a Macrozamia density of 1270-1590 plants ha^{-1}. Comparable measurements for this species have also been recorded by Grove et al. (1980).

Litter and Soil

Nitrogen fixation has been recorded in both litter layers and the soil of forest ecosystems. This is caused by free-living bacteria, blue green algae and lichens. Comparisons between studies are difficult because of differences in environmental conditions, particularly moisture contents at the time of sampling, frequency of sampling during the year and the various ways in which the results are expressed. Never-the-less, fixation has been widely observed in both hardwood and coniferous forest ecosystems (Jones et al. 1974; Granhall 1975; Knowles and O'Toole 1975; Todd et al. 1978).

In litters, Todd et al. (1978) measured an annual nitrogen input of 2.3 kg N ha^{-1} in a deciduous hardwood forest and Jones et al. (1974) recorded 0.3-0.6 kg N ha^{-1} $year^{-1}$ in a conifer plantation (Table 4). Comparable rates have been measured in a number of other forest ecosystems including eucalypt forests (O'Connell et al. 1979). The only study to report insignificant fixation in forest litter was that of Tjepkema (1979) but he noted the area had very acid rainfall and soils.

Nitrogen fixation rates in soil vary widely, ranging from a high value of 8.5 kg N ha^{-1} $year^{-1}$ in one temperate hardwood forest soil to 0.15 kg N ha^{-1} $year^{-1}$ in a tropical forest soil (Table 4). The low value for the temperate soil was at the site with acid soils noted above (Tjepkema 1979) while the tropical soil seems to have been limited by available energy and was capable of fixing much higher rates when given an energy supplement (Spiff and Odu 1972). There appear to be no measures of fixation in Australian forest soils, although Rogers et al. (1966) have detected fixation in soil lichen crusts in inland South Australia.

Fixation can occur in decaying logs in the forest floor. Cornaby and Wade (1973) measured fixation rates in decaying chestnut logs in the U.S.A. that were greater than rates in the soil and of the same magnitude as that of the litter (Table 4). Expressed on an annual basis, the 0.9 kg N ha^{-1} $year^{-1}$ fixed represents about 4% of the nitrogen content of the log and appears to be an important auxillary nitrogen source for decomposer organisms. In this respect it is interesting to note that Benemann (1973) and Breznak et al. (1973) have also recorded fixation occurring in the gut of a variety of termites. Termites are widespread in many eucalypt forests and, if fixation in these is common, they may have a disproportionate influence on the increase in the mobilisation and cycling of nitrogen immobilised in woody material.

Table 4. Various measures of nitrogen fixation in litter, logs and soil in forest ecosystems showing whether a single measurement or based in measurements throughout the year.

	Litter			Soil			Logs		
	$kgN\ ha^{-1}yr^{-1}$	$\mu gNg^{-1}day^{-1}$	$nmC_2H_4g^{-1}day^{-1}$	$kgNha^{-1}yr^{-1}$	$\mu gg^{-1}day^{-1}$	$nmC_2H_4g^{-1}day^{-1}$	$nmC_2H_4g^{-1}day^{-1}$	Sample times	Reference
(a) **Deciduous Hardwood Forest**									
Mixed spp, U.S.A.	2-3			8.5				Multiple	Todd *et al.* 1978.
Mixed spp, U.S.A.	slight			0.15				Multiple	Tjepkema 1979.
Mixed spp, U.S.A.			23.7			1.2	30.5	Single	Cornaby & Wade 1973.
Aspen, Maple; Canada			7.6	0.5-1.0				Single	Knowles & O'Toole 1975.
(b) **Conifer Forest**									
Douglas Fir plantation; U.K.	0.3-0.6	2.6		2.5-4.8	1.04			Multiple	Jones *et al.* 1974.
Native Conifers; N.Z.		6.7			0.10			Single	Silvester & Bennett 1973
(c) **Eucalypt Forest**									
E. marginata			25.4					Single	O'Connell *et al.* 1979.
E. diversicolor			51.4					Single	O'Connell *et al.* 1979.
(d) **Tropical Soil Rainforest**				0.06					Spiff & Odu 1972.

Table 5. Phyllosphere nitrogen fixation in forest ecosystems

Forest	Fixation Rate kg N ha^{-1} yr^{-1}	Method	Sample times	References
Rain forest	61	estimated from water N concentrations above and below canopy	4	Edmisten 1970
Rain forest	25-75	C_2H_2 reduction	1 (?)	Harrelson 1970
Deciduous hardwood	1.7	C_2H_2 reduction	multiple	Todd *et al.* 1978
Douglas Fir	14.4-14.6	^{15}N	multiple	Jones *et al.* 1974
Canopy lichens only				
Rainforest	1.5-8	measure lichen biomass & assume fixation rate	-	Forman 1975
Douglas Fir	1.5-10	measure lichen biomass & assume fixation rate	-	Denison 1973

Rhizosphere

There have been a number of reports of nitrogen-fixing activity in plant rhizosphere. Work by Richards and Voigt (1964) and Silvester and Bennett (1973) on conifers suggests the centre of activity is outside the root and is probably associated with rhizosphere bacteria. The rates of fixation reported have often been quite low and Knowles (1977) quotes data from *in situ* assays in tropical and temperate forests suggesting fixation rates of 1-5 kg N ha^{-1} $year^{-1}$. On the other hand, Day *et al*. (1975) concluded that most of the fixation in an English deciduous woodland of 30 kg N ha^{-1} $year^{-1}$ was probably due to fixation in the rhizosphere of a weedy dicotyledonous understorey.

Phyllosphere and Upper Plant Surfaces

A variety of nitrogen fixing organisms may inhabit leaf surfaces, branches and tree boles, particularly in the tropics where the canopy microclimate favours year long activity (Ruinen 1975). Estimates of phyllosphere fixation in rain forests suggest annual rates of up to 75 kg N ha^{-1} (Edmisten 1970; Harrelson 1970), but smaller rates of 4-15 kg N ha^{-1} $year^{-1}$ have been measured in temperate conifers (Jones *et al*.1974) and 0.2-1.7 kg N ha^{-1} $year^{-1}$ measured for temperate deciduous hardwoods (Todd *et al*. 1978). Some of the data are shown in Table 5. This difference between hardwoods and conifers in the temperate region is probably related to the difference in leaf longevity and to the fact that the maximum fixation rates measured in Douglas fir by Jones *et al*. (1974) occurred in April and May when the deciduous hardwood species leaves were only just beginning to appear. No measurements have been made in Australian forest ecosystems although some phyllosphere fixation may occur in native forests growing in wetter areas and phyllosphere fixation may account for some of the suggested nitrogen accretion that Richards (1964) has suggested occurs in *Pinus* plantations.

Appreciable amounts of fixation probably occur in lichens growing on leaves, twigs and branches in tree crowns. Forman (1975) and

Denison (1973) have both estimated an annual input of up to nearly 10 kg N ha^{-1} in both tropical and temperate forests although no actual measurements of fixation were made in either case (Table 5).

TOTAL NITROGEN FIXATION IN FOREST ECOSYSTEMS

There are comparatively few attempts to estimate the total nitrogen input into a forested ecosystem. Some of these are shown in Table 6. These include estimates based on a summation of fixation in various ecosystem components, such as those described above, and estimates based on direct assessments of nitrogen accretion in the ecosystem (or soil) which indicate nett rather than total nitrogen inputs.

The highest values are those estimated for tropical rainforests (up to 88 kg N ha^{-1} $year^{-1}$) and for plantations of known nitrogen fixers such as Acacia or Alnus (up to 202 kg N ha^{-1} $year^{-1}$). In temperate woodlands with mixtures of N fixing and other species most studies report values of about 20 kg N ha^{-1} $year^{-1}$. Perhaps the most reliable value is the indirect measure of nett nitrogen fixation by Borman et al. (1977) who calculated the input after allowing for rates of biomass incorporation, losses in stream water and denitrification.

Fixation in the various components (soil, litter, phyllosphere etc.) of eucalypt forest ecosystems should be comparable to rates measured in forests of similar structure and in similar climates elsewhere. There may be a difference however in the nature of the input from the understorey of eucalypt forests which commonly have a strong legume component. Table 6 shows these may be capable of a large nitrogen input. This understorey component may change in time depending on the fire regime. Hence nitrogen inputs to the ecosystem may also vary strongly with time.

Table 6. Nitrogen inputs from fixation in forest ecosystem

Forest	Rate kg N ha^{-1} yr^{-1}	Method	References
Rainforest	88	Estimated from water N concentrations at various points in ecosystem; allows for losses from ecosystem.	Edmisten 1970
Deciduous hardwood U.S.A.	14	Estimated indirectly from known rate of ecosystem N accrection, outputs and other ecosystem inputs.	Borman *et al.* 1977
Deciduous hardwood U.S.A.	12	Periodic C_2H_2 reduction measures in various ecosystem components.	Todd *et al.* 1978
Decidous hardwood U.S.A.	14	?	Metillo quoted by Todd *et al.* 1978
Deciduous hardwood U.K.	49 (Soil only)	Estimate based on accretion rate in soil less inputs due to rain (1.4) birds/dust (1.5) and dry sorption of ammonia (13). No allowance for amount in biomass.	Day *et al.* 1975
Deciduous hardwood U.S.A.	0.2	Periodic C_2H_2 reduction measures in various ecosystem components.	Tjepkema 1979
Alnus U.S.A.	85	Calculated from rate of N accretion in soil and plants in forest of known age.	Voight & Steuck 1969
Douglas Fir	8-20	Periodic measurements using ^{15}N of fixation in various ecosystem components.	Jones *et al.* 1974
Acacia plantation	202 (Soil only)	Estimate based on accretion rate in top soil. No allowance for amount in biomass or other inputs (e.g. rain).	Orchard & Darby 1956
Casuarina planatation	52	Based on accretion in 13 year old plantation ecosystem less the amount added in rain.	Dommerques (1963); quoted by Silvester 1977.

CHANGES IN ECOSYSTEM NITROGEN INPUT WITH TIME

In most studies of primary successions to date, nitrogen input from symbiotic N fixers are high early in the succession but, with time, diminish as the N fixing-plants are eliminated (Stevens and Walker 1970). Less work has been carried out in secondary successions but Gorham et al. (1979) have speculated that "in systems with a high fire frequency, nitrogen fixers will be more prevalent in a secondary succession, since fire removes nitrogen by volatilization and releases phosphorus". Where secondary successions have been induced by other mechanisms (i.e. logging, windthrow) they suggest nitrogen is not lost and changes in nitrogen fixation may be less important.

The evidence from Australian forest ecosystems broadly supports these views. Fires commonly stimulate leguminous species (Floyd 1966; Christensen and Kimber 1975; Purdie 1977; Shea et al. 1979; Specht et al. 1979; Bell and Koch 1980;). In the absence of further fires, or where fire intensity is low, these legumes will eventually die and be excluded from the succession. Thus Specht et al. (1958) noted that the legume Phyllota disappeared from a heath community about 20 years after a fire and populations of the only other nitrogen fixer present, Casuarina pusilla, also diminished with time. Likewise, Bell and Koch (1980) found the understorey species diversity in jarrah forest increased to a maximum 3-5 years after fire and then subsequently diminished, due mainly to senescence of Acacia, Bossiaea and Kennedya. In the absence of fire such species usually remain in the ecosystem as seed stored in the soil and regenerate again after the first hot fire. Since these species are often nitrogen fixers, the normal pattern of nitrogen inputs in a mature eucalypt forest is probably a series of major pulses corresponding to the fire frequency rather than a steady input over time. These pulses lag well behind the pulse of phosphorus originating at the time of the fire, suggesting that the N/P ratio in soil may fluctuate appreciably in the post fire period. Eucalypts appear to have an optimal N/P ratio (Lamb 1977; Cromer et al. 1980) and marked changes, if they occur, may impose temporary stress conditions.

There may be exceptions to this broad pattern. Some species, including some Acacia and Casuarina, may be favoured by the absence of wildlife (e.g. Coaldrake 1971; Langkamp et al. 1979). An unusual case of this occurs in a dry sclerophyll E. ovata forest near Pt. Phillip Bay in Victoria which has escaped fire for over 90 years because it is surrounded by farmland (Withers and Ashton 1977). At this site the dominant eucalypts are now dying and being replaced by Casuarinas and some Acacia. The increase in the proportion of the supposed nitrogen fixing genera does not appear to have yet sponsored any major difference in the total soil nitrogen concentration between the stagnating eucalypt stand and the Casuarina community, although there may be differences in the total nitrogen pool in the two sites.

In the cooler, wet sclerophyll forests of Tasmania, the absence of wildfire eventually leads to the replacement of the eucalypt dominated forest by a cool temperate rainforest. In the moist micro-environments of these forests nitrogen inputs may increasingly come from soil and phyllosphere fixation rather than legumes.

Management can alter these successional patterns by altering fire intensity and frequency. If hot fires are excluded many hard seed coat species will fail to germinate and Floyd (1976) has described how changes in fire frequency can drastically alter understorey species composition. Likewise, post-logging seed beds left by bulldozers rather than fire may produce lower understorey species numbers generally and lower legume numbers in particular (Floyd 1966). In both cases the nitrogen inputs to the successional ecosystems are likely to be comparatively small and the long term effects of such changes are unclear. The extent to which a particular fire regime will alter the population of understorey nitrogen fixers will also depend on the extent to which grazing of these species by native herbivores occurs (Leigh and Holdgate 1979).

It is well known that fixation rates in various ecosystem components vary throughout the year because of changes in factors such as temperature and moisture. There is also evidence that in some symbiotic relationships the amount of fixation varies during the life of the host species. Grove et al. (1980) have measured a decrease in fixation in Macrozamia roots from a value of 8.4 kg N ha^{-1} $year^{-1}$ in the first year after a fire to 1.4 kg N ha^{-1} $year^{-1}$ seven years after a fire. Likewise, Daly (1966) has commented on an apparent decrease in the efficiency of fixation by Alnus root nodules with time.

FACTORS AFFECTING FIXATION RATES

It has been proposed by Beadle (1962) and Walker (1965) that nitrogen fixation in an ecosystem will become reduced when phosphorus available to plants is limited by chemical immobilisation or diminished weathering of primary phosphate minerals, and Gorham et al. (1979) suggest this indicates a possible control of one nutrient cycle by another. While this phosphorus induced limitation may apply to agricultural legumes, the evidence so far suggests it is not a significant limitation for native forest legumes. Moore et al. (1967), for example, have found native communities of Acacia harpophylla (Brigalow) are capable of growing well and presumably fixing nitrogen under conditions of poor phosphorus availability. Likewise Shea and Kitt (1976) in a glasshouse study found that the addition of superphosphate, potassium sulphate and trace elements had no effect on nodule nitrogenase activity in several W.A. Acacia species although the nodule weight itself increased. If phosphorus is limiting fixation in these species it may be doing so by simply limiting nodulation.

Nitrogen fixation in agricultural legumes is commonly reported to be depressed by high levels of available nitrogen although evidence from field studies done without added nitrogen is difficult to find (Gibson 1977). Such a depression does appear to have occurred during successive rotations of Acacia mollissima in South Africa where less fixation occurred in later rotations (Orchard and Darb 1956). Withers (1979) has also noted a reduction in Acacia nodulation (and hence fixation?) when the young seedlings were shaded. However she found the overall plant weight was also reduced and the proportional weight of nodules remained constant.

Although not a great deal is known about fixation rates in Acacia and the factors that affect them, even less is known about the other potential nitrogen fixers in Australian forest ecosystems. There is also a particular gap in knowledge concerning the endophytes involved with Acacias and other species. For example, there appears to be a high fixation capacity in Acacia and Casuarina plantations overseas compared with fixation rates by these and other legumes in forest ecosystem in Australia. Part of this difference, of course, concerns the difference in stocking rates, but it seems possible there may be relatively sparse population of suitable microorganisms in native forest soils (F. Bergersen, pers. comm.).

Given, then, that the rates of nitrogen fixation by various nodulated species found in eucalypt forests can vary and that the populations of these species can change in time, what scope is there for the forest manager to increase nitrogen inputs into the forest? In the first place, it may be possible to increase the population of nodulated species by manipulating fire regimes and overstorey canopy cover. Obviously more work needs to be carried out on the ecology of particular understorey species and of possible disadvantages arising from competition before this can be done. Secondly, it may be possible to introduce non-native nitrogen fixers into forests. This has been very successfully done in rubber plantations in Malaysia, and Broughton (1977) reports gains of 150 kg N ha^{-1} $year^{-1}$ were achieved over a five year period.

Other papers in this volume describe similar approaches being tried in Pinus plantations in Australia and New Zealand. There seems to be less scope for increasing inputs from free-living nitrogen fixers in the soil, litter or phyllosphere, although the ecology of these organisms has scarcely been studied and so the possibilities remain unknown.

CONCLUSIONS

1. Ionic nitrogen inputs in rainfall are likely to be less than 9 kg N ha^{-1} $year^{-1}$ although organic forms of nitrogen may increase this amount. The ecological significance of direct absorption of atmospheric ammonia by plants remains to be assessed.

2. Fixation rates of about 20 kg N ha^{-1} $year^{-1}$ have been measured in temperate forest ecosystems. This amount is made up of inputs from the phyllosphere, litter, soil and rhizosphere and although there are few comparable measurements in Australian forest ecosystems, the diversity of forests in which fixation has been measured suggests comparable inputs can be expected in similar ecosystem components.

3. Much greater nitrogen inputs into Australian forests are likely to originate in nitrogen fixing plants in the understorey. The composition of the understorey is strongly influenced by fire but the relationship between fire regime and nitrogen fixation in the post fire succession is not well understood. In particular, the advent of controlled burning and the reduction in the frequency of hot fires had undoubtedly changed the nature of forest understoreys and hence nitrogen fixation patterns. The long term significance of this for the forest nitrogen balance is not clear.

4. The genus Casuarina is widespread in many forest ecosystems and may be an important source of nitrogen. The limited amount of evidence available, however, suggests not all species capable of significant rates of fixation under normal conditions and the importance of Casuarina needs to be studied.

5. There appears to be some scope for increasing natural nitrogen inputs into forests by manipulating the natural understorey and by planting exotic legumes.

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INTERRELATIONSHIPS BETWEEN FOREST FAUNA, NITROGEN FIXING PLANT SPECIES AND FOREST HEALTH

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INTRODUCTION

In tackling a subject as broad as this one it is easy to become overawed by the mass of detailed information which is available on the topic. Reviewing this vast treasure house of knowledge is not my object; I have no intention of tackling such a task for which I feel there are others far better qualified than myself. Besides, beyond serving as a useful reference for others, reviews seldom achieve a great deal. They are rarely stimulating reading and they mostly fail to identify the real problem areas. Since one object of this symposium is to identify areas of concern relating to the managing of the nitrogen economies of natural and man-made forest ecosystems, a review is in any case inappropriate. For these reasons I have chosen to concentrate on local aspects in the field of applied forest ecology and unashamedly ignore the rest of "Pandora's box".

As we shall see, forest fauna, nitrogen fixing plants, and forest health are all interrelated. It is reasonable to assume that in the past some kind of balance, a dynamic equilibrium, existed between these factors. In recent times, following the arrival of European man to Western Australia, certain changes have taken place which are altering this equilibrium or former natural balance. It is my intention to examine certain aspects relating to two factors which may be causing changes. One of these is the widespread practice of low intensity prescribed burning which is carried out for fuel reduction purposes in our forests. The other is the introduction of the European red fox (Vulpes vulpes) to this continent.

For the purpose of this paper the term 'forest fauna' is taken to include both vertebrate and invertebrate forms. 'Nitrogen-fixing plants' are taken to be native leguminous plants with root nodules harbouring nitrogen-fixing organisms. It is accepted that there are other nitrogen-fixing plants, for example Macrozamia reidlii (Halliday and Pate 1976), Casuarina sp. and others, but these are not as widely distributed as the legumes and are therefore not treated in detail. Lastly, 'forest health' though it could be widely interpreted, is taken as referring primarily to the condition of the dominant tree species, the eucalypts, for it is these which essentially form the forest per se. In addition, this paper deals in particular with the dry sclerophyll jarrah (Eucalyptus marginata) forest of Western Australia.

SUMMARY

Nitrogen is lost from the forest system during fires as a part of the natural process. It is believed to be returned largely by native legumes, the germination and development of which depends on fire. The type of fire, and the activities of animal grazers have a profound influence on germination and development.

The level of nitrogen in the system may influence sporocarp production in mycorrhizal fungi. These fungi are essential to maintain the health and vigour of the forest. Dispersal of the fungi is through the agency of mycophagous animals.

In recent times there have been changes to the forest ecosystem which may be affecting these natural processes. Thus the practice of regular and frequent cool prescribed burning for fuel reduction in the forest is reducing the legume component in the jarrah forest understorey. In addition the introduced fox has almost exterminated mycophagous animals in some forest areas. These two factors may affect the health and vigour of our forest ecosystem in the long term.

LEGUMES, FIRE AND FOREST FAUNA

Australian forest soils are generally low in nutrients (Leeper 1970) and nitrogen is at a premium. Under such conditions, animals may select nitrogen rich foods (Leigh and Holgate 1979); indeed it has been proposed that the carrying capacity of the land, with respect to kangaroos and wallabies, may be defined by the amount of nitrogen fixed in the system (Main 1968). Grazing animals influence the survival of seedlings, in particular the nutritious legumes (Leigh and Holgate 1979). Both vertebrates, kangaroos, wallabies and wombats (Christensen 1977, Leigh and Holgate 1979, Oliver, pers. comm.), and invertebrates, principally native grasshoppers (Wheelan 1977), may be involved. As a consequence nitrogen rich leguminous plants are frequently under greater pressures from grazing animals than are other types of plants.

Fire is a natural factor in dry sclerophyll forest ecosystems such as the jarrah (Eucalyptus marginata) forests. Nitrogen is known to be released during fires. In the short term this is compensated for by an improved availability of nitrogen, the extent of which varies according to the degree of soil heating, the amount of ash produced, pH changes and other factors (Humphreys 1966, Raison 1976). In the long term, nitrogen-fixing bacteria in the roots of native leguminous plants appear to play an important role in maintaining the nitrogen status of the soil (Shea and Kitt 1976, Malajczuk pers. comm.).

The majority of native legumes possess 'hard seeds' which germinate most prolifically following fire (Christensen and Kimber 1975).

Under certain circumstances fire may compound the damaging effects of the herbivores (Wheelan 1977, Shea et al. 1979). The scrubby native legumes, unlike for example grasses, are not well adapted to grazing by herbivores, and the small seedlings are often damaged or destroyed. Thus following spring fires, which are generally of low intensity and germinate few legumes, the grazing pressure on the limited seedling resource may be extraordinarily high, resulting in the survival of very few seedlings (Wheelan 1977, Christensen 1977). Following fires of high intensity, when widespread prolific germination of seedlings occurs, grazing animals make little inroad on the vast germinant resource and a high proportion of seedlings survive (Christensen 1977).

The deleterious effects of low intensity fires are compounded because such fires have a tendency to burn unevenly, resulting in a mozaic of unburnt patches of understorey vegetation. Unburnt areas are known to provide a refuge during burns as well as centres from which populations of invertebrate grazers can rapidly expand following a fire (Wheelan 1977). Similarly the larger grazers, kangaroos and wallabies, utilize unburnt areas as refuges and centres from which to operate within recently burnt areas of forest. Under such circumstances grazing pressures may be at a maximum. Prescribed fires of low intensity occurring at regular and frequent intervals exaggerate these effects. Consequently, in areas under such a fire regime, we may expect the legume seed resource in the upper soil layers to become depleted over a period of time. There is some evidence that this is indeed occurring in the northern jarrah forest (Shea et al. 1979).

In the past, a natural balance between herbivores and leguminous plants was maintained by natural selection of adaptive traits which tended to reduce grazing pressures on these plants. One example is the common trait of hard-seededness referred to earlier. As a result of this trait, 'mass germination' of legumes occurs following intense fires. This has the effect of 'flooding the market' with food for the grazers, and ensuring that a high proportion of seedlings survive to maturity. In a similar manner the highly synchronized calving of species of African plains antelope protects the young from predation, ensuring that a high proportion of individuals survive to maturity.

In addition, many plants have developed unpalatable chemicals, for example alkaloid compounds which tend to deter grazing animals (Wheelan 1977). The widespread south-west genera Oxylobium and

Gastrolobium contain a highly poisonous compound, sodium fluoroacetate. Very small amounts of this compound is fatal to non-native grazing animals such as for example sheep. Native grazers, kangaroos, wallabies and others, have developed a very high level of tolerance to this compound, evidence which attests to the long association of grazing marsupials and native legumes in the south-west (Oliver et al. 1977). Despite the high tolerance of native herbivores the poison confers a high level of protection to the seedlings as the grazers may ingest only limited quantities of such plants.

These adaptive traits operate effectively under a system of natural fire diversity. Under natural conditions, should a succession of one or more cool fires occur, inevitably these will be followed by a fire of higher intensity sooner or later. The destruction and losses incurred as a result of a succession of cool fires would therefore have been balanced by the effects of the occasional more intense fire. The plants' adaptive traits may not be capable of coping with a continued regime of frequent cool fires without the occasional more intense fire to break the sequence. Hence we should be concerned about the current system of prescribed burning which may be affecting the relative frequency of occurrence of species of native legumes. There is already some evidence that the cumulative effects of prescribed fires and grazing by native fauna may have resulted in a reduced legume component in the understorey scrub layer of the northern jarrah forest (Shea et al. 1979).

In the long term, under a prescribed burning regime of regular and frequent cool fires, a lowering of the soil nitrogen status might be expected. On this point however, there is conflicting evidence, Floyd (1966) reported negligible available nitrogen production in soils under spotted gum (E. maculata) following eleven years of control burning as compared with unburnt soil. Hatch (1959) on the other hand found no significant differences between the nitrogen status of regularly burnt firebreaks and nearby unburnt jarrah forest.

MYCORRHIZAE AND FOREST HEALTH

Microorganisms are an important link in the complex web of inter-relationships and inter-actions between forest plants, animals and nitrogen. Amongst the more prominent groups of microorganisms which play a role in the cycling of nitrogen, are the group of symbiotic hypogean fungi which form mycorrhizae with the roots of trees and woody plants. Mycorrhizae have been found associated with the roots of most families of the world's vascular plants and are considered to play an important role in plant nutrient uptake. Woody species of the Pinaceae, Fagaceae and Betulaceae in particular are known to be dependant on mycorrhizae, especially in nutrient deficient situations (Harley 1969; Marks and Kozlowski 1973).

In addition to their role in nutrient uptake, mycorrhizal fungi also play an important role in protecting the host roots against disease organisms. By shielding root tips with a protective mantle and producing metabolites that often inhibit pathogenic growth, mycorrhizae may protect rootlets from pathogens (Harley 1969; Marks and Kozlowski 1973).

Eucalypts are known to have distinctive mycorrhizal associations (Chilvers 1968, Malajczuk *et al*. 1980). In addition Malajczuk (1979) suggests that the differential susceptibility of the two major species of eucalypt, jarrah (*Eucalyptus marginata*) and marri (*E. calophylla*), to the plant root pathogen *Phytophthora cinnamomi* may be at least partially explained in terms of their mycorrhizae and associated microflora. It is perhaps pertinent that the plants most susceptible to this pathogen, *Banksia* sp., *Macrozamia reidlii* and *Xanthorrhoea* sp. do not form mycorrhizae (N. Malajczuk, pers. comm.).

Mycorrhizae therefore are of critical importance in tree nutrient uptake and in the tree's defence against disease organisms.

This association between fungi and the higher plants is a very ancient one indeed. Mycorrhizae occur in the oldest fossils of rooting structures, rhizomes of lycopods, from some 400 million years ago (Harley 1969). Sometime during this immense timespan there evolved a tri-partite relationship between mycorrhizal fungi, the vascular plants and animals. In one species, the West Australian rat kangaroo or woylie (Bettongia penicillata), this association has has been demonstrated to be a very ancient one indeed (Kinnear et al. 1979).

Animals eating the fruiting bodies of hypogean mycorrhizal fungi, which form an important food source for many mammals (Fogel and Trappe 1978; Christensen 1977, 1980a), in turn disperse the spores (Maser et al. 1978a, 1978b; Christensen 1980a).

Mammals in particular are important fungus eaters, and mycorrhizal fungi may account for 75% of small mammal mycophagy. Many animals are involved, a range of herbivores, carnivores, insectivores and omnivores all feed on different fungi. Some species rely on fungi as their primary food and there has evolved a high level of interdependence between fungi and animals in some cases (Fogel and Trappe 1978; Maser et al. 1978a; Christensen 1980a). The sporocarps, which they apparently detect by odour, are digested, but the spores pass through the alimentary canal and are deposited onto the soil in the animal faeces. A mechanism for long range dispersal also exists through the agency of native dung beetles, which can fly. Several species of these beetles have been shown to feed on the faeces of fungus eating animals (Christensen 1980a).

Maser et al. (1978b) hypothesize an obligatory symbiotic relationship between hypogean mycorrhizal fungi and most higher plants, together with mycophagous mammals which disperse their spores. The relationship, they maintain, is of critical importance to the optimum functioning of the coniferous forest ecosystem of North America. Christensen (1980a) suggests that a similar tripartite relationship may be of special significance under the peculiar conditions prevalent in Australian forests. Thus low soil nutrient levels, together with frequent fires, followed by rain, create conditions which might result in high nutrient losses, were there not some efficient mechanism such as mycorrhizal fungi for absorbing them quickly and retaining them in the system.

In recent years events which have made non-effective the dispersal mechanism of mycorrhizal fungi have occurred. Over the last 40-50 years dispersal of the spores of these fungi has been almost non-existent in the northern jarrah forests. The introduced European red fox (Vulpes vulpes) caused widespread disappearance of native mycophagous animals during the 1930s (Christensen 1980b). A new equilibrium has been established involving the fox, the introduced rabbit (Oryctolagus cunninculus), the rabbit disease myxomatosis, the rabbit flea (Spilopsyllus cuniculi), the rabbit poison 1080 and in some areas native poison plants of the genus Gastrolobium. This complex system of largely exotic species now apparently determines population levels of native phytophagous animals (Christensen 1980a, 1980b).

We may only speculate about the consequences of this lack of dispersal. For example, how essential is dispersal of the spores? If there is no dispersal, will a large proportion of the new roots produced by trees remain uninfected and therefore less effective in nutrient uptake and more susceptible to disease? It has been speculated (Christensen 1980b) that the lack of spore vectors from the northern jarrah forests over the last 30-40 years may be a factor in the spread of the forest tree disease (Phytophthora cinnamomi) in recent years.

In addition to the introduced fox, which is now a major factor regulating spore dispersal, nitrogen also appears to be a limiting factor in the spread and growth of mycorrhizal fungi. Both the sporocarps and the spores of mycorrhizal fungi contain very high levels of this element (Kinnear et al. 1979). Sporocarp production in the field has also been demonstrated to be most prolific under young vigorously growing stands of native legumes which have a high nitrogen fixing capacity (Christensen 1977, 1980a). High levels of soil nitrogen thus appears to favour sporocarp production and therefore their mycophagous animal vectors as well. Nitrogen therefore may be a further limiting factor in the growth and spread of mycorrhizal fungi.

DISCUSSION

The relationship between nitrogen-fixing plant species, forest fauna and forest growth and health is a delicate one. The nitrogen status of the forest appears to depend in no small measure on fire diversity which affects the abundance of animal grazers and leguminous plants. Nitrogen levels ultimately influence mycorrhizal development and hence nutrient absorption, tree health and the mycophagous animals. Changes in the abundance of the animal spore vectors may in turn affect mycorrhizal distribution and growth.

In the short time since European settlement of the south-west, changes have occurred which may be altering former balances within the forest ecosystem. Fire is a natural agent in our forests (Christensen *et al*. 1980), but in recent times a new fire regime, broadscale cool spring prescribed burning on a short rotation has been introduced (Peet 1967). This new fire regime appears to be resulting in changes in the abundance of hard-seeded nitrogen-fixing leguminous understorey species in the jarrah forest. If such changes were to become irreversible it might adversely affect the nitrogen balance in the system with resulting problems in forest growth and health. Such a situation seems unlikely since there still appears to be a store of legume seeds at depth in the soil profile which may be made to germinate simply by introducing one intense fire (Shea *et al*. 1979).

Nevertheless how long can the system remain in temporary 'imbalance' without resulting in serious changes? There appears to be no answer to this question at the present time since there are too many imponderables. For example, are native legumes as important a factor in the total forest nitrogen budget as we believe they are? This is a difficult question. Certainly it may be demonstrated that they fix considerable quantities of nitrogen, but it has not yet been satisfactorily demonstrated that soil nitrogen declines significantly in their absence. The difficulty is to establish a 'natural' or 'base' level of nitrogen for the system. In the absence of concise pre-European fire history data, the relative frequency of occurrence of legumes in the forest and hence the rate of nitrogen fixation cannot be established with any degree of accuracy. As a consequence, there is nothing with which to compare present nitrogen levels and turnover rates in the jarrah forest in order to determine whether or not they are adequate. Nevertheless nitrogen levels could be measured on long term plots given different fire treatments resulting in a variety of legume populations. Such data would provide valuable information.

In addition to the lack of information concerning nitrogen input into the system, we also lack data on its real significance. For example, what are the precise relationships between spore production in mycorrhizal fungi and the levels and availability of nitrogen? Is the continuous distribution of the spores of mycorrhizal fungi essential to ensure adequate levels of root infection of forest trees? If it is, then the problem of the introduced fox and predation of spore vectors needs to be given more serious consideration.

To what extent is the capacity of eucalypts to take up nutrients and to resist disease affected by reduced mycorrhizal infections? Introduced plantation pines, for example, seem to manage throughout the entire life span with only one infection of mycorrhizae, carried out whilst they are in the nursery. Does the fungus in this case manage to spread by mycelial contact without the aid of animal vectors, or can the pines cope with lower levels of root infection only because of the artificially high nutrient levels?

To these and many other questions we do not yet have the answers. However, they are not impossible to test experimentally and this should be done. Having once done so we may find that for one reason or another the changes which we have imposed upon the forest ecosystem are causing no significant impact. On the other hand, if they should be found to be having harmful effects, it will still be possible to institute changes to negate or reverse these effects before they become irreversible and cause irreparable damage.

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NITROGEN ECONOMY IN JARRAH FOREST CATCHMENTS

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ABSTRACT

Initial data for nitrogen input and output for jarrah forest tributary catchments of the Yarragil Brook, southeast of Dwellingup, Western Australia, are presented. The catchments are representative of aggrading ecosystems with forestry management histories of selective logging and controlled burning. Bulk precipitation input for total nitrogen was 3.5-3.7 kg/ha/yr. Input nitrogen was primarily in organic form. When compared to clearfall values, canopy throughfall was lower in inorganic nitrogen and higher in organic nitrogen. Streamflow outputs of nitrogen forms were extremely low despite the history of disturbance. A better understanding of the ecosystem mechanisms of nitrogen retention would provide information for better management of the resources of the jarrah forest ecosystem.

INTRODUCTION

Jarrah forest catchments supply Western Australia with major economic resources in timber, bauxite, fresh water and recreation. With increased pressure of industrial, agricultural and domestic use of the Darling Range, an understanding of the existing forest ecosystem and its response to modification and management by man becomes extremely important and timely. Given the basic abiotic and biotic complexity of land, the phenomena of succession and retrogression, a multiplicity of managerial goals, and a desire for more efficient use of the land, it is obvious that some theoretical framework upon which we can assemble and interrelate these diverse components is a necessity (Bormann and Likens 1969). In one form or another, foresters and range managers have long been aware of this need (Lutz 1957, 1963; Costello 1957). The ecosystem concept provides this framework (Evans 1956).

In the past year ecosystem monitoring in the Yarragil Brook tributary catchments southeast of Dwellingup, Western Australia, has been initiated (Fig. 1).

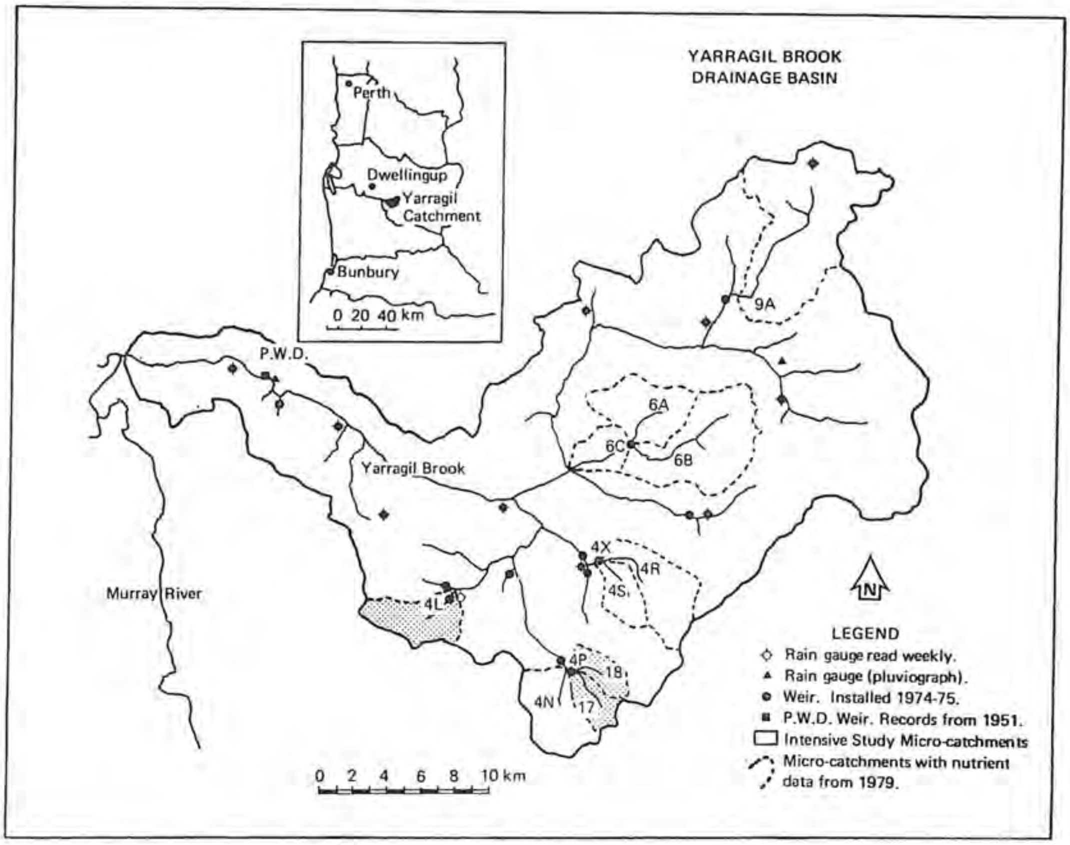

Fig. 1. Yarragil Brook Drainage Basin southeast of Perth, Western Australia. Locations of nutrient monitoring Catchments, weirs and rain gauges.

Major objectives of the study are to measure compartment levels and transfers of major essential elements in forested microcatchments and to assess impacts of a number of forest management practices. A basic conceptual model has been developed (Fig. 2) and a number of representative sites have been delineated to measure the levels of the ecosystem state variables and transfer rates. At each site samples of the overstorey, understorey, standing and fallen logs and litter provide values for the above-ground primary producer ecosystem components. Litter fall traps and litter decomposition bags monitor the transfer of elements via the leaf fall-decomposition cycle. Collections of rainfall, throughfall, stemflow, tension-cup lysimeters and the microcatchment v-notch weir provide data on hydrologic transfers. In the current report, initial data for the input, conservation and output of nitrogen in these jarrah forest catchments for 1979 are presented.

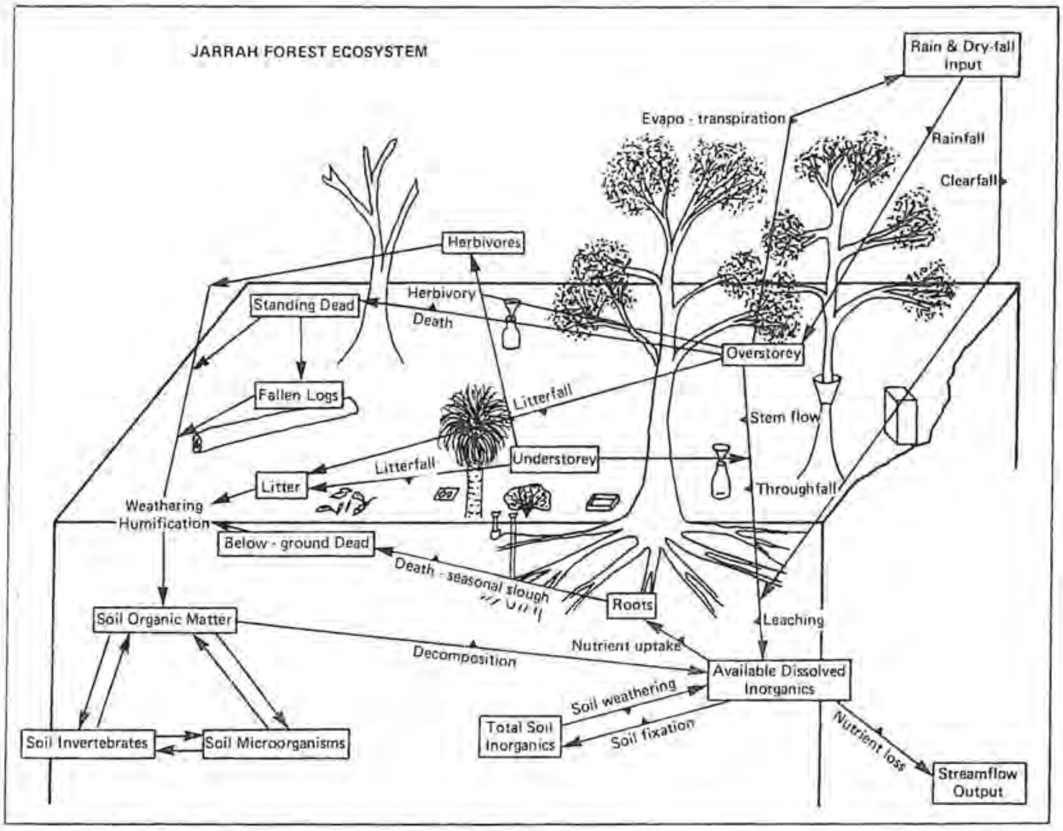

Fig. 2. Conceptual model of the jarrah forest ecosystem and diagrammatic representations of field sampling intensive study sites.

JARRAH FOREST NITROGEN BUDGETS

Measurements of nutrient inputs from rain and outputs in stream water can provide the information to calculate nutrient budgets for watershed-bounded ecosystems (Bormann and Likens 1967). Negative input-output balances tend to occur in early successional vegetation, become positive when net ecosystems production is highest and then tend to achieve a balance between inputs and outputs when net ecosystem production approaches zero (Gorham et al 1979). Accumulating levels in productive ecosystems have been measured despite periodic wildfires volatilizing some 80% of the exposed nitrogen (Gessel et al 1973). Documentation of ecosystem nitrogen budgets are complicated primarily because of the predominantly gaseous phase.

Nitrogen losses in streamflow for selected jarrah forest catchments of Yarragil Brook are shown in Table 1. Despite a history of logging and control burning which has kept these communities from reaching ecological maturity, both inorganic and total nitrogen outputs were extremely low. The range of NO_3/NO_2 losses from .0000047 to .000413 kg/ha/yr are substantially below the values 0.011 to 0.013 reported for Eucalyptus radiata dry sclerophyll forests in northeast Victoria (Flinn et al 1979). Nitrate loss from a diversity of forested streams in the northern hemisphere is also several orders of magnitude higher : .03-4.5 kg/ha/yr (Vitousek and Melillo 1979). Nitrogen output in Yarragil Brook microcatchments showed a strong relationship with total streamflow (r = 0.979, Fig. 3). However, streamflow itself was poorly correlated to catchment area or rainfall.

Nitrogen inputs in clearfull and throughfall during 1979 have been estimated for 4 L and 4 P microcatchments (Table 2). Comparative Australian data are, at present, scant and varied. Studies by the Engineering and Water Supply Department of South Australia (Wood 1975) give values similar to those of the present study (total N of 3.19 and 3.69 kg/ha/yr). Westman (1978), however, recorded an annual accession of 60 kg/ha total N, and 0.17 kg/ha NO_3. O'Connell (cited in Congdon 1979) records a figure of 0.7 kg total N/ha/yr in rainfall at Dwellingup. These differences highlight the need for further Australian studies, though the variation observed may indeed be real, being dependent upon differences in rainfall duration, proximity to industry or to the sea. Clearfall values for total and soluble nitrogen inputs to Yarragil Brook are at the extreme low end of the range reported for overseas by Loehr (1974): 5.6 to 100 kg total N/ha/yr (the high value including industrial areas); 0.8 to 12.9 kg/ha/yr inorganic nitrogen.

Table 1. Nitrogen outputs in streamflow for selected jarrah forest catchments of Yarragil Brook during 1979.

Catchment name	Area (ha.)	Years since last burn	Streamflow total (m^3)	Weighted average rainfall (mm)	Catchment Output NH_4–N		NO_3/NO_2–N		Organic N		Total N	
					kgs	kg $ha^{-1}yr^{-1}$	kgs	kg $ha^{-1}yr^{-1}$	kgs	kg $ha^{-1}yr^{-1}$	kgs	kg $ha^{-1}yr^{-1}$
4P–18	52	Before 1972	4885	776.8	.0956	.0018	.0165	.000317	2.2519	.0433	2.3640	.0455
4P–17	78	Before 1972	8224		.1521	.0019	.0322	.000413	2.7882	.0357	2.9725	.0382
4L	123	Spring 1973	No flow-ponded	755.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6C	461	Spring 1972	4460	685.0	.0705	.00015	.0182	.000040	1.9641	.0043	2.0528	.0045
9A	580	Spring 1972	689	648.3	.0088	.000015	.0027	.0000047	0.3593	.0006	0.3708	.0006

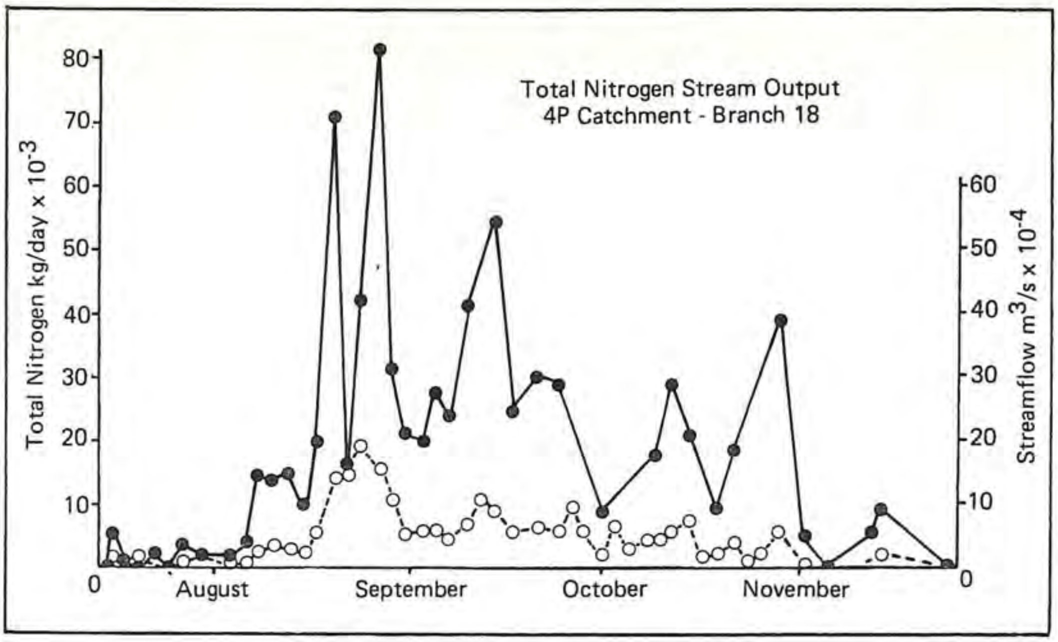

Fig. 3. Total nitrogen (open circles) and streamflow (closed circles) output for the Yarragil Brook forested tributary 4P-18 during 1979.

Table 2. Yarragil Brook catchment nitrogen input.

Catchment name	Sample	Catchment Input (kg ha^{-1} yr^{-1})			
		NH_4–N	NO_3/NO_2–N	Organic N	Total N
4L	Clearfall	0.291	0.211	3.047	3.549
4P	Clearfall	0.395	0.230	3.065	3.691
4L	Throughfall	0.217	0.112	4.120	4.448
4P	Throughfall	0.142	0.068	4.629	4.839

DISCUSSION

Jarrah forest ecosystems receive very low levels of nitrogen input in rainfall. In turn, losses in streamflow appear correspondingly meagre (<1% of clearfall inputs during 1979). The vagaries of the hydrological cycle in this Mediterranean climate region have an important influence on nutrient budgets for jarrah forest catchments, emphasizing the necessity for long-term monitoring. It may be possible, however, to predict total nitrogen output for more mature Yarragil Brook microcatchments from longer-term streamflow records, given the close relation between these two parameters.

Jarrah forest catchment streams rarely yield more than 15% of annual rainfall input and it is common to have no streamflow for some forested catchments (Shea and Herbert 1977). Lack of water for nitrate transport is one of the main processes delaying or preventing solution losses of nitrate from disturbed forests (Vitousek et al 1979). The development of hardwood eucalypt forests of considerable biomass, growing on old lateritic soils, is the product of centuries of evolution towards efficient nutrient accumulation, retention and recycling. The evolution of a deeply-rooting overstorey capable of transpiring substantial amounts of water throughout the dry summers, serves to reduce losses of soluble nitrogen from the ecosystem.

Nutrient retention in jarrah forest catchments must be considered when judging the long-term impact of various management options. This applies particularly to the proposed use of periodic hot fires (Shea et al 1979) to actively manage site deterioration caused by fungal dieback spread. The rapid recovery following fire by jarrah forest vegetation is well documented (Peet and McCormick 1971, Shea et al 1979, Bell and Koch 1980). However, we need to know whether the increased fixation of nitrogen by regenerating legumes is sufficient to balance volatilization and streamflow losses following fire (Raison 1980).

Considering that the environment is only marginally suitable for forest growth (Shea et al 1975), rehabilitation of degraded areas with species capable of maintaining the high rates of water usage typical of jarrah is a difficult problem. Effects of reduced evapotranspiration upon the hydrological cycle in turn, pose problems for continuing water quality and quantity. If the northern jarrah forest is to continue to provide economic resources in timber, bauxite, fresh water and recreation, a better understanding of the dynamics of existing ecosystems must be established. The ecosystem study now under way and co-operative efforts with the W.A. Forests Department, the Western Australian Institute of Technology, Murdoch University and CSIRO are designed to assist in the development of this understanding.

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SOIL AND LITTER INVERTEBRATES OF THE JARRAH FOREST AND WOODLAND REGIONS

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ABSTRACT

This paper confines itself to those invertebrates which occur in soil and litter layers of the region which was, or still is, vegetated by jarrah (Eucalyptus marginata). Invertebrates from other strata of the forest such as the canopy defoliators, although also important in nutrient cycling, are not considered here.

The aim of this paper is threefold. It commences with a discussion of the ways in which soil and litter invertebrates may influence the decomposition process in terrestrial ecosystems. The published work on soil and litter invertebrates from the jarrah forest or woodland region is then reviewed in chronological order and certain points of interest are discussed. Finally, the relevant projects which are currently in progress in this region are outlined. Most work is in its early stages, so the findings will not be mentioned in detail here. It is hoped, however, that its description here will alert interested persons to its existence and enable them to contact the relevant workers if so required.

INTRODUCTION

The basic components of terrestrial plants and animals are ultimately returned to the soil or soil surface in the form of fallen leaves, wood and other parts of plants, dead roots, or as faeces and carcasses of animals. The decomposition process which subsequently takes place prevents the build-up of detritus and returns elements such as nitrogen to the biogeochemical cycles of the biosphere. It occurs because heterotrophic organisms metabolise the detritus as their energy base.

It has commonly been assumed that decomposition, and hence nutrient mineralization, results from the activities of the soil microflora and that soil fauna has only a relatively insignificant direct effect. The evidence now suggests that the soil and litter fauna plays a regulating role in nutrient cycling and that its contribution is by no means insignificant. This paper commences with a brief summary of current ideas on the role of soil and litter invertebrates in the decomposition process. It then outlines the relevant work which has been performed to date in the jarrah forest and woodland regions of Western Australia and, finally, it describes the projects which are currently being performed in this region. The first section of the paper draws on four reviews of the same subject (Edwards et al. 1970; Reichle 1977; Kitchell et al. 1979 and Springett 1979a). The primary sources of information are not generally referenced in the text here.

Soil organisms may be grouped into three categories: the mesofauna which includes animals such as worms and ants which can burrow and tunnel in the soil; the microfauna which comprises animals small enough to move through existing soil spaces; and the microflora such as the bacteria, fungi and actinomycetes. The microflora break down the complex molecules, including cellulose, lignin and suberin, of the detritus and hence assist in the encouragement of mineralization of nutrients. The principal role of the fauna in decomposition has generally been considered to result from comminution, or reduction in particle size, of the detritus. This was thought to increase the surface area of the detritus and hence to promote leaching and microbial attack.

Following on from the fact that the microflora and fauna mainly use detritus as their food base, the view has arisen that the impact of soil flora and fauna is correlated with the magnitude of energy flow through the population or community. Reichle (1977) cites one study which was performed in mesic deciduous forest in which $2500gCO_2/m^2$/year is respired by the total soil heterotrophic community. The microflora contributed 90.3 per cent of this amount and the fauna produced the residue. It is tempting to use figures such as these to express the relative importance of different components of the biota in the decomposition of detritus. The problem with this approach is that CO_2 production gives an indication of how much is going on in the system while failing to provide information on the type of activities which are taking place. For instance, this method fails to provide information on the interaction between fauna and microflora and the possible synergistic effect of the former on the microflora. This is illustrated by a simple laboratory experiment described by Springett (1979a). The decomposition rate of cellulose was increased by 40 per cent when one species of Collembolan was incubated with microflora in a culture; it was increased a further 20 per cent when a predacious mite was also added.

As a result of such problems, there is now an interest in looking at the role of fauna in regulating decomposition and hence, ultimately, nutrient cycling (Kitchell et al. 1979). In their review paper, the regulating influences are grouped into two categories; translocation and transformation. Neither of these processes are directly related to energy flow.

Translocation refers to the processes whereby detritus, or its component compounds, are redistributed between subunits of the ecosystem so that detritus availability to decomposers, and utilization of the resulting nutrients by primary producers, is facilitated. For instance, leaf litter may be consumed by mesofauna at one site while defecation or mortality of the animal may occur in another area. In cases where the organic matter is moved upwards through the soil, increased exposure to physical and biological agents may accelerate decomposition. In Australia ants and termites are particularly important agents which carry organic matter from above ground into the soil where decomposition then takes place. A further regulating influence, not directly related to decomposition, is the upward movement of mineral soil by earthworms, ants and other animals to the surface where the availability of nutrients to certain plants is increased.

Transformation describes the processes which result in the alteration of organic matter particle size and hence susceptibility to leaching and microbial attack. One obvious example of transformation is the conversion of litter to faeces. This can produce different outcomes. Large arthropods may produce faeces with a lower surface area than the original litter and therefore decrease decomposition rates. The microfauna may have the opposite effect by producing faeces of increased surface area although, with smaller particles, this effect may be counteracted by the agglomeration of small particles and hence loss of surface area. Also included in this category is the channelization of wood. Studies have shown that logs decompose very little until invasion by various decomposer organisms is permitted by the works of primary channelizing organisms such as termites, ants and beetles.

One additional influence of fauna on decomposition, which does not naturally fall into either of the above two categories, is the selective grazing of arthropods upon microflora. This may regulate the rate of decomposition so that nutrient release occurs in a more controlled manner. Selective grazing may also promote the diversity and activity of certain components of the microflora.

The data from which the above comments emanated, were obtained from studies performed in numerous geographical, often moist, regions. Their relevance to the drier jarrah forest and woodland regions is uncertain. Comparable studies on the role of soil and litter fauna in decomposition here are scarce as most work performed to date has largely been confined to the base-line data gathering stage. The remainder of this paper outlines the previous and current work on soil and litter invertebrates in the jarrah forest and woodland regions so that this Workshop may reflect on the adequacies of, and needs for further, information on this potentially important component of the decomposition and nutrient cycling system.

PREVIOUS STUDIES ON SOIL AND LITTER INVERTEBRATES

In what follows I discuss only those studies directly involving soil or litter invertebrates in the region of interest. It should be noted that invertebrates from other strata, such as the canopy defoliators, are also important regulators of nutrient cycling. A complete list of current and published work on terrestrial invertebrates in Western Australia is to be found in Majer and Chia (1980).

Table 1 documents in chronological order the past and present work on jarrah forest or woodland soil and litter invertebrates. Although not specifically concerned with invertebrates, the work of Hatch (1955, 1964) is listed since it laid the ground work on jarrah litter fall, litter biomass, decomposition rate and chemical composition.

In his pioneer work, McNamara (1955) studied the invertebrates of the soil and humus in jarrah forests and compared burnt and unburnt compartments and also areas suffering from crown deterioration. He concluded that the microfauna contained more individuals and taxa in places with accumulated organic matter. Over a decade later Bornemissza (1969) reported a study of soil and litter invertebrates in a burnt area of native bushland at Kings Park, Perth. He concluded that most of the soil and litter dwelling invertebrates had regained normal population levels after 2 or 3 years.

Springett (1971, 1976a) compared the soil and litter fauna of Pinus pinaster plantations and native woodlands at Gnangara, north of Perth. This study suggested a lower species diversity of soil microarthropods occurred in pine plantations than in native vegetation, but abundance levels were similar. Associated decomposition experiments suggested that the impoverished

Table 1. Chronological review of past and present works on jarrah forest or woodland floor invertebrates which have direct relevance to the consideration of nutrient cycling.

Reference to and/or status of project	Project Description	Consideration given to invertebrates	Consideration given to litter decomposition
Hatch (1955, 1964)	Quantification of jarrah litter fall, litter accumulation, gross decomposition and influence of decomposition on forest soil.	No experimental work.	Decomposition of jarrah leaves studied over a two year period.
McNamara (1955)	Quantification of soil and humus layer invertebrates in relation to burning, crown cover and amount of organic material.	Soil cores from selected plots sampled using Berlese funnels.	No experimental work.
Bornemissza (1969)	Study of reinvasion of soil and litter invertebrates to woodland following burning.	Sequential samples taken at various times after burning.	No experimental work.
Springett (1971, 1976a)	Comparison of soil micro-arthropod density and diversity and litter decomposition rates in pine plantations and in native vegetation.	Monthly or bimonthly soil cores taken from plots for extraction of arthropods.	Decomposition assessed using mesh bags of leaves and by buried calico strip method.
Springett (1976b)	Effect of prescribed mild burning on soil and litter fauna in pine, jarrah and karri forests or plantations.	Fauna sampled by hand sorting and from soil cores collected once. only from plots of differing age since burn.	Decomposition assessed only in the pine plots using mesh bags of leaves.
Majer (1977)	Survey of surface active fauna in areas of different land use at Dwellingup.	Pilot pitfall trap samples taken to study how land use influences invertebrate abundance and diversity.	No experimental work.

Majer (1978), Majer and Kabay (1979), Van Der LInden (1979) ONGOING WORK	Study of influence of various bauxite mined area rehabilitation practices on invertebrate fauna, litter decomposition and soil nutrient status.	Invertebrates assessed by pitfall traps, soil cores and litter sampling in range of rehabilitated mined areas.	Role of invertebrates and microflora currently being assessed by litter bag techniques.
Springett (1979b)	Effects of a single hot summer fire in jarrah on soil fauna and litter decomposition.	Arthropod fauna sampled three times following burn.	Decomposition estimated using calico strips. Litter feeding experiments using millipedes performed.
Koch and Majer (1980) Majer and Koch (in prep.)	Elucidation of seasonal activity of forest floor invertebrates in jarrah forests and woodland.	Monthly pitfall trap data correlated with climatic variables.	No experimental work.
Majer (unpublished)	Influence of various prescribed burns on surface active and soil fauna.	Monthly pitfall trap data obtained before and after five prescribed burns. Monthly litter and soil core samples examined following one prescribed burn.	No experimental work.
Postle A.C. ONGOING WORK.	Influence of site characteristics and forest management practices on soil/litter fauna, litter decomposition and nutrient cycling.	Details of study summarised in Table 3.	Details of study summarised in Table 3.
Abbott, I. ONGOING WORK.	Influence of Moderately hot summer burns on large soil and litter animals.	Fauna sampled by a range of complimentary methods both before and after the burn.	No experimental work.

microfauna of pine plantations was associated with a lower decomposition rate than in native vegetation. Springett (1976b) also performed work on soil and litter fauna in burnt and unburnt forests of jarrah at Dwellingup, karri at Pemberton and plantations of pine at Gnangara. She found that, in the plantation, litter decomposition ceased until four years after burning. Both species diversity and microfauna density were reduced following burning of the native forests.

In 1977 Majer published the results of a pilot survey of surface active fauna in unburnt jarrah, burnt jarrah, Phytophthora cinnamomi affected jarrah, pine plantations and urban, farmed and mined areas. Analysis of similarity of the ant fauna revealed two groupings of sites; the first group consisted of sites with a rich ant fauna of moderate equitability and was associated with only slightly modified native forests. The second group consisted of sites with a less rich and, to some extent, less equitable ant fauna and was associated with areas of highly modified vegetation. A further study (Majer, 1978) described a two year continuous pitfall trap monitoring programme performed in a forest control plot and in bauxite mine pits which had been planted with marri (Eucalyptus calophylla), revegetated by seeding with native plants, and in one which had not been subject to any form of revegetation. The study revealed that a great variety of invertebrates recolonized the mine pits and that revegetation was not a prerequisite for many taxa to be present. Of the mine plots, the unplanted plot supported the least variety, and lowest numbers of invertebrates. The variety of invertebrates, when classified at broad taxonomic levels, was similar in the planted and seeded plots although invertebrate numbers were generally higher in the latter. The richness of the ant fauna in the seeded plot was considerably greater than in either of the other mine plots.

This work has since been extended, in conjunction with Mr E.D. Kabay of Alcoa of Australia Ltd., to look at the influences of time and the large range of rehabilitation practices on invertebrate recolonization. Invertebrates have been sampled from all strata of 30 mined areas and 3 forest control plots and the data are still being analysed. Some preliminary findings on the soil and litter fauna are given in Table 2 and they indicate that different taxa recolonise the mines at different rates.

Table 2. Comparison of invertebrate numbers sampled from soil and litter in forest and bauxite mined areas during August-October 1979.

(a) *Soil*			(b) *Litter*		
Year 1	Acarina	∿*	Year 1	Acarina	<↑
	Collembola	∿		Araneae	<↑
	Homoptera	∿		Collembola	<↑
	Coleoptera (larvae)	∿		Blattodea	<↑
	Diptera (adults)	<		Pscocoptera	<↑
				Heteroptera	<↑
				Thysanoptera	<↑
				Coleoptera (larvae)	<↑
				Diptera (adults)	<↑
				Lepidoptera (larvae)	<
				Hymenoptera (not ants)	<↑
Year 2	Araneae	∿	Year 2	Isopoda	<↑
	Symphyla	<		Diplopoda	<↑
	Isoptera	<		Chilopoda	<↑
	Staphylinidae	∿		Isoptera	<↑
	Diptera (larvae)	<		Homoptera	<
				Diptera (larvae)	<↑
Year 3	Chilopoda	<↑	Year 3	Staphylinidae	<
	Protura	<↑			
Year 4	Diplura	>	Year 4	–	
	Heteroptera	∿			
Year 5	–		Year 5	Thysanura	<↑
Year 6	–		Year 6	–	
Year 7	–		Year 7	–	
Year 8	Thysanura	∿	Year 8	–	
	Lepidoptera (larvae)	<			

The following taxa were not collected in the mined area samples although they were present in those taken in the forest:

(a) Soil	(b) Litter
Pseudoscorpiones	Annelida
Isopoda	Onychophora
	Scorpiones
	Pseudoscorpiones

* (∿, no detectable difference from forest levels; <, less than forest levels; >, greater than forest levels; ↑, levels increase with age of mined area.)

Although the density (but not necessarily diversity or species composition) of many soil fauna groups has attained forest soil levels, the litter fauna is generally of lower density in the mined area. This is largely associated with the lower amount of litter here. The litter decomposition rate in the 33 study areas is currently being monitored using jarrah leaves confined in bags of three mesh sizes; large mesh to allow entry of all biological agents, intermediate mesh size for small invertebrate and microflora entry and small mesh size for access by microflora only. The leaves will shortly be collected after two winter periods and it is anticipated that the data will provide information on the degree of decomposition and hence nutrient cycling, which has been re-established in the mined areas.

Recently, Springett (1979b), published the results of an investigation into the effects of a single hot summer fire on soil fauna and litter decomposition in jarrah at Dwellingup. Burning reduced the numbers of arthropods, the proportion of juveniles and the proportion of fungal feeders in the micro arthropod populations. The rate of decomposition was also reduced. Feeding studies were also performed on a litter comminuting millipede (Podokipus sp.) which was common at the site. Subsequent jarrah seedling pot growth trials showed that growth was greatest under leaf litter and millipede faeces and least under leaf ash. Majer (unpublished) has also looked at the influence of five prescribed burns (30, 175, 175 and 500 KW/m autumn burns, 1500 KW/m spring burn) over extended periods of time. As yet this work has not been written up. Currently Dr I. Abbott of the Forests Department is monitoring the effect of moderately hot summer burns on large soil and litter animals.

One important influence on decomposition is season. This is associated with changing temperature and moisture regimes. Koch and Majer (1980 and in prep.) have attempted to elucidate the activity of surface active invertebrates within the jarrah region. They used total number of species of particular feeding groups obtained by pitfall trapping as an index of activity of that particular group. Figure 1, which shows the results for the Perth and Dwellingup sites, suggests that decomposer activity is confined to periods of high moisture availability and that the duration of activity varies with the length of moist periods. It would be of interest to compare decomposition rates at the sites where this study was performed.

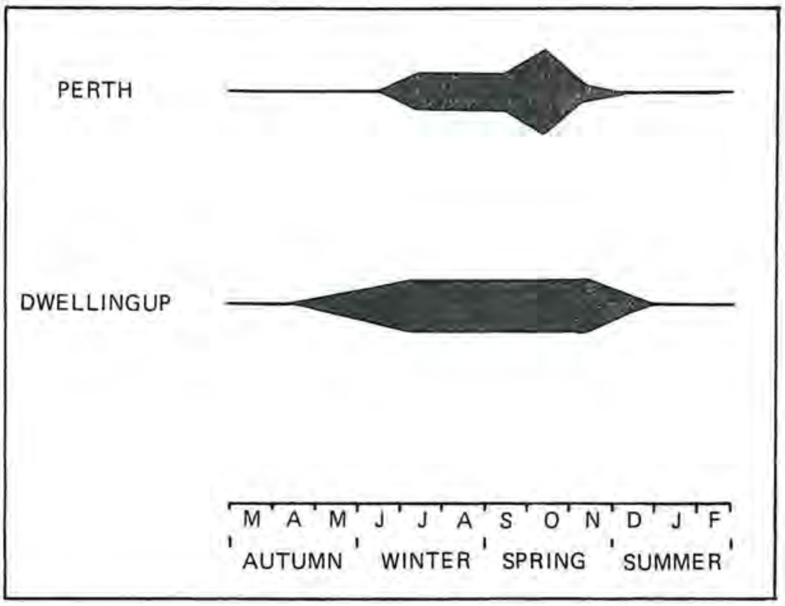

Fig. 1. Kite diagrams showing variation in decomposer activity at two jarrah vegetated sites of differing moisture availability (ref. Koch and Majer, 1980).

Mr A. Postle has recently commenced a comprehensive study on soil and litter invertebrates and decomposition under the joint supervision of myself and Dr D. Bell of the University of Western Australia's Department of Botany. This study is funded by the Dieback Research Fund and is looking at the influence of site characteristics (including so-called dieback conducive and suppressive soils), forest management practices (logging and burning) and forest degradation by dieback on the composition of the soil and litter fauna, litter decomposition rate and nutrient cycling. The sampling programme used in this project and also the study plots are shown in Table 3 and Figure 2 respectively.

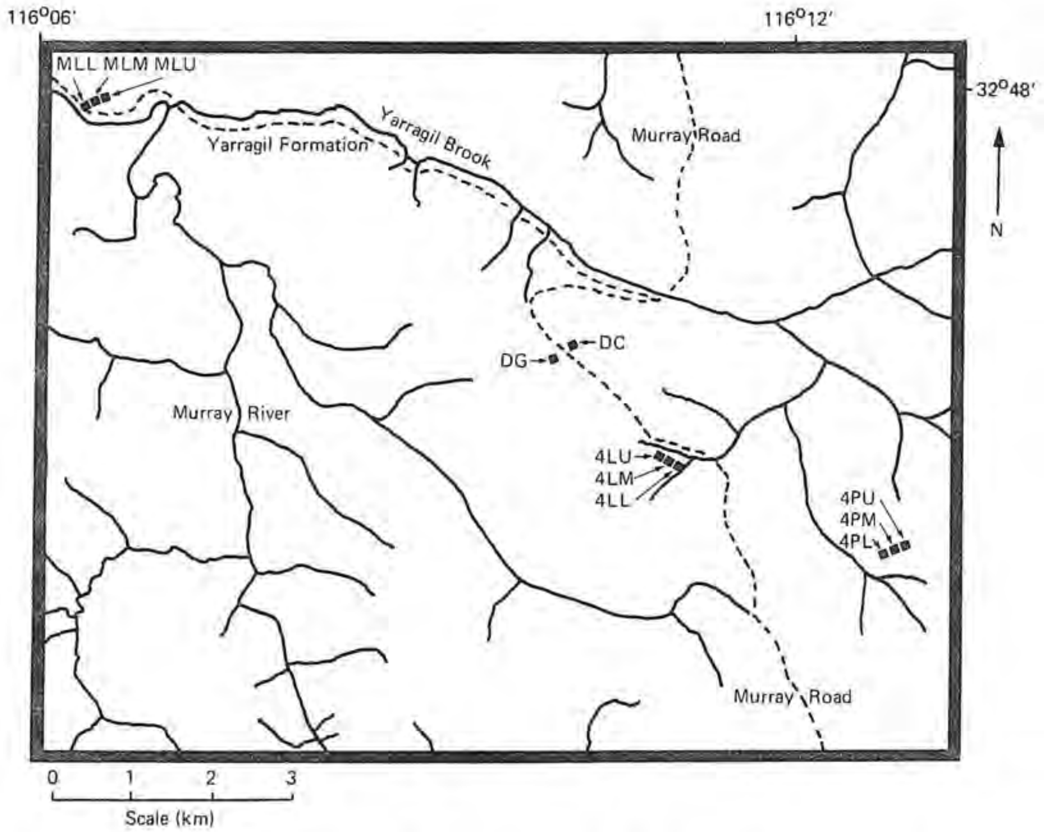

Fig. 2. Position of study plots used in A. Postle's study of soil and litter fauna and litter decomposition (Ref. Table 3).

The relevance of this project to dieback research is that soil fertility, microclimate and soil microbial population make-up all influence the performance of the pathogen and/or the way in which plants respond to it. Since invertebrates influence these three variables, this study is a logical component of a multi-disciplinary research effort aimed at understanding the biology of P. cinnamomi. One further role of this study is that it will provide a necessary input into Dr Bell's study of biomass, energy and nutrient cycling which, like this study, is being performed in the Yarragil Brook catchment, south-east of Dwellingup.

Table 3. Description of plots and methods of study used in the current forest invertebrate/litter decomposition project of Postle and Majer.

				Litter decomposition monitoring					Invertebrate monitoring		
Plot	Plot description	Vegetation type (Havel 1975)	Reasons for plot selection	Jarrah leaves confined in bags of three mesh sizes	Jarrah twigs bark & fruit in bags	Untreated leaves attached to forest floor	Buried calico strips	Pesticide treated leaves in cages	Twenty pitfall traps	Twenty litter samples	Twenty soil cores
4PU	Upland plot on 4P catchment transect	S–T transition	Dieback conducive soils. Controls for 4L plots.	Ten bags of largest mesh size analysed from each plot at bi-monthly intervals.	Ten bags of each litter component will be left in each plot for two years.	Twenty clusters of leaves will be left in each plot for two years.	Ten strips analysed from each plot at bi-monthly intervals.	Twelve of each treatment will be left in plot for two years.			
4PM	Midland plot on 4P catchment transect	0									
4PL	Lowland plot on 4P catchment transect	W–C transition									
4LU	Upland plot on 4L catchment transect	P–W transition	Dieback conducive soils. To be burnt and logged.								
4LM	Midland plot on 4L catchment transect	W–P transition		Ten bags of each mesh size will be left in each plot for two years.							
4LL	Lowland plot on 4L catchment transect	W							Monthly	Monthly	Monthly
MLU	Upland plot on Murray loam transect	T	Examples of die-back suppressive soils.								
MLM	Midland plot on Murray loam transect	T									
MLL	Lowland plot on Murray loam transect	Q									
DG	Dieback graveyard	P	Effects of severe dieback attack.								
DC	Control to plot DG	P	Control for plot DG								

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VARIABILITY IN SOME POOLS AND TRANSFERS OF NITROGEN IN THREE EUCALYPT FORESTS

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SUMMARY

Information on the spatial variation in pools of nitrogen in soil and litter, and of spatial and temporal variation in transfers of nitrogen via litterfall and litter decomposition are presented to demonstrate the intensity of sampling that can be required in eucalypt forests to obtain reasonably precise estimates of these parameters.

Nitrogen transfers were generally found to be less spatially variable than the nitrogen pools examined. Management-induced changes in transfer rates of nitrogen may be easier to detect than changes in pools of nitrogen. In soils containing large pools of nitrogen, changes in nitrogen levels would need to be very great (approx. 200 kg ha^{-1}) before they could be detected by sequential sampling and analysis.

INTRODUCTION

Most of the pools and fluxes of nutrients in Australian eucalypt forests have a high variability, both in space and in time (see Bevege 1977; Richards and Charley 1977). This creates special problems related both to the formulation of effective as well as economical sampling procedures, and to the interpretation and use to which the data on nutrients can be put. In view of the importance of this topic, it is surprising that it has not received much attention from researchers.

In this paper we present data on means and associated variability for several pools and fluxes of N in three sub-alpine eucalypt forests. The implications of the findings for sampling and interpretation in nutrition research in eucalypt forests are briefly discussed.

SITES AND METHODS

Sites

Data are presented for the following three long unburnt (>20 yr) sites: *Eucalyptus pauciflora* (snowgum); *E. dives/E. dalrympleana* (dives) and *E. delegatensis* (alpine ash).

Sampling and Measurement

(i) Soil.

Two soil cores (8 cm diam.) were taken from each of 5 (8 at *E. delegatensis*) 0.5 m^2 randomly located quadrats within a 0.25 ha area at each site. Each core was separated into 0-5, 5-15 and 15-25 cm depths before sieving and weighing of the fine (<2 mm) fraction which was then analysed for total N after Kjeldahl digestion. The mean (of the two cores) was calculated for each quadrat, and these data used to compute the mean (n=5 or 8) and the associated variance for each site. The standing crop of NH_4-N was measured on three composite samples (each comprised of 5 soil cores) from each site. NH_4-N was extracted from field moist soils by shaking with 2N KCl (1:5, soil:KCl) for 1 h.

(ii) Accumulated litter

Litter (excluding wood >8 mm diam.) was collected from 10 randomly located 0.5 m^2 quadrats at each site. After measurement of dry weight, a sub-sample from each quadrat was ground, digested in H_2O_2/H_2SO_4 and analysed for N.

(iii) Litterfall

The dry weight of litter falling into 20, 0.5 m^2 circular traps at each 0.25 ha site was determined monthly. The total weight per trap was summed over 3 monthly periods and the mean (n=20) and variances calculated for the site. The concentration of N in litterfall was measured after bulking of material from 5 traps so as to give 4 spatial replicate samples per site for each 3 monthly period.

(iv) Decomposition of litter.

(a) Loss of weight and N from leaves.

Eighty litterbags each containing 10 g of leaf litterfall were placed on the surface of the litter utilising a 5 x 5 m grid at each site. Ten bags were collected at random at each of eight dates with the final collection being made 55 weeks after placement. The residual leaf material in each bag was dried, weighed and analysed for total N. This enabled the calculation of the loss of weight and of N from the bag to be made. Data are presented for the loss of weight and N after 9, 22 and 55 weeks of exposure in the field.

(b) NH_4-N in litter leachate

Water percolating through the litter layer was collected in triangular trays (125 cm^2 area, with 1 cm lipped edges) which were carefully inserted underneath the intact litterbed. Eight trays were installed at each site in February 1978. Analysis of the water, which is enriched by soluble and organic decay products provides a measure of the net release of nutrients from decaying litter. The input of N in the throughfall is very low and was therefore neglected in the present calculations. Data on the amount of leached soluble NH_4-N are presented for the period October 1978 to January 1979.

Statistical calculations

On the basis of the measured mean and variance, the number of samples (ns) required to predict the mean with an accuracy of ±10 or 20% of the mean was calculated (Mader 1963; Peterson and Calvin 1965; Snedecor and Cochran 1967) with the probability of prediction being 95%. From the confidence limits (CL) which were also calculated, the 'least significant difference' (smallest measured change in a parameter that could be considered statistically significant) can be calculated from the formulae, LSD = $CL\sqrt{2}$. The formulae used were:

$$ns = \frac{t_\alpha^{\,2}\ SD^2}{D^2} \qquad CL = t_\alpha(SE)$$

where t_α is students t value at 0.05% level;

SD is the measured standard deviation of the mean;

D is specified limit (e.g. 10 or 20% of the mean);

SE is the standard error of the mean.

For these calculations to be valid the implied assumption that the initial sampling gave an accurate estimate of the population mean and the variance has to be made. The ns is a measure of variance relative to the mean, while the CL is an index of the absolute (e.g. kg ha^{-1}) resolution that was achieved in the sampling.

RESULTS AND DISCUSSION

Pools of nitrogen

A large pool of total N is contained in the upper 25 cm (the intensively rooted zone) of these soils (Table 1). Spatial heterogeneity decreased with soil depth; 10-14 spatial locations each consisting of two core samples would need to be sampled to estimate (within ± 20% of the mean) the 0-5 cm soil N store, while only 4-7 would be required at 15-25 cm (Table 1). Although the total N stored in 0-25 cm layer was less variable than in the surface soil, the confidence limits of 400-680 kg N ha^{-1} indicate that sequential measurement of total soil N would be an insensitive method for attempting to measure the effect of management practices such as low intensity burning, or for studying the fate of applied fertiliser. Estimation of total soil N (in <2 mm fraction) is more accurate when based on calculation of the weight of N in individual core samples. Overestimates may occur when pools are calculated by multiplying plot mean weight of fine earth by plot mean concentration of N in this fraction. In stony forest soils the correction for volume occupied by stones, roots and >2 mm earth is essential. Overestimation of soil N stocks by up to 50% can result from the assumption that the entire 0-25 cm horizon consists entirely of fine (<2 mm) earth (Raison and Woods 1979).

Table 1: Pools of total N (kg ha^{-1}) in soil (<2 mm fraction layers and associated measures of variability.

Site, depth (cm)	Mean	SD	ns (±20%)	CL (P<0.05)
E. pauciflora				
0-5	750	170	10	210
5-15	1150	210	7	260
15-25	880	120	4	150
0-25	2780	325	3	400
E. dives				
0-5	640	160	12	200
5-15	1100	380	23	470
15-25	1000	190	7	230
0-25	2740	550	8	680
E. delegatensis				
0-5	650	200	14	170
5-15	1340	340	9	280
15-25	1020	235	7	200
0-25	3010	710	8	590

Calculations based on 5 (for *E. pauciflora* and *E. dives*) and 8 (*E. delegatensis*) replicate measures. Each replicate represents the mean of two cores taken from a 0.5 m^2 quadrat.

Table 2. Pools of exchangeable NH_4-N (kg ha^{-1}) in soil (<2 mm fraction) layers and associated measures of variability.

Site, depth (cm)	Mean	SD	ns (±20%)	CL (P<0.05)
E. pauciflora				
0-5	1.2	0.2	15	0.52
5-15	1.5	0.4	31	0.95
15-25	1.7	0.1	3	0.34
0-25	4.3	0.5	5	1.11
E. dives				
0-5	2.0	0.7	67	1.81
5-15	4.9	1.8	60	4.39
15-25	3.8	0.7	18	1.85
0-25	10.6	2.0	17	5.08
E. delegatensis				
0-5	0.8	0.1	14	0.34
5-15	2.6	0.6	28	1.59
15-25	1.7	0.5	37	1.16
0-25	5.0	0.8	10	1.97

Calculations based on analyses of 3 bulk samples, each comprised of 5 randomly sampled cores. Sampling in autumn.

The quantity of NH_4-N in the soil will vary seasonally as a result of seasonal fluctuations in the relative rates of mineralisation and root uptake (Richards and Charley 1977). The data for one sampling (Table 2) provides an example of the high spatial variation that can be encountered. As with total N the variability decreases with increasing soil depth.

Where there is a basis for stratification of sampling, e.g. in relation to the location of large trees (Ryan and McGarity 1978) or when a mosaic of burning intensities exists, it is possible to increase the precision of the estimate of soil N for each stratified location.

In accumulated litter, it appears that the spatial variation in both dry weight and N store is higher than that for the concentration of N (Table 3). Spatial variation in the amount of N in the litter needs to be considered in studies aiming to estimate the loss of N from this layer during burning. High variation in the dry weight and nutrient store in litter also presents constraints to the use of decomposition constants (k) for the study of turnover rates (Richards and Charley 1977), or to the use of sequential sampling to detect seasonal or annual changes in litter weights.

Table 3. Weight and concentration of N in accumulated litter, and weight of N in the litter layer; with associated measures of variability.

	Mean	SD	ns (±20%)	CL ($P<0.05$)
		Litter weight (t ha^{-1})		
E. pauciflora	17.4	3.6	5	2.6
E. dives	14.5	3.9	9	2.8
E. delegatensis	22.7	6.3	10	4.5
		Litter N concentration (%)		
E. pauciflora	0.582	0.089	4	0.110
E dives	0.523	0.066	3	0.082
E. delegatensis	0.531	0.060	1	0.049
		Litter N (kg ha^{-1})		
E. pauciflora	101	22	8	18.7
E. dives	75	20	12	16.2
E. delegatensis	120	32	11	25.7

Weight data based on 10 randomly located 0.5 m^2 quadrats; concentration measurements are for 8 quadrats at the *E. delegatensis* site and 5 quadrats at the other two sites.

In addition to the natural spatial variability in litter weight, the difficulty in defining a distinct boundary between soil and litter probably contributes to variation in the quantity of litter collected. This problem is greatest on long-unburned E. delegatensis sites where much fragmented material accumulates at the base of the litter-pack. Larger components of litter (e.g. wood and bark) contribute greatly to spatial variability in dry weight and thus to the N storage in litter. This occurs despite the fact that these components contain a relatively low concentration of N. An increase in sampling precision could therefore be gained by sampling a larger area for these components. Total litter storage could then be calculated by addition of the amounts in the individual components (Richards anc Charley 1977).

The weight of post-fire residual litter was found to be more spatially variable than the weight of prefire litter, with 14-30 samples required to estimate the mean within ±20% compared to 7 samples for pre-fire litter (10, 0.5 m^2 quadrats taken from burnt sites). Stratification, e.g. in relation to tree boles, could be used to increase the precision of accumulated litter sampling.

Transfers of nitrogen

Litterfall

Spatial variation in the dry weight of leaf litterfall was less than that for total litterfall at all sites (see also Birk 1979). However, since leaves contribute only about one half of the dry weight and the N transfer in litterfall, other litterfall components must be considered. Spatial variation in the return of N in litterfall (Table 4) shows that it is not feasible to accurately estimate N return during periods when the rate of litterfall is low. However, return of N during the season of peak litterfall (November-January in the ACT), and during one whole year, could be estimated within ±20% of the mean with 5 or fewer bulked samples at all sites except E. pauciflora where about 10 samples would be required (Table 4). A possible explanation for the greater variation in E. pauciflora is that the trees are widely spaced and shed large ribbons of bark while the trees on the other sites produce small particles of fibrous bark which fall more evenly. Variable sheeding of material during windy periods is also likely to be more important on exposed E. pauciflora sites. Increased precision could be achieved by sampling large and variable components like bark and wood with larger traps. Although data is presented for only one year, the spatial variability is likely to be similar from year to year as found by Richards and Charley (1977).

Table 4. Return of N in litterfall (kg ha^{-1}), and associated measures of variability.

Site, period (months)	Mean	SD	ns (±20%)	CL (P<0.05)
E. pauciflora				
Aug–Oct	2.4	0.7	23	1.2
Nov–Jan	9.4	1.8	9	2.9
Feb–Apr	3.7	1.3	31	2.1
May–July	1.1	0.1	1	0.1
Total	16.7	3.4	10	5.4
E. dives				
Aug–Oct	2.0	0.3	6	0.5
Nov–Jan	10.0	1.3	4	2.1
Feb–Apr	5.0	1.1	12	1.7
May–July	1.8	0.3	5	0.4
Total	18.8	0.9	1	1.4
E. delegatensis				
Aug–Oct	2.5	1.5	85	2.3
Nov–Jan	12.8	1.8	5	2.8
Feb–Apr	11.8	0.5	1	0.8
May–July	2.2	0.2	3	0.4
Total	29.3	3.5	3	5.5

Calculations based on 4 replicates, each representing a bulked sample from five 0.5 m^2 litter traps.

Decomposition of litter.

The concentration and content of N in leaves enclosed in litterbags and exposed in the field for 55 weeks did not show high spatial variability (Table 5). The mean values could be estimated to within ±10% with generally less than 10 replicates. A larger number of replicates would be required for the same level of precision at the snowgum site during the early phases of decay.

Table 5. Concentration and content of N in litterbags after 0, 9, 22 and 55 weeks decay in the field.

Site, exposure (weeks)	Mean	SD	ns (±10%)	CL (P<0.05)
		Concentration (%)		
E. pauciflora				
0	.77	.070	5	.050
9	.89	.229	34	.163
22	.91	.149	14	.106
55	.89	.117	9	.084
E. dives				
0	.75	.069	5	.049
9	.95	.075	3	.054
22	.82	.081	3	.058
55	.84	.065	2	.046
E. delegatensis				
0	.56	.080	5	.057
9	.66	.139	10	.099
22	.82	.168	10	.120
55	.90	.140	6	.100
		N content (mg bag^{-1})		
E. pauciflora				
0	69.5	6.9	5	4.9
9	72.2	19.3	16	13.8
22	64.0	11.1	7	7.9
55	55.5	6.9	4	4.9
E. dives				
0	64.3	6.0	5	4.3
9	67.4	4.9	2	3.5
22	53.9	5.1	2	3.6
55	53.0	4.9	2	3.5
E. delegatensis				
0	48.8	7.3	11	5.2
9	45.2	9.6	11	6.9
22	52.2	10.4	9	7.4
55	52.1	10.8	10	7.7

Actual spatial variation in decay and N release from the entire litterpack is likely to be greater than that in N concentration and N content in litterbags. This is because the decay in litterbags represents only the initial stage of decomposition during which very little net release of N occurs. Although the loss of weight and N from leaves in litterbags can be measured quite precisely, the major limitations of this technique are that other litter components are excluded, and that the release of N in significant amounts may be delayed until the litter becomes partially fragmented and incorporated into the soil.

Collection of litter leachate overcomes some of the above problems and so should provide a good measure of the mean and spatial variability in the net release of nutrients from the entire litterpack (see Feller 1978). Preliminary data available for October 1979 to January 1980 (Table 6) show that spatial variability for N release was much greater for leachate trays than that for litterbags mainly because of the more variable nature and amount of litter on the trays than in the bags. Spatial variability in annual release of N will probably be less than that suggested by these results because during the reported period decay of litter was probably at a minimum due to lack of moisture. Note that there was a large difference between the sites in the weight of N leached, indicating more rapid turnover in the E. delegatensis forest.

Table 6. Weight of dissolved NH_4-N (g ha^{-1}) in litter leachates at two sites.

Site, period	Mean	SD	ns (±20%)	CL (P<0.05)
E. dives				
10/79	138	46	15	38
11/79	78	48	53	40
12/79	20	38	*	*
1/80	8	9	*	*
10/79 – 1/80	244	77	14	63
E. delegatensis				
10/79	506	247	33	206
11/79	387	152	22	128
12/79	210	111	38	92
1/80	65	56	*	*
10/79 – 1/80	1168	322	10	262

* Very high values.

Calculations based on 8 spatial replicates; 3, 3, 1 and 3 collections in October to January respectively.

CONCLUSIONS

Relative spatial variation appears to be greater for the measurement of the pools than for the transfers of N in the three forests. This means that for assessing the effects of forest management practices on nutrient cycling and tree nutrition, changes in the magnitude of transfers should be easier to detect than changes in the pools. Added to this is the fact that nutrients actively cycling within the community are of greater ecological significance in the short-term than those bound in the immobile forms in soils, roots and above-ground biomass.

The snowgum site exhibited less spatial variation than the other sites for all the N parameters except for the transfer of N in litterfall and the N content in litter bags. The E. dives and E. delegatensis sites displayed similar spatial variation in total N in the surface 25 cm of soil and in accumulated litter but for the other parameters there were no consistent trends related to site.

Further detailed sampling would be required to explain the differences in spatial variability between sites. The data presented do however provide a general guide to the approximate degree of spatial variation typical of a range of eucalypt forests.

Stratification of sampling provides a technique by which the precision of measurement within recognisable units within the forest can be increased (Fergus 1977). This, however, depends on the property in question being spatially related to visible features, a requirement which may be difficult to achieve for some nutrient pools and fluxes in natural eucalypt forests.

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AN ESTIMATE OF THE IMPORTANCE OF MACROPOD GRAZING IN THE NUTRIENT CYCLING OF THE JARRAH FOREST UNDERSTOREY

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ABSTRACT

The amount and nutrient composition of faecal pellets deposited by macropods was estimated at a site in a jarrah forest (Eucalyptus marginata) near Perth, Western Australia. More faecal pellets were found in swampy areas than elsewhere, particularly during summer. Pellets appeared to decompose more rapidly in the wet winter than during the hot, dry summer. A comparison of the nutrient composition of fresh pellets with older ones suggested that some elements are released as the pellets age and others are retained.

It is estimated that macropods deposited onto the forest floor 29 kg dry weight of pellets per ha per year, representing an annual addition of 0.36 kg nitrogen in faeces. This annual cycle of nitrogen through macropod faeces is equivalent to 8% of the nitrogen contained in potentially edible understorey plants, and about 3.8% of the nitrogen deposited by litterfall.

INTRODUCTION

Springett (1978) recently drew attention to the lack of work on biological regulatory mechanisms in eucalypt forests. He suggested that a two-pathway nutrient cycling system has developed to buffer the irregularity and harshness of the climate in the eucalypt forests of Australia. Larger trees maintain a slow, conservative, long-term nutrient cycle, while the understorey shrubs and litter are part of a rapid, short-term cycle.

Marsupials, particularly the macropods, are grazer components of the short term cycle. Most of the available information on the nutritional requirements, grazing behaviour and diet selection of macropods relate to their interactions with domestic stock, particularly in arid or semi-arid situations. However, Hume (1977) suggests that the nutritional requirements and digestion by temperate forest macropods may be very different from those of animals from arid environments. The current study was designed to obtain an estimate of the proportion of the annual nitrogen turnover of the understorey of a eucalypt forest which passes through the macropod pathway.

METHODS

During 1978 a study was set up in the jarrah (Eucalyptus marginata) forest near Gleneagle Pine Plantation, 55 km SE of Perth, in south-western Australia. Mean annual rainfall at the site is approximately 1200 mm. The area last had a hazard reduction burn in spring 1975. Two transects, each 500 m long, and 25 m apart were constructed using small pegs to minimise disturbance to the animals' behaviour. The pegs were placed at 5 m intervals and on each sampling occasion all recognisable macropod faecal pellets were removed from a one metre square quadrat at each of the two hundred pegs. The transects extended from a swamp occupied by Melaleuca sp, Hypocalymma angustifolia, Xanthorrhoea preissii and Eucalyptus patens, corresponding with Havel's (1975) site-vegetation type 'A', through a transition zone with Banksia littoralis, and to a laterite slope jarrah forest with Eucalyptus calophylla, Banksia grandis, Persoonia longifolia, P. elliptica and Casuarina fraserana as the other main tree species (Havel's Type 'P').

Samples were collected in autumn (April/May) and again in spring (October/November) almost all annual rainfall occurring between these two periods. During each period three collections were made at 14 day intervals. Faecal pellets collected after longer intervals were classified as fresh (no deterioration of the brown or black colour, or texture), medium (some deterioration of colour and texture) or old (bleached and/or leached to an even, grey colour). Pellets were dried to constant weight at 70°C and their weights recorded. Faeces collected in April and May were analysed for sixteen nutrient elements. Kjeldahl digestion, automated distillation of ammonia, and spectrometry were used for the nitrogen analysis (Keay & Menagé 1970), and X-ray spectrometry for the other elements (O'Connell 1977).

RESULTS AND DISCUSSION

Patterns of faecal pellet deposition

The amounts of faeces deposited in each of the two transects were very similar in each of the six collections (product moment correlation coefficient r_4 = +0.998). The results from both transects have been combined. The transects were not cleared prior to the first collection on 12 April, thus the old pellet category in this sample may include some pellets accumulated over several years. All subsequent estimates were based upon fresh pellets collected two weeks after clearing a quadrat. More fresh faeces were deposited in the 200 x 1 m^2 sample areas in the April/May period (62.2 g/month) than in October/November (32.9 g/month).

The lower 20% of each transect had a different vegetation from the remainder and will be referred to as "the swamp". In all faecal collections, except those of 28 April and 12 May, a significantly higher percentage of pellets was found in the swamp than would be expected by chance (Table 1). Faeces collected after the long summer interval showed a high percentage in the swamp, then a much lower percentage as the autumn rains started in late April/early May. The percentage of faeces deposited in the swamp over winter was fairly low, rising again as the dry, hot summer started in November (Table 1). This suggests that, while the swamp is used preferentially throughout the year, this preference is most marked in the summer and least obvious during the winter. In the remainder of the transect there is no apparent tendency for pellets to be aggregated, since 95% confidence limits lie within 6.4% of mean weight per $1m^2$ quadrat, and the variance: mean ratio is 1.24. From the faecal collection data it is not possible to say whether the swamp is preferred for food, or shelter, or both, but Caughley (1964) observed that kangaroos defecate mostly at night and in the areas where they feed.

Table 1. The dry weights (in grams) of faeces collected from the two 500 m transects, on six occasions during 1978. The value shown in parentheses for each sample represents the percentage by weight of the faeces collected from the lower (swamp) parts of the transect. The swamp represented 20% of the transects, and the χ^2 values test for the amount of faeces deposited in the swamp being significantly greater than 20% of the total amount collected on that date.

	12 April	28 April	12 May	12 October	27 October	10 November
Fresh	148.0 (36%)	29.0 (25%)	33.2 (17%)	51.8 (29%)	17.5 (69%)	15.4 (59%)
Medium	223.8 (39%)			148.0 (26%)		
Old	378.0 (52%)			38.5 (44%)		
Total	749.8 (45%)			238.3 (36%)		
χ^2_1	13.13	0.46	0.13	5.58	46.64	30.21
P	< 0.001	>0.4	>0.7	<0.02	<0.001	<0.001

The most common macropods in the area, and those likely to have contributed most to the results, are the Brush Wallaby Macropus irma and the Grey Kangaroo Macropus fuliginosus. These animals might co-exist by feeding at different levels of the vegetation but our observations suggest that most grazing is confined to the region between ground level and one metre high.

Christensen (1977) has noted that scarab beetles may bury considerable numbers of faecal pellets; however in this study only a small amount of activity was noted for the native dung beetle Onthophagus haagi. The number of pellets decomposed by other organisms can only be inferred from the data. The small proportion of older pellets in the first spring collection, compared with the first autumn collection, suggests that pellets are decomposed more rapidly in winter, although it should be remembered that the latter collection may include pellets accumulated over several seasons. Conversely, during hot, dry conditions, such as those which prevail during summer, it is known that decomposition by organisms within the litter effectively ceases (Springett 1976). The higher proportion of older pellets found in the swamp, in both April and in October, suggests that there is less decomposer activity there. The swamp is seasonally water-logged in winter and the soil surface becomes hard and dry in summer. These widely varying conditions may be less favourable for decomposer organisms than the more equable environment of the forest litter layer. Decomposer activity was not observed to be significant during 14 day intervals, and therefore amounts of material collected during these periods are measures of faecal deposition.

Estimating nitrogen cycling by macropods

A comparison of the concentrations of elements in the oldest pellets with those in the freshest pellets (28 April and 12 May collections combined; the 12 April fresh pellets were of unknown age) showed the amounts of all except phosphorus and sulphur to be significantly lower in the older pellets (Table 2). This suggests that many elements may be leached from pellets as they age. Only fresh pellets from the 28 April and 12 May collections were used in the following estimates in order to minimise any errors due to nutrient loss from pellets. It was assumed that due to the relatively dry conditions (<7 mm rainfall in 2 weeks) no significant NH_3 loss or nitrogen fixation took place. The two estimates of faecal deposition were 38 kg dry weight ha^{-1} $year^{-1}$ for April/May and 20 kg ha^{-1} $year^{-1}$ in October/November. Using an intermediate value of 29 kg ha^{-1} $year^{-1}$ for the whole year, the amounts of each of eight macronutrients deposited in faeces during the year were calculated, and are shown in Table 2.

Macropods are assumed to feed from plants between ground level and 1.5 m high. In this study no plants known to be eaten by macropods were seen to exceed this height. Although no measurements of the above-ground biomass of shrubs <1.5 m high and groundcover plants have been made at the macropod study site, it

Table 2. The amounts of eight elements in faecal pellets and in understorey shrubs and groundcover.

		Element							
		N	K	Cl	Na	Ca	S	P	Mg
Mean percentage (±S.E.) of element in dried faeces of collection	12 April : Old	0.88 ±0.07	0.08 ±0.01	0.04 ±0.01	0.01 ±0	0.57 ±0.04	0.17 ±0.01	0.08 ±0.01	0.11 ±0.01
	12 April : Medium	1.34 ±0.08	0.12 ±0.01	0.04 ±0.01	0.02 ±0	0.86 ±0.04	0.21 ±0.01	0.10 ±0.01	0.15 ±0.01
	12 April : Fresh	0.90 ±0.08	0.22 ±0.02	0.04 ±0.01	0.05 ±0.91	0.84 ±0.06	0.16 ±0.01	0.09 ±0.01	0.14 ±0.01
	28 April : Fresh	1.09 ±0.14	0.36 ±0.05	0.09 ±0.02	0.09 ±0.03	0.92 ±0.08	0.17 ±0.01	0.09 ±0.01	0.15 ±0.02
	12 May : Fresh	1.41 ±0.16	0.31 ±0.07	0.09 ±0.02	0.08 ±0.09	0.76 ±0.09	0.17 ±0.01	0.10 ±0.01	0.13 ±0.02
t-test for differences in percentages of elements between 12 April old pellets and combined 28 April and 12 May fresh pellets	t_{28} =	2.18	4.39	2.09	2.80	2.93	ϕ	1.07	2.42
	P	<9.05	<0.001	<0.05	<0.01	<0.01	-	>0.2	>0.05
kg ha^{-1} year^{-1} of element in faeces		0.36	0.10	0.03	0.02	0.26	0.05	0.03	0.04
*kg ha^{-1} of element in ground cover and shrubs <1.5 m high		11.7	9.1	5.0	1.2	9.5	1.7	0.9	3.0
Annual amount of element in faeces as a percentage of amount in	All shrubs < 1.5 m high	3.1%	1.1%	0.6%	1.7%	2.7%	2.9%	3.2%	1.3%
	**"Edible shrubs" < 1.5 m high	7.9%	2.0%	0.9%	3.7%	5.5%	5.4%	4.3%	2.7%

* Data from Hingston *et al.* (1979).
** Excludes *Macrozamia*, *Xanthorrhoea* and dead *Pteridium* species.

is assumed to be the same as on the jarrah forest site near Dwellingup studied by Hingston et al. (1979), namely 1700 kg dry weight ha^{-1}. Plant species distribution and density at both sites appear similar, despite the slightly higher mean annual rainfall of 1300 mm at Dwellingup.

The amount of eight elements contained in the understory plants are presented in Table 2. Although Macrozamia riedlei, Xanthorrhoea preissii and dead Pteridium esculentum comprise over half the understory biomass they are generally not eaten by marsupials. Other shrub and groundcover species are potentially "edible", but macropods probably select particular species and parts of them when feeding. There is 4.6 kg N ha^{-1} in potentially "edible" shrubs.

Given the assumptions made previously it is estimated that macropods deposit 0.36 kg N ha^{-1} $year^{-1}$ in faeces. This is 3% of the amount contained in all understory shrubs and 8% of the amount in "edible" shrubs (Table 2).

The amount of nitrogen in macropod faeces when compared with that in litterfall (9.5 kg N ha^{-1} yr^{-1}; Hatch 1955, O'Connell 1979) amounts to only 3.8%. However faecal nitrogen is a component of the short-term pathway discussed by Springett (1978) and may be more important than the quantities of N involved suggest.

The significance of the contribution of urinary nitrogen to the ecosystem is unknown but several studies have been made which may give some indication of the amount of N in this component. Laboratory trials with animals on both restricted and unrestricted diets indicate that macropods deposit at least as much nitrogen in urine as in faeces (Forbes and Tribe 1970, McIntosh 1966). However results from these laboratory trials need to be interpreted with caution, because Kinnear and Main (1975) have shown that macropods may recycle body nitrogen which would otherwise be excreted. Thus the amount of N excreted appears to depend on a number of environmental conditions. For example the urinary nitrogen excreted by tammar wallabies (Macropus eugenii) was shown to be five times greater in winter than in summer. We conclude that although the amount of nitrogen excreted in urine has not been estimated for animals in the jarrah forest it could possibly make at least as significant a contribution as the nitrogen in faeces.

The estimates of the contribution by macropods to the nitrogen cycle given here are from a limited study. Both temporal and spatial variation in the numbers of animals in relation to their habitat are likely to affect the local contribution of faeces and urine but the significance of these factors needs further investigation.

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SESSION 2.
Management of Nitrogen in Forests

SILVICULTURAL AND MANAGEMENT PROBLEMS IN SUPPLYING NITROGEN FOR PRODUCTION FORESTRY

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INTRODUCTION

Forestry with a relatively low return on capital invested has tended to develop and use silvicultural practices that are convenient, cheap or both. Little effective research has been done on the likely effects of continued harvesting on the capacity of sites to sustain optimum production. During recent years a number of changes have occurred in management which collectively have the potential to drastically reduce the productivity of a given site. The changes referred to include the increasing scale of operations, increasing mechanisation, widespread clearfelling (frequently large coupes), burning of large areas to encourage regeneration, change of species or provenance as a result of seed shortages when faced with regeneration of large areas, planned shorter rotations and greater utilisation of biomass with consequent increased nutrient drain on the site. These changes are occurring relatively rapidly and in spite of enhanced perception of environmental effects, few people have become sufficiently concerned for adequate research to be initiated.

Unless the effects of the above and other (e.g. use of frequent low-intensity prescribed burning) management practices are closely monitored and action taken when necessary to prevent deterioration, complex problems could be induced which will be difficult if not impossible to overcome.

Many Australian forest environments are characterised by:

(a) Soils of low total nutrient content compared to those overseas. Fertilizer experiments also indicate that the nutrient-supplying capacity of our soils is low.

(b) Low inputs of nutrients from weathering of soil minerals (many of the parent rocks are old re-worked sediments) or from atmospheric input (our atmosphere over forest is relatively unpolluted).
(c) Vegetation which is adapted to poor soils and plant communities which when undisturbed appear to be effective in retaining and recycling nutrients.

On most Australian forest sites productivity is nutrient-limited, and the forest which exists today reflects efficient nutrient accumulation, retention and recycling over long periods of time.

Since almost all forest management practices have at least the potential to deplete a site of nutrients, the effects of management on future nutrition of our forests is a key long-term research question. In the past, forest nutrition research has attempted with some success to define the role of mineral nutrition and to improve diagnostic and ameliorative procedures in Australian forests. It is now urgent that additional resources be allocated specifically to long-term studies of changes in soil characteristics, especially under semi-intensive and intensive forest management.

Up to the present there has been no comprehensive study of the N cycle or budget as it exists in an Australian forest. Various authors have provided partial information about the distribution of N but there has been little accurate data on fluxes and practically nothing at all on the implications for management of various types of disturbance or of fertilization.

In terms of nutrition, the following are some of the more specific questions which need to be answered in order to predict the effect of a management practice (Kimmins 1977):

(a) What proportion of the site nutrient capital is removed either directly or indirectly as a result of the management practice? This question must be considered for both the total and 'available' or mobile site nutrients.
(b) How rapidly does the remaining site nutrient capital cycle? How 'available' is it to the vegetation?

(c) How rapidly are the losses from either the total or the available soil capital replenished and by what mechanisms? Are these mechanisms affected by the management treatment?

(d) What is the subsequent nutrient requirement of the tree crop? How does the nutrient demand on the soil vary with the life of the crop?

(e) How frequently is the management practice applied? What is the total impact of all the nutrient-depleting practices applied to the site during the forest rotation?

There is already considerable evidence that particular care will be necessary if sustained forest production is to be achieved on many Australian forest soils. When an equilibrium is disturbed resulting in net loss of important nutrients, a considerable time frequently elapses before the deterioration is detected. This is particularly true under a long-term crop such as forest trees. There are many examples in Australia where the first rotation of exotic pines failed without fertilizer; there is considerable evidence to show that many areas where pines have succeeded at a marginal level will not be capable of growing a second rotation unless given considerable silvicultural assistance. There are forests where it is by no means certain that the cultural treatments currently proposed will be sufficient to achieve sustained production. The majority of areas planted to exotic species, or fast-growing eucalypts, have not yet come into second rotation. Thus there have been limited opportunities for comparison of the productivity of first and second rotation crops.

Study of factors affecting the nutrient budget and cycle under management can give an indication of the likely effects of silvicultural practices on productivity before they become manifest. Such studies can indicate the rate of soil depletion (and hence the likely fertilizer inputs required), silvicultural practices which may be particularly damaging (e.g. slash burning or cultivation between rotations) or ways in which inputs can be increased (use of management to favour legume growth). Clearly, detailed studies on the effects of management on ecosystem processes and the significance of any changes in these to the long-term function of the forest should be given a high research priority.

NUTRIENT BALANCE SHEETS

Remezov (1959) suggested that nutrient balance sheets and cycling were concerned with nutrient imports and exports to the geochemical system and with internal biological plant-soil exchanges. Nutrient imports and exports can be listed as follows:

Nutrient import	Nutrient export
Rainfall	Harvesting-nutrients site perturbation, erosion compaction
Airborne aerosols and dust	Soil leaching and run-off
Rock weathering	Fire
Fertilizer	Volatile (gaseous) losses
N fixation - legumes	Erosion (general).
- non-legumes	

Silvicultural procedures influencing nutrient losses and gains include:

Rotation change (eucalypt-pine; pine-pine), clearing including clearfelling, cultivation, windrowing, weed control (burning of logging slash after harvest).
Thinning
Controlled burning
Fertilization.

Events of importance include wildfire and unusual storms with consequences such as windthrow and erosion.

Bevege (1978) drew attention to the fragmentary nature of Australian studies on biomass and nutrient distribution in indigenous forests. Turvey (1979) reviewed several mineral cycling studies subsequent to those reported by Bevege but was able to add little additional information on the details of N cycling in Australian ecosystems. In the case of Pinus radiata several estimates of N distribution in compartments of the ecosystem have been made (Will 1968; Mitchell 1970; Snowdon and Waring 1974) but there are many important gaps. Many conclusions are made on a basis of assumptions or of borrowed data. A recent more complete estimate has been made by Nambiar and Woods (1979).

Raison (1977) summarised N pool sizes, fluxes and budget (Tables 1 and 2) for a Eucalyptus wet sclerophyll forest and for a P. radiata plantation age 40. He concluded that although it is not

Table 1. N cycle and budget for Armidale wet sclerophyll forest. (from Raison 1977) (E = measures from elsewhere)

N Pools (kg ha^{-1})	
Soils (0-15 cm)	4500
Litter	92
Soil NH_4-N	2
NH_3-N	1
Biomass above ground (E)	170-320
Roots	?
N Fluxes (kg ha^{-1} yr^{-1})	
Litterfall	83
Transfer from forest floor to soil	77
Ammonification	335
Nitrification	114
Plant uptake	=80 ?
Internal recycling	?
N fixation (E)	15-19
Rainfall accretion	<2
Leaching	Low ?
Gaseous loss	?
Budget kg ha^{-1} (E)	
Clearfelling	– (104-141)
Selective logging	– (variable)
Wildfire/slash burning	– ? (200+)
Prescribed burning	– (50-60)+
Leaching, run-off	?
Other gaseous loss	?

Table 2. N cycle and budget for *P. radiata* forest growing on South Australian sand podzol – SQ V, age 40 (from Raison 1977).

N Pools (kg ha^{-1})	
Biomass wood + bark	83
other	260
roots	?
Soil (0-60 cm)	2000
Litter	400-670
N Fluxes (kg ha^{-1} yr^{-1})	
Litterfall	=27
Mineralisation	27 (?)
Plant uptake	?
Internal recycling (IMPT)	?
N fixation	low (?)
Rainfall accretion	<2
Leaching, gaseous loss	?
Budget (ka ha^{-1} rotation^{-1})	
Budget (kg ha^{-1} rotation^{-1})	
Thinnings	-130
Final harvest	-80
Fire	-(500-700)
Leaching	?
Other gaseous loss	?
Fertiliser	+ variable (300 to age 5)
Rainfall accretion	+80

possible to construct a complete budget for any Australian forest ecosystem, studies to date have quantified some pool sizes and flux rates for N and have provided a base for future work.

A schematic mineral and nitrogen cycle broadly applicable to most forested regions was presented by Webber (1977, Fig. 1). The maintenance of productivity requires a balance between the left and right hand sides (output and input). The manager must be concerned to ensure that balance is not upset by an increase in output unless accompanied by a commensurate increase in input. In order to be able to do this, values must be available to quantify nutrient pools and fluxes under different management options.

THE SOILS

Stephens and Donald (1958) attempting to explain the widespread occurrence of low fertility soils in Australia listed the following as some of the contributing factors:

(1) The large areas of Tertiary soils such as the extremely leached lateritic podzolic soils and red earths.

(2) The prevalence of new soils developed *in situ* on lower horizon remnants of the above soils and on their colluvial and alluvial residues.

(3) The extreme susceptibility of several soil groups to leaching under present-day climatic conditions. The highly flocculated krasnozems, the aeolian and fluviatile sands, and the soils developed on coarse-textured sedimentary rock all show great porosity and all occur extensively in regions of moderate to high rainfall.

Low fertility and especially paucity of phosphorus has long been recognised and superphosphate has been successful in increasing the growth rate of *P. radiata*.

Large areas of infertile sand podzols have been planted in South Australia. Florence and Lamb (1975) showed a realistic appreciation of the problems of productivity maintenance there and

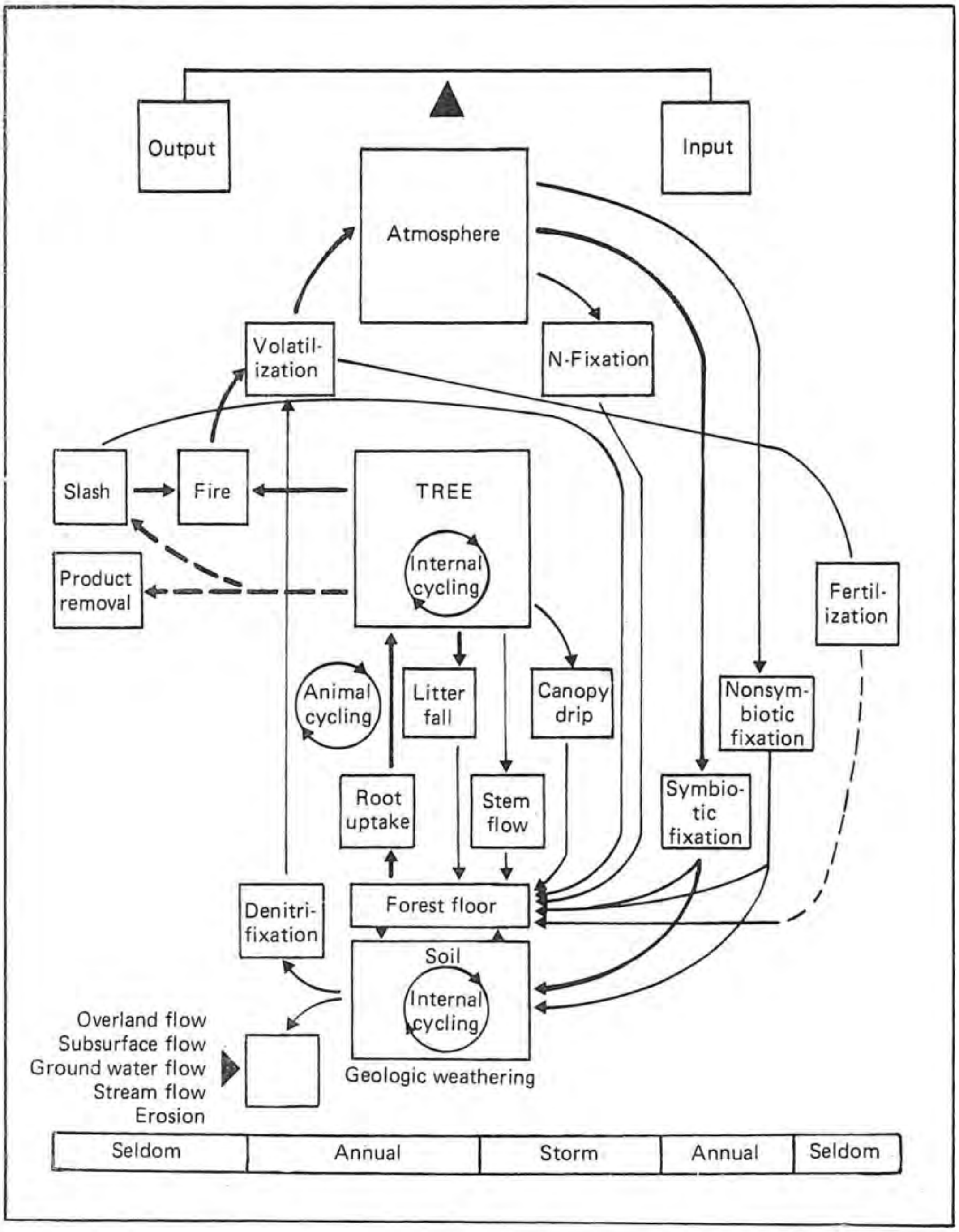

Fig. 1. A modified mineral and nitrogen cycle applicable to any forested region. Broken pathways indicate areas subject to modification by forest managers. The thickest lines also indicate major transfer pathways (Jorgenson, Wells and Metz 1975; Patric and Smith 1975). (After Webber 1977)

recommended that use of a fallow period between rotations in order to allow N to be replenished. Waring (1971) suggested that, on the basis of location, rainfall and availability, future soils available for pine plantations would consist mainly of solodics and podzolics. Solodic soils are a logical choice for pine plantations, having a better nutrient status than the podzols. The podzolics have better physical and chemical characteristics but may also exhibit poor internal drainage. The earths are better again but in general are less available for plantation establishment. All these soils have inherently greater physical and chemical problems then the soils commonly available in other countries for plantation forestry.

Soil P Deficiency, Legumes and N Supply

The Australian indigenous *Eucalyptus* forest is remarkable for the range and diversity of N-fixing plants, especially legumes, growing in association in overstorey and understorey. Traditional management practices such as control burning and timber stand improvement (TSI) have tended to reduce their frequency of occurrence, particularly of legumes (e.g. Malajczuk and Grove 1977). Recently in Western Australia, however, steps have been taken to reverse this trend by using hotter burns to encourage legumes in the understorey. From an evolutionary point of view the high proportion of N-fixing species may have developed as a mechanism to cope with periodic bushfire and leached soils low in nutrient reserves. Hannon (1958) suggested that the N lost in fires was quickly replaced to a level dictated by soil P deficiency which limited the growth and efficiency of legumes. This natural method of maintaining the N supply to the forest could be encouraged much more than has been the practice in the past. Although tree forms of *Casuarina* and *Acacia* may sometimes need to be reduced or eliminated in the interests of timber production, shrub forms and herbaceous legumes could be carefully favoured in silvicultural operations. Even more useful in areas showing signs of N depletion, would be the deliberate addition of P fertilizer to the forest to encourage legume growth. If necessary, useful understorey plants could be re-seeded.

A wide range of field experiments in Australia have shown that most forest soils are deficient in phosphorus and nitrogen (at least) for optimum forest production which indicates that the supply is inadequate on certain occasions even under traditional logging regimes where the rotation length is long, only the sawlog is harvested, and the demand on the soil for nutrients is low. Such deficiencies are not experienced in New Zealand or North America to anywhere near the same extent and this places Australia under a handicap when trying to ensure a permanent N supply at an adequate level for maximum production.

THE USE OF FERTILIZERS

Second Rotation Decline in Productivity

Many research workers have found evidence about site deterioration under forestry monocultures to be equivocal. In South Australia a production drop in second rotation *P. radiata* was reported in 1966 (Keeves 1966). Workers in other States have reported inability to find any evidence of decline. Variable results have also been reported from overseas workers. The differing results are explicable when consideration is given to the difficulty of controlling the factors involved for a relatively long period of time. Some of the factors affecting site productivity under successive rotations are listed below:

Species	Silvicultural regime	Management	Site
Growth rate	Weed control Rotation length	Economic demand	Organic matter Soil texture
Nutrient demand	Natural regeneration or planted seedling	Environmental impact	Soil depth Soil nutrients
	Clearfell or thin	Harvesting intensity	Rainfall
	Prescribed burning Fertilizer		

Even minor variations in the combination of factors operating during the rotations studied will affect yield and, depending on the particular variation, will result in an increase or decrease in productivity. Most studies reported in the literature do little to establish the cause of variation because they have not resulted from precise experimentation. There is evidence that some of the authors reporting decline may have measured changes due to altered establishment procedures rather than nett nutrient loss as such.

I believe that on many sites (even under the best management conditions) timber production will result in nett nutrient drain. The loss will be greater for demanding species, short rotations, whole tree harvesting and also with a clearfelling and replanting regime than for natural regeneration. To the extent that there is a departure from optimum management towards shortterm objectives of maximum profit, probability of loss will be greatly increased. (An example would be wet weather logging.) The loss of fertility will be easier to detect on sites where production strains are likely to be reflected in distinct, and sometimes spectacular, deficiencies. A possible example is the relatively infertile sand podzols where Keeves (1966) reported second rotation decline. Based on South Australian yield tables (Lewis et al. 1976) N.Z. Forest Products Ltd plantations at age 10 are growing at only S.Q.III-IV, yet by age 30 they have achieved the total production of S.Q.I (Woollons, pers. comm.). The falloff in growth at older ages in South Australia may indicate the effect of nutrient depletion during the latter half of the first rotation.

The nature of growth responses by forests

The results from 25 years of research have enabled the development of a conceptual model for the description of growth responses obtained to fertilization, weed control and other silvicultural treatments. The model is based on three major premises.

1. Some treatments (e.g. fertilization and irrigation) may result in a long-term change in site quality as measured by maximum current annual volume increments;
2. Some treatments (e.g. weed control, cultivation) may reduce the time required to attain maximum production.

3. In older stands, particularly those which have not received optimum silvicultural treatment or those on sites of low quality, responses might be delayed by factors associated with crown structure.

<u>Responses to NP treatment at establishment and the effect of weeds</u>

The first two premises are important for evaluating responses obtained at establishment. These are illustrated with data from a long-term experiment (Belanglo LT4) on a first rotation site at Belanglo State Forest, N.S.W., which tested combinations of complete fertilizer with weed control (Figs. 2 and 3). The following observations can be made (Fig. 2):

1. Volume increment at age 12 yr on fertilized plots (i.e. the change in slope of the volume curve) is about twice that obtained on unfertilized plots;
2. On fertilized pots the effect of weed control has been to reduce by two years the time required to attain maximum volume increment;
3. On unfertilized plots weed control has reduced the time to attain maximum increment by at least four years but possibly by as much as eight years.

This experiment demonstrates the responses which can be obtained by special care with establishment procedures and with adequate rainfall (850 mm) during the first year of growth. Figure 2 also illustrates data from another experiment (Belanglo LT3), a second rotation site where the methods of fertilization and weed control were less than optimum and subsequent meteorological conditions were less favourable for growth responses. Although the maximum volume increment is similar to that on the first experiment, the time taken to reach this maximum was delayed by two to four years.

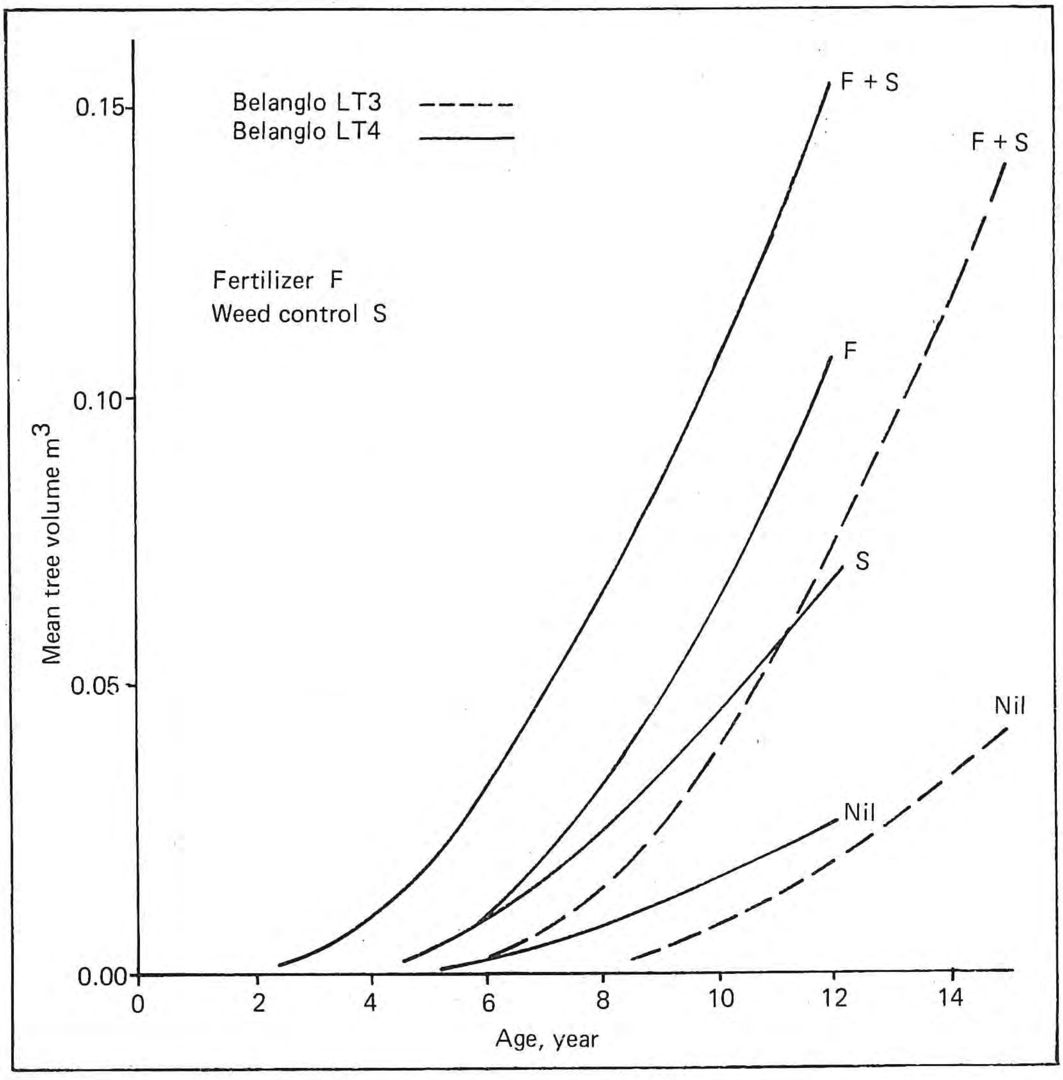

Fig. 2. Effects of fertilizer and weed control on volume of *P. radiata* in two experiments at Belanglo S.F., N.S.W.

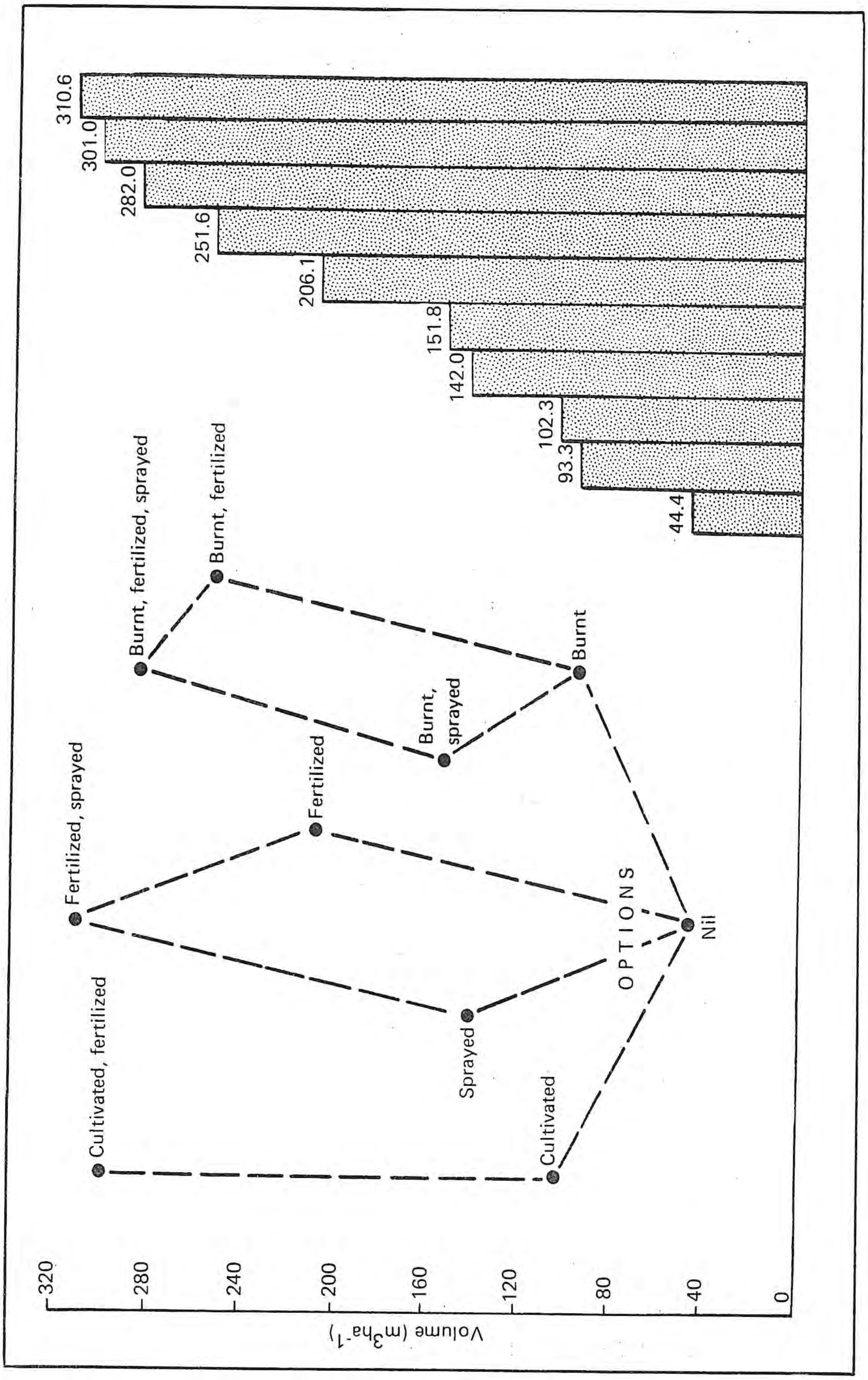

Fig. 3. The effect of different methods of site preparation on the volume of *Pinus radiata*, aged 12 years, Belanglo S.F. The histogram shows the volume in ascending order of each treatment.

Figure 3 shows that various plantation establishment treatments commonly available to forest managers have, 12 years after planting, resulted in a wide range of growth responses. Volume (by sectional measurement of bole) indicates that various combinations of treatments have produced a range of site qualities (South Australian Yield Tables) from S.Q. VII to S.Q. III.

This confirms conclusions from this experiment made in 1971: 'Early growth responses are very sensitive to a range of site preparation techniques and degrees of weed control. Both the extent and persistence of the response are affected by these factors.' (Waring 1973). There has, however, been an interesting change in the relative position of the responses to fertilizer alone and to weed control alone. By 1973 these two treatments had produced equal responses, but since that time the fertilizer treatment has achieved a higher growth rate and is currently parallel to F & S treatment (Fig. 3).

The species of weeds and types of growth interact with factors such as light, nutrients and water supply. The forest manager has the opportunity to manipulate establishment procedures which restrain weeds sufficiently to ensure that the stand achieves the maximum increment for the site at an early age. Thus the option for long-term maximum growth rate is not foregone. Effective weed control is essential for good survival and rapid early growth. It is a pre-requisite for responses to fertilizer; fertilizer without weed control may not only be ineffective, it may be damaging. Satisfactory weed control can be achieved by appropriate cultivation, by chemicals, or by a combination of the two.

Later Age Response

To test the effect of time of fertilizer application on productivity gain, an experiment (Long Term Experiment No. 3) was established at Belanglo State Forest, N.S.W., in 1963 using P. radiata at an espacement of 2.4 x 2.4 m. The design used was a complete factorial testing three treatments (Nil, N, NP), six application times and eight replicates. Nitrogen was applied as urea at a rate of 224 lb ac^{-1} (250 kg ha^{-1}) and phosphorus as superphosphate at 448 lb ac^{-1} (500 kg ha^{-1}) at planting ('0'), year 2 and at year 4.

Table 3 presents the percentage response of treatments over the control for height, diameter, sectional area and volume. The results show that the time of fertilizing can be responsible for differences in production similar to those caused by varying site preparation techniques or by levels of fertilizer.

Table 3. Percentage response of various treatments over the Nil for height, diameter sectional area and volume. (*P. radiata* planted 1963 at 2.4 x 2.4 m, Long Term Experiment 3, Belanglo, S.F. 1971 measurements.)

Fertilizer and time of application	Per cent response over nil			
	Height	Diameter	Sectional area	Volume*
P 0 years	67	51	100	235
P 2 years	51	40	73	161
P 4 years	38	33	58	118
NP 0 years	86	75	156	376
NP 2 years	67	58	125	276
NP 4 years	37	42	77	137

* 0.7854 D

Some treatments were thinned at age 9 and P and NP fertilizer treatments were then re-applied. Results at age 14 are shown in Table 4.

Table 4. Response to fertilization Belanglo LT3.

Treatment at planting	Nil	P	P	NP	NP
Treatment at thinning (age 9 years)	Nil	Nil	P	Nil	NP
Total volume production to thinning at age 9 yr (m^3ha^{-1})	5.8	21.8	24.8	29.2	33.1
Total volume production to age 14 yr (m^3ha^{-1})	39.0	108.1	123.8	118.5	146.4
Growth, age 9-14 (m^3ha^{-1})	33.2	86.3	99.0	89.3	113.3

Refertilization with NP at age 9 resulted 5 years later in an additional volume increment of 24 $m^3 ha^{-1}$, double that of the increment obtained on plots refertilized with P.

It is apparent that the fertilizer treatment which resulted in the largest response (NP, 0 + 9 yrs) is necessary at the site in order to maintain the volume increment curve at the maximum rate (Fig. 2). The use of P fertilizer alone allows the curve to fall away.

Crane (1981) described three row-thinning x fertilizer trials in which stands of P. radiata 16 to 25 years old at Uriarra (A.C.T.), Kowen (A.C.T.) and Belanglo (N.S.W.) were thinned and fertilized with 423 kg N ha^{-1}, 128 kg P ha^{-1} applied as ammonium phosphate and urea. As N and P were added together, the individual effect of each element is not clear and remains for later investigation (Table 5).

Table 5. Response of total stand volume to fertilizer.

Site	p.a.i. over 4 years (1980-1976) $m^3 ha^{-1}$		
	Nil	NP	Difference
Belanglo	80.2	84.5	4.3 ± 2.0
Kowen	51.3	71.5	20.2 ± 4.3
Uriarra	75.8	102.7	26.9 ± 4.4
ACT mean	63.6	87.1	23.5 ± 4.3

Note: (a) The Belanglo difference is not significant at the 5% level.
(b) The ranges after the differences depict 95% confidence intervals.
(c) The volumes are not estimated from sectionally measured trees, but calculated using D^2H.

Ballard (1978) was concerned about the lack of success in maintaining foliar levels of nutrients, especially of P, after applying fertilizer at time of planting. In advocating continuous maximum productivity he is probably pursuing a benefit with too high a cost. Although we certainly need more information on this point (i.e. the degree to which growth falls away in the absence of re-fertilization), we need an accurate budget which will inform on the cost and benefit of the likely response from refertilization. With regard to early fertilization of P. radiata, evidence is already in hand of N application in the presence of P deficiency resulting in a depression of growth (e.g. Waring 1969). It is therefore highly probable that later age response to N or NP depends upon the level of soil available P. The decline in available P after fertilization will depend (for most sites) on the P fixing status of the soil. It appears as though for Belanglo and most A.C.T. sites (already discussed above) the fall-off in growth is only slow and small, but refertilization at wide intervals will still be profitable. In areas of high P fixation the fall-off can be rapid and large, lifting the problem to a different level - one of success or failure depending on timely refertilization.

In view of the (at present) relatively unpredictable nature of response to refertilization there is a great need for more data within forest regions. Later refertilization should be built into experiment designs right from the start in order to allow a comparison to be made with and without refertilization.

Foliar Analysis

Foliar analysis has become widely accepted as a tool for detecting nutrient deficiencies and to follow nutrient uptake from fertilizers. In particular, it shows some promise as a technique for managing phosphate fertilizer prescriptions for P. radiata and other conifers. Foliar levels of other nutrients have proved useful for indicating the presence of nutrient deficiencies, but since insufficient is known about their interaction with other factors of the environment and other nutrients they cannot be used with any confidence for predicting fertilizer requirements. Considerably more research is required into appropriate sampling procedures for nutrient levels and into the relationships between growth and foliar elemental concentration before crop logging (Richards and Bevege 1972) will be useful. Most workers have neglected to do this - as a consequence their results may be unreliable.

Chemical analysis of about 3000 foliage samples taken from trees in experimental plots (25 trees per plot) have allowed estimates of between-tree variation for foliar nitrogen concentration (Snowdon and Waring, unpublished). The average coefficient of variation was 20%, the range being from 7% to 35%. On this basis 12 of the 25 trees would need to be sampled in order to estimate the plot mean within ± 10% ($P<0.05$). For a forest compartment, 18 samples or more would be required depending on variability within the compartment. As no consistent relationship was found between N content of foliage and height, trees to be sampled should be chosen at random.

In recent years workers have sampled a variable number of trees for N analysis - for example, Gentle _et al_. (1965) sampled 1 tree per plot; Raupach _et al_. (1969) sampled 6; Mead and Will (1976) 8-10; Raupach and Hall (1974) 4. Waring (1964) and Anon. (1968) reported that the percentage content of N in the foliage of _P. radiata_ was unreliable as an indicator of element deficiency or sufficiency. As a result of extensive foliar analysis associated with field trials it was concluded that, in general, the percentage content of N increases with higher rates of fertilizer N and decreases where increased application of P gives growth responses. The concentration of N in foliage falls with time from the last application of N fertilizer.

Raupach (1967), after extensive work on foliar analysis of _P. radiata_, recommended the use of the following levels of diagnostic purposes:

>1.4% good growth
1.2% marginal growth
<1.0% poor growth

These diagnostic levels are lower than figures given by Will (1961). Ballard (1977) recommended:

>1.5%	satisfactory
1.2-1.5%	marginal
<1.2%	low.

However, shortly afterwards Ballard (1979a) wrote 'apparently total N in conventionally sampled tree tissue does not provide a sensitive indication of the tree's N status'.

There are indications that foliar N is no better as a predictor of N status for Eucalyptus than it is for P. radiata.

It can be concluded that in the light of current information, foliar analysis for total N is not useful for the precise monitoring of N status we will need in future production forests. In view of this it is urgent that further research be carried out on the possibility of using some of the N fractions found in the tree for the above purpose.

Any examination of the role of N as a foliar nutrient would be incomplete without some discussion of the importance of the supply of sulphur (S). As S and N are both important components of amino acids it would be logical to expect that the demand for sulphur should rise when large growth responses are obtained to additions of N fertilizer. In pot trials in Canberra deficiencies of S were shown to accompany responses to NP (Waring, unpublished) for P. radiata, P. elliottii and P. pinaster using surface soil (0-7.5 cm) from sand podsol (Jervis Bay) yellow podzolic soil (Belanglo) and red-yellow earth (A.C.T.). When S was carefully tested in the field no response could be shown at any of the locations (e.g. Waring 1963, 1969). Any explanation of nutritional chemistry/ physiology of foliar S (Lambert and Turner 1978) will need to take into account the lack of growth response to the element on the three separated locations described above.

Efficiency of Fertilizer Use

When urea is added to a forest soil it is usually quickly hydrolysed to positively charged ammonium ions which move slowly in the presence of clay and organic colloids. Much of the nitrogen will be immobilised in similar forms as already exist in the soil. However, under the influence of heavy rainfall soon after application, urea can be leached unchanged through sandy profiles. Ballard's (1976b) study on movement and transformation of N fertilizers on pumice soil is one which should be repeated on other soils even though the absence of active roots render the study somewhat artificial. The author discounted the significance of his evidence of rapid leaching as he considered it may not be relevant to field conditions. He cited Knight and Will (1977) as evidence of stability in the field. Nambiar and Woods (1979) also studied the movement of N from fertilizers in Mount Burr Sand. They found considerable leaching of both ammonium and nitrate occurred to a depth of 40 cm 11 weeks after application.

Ballard (1979a) says that the recovery of N fertilizers by trees is well below that reported for agricultural crops. He discusses short-term recovery in trees only and quotes the short response duration and low recovery as reasons for further research on methods of N fertilization. Adding that the need for replacement cannot be predicted and that there are 'dangers of nutrient imbalance from initial luxury consumption', he concludes that 'existing technology thus appears to be inadequate to meet the challenge of efficiently replacing N in forest ecosystems and sustaining site productivity'.

I agree with Ballard in urging the necessity for further research on N fertilization but I consider this statement far too sweeping. He does not refer to the fate of applied N which is not taken up into the tree. Pritchett (1978) has a different attitude and implies that recovery consists of applied N minus losses due to volatilisation and leaching. He quotes Cole and Gessell (1965) in support of almost negligible losses from the latter.

N Fertilization and Soil Organic Matter

Australia is famous for having raised the productivity of its pastures by using P fertilizers and legumes to ensure an increase of N into the soil-legume-grass system. This resulted in an increase in soil organic matter and permanent improvement in soil fertility (e.g. Henzell et al. 1966). Having this well documented efficient pattern of successful incorporation of 'cheap' N (Donald 1960) into the pasture system available to us, it would be expected that we in Australia would apply similar methods to the forests and in particular to forest plantations. If the level of soil organic matter and total N can be increased, mineralizable N in the soil should increase with consequent growth increases. Schumway and Atkinson (1978) suggest that mineralizable N may be useful in predicting N fertilizer response of Douglas fir.

Waring (1969) reported that in a stand of P. radiata aged 3½ years and broadcast fertilized with N (500 kg ha^{-1}) and P (188 kg ha^{-1}), 296 kg ha^{-1} N or 59% was retained in the aerial part of the tree plus 0-7.5 cm of soil. The surface soil (0-7.5 cm) level of total nitrogen and organic matter was increased by 23%. This is considered to be of reasonable accuracy as variation was covered by five constant volume samples per .001 ac plot. The difference between NP and Nil plots was significant at the 5% level.

Snowdon and Waring (1974) reporting the same experiment at age 7, wrote 'when nitrogen (700 kg ha^{-1}) was added in the presence of phosphate 41.2% of the extra N was recoverable from the biomass and the remainder could be located in the soil'. In this paper litter, roots and soil (to 30 cm depth) were included in the balance sheet (Table 6).

An attempt to gain further data was made in 1962 when a field trial was established at Belanglo to compare the ability of clover and urea to supply nitrogen to P. radiata and to measure the effects of both sources of nitrogen on organic matter and total soil nitrogen (Waring 1966). Twelve replications of a 2 x 3 factorial design were established with a plot size of 11 x 11 m and tree spacing of 1 x 1 m. Mineral soil from 0-7.5 cm layer was sampled as in the earlier experiment before treatment and three years later and total nitrogen was determined. Results showed

Nil	0.076% N
Clover	0.103% N
Clover + Urea	0.109% N
Urea	0.090% N

Table 6. Amounts of dry matter nitrogen and phosphorus in various components of *Pinus radiata* ecosystem 7 years after fertilization.

Component	Nil	N	P	NP
		Biomass (t ha^{-1})		
Crown	7.2	5.2	23.1	42.7
Stem	8.6	5.0	38.0	93.8
Litter	1.3	1.3	2.9	6.5
Root	3.8	2.1	15.5	32.0
Total	20.9	13.6	79.5	175.0
		Phosphorus (kg ha^{-1})		
Crown	4.2	3.7	22.1	40.1
Stem	1.6	0.9	11.9	26.4
Litter	0.6	0.5	2.6	6.2
Root	0.7	0.4	4.9	9.0
Total biomass	7.1	5.5	41.5	81.7
Soil to 30 cm	155	156	373	350
Total	162	162	415	432
		Nitrogen (kg ha^{-1})		
Crown	67.5	67.2	139.5	257.7
Stem	16.7	14.1	57.4	145.5
Litter	15.0	20.3	35.4	91.4
Root	7.5	5.9	23.5	49.6
Total biomass	107.7	107.5	255.8	544.2
Soil to 30 cm	1967	2567	1816	2227
Total	2075	2675	2072	2771

The increase in total nitrogen due to clover was highly significant (0.1% level). Clover incorporated 49 kg ha^{-1} yr^{-1} of N into the organic matter whereas urea at a level supplying 45 kg ha^{-1} yr^{-1} only incorporated 25 kg N. A similar result was obtained from addition of urea fertilizer in the earlier experiment (Waring 1969). An important point about the clover experiment was that it illustrated the fine line dividing beneficial and adverse effect when using N-fixing ground cover. Although rainfall during the first 12 months after planting was well above the average (984 vs. 850 mm) the trees were significantly retarded in growth on plots in the 'clover' treatments as a result of competition for water with the rapidly growing crimson and white clover sward. During the second 12 months this effect disappeared as trees responded to N and 1057 mm rainfall. Tree response continued to widen during the third year (760 mm rainfall) although the clover was severely set back as a result of very low summer and autumn rainfall (37% of average). These results indicate that with this type of clover, growth should be controlled in the immediate vicinity of the tree to lessen competition for water in dry seasons.

It is fortunate that a leguminous understorey can be grown in association with plantations during the establishment period when great demands for nutrients are made on the soil by the tree. When following a regime aimed predominantly at the production of sawn timber, another opportunity to establish legumes will occur at the end of the rotation after the stand has been thinned. Where this is not possible, consideration could be given to growing a legume for a period between rotations (Stephens and Bond 1957; Anon. 1968; Florence and Lamb 1975). The feasibility of this was confirmed by planting P. radiata in 1966 on two adjacent areas at Belanglo, both of which had previously produced a 30-year crop of that species. One of these areas had been laid down to clover with an application of 1550 kg ha^{-1} of superphosphate 3 years earlier, while the other had received no fertilizer and had remained under native grasses. By the time of planting, the clover had largely died, and the treatments in both areas consisted of applications of P and NP with unfertilized plots as controls. After 2 years, highly significant responses to fertilization were obtained in the native grass areas, whereas no responses were obtained in the clover area. Apparently the addition of P fertilizer plus the N input from 3 years of occupancy of the site by clover, produced an environment where N and P supply was adequate for optimum growth. If the clover had been grown during the last 5 years of a sawlog rotation, the result as described would eliminate the need to apply fertilizer N and P at time of planting the new rotation and would enhance, on an average, the prospects of tree survival in dry seasons. It would thus be possible to eliminate most of the major problems

Ballard (1978) listed as being associated with the current practice of early fertilization, i.e. the short-term effectiveness of spot applications, lack of precision and high cost of application.

The management problems of growing an N-fixing crop beneath plantation trees should not be underestimated. The establishment and proper control of such a crop requires considerable skill in addition to those normally required of a forester. An increase in the range of decision-making is required which may not be generally welcome. For example, decisions are required on:

1. whether to graze and if so under what circumstances,
2. which N-fixing plant to use.

In areas of lower rainfall or of winter incidence, subclover may suit for immediate use. In a relatively adverse environment clustered clover has some advantages. Lupins are a probable alternative.

In the slightly longer term there would need to be careful trials and selection from the bewildering variety available of untested, possibly suitable plants.

If the understorey crop is not well managed or the wrong type of plant is used, the results could be as unfortunate and as little publicised as most of the attempts around the world to grow mixed leguminous and nonleguminous trees. Most of these have been unsuccessful.

The results from these experiments indicate that overall retention of N in the soil system at Belanglo is high. This may be the situation in most forest soils where conservation mechanisms include (for relatively long periods) the absence of cultivation, presence of a litter layer and permanent occupation of the soil by roots. Careful studies should be initiated on the effectiveness of various types of N input in increasing soil organic matter because if this can be achieved efficiently it is the best way to counter the expected drain of total soil nitrogen in plantations and perhaps to reverse that trend while increasing productivity (Donald 1960). To enhance biological productivity one must either increase the rate at which N cycles or add N to the system (Davey and Wollum 1979). It appears as though the deliberate encouragement of selected N-fixing ground cover when sufficient light is available will perform both functions.

INTENSIVE MANAGEMENT

Miller et al. (1980) summarised the considerable progress made in recent years towards utilising the 20-50% of biomass which traditionally has remained in the forest after logging. The authors also discuss the environmental consequences of a shift towards more complete harvesting such as the increased drain on the nutrient capital of a site, the risk of erosion and possible damage to soil structure. The conclusion is made that 'only very intensive harvesting of fast grown trees is likely to remove more than the expected input of nitrogen, whereas for phosphorus input will seldom match removal - even by conventional harvesting'. This conclusion is based upon evidence from European sources of high nitrogen inputs to the ecosystem mainly in rainfall (4.0 to 21.9 kg ha^{-1} yr^{-1}.

Referring mainly to North America, Pritchett (1978) suggests that soils which do not contain adequate soil nutrient reserves to maintain production under intensive management are exceptional but comments that 'the trend towards more complete utilisation of tree components and the adoption of shorter rotations could significantly reduce the capacity of many marginally deficient soils to replace nutrients removed in harvests'.

Kimmins (1977) and Wells and Jorgensen (1979) agree that information about biological, chemical and physical processes is not complete or reliable enough for predicting the effects of intensive harvesting practices on the nutrient reserves and long-term forest production. However, the latter authors suggested that there was general agreement that normal rotation length and harvesting of sawlogs only would not deplete the soil of nutrients, but that short rotation and whole tree logging would result in decline.

Webber (1977) expressed the opinion that 'for traditional management operations on the soils where nutrient deficiencies are non-existent the impact of harvesting on productivity is unlikely to be a major problem'.

Kimmins (1977) suggested that longer rotations should be used if whole tree harvesting is to be practiced on infertile sites and advanced the concept of an 'ecological rotation' - one which permits the return of the site to the ecological condition that existed prior to rotation. If long-term maintenance or improvement of the site nutrient status is an objective of management, rotations should not be shorter than the ecological rotation.

It is obvious that intelligent management demands evaluation of the alternatives of fertilisation, rotation length and harvest intensity in relation to the expected degree of depletion. In order to do this the 'reliable information' (Wells and Jorgensen 1979) will need to be available. There has been hardly any effective research in Australia which will assist in answering questions such as:

> To what degree can N be allowed to be depleted on a site and still be able to replenish using fertilizer?

Recent reports indicate that hardwood framing for house construction has dropped from c. 90% to 60% with an accompanying rise in softwood framing. This trend is expected to continue, and to strengthen conviction that Australia will in the foreseeable future continue to produce sawlogs as the most valuable end product around which the management of forests must revolve (Bunn 1971). It appears as though this policy of producing pulp as thinnings from a predominantly sawlog regime will continue in South Australia (Lewis et al. 1976).

It is therefore more likely that intensified management will concern whole tree logging to a greater extent than short rotations. Within pine plantations stands will probably be established to maximise the yield of both pulpwood and sawlogs (Kerruish and Moore 1980) in the immediate future. Estimates of the increase in nutrient removal by whole tree harvesting range from about two to four times as much of each element removed compared to sawlog harvesting only. A realistic estimate for Australian pine plantations might be at least twice as much (Will 1968, P. radiata; Pritchett and Smith 1974, P. elliottii).

Nutritional deficiencies are common in Australian plantations during the first rotation and frequently necessitate the addition of substantial quantities of fertilizer, particularly N and P. Evidence presented earlier in this paper shows that we lack clear evidence of the quantity of fertilizer it is necessary to apply to achieve maximum production for the rotation/site or whether the rotation is an 'ecological rotation' as defined by Kimmins (1977). If whole tree logging more than doubles the demand for N, the site might well be depleted beyond the point where reserves can still be restored by N fertilizer. It is urgent that accurate answers be obtained to the question raised above for Australian species and sites because of economic pressures which are currently being applied. In the meantime it would be merely sensible to accept that preventative action is called for as an interim measure to ensure on average to above average sites all possible measures are taken to conserve N. I am aware that this is in the process of being implemented on sand podzols in Victoria, South Australia and Western Australia, but urgent consideration should be given to extending the practices to better sites.

THE EFFECT OF FIRE

Byrne (1977) indicated that the situation in Australia regarding prescribed burning was as follows:

1. N.S.W. and S.A. accepted prescribed burning in Eucalyptus forest as being necessary but had reservations about the long-term effect. No burning in pine plantations.

2. Victoria, A.C.T., and Tasmania accepted prescribed burning in *Eucalyptus* forests and regarded burning in pine forests as under investigation.
3. Western Australia and Queensland accepted prescribed burning in *Eucalyptus* and in pine forests under specific conditions but on a fairly large scale.

Eucalyptus and Other Indigenous Ecosystems

At present there is widespread use of prescribed burning in indigenous forests, but there is a paucity of data on the nutrient balance particularly in the long-term. When the export of timber from the forest was small as in the traditional selection silviculture for sawlogs, the presumption that N lost in prescribed burning was replaced by N-fixing plants was probably correct. With increasing intensity of management (group fellings etc.) and in the absence of a positive policy of legume retention, the presumption becomes increasingly suspect. There is a great need for accurate data on the cycling of N in indigenous ecosystems (especially managed *Eucalyptus* production forests) under prescribed burning regimes.

Pine Plantations

From the nutritional viewpoint I believe that the following would supply a reasonable rationale for prescribed burning in pine plantations:

The Manager -

1. Should accept that
   - there are long-term problems of N-supply in plantations in most countries;
   - Australia has special problems because of the widespread occurrence of soils with low nutrient reserves;
   - with a few notable exceptions, current plantation management effectively excludes an N-fixing plant understorey;
   - available evidence shows that the export of litter from plantations interrupts the biological cycle and is deleterious to the nutrient status of the forest.

2. Should be aware of

   - the complexity of the task of proving the net effect of prescribed burning on plantations and that it will form part of other urgent nutrient cycling research;
   - the desirability of pursuing a policy of management with the objective of minimising loss of currently held N reserves in the system.

3. Should decide that

   - prescribed burning in pine plantations will be kept to a strict minimum or completely excluded until clear evidence is available that the procedure has no detrimental effects in the long-term.

MECHANISATION

Harvesting and clearfelling are inextricably interwoven with re-establishment of the next rotation and they must be considered together particularly as harvesting intensity is crucial to the degree of nutrient demand on the site. Harvesting has biological and physical effects on the site and in some circumstances these can dominate the situation and render fertilization irrelevant. Examples are effect of disturbance on the microbial population and water table problems resulting from clearfelling.

Changes in harvesting are likely to occur at a rapid rate and on a number of fronts simultaneously. Harvesting costs represent a large percentage of costs of wood 'at the mill door' and the technologically minded Australian forester will press on towards systems which will be increasingly mechanised and will be adopted because cost savings will be large and easily demonstrable. Kerruish and Moore (1980) argue for automated processing of thinnings from young plantations. Replacement of the high labour input associated with chainsaw thinning will allow a substantial reduction in costs. Pine plantations have been established increasingly in recent years on prepared sites with moderate topography. This encourages the use of machines. The position is less clear with regard to eucalypts.

Another aspect under consideration for mechanisation is that of stump removal and site preparation for machine planting of the subsequent rotation. What is the effect of such disturbance on long-term soil fertility and especially N supply? We need to be able to supply answers quickly since these are current problems. Forest nutrition researchers can only hope to influence the development of mechanisation if convincing data can be presented which clearly shows other benefits foregone, e.g. site productivity. This evidence is most likely to be obtained by concentrating available Australia-wide resources on research of a basic nature into the area of crop replacement or rotation change. This means an intensive study of the nutritional consequences involved in harvesting and forest establishment procedures.

Once soil disturbance is accepted as a major factor causing loss of nutrients on marginal sites, then consideration must be given to minimising it. If in addition it is accepted that the use of fire between rotations should be avoided where possible then the manager must give serious consideration to using natural regeneration to establish the successive rotation wherever it is practicable. Suitable locations/conditions would include:

- where the advance growth present would provide adequate stocking,
- where the residual slash from the first rotation is not excessive,
- where the need for improved planting stock is not given the highest priority (or perhaps because 1R was of improved planting stock),
- where the site is so vulnerable that minimal disturbance is of highest priority.

FOREST INDUSTRY DEVELOPMENTS

There are indications in the forest industries that there will be a surge in demand in the near future, especially for softwood from conifer plantations. My knowledge of industry is very limited but I wish to mention five developments which will apply pressure to plantations at least on the east coast of Australia. There are probably similar factors operating in other parts of the country.

1. A feasibility study is being carried out by APM regarding the possible construction of a $2000 million kraft pulp mill to use wood from south-eastern Queensland and a doubling of production at its Maryvale Mill.
2. A paper mill is being built in the Albury area by Australian Newsprint to use over 300 000 tonnes yr^{-1} of pulp wood from Tumut.
3. For sawmills operating on Eucalyptus old growth forests in N.S.W. and Tasmania, there has been a recent intensification of the supply problem with a reduction in log quotas. In Australia generally a decline is occurring in the production of hardwood framing timber with a related increase in softwood framing.
4. A medium density fibreboard plant to use 170 000 tonnes yr^{-1} roundwood will open at Wagga 1982.
5. A thermo-mechanical pulp mill capacity of 380 000 tonnes yr^{-1} Bathurst N.S.W., 1981.

All five developments tend to increase the pressure for a much greater area of plantations and for increased intensity of use of those plantations at present in existence.

Wilson (1980) argued that there are good prospects for the export of forest products from softwood plantations in Australia and New Zealand and much of the above development appears to be a response to these trends which will take some time to develop. Also in the longer term is a possibly important development named the SCRIMBER process. This involves the crushing of the stems of young trees and combining the web of strands with adhesives into moulded products (Higgins, pers. comm.).

THE MOST IMPORTANT TEN YEARS

In the normal course of forest production the greatest possibilities for loss of N from the system occur during the rotation change period which includes operations from clearfelling through planting/regeneration and on to the early years of the new forest. Important features of this period likely to affect the loss of N include:

- nutrient export due to wood taken off-site,
- fate of nutrients held in logging slash
  - (a) burn - large loss
  - (b) mulch - unknown loss
  - (c) plough in - unknown loss
- removal of stumps and/or soil preparation for planting
- planting, natural regeneration or seeding
- weed control
- fertilization.

This period is one of considerable disturbance with the probability of nutrient leaching and the possibility of soil erosion and/or soil compaction. This continues until the site is fully reoccupied by vegetation which may be modified by weed control. True forest conditions appear at 5/6 years with accumulation of litter and are consolidated (for pine plantations) at canopy closure with suppression of understorey.

Forest management practices are influential in affecting soil properties more during this period than at any other stage in forestry production. This is because the period is an abrupt interruption to nutrient cycling which is the process largely responsible for the small net demand made on soil nutrients by mature forest stands and for the small net losses from leaching.

At best, operations during this period will result in considerable losses of N, but the total effects have the potential to be disastrous because it is sometimes easier to impose violent solutions. If managers understand that many of the possible treatments have great potential to enhance or degrade soil fertility then they will be able to take steps to modify damaging procedures which appear superficially attractive because of convenience or cost.

Research into this area is being conducted mainly by those working on _P. radiata_ plantations on sand podzols in Victoria, South Australia and Western Australia. Squire _et al_. (1979) showed that early growth of second rotation trees was greater than first rotation trees when logging slash was left on site. An important question yet to be answered is how much of the nutrient content of slash is held in the system in the long-term and what proportion is lost during the decomposition process in the absence of physiologically active roots?

On these and on the more normal soils which will carry most of the future plantations in Australia we urgently need _accurate_ figures giving the nett nutrient position (especially N) for the decade extending from just before clear-felling to just after canopy closure in the subsequent rotation.

A NUTRITION BASED MANAGEMENT PLAN

I must emphasise that I have always been an advocate of maximum productivity with the concurrent maintenance of soil fertility. I want to dispel any impression that my 'conservative' approach to forest nutrition indicates any underlying belief that we should not exploit our forests. On the other hand anyone who still thinks that the maintenance of N to our forests at a rate adequate for maximum production does not present immediate complex problems is at least being careless and irresponsible.

With this introduction I will suggest a management plan for _P. radiata_ plantations. (These are the single most important factor determining forest production in Australia.) A nutrition oriented management plan should be based on three assumptions:

1. We in Australia are operating on a different scale of forest nutrition compared to countries like New Zealand, Canada, U.S.A., Brazil, Scandinavia, Germany, France and Britain.
2. Our soils are relatively poor, our climate sometimes harsh and our plantations commonly suffer deficiencies during the first rotation. Our nutritional strategy will necessarily be different from that of the above countries.

3. In order to have a successful plan we will have to rapidly initiate procedures that others see only as future possibilities. Australian foresters established the early pine plantations in difficult environments and in the face of almost complete indifference by the politicians of the day and by the general population. The difficult environment is still with us (perhaps with depleted soils) and a special nutritional strategy is required in order to maintain or increase productivity in all present and future plantations.

The Plan.
It is accepted that N + P present major problems of supply in the majority of forest areas during the first rotation and that in addition B and Zn will need to be added in specific areas. Other elements will be included in future for some situations, e.g. S, K, Cu.

Also that for most areas the only safe program for the maintenance of productivity and fertility is one that is preventative in nature - one which continually gives high priority to the conservation of the nutrient reserve already present and actively pursues strategies which add to the reserves. This is designed to prevent severe depletion occurring before the problem is perceived. Restoration of such soils is very difficult. There are large areas of depauperate soils in many countries which defy amelioration at reasonable cost. A preventative program will necessarily exclude the use of prescribed burning in pine forests until the long-term effect of the treatment is clear.

For most of our forest areas the decision should be made to forego opportunities to introduce high degree intensive management, i.e. the combination of short rotation, whole tree logging and automation of many harvesting/establishment procedures. The existing traditional long-rotation predominantly sawlog regime (Lewis et al. 1976) must continue to operate for nutritional reasons quite apart from the other silvicultural and economic reasons responsible for its current acceptance. The excessive additional nutrient strain associated with high degree intensive management cannot be accepted until success is demonstrated at maintaining nutrient reserves under normal long-rotation regimes.

High degree intensive management because of its importance should become a long-term research project in several areas where soil fertility and forest productivity would be monitored using fertilizer prescription technology. Alternatives such as fertilization, adjustment of rotation length and harvesting intensity would be varied leading to realistic production objectives which will be within the nutritional limitations of the system.

On most sites (covering a range from poor to above average) plans should include a legume ground cover at some stage in the rotation, either early (from time of planting) or late (where final crop trees are spaced widely enough to permit), applying sufficient fertilizer (P, Mo?) to ensure health of legume. If not establishing ground cover at planting apply NP fertilizer on a per tree basis in conjunction with effective weed control and consider a non-commercial thinning at age 4 to 7 years in order to obtain additional response by early restoration of free growth (Waring 1972). Refertilize with NP fertilizer broadcast at this stage or after normal first commercial thinning if no non-commercial thinning is carried out.

The degree and nature of fertilization necessary during the remainder of the rotation will vary with the particular site and should be found by using test plots.

When considering options at time of clearfelling the aim should be to minimise compaction and soil disturbance/erosion. The hazard will vary with the nature of the soil. Logging slash should not be burnt because of its value as a mulch and as a source of nutrients; the advantages of chain saw felling and hand replanting should be considered as should also the possibility of using natural regeneration for re-establishing the forest.

DISCUSSION

The most important function for forestry research organisations is to provide the data which will allow timber, paper and associated products to be produced efficiently and in perpetuity, while simultaneously improving, or at least maintaining, the fertility of the soils involved. No other group will do this; no one else has sufficient knowledge of the complexities involved in coordinating research with silvicultural and forest management problems.

I am not advocating a policy of diminished research into the other uses of the forest. I believe that wood production is an important primary aim and that the spin-off from detailed studies of nutrient cycling in production forests will result in management procedures more sensitive to the needs of the environment and that this will be of direct benefit to all forest users.

Now and for the 1980s in Australia there is more than ever before a need to establish priorities, to collaborate in the more complex studies and to relate results progressively to the needs of management. If the research workers themselves recognise this, much can be done by way of direct collaboration without waiting for formal structures and for authorities to recruit and fund teams to conduct inter-disciplinary studies. This will not occur until urgent problems are more clearly delineated by research results than is the situation at present.

We have been managing our native Eucalyptus forest for almost a century. It is a conservative ecosystem adjusted to fire and to soils with low nutrient reserves. Many N-fixing plants are present and play an important role in maintaining N supply. Large areas of this forest have been cleared and converted to pine plantations which are more demanding when the ratio of nutrient to biomass is considered (Crane and Raison 1980). Normally no legumes are associated with the plantations. Variations in rotation length and harvesting intensity are probably imminent which may more than double the nutrient demand on the site compared with that experienced by a plantation with a traditional long rotation sawlog regime.

It is now generally accepted that substantial quantities of fertilizer will need to be used to maintain the productivity of our forests but details like type, quantity, frequency of application etc. are only clear for a limited number of locations. I have endeavoured in this paper to point to some gaps in our knowledge and I have suggested that many of these can only be closed by collaborative teamwork on studies designed to provide data on nutrient cycling of important species and locations. However, studies of this type are complex and offer almost unlimited opportunities for dispersal of effort, fragmented results and a widening of the gulf which is sometimes apparent between research workers and forest management (Saucier 1979). I believe this trend is already evident.

Looking at nutrition from the managers' viewpoint is instructive. He is told that fertilizer and other ameliorative procedures are essential to maintain productivity but the amount of information coming forward is not sufficient to justify costly alternative procedures. We have no national grid of fertilizer trials from which to formulate predictive models. Rosvall (1979) developed equations which estimate fertilizer response under different stand and site conditions and are based on 234 fertilizer trials distributed throughout Sweden. Many of Pritchett's (1978) conclusions are drawn from the results of similar trials established by collaboration within regions between private companies and government forest agencies. These may serve as a more useful pattern in Australia where collaboration within regions could be valuable and probably already operates to a certain extent, e.g. Gippsland, southern New South Wales and A.C.T.; Mount Gambier and western Victoria. There is a need for collaboration to establish a set of calibration experiments as a basis for regional operational information as well as providing locations for important basic studies.

Thus I have suggested nutritional work on two fronts : nutrient budget and cycling which could be called 'basic' and studies aimed at fine tuning fertilizer prescription technology currently and in the immediate future. We need the former to understand ecosystem processes and allow accurate strategies to be devised; we need the latter to assist the manager to get on with the job of adjusting nutrient supply <u>now</u> to avoid unnecessary nutrient depletion of existing forests. Both objects need to be pursued simultaneously to avoid a serious breakdown in research and development in forestry in Australia.

Priority nutrition research:

1. Nitrogen changes
   Input from N-fixing plants
   Input from inorganic N

   Output from fire - wildfire and prescribed burning
   Output from disturbance - erosion, volatilisation, denitrification, leaching, loss of soil OM, changes in bulk density, micro-organisms

   Fate of nutrients in unburnt slash
   Weeds or N-stores?

2. Methods of establishing and maintaining N-fixers
   Prescriptions for burning, introduced species v. natives, fertilizers for N-fixers

   Fertilizer timing and efficiency - effect of thinning, fate of applied nutrients, demand at different ages

   Harvesting to minimise N-loss

3. Short rotation, whole tree utilisation, biomass studies, genotype x fertilizer interaction, mensuration and modelling

4. Soil and plant chemistry.

This list of research projects is advanced for consideration by the workshop. I accord items under 1 the highest priority but I believe they deserve and should be allocated additional new resources in order to ensure that adequate planning is devoted to the task.

The remaining items are important and I cannot agree with any suggestion that resources going to them should be diminished. Some research organisations may be able to make some internal re-arrangement which would result in some extra resources being transferred from what appear to be projects of lower priority.

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BIOLOGICAL AND ECONOMIC CRITERIA FOR ESTABLISHING A NITROGEN FIXING UNDERSTOREY IN PINE PLANTATIONS

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ABSTRACT

This paper investigates the rates of nitrogen fixed by tree and understorey nitrogen fixing species. The probable methods of cropping systems are discussed and the potential for a legume understorey in forestry is investigated. Eleven biological criteria are defined for a legume understorey species in forestry. The main cost of establishing a legume understorey is weed control to prevent competition with the planted trees. Cultivation and special fertilization may also be additional costs. In an economic analysis it was found that inorganic N fertilization was cheaper by \$88 ha^{-1} than the most probable legume establishment treatment. This required an increase in urea cost of 2.75 x to equal the cost of legume establishment. Legume establishment became a proposition if the tree MAI was 4.4 to 5.6% better than predicted.

The particular problems in chosing a legume understorey species and symbiotic Rhizobium suitable for plantation forestry in south eastern Australia are discussed.

NITROGEN FIXING PLANTS IN FORESTRY

The need to raise and maintain nitrogen in plantation forest ecosystems has been established elsewhere in this Workshop. This paper builds on the axiom that nitrogen is necessary for maintenance of forest productivity, always assuming that phosphorus present is adequate to sustain tree growth. Thus, given the rapidly rising cost of nitrogen fertiliser shown in Fig. 1, and the inefficiency of uptake, by the trees, of inorganic fertilizer due to leaching losses and volatilisation (Bengston 1978), it has become very necessary to examine the biological efficiency and costs of nitrogen fixing plants in plantation forestry.

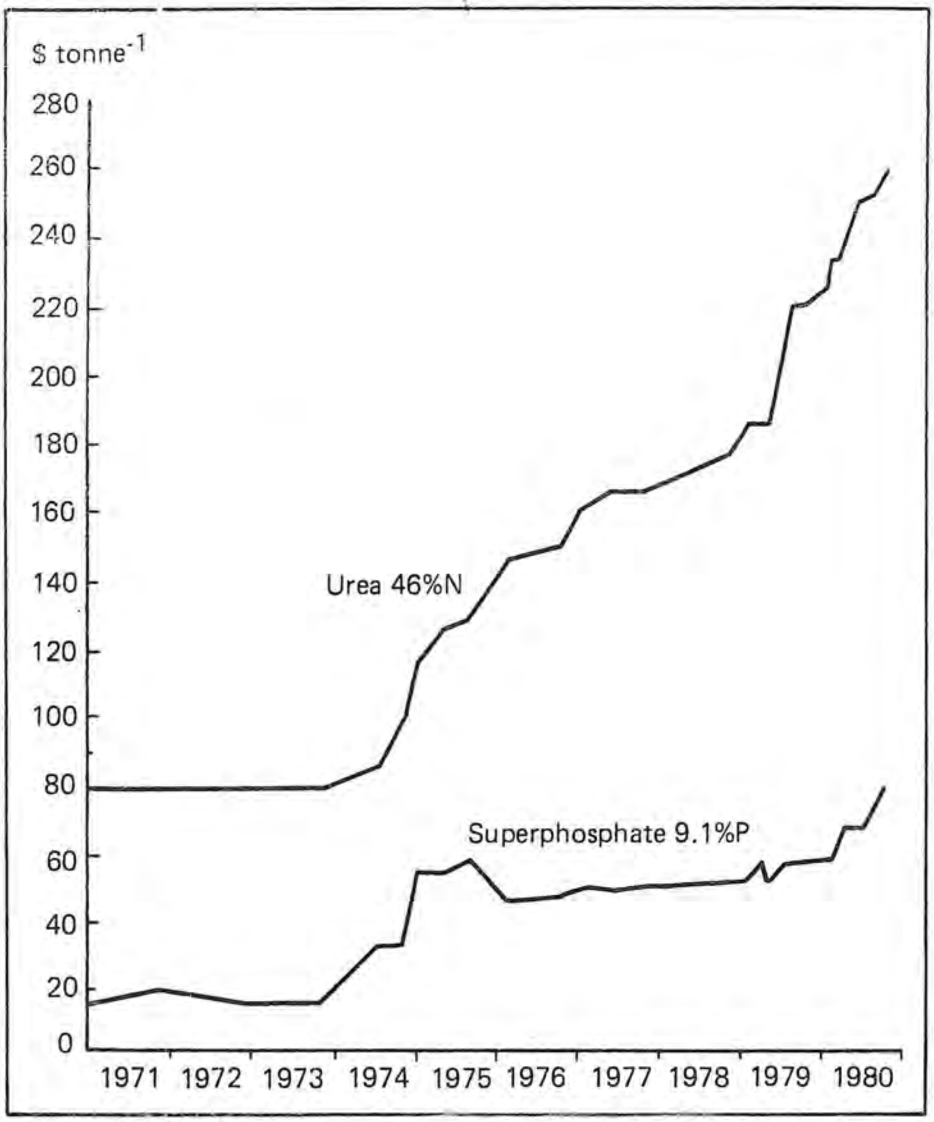

Fig. 1. The costs of urea and superphosphate fertilizers over the period 1971-1980 (Pivot Fertilizers price lists).

Nitrogen fixation by non-symbiotic organisms is low (average 1 to 5 kg N ha^{-1} yr^{-1}) in comparison to the symbiotic systems (average 30 to 200 kg N ha^{-1} yr^{-1}) (Davey and Wollum 1979) (Table 1). While the former are important in long forest rotations with extensive management, the latter offer the best opportunity for increased inputs under intensive forest management.

Table 1. N-fixation Rates of Some Symbiotic Systems.

Genus	N_2 fixed* (kg N ha^{-1} yr^{-1})	Source
AGRONOMIC		
Glycine	80 – 105	Hardy *et al.* (1973)
Medicago	200 – 300	Ambrus (1977)
Picum	100	Ambrus (1977)
Trifolium	58 – 183	Philips and Bennett (1978)
Trifolium	121	Waring (1966)
NON-AGRONOMIC		
(a) *Trees*		
Acacia	8 – 16	Langkamp *et al.* (1979)
Alnus	40 – 325	Cited in Haines and De Bell (1979)
Casuarina	50 – 200	Haines and De Bell (1979)
Robinia	55	Ashley and Baker (1968)
(b) *Shrubs or herbs*		
Acacia	3.0	Malajczuk and Grove (1977)
Bossiaea	2.8 – 8.6	Malajczuk and Grove (1977)
Ceanothus	72 – 108	Youngberg and Wollum (1976)
Lespedeza	18	Bengtson and Mays (1978)
Lupinus	160	Gadgil (1971)
	180	Palaniappan *et al.* (1979)
Macrozamia	16	Halliday and Pate (1976)
Purshia	0.057	Dalton and Zobel (1977)

* Actual or inferred.

The value of a nitrogen fixing crop in forestry depends much upon the choice of species. Of the symbiotic systems available, it appears that only two offer short term practical application; these being legumes and actinomycete-nodulated nonlegumes. These can be grouped broadly into tree and understorey species.

N-Fixing Tree Species

Mixed species systems of Robina pseudoacacia (black locust) and conifers were reported in the early 1930's (Haines and DeBell 1979), but overtopping of the conifers lead to failure of some stands. Finn (1953) reported increases in soil nitrogen status, foliar nitrogen levels and growth of several tree species planted in association with R. pseudoacacia. Robina spp. have also been used in revegetation of mine affected areas (Carpenter and Hensley 1979).

Tarrant and Trappe (1971) listed 23 well-documented instances of the use of alder for soil improvement and advocated the increased use of red alder (Alnus rubra) in rotation, or mixed planting, with Douglas fir (Pseudotsuga menziesii) in the Pacific Northwest. Subsequently, Atkinson et al. (1979) proposed the use of red alder in alternate commercial cropping systems with Douglas fir. They concluded that all utilisation systems were profitable, but that under the then existing wood market conditions, systems utilisating Douglas fir only were the most profitable. However, it was noted that expanded wood markets (particularly for Alnus) and increased fertiliser costs could enhance profitability of the alternate cropping systems.

A number of Casuarina and Acacia species are native to Australia and may have potential as nitrogen fixers in some plantation forest systems. Casuarina species have been used in land reclamation in West Africa and Asia, and as well as Myrica species, have seen limited use in wood production forests of tropical and subtropical environments (Gordon and Dawson 1979). Acacia pellita has been used successfully in the revegetation of mined areas in Northern Australia (Langkamp et al. 1979).

N-Fixing Understorey Species

Waring (1966) showed clovers to be of potential value to forestry in replacing soil nitrogen lost during the first rotation. However, Richards and Bevege (1967) found the growth of exotic conifers to be depressed, and that of native conifers to be increased, in the presence of perennial legumes.

A successful green manuring mixed species system is used in New Zealand where tree lupin (Lupinus arboreus) enables the establishment of Pinus radiata on nitrogen-poor sand dunes. Lupins are allowed to grow for about 3 years before being crushed, or sprayed with herbicide, to allow pine establishment. The lupins regenerate and persist until canopy closure, and also regenerate at each thinning. Nitrogen fixed by the lupins is the major source of N for the site (Gadgil 1977). Perennial lupins have also been used in the USSR where they were introduced into a 33-year-old stand of Pinus sylvestris. The increase in profitability of forest production at 40 years, as a result of lupin introduction, was estimated at 19% (Lakhtanova and Beregova 1976). Green manuring of yellow lupin is also recommended for some humus-poor sandy soils in the USSR (Mangalis 1975).

Lupinus polyphyllus is used in the USSR to increase the N content of pine plantations, thereby increasing the resistance to insect attack (Vorontsov 1975). Soil infestations of chafers (Melolonthinae) are also overcome by Pinus - Lupinus associations (Nikitin et al. 1976). L. polyphyllus is also used in West Germany to ameliorate forest soils degraded by litter gathering in former times (Rehfuess 1979).

Legumes also play an important role in agroforestry systems (Cook and Grimes 1977, Anon. 1978a) and erosion control of forested, clearfelled or afforestation areas (Anderson and Brooks 1975, Anon. 1976, Bengtson and Mays 1978).

Other Considerations

Irrespective of N-fixation, N-fixing understories may be important not only in the cycling of N but also in the cycling of all nutrients by maintaining the nutritional integrity of the system and serving as a "sink" of "available" nutrients while reducing losses from litter and soil layers (Outcalt and White 1979).

Similarly, Zhilkin and Rikhter (1976) found that cultivation of perennial lupin in 90-year-old Pinus sylvestris stands promoted more rapid decomposition of the litter and the liberation of N and ash elements into the biological cycle. Such responses are likely to result from a lower C/N ratio developed through the addition of N rich leguminous litter.

Boring et al. (1979) emphasised the importance of some understorey species in the revegetation of clear-cut sites, and claimed it to be a nutrient conserving process that minimised hydrologic losses of elements and initiated a rapid recovery of nutrient cycling.

Swaby and Sperben (1958, cited by Gadgil 1977) have shown that some legumes are capable of utilizing insoluble phosphate (apatite) in sandy soils. This could increase the availability of phosphorus in the plantation ecosystem.

Haines et al. (1978) reported the successful control of weeds in a sycamore plantation through the introduction of a leguminous understorey. Weed control costs would be saved in such a case provided that the understorey did not inhibit tree growth by competing for soil moisture in critical periods.

Shea (1979) has also shown that native legumes may suppress Phytophthora cinnamomi and subsequent jarrah dieback in Eucalyptus marginata forests of Western Australia.

Thus, in addition to raising soil nitrogen levels, N fixing species may also be incidental in improving rates of mineral cycling; improving soil organic matter content, soil structure and cation exchange capacity; providing effective control of competing species; and inhibiting soil-borne pathogens. The rapid establishment of a cover crop after clear felling will reduce surface run-off and soil movement, and may temporarily immobilise nutrients otherwise lost from the site following rapid mineralisation of soil organic matter.

There are, however, several potential disadvantages in using nitrogen fixers in forestry. These include: the cost of establishing the species and supplying minerals essential for successful root nodulation; the cost and supply of seed and innoculum; the opportunity cost of land occupied by a non commercial crop; the cost of reducing competition with trees using weedicides; and a potentially increased fire hazard from the understorey.

THE CHOICE OF CROPPING SYSTEM

Concomitant with a choice of nitrogen-fixing species is the choice of cropping system to use. Haines and De Bell (1979) suggested six potential cropping systems for utilising root nodulated nitrogen fixing plants in forestry. These systems are divided into two groups:

1. Crop rotation systems
    - 1.1 Green manuring with a non-commercial nitrogen fixing species, in which the crop is ploughed in its green state prior to planting the commercial tree crop.
    - 1.2 Alternate commercial cropping of a nitrogen-fixing plant with the tree crop.
2. Mixed species systems
    - 2.1 Mixtures of two commercial nitrogen fixing species.
    - 2.2 Nitrogen fixing trees as the principal crop.
    - 2.3 Nitrogen fixing species understorey for the whole rotation.
    - 2.4 Nitrogen fixing understorey for the early phase of the rotation.

Crop Rotation Systems

Crop rotation systems involve growing the N fixing crop by itself for a given period, followed by one or more crops of non-nitrogen fixing (principal crop) species. The N fixing crop may or may not have commercial value. Green manuring utilizes N fixing crops of no commercial value, and are therefore not harvested, whereas those used in alternate cropping systems do have commercial value. In both systems, incompatability of growth patterns of the two crops are avoided and each crop receives full sunlight allowing growth and N fixation to proceed at maximum rates. They also provide for amelioration of soil-borne pathogen problems (Russell 1973), and have been used in agriculture for this purpose for at least 2000 years.

The principal disadvantage of crop rotation is the opportunity cost of the time that the land may not be producing the crop of highest value. The value of the ameliorative function of the crop must then be equal to, or greater than, this cost.

Mixed Species Systems

Haines and De Bell (1979, p.290) defined these systems as involving "... a sharing of site resources between the nitrogen-fixing species and principal crop during all or selected portions of a rotation."

Advantages of mixed species systems include the absence of any period during which the principal crop is not growing on the site, and the ability of the N fixing species to increase the supply of nitrogen, and perhaps other nutrients, to the principal crop throughout the rotation or at time of greatest demand (e.g. during the years of fastest growth or after a thinning).

Disadvantages of mixed species systems stem from competition between each species for space, moisture, nutrients and light. For this reason production from the principal crop, and N fixation by the other species, may be less than could be achieved under a system of crop rotation. If N fixing trees rather than understorey species are used, disadvantages related to occupation of growing space might be greater. However, most N fixing understorey species are intolerant of shade and under such conditions N fixation rates are much reduced.

OBJECTIVES AND CRITERIA FOR USING N FIXING SPECIES IN PINE PLANTATIONS

The permutations of the above systems are numerous and in pursuing these the initial objective of fixing nitrogen in the forest ecosystem may become lost. So for the purpose of this examination we have used the clear but limited objective of primarily growing pine for pulpwood production in Victoria. This land use system mitigates against non commercial rotational cropping unless the opportunity cost of "vacant" land is met by the returns in raised productivity resulting from the non commercial crop. Or, putting it in a quasi-equation:

$$\begin{array}{l} \text{\$ value of increased} \\ \text{wood growth from N} \\ \text{fixed by crop and} \\ \text{improved soil} \end{array} \geq \begin{array}{l} \text{\$ opportunity} \\ \text{cost of non} \\ \text{tree growing} \\ \text{land} \end{array} + \begin{array}{l} \text{\$ cost of} \\ \text{inorganic} \\ \text{N fertiliser} \\ \ \end{array} + \begin{array}{l} \text{\$ cost of} \\ \text{improving} \\ \text{soil} \\ \text{condition} \end{array}$$

The equation becomes biased against the nitrogen fixing crop if expensive measures are needed to remove it or reduce its competitive effects, i.e. by ploughing, slashing, crushing, or weedicide. The extreme case of this situation would be the removal of a nitrogen fixing tree crop before pine establishment. In this case the value of the nitrogen fixed by the trees and used by the pines for increased growth will be substantially offset by the cost of clearing and prevention of competing regeneration.

For pine plantations in Gippsland, Victoria, we consider that an understorey nitrogen fixing crop should be established at, or at the most 2 years prior to, pine establishment. The nitrogen fixed should be available to the trees during their maximum early growing phase, be shaded out at canopy closure, and return to supply nitrogen and promote mineral cycling after thinning. Using this system we have defined some biological criteria for such a nitrogen fixing understorey.

These criteria are:

1. Have a minimum N_2 fixing capacity of 50-100 kg N ha^{-1} $year^{-1}$
2. Maintain a low growing habit and be non-climbing
3. Be shade tolerant
4. Be herbaceous rather than woody to provide rapid litter decomposition
5. Provide weed control through good ground cover
6. Grow during the wet cool seasons and not compete with pines for moisture
7. Be perennial or self seeding annual
8. Easy to germinate
9. Low additional fertilizer requirements
10. Have available seed or be adaptable to seed farming

11. Be non-prickly so as not to inhibit harvesting or fire suppression activities.

It would be unrealistic to expect any nitrogen fixing understorey to meet all the above criteria, but there is a penalty for each criterion that is not met. This penalty is in the form of either increased costs to silvicultural operations, or reduced growth of pine trees.

INTENSIVE SILVICULTURAL TREATMENTS AND THE GROWING COST OF WOOD

Before any detailed analysis of the cost of legume establishment, we will examine the way in which money spent on pine establishment affects the growing cost of the harvested wood.

In an economic evaluation of the cost efficiency of silvicultural treatments on the growing cost of wood, Cromer et al. (1977) based their decision on the break-even growing cost of wood fibre. The break-even cost is the price per unit wood volume that must be received to cover costs, and is found by dividing the discounted costs of land, establishment, and maintenance, by the discounted wood yields. They found in their analyses that, in a capital rationing situation as land became more expensive and treatment and maintenance costs increased, it became economically preferable to spend money on intensive silvicultural treatments (fertilizers and weedicides) that produced more wood, than to buy more land, i.e. the break-even treatment cost increased with increasing land prices. Moreover, as land prices rose, the opportunity cost of not implementing intensive silviculture increased dramatically.

In their analysis of weed control and rates of NPK fertilization on a soloth soil in Gippsland, Cromer et al. (1977) found that the break-even silvicultural treatment was weed control with 67 kg P ha^{-1}. However, the greatest wood volume production was obtained with 202 kg P + 232 kg K + 807 kg N ha^{-1} with weed control. Thus, although high fertilizer rates increased wood volume grown, the high cost particularly of N fertilization offset the value of the wood grown. In a subsequent analysis of the energy involved in establishing these treatments, Dargavel and Cromer (1979) found that on energy criteria the break-even treatment was unchanged, but nitrogen fertilization incurred a heavy energy cost which was not associated with commensurate increases in energy production. However, the N:P ratios used in this experiment were very high at 4:1 and there are no direct measures of the growing cost of wood using much lower nitrogen rates to complement phosphorus fertilization. Tree responses to N:P ratios of 3;1 and 1.5:1 for 30 and 60 kg P ha^{-1} respectively are estimated in the following section. These moderate treatments reduced wood growing costs below that for phosphorus alone.

From these considerations it is clear that there is a response to nitrogen fertilization but that for high levels of nitrogen this response is uneconomic in both money and energy terms. Thus, if both the cost and the energy component of placing nitrogen in forests can be reduced, then wood growing costs can also be reduced. As land prices rise it becomes imperative to use the increase in wood volume produced by nitrogen fertilization; thus the solution to the problem of nitrogen supply in forests has an increasing economic benefit attached to it.

THE COSTS OF LEGUME ESTABLISHMENT

When compared with inorganic fertilizer application there may be higher costs associated with establishing legumes. These may include costs for seed, inoculum, sowing, cultivation, special fertilization, and weed control. These costs are shown in Figure 2 with the costs accumulated into establishment treatments. Included for comparison in Figure 2 are the costs of establishing pines with inorganic fertilizers and weed control. Throughout these economic considerations the cost of urea has been used as the cost of supplying nitrogen in a fertilizer. Because of its high nitrogen content (46%), urea is a cheaper way of supplying nitrogen than either ammonium nitrate or ammonium sulphate (Table 2). Urea may not be the most efficient way of supplying inorganic nitrogen however, and this must be borne in mind.

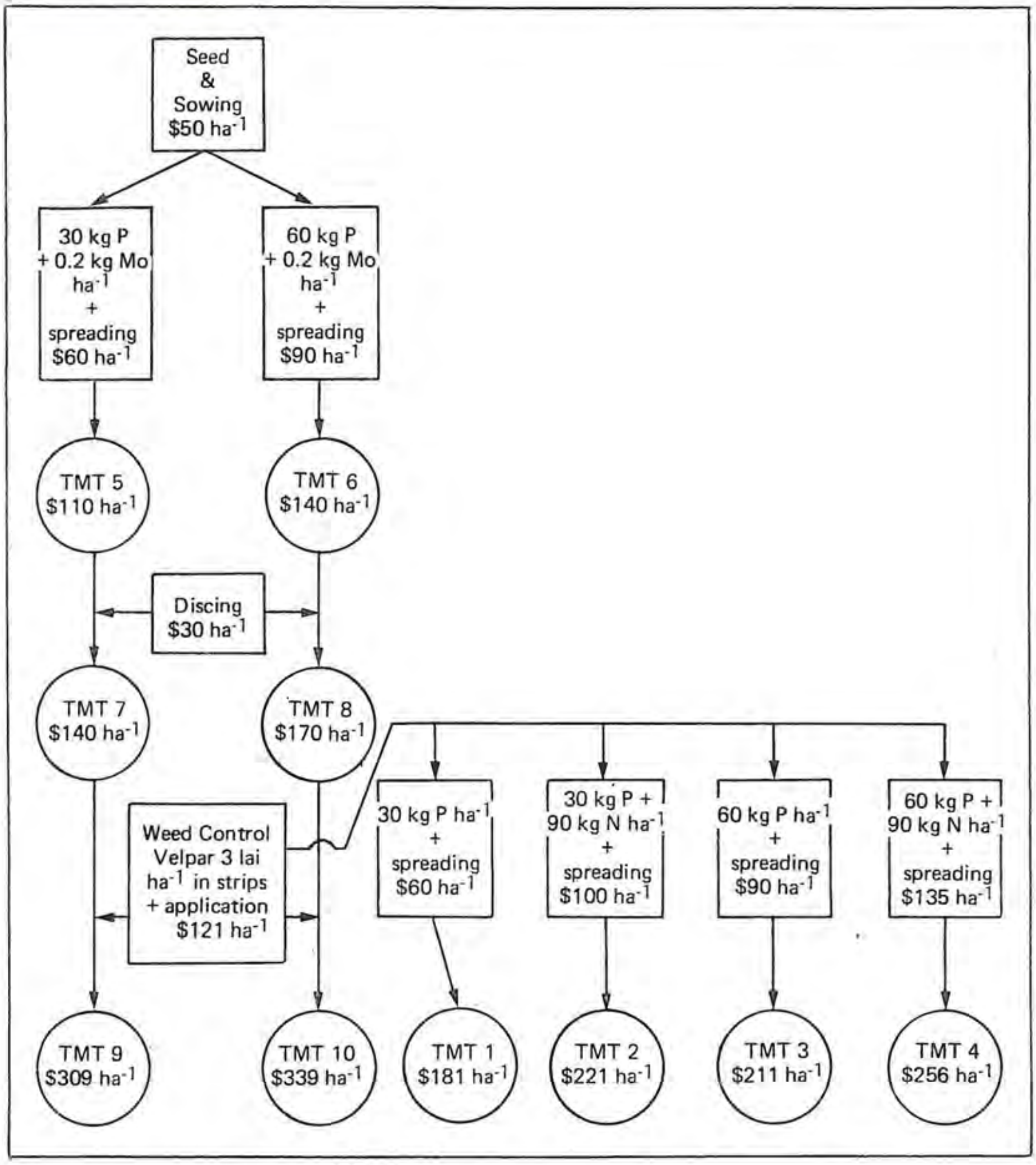

Fig. 2. Site preparation treatments (TMT) and associated costs per hectare. (Treatments 9 and 10: All operations except weed control discounted for two years prior to establishment of pines.)

Table 2. The Relative Costs[1] of some Nitrogen Fertilizers

	%N	\$/tonne^{-1}	\$/kg N^{-1}
Urea	46	263.15	0.57
Ammonium nitrate	34	214.51	0.63
Ammonium sulphate	21	156.07	0.74

[1] Based on Pivot Fertilizer price list August 1980.

If successful establishment of legumes can be achieved with sowing and some P + Mo fertilizer for nodulation (Anon. 1978b), then the cost of legume establishment will be c. \$60-90 ha^{-1}. But, if discing is required for successful germination, a two year growing period used to accumulate nitrogen, and weedicide required to prevent competition with pine seedlings, then legume establishment may cost \$309-\$339 ha^{-1}, compared with \$221-\$251 ha^{-1} for inorganic fertilizer and weed control. Thus there is much to be gained in finding a legume that will germinate readily without cultivation, will fix and liberate nitrogen rapidly, and will not compete with pine seedlings for moisture (i.e. will not require controlling with weedicide). As discussed previously, however, if the tree growth response to legume nitrogen is high then the cost of legume establishment may be offset by the reduced growing cost of wood. So in calculating the value of a legume crop, some estimation must be made of the nitrogen fixed by the legumes and utilised by the trees.

In the following calculations of the value of a legume crop, the amount of fixed nitrogen available to the trees has been varied between 0 and 90 kg N ha^{-1} (Figures 3 and 4). The value of the crop as a soil improver has not been taken into account but this will be, nevertheless, of long term value in subsequent pine rotations.

The basis for a response by pine trees to nitrogen fertilization on the majority of soils in Gippsland is phosphate fertilizer, so in this evaluation two levels of phosphorus were used; 30 and 60 kg P ha^{-1}. The responses to these levels of phosphorus and nitrogen fertilizer were taken from Dargavel and Cromer (1979). By taking 30 kg P (treatment 1) and adding 90 kg N (treatment 2), MAI was raised from 15.4 m^3 ha^{-1} yr^{-1} without nitrogen to 18.4 m^3 ha^{-1} yr^{-1} with nitrogen. The responses to inorganic nitrogen at 90 kg N ha^{-1} (0.6 m^3 ha^{-1} yr^{-1} at 30 kg P ha^{-1}, and 1 m^3 ha^{-1} yr^{-1} at 60 kg P ha^{-1}) were assumed to be the maximum responses obtainable to legume fixed nitrogen.

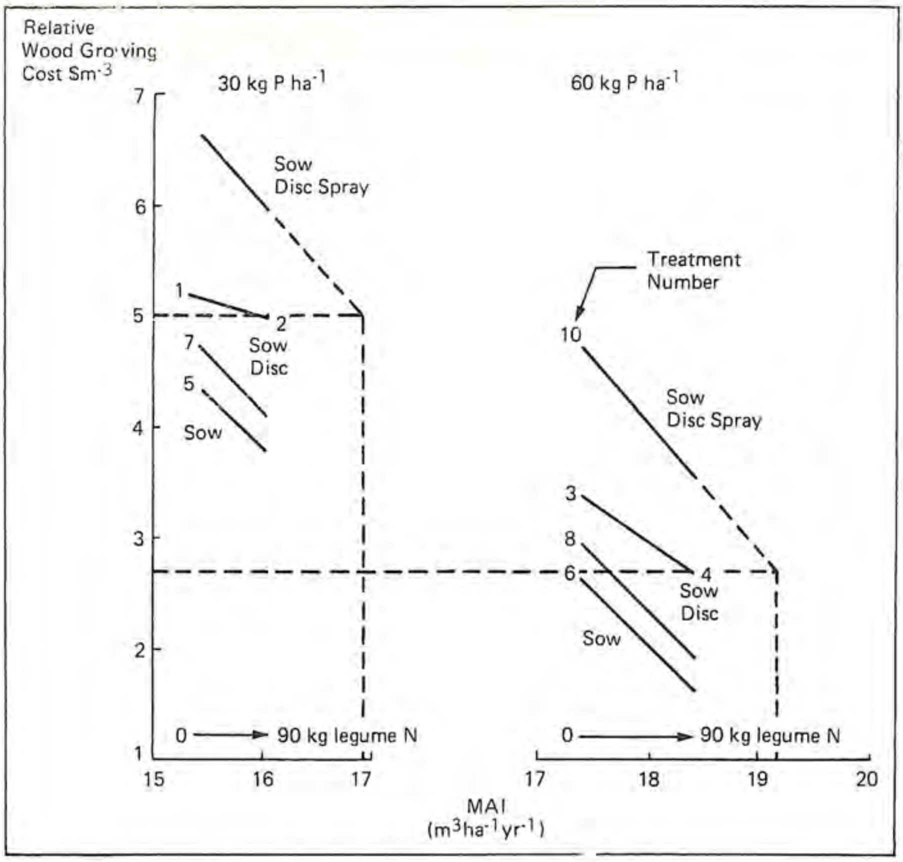

Fig. 3. Predicted wood volume production and relative wood growing costs for selected legume establishment and fertilizer treatments.

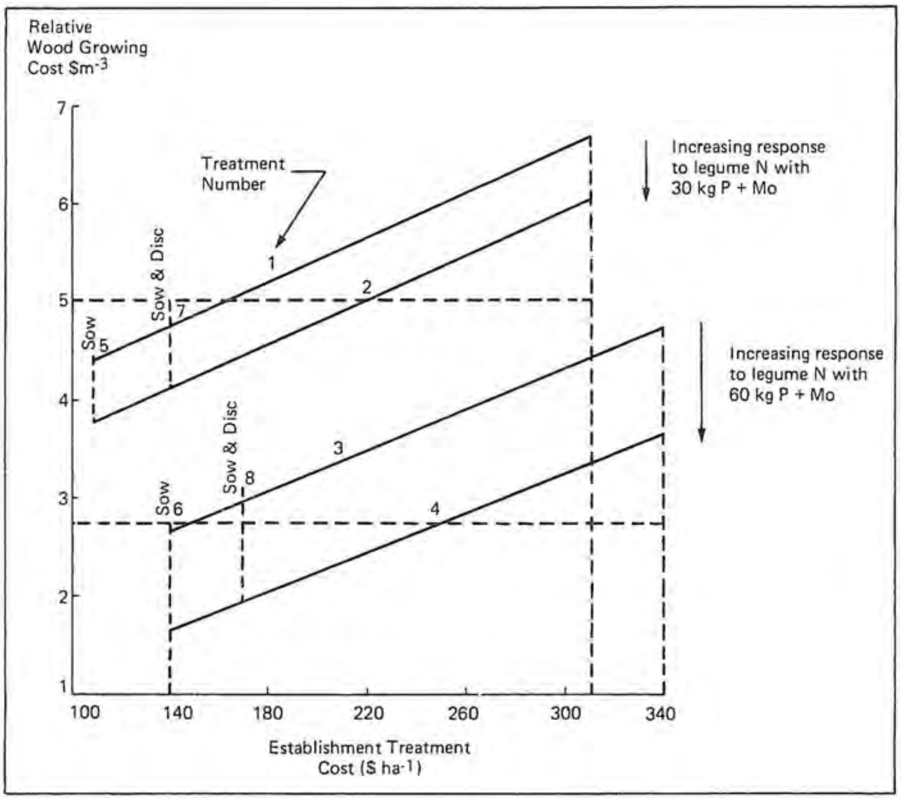

Fig. 4. The relative wood growing cost for selected legume understorey establishment and fertilizer treatment costs.

Figure 3 shows that as there is a response to nitrogen, MAI increases, and the growing cost of wood is reduced. The growing cost of the wood is reduced overall by increasing phosphorus to 60 kg P ha^{-1}, and is further reduced by a response to nitrogen. If weed control is not needed the growing cost of the wood is much reduced.

The treatment costs (Figure 2) and wood growing costs (Figure 3) have been combined in Figure 4. This shows that the growing cost is reduced at the higher levels of fertilizer, and that as the response to legume nitrogen increases there is a marked reduction in wood growing cost. Thus the potential reduction in wood growing cost from a response to legume nitrogen is greater at the higher level of phosphorus fertilization. The data show that if weed control has to be used to obtain a response to legume nitrogen, then inorganic nitrogen fertilization is cheaper, and cheaper wood is grown.

Since nitrogen fertilizer (urea) has risen in the past six years by \$29.53 $tonne^{-1}$ yr^{-1} or increased approximately three times (Figure 1), some estimate needs to be made as to when the 'worst' legume establishment treatments 9 and 10 (Figure 2) will become economic. Treatment 9 (30 kg P + Mo ha^{-1}, sow, disc, weed control after 2 years when pines are planted) cost \$88 ha^{-1} (40%) (Figure 4) more than treatment 2 (30 kg P + 90 kg N ha^{-1}, weed control). Since all components of treatment 2 excluding nitrogen are included in treatment 9, the cost difference between the treatments must be borne by the nitrogen fertilizer. Thus, if the nitrogen component of treatment 2 increased \$88 then legume establishment becomes economic. Similarly the legume treatment 10 (sow, disc 60 kg P + Mo ha^{-1}, weed control) is \$88 ha^{-1} (35%) more expensive than treatment 4 (60 kg P + 90 kg N, weed control). Thus, in both cases \$88 has to be spread over 90 kg N, or c. \$1 kg^{-1} N. This is \$460 $tonne^{-1}$ urea increase on current price, or a total price of \$723 $tonne^{-1}$. This would necessitate a urea price rise of 2.75 times its current value, which is a substantial price rise even at the current rate of increase.

The growing cost of the wood can be reduced if MAI is increased. Thus, if the pine response to legume establishment is greater than that obtained from 90 kg N ha^{-1} (i.e. the maximum response used in these calculations), then legume establishment may become economic. From Figure 3 it can be seen that with an increase in MAI of treatment 9 to 16.9 m^3 ha^{-1} yr^{-1} (5.6%), the growing cost of the wood is reduced to that for treatment 2, and legume establishment becomes economic. Similarly if the response to treatment 10 is increased to 19.2 m^3 ha^{-1} yr^{-1} (4.4%) then legume establishment will grow wood as cheaply as treatment 4.

Thus for legume establishment to reduce the growing cost of pine wood for pulp, there must be either a substantial increase in the cost of nitrogen fertiliser (c. 3x), or 4.4 to 5.6% better than predicted response to nitrogen fixed by legumes. If weed control is not necessary then legume establishment is an economic proposition. However, it is likely that these three factors will combine. The cost of nitrogen fertilizer will continue to increase at a rate greater than the cost of establishing legumes. It is also probable that nitrogen fixed by the legumes will be available to pines longer in the rotation than inorganic nitrogen applied at establishment. It may be possible to apply weedicide at a rate lower than that used here for broad spectrum weed control, or crushing of legumes at planting may provide adequate control of competition.

If these three factors change synchronously then legume establishment in pine plantations will rapidly become an economic proposition.

NON AGRONOMIC OR AGRONOMIC NITROGEN FIXERS IN FORESTRY

Having chosen the legume understorey system for forestry, much of the success of its establishment depends upon the choice of species.

Most introduced legumes of agronomic importance exhibit high rates of nitrogen fixation under specific agricultural conditions. However, their rates of nitrogen fixation and persistence may not be adequate under adverse soil conditions, low rates of fertilisation, no grazing, no pest control, or no competing weed control. The nitrogen fixing capacities of dense stands of non agronomic species is largely unknown, but they may be more tolerant of otherwise adverse soil and environmental conditions. Because of the uncertainty over the performance of agronomic legumes under forestry conditions, and the largely unknown entity of non agronomic legumes, we have established a legume screening trial for pine plantations in Gippsland, Victoria. Fifteen legumes listed in Table 3 are being screened on a range of sites; the natives are all endemic to Gippsland.

Table 3. Leguminous understorey species screened by A.P.M. forests in Gippsland, Victoria.

Species	Cultivar or Provenance	Prostrate (P) or erect (E) growth
NATIVE		
Acacia brownii	Goonoo Forest, N.S.W.	E
Aotus ericoides	Macquarie Pass, N.S.W.	E
Bossiaea buxifolia	Pilliga State Forest, N.S.W.	P
Gompholobium latifolium	N.S.W.	E
Goodia lotifolia	Robertson, N.S.W.	E
Indigofera australis	Gippsland, Vic.	E
Kennedia prostrata	Borden, W.A.	P
INTRODUCED		
Lupinus angustifolius	New Zealand blue	E
L. arboreus	Woodhill, New Zealand	E
L. cosentinii	Perth, W.A.	E
L. polyphyllus	Russell Prize Mix	E
Medicago sativa	WL451	E
Trifolium pratense	MP New Zealand	E
T. subterraneum	Woogenallup	P
T. repens	Haifa	P

The nitrogen fixing potential of any legume is dependent upon the correct symbiotic Rhizobium species for root nodulation. Several strains have been purified and reproduced in peat for routine inoculation of agronomic legumes (Roughley 1970). However, the efficacy of any strain of Rhizobium is dependent upon favourable environmental factors including moisture, soil pH, and nutrient availability. Rhizobium strains are now being selected for adverse acid soils (Date and Halliday 1979), and for improved mineral nitrogen production with legumes. Most Rhizobium strains selected for agriculture may not be suitable for forest soils or native legumes. The native legumes/Rhizobium symbioses are poorly defined, and no commercial innoculum exists specific to native legumes of south eastern Australia. Therefore, as an adjunct to the legume screening trial we have tested the ability of commercial cow pea inoculum (group I) to increase root nodulation of seven native legumes listed in Table 3. This is a glasshouse trial and is being assessed for species biomass and nitrogen content, mineral and total soil nitrogen, and nodule activity by acetylene reduction assay. Early indications are that Indigofera australis at least has shown a positive response to inoculation.

In selecting legumes for use in plantation forestry we are faced with many of the same questions that agronomists have faced and largely solved. The main questions are, which species, which symbionts, and what environmental tolerances? The answers to these questions require experimentation with a range of soil climatic variables. The question of which symbiont is one that will need to be answered in co-operation with microbiologists. This is a difficult question to answer, but much of the success of legume establishment and the nitrogen fixed by them is dependent upon the symbiotic association between the Rhizobium species and its legume host.

CONCLUSIONS

Although the inflating cost of supplying nitrogen to forests as inorganic nitrogen fertiliser has provided a stimulus to the investigation of legumes for forestry, it is unlikely that fertiliser will be superseded as a cheap source of nitrogen in forestry in at least the next five years or maybe ten. The main cost involved in establishing a legume understorey is strip weed control to prevent competition with pine seedlings. If a legume can be found to be non-competitive, or easily killed at the time of planting, then the probable nitrogen supplied by the legume becomes an economic proposition.

The full potential of a legume understorey will not be realised without a great deal of investigation of legume/Rhizobium symbioses, for native legumes in particular, across a range of forest soil environments.

In the long term it is quite probable that a legume understorey will fix more nitrogen than is economically possible through inorganic fertilization. Moreover the nitrogen supply will last through the rotation to improve rates of mineral cycling, soil structure and nutrient status, and utlimately the growth of trees.

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NITROGEN IN RADIATA PINE FORESTS IN NEW ZEALAND*

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BIOLOGICAL NITROGEN INPUTS

Non-symbiotic nitrogen fixation by bacteria, blue-green algae, and lichens is unlikely to exceed or even reach 5 kg ha^{-1} yr-1 in temperate forests (Jurgensen _et al_ 1979; Tjepkema 1979). Much larger N inputs can be expected from symbiotic N-fixing plants commonly found in New Zealand exotic forests. Shrubs such as perennial yellow tree lupin (_Lupinus arboreus_), tutu (_Coriaria arborea_), gorse (_Ulex europaeus_), and broom (_Cytisus scoparius_) can fix up to 200 kg N ha^{-1} yr^{-1} (Egunjobi 1969; Gadgil 1971; Helgerson _et al_ 1979; Silvester _et al_ 1979).

The use of N-fixing plants as an alternative to fertilizer-N in exotic forests is theoretically attractive but poses problems for the forest manager. The typically vigorous growth of these plants in open situations means that trees must be protected from competition during the first years of forest establishment. Later in the rotation the plants are unlikely to realise their N-fixing potential unless tree stands remain relatively open-grown or are thinned sufficiently for understorey plants to thrive.

A study of nitrogen distribution in the ecosystem of a developing sand-dune forest has drawn attention to the importance of marram grass and plant litter which act as reservoirs for nitrogen fixed by perennial tree lupin (Fig. 1).

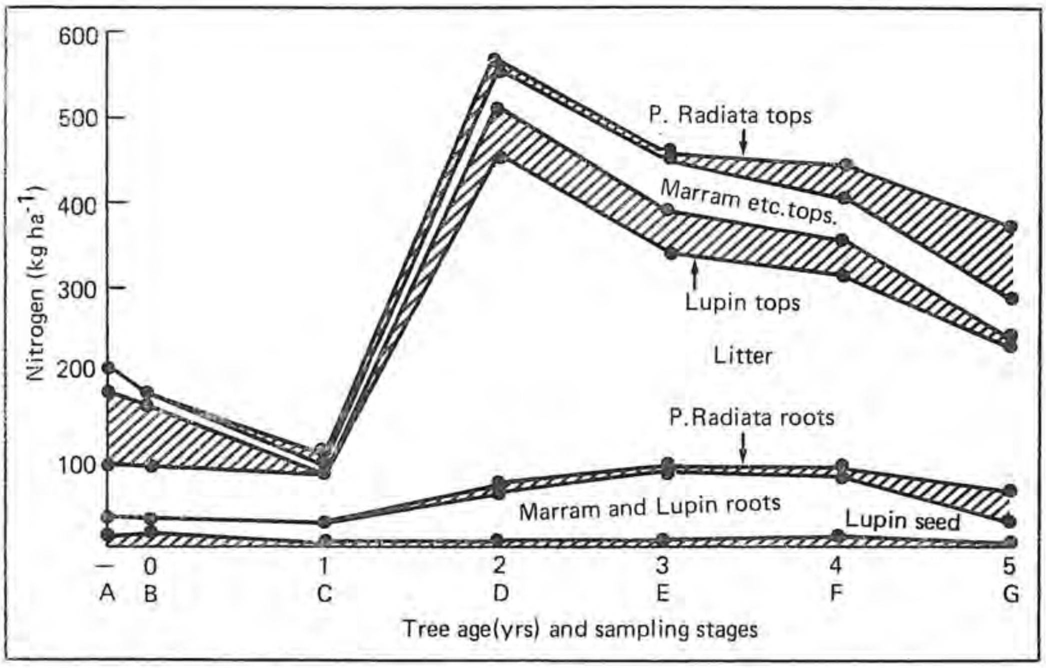

Fig. 1. Nitrogen distribution in the biomass and litter fraction of the developing sand dune forest ecosystem. Data from Gadgill 1979.

N.B. A change of sampling site may have exaggerated the magnitude of differences between stages C and D.

NITROGEN FERTILIZERS AND GROWTH RESPONSES

Increasing areas of radiata pine forests are being treated with N fertilizers. In a few forests approximately 15 g of N (usually as D.A.P.) are applied alongside each tree at time of planting. Applications later in the life of stands are aerially broadcast; in 1979 over 4000 ha were treated (mainly with urea) and this is likely to increase but probably not to the 1985 level projected by Ballard and Will (1978).

Recent trials have shown that application of N fertilizer to young pole-stage stands mainly increases B.A. growth-height is increased only in very deficient stands and form factor changes are largely ephemeral at this age. Twelve rates-of-N trials and four N x P factorial trials in 9-year-old radiata are the basis for the following presentations. In Fig. 2 expected growth responses to N are given in relation to (1) three nitrogen states (% N in foliage) and (2) three canopy conditions. In Fig. 3 basal area response curves are given for four trials; the larger the growth response the later the peak in response. Other trials have shown that the net volume gain after 5 years is maintained through to the end of the rotation. Figure 4 shows that the maximum response is produced by an application of 200 kg N ha^{-1}; since there is apparently a linear response between 0 and 200 kg N ha^{-1} the latter is the economic optimum for deficient and low-marginal stands.

Nutritional State				
A. V deficient N < 1.2%	B. Low-Marginal >1.2–1.4% N	C. Marginal-Adequate > 1.4% N		
25% √√	15% √√	5% ?	1	Recently thinned
√√	√	?	2	Open canopy
Does not occur	?	No	3	Closed canopy

√√ – Response confidently expected
√ – Response expected
? – Response uncertain
No – Lack of response confidently expected

Figures give average percentage by which basal area in plots is fertilized at 200 kg N ha^{-1} exceeded unfertilized plots three years after fertilizing

Fig. 2. Expectation of basal area response to nitrogen fertilizer in radiata pine.

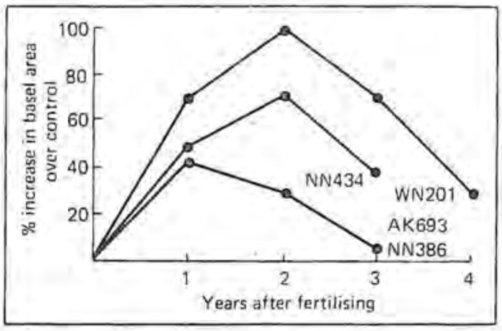

Fig. 3. Annual basal area response to nitrogen fertilizer.

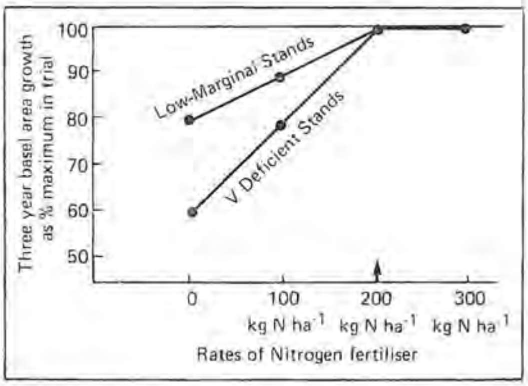

Fig. 4. Three-year basal area increment as % maximum for varying nitrogen rates.

NITROGEN UPTAKE IN RADIATA PINE FORESTS

Tree foliage and branch weights increase rapidly in the years immediately after planting. The rates of increase are dependent on the site and the number of plants established, but by age 4 years foliage mass may be 10 t ha^{-1} or more. Once canopies close, the amounts of foliage and live branch material tend to stabilise though branch mass may continue to increase slowly as stands mature and the remaining trees become more widely spaced. Total nitrogen in the foliage of a closed radiata pine stand would be about 120 kg ha^{-1} and would be expected to be affected by site conditions in, as yet, undefined ways. The nitrogen content of branches of closed stands is very variable but averages about 30 kg ha^{-1} according to published data.

Nitrogen in stems increase with stand age as the weight of stem material accumulates. However, the lower concentration of nitrogen in larger stems implies that the rate of accumulation is slower for nitrogen than for dry weight. The total amount of stem nitrogen (kg ha^{-1}) may be estimated from mean stand height (m) and basal area (m^2 ha^{-1}) using the relationship:

stem nitrogen = 13.1 + 0.20 (basal area).(height).

CYCLING OF NITROGEN IN LITTER

Weight of litterfall is of the order of 5000-6000 kg dry wt ha^{-1} yr^{-1}; this returns to the forest floor 30-40 kg N ha^{-1} yr^{-1} (Will, 1959). Recently M.L. Carey (unpubl.) has studied litter accumulation in fortyone 18- to 20-year-old first-rotation stands in a wide range of soils and climate. Dry weight of organic material in the litter layers (above the mineral soil boundary) ranged from 5.9 to 59.5 t ha^{-1}; these contained 55 to 660 kg N ha^{-1}. Thus on some sites only 2-3 years' litterfall remain while on others 10-15 years' accumulation is present; the latter indicates that very little decomposition has occurred during the life of the crop. Physical appearances ranged from a loose layer of easily recognisable needles resting on the mineral soil to a dense fibrous mat up to 10 cm in depth. The concentration of N in the combined litter layers ranged from 0.82% to 1.56% but was not correlated with the weight of litter present. Factors favouring fast decomposition appeared to be:

1. low tree stocking (but still full canopy)
2. high winter rainfall
3. high Ca content of foliage.

Litter decomposition studies on a site where litter accumulation is moderate (20 t ha^{-1}) have shown that needle litter loses about half its weight during the first 2 years but little or no N is lost up to that stage (Will, 1967). More recent studies in the same locality have indicated that thinning a 14-year-old stand does not affect the rate of litter decomposition or N loss. A simulated broadcast application of 200 kg N ha^{-1} as urea raised the N level in the litter from 0.65% to 1.20%; this difference of approximately 0.5% was maintained over the following 4 years but was not associated with any increase in dry weight loss.

Gadgil and Gadgil (1978) reported increased rates of litter decomposition after clearfelling. They suggested that release of saprophytic micro-organisms from competition with pine mycorrhizal fungi was responsible rather than changes in microclimate.

LOSSES OF NITROGEN ASSOCIATED WITH MANAGEMENT OPERATIONS

Undisturbed forests tend to accumulate N (Likens et al 1977). A catchment study in Tairua Forest has shown a net gain of 1.1 kg N ha^{-1} yr^{-1} (3.7 kg N ha^{-1} yr^{-1} in precipitation minus 2.6 kg N $ha^{-1}yr^{-1}$ in streamwater output). B. Webber (unpubl.) found that 214 kg N ha^{-1} were removed from the site when harvesting a 29-year-old radiata pine stand; this represented 6% of the N present in the mineral soil. Whole-tree removal would have doubled the amount of N removed.

A lysimeter study has shown that increased leaching losses of N occur after clearfelling; NO_3-N concentrations in leachate below the rooting zone rose from 0.04 mg l^{-1} to an average of 0.7 mg l^{-1} during the first 2 years after felling. However the total quantity lost over this period was less than 16 kg N ha^{-1}.

Tube lysimeters have been installed in trenched plots which simulate some of the effects of clearfelling (Vitousek et al 1979). Soil NO_3-N levels in control areas were 0.002 mg N l^{-1}; trenched plot concentrations showed a response after 11 weeks and a year later had risen to 8.0 mg l^{-1}.

Broadcast burning is a common method of site preparation in New Zealand but no detailed studies of N or other nutrient losses have been made. Mechanical methods of site preparation can relocate nutrient within a site to the detriment of tree growth. Ballard (1978) showed that tree volume growth can be seriously reduced (20%) as a result of improperly conducted windrowing. Better growth on windrows was more than counter-balanced by poorer growth on interwindrow strips. Soil and foliage N analyses strongly suggest N deficiency as the cause of this reduced growth.

Losses of N from forests after fertlizer applications seem to be restricted to the amounts falling into or immediately adjacent to stream channels (Neary and Leonard 1978). Volatilisation and denitrification losses of N have not been measured in New Zealand but it is thought that conditions do not favour such losses.

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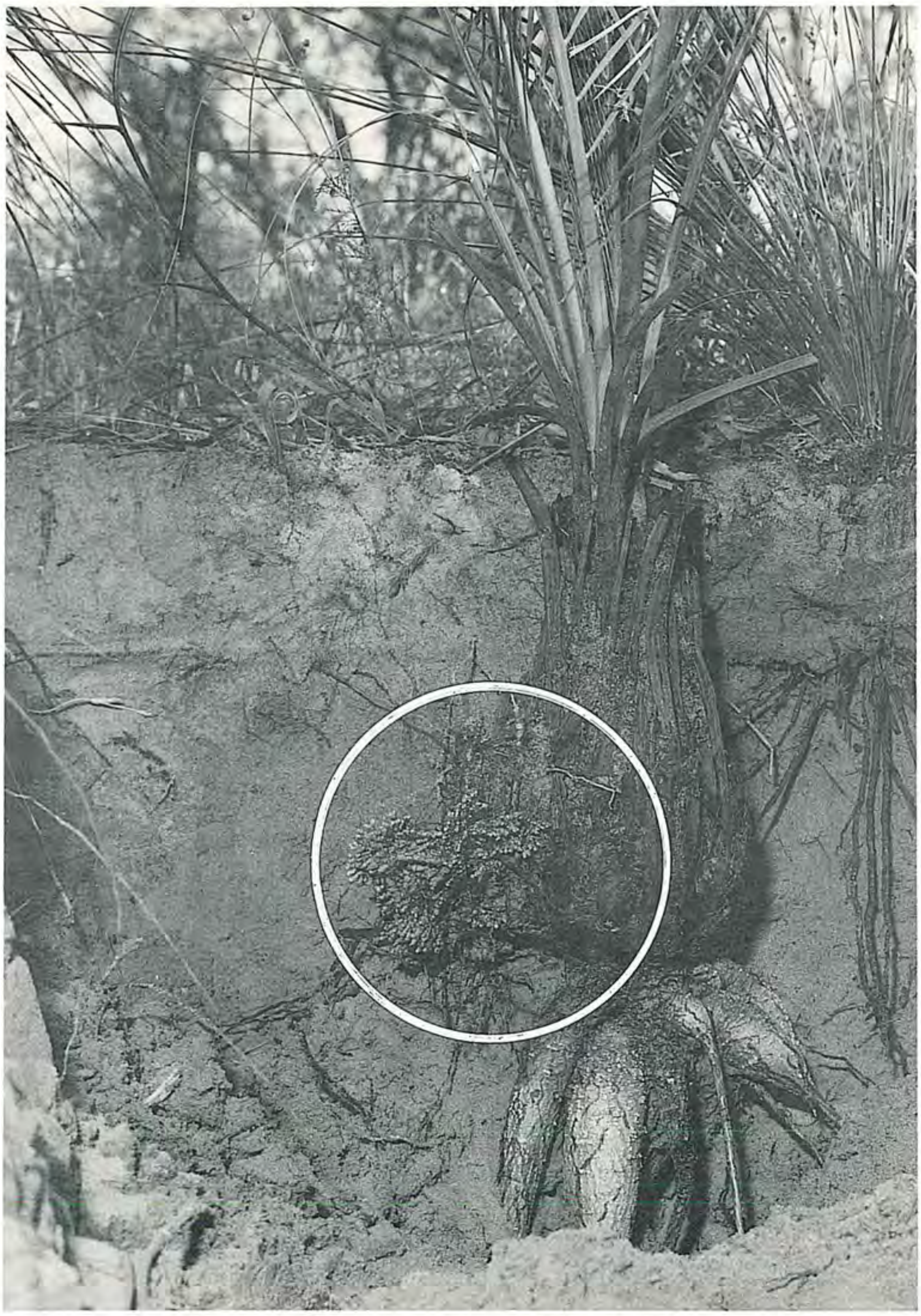

SESSION 3.
Basic Biological Processes
(a) N-fixation

SYMBIOTIC FIXATION OF NITROGEN IN FORESTS

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SUMMARY

Some general properties of symbiotic nitrogen-fixing systems are outlined and discussed in relation to aspects of the ecology of the symbionts and some of the environmental characteristics of forests. Some symbiotic components of forest systems are described and methods for quantifying N_2 fixation are outlined. A plea is made for inventories of N_2-fixing components of representative forests to be compiled, along with <u>in situ</u> or laboratory measurements of their rates of activity. On the basis of such information, the more quantitatively important components could be identified for urgent study.

INTRODUCTION

Although the symbiotic fixation of N_2 from the atmosphere has been known with certainty for almost 100 years, it is still difficult to measure rates of activity in the field. This arises from analytical difficulties (it is difficult to measure a small incremental change in a large pool of N), from the heterogeneity of natural systems which generate sampling problems and from limited knowledge of the occurrence, quantitative distribution of, and environmental restraints on N_2 fixing components of ecosystems. These qualifications apply to the simplest agricultural crop and are of much greater magnitude in forest systems.

SOME BASIC PROPERTIES OF SYMBIOTIC N_2-FIXING SYSTEMS

For the purposes of this discussion I regard a symbiotic system as one in which the non-N_2-fixing component plays a nutritional or micro-environmental role in support of a diazotrophic micro-organism(s) and derives a portion or all of its combined N from the activities of the diazotroph(s). In forests, symbiotic systems range all the way from simple associations between micro-organisms to nodulated legumes with highly developed symbioses which function efficiently and have high specific activities. Some symbiotic diazotrophic microorganisms have the capacity to fix N_2 in free-living situations, provided that the environmental and nutritional conditions are suitable. However, generally in the more highly developed symbioses, the diazotroph fixes little or no N_2 apart from its host, although it may have an extensive free-living existence as a saprophyte, or even as an autotroph in the case of some cyanobacteria (formerly known as blue-green algae). The study of the ecology of the free-living stage of symbiotic diazotrophic microorganisms must form an essential part of the study of forest systems.

Symbiotic systems are all adapted in various ways to the requirements governing the synthesis and functioning of nitrogenase. This enzyme, essentially the same in all N_2 fixing organisms, is a very complex one. It consists of two proteins. The enzyme (dinitrogenase) and its specific reductase, whose Mo, Fe and S contents (a total of 1-2 Mo, and up to 36 Fe and labile S atoms per functioning nitrogenase molecule) generate specific requirements for these elements (Fig. 1), in addition to requirements for non-N_2-fixing growth. In a simple saprophytic organism such as _Klebsiella pneumoniae_, synthesis of nitrogenase is specified and controlled by a cluster of 15 cistrons (_nif_) on the chromosomal DNA (Merrick _et al_. 1980); in other organisms, the details of _nif_ are not yet clear, but these genes are sometimes located on plasmid DNA (Higashi 1967). In all organisms, there are additional specific biochemical pathways of electron flow to nitrogenase, the components of which must also be synthesised coordinately with nitrogenase. In symbiotic diazotrophs additional genes concerned with infection and symbiotic development must be involved. To these must be added the genes of the host which are concerned with the recognition of the symbiont, infection, the development of the symbiosis, and often with the development of specific pathways for the assimilation of fixed N into utilizable forms (Scott et al. 1976; Streeter 1979). It is clear that the genetics will be found to be very complex. The functioning of nitrogenase is also very complex (Orme-Johnson et al. 1977). I do not propose to go into that here, except to highlight some major requirements which govern the conditions for N_2 fixation in nature.

1. Nitrogenase is rapidly and irreversibly destroyed by O_2 (e.g. Bergersen and Turner 1968). Furthermore, at least in some microorganisms, nitrogenase synthesis is negatively regulated by O_2 (S. Hill and C. Kennedy, pers. comm.; Ching et al. 1980; Yates 1977). It is therefore essential that microsites with very low concentrations of free O_2 be provided. Generally, truly anaerobic N_2 fixation is inefficient in energetic terms, and therefore efficient systems require O_2 at vanishingly low concentration, but with fluxes adequate to meet metabolic requirements. This problem seems to be best solved in the legume root nodule (Bergersen 1978).
2. Nitrogenase requires at least 6-15 ATP molecules for every N_2 molecule reduced to $2NH_2$ and 6 electrons must be supplied from substrate oxidation via the nitrogenase reductase. Therefore readily available energy must be in good supply (Fig. 1).
3. Synthesis of nitrogenase is negatively regulated by NH_3 (Yates 1977). Therefore the symbiotic microorganisms must be located in an environment from which the product of N_2 fixation is efficiently removed, and from which exogenous NH_3 is excluded. Further, the production of symbiotic N_2-fixing organs such as root nodules, is often specifically inhibited by combined nitrogen such as nitrate, in the soil.

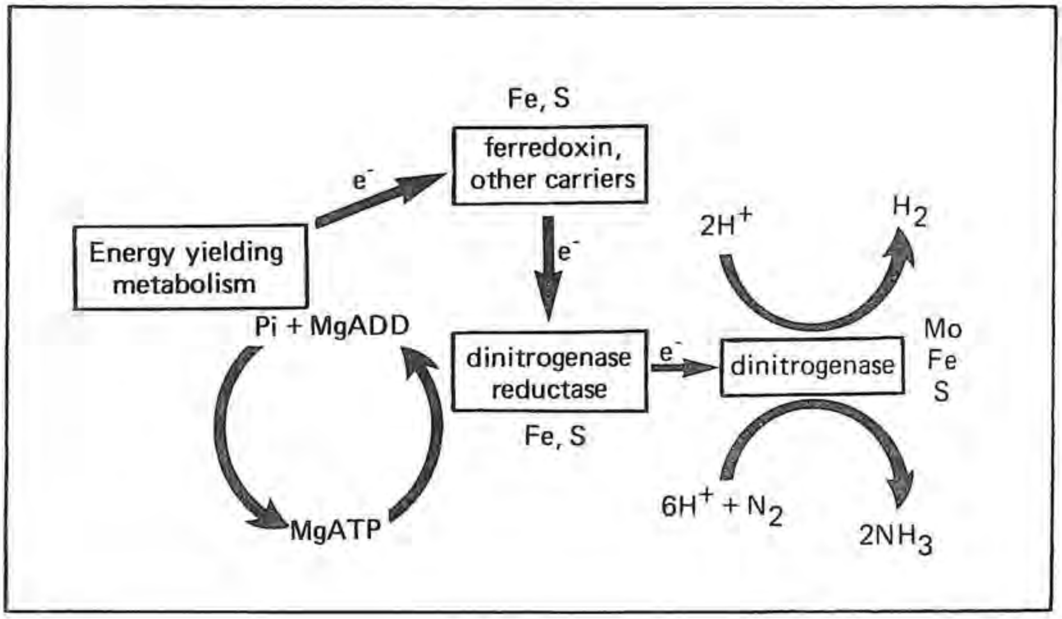

Fig. 1. The over-all reaction of nitrogenase.

FOREST ENVIRONMENTS AND N_2 FIXATION

Generally speaking, the mature forest environment would appear to favour biological nitrogen fixation, since it is generally of high C:N ratio, and in many climates, moderation of moisture and temperature compared with unshaded environments, would favour microbiological activity. However, most of the potential carbon energy sources are locked up in forms which are only available to the relatively rare cellulolytic and even rarer lignolytic organisms. No examples of N_2 fixing microorganisms are known among these. Consequently such carbon resources are available only to N_2 fixing components which form 'symbiotic' associations with other organisms which are able to degrade them. Therefore, in terms relevant to N_2-fixing microorganisms, the forest environment is characterized by low availability both of carbon energy sources and of combined nitrogen. Consequently most symbiotic systems of significant productivity involve photosynthesis as the source of energy for nitrogenase activity. There is also a great difference in the significance of symbiotic systems between establishment or regeneration phases and the near equilibrium conditions of mature forests. Some of these matters arise when considering the various known symbiotic systems in forests.

EXAMPLES OF FOREST N_2-FIXING SYMBIOSES

Associations with Decomposers

A number of studies have detected nitrogenase activity in decomposing litter and rotting logs (e.g. O'Connell *et al*. 1979; Ichioh Nioh 1980; Cornaby and Waide 1973; Roskoski 1980), and some of these systems appear to consist of specific associations which can be regarded in the broadest sense as being 'symbiotic' (Konokov *et al*. 1979). These Russian studies showed the involvement in pine and spruce litter of *Trichoderma* spp. and a *Penicillium* sp. with several facultative *Bacillus* sp. and *Arthrobacter globiformis* (probably *Corynebacterium autotrophicum*; Dalton 1980) as diazotrophic microorganisms.

Many species of termites fix N_2 (Breznak *et al*. 1973) due to the presence in the hind gut of populations of *Citrobacter freundii* (French *et al*. 1976). These bacteria appear to utilize carbon compounds made available by anaerobic cellulolytic organisms in the gut.

Symbioses with Cyanobacteria

Lichens. Many lichens contain N_2-fixing cyanobacteria as the photosynthetic component: some additionally contain green algae (Millbank 1977). Lichens are widespread in nature and some occur extensively in woodlands and forests on limbs and tree trunks and on exposed rocks. Nitrogenase activity of significant proportions was detected within a few hours when a piece of desiccated thallus of a *Sticta* sp. (collected from a *Eucalyptus meliodora* woodland near Canberra) was moistened (author's observations). Table 1 lists genera in which N_2 fixation has been detected. The present author is not aware of any Australian study of the role of such lichens in forests, but personal observations suggest that lichens may sometimes be important.

Table 1. Genera of N_2-fixing lichens (from Millbank, 1977)

Lichen	N_2-fixing components	No. of species tested
Collema	*Nostoc*	9
Dendriscocaulon	*Scytonema*	1
Ephebe	*Stigonema*	1
Leptogium	*Nostoc*	4
Lichina	*Calothrix*	2
Loabaria	*Nostoc*	2
Massalongia	*Scytonema*	1
Nephroma	*Nostoc*	2
Pannaria	*Nostoc*	2
Parmeliella	*Nostoc*	2
Peltigera	*Nostoc*	7
Placopsis	?	1
Placynthium	*Dicothrix*	2
Polychidium	*Scytonema*	1
Pseudocyphellaria	*Nostoc*	1
Solorina	*Nostoc*	3
Stereocaulon	*Nostoc*	2
Sticta	*Nostoc*	2

Bryophytes. There are N_2-fixing species of liverworts (usually with a species of Nostoc as the endophyte; Millbank 1977), some of which show impressive rates of activity. They seem to be significant in local situations in cool forests of the northern hemisphere. Diana Duncan (unpublished Honours Thesis, University of Tasmania) has measured the development of a primary vegetation sequence of 'fire mosses' and other mosses following clearfelling and burning prior to the re-establishment of forests in Tasmania (Fig. 2). Heather Brasel (CSIRO Division of Forest Research, Hobart) has followed up this observation with measurements of nitrogenase activity using acetylene reduction methods and $\delta^{15}N$ measurements have been made in our laboratory (analysis by G. Turner). The results indicate that some of these mosses may be fixing all of the nitrogen needed for their growth at certain stages. The N_2-fixing components of the symbioses have not been identified but in Britain a species of the cyanobacterium Hapalosiphon has been found as an occasional endophyte of Sphagnum (Millbank 1977).

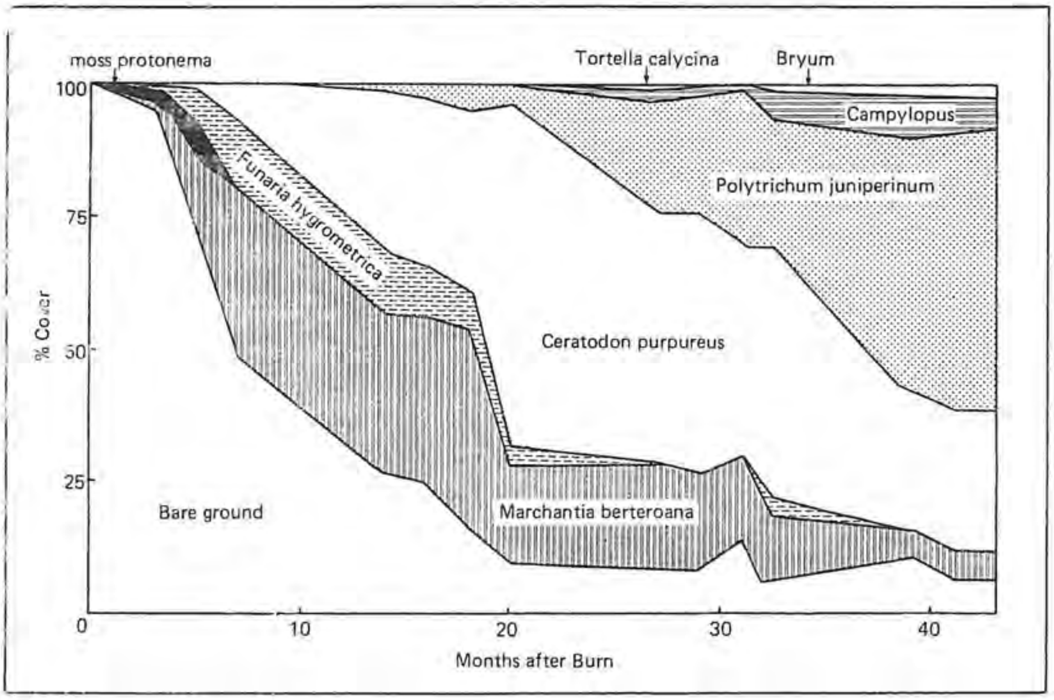

Fig. 2. Changes in percentage cover of bryophytes with time in quadrants on newly clearfelled and burned land. Redrawn from an Honours Thesis by Diana Duncan, Uni. of Tasmania.

Cycads. Cycads are prominent in some tropical and sub-tropical forests. Many species bear coralloid roots which branch out from beneath the swollen stem bases beneath the soil and in which a zone of intercellular spaces contains masses of cyanobacteria (Nostoc or Anabaena spp.) whose activity produces N for growth of the host (Bergersen et al. 1954). In Australia, N_2 fixation has been studied in Macrozamia communis in a Eucalyptus maculata forest on the S.E. coastal escarpment of New South Wales (Bergersen et al. 1965) and in Macrozamia riedlei in a Eucalyptus-Banksia woodland in coastal Western Australia (Halliday and Pate 1976). Rates of activity recorded indicated that this system could be an important source of nitrogen, although its activity is greatly affected by high temperatures and drought (Halliday and Pate 1976).

Gunnera. Species of the Gunneraceae, formerly a genus of the Haloragaceae, bear glands or domatia, in the bases of the leaves. Within the domatia are numerous intracellular cyanobacteria identified as Nostoc punctiforme. They are enriched with heterocysts. Nitrogen fixed by these symbionts is distributed throughout the plant and is sufficient to support growth in N-free conditions (Silvester and Smith 1969). Ten species of Gunnera occur endemically in New Zealand where they form a significant component of sub-tropical rain forest understorey. These species are small herbaceous plants. In contrast, very large species occur in tropical rain forests in Asia and South America. One of these, G. macrophylla, has been studied in montane forests in Java (Becking 1974). In both situations where Gunnera species have been studied, they make significant contributions of N (12-21 kg N ha^{-1} yr^{-1} in Java, (Becking 1974); up to 72 kg N ha^{-1} yr^{-1} in New Zealand (Silvester and Smith 1969)). One species, G. cordifolia, occurs in Tasmania, but N_2 fixation has not been studied. In view of the occurrence of G. macrophylla in New Guinea it is surprising that this or a related species has not been recorded in rainforests of north Queensland.

Nodulated Legumes

Symbiotic N_2-fixation reached a culmination in efficiency and often magnitude, in the legume root nodule, whose physiology and biochemistry have been extensively studied. One view of the cellular structure of nodules and of the process with its supporting metabolism is given in Figs. 3a and b, which represent the activities within one of the bacteroid-containing envelopes of which there are several thousand in each cell of the central tissue of each nodule. The process of infection and nodule development has been described by Dart (1974).

Although legumes are prominent components of most Australian forest systems, especially during regeneration following fire, there is surprisingly little published information about their role as symbiotic N_2 fixing plants. Bowen (1956) listed 135 species in 48 genera of native legumes, whose nodulation has been recorded. Many were species which are characteristic of heath and scrub lands, but some are also prominent in forest successions. Lange (1959) added 137 species in 24 genera, from Western Australia, to the list of nodulated native legumes. In an

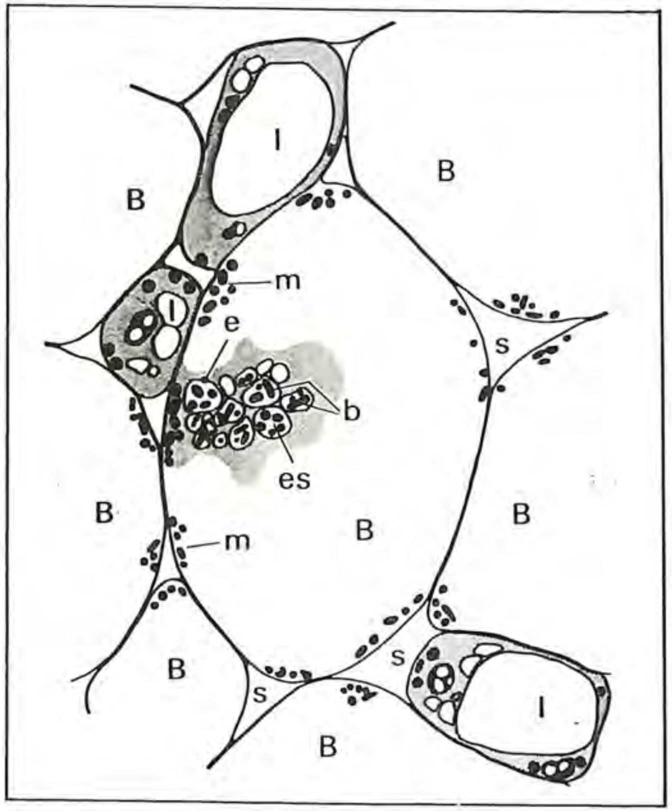

Fig. 3. (a) The essential features of N_2-fixing tissue of legume root nodules. B, bacteroid containing host cells; I, uninfected interstitial cells; b, bacteroids; e, membrane envelopes; es, envelope space; s, intercellular space, gas filled; m, mitchondria.

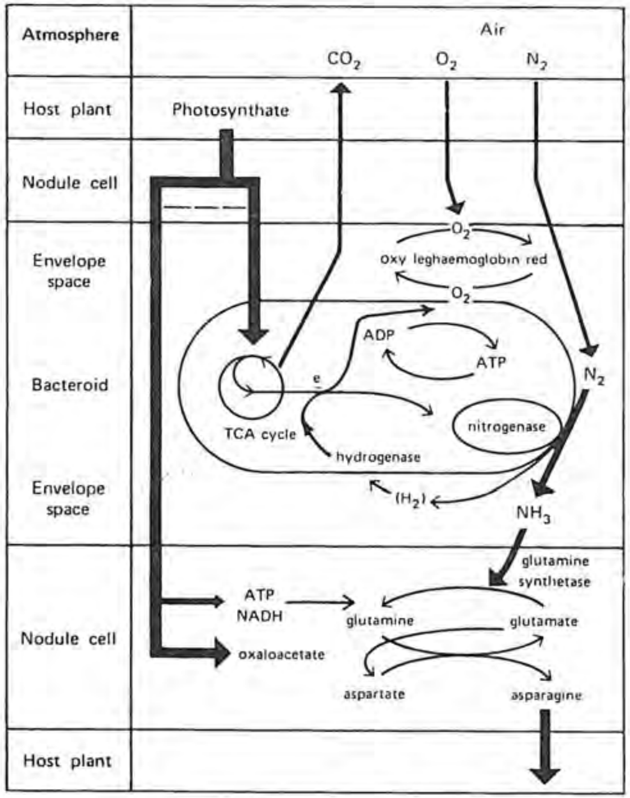

Fig. 3. (b) The main metabolic pathways supporting N_2-fixation in legume root nodules. The assimilatory pathway for NH_3 is that for a typical amide plant. In others the major assimilate may be different.

unpublished report to a SCOPE workshop in December 1977, Dr. Ann Lawrie reported acetylene reduction studies of nodulated legumes in various sites around Port Phillip Bay near Melbourne (see also the paper by Lawrie, these proceedings). One was a dry sclerophyll woodland (Lysterfield) whose understorey had been burned four years prior to the beginning of the study. Three species, Acacia armata, A. meansii and A. melanoxylon were found to have averages of 148, 67 and 45 mg (f.wt.)/plant of nodules respectively, were collected with maximum activities of 2-12 nmol C_2H_4 $h^{-1}mg^{-1}$ f.w. in November-December, and lowest values (0-1 nmol h^{-1} mg^{-1}) in February-March. Dr. Lawrie emphasized the need for accurate estimates of nodule density, of plant distribution and of seasonal variation in nitrogenase activity before such studies could begin to yield really useful data. The present author is aware of current research on N_2 fixation by Acacia spp. but few data appear to have been published as yet (Shea and Kitt 1976; Langkamp et al. 1979; see also paper by Langkamp and Dalling, these proceedings).

In a quite different sense, the effects of sowing herbaceous legumes to provide fixed nitrogen during the establishment and early growth phases of Pinus spp. have been studied in eastern and Western Australia. This is the subject of another paper in this workshop.

There are many leguminous forest trees which are commercially valuable in some countries. The present author is not aware of any systematic study of N_2 fixation by such species. However, there is an increasing interest in the exploitation of leguminous trees. For example, a recent study (Anon. 1977) has advocated multi-purpose utilization of Leucaena leucocephala. Some new varieties have been developed which emphasize its value in reforestation projects with uses ranging from a role in slash and burn farming to wood for fuel and pulp uses. Annual wood growth rates as high as 100 m^3 ha^{-1} yr^{-1} have been recorded for some newer Salvador types. It is stated in this report that nodulated L. leucocephala is capable of fixing as much as 500 kg N ha^{-1} yr^{-1}

(Anon. 1977). The species was shown to have symbiotic specificity, being nodulated only by fast-growing strains of Rhizobium isolated from Acacia farnesiana, Mimosa invisa, MI. pudica and Sesbania grandiflora but not by slow-growing strains isolated from other members of the "cowpea miscellany" (Trinick 1968). In another report (Anon. 1979), the following species are listed as being potentially commercially exploitable, with fast growth rates: Acacia auriculiformis, A. mangium, Acrocarpus fraxinifolius, Albizia falcataria, A. lebbek, A. acle, A. chinensis, A. minahassae, A. pedicellata, A. procera, A. adianthifolia, A. ferruginea, A. gummifera and A. zygia, Calliandra callothyrsus, Dalbergia sissoo, Enterolobium cyclocarpum, Mimosa scabrella, Samanea saman, Schizobolium parahyba and S. amazonicum, Sesbania grandiflora and Tipuana tipu. However, the report also points out that nodulation or N_2-fixation has not been investigated for many of these species, although their fast growth and N-rich foliage suggests that they do fix N_2.

Three other genera are listed as slower growing luxury timbers of high value, one of them Intsia bijuga, occurring in northern Australia.

Nodulated Non-leguminous Angiosperms

There are several known and important nodulated non-leguminous plants of significance for forest systems in Australia. The main group is that which bears 'Alnus' type nodules on the roots. There are at present 168 known nodulated species scattered among 16 genera (Table 2) in several families.

The nodules are transformed lateral roots with the endophyte, an actinomycete of the genus Frankia, located in parenchyma cells of the inner cortex. The endophytes from a few species have recently been cultured as very slow-growing organisms in broth media, where nitrogenase activity has been detected (Torrey, pers. comm.).

Probably the best known representatives of this group in Australia are found in the genus Casuarina, species of which have been exploited for fuel and timber in the past (see also the paper by

Galbraith, these proceedings). Some species are possibly important in regeneration of forests in former rain forest areas of N. Queensland. Nodulation has been recorded in Australia for C. cunninghamiana, C. cristata, C. glauca, C. torulosa, C. littoralis and C. decussata, but nodules were not found on C. inophoia and C. luehmannii, but this may have been due to the nodules being lower on the root systems than could be excavated (results of various Australian observers, recorded in Bond 1976). other genera listed in Table 2 occur in Australian woodlands and forest, but there is no record of nodulation. Hannon (quoted in Bond 1976) did not find nodules on Discaria pubescens in the Canberra and Armidale, N.S.W., districts.

Table 2. Genera of plants bearing *Alnus*-type root nodules (from Bond & Wheeler, 1980, with additions from recent literature).

Genus	No. of known nodulated species	Total No. species*
Coriaria	13	15
Alnus	35	35
Myrica	35	35
Casuarina	24	45
Hippophaë	1	3
Eleagnus	17	45
Shepherdia	1	3
Ceanothus	31	55
Discaria	5	10
Colletia	3	17
Dryas	3	4
Purshia	2	2
Cercocarpus	4	20
Rubus	1	250
Datisca	2	2
Cowania	1	5

* According to Willis' Dictionary of Flowering Plants and Ferns. Ed. H. Airy Shaw, Cambridge Press, 1966.

Nodulated Alnus spp. are common components of woodlands in North America and Europe and are dominant trees in some locations in Alaska. A. rubra is involved in interplantings in managed forests of Douglas fir and Hemlock in Washington and Oregon. These examples are given merely to indicate the important role which nodulated plants of this type can play in forest systems.

In this section mention must be made of nodules initially discovered by Trinick on Parasponia rugosa (originally described as Trema aspera by Trinick 1973). The anatomy of these nodules (Trinick 1979) resembles the Alnus type, but the diazotrophic endophyte is clearly a Rhizobium of the 'cowpea' type. Parasponia spp. are endemic in Indonesia and New Guinea but closely related members of the Ulmaceae occur in coastal forests in eastern Australia. None have been examined for nodulation.

EVAULATION OF SYMBIOTIC N_2-FIXATION IN FORESTS

Knowles (1980) has recently reviewed methods for estimating N_2 fixation in natural plant communities. Methods employing acetylene reduction and ^{15}N techniques are described but he emphasizes the difficulties which arise from the heterogeneous nature of most forest communities, the choice of appropriate non-fixing reference plants and the sheer size of trees. The only solution immediately available would seem to be to isolate individual N_2 fixing components, such as root nodules, and estimate the rates of activity, preferably at intervals over several seasons. An estimate of the amount of tissue present per unit area would then allow an estimate of the total N_2 fixation achieved by that component. This approach was used by Halliday and Pate (1976) for coralloid roots of Macrozamia riedlei which was estimated to fix 18-19 kg N ha^{-1} yr^{-1}, based on plant numbers weight of coralloid roots per plant and acetylene reducing activity per plant over a 13 month period.

The following is an estimate of the magnitude of the N-contribution of termites. Estimates of termite populations in forests and woodlands range from 1000-10,000 m^{-2} in Africa to 600-1000 m^{-2} for Nasutotermes exitosus in a S. Australian woodland (Lee and Wood 1971). Their size ranges from 100 mg/animal for N. exitosus to 50 mg or more in a large species such as Macrotermes darwiniensis. Nitrogenase activities measured in our laboratories (G.L. Turner, pers. comm.) range up to peak values of 50 nmole C_2H_4 h^{-1} g^{-1} f.w. for Coptotermes acinaciformis. Such rates were sustained for about a month. At other times activities were only about 1/5 of this value. Considering a population of 1000 m^{-2}, each weighing 10 mg, and assuming a realistic $C_2H_2:N_2$ ratio of 4, for one month at peak activity, N_2 fixed by these termites could be estimated at

$$28 \times \frac{50 \times 10^{-9}}{4} \times (0.01 \times 1000 \times 104) \times 24 \times 30) = 25.2 \text{ g N ha}^{-1}$$

Thus, although this N_2-fixation may be of great importance to the role of termites in litter decomposition, it is unlikely that it is of great significance to the over-all N-economy of a forest.

The limitations of the C_2H_2-reduction assay for nitrogenase are well-known (e.g. Turner and Gibson 1980). However, when used carefully, with internal standards and properly calibrated against an $^{15}N_2$ assay, it is probably the only practicable method for use in natural systems. It is difficult to conduct ^{15}N experiments in forests (Knowles 1980) but a calibration of the C_2H_2 reduction assay is essential. Perhaps a calibration for a standard set of conditions using a typical sample of a N_2-fixing component such as nodulated roots or pieces of lichen thallus, could be widely applied to similar material. It could certainly be preferable to using an untested $C_2H_2:N_2$ ratio.

It is certainly preferable to make estimates using the approach outlined above, than to continue to tolerate the almost complete lack of N_2 fixation data in forest and indeed also in agricultural systems. At least such an approach will permit a realistic relative assessment so that the most important systems can be selected for further study.

Nitrogen fixation in an ecosystem is nearly always the sum of activities of a range of organisms. The few data so far available tend to concentrate on the contributions of individual components. In my view the time has come to construct accurate inventories of N_2-fixing components by means of simple C_2H_2-reduction assays, perhaps supported with $\delta^{15}N$ measurements. The next stage would be to obtain accurate estimates of the abundance of these components. Finally, more accurate determinations of the activity of the more important components will allow a more realistic estimation of the part played by symbiotic N_2-fixation in a forest.

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MANAGING THE NITROGEN ECONOMIES OF REHABILITATED SITES ON GROOTE EYLANDT

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Most mining operations on Groote Eylandt take place in a Eucalyptus tetrodonta open-forest (Langkamp and Dalling 1979). The natural regeneration[1] program following surface mining has the objective of encouraging plant community development back towards this pre-mining state. This objective is partly realized by sowing plants onto the restored areas[1] that are endemic to the mine lease.

In the short term the availability of nitrogen is of major importance in determining the growth and establishment of these sown plants. However in the longer term nitrogen availability can have a profound influence on the progression of the restored areas towards their pre-mining condition.

The reestablishment of a N-nutrient bank on restored areas has been investigated on Groote Eylandt over the past two years. We have previously reported (Langkamp et al 1979)[2] some aspects of the N_2 -fixation capacity of Acacia holosericea, one of the most vigorous colonizers of the restored areas. It was concluded that N - accretion over a wet season would be low (12 ± 4 kg ha^{-1}) even with planting densities of 1111 trees ha^{-1}. This estimate was calculated using a ratio for acetylene reduced to nitrogen of 3.9 (Hardy et al 1973) and an estimated 4.9×10^2 nmol acetylene reduced mg $f.wt^{-1}$ of nodule for a measured 24 hour period with a season length of 182 days. We have now measured the acetylene

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1 Terminology follows that of Langkamp, 1979.

2 In that paper the plant was incorrectly named as A. pellita O. Schwarz : see Corrigendum Aust. J. Bot. 1980, 28: 269.

reduction rates of rooted nodules over one complete season (Fig. 1). A distinct seasonal trend is obvious, with peaks in activity coinciding with each wet season in January 1979 and February/March 1980.

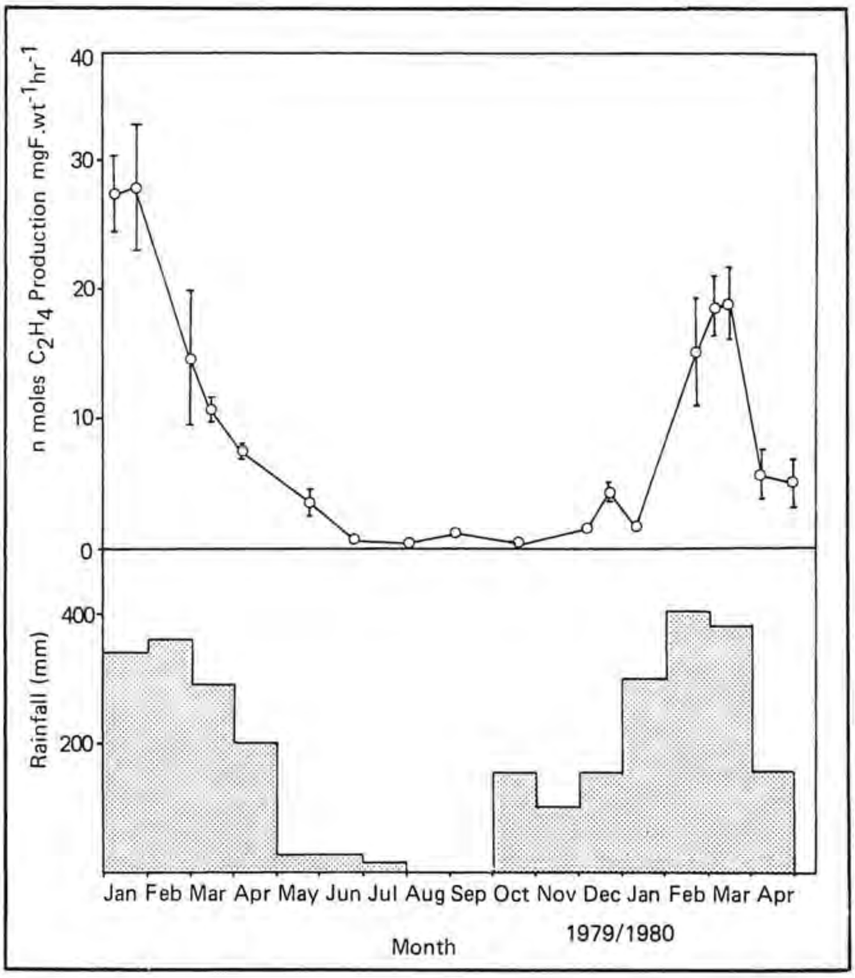

Fig. 1. Mean monthly rainfall at Angurugu, Groote Eylandt and acetylene reduction rate for *Acacia holosericea* over the 1978/79-1979/80 wet season.

Because of the decline in nodule specific activity and an observed decline in nodule abundance during the dry season it would seem that our suggested accretion of 12 kg N ha^{-1} yr^{-1} is too high.

Acetylene reduction measurements made on root nodules of other legume species from various sites on Groote Eylandt are shown in Table 1.

Table 1. Acetylene reduction rates by various legume species on Groote Eylandt.

Plant Species		Site	C_2H_2 Reduction Rate (nmole C_2H_4 gm D. $wt^{-1}hr^{-1}$)
CYPERACEAE			
Fimbristylis dichotoma	(L.) Vahl.	FWS	70(30)
Fimbristylis bisumbellata	(Forsk.) Bubani *vel. aff.*	FWS	1.2(1.0)
POACEAE			
Alloteropsis semialata	(R.Br.) Hitchc.	OTF	n.d.
Aristida capillifolia	Henr.	OTF	n.d.
Brachiaria pubigera	(Roemer & Schultes) S.T. Blake	OTF	0.7(0.1)
Chloris gayana	Kunth.	RA	1.4(0.4)
Heterpogon triticeus	(B.Br.) Stapf	OTF	n.d.
Imperata cylindrica	(L.) Beauv.	FWS	151(69)
Paspalus vaginatum	Swartz, now *P. distichum* L.	FWS	23(15)
Pletrachne pungens	(R.Br.) Hubbard	OTF	0.3(0.1)
Rhynchelytrum repens	(Willd.) C.E. Hubbard	RA	n.d.

Measurements were made in May 1979 (mid dry-season PAR 1650 µmoles $m^{-2}sec^{-1}$, Air temperature, 31°C; Soil temperature, 36°C) and February 1980 (mid wet-season. PAR 2100 moles m^{-2} sec^{-1}; Air temperature, 34°C; Soil temperature, 34°C). Sampling sites were a *Eucalyptus tetrodonta* open-forest on Laterite (OTF), a reclaimed area covered with topsoil from the *E. tetrodonta* open-forest (RA), a *Melaleuca leucadendron* fresh-water swamp and marsh complex (RWS) and a *E. tetrodonta/Callitris* intratropica open-forest on Sandstone (SS). Nodule characteristics follow that described by Lim and Ng (1977). Standard errors are in brackets (n=3). n.d. not detected.

*Lack of nodules allowed for a single determination only.

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As with Acacia holosericea a distinct seasonal trend in C_2H_2 reduction is suggested, with greater activity recorded in the wet season, but in addition there is a trend for members of the Mimosaceae to show greater activity than those of the Caesalpinaceae and Fabaceae. Nodules on the Mimosaceae were larger and occurred abundantly on the roots in the wet season. By contrast nodules on the Caesalpinaceae and Fabaceae were generally smaller, more difficult to find, and often light brown in colour with a smooth surface. Nodules on Abrus precatorius appeared different in that they showed white fluffy streaks on the surface, similar to those observed on Calopogonuim mucinoides by Lim and Ng (1977). In general, nodules were more difficult to find in the dry season and these were often dried shells or small and inactive.

Associations between nitrogen-fixing microorganisms and the roots of grasses has previously been found with some temperate grasses but higher activities have usually been found with tropical grasses. Since a flush of grass growth occurs with a beginning of the wet season on Groote Eylandt, it is not unreasonable to assume that some of these microorganism:root associations may be active in both the undisturbed eucalypt open forest and areas disturbed by mining activities.

To establish the importance of these non legume associations in the eucalypt open forest, a survey of the N_2 fixing ability of several grasses and sedges found in the mine lease areas (Langkamp et al 1980) was carried out in February 1980. The results of this survey are shown in Table 2, where the acetylene reduction activity was measured using the excised root assay of Dobereiner and Day (1976).

Seven out of the 11 species listed show a positive C_2H_2 reduction ability, but the values obtained for each species were variable. The results indicate that C_2H_2 reducing organisms are present and strongly associated with viable roots. More than likely their C_2H_2 reduction ability is severely limited by energy. Of the species studied, high rates of non-legume C_2H_2 reduction were

Table 2. Acetylene reduction rates (8-16 hour assay) by various non-leguminous species on Groote Eylandt in February, 1980 (mid-season).

Plant Species	Site Size (n=10)	Nodule Characteristics (February 1980) Morphology	Mean Diam	C_2H_2 Reduction Rate nmole C_2H_4mg F.wt.$^{-1}$hr^{-1} Dry Season	Wet Season
CAESALPINACEAE					
Cassia mimosoides L.	OTF	Elongate/lobed. Dark brown. Smooth surface.	5mmx1mm	0.7(0.4)	8.5(0.1)
FABACEAE					
Abrus precatorius L.	OTF	Globose. Pale brown white streaks on surface.	2mm	0.8(0.1)	-
Brachysema uniflora R.Br.	OTF	Elongate/lobed Light brown. Rough surface	8mmx1mm	-	12.0*
Glycine tomentella Hayata	OTF	Globose. Light brown. Smooth surface.	1mm	-	9.1(4.1)
Jacksonia dilatata Benth.	SS	Elongate/lobed. Light brown. Rough surface.	6mmx1mm	-	18.7*
Vigna lanceolata Benth.	OTF	Globose. Light brown Smooth surface.	1mm	n.d.	7.6*
MOMOSACEAE					
Acacia aulacocarpa A. Cunn.	OTF	Clobose/irregular. Light brown. Rough surface.	2mm	0.8*	18.2(1.2)
Acacia holosericea A. Cunn. ex G. Don	RA	Elongate/lobed. Pink, Dark brown. Rough surface.	6mmx2mm	3.7(1.0)	18.5(2.1)
Acacia humifusa A. Cunn. ex Benth	SS	Globose/elongate. Dark brown. Rough surface.	8mmx3mm		22.4*
Acacia simsii A Cunn. ex Benth	RA	Fan/coralloid. Pink brown. Rough surface.	9mmx3mm	-	20.9(5.3)
Acacia torulosa Benth	OTF	Globose. Dark brown rough surface.	3mm	-	22.1(0.6)
Acacia yirkallensis Specht	OTF	Elongate. Dark brown rough surface.	6mmx2mm	0.6(0.1)	-

Conditions at the time of sampling were: PAR 2100 μmoles m^{-2}sec^{-1}, Air temperatures 35°C, Soil temperature 39°C. Standard errors are in brackets (n=3). n.d.: not detected. Sampling sites were the same as those in Table 1. Reproduced with permission Aust. J. Botany.

associated only with plants found in a Melaleuca leucadendron open forest swamp complex : the sedge, Fimbristylis dichotoma; and the grasses Imperata cylindrica and Paspalum vaginatum. No species tested in the eucalypt open forest or rehabilitated area exhibited appreciable activity.

We have discussed the uncertainty of using these data (Langkamp et al 1980) in regard to calculating the contribution of these plant: microorganism associations to the overall N Budget of the study area. With that qualification we conclude that nitrogen accretion in the Eucalyptus tetradonta open forest will be low, and based on our results, would be limited by the low N_2 fixation (C_2H_2 reduction) activity of the non legumes and the low frequency of occurrence of the legumes. On an individual plant basis the potential for N_2 fixation by legumes does not appear to be limited by nodule specific activity as the rates of C_2H_2 reduction were comparable with those listed for a wider range of legumes (Hardy et al 1973). If similar speculation is made in regard to comparing C_2H_2 reduction with N_2 fixation as was done for Acacia holosericea (Langkamp et al 1979), then a total annual increment from both legumes and non legumes of 0.05 to 1 kg N ha^{-1} may be possible. These values are low in comparison with measurements we have made on N biomass of the grasses associated with the Eucalyptus tetrodonta open forest. For example on a site that had been burnt in the previous dry season, the mid wet season above ground biomass of all grasses was 1030 ± 490 kg ha^{-1} and contained approximately 25 kg N ha^{-1}. This value is of the same order of magnitude as the annual amount of inorganic N (68 kg ha^{-1}) we have estimated to be made available over a wet season.

The implications of these studies for the successful management of the rehabilitated areas on Groote Eylandt are several. Firstly, the importance of topsoil conservation is emphasized, since the mineralization of soil organic N appears to play an important role in the seasonal growth of understorey species. Secondly N accretion through non legume N_2 fixation is likely to be minimal on the rehabilitated areas, especially if the sites are dry. Thirdly, N accretion by legumes is likely to be limited by the choice of species used, their density over the restored area and such factors as nodule load and health.

The questions being considered at this workshop are basic to nearly all natural regeneration programs. The implications of nitrogen fertilizer application on the regeneration of restored areas is a particularly important aspect which has been little investigated and deserves more consideration at many minesites round Australia.

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NITROGEN FIXATION AND NODULATION IN NATIVE AUSTRALIAN LEGUMES*

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The acetylene reduction technique was used to study nitrogenase activity in root nodules of three Acacia spp. in peppermint woodland at Lysterfield, near Melbourne, Victoria. A. mearnsii De Wild., A. melanoxylon R. Br. and A. peradoxa DC. Seasonal studies of activity showed that a maximum was reached in spring; diurnal fluctuations in activity reached a maximum soon after midday. Nodule abundance varied widely, due to wide variations in both plant abundance and nodulation per plant. Estimates of nitrogen fixation for each species were derived from seasonal and diurnal studies on acetylene reduction and nodule abundance data by using the theoretical ratio of 3 acetylene: 1 nitrogen reduced: for A. mearnsii-0.746 kg N_2 fixed $ha^{-1}yr^{-1}$, for A. melanoxylon-0.005 kg N_2 fixed $ha^{-1}yr^{-1}$ and for A. paradoxa-0.043 kg N_2 fixed $ha^{-1}yr^{-1}$. The main reason that these estimates were lower than similar estimates for agricultural systems may be the low densities of plants and nodules and nitrogen fixation would be higher than this in denser stands. However, real differences occurred among species: nodulation of both A. mearnsii and A. paradoxa was much more abundant per plant than nodulation of A. melanoxylon, and the nitrogenase activity in nodules of A. mearnsii was much higher than in nodules of the other two species.

Investigations on the inter-relationships among the rhizobia and their hosts were conducted, using serological and cross-inoculation techniques. Serological techniques showed that there was a large number of rhizobial strains at the site, but that strains from this site were related more closely serologically to strains from the same site than to strains from different sites. From cross-inoculation tests, considerable

* For further details of field work see A.C. Lawrie (1981), Aust. J. Bot. 29: 143-157.

differences in effectiveness of the symbioses formed were seen, although all isolates nodulated all three species. All isolates appeared to belong to the cowpea group, with a characteristically wide host range. As combinations of rhizobia and their hosts found in the wild were seldom optimal in cross-inoculation tests, considerable scope exists for increasing nitrogen fixation by inoculation with more effective rhizobia.

Current microscopical studies are aimed at elucidating the processes of infection and nodulation in these legumes.

EFFECTS OF ENVIRONMENTAL FACTORS AND ASSAY PROCEDURES ON RATES OF ACETYLENE REDUCTION IN EUCALYPT LITTER

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ABSTRACT

The initial phase of a study of non-symbiotic nitrogen fixation in the litter layer of jarrah (Eucalyptus marginata Donn ex Sm.) and karri (E. diversicolor F. Muell.) forests involved measurements of the effects of moisture content, temperature, gas composition, length of assay, sample storage, and type of litter on rates of acetylene reduction. The results of these tests are summarized and their implications in relation to procedures adopted for field measurements are discussed. In leaf litter, rates of acetylene reduction increased with increasing moisture content throughout the range 30% to 200% of oven dry weight, and were maximal from 22.5°C to 27.5°C. Thus, in the Mediterranean climate of south-western Australia, conditions are sub-optimal for nitrogen fixation at all times of the year.

INTRODUCTION

Estimates of rates of acetylene (C_2H_2) reduction in the litter layers of jarrah (Eucalyptus marginata Donn ex Sm.) and karri (E. diversicolor F. Muell.) forests indicated that non-symbiotic nitrogen fixation may be a significant nitrogen input to these ecosystems (O'Connell et al 1979). The study has been extended to measure seasonal variation in nitrogenase activity at sites in both jarrah and karri forests. Preliminary experiments were conducted to determine the effects of litter moisture, temperature, gas composition, assay time, and of different litter components on rates of acetylene reduction. In this paper we summarize the results of these experiments.

EXPERIMENTAL

Moist litter, collected during winter, was prepared by cutting decomposing leaves into fragments (< 1 cm^2) and mixing to produce a bulk sample of homogeneous material for analysis. Acetylene reduction assays used 7 g (wet weight) of this material in 50 ml glass tubes closed with Suba-Seals. Ethylene (C_2H_4) concentrations in three replicate tubes of each treatment were determined using a Varian Aerograph 2700 2-channel gas chromatograph with flame ionization detector. Peak heights were corrected according to ethylene levels in reagent blanks or to ethylene levels measured immediately after introduction of acetylene into the sample tubes. Measured rates of acetylene reduction are not directly comparable between experiments since there was some variation in degree of leaf decomposition, sample storage procedures, moisture content, and assay conditions.

Acetylene concentration

Karri leaf litter (270% moisture based on O.D.wt.) was incubated in 50 ml glass tubes from which 15 ml air (STP) was removed and replaced by combinations of acetylene and argon to give a range of pC_2H_2 (0-0.30 atm) at constant pO_2(c.0.14 atm). Eight levels of acetylene were tested at 20°C and four levels at 16°C. Ethylene and acetylene concentrations were determined for each sample at five times over a period of 55 hours.

At both temperatures and at each sampling time ethylene production was negligible in the absence of acetylene and increased rapidly with increasing acetylene concentrations until saturation was reached at c.0.10 atm pC_2H_2 (Fig. 1). This level is commonly used in acetylene reduction assays and was chosen for other experiments in this series.

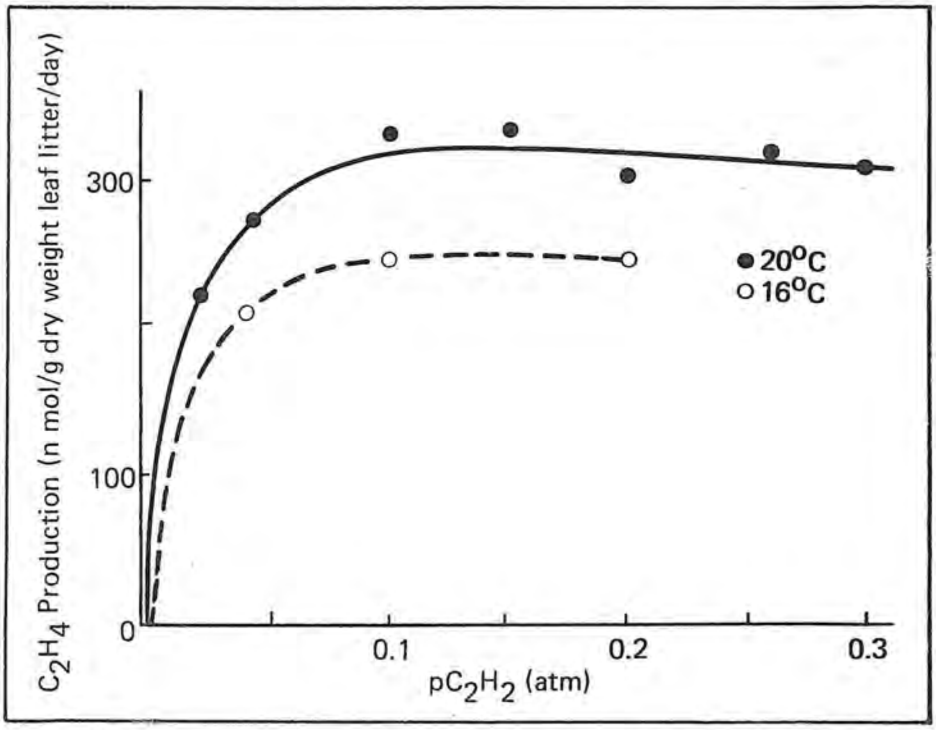

Fig. 1. Effect of pC_2H_2 on ethylene production by karri leaf litter incubated at 16°C and 20°C. Each value plotted is the mean of three replicates and the vertical bar represents the confidence interval ($P<0.05$) of the difference between any two means.

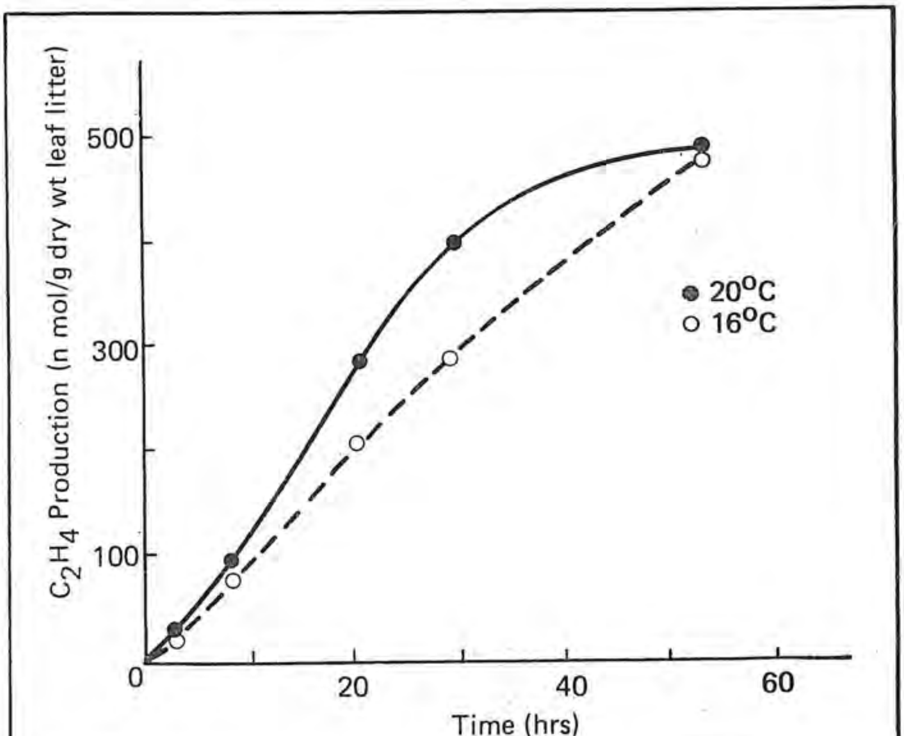

Fig. 2. Time course of acetylene reduction (0.1 atm pC_2H_2) by karri leaf litter incubated at 16°C and 20°C. Each value plotted is the mean of three replicates and the vertical bar represents the confidence interval ($P<0.05$) of the difference between means at 20 hours.

Time course of acetylene reduction

Repeated measurements of ethylene production over a time span of 55 hours in the previous experiment provided information on the effect of assay time on acetylene reducing activity. At 20°C and 0.1 atm pC_2H_2, the rate of ethylene production appears to increase gradually during the first 20 hours of incubation after which the rate begins to diminish (Fig. 2). These trends may partly result from changes in pO_2, since oxygen levels are known to markedly affect acetylene reducing activity. At the lower temperature (16°C), where acetylene reduction and presumably litter respiration are lower, the change in the rate of ethylene production with time was less apparent and the fitted curve is closer to linearity throughout the incubation period. The results indicate that the time course of acetylene reduction may vary according to assay conditions. This may influence the magnitude of treatment differences for the factors examined in this paper but it is unlikely to alter the general shape of the response functions.

Moisture content

Samples of jarrah and karri leaf litter having a range of moisture contents (10%-210%) were prepared by air drying field moist litter for varying periods of time at room temperature. Rates of acetylene reduction measured after incubation at 20°C for 17 hours were negligible below c.40% moisture and then increased throughout the range, being maximal at the level of field moisture (Fig. 3). Greatest changes in the rate of ethylene production occured in moisture range 50-100% of dry weight.

Temperature

Leaf litter (c.200% moisture) was incubated at ten temperatures ranging from 4°C to 43°C for 15 hours before measurement of ethylene production. For both jarrah and karri leaf litter maximum rates of acetylene reduction occurred at temperatures between 22.5°C and 27.5°C. Rates were zero or negligible below 10°C and above 34°C (Fig. 4).

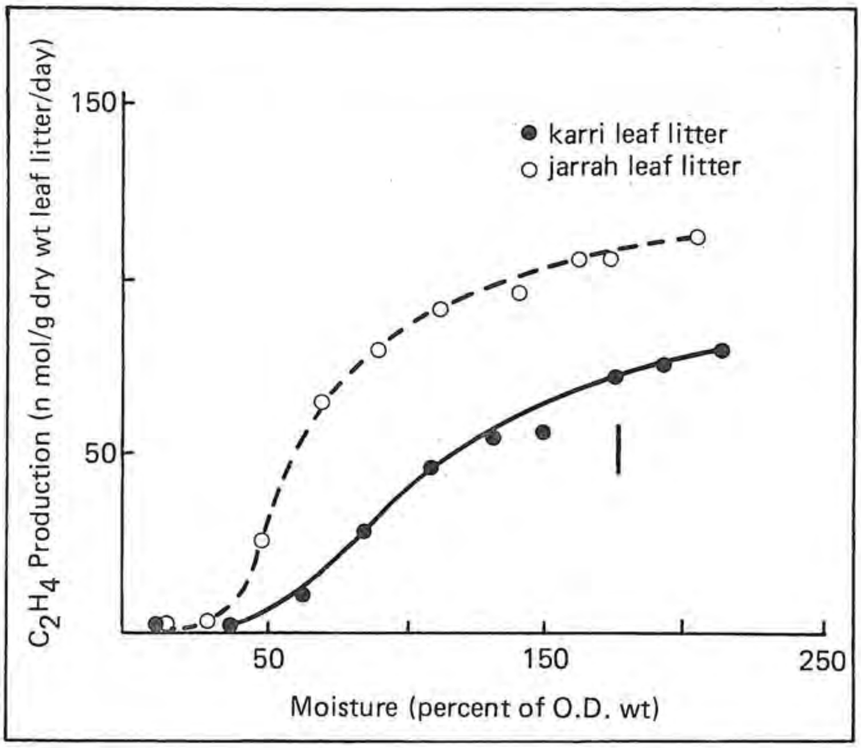

Fig. 3. Effect of moisture content of litter on acetylene reducing activity of jarrah and karri leaf litter. Each value plotted is the mean of three replicates and the vertical bars represent the confidence intervals ($P<0.05$) of the difference between any two means.

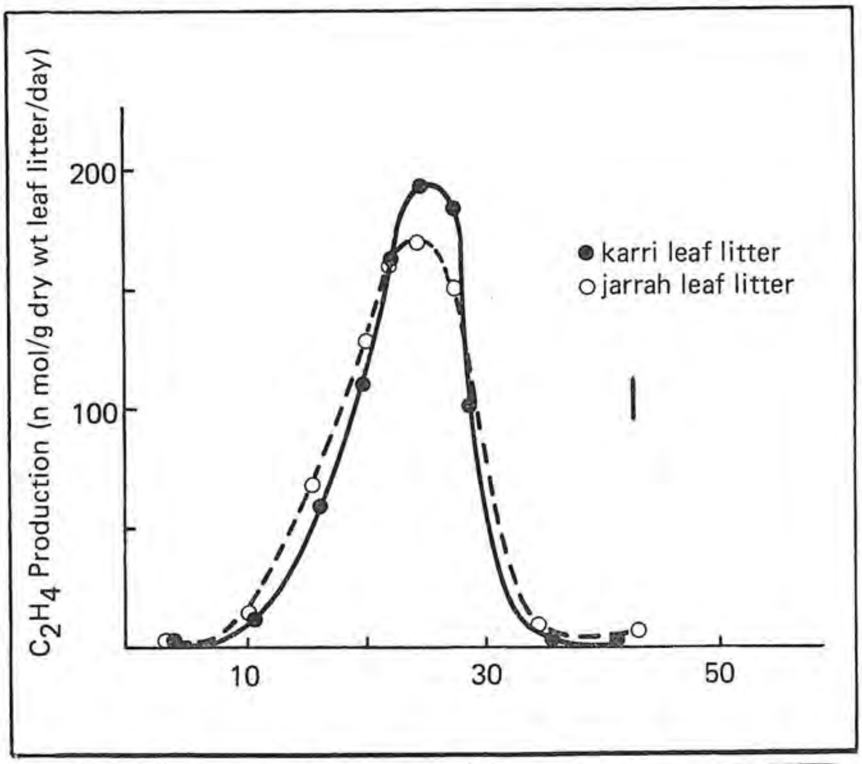

Fig. 4. Effect of temperature on ethylene production by karri and jarrah leaf litter. Each value plotted is the mean of three replicates and the vertical bars represent the confidence intervals ($P<0.05$) of the difference between any two means.

Oxygen concentration

Assay tubes containing leaf litter (c.230% moisture) were evacuated and gases introduced to give 0.1 atm pC_2H_2 and a range of oxygen levels (0-0.4 atm). Tubes were brought to 1 atm by addition of varying amounts of argon and incubated at 25°C for four hours. The pO_2 had marked effects on acetylene reducing activities of both jarrah and karri leaf litter. Maximum rates of ethylene production occurred between 0.05 atm and 0.1 atm (Fig. 5). At oxygen levels above 0.1 atm acetylene reducing activity declined almost linearly and at ambient oxygen levels ethylene production was only 40-50% of the maximum rates measured. Thus, even small changes in oxygen levels which may be induced by biological or environmental factors or by experimental procedures could have significant effects on rates of acetylene reduction.

Other gas mixtures

The production of ethylene from sources other than reduction of acetylene is often tested during acetylene reduction assays by incubating samples in the absence of acetylene. These control samples measure net production of ethylene, since endogenously produced ethylene is oxidized under aerobic conditions (Cornforth 1975). However ethylene oxidation is suppressed in the presence of acetylene and can therefore lead to overestimation of the rate of acetylene reduction (Witty 1979).

A series of experiments was conducted to assess the contribution of endogenous ethylene to total ethylene production during acetylene reduction assays of karri leaf litter. There was no net ethylene production (i.e. endogenous ethylene production less ethylene oxidation) under aerobic conditions in the absence of acetylene (see pC_2H_2 function, Fig. 1). In the presence of 0.1 atm pC_2H_2 and under anaerobic conditions (0.9 atm pA) no ethylene was produced (see pO_2 function, Fig. 5). Where nitrogen replaced air in assay tubes no detectable levels of ethylene were produced either in the presence or absence of acetylene. To assess losses

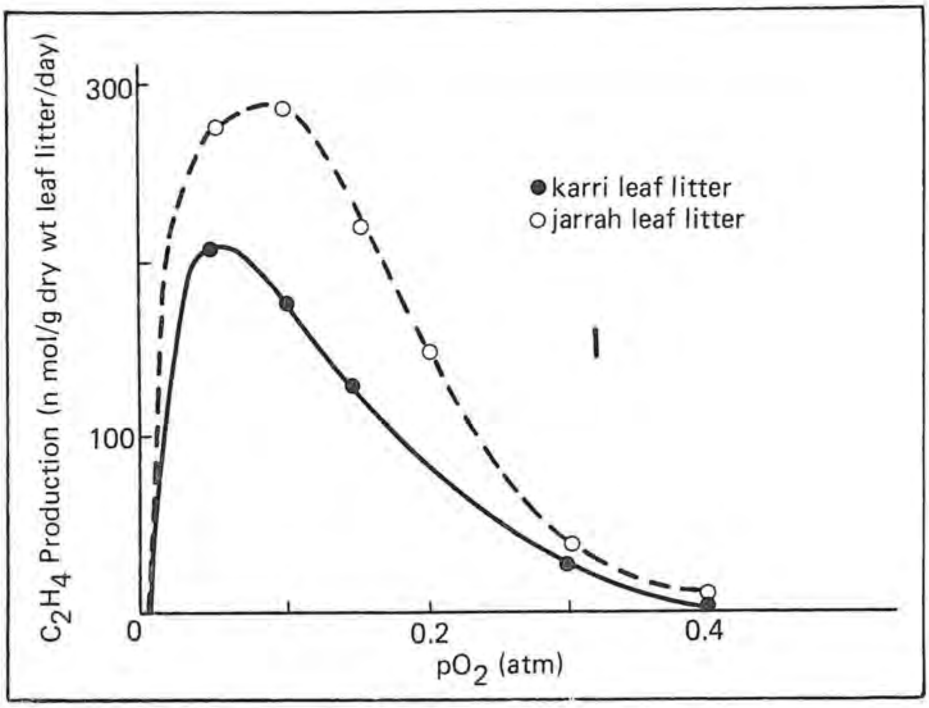

Fig. 5. Effect of pO_2 on ethylene production by karri and jarrah leaf litter. Each value plotted is the mean of three replicates and the vertical bar represents the confidence interval ($P<0.05$) of the difference between any two means.

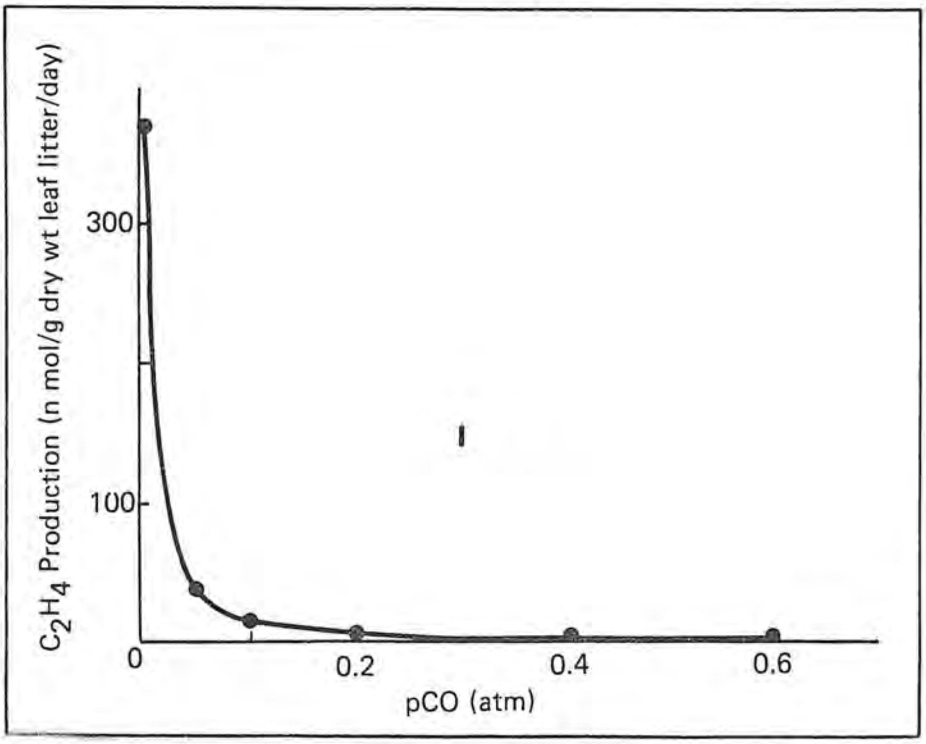

Fig. 6. Effect of pCO on ethylene production by karri and jarrah leaf litter. Each value plotted is the mean of three replicates and the vertical bar represents the confidence interval ($P<0.05$) of the difference between any two means.

of ethylene (oxidation or experimental losses) in the absence of acetylene, known amounts of ethylene were introduced into tubes containing leaf litter and ethylene concentrations were measured several times over a period of 21 hours. Some losses occurred but these were small relative to rates of ethylene production by reduction of acetylene.

Carbon monoxide is known to inhibit the reduction of both nitrogen and acetylene by nitrogenase (Dilworth 1966). In karri leaf litter ethylene production was shown to be strongly inhibited at low levels of carbon monoxide (Fig. 6). Rates of ethylene production at 0.04 atm pCO were less than 1% of those obtained without carbon monoxide, suggesting that ethylene production arises predominantly from acetylene reduction by nitrogenase.

Acetylene reduction by other components of litter

Comparison of acetylene reducing activities and the percentage contribution to total litter nitrogenase activity for various components of litter from jarrah and karri litter has been reported (O'Connell et al 1979). A limited number of samples of decaying wood and litter from different forest communities have also been tested for nitrogenase activity. This preliminary data indicates that activities are considerably lower in decomposing wood than in the leaf component of jarrah and karri litter. However, in these forests the weight of wood on the forest floor may be large relative to the weight of litter (Hingston et al 1981) and thus may be an important source of non-symbiotically fixed nitrogen.

CONCLUSIONS

The results of these experiments show that rates of acetylene reduction by eucalypt litter are highly sensitive to variations in environmental factors. In the jarrah and karri forests of south west of Western Australia optimal conditions for nitrogenase activity are rarely met under field conditions. Temperature is limiting when litter contains high levels of moisture in winter and during the hot dry summer months moisture levels in litter are generally low.

In ecosystem studies which attempt to quantify nitrogen fixation by the acetylene reduction method, recognition of the sensitivity of the technique to environmental factors as well as to factors determined by assay procedures is essential if reliable estimates of nitrogen inputs are to be obtained. When estimating rates of acetylene reduction in the field it is important that moisture and temperature levels are not altered by the assay procedure. The acetylene reducing activity is also highly sensitive to change in pO_2 which may vary in the field as a result of biotic and antibiotic factors. Of particular importance is the effect of assay procedures on oxygen levels. Sample disturbance may change oxygen tension at the site of nitrogenase activity; replacement of air in the assay vessel with acetylene or other gases reduces the pO_2; and small gas/sample volume ratios may cause significant depletion of oxygen during the assay.

Our results show that during the assay period ethylene production in litter arises principally from the reduction of acetylene. Further studies involving parallel assays of $^{15}N_2$ uptake and acetylene reduction are required to confirm these findings and to provide an estimate of the conversion factor between acetylene reduced and nitrogen fixed.

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THE POTENTIAL OF *CASUARINA* SPP.

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NATURAL DISTRIBUTION

The natural distribution of casuarinas extends from India and Malaysia through Australia to the islands of the South Pacific Ocean. The greatest development of the species is in Australia where they grow under climatic conditions ranging from those in the arid zone to those of the higher rainfall regions along the coast (Hall 1972). In the south west of Western Australia two species are common in the understorey of the indigenous forests. These are the karri oak (*C. decussata* Benth.) growing in the wet sclerophyll (karri) forest of the lower south west and the sheoak (*C. fraserana* Miq.) a component of the understorey in the dry sclerophyll (jarrah) forest of the Darling Range (Forest and Timber Bureau 1957).

In the Cobiac study area of the jarrah forest, casuarinas predominate on the lower slopes (Figure 1a) which are characterised by yellow gravels and yellow fine gravels (Figure 1b). Areas with high concentrations of casuarinas are also noted for their lack of *Macrozamia riedlei* and thin populations of jarrah.

NITROGEN FIXATION BY *Casuarina* spp.

Although it has been known since 1932 that some *Casuarina* spp. are able to fix N_2 (Aldrich-Blake 1932; Mowry 1933), relatively few studies have been made of these species compared with those made of legumes. To date 24 of the 45 known species have been shown to fix N_2 (Bergerson, pers. comm.). In Western Australia 18 species are endemic, 9 have been examined for nodulation and nodules have been found only on *C. obesa* and *C. fraserana*.

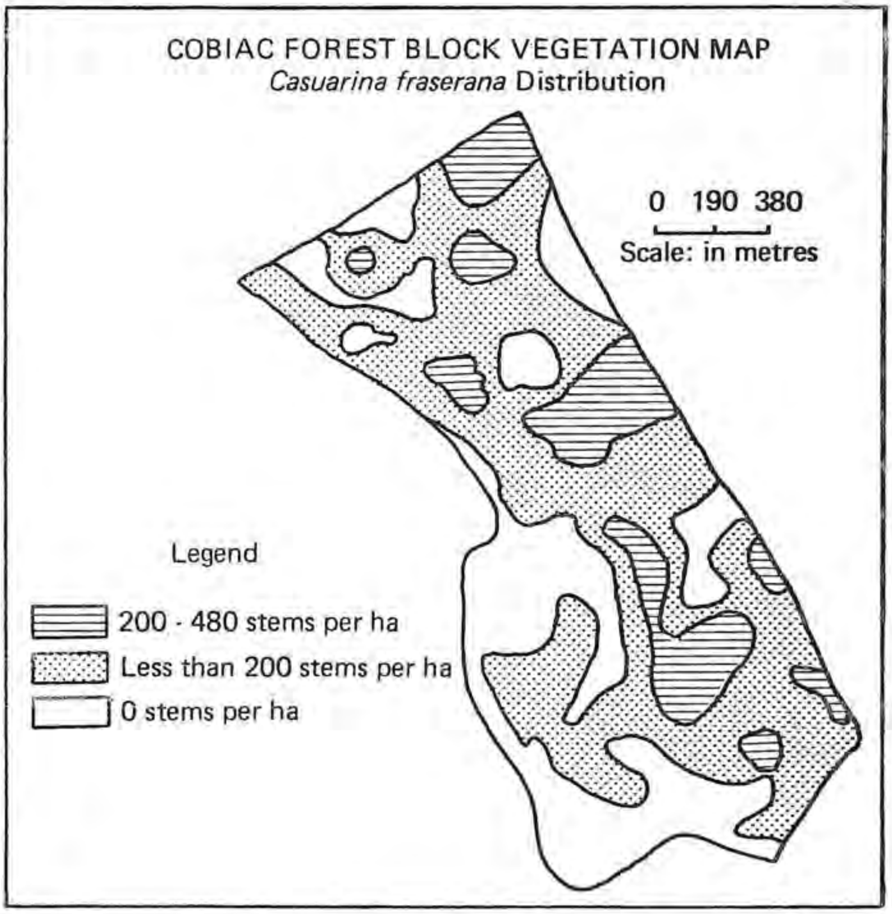

Figure 1a

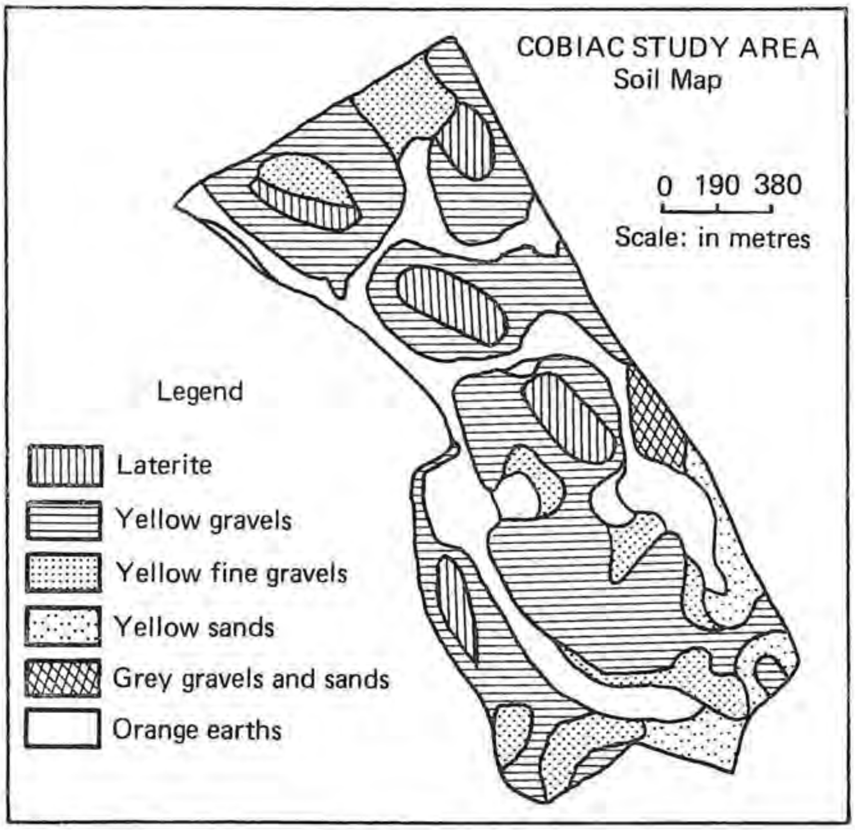

Figure 1b

There are few estimates of the amount of nitrogen fixed by Casuarina spp. or of the specific activity of casuarina nodules. Dommerques (1963) estimated that C. equisetifolia fixed about 58 kg of nitrogen per hectare per year at Cape Verde in South Africa. The estimate was obtained from an analysis of the build-up of nitrogen on a site with casuarinas compared with an adjacent control site without casuarinas. Specific activities of nodules from three species of Casuarina have been determined by Slogar (1968), with the following results:

C. cunninghamiana 0.1 μ mol C_2H_4 produced/g fresh wt of nodule^{-1} hour^{-1}

C. equisetifolia 0.2 to 0.7 μ mol C_2H_4 produced/g fresh wt of nodule^{-1} hour^{-1}

SOME FACTORS AFFECTING NODULE FORMATION AND NITROGEN FIXATION

The optimum temperature for nitrogenase activity of casuarina nodules measured using the acetylene reduction technique varies from 35°C for C. equisetifolia (Waughman 1977) to 24-38°C for C. equisetifolia and C. cunninghamiana (Tyson and Silver 1979).

The nutritional requirements of the species appears to be similar to legumes, cobalt and molybdenum being essential for nodulation (Bond and Hewitt 1961, Hewitt and Bond 1961, Bond and Hewitt 1962, Hewitt and Bond 1966).

INFECTION AND NODULE FORMATION

By means of electron microscopy the endophyte in C. cunninghamiana nodules has been identified as an actinomycete (Becking 1970). It is classified as Frankia casuarinae under the classification system proposed by Becking. However the endophyte has not yet been successfully isolated and cultured.

Torrey (1976) showed that nodules are formed by repeated endogenous lateral root initiations one placed over the other in a branched and truncated root system. Cortical tissues infected by the endophyte are derived from successive root primoidia and form a swollen nodular mass. Root hairs are deformed on inoculated roots but there are no infection threads in the root hairs. The mode of infection has not been determined.

The red pigmentation in nodules was considered by Bond (1958) to be due to anthocyanins rather than haemaglobin which is found in legume nodules. However, Davenport (1960) has observed deoxygenated haemaglobin firmly bound to cell debris. Anthocyanins have been observed in the negative geotropic roots growing from the lobes of the nodules (Bond 1958). These roots, termed rhizothamnia, are considered by Silver *et al*. (1966) to form due to a lack of the auxin, indol-acetic acid. The rhizothamnia contain a very active indol-acetic acid oxidase enzyme system.

USES FOR *Casuarina* spp.

In the past in Western Australia the main use of *Casuarina* spp. has been as a source of wood for barrel making, shingles and firewood.

In New Guinea *Casuarina* species are used to improve the nitrogen status of the soils. Chapman (1974) reports that indigenous species of *Casuarina* are grown in rotations. Five year old trees are removed and used as building timber and firewood. The land is then cropped. The same system is used to reclaim land in West Africa and Asia (Gordon and Dawson 1979).

In Egypt *Casuarina* spp. are grown to stabilize and revegetate sand dunes (Badran and El-Lakany 1977). They were chosen for this purpose because they tolerate drought and salinity and can fix N_2.

CONCLUSION

Very little research has been done to determine the contribution Casuarina spp. make to the nitrogen economy of forest ecosystems. However they show promise as useful nitrogen fixing plants with a wide range of tolerance of harsh conditions and a variety of uses. On this basis their potential needs to be investigated more fully.

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VESICULAR ARBUSCULAR MYCORRHIZAE - A POSSIBLE LINK IN THE TRANSFER OF NUTRIENTS BETWEEN LEGUMES AND EUCALYPTS

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ABSTRACT

The ecological significance of mycorrhizae in the transfer of nutrients is discussed. An experiment is described showing that *Glomus fasciculatus* forms vesicular arbuscular mycorrhizae with seedlings of *Eucalyptus marginata* and *E. diversicolor* and a common understorey legume, *Acacia pulchella*. It is postulated that nitrogen may be transferred directly between legumes and non-legumes in natural ecosystems via common mycorrhizae forming fungi.

INTRODUCTION

Understorey legumes in the eucalypt forest of the south west of Western Australia are considered beneficial in that inputs of symbiotically fixed nitrogen may help to alleviate losses of N through fires as discussed by Grove and Malajczuk elsewhere in this workshop proceedings. However, acquisition of this fixed nitrogen by non-legumes (*Eucalyptus* spp.) is poorly understood in these natural ecosystems.

In agricultural crop systems, where the legume precedes the non-legume in rotation, the principle transfer mechanism for nitrogen is the decomposition of legume root and shoot tissue and the subsequent uptake of mineral nitrogen by the non-legume (Simpson 1976; Henzell and Vallis 1977).

In eucalypt forests, legumes and non-legumes occur together with their roots forming an interwoven pattern in the soil. The period of active root growth of eucalypts and legumes and of maximum nitrogen fixation by the legume is synchronized during late winter and spring. It would be expected that some nitrogen would be transferred to the eucalypt via the decomposition process. Exchange of nitrogen may also occur via exudation of organic substances from roots, as has been suggested by Virtanen et al. 1937. Vallis (1978) considered the latter process to be of minor importance considering the amount of nitrogen in legume tissue relative to the amount exuded. However, a further mechanism for nitrogen transfer in forests with legume understoreys may be the direct movement of nitrogen between hosts through the connections made by fungal hyphae.

Fungi have been found to form a significant proportion of the biomass in some forest soils (Fogel 1980). In the karri forest, for example, we have estimated that the biomass of sporocarps of a hypogeous basidiomycete (Mesophellia spp.) may be as high as 100 kg ha^{-1} and contain 3 kg N.

Fungi are associated with decomposition of litter and wood and also form intimate associations with unsuberized roots (mycorrhizae). These symbiotic associations can increase plant growth through the active transfer of nutrients from soil and/or litter via hyphae to the host. Radioactive tracer studies have shown enrichment of phosphorus at the surface of mycorrhizal roots compared with non-mycorrhizal roots (Bowen 1973). Recent studies by Bevege et al. (1978) reported enrichment of biologically fixed nitrogen (tagged using ^{15}N) in the roots of indigenous and exotic conifers. They suggested that non-symbiotic nitrogen fixing bacteria in the mycorrhizosphere were responsible and that ^{15}N uptake and translocation occurred via fungal hyphae. Pate (1980) analysed the tracheid sap of a number of woody species and found transport of nitrogen occurred entirely in organic form. He suggested that nitrogen may be taken up and metabolized by associated mycorrhizae prior to xylem loading in the plant.

In eucalypt forests it is possible that trees and understorey legumes have common fungal symbionts and that nutrient transfers may occur directly through hyphal connections. Recent work by

Heap and Newman (1980a,b) reported the exchange of labelled phosphorus between Trifolium repens L. and Lolium perenne L. via a common mycorrhizal symbiont. It is feasible therefore that there may also be direct exchange of other nutrients. For example, nitrogen could be transferred from a sink with a high nitrogen concentration in the legume to that with a low nitrogen concentration in the non-legume.

It has been shown that the understorey legume (Acacia pulchella R. Br.) and eucalypts (Eucalyptus diversicolor F. Muell. and E. marginata Donn ex Sm.) form vesicular arbuscular mycorrhizae with a known fungal symbiont Glomus fasciculatus Thaxter sensu Gerd. and Trappe (Table 1) (Malajczuk et al. 1981). We therefore postulate that nitrogenous compounds may be translocated between hosts, from legume to non-legume, though common fungal symbionts such as G. fasciculatus.

Table 1. Extent of vesicular arbuscular mycorrhiza formation by *Glomus fasciculatus* on *Eucalyptus* spp. grown singly or with *Acacia pulchella* as a companion plant.
Percentage of root length with VA Mycorrhizae*

Host plant	Grown alone	Grown with *Acacia pulchella*
Eucalyptus diversicolor	31 ± 2.5	30 ± 2.5
Eucalyptus marginata	30 ± 2.1	34 ± 5.3
Acacia pulchella	61 ± 3.0	

*Data are mean percentages ± standard deviations of three replications, based on observations of 25 root pieces approximately 1 cm long.

CONCLUSION

There is obviously a need for further experimentation to test this hypothesis and to determine the significance of the various nitrogen transfer mechanisms in the forest ecosystems. In contrast to the uptake of soil nitrogen which is influenced partly by decomposition rates and microbial immobilization, the direct transfer of nitrogen through fungal hyphae would offer a rapid and efficient means for the non-legume to obtain nitrogen.

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NITROGEN INPUTS TO EUCALYPTUS MARGINATA AND E. DIVERSICOLOR FORESTS

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ABSTRACT

Nitrogen is a major factor limiting the productivity of many forest ecosystems. Biological inputs of nitrogen are particularly important in the eucalypt forests of south western Australia since fires may cause substantial losses of nitrogen.

In this paper we report on measurements of nitrogen fixation using the acetylene reduction technique. Some estimates of rates of nitrogen fixation by legumes, a non legume, and by free-living organisms in the litter layers of jarrah and karri forests are presented. The influences of fire and phosphorus application on rates of nitrogen fixation are discussed.

INTRODUCTION

Nitrogen is the essential element which most commonly limits productivity in forest ecosystems (see Gordon et al 1979). In the eucalypt forests of south western Australia growth responses to applied nitrogen have been recorded for jarrah (Eucalyptus marginata Donn ex Sm.) (Kimber, pers.comm.) and more recently in regrowth karri (E. diversicolor) F. Muell.) (Grove, unpublished data). This implies that there is a necessity to maintain the nitrogen balance if the productivity of these forests is to be sustained. Furthermore, raising the level of nitrogen inputs may enhance growth and stability of the forest ecosystems.

Fire is a major factor responsible for nitrogen losses in forests, since a high proportion of the nitrogen bound in forest debris can be lost to the atmosphere during combustion (Debell and Ralston, 1970). In the eucalypt forests of southwestern Australia mild intensity burns are carried out every 5-7 years for the purpose of fuel reduction (Christensen and Kimber 1975). A major portion of this fuel is litter, which after 6 years litter accumulation can contain 50kg N ha^{-1} and 220kg N ha^{-1} in the jarrah and karri forests respectively (O'Connell *et al* 1978; Hingston *et al* 1979). Assuming a 70% loss of this litter nitrogen during burning, average annual accessions of 6kg N ha^{-1} in the jarrah forest and 26kg N ha^{-1} in the karri forest would be required to replace this loss.

Since inputs from rainfall are small (about 1kg N ha^{-1} $year^{-1}$, O'Connell, pers.comm.), biological fixation of nitrogen is likely to be the principal source of input. This paper summarizes current work on some of the biological nitrogen fixing systems in the jarrah and karri forests. All measurements have been made using the acetylene reduction technique (Dilworth 1966).

NITROGEN FIXATION BY LEGUMES

Jarrah Forest

Rates of nitrogen fixation have been estimated for legumes germinating after an intense fire in the jarrah forest (Hingston, Malajczuk and Grove, unpublished data). Maximum rates of acetylene reduction for legumes were recorded in late winter and spring. In the 18 month period following germination, the major legume species, *Acacia pulchella* R. Br., fixed approximately 1.5 kg N ha^{-1} at a site where the plant density was 6 m^{-2}. Measurements in older stands are too limited to predict annual rates of nitrogen fixation. However, an estimate for plants growing on yellow sandy gravels indicated that higher rates can be attained in older unfertilized stands and that application of 50 kg phosphorus ha^{-1} can produce a six fold increase in yield and a significant increase in the rate of acetylene reduction.

Karri Forest

Bossiaea laidlawiana Tovey and Morris is the dominant understorey species in much of the northern karri forest. Rates of acetylene reduction by nodulated roots extracted from soil blocks were measured at four sites representing karri and understorey stands of different ages. The highest rates of acetylene reduction were recorded in spring and early summer before soil moisture became limiting. Estimated rates of nitrogen fixation ranged from 6kg N ha^{-1} $year^{-1}$ in a 7 year old karri/understorey stand to 14kg N ha^{-1} $year^{-1}$ in a mature stand of karri with an 11 year old understorey. Since the standing biomass of B. laidlawiana contained 56kg N ha^{-1} and 165kg N ha^{-1} in the 7 year old and mature karri stands respectively, rates of fixation are similar to the average net rates of nitrogen accumulation. However, as the nitrogen content of litter fall from B. laidlawiana generally exceeds the rate of nitrogen accumulation in aboveground biomass (O'Connell, pers.comm.), the nitrogen fixation estimates represent less than half of the total nitrogen uptake. The application of phosphorus (200kg P ha^{-1}) to young regenerating Bossiaea resulted in a three-fold increase in yield after one year.

NITROGEN FIXATION BY NON-LEGUMES

Jarrah Forest

A study of the cycad Macrozamia riedlei (Fisch. ex Gaudich) C.A. Gardn., a common understorey species in the jarrah forest, has shown that fire influences its growth and nitrogen fixing capacity (Grove, O'Connell and Malajczuk 1980). Rapid leaf growth occurs in the first year following fire, and declines in the fifth year after fire. Rates of acetylene reduction were greatest for plants in recently burnt forest and declined to a minimum in forest areas burnt seven years previously. This decline in the acetylene reduction rate was attributed to a decrease in both the weight and nitrogenase activity of coralloid roots with increasing time after burning. Over a seven year period following fire, it was estimated that c. 40kg N ha^{-1} would be fixed where the cycad density was 1370 ha^{-1}.

NON-SYMBIOTIC NITROGEN FIXATION

Jarrah and Karri Forests

A preliminary study of the rates of acetylene reduction in the litter layer of the jarrah and karri forests has suggested that the rates of nitrogen fixation may be significant in relation to the nitrogen budget of these ecosystems (O'Connell, Grove and Malajczuk 1979). Nitrogen fixation rates of 9.9g N ha^{-1} day^{-1} for jarrah litter and 14.3g N ha^{-1} day^{-1} for karri litter were obtained during a winter sampling. Subsequently this study has been extended to examine the effects of season and litter amounts on rates of acetylene reduction.

CONCLUSION

Field variability and inherent difficulties in the acetylene reduction technique can cause under- and over-estimations of the nitrogen fixing capacity of the various systems. Values derived are semi quantative; however, they do indicate the relative importance of each system in the natural ecosystem.

Fire in south western Australia is a significant factor influencing nitrogen inputs of eucalypt forests. Its frequency and intensity will have a differential effect on the rates of nitrogen fixation and total gains from various legumes and non-legumes. In using fire as a management tool, its effects on the nitrogen fixing systems should be recognized and further investigated. The present study provides an insight into nitrogen inputs by the dominant species in selected communities. However, it is recognized that there is a diverse range of nitrogen fixing plants throughout the jarrah and karri forests (Havel 1975; McArthur and Clifton 1975) for which fixation data is not available.

We have found that the growth of legumes in jarrah and karri forests is stimulated by the application of phosphorus. Fertilization may therefore provide an additional management option for improving the nitrogen economy of these forests.

Rates of non-symbiotic nitrogen fixation in the two eucalypt forests are low relative to the symbiotic nitrogen fixing systems. However fixation by free-living bacteria will occur in all forest areas and may be particularly important where there is a low density of nitrogen fixing plants. Measurements to date have been restricted to the litter layer, but other sites of fixation (e.g. rhizosphere, decaying logs) may add appreciable amounts of nitrogen.

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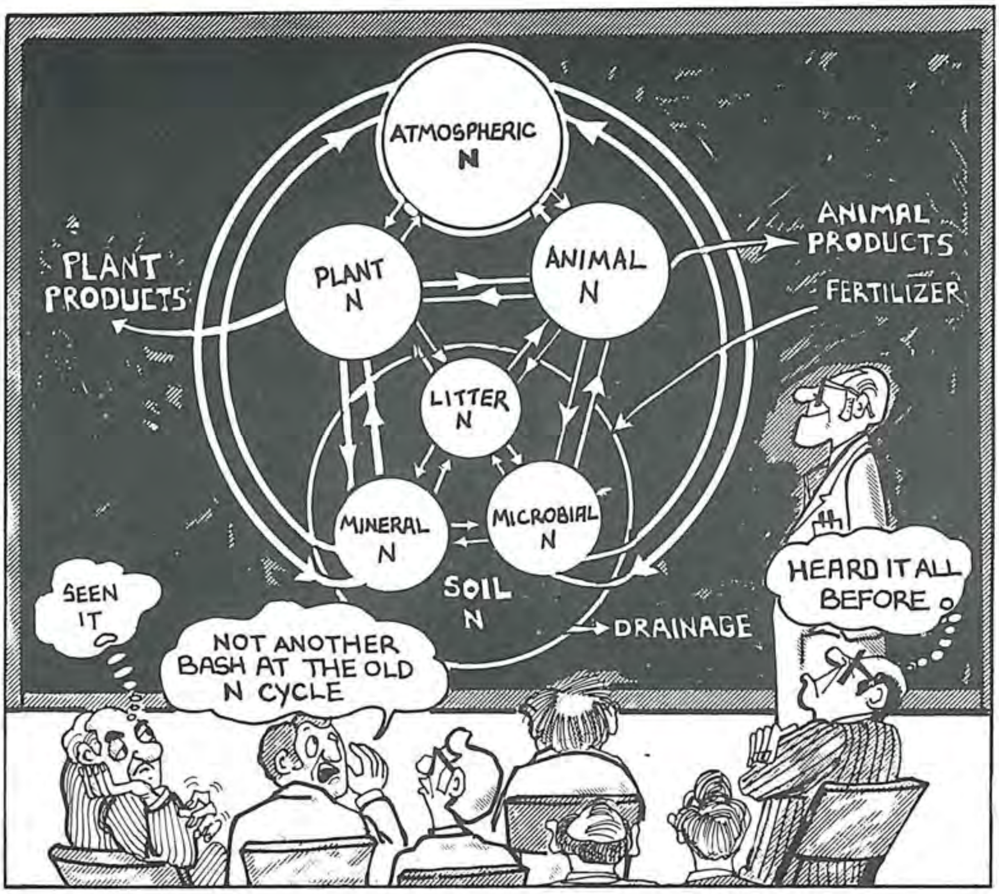

SESSION 4.
Basic Biological Processes
(b) Soil Nitrogen

EVALUATION OF NITROGEN REQUIREMENTS AND SOIL NITROGEN AVAILABILITY IN AGRICULTURE AND FORESTRY

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INTRODUCTION

The nitrogen (N) requirements of many agricultural and horticultural crops have been reasonably well defined for a century or more. Within the past 4 to 5 decades, however, crop nutrient requirements gradually have increased because of the greater yields associated with improved varieties, cultural practices, irrigation, pest control, and other factors. Fertilizer use has increased dramatically throughout the world to keep pace with rising nutrient demands that accompanied improvements in agricultural technology.

Until recently, research on forest nutrition mainly consisted of measuring the total nutrient content and associated weights of the unfertilized tree and its components (foliage, branches, bark, and bole wood), of the forest floor, and of underlying soil. Estimates for roots sometimes were included. These studies have done much to improve our knowledge of the dynamics of nutrient cycling in forest ecosystems. Information obtained from sampling trees of varying ages within a given species grown on differing sites has prompted considerable speculation regarding the intrinsic internal nutrient requirements of trees grown to a given age under a specified set of soil and climatic conditions.

Experiments on forest fertilization during the past 3 or 4 decades posed additional questions with respect to predicting and interpreting growth and yield responses to fertilizer treatments in relation to external as well as internal nutrient requirements of forest tree species (Tamm 1964). Such experimentation in forestry is very costly and difficult to interpret.

The remainder of this discussion will emphasize some of the problems encountered in defining the nitrogen requirements of trees and agricultural crops and explore opportunities for assessing soil nitrogen availability and supplemental fertilizer-N requirements in both systems.

AN APPROACH TO ACHIEVING MORE EFFECTIVE USE OF N IN AGRICULTURE

The importance of minimizing overuse of N first became of particular interest to me in studies with N fertilization of sugarcane in Hawaii. If sugarcane takes up more N than is required for optimal balance between yield of total dry matter and sugar, the quality of juices and recovery of sugar usually declines (Stanford 1963). Based on uptake-yield results from rate-of-N field experiments on irrigated plantations, Stanford and Ayres (1964) determined that optimal N uptake for 2-year-old cane was about 4 lb. N ton^{-1} of total dry matter, TDM (2 kg $tonne^{-1}$). This value corresponds to 0.2% N in TDM, or about 1 kg $tonne^{-1}$ of millable cane (field weight) and defines the internal N requirement of 2-year-old sugarcane for near maximum yield. In these experiments, a broad range of yield maxima (100 to 190 tonnes ha^{-1}) were obtained owing to diverse climatic and cultural conditions and different varieties. The internal N requirement, together with estimates of soil N-supplying capacities and efficiency of N use, provided a reasonable basis for estimating the amounts of supplemental N fertilizer needed for a specified yield level (Stanford _et al_. 1965; Stanford 1966).

A less empirical approach to estimating amounts of N derived from the soil during the cropping season, suggested by Stanford (1973) and Stanford _et al_. (1977), has been discussed in depth by Campbell (1978). Estimates of soil N made available during the season, used in conjunction with estimates of internal N requirements for specified yields of various crops, may result in more reliable predictions of supplemental N fertilizer needs (Oyanadel and Rodriguez 1977; Prado and Rodriguez 1978; Sanchez 1973) than were obtained from earlier studies. Estimating the

N-supplying capacities of soils will be discussed more fully in a later section.

BASIC CRITERIA FOR EFFECTIVELY USING N IN FORESTRY

N Requirements of Trees

The average annual removal of N from short rotations, with whole-tree removal, is much higher than for long rotations (Wollum and Davey 1975; Malkonen 1976; Kimmins 1977). The shorter the rotation, of course, the greater will be the cumulative nutrient demand on the site. The practice of short rotations with whole-tree removal has been referred to as "fibre" farming. Rotation periods often are in the range of 5 to 25 years, depending on how the product is to be used and on potential growth rate as affected by site characteristics (soil fertility, fertilizer additions, water supply and temperature regime). Short rotations (less than 10 years) for pulp wood production from eucalypts in Australia as related to stand density, cultivation, and fertilization have been discussed by Opie *et al*. (1978) and Cremer *et al*. (1978). Most of the experience in intensive wood production in Australia has involved introduced conifers, mainly *Pinus radiata* (Edgar 1978).

Cromer *et al*. (1975) presented a striking demonstration of the potential for bringing about rapid growth of *Eucalyptus globulus* under intensive cultivation and fertilization. Their experiment was carried out in a 1000 mm rainfall area in Victoria and compared N rates of 34, 101, and 202 kg ha^{-1} in combination with 15, 45, and 90 kg ha^{-1} of P, respectively. The controls received no N or P. Although independent effects of N and P or their interactions cannot be evaluated, it is interesting to note that the relationships between yields of TDM and N yield at the end of 2 and 4 years (Fig. 1) were essentially linear. What do these data suggest regarding the internal N requirement of *E. globulus*? With further increments of N, and adequate P, would the TDM-N yield curve continue to be linear or would luxury consumption become manifest? Additional rate-of-N experiments with suitable modification in design might reveal important information about the internal N requirement of eucalypts with increasing age, especially in short rotations. The recoveries of applied N, shown adjacent to each point in Fig. 1, are higher than generally are reported in the literature from Europe, Canada, and the United States (Keeney 1980) with fertilization of established stands.

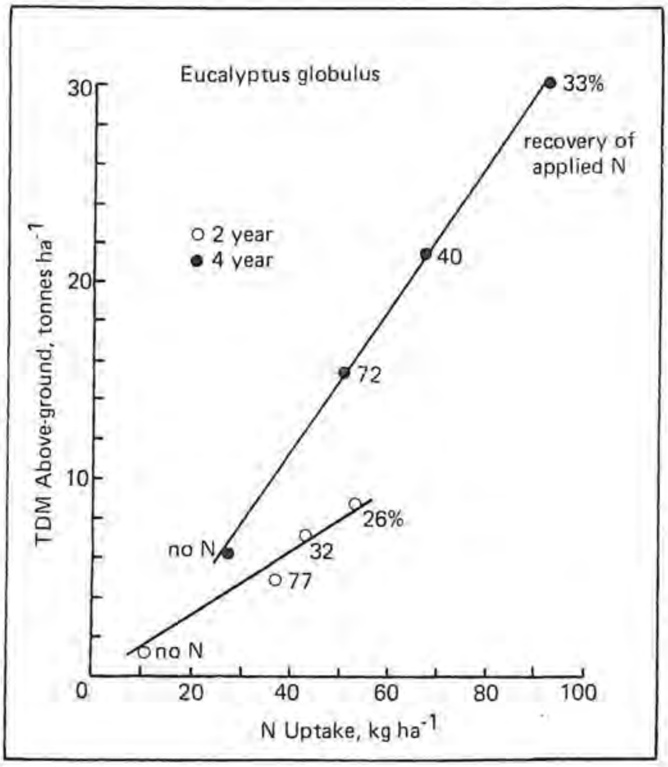

Fig. 1. Total above-ground dry matter production of *Eucalyptus globulus* in relation to N uptake, 2 and 4 years after planting. Adapted from Cromer *et al*. (1975).

Short rotations of loblolly pine (*Pinus taeda* L.) and other species of pine are becoming prevalent in the southeastern United States where climatic and soil conditions are particularly conducive to rapid growth. Relatively little appears to be known about the optimal N requirements of loblolly pine stands of different ages. Few, if any, comprehensive rate-of-N experiments involving TDM and N uptake measurements seem to have been reported. Switzer *et al*. (1966) harvested whole unfertilized trees from poor upland and good bottomland sites in Mississippi and determined TDM (whole trees) and associated yields of N. Ages of trees from poor and good sites ranged between 5 and 60 years. In Fig. 2, the relation of TDM (above ground) to total N uptake is seen to be almost linear for trees 20 years or more of age. With an annual crop such as sugarcane or maize, such a relationship would indicate that N became the primary limiting factor on the good as well as the poor sites (Stanford 1966). Switzer et al. (1966)

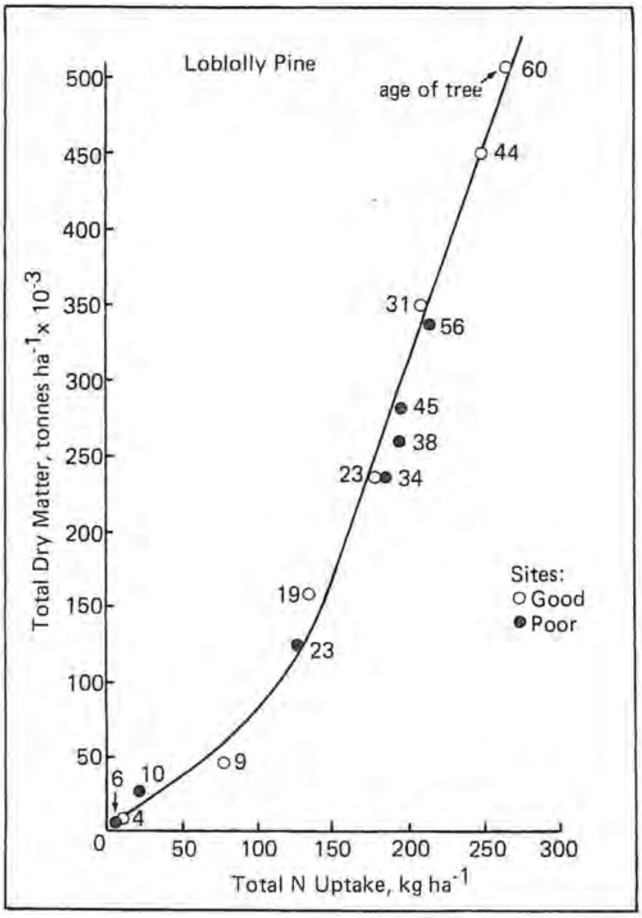

Fig. 2. Total above-ground dry matter production of *Pinus taeda* L. in relation to N uptake for different ages of trees grown on good and poor sites. Adapted from Switzer *et al.* (1966).

concluded, however, that N was not a limiting nutrient even on the poor upland sites. Again, a need is indicated for rate-of-N experiments on loblolly pine, extending for at least 2 or 3 decades, to determine under what conditions, if any, luxury consumption of N occurs, and its importance in relation to maintaining optimal N nutrition. For stands older than 2 decades, Switzer and Nelson (1972) concluded that a sizeable fraction of the annual N (and other nutrient) requirement of loblolly pine is met by transfer within the living system. Based on this premise, the N requirement for foliage production at 20 years of age constitutes about 85% of the total requirement. After this time, luxury consumption of N by foliage and distribution of the excess N to the other tree parts and the forest floor might be expected to play a key role in maintaining optimal rate of growth.

That luxury consumption of N can be induced by fertilization of standing Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) of various ages seems to be implicit in results reported by Heilman and Gessel (1963). From the data presented for 5 sites in the Pacific Northwest, the general relationship between total dry matter production and N uptake of Douglas-fir for N-fertilized and control plots can be examined. At the time of whole-tree sampling, stands varied in age from about 30 to 52 years. Over the

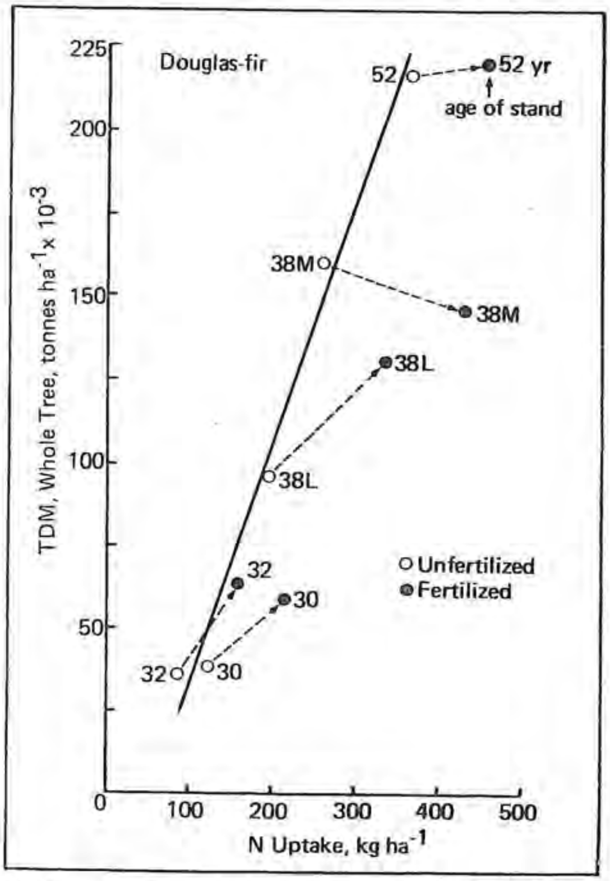

Fig. 3. Total above-ground dry matter production of Douglas-fir in relation to N uptake for N-fertilized and control trees of varying ages. Adapted from Heilman and Gessel (1963).

several-year period preceding whole-tree harvest, plots received 250 to 700 kg ha^{-1} of fertilizer N in unspecified increments. In Fig. 3 is presented the relationship between total dry matter (whole trees) and corresponding N uptake values for N-fertilized and control (no-N) trees of varying ages. The relation appears to be near-linear for the control trees as also occurred with loblolly pine (Switzer et al. 1966). Significant TDM and N-yield responses to applied N seem evident for the stands that were 30 and 32 years of age and for the 38-year-old site labelled 38L. On the two remaining sites (38 M and 52-year), N uptake in fertilized trees exceeded the growth requirement (i.e. luxury consumption is indicated). More recently Turner (1977) measured the effects on short-term N cycling of altering the availability of N in the soil-humus complex under a 45-year stand of Douglas-fir. Extreme N deficiency was induced by broadcasting 18,000 kg ha^{-1} of sucrose and sawdust on the forest floor. The control plot received nothing. The two remaining treatments were 220 and 880 kg of N ha^{-1} as

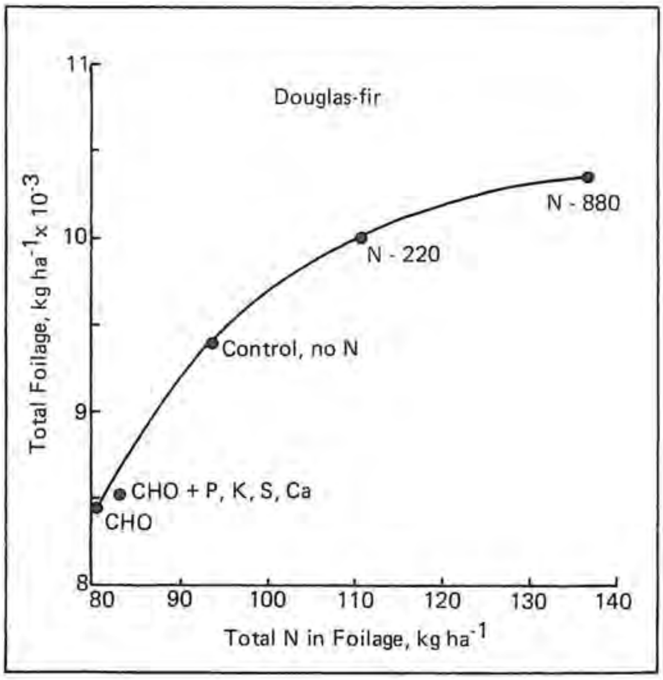

Fig. 4. Total yield of Douglas-fir foliage in relation to uptake of N by foliage one year after treatments which gave rise to levels of N availability greater than (220 and 880 kg N ha^{-1}) and less than (18,000 kg ha^{-1} of sucrose plus sawdust:CHO) that of the unfertilized control. Adpated from Turner (1977).

urea. Total foliage yields in the standing crop, after one year, and corresponding total N uptake by foliage, plotted in Fig. 4, indicate approaching luxury consumption, if one assumes that yield of foliage was near maximum with the highest rate of N applied.

Some of the least productive soils of the world pose technological and economic constraints from the standpoint of supplying adequate nutrition to trees. Often aesthetic or recreational considerations and conservation needs, however, dictate the course of action. Ballard (1976) points out that "even if a forest is seriously N-deficient and responds dramatically to fertilizer application, it is often uneconomic to fertilize". The work of Miller and Miller (1976) and Miller et al. (1976) in northeast Scotland is of particular interest in that it involves some unique studies with rates of N applied to a 35-year-old stand of Corsican pine (Pinus nigra maritima) on mobile sand dunes inherently low in productivity. Basal applications of P and K were made. Annual rates of N as ammonium sulphate, applied for three consecutive years, were 0, 84, 168, 336, and 504 kg ha^{-1}. In the fourth year, growth response had leveled off at the 168 kg ha^{-1} yr^{-1} N rate, although N uptake continued to rise linearly through the maximum rate applied. Few N rate studies with forests have demonstrated luxury consumption so vividly. From these results, Miller et al. (1979) constructed a model depicting N fluxes through the tree-soil system in relation to growth responses associated with varying N rates. With no N applied continuing immobilization of N in trees and forest floor occurred, resulting in dying of older tissues and utilization of the N thus released for new growth. The excess N stored in the trees that initially appeared to be excessively fertilized gradually was expended in enhancing tree growth and building of N in the forest floor. Differential responses of basal area growth to the three highest N rates developed during the latter part of the decade following the period in which 500, 1000, and 1500 kg of N ha^{-1} was applied. Thus, luxury consumption prolonged the duration of response to N.

Amounts and Availability of N in Soil and Forest Floor

The forest floor and underlying mineral soil are the dominant sources of N to trees. Redistribution of the internal N reserves of the tree contribute primarily to the short term needs (Turner 1977). The soil is the ultimate source, therefore, of a large proportion of the N accumulated in trees and in forest floor (Wells and Jorgensen 1975). In studies of nutrient accumulation and cycling in a 20 year-old loblolly pine ecosystem, Switzer and Nelson (1972) used a system of accounting that indicated minor contributions of soil N at this stage of development. On the other hand, Wells and Jorgensen (1975) clearly demonstrated declines in total N and other nutrients in the layers of mineral soil after 5, 11 and 15 years. Thus, to an unknown extent, the apparent decline in N requirement of loblolly pine with age may reflect decline in available soil N availability over time.

One of the formidable problems in studying distribution of N among components of the forest ecosystem is that the total N in the system is dominated by soil N (Heilan and Gessel 1963; Gessel et al. 1973; Klemmedson 1975; Kimmins 1977; Hingston et al. 1979; Keeney 1980). With increasing age of stands, the N builds up in the forest floor. The primary source of this N is the soil. Ultimately, amounts of N in the trees and in the forest floor are of similar magnitude (Switzer and Nelson 1972; Keeney 1980). The need for developing reliable means of assessing the relative N contributions from soil and forest floor or from the soil-humus complex as a whole is apparent.

The total N content of soils should not be ignored as a possible means of distinguishing among soils with respect to N-supplying ability. In areas or regions where little is known regarding the range in N status of soils, determining the total soil N contents in the main rooting zone, by depth increments, may be useful as a first step in exploring the soil N-uptake relationships for a given crop.

Zinke (1960) determined the total N contents of soils associated with 23 ponderosa pine (*Pinus ponderosa* Laws.) sites located throughout California and found that site indexes at age 300 and total soil N were correlated significantly (r=0.71). Site indexes ranged from 20 to 64 meters, and soil N contents (to the 120 cm depth) ranged from 2200 to 14,000 kg ha^{-1}. This range in total N is similar to that cited by Gessel et al. (1973) who suggested that the supply of soil N may be inadequate for optimal growth of Douglas-fir if the total amount of N to effective rooting depth falls below 5000 kg ha^{-1}.

In another study in the Pacific Northwest, total soil N (kg ha^{-1}) to rooting depth was evaluated as a predictive index for response of Douglas-fir to N fertilizer, on different parent materials. On low N pumice soils (less than 2400 kg N ha^{-1}) growth response to applied N did not occur because S was extremely deficient (Turner et al. 1979). Tree growth responses (diameter at breast height over bark) to N applied did not occur when soil N exceeded 8,000 kg ha^{-1} (6 sites, ranging from 10,000 to 17,000 kg ha^{-1}). In the soil N range of 3000 to 8000 kg ha^{-1}, growth responses occurred on 10 of 11 sites.

Mineralization Characteristics of N in Soil and Forest Floor

Abundant evidence shows that net release of N from litter in standing forests is relatively slow under a broad range of climates (Gessel et al. 1973; Wells and Jorgensen 1975; Wollum and Davey 1975; Rapp et al. 1979). This is illustrated by the fact that concentration of N in litter increases over time (Wells and Jorgensen 1975). Net mineralization occurs briefly when fresh needles or leaves undergo initial decomposition. Decomposing residual forest litter, however, competes with the living roots for the N thus released. As a further complication, the soil N mineralized beneath the forest floor supplies an unknown portion of the N required in decomposing the annual flush of high-carbon litter fall as well as the more slowly-decomposing residual material.

According to Vitousek and Melillo (1979), considerable study has been done in Europe and Africa on amounts of N mineralized *in situ*. The studies cited were not examined by this reviewer.

Vitousek and Melillo (1979) present evidence that higher rates of N mineralization generally occur under deciduous rather than under coniferous forest. Under a 35-year-old stand of *Pinus pinea*, Rapp *et al*. (1979) evaluated total N uptake and N distribution in the system, together with *in situ* measurements of N mineralization, and were able to account for essentially all of the N cycled within a 2-year period. Their method of measuring N mineralization in the field warrants further investigation both in agriculture and forestry. It permits measuring, simultaneously, the N mineralized in discrete humus layers (e.g., F_1, F_2, and F_3) and in the underlying soil. During one year, the amounts of N mineralized in the F_1, F_2, F_3, and A (soil) layers, respectively, were 3.7, 4.2, 1.0 and 2.6 kg ha^{-1}. Eighty-seven per cent was present as NH_4^+-N. Only 1.6% of the total organic N in these layers (706 kg ha^{-1}) was mineralized in one year. Other less successful attempts at characterization of N mineralization under field conditions have been reviewed by Keeney (1980).

EVALUATION OF SOIL N AVAILABILITY UNDER CONTROLLED CONDITIONS IN THE LABORATORY

Biological Methods

Aerobic mineralization.

Methods involving incubation of soils under controlled environmental conditions and measurement of mineral N generally are accepted as being more reliable than chemical methods as a basis for estimating the relative N supplying capacities of soils (Keeney 1980; Stanford 1981). This is because mineralization of organic N under laboratory conditions is mediated by the same organisms and biological processes that occur in the field.

Bremner (1965) critically discussed more than 30 aerobic incubation procedures that had been published over a span of several decades. Keeney and Bremner (1966) concluded that most of the proposed methods were unsatisfactory because results often were influenced by method of sample treatment prior to incubation (e.g. extent of drying, method of storage). The problem of moisture control during short-term incubation of soils differing in texture and exchange capacity was solved (Keeney and Bremner 1966) by mixing 30 g of sand with 10 g of soil in a bottle containing 6 ml of water. They also stressed the importance of measuring both NH_4^+ and NO_3^- (and NO_2^-, if present). This is of particular significance in forest soils where mineral N usually accumulates predominantly in the NH_4^+ form (Vlassak 1970; Nommik 1976; Geist 1977; Rapp et al. 1979; Hopmans et al. Keeney 1980; Stanford 1981).

Methods involving short-term aerobic incubations have received limited acceptance in predicting N fertilizer needs for either arable or forested soils as discussed by Stanford (1981). Stanford and Smith (1972) developed a method of estimating N mineralization potentials of soils, N_o, based on cumulative release during a series of consecutive aerobic incubations. Calculations of N mineralization potential, N_o, is based on the first-order expression, $dN/dt=-kN$ (Note: initially $N=N_o$; t=time) as described by Stanford and Smith (1972), Stanford and Smith (1976), and Campbell (1978). Using N_o, the amount of N mineralized during the growing season or other specified time periods can be estimated by taking into account the effects of temporal variations in soil water content and temperature (Stanford et al. 1977; Oyanadel and Rodriguez 1977; and Campbell 1978). The method is useful as a research tool for examining the long-term mineralization characteristics of soils, but is too laborious for routine use in advisory work. It serves as a reliable biological basis, however, for developing and selecting more rapid methods for assessing soil N availability as will be discussed later.

The mineral N produced during aerobic incubation of forest soils usually is predominantly NH_4^+ as contrasted to cultivated land and pastures where nitrification usually proceeds rapidly except for occasional initial lag periods when NH_4^+-N may build up temporarily. This is illustrated in the studies of Vlassak (1970) who concluded that soils under deciduous as well as coniferous forest were mostly ammonifying. Owing in part to the higher base content of deciduous leaves than of conifer needles, nitrification under hardwood becomes of importance particularly in the period between clear-felling and initiation of new ground cover (Vitousek and Melillo 1979). Hence, as mentioned earlier, both NH_4^+ - N and NO_3^--N should be measured after incubation. Often (NH_4^+ +No_3^-)-N suffices if the goal is to measure total available mineral N, without regard to specific amounts of ionic forms present. Only traces of NO_2^- usually are present.

Anaerobic mineralization.

Incubation of soils under anaerobic (water-logged) conditions and measurement of NH_4^+-N released is attractive because of its simplicity as compared to most aerobic procedures (Stanford 1981). Waring and Bremner (1964) with a number of Australian soils, found high correlation between the amount of NH_4^+ - N produced anaerobically and the (NH_4^+ + NO_3^- + NO_2^-)-N mineralized during aerobic incubation. Following incubation, they determined the NH_4^+-N by steamdistilling the soil-water system made alkaline with MgO. Robinson (1967) modified the Waring-Bremner method by determining the NH_4^+-N in the liquid after filtration in order to eliminate release of NH_4^+-N by decomposition during boiling of soil organic

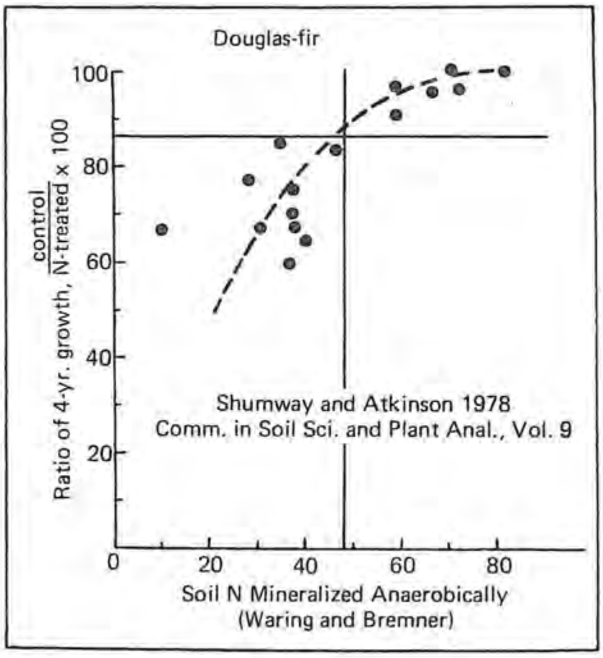

Fig. 5. Effect of N fertilizer treatment on percentage growth responses of Douglas-fir at 5 sites in relation to soil N released during anaerobic incubation. Adapted from Shumway and Atkinson (1978).

matter. Stanford and Smith (1971) further modified the Waring-Bremner method by extracting mineral N with 0.01 M $CaCl_2$ before incubating soil residues anaerobically. Thus, only the N ammonified during incubation was measured. The significance of proposed modifications of the Waring-Bremner procedure are discussed more fully by Stanford (1981).

Recent studies have demonstrated significant relationships between N released during anaerobic incubation by the unmodified Waring-Bremner method (1964) and 4-year growth responses (diameter breast height) of Douglas-fir to N fertilization (Sumway and Atkinson 1977, 1978). Ammonium production during incubation represented the difference between final and initial NH_4-N content. In Fig. 5, the relative increases (percent) in diameter growth vs N index are shown, based on data from Shumway and Atkinson (1978). Correlation coefficients relating growth response and mineralizable N, based on soil samples from 0-15 cm, 0-30 cm and 30-60 cm, respectively, were -0.82, -0.72, and -0.70, indicating that the most effective root-feeding zone, on average, extended to about 30 cm. Site index also was negatively correlated (r = -0.5) with growth response. Taken together, relative stand density and mineralizable N accounted for 86% of the variation in growth response.

Criteria for Choosing a Suitable Chemical Index of Soil N Availability

The potential usefulness of a particular chemical index for assessing soil N availability is determined by its reliability as a basis for predicting the capacity of soils to mineralize N in the natural environment. A given chemical index usually is not worthy of further attention if results do not correlate highly with amounts of N released biologically under controlled conditions in laboratory incubations or glasshouse cropping for a particular array of soils. Stanford and Smith (1976) were able to estimate potentially mineralizable N, N_o, with reasonable accuracy, for a broad range of soils, based on the regression of N_o on amounts of NH_4^+-N released by 16-hour autoclaving in 0.01 $CaCl_2$. Since it is not feasible to devise a chemical method that simulates the action of microorganisms in releasing plant-available forms of soil N, relationships involving chemical extraction must always be empirical. When a reliable and reproducible chemical method has been developed and its relationship to the soil N mineralization capacity has been established, the challenge of adapting the method for use in predicting N release under field environmental conditions becomes of primary importance as alluded to earlier.

Relatively mild extraction methods.

The hot-water extraction method of Keeney and Bremner (1966) involves 60 minutes of boiling in water followed by determination of total N in the clarified extract. This method frequently has given excellent correlations with biological methods in laboratory and glasshouse (Stanford 1981). A disadvantage is the need for acid digestion and distillation to determine total N in the extract. A possible advantage is that the Keeney-Bremner method, in extracting only 1 to 2% of the total soil N, may selectively remove the N from organic fractions that are relatively susceptible to mineralization.

The distillable NH_4^+-N released by 16-hour autoclaving or by 16-hour boiling (100°C) in the steam chest correlated well with potentially mineralizable N for a broad range of soils (Stanford and Smith 1976). A disadvantage of this method is that certain calcareous soils of western United States did not conform to the general relationship applicable to most soils. Selective removal of mineralizable N may be advantageous (Stanford 1981). Another method involving 1-hour, room-temperature extraction of soils with acid $KMnO_4$, and measurement of the NH_4^+-N released by distillation seems to offer promise, but the method has not been adequately tested by others (Stanford and Smith 1978).

The NH_4^+-N released by boiling alkaline permanganate solutions does not appear to provide a generally useful index of soil N availability (Keeney and Bremner 1966; Stanford 1978). Mild alkaline permanganate extraction, however, may be worthy of further study based on preliminary evidence (Stanford, unpublished). The following procedure was found to be very reproducible: (1) Weigh

1 gram of air-dry soil into a steam-distillation flask; (2) add 1 gram of solid $KMnO_4$, 0.4 gram of powdered MgO, and 10 ml of distilled water; (3) steam-distill 25 ml of liquid into 5 ml of 1% boric acid-indicator solution (Bremner 1965), and titrate with 0.005 N H_2SO_4 to determine NH_4^+-N. For 72 selected soils the relation between amounts of NH_4^+-N released chemically (X, ppm) and the amounts mineralized (Y, ppm) during anaerobic incubation (2 weeks at 35°C) was as follows: Y=0.5X - 7.5 (r = 0.85). For these same soils, the regression of Y on autoclave distillable NH_4^+-N (X), was Y=1.1X - 6.2 (r = 0.84). Other chemical methods involving extractions of mild to intermediate intensities have been reviewed (Stanford 1981).

Intensive Extraction Methods.

The possible utility of total soil organic N for distinguishing among soils of low, medium, and high N-supplying capacities should not be ruled out under appropriate circumstances. Hagin and Amberger (1974) developed a model for predicting N release from the total organic N pool, taking into account the effects of temperature, soil water content, pH, oxygen, and C/N ratio on mineralization rate. They concluded that potentially mineralizable N, N_o, and total soil N were well enough correlated that the latter reliably depicted mineralizable N in their model. Kafkafi et al. (1978) also developed a fertilization decision model in which total N was treated as the source of mineralizable N under Israeli conditions.

Determining total soil organic N is a laborious process. In our laboratory we found that the alkali-distillable NH_4^+-N released by a modified procedure for estimating organic carbon (Walkley 1947) correlated highly with total N as determined by conventional Kjeldahl digestions. We use the following version of the Walkley-Black method: (1) Weigh 1 gram of soil into a 250 ml Erlenmeyer flask; (2) add 10 ml of 1N $K_2Cr_2O_7$; (3) add 20 ml of concentrated H_2SO_4, swirling the flask during addition; (4) after 15 minutes, add 100 ml of distilled water and allow to cool to room temperature (final liquid volume is 125 ± 1 ml); (5) place suitable aliquot (e.g. 10 to 25 ml) in steam distillation flask, make alkaline with 50% (w/v) NaOH, and steam-distill the NH_3 as described above for the mild alkaline $KMnO_4$ procedure.

We have compared total Kjeldahl N and Walkley-Black distillable N for a large number of soils from the United States. Results for the 72 soils mentioned earlier are summarized in Table 1.

Table 1. Regressions of Walkley-Black distillable NH_4^+ – N on total soil organic N for 6 soils from each of 12 series in the Coastal Plain and Piedmont Plateau regions of eastern United States.

Soil series (6 soils within each series)	Regression coefficient	Correlation coefficient, r	Range, total organic N ppm
		Coastal Plain	
Beltsville sil	0.74	0.982	513-963
Fallsington sl	0.79	0.998	415-1257
Lakeland ls	0.83	0.990	242-581
Matapeake sil	0.83	0.996	457-1265
Othello sil	0.68	0.985	736-1208
Sassafras sl	0.76	0.978	442-864
(si = silt, s = sand, 1 = loam)			
		Piedmont Plateau	
Salvin sil	0.73	0.991	528-2140
Chester sil	0.79	0.968	827-1197
Gilpin sil	0.77	0.995	1031-2525
Hagerstown sil	0.74	0.990	853-2148
Myersville sil	0.72	0.989	1140-1472
Penn sil	0.82	0.995	880-1422
(sil = silt loam)			

Regression equation (Y = Walkley-Black; X = total N, ppmN)

Coastal Plain (36 soils):	$Y = 0.74X - 16.5$	$r = 0.992$
Piedmont Plateau (36 soils):	$Y = 0.70X - 0.44$	$r = 0.974$
72 soils:	$Y = 0.70X + 8.5$	$r = 0.987$

Included in the study were 6 surface soils from each of 12 soil series, equally divided between soils developed on the Atlantic Coastal Plain and the adjoining Piedmont Plateau. Soils were supplied through the courtesy of Dr. J.E. Foss, Agronomy Dept., University of Maryland. Since most agricultural and forestry laboratories have a soil collection of known total N contents, it might be informative to further explore the relation to Walkley-Black NH_4^+-N. Comparison of forest humus layers with underlying soil layers might be of interest. For the soils of Table 1, we obtained the following regression of Y (N mineralized anaerobically, 4 weeks) on X (total N):

$$Y = 0.056X - 6.0 \qquad r = 0.877$$

The regression of Y on Walkley-Black NH_4^+-N (X) was:

$$Y = 0.079X - 5.7 \qquad r = 0.874$$

It may be worth noting that the small Y-intercepts indicate that these relationships are highly linear.

DISCUSSION

A practical understanding of intensive cropping in agriculture and horticulture in relation to nutrient removal and replenishment existed long before extensive efforts in nutrient management of forests began. Contrary to common belief, however, the use of fertilizers in cultivated crops and pastures, today, is more an Art than a Science. Despite all that is known about N requirements, N cycling, and N management, progress in development and acceptance of methods for predicting optimal N fertilizer needs has been exceedingly slow. In this respect, foresters may not be far behind agriculturists.

The problems of N management in forestry, however, are much more complex than with cultivated crops. The forester is the first to concede that more detailed information is needed about the amounts and distribution of N within forest ecosystems and the nutrient-cycling processes. Development of methods for assessing year-to-year changes in the contributions of N from the soil and forest floor in relation to optimal N uptake for a given tree species and climatic regime (e.g. temperature, soil water) can progress as information about the system improves.

A direct approach to estimating needs of crops may be described as follows (Stanford 1973; Stanford et al. (1977).

$$N_c = N_i + N_m + N_f \qquad (1)$$

In this equation, N_c denotes the uptake of N associated with some specified attainable yield; N_i and N_m, respectively, denote the measured initial quantity of mineral N in the soil and the estimated N mineralized during the cropping season or specified period of time; N_f denotes the amount of fertilizer N uptake needed to meet the deficit. If the recoveries or efficiencies, e, of N_f N_i, and N_m differ, equation 2 may be written. Solving for N_f gives equation (3). If, as a first approximation, $e_i = e_m = e_f$, the N fertilizer requirement may be expressed as in equation (4).

$$Nc = e_i N_i + e_m N_m + e_f N_f \quad (2)$$

$$N_f = (N_c - e_i N_i - e_m N_m)/e_f \quad (3)$$

$$N_f = [N_c - e_f(N_i + N_m)]/e_f \quad (4)$$

In forest situations, mineral N, N_i, initially present in the soil and forest floor may be very low (Rapp et al. 1979; Hopmans et al. 1980). If present, most will be in the form of exchangeable NH_4^+. The amount of N mineralized during the season can be estimated from soil N mineralization potential, N_o (Stanford 1981) by adjusting for effects of temperature and soil water fluctuation in the field. It is possible that results obtained in this manner could be verified in the field using the method of N mineralization in situ as described by Rapp et al. (1979). The efficiency coefficient, e_f, can be based on evidence derived from recoveries of applied N in the field (Cromer et al. 1975).

It would seem reasonable to explore such an approach initially using short rotation experiments (e.g. up to 20 years) involving multiple N rates that range from zero through excessive. In addition to the kind of results obtained by Cromer et al. (1975) and illustrated in Fig. 1, the changes in the total N status and mineralization characteristics of soil and forest floor should be examined frequently. As we have found with agricultural crops, only a few such experiments are needed for a given species and age, because the internal N requirement per unit of product (e.g. % N in whole tree) is independent of the level of attainable yield (Stanford and Ayres 1974; Stanford 1966, 1973). Despite the greater complexities involved in studying forest N nutrition, I see no reason why this view should be less valid for trees than for agricultural crops.

Experiments involving fertilization of the standing forest and measurement of diameter growth responses as reported by Shumway and Atkinson (1978) offer a means of studying soil N-tree response-N fertilization relationships with uneven-aged as well as uniform stands. The studies of Turner (1977) and Heilman and Gessel (1963) suggest the possibility of using total foliage yield and N uptake by foliage as the basis for evaluating fertilizer N responses in established stands. To facilitate general interpretation, basic information may be needed on the characteristic ratios of foliage yields to total tree yields in relation to age for different species. Although the foregoing suggestions may seem inappropriate to some, they may provide food for thought in planning and conducting experiments aimed at evaluating N requirements and soil N availability in forestry.

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NITROGEN IN LITTER AND SOILS WITH REFERENCE TO THE JARRAH FOREST ECOSYSTEM

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INTRODUCTION

Research by workers in many disciplines has contributed to understanding of transfers and transformation of nitrogen in forest and agricultural ecosystems. The concepts developed from these detailed studies of processes have been outlined in a number of integrative papers and reviews, including those by Campbell (1978) and Keeney (1980). An excellent treatment of decomposition processes is given in a recent book by Swift et al (1979), which has been extensively drawn on in this paper.

My purpose here is to examine some of the available concepts, their applicability to litter and soil N in general and their possible relevance to managing the nitrogen status of the jarrah forest ecosystem in particular.

Concepts of the Decomposer Sub-System for Litter and Soils

In earlier times, N in litter and soils was simply considered as an elemental component of a nebulous material termed 'soil organic matter'. It was widely understood that this was a gross over-simplification since N occurs in many different forms including, for example plant debris, soil meso- and micro-organisms and humus. However, from the applied viewpoint, researchers were faced with a problem. How can this complex mixture be characterised to relate the soil N to its availability to plants? The techniques required needed to be simple and convenient so that adequate account could be taken of sampling problems associated with variability. Broad concepts such as C:N ratios, net mineralization of soil N, and chemical decomposition of organic N provide useful information but have not provided answers for many of the questions about N cycling and availability. Correlations between soil tests and responses to nitrogen are rather poor, even for agricultural crops where conditions are more favourable for obtaining good correlations than they are in forestry.

More recently, there has been greater emphasis on the 'living' component of soils and litter in relation to N cycling and availability. Newer approaches have been tried and techniques refined to increase understanding of N in the whole system. Some of the more notable of these approaches are:

1. Study of the decomposer sub-system recognizing the importance of decomposer organisms; the influence of the quality of detritus; and the relevance of biochemical reactions involving enzymes in decomposition (studies reviewed and integrated by Swift *et al*. 1979).

2. Development of techniques to study the microbial component of 'soil organic matter' (Jenkinson, Powlson and Wedderburn 1976; Jenkinson 1976).

3. Development of techniques to estimate the mineralizable N component of soils and the effects of moisture and temperature on ammonification, nitrification, de-nitrification and immobilization (Stanford and Smith 1972; Stanford *et al*. 1973; Watts and Hanks 1978).

Decomposition in the Litter and Soil Sub-Systems

The complex process of decomposition can be simplified by viewing the overall process as a combination of leaching, comminution and catabolism (Swift *et al*. 1979).

Leaching is essentially an abiotic process. It is more significant for soluble inorganic and organic components than for N which is generally incorporated in proteins and other non-leachable forms.

Comminution, the reduction of particle size of organic detritus, is mainly a biotic process and involves invertebrates in litter and soil.

Catabolism is an enzymatic process, mediated by animals, fungi and bacteria. The reactions are energy-yielding, often combined in sequence to form reaction chains and usually involve the transformation of complex organic molecules to smaller, simpler molecules. For example, the release of N can be represented as

$$\text{Protein} \rightarrow \text{Amino-acids} \rightarrow NH_4^+ \rightarrow NO_2 \rightarrow NO_3^-$$

Leaching, comminution and catabolism are generally inseparable in the decomposer sub-system but the sub-system can be represented by conceptual models such as that reproduced in Figure 1.

This model illustrates the breakdown of a primary resource (leaf litter) through a series of steps in a 'cascade structure'. At each step there is release of some simple organic and inorganic molecules (e.g. NH_4^+ and NO_3^-). These molecules are either 'immobilised' as part of the decomposer organisms or added to the pool of available nutrients. 'Branching' results when the different processes, leaching, comminution and catabolism, produce different resources from the same initial resource. 'Convergence' occurs when the same product is formed from different resources. Both these processes are illustrated in Fig. 1.

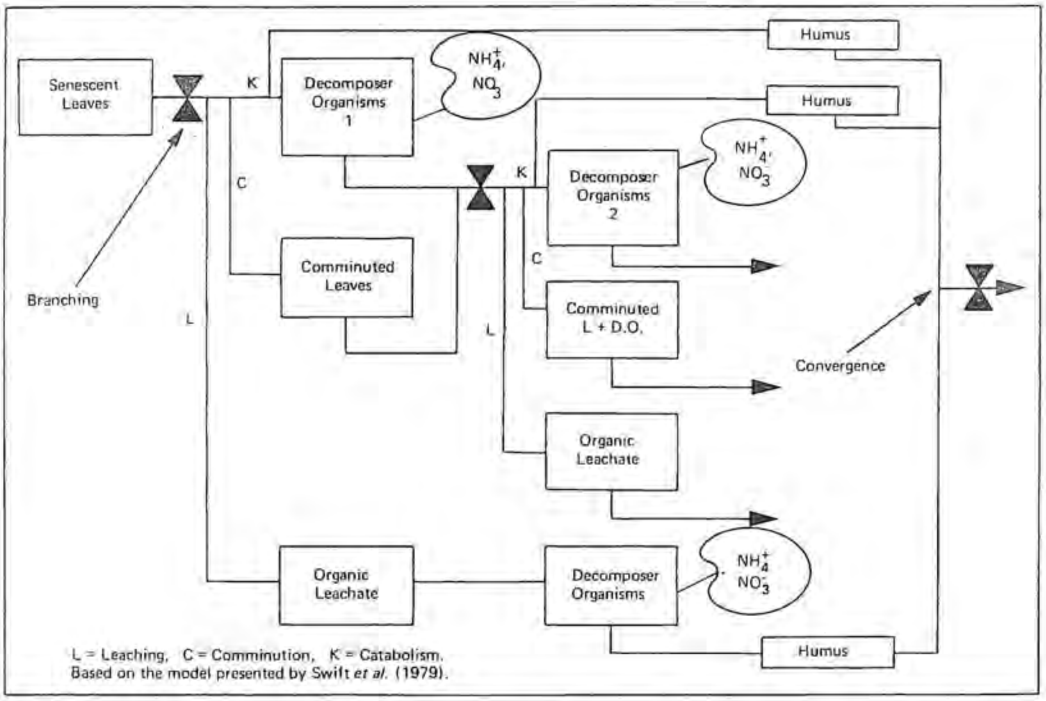

Fig. 1. A model of the decomposer-subsystem for leaf litter.

Factors Affecting the Rate of Decomposition

Organisms

There is a large degree of diversity in the types and functions of organisms operating in the cycling of N. Added to this, interactions involving meso-fauna, fungi, nematoda, protozoa and bacteria are the rule in decomposer food webs. As an aid to interpretation, Swift et al. (1979) group decomposer organisms, on the basis of their function, into necotrophs, biotrophs and saprotrophs. Necotrophs attack living organisms and kill their prey to provide a food source; biotrophs also feed on living organisms but they establish a host-parasite type of relationship with the host remaining alive; and saprotrophs utilize the nutrients in dead material. An indication that this grouping could be useful for considering mineralization of N is given in some recent papers by Elliott et al. (1979) and Anderson et al. (1979). Using microcosms containing soil to study biotic interactions and trophic dynamics, these authors found heavy amoebal grazing pressure significantly increased mineralization of

C, N and P over the action of bacteria alone. Similarly, nematodes increased the mineralization rate of nitrogen and phosphorus over the rate for bacteria alone. Both ameobae and nematodes in these experiments function as grazers on bacteria and fungi, probably as necotrophs. The suggestion from the results is that a considerable proportion of the mineralization in soils may be due to organisms in this trophic role. It could reasonably be hypothesized that bacteria, acting as necotrophs, would also release mineral forms of nutrients. On the other hand, many fungi function as saprotrophs, collecting nutrients from the dispersed state, i.e. at low concentrations in dead wood and litter, and concentrating the nutrients in their tissues. These provide higher energy and nutrient enriched substrate for the biotrophs and necotrophs. As Swift et al. (1979) point out, although this framework of trophic groups is useful for interpreting decomposition, the same organisms can perform in different groups under different circumstances. Clark (1969) characterising the soil sub-system, described it as an 'ecological jungle' with a maze of interactions and associations, thus some simplification is necessary to be able to interpret the functions of the sub-system.

Physico-chemical environment

The importance and effects of environmental factors (including air temperatures, soil temperatures, rainfall, distribution of rainfall throughout the year, nutrient levels in soils, soil chemical characteristics and soil physical characteristics) on the activities of organisms are generally well understood (Swift et al. 1979). To a large degree the differences between decomposer activity in different forest ecosystems can be attributed to the physico-chemical environment.

Resource quality

The composition and cellular structure of organic debris in the decomposer sub-system will influence decomposition rates. The physical state of debris, i.e. logs, branches, twigs, bark or leaves, to some extent determines the identity of the decomposer organism that is effective and the rate of decomposition. The availability of nutrients in organic debris as indicated at a broad level by C:N and C:P ratios for example, is also relevant. It has been shown that the rate of decomposition of organic components decreases in order from sugars to hemicelluloses, celluloses, lignin, waxes and phenols. Thus the organic compounds making up the organic matter are important, but the organization of these substances in cellular tissues has a modifying effect (Swift *et al.* 1979), as does the presence of chemical modifiers such as polyphenols.

Techniques for examining Soil Microbial Biomass

A useful method for studying the microbial biomass in soils has been presented in a series of papers by Jenkinson and his co-workers (Jenkinson and Powlson 1976; Powlson and Jenkinson 1976; Jenkinson, Powlson and Wedderburn 1976; Jenkinson 1976). In these studies, fumigation was used to kill micro-organisms and their later decomposition during incubation with freshly introduced soil micro-organisms was analysed. Jenkinson found that of the total cellular carbon in a diverse group of micro-organisms added to soil and killed by fumigation, a remarkably constant proportion (50% with a standard deviation of 8%) was evolved as CO_2 during a subsequent 10 day incubation. The flush CO_2, obtained during incubation following soil fumigation, is the basis for his proposed method for measuring soil biomass. Reasonable agreement between this method and direct microscopic measurement of soil biovolume (Jones and Mollison 1948) was found for 7 of the 8 soils Jenkinson tested. Other techniques used to estimate microbial biomass in sediments include extraction of ATP (Macleod *et al.* 1969; Ausmus 1973; Oades and Jenkinson 1979; Ross *et al.* 1980a) estimation of muramic acid (Millar and Casida 1970) and estimation of extractable lipid phosphate (White *et al.* 1979). The relationship between biomass-C, the mineral N flush and extractable ATP have been examined by Ross *et al.* (1980a) for soils from tussock grasslands in New Zealand and Oades and Jenkinson (1979) for some Australian soils. Increasing use of these techniques will provide useful data to clarify aspects of decomposition studies.

It was more difficult to generalise from the net mineralization of nitrogen than of carbon after soil fumigation, because the proportion of the biomass-N involved was more variable than the proportion of biomass for carbon. Jenkinson (1976) recovered 43% (with a standard deviation of 23%) of the nitrogen added to soils in specific micro-organisms. Studies by Ladd and Paul (1973) of nitrogen mineralization - immobilization and the effects of fumigation of soils in the field on enzyme activities, bacterial numbers and extractable ninhydrin reactive compounds (Ladd et al. 1976) illustrate some of the biochemical complexities of reactions in soils. Interactions of micro-biological and biochemical processes contribute to the difficulties of simple interpretations of microbial biomass estimates in relation to mineralization of N. Both the biomass-C and the mineral N flush were found to vary significantly between storage treatments of 28 and 56 days' storage at 25°, 4° and -20°C for four New Zealand soils (Ross et al. 1980b). The effects on biomass-C, mineral N flush and ATP differed and it was considered that no storage temperature was satisfactory for all three indices of microbial biomass. Generally the mineral-N flush changed more with soil storage than other microbial biomass indices. Storage at 4°C appeared to result in least change with time.

Amato and Ladd (1980) followed the incorporation of ^{14}C and ^{15}N labelled Medicago littoralis leaf material into microbial cells formed during leaf decomposition. They estimated that the labelling of microbial biomass reached a maximum after about 62 days when ^{14}C and ^{15}N in microbial biomass reached about 23% of the original material added to a calcareous soil. Techniques involving use of stable isotopes appear to have considerable potential for study of the changes occurring during decomposition of plant material.

Spalding (1977) reports correlations between enzymatic activities and decomposition of coniferous leaf litter resulting in production of extractable substances. His simplified conceptual model is put forward as a basis for examining the relationships between the cellular organic constituents of litter, enzymes and respiration. Spalding (1978) also concluded from his studies on litter that the decomposition of carbohydrates and proteins released from microbial biomass was responsible for the flush of CO_2 evolution following biocidal treatment. He considers that enzymatic assays are useful for following processes which release substrate for microbial assimilation from plant litter.

Modelling Nitrogen Mineralization in Soils

This topic is dealt with in detail elsewhere in this Workshop by Dr G. Stanford. Evidence that the nitrogen mineralization potential of soils offers a reliable basis for estimating mineralization (Smith *et al*. 1977) and N uptake by plants (Stanford *et al*. 1973) suggests that these techniques should receive greater attention in the forest situation. An example of the manner in which modelling of nitrogen might be applied using Stanford's methods is given in the soil - water - nitrogen model described by Watts and Hanks (1978).

APPLICATION OF CONCEPTS TO THE JARRAH FOREST ECOSYSTEM

The distribution of nitrogen in the jarrah forest ecosystem and estimates of the amounts of N involved in transfers are shown in Fig. 2.

The estimates of N capital are from a site within a pole stand located near Dwellingup, W.A. (Hingston *et al*. 1981a). Inputs of N in rainfall and in throughfall were estimated by O'Connell *et al*. (1979); symbiotic fixation of N by *Macrozamia riedlei* by Grove *et al*. (1980); fixation of N by legumes by Hingston *et al*. (1981b); non-symbiotic fixation of N in litter based on studies by O'Connell *et al*. (1979b); and N in litterfall by O'Connell *et al*. (1979a). Seven other sites in the Dwellingup area had N in the above-ground biomass of trees ranging from 151 to 401 kg ha^{-1} with a mean of 264 kg ha^{-1}; N in litter ranging from 35 to 83 kg ha^{-1} with a mean of 52 kg ha^{-1} for sites sampled 6 years after fire hazard reduction burns; and N in soils ranging from 1019 to 2391 kg ha^{-1} with a mean of 1682 kg ha^{-1}.

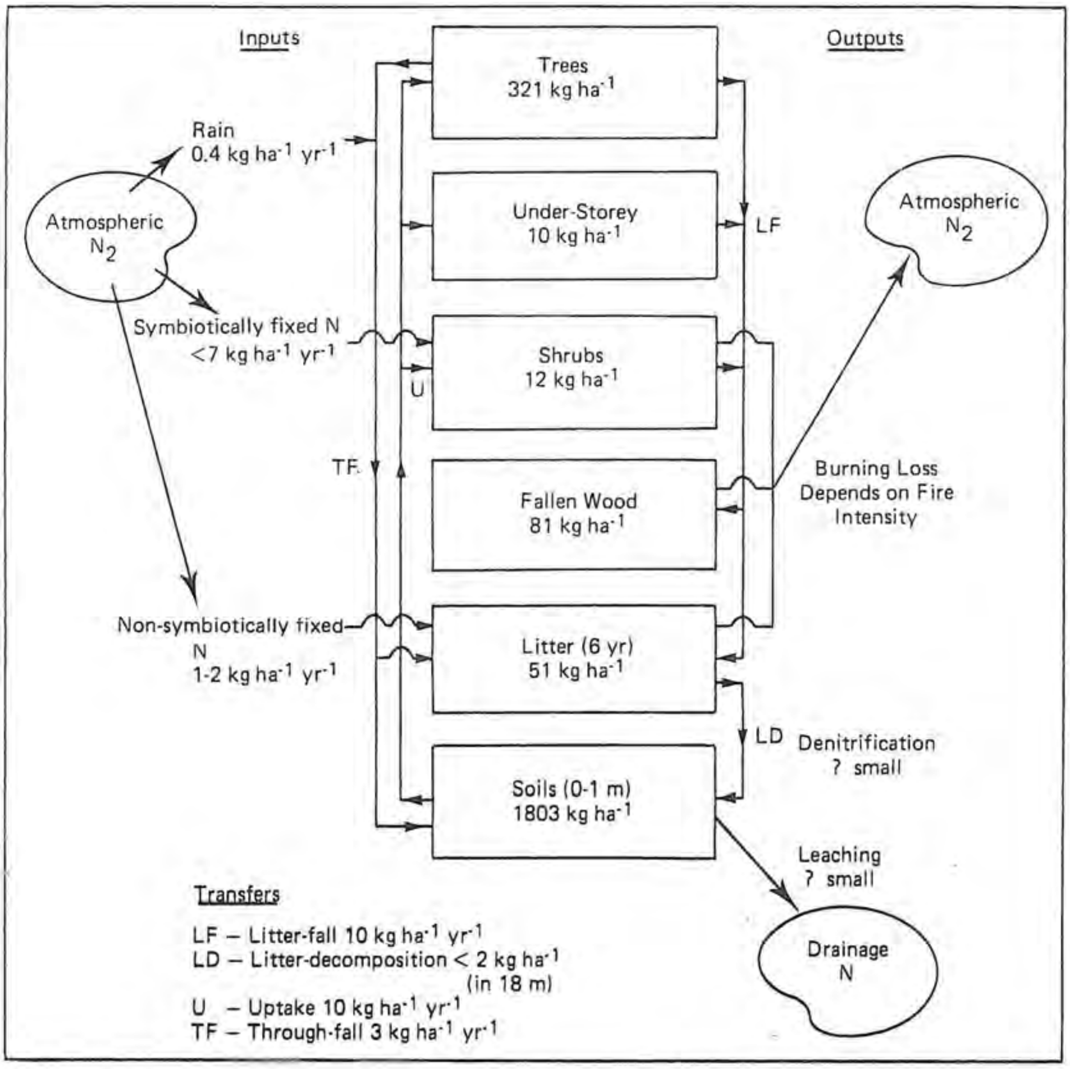

Fig. 2. Estimates of nitrogen distribution and transfers in jarrah forest sites.

The data in figure 2 indicate the small store of N in the soil; the low rate of transfer of N from litter to soil; the potential for loss of N from the ecosystem through burning of litter, fallen dead wood and low growing shrubs; and the low inputs of N through fixation from the atmosphere.

Litter decomposition

The low rates of litter decomposition, which lead to accumulation of significant quantities of fuel on the jarrah forest floor, provide problems for managing the forest. Firstly, the annual prolonged drought period characteristic of the Mediterranean climate combined with accumulation of flammable fuel creates a serious wildfire hazard. Secondly, nutrients are in short supply in the jarrah forest ecosystem and a large proportion of nutrients such as N become locked up in litter. This may limit vegetative production and, in the extreme, possibly contribute to disease related to various nutrient deficiencies. However accumulation of litter at the soil surface also has a positive role in forest management. It insulates the soil from excessively high summer temperatures, helps to conserve soil moisture through its mulching effect and may have a beneficial effect in providing a habitat for mycorrhizae and other useful micro-organisms. There is considerable evidence that development of mycorrhizae provides forest trees with a very effective means of increasing uptake of nutrients from soils where concentrations are low. It has also been suggested that ectomycorrhizae can provide protection to plant roots against soil-borne pathogens.

Thus forest managers are faced with a dilemma. How do they avoid the risk of wildfires, with consequent damage to the forest resource, destruction of property and possibly loss of lives, and yet maintain the beneficial effects of a litter layer in Mediterranean forests? Prescription burning is the method for control of litter build-up. This has already proved effective for reducing the wildfire hazard and experiments to improve techniques further are continuing. Research aims to determine the intensity, season and frequency of burning required to maintain the forest in a safe and healthy state. However the time may be approaching when alternatives to burning, or a combination of burning and other techniques, could be explored. Taking a long term view, the increasing demand for fuel may make it an economic proposition to remove waste logs and large branches from the forest and perhaps a way can be found to increase the rate of decomposition of leaf litter. This approach is probably impractical at present. However, if the decomposition rate for litter could be increased, benefits such as retention of N in the ecosystem and improvements in soil physical properties could result in higher forest productivity and better forest health.

Factors likely to affect rates of litter decompostion are environmental conditions, nutrient levels, litter quality, decomposer organisms and interactions between these factors.

The Effect of Environmental Conditions on N Release from Litter

The Mediterranean climate (with its long, hot and dry summer period) has a dominating influence on most processes in the jarrah forest. It affects the survival and activity of decomposer organisms (Springett 1979; Koch and Majer 1980) and limits the period of the year when N is mineralized. Although the climate is an unavoidable constraint, the microclimate at the forest floor may be modified by altering the tree density, shrub type and density and the thickness and type of litter. Such modifications of microclimate have been observed (Shea 1975).

Litter Quality, Decomposition and N Release from Litter

The senescent leaves, branches, bark and fruit deposited from jarrah and marri comprise most of the litter in the jarrah forest. This material has characteristically low concentrations of nutrients (O'Connell *et al*. 1978) which probably contributes to its slow rate of decomposition.

The weight of litter from leguminous species and macrozamias, N_2-fixing species, is small but high concentrations of nitrogen and other nutrients in their tissues predisposes them to rapid decomposition and adds to their significance in nutrient cycling.

Another contribution to the organic debris in litter comes from the fresh, rather than senescent, comminuted material deposited by insect grazers. This is also relatively nutrient rich and decomposes more rapidly than senescent material. Springett (1978) estimates that as much as 20% of green leaf material could be involved. If the annual addition of green leaf to the eucalypt canopy is equivalent to the leaf litter fall (3.8 tonnes ha^{-1}, O'Connell et al. 1978), then Springett's estimate suggests that the rain of insect frass and debris would contribute 3 kg N ha^{-1} yr^{-1} to the litter.

Macropod grazers also contribute a small amount to the litter decomposer system (Jones et al. in this workshop) but their total contribution to the N cycle is uncertain.

Accepting the C:N ratio of organic debris as a guide to its rate of decomposition, senescent eucalypt leaves with a ratio of 177 (O'Connell and Menagé, pers. comm.) are expected to decompose slowly. The more comminuted litter has a C:N ratio of 60, the lower ratio probably resulting from removal of soluble constituents of litter by leaching, inclusion of microbial material with a lower C:N ratio, and non-symbiotic fixation of N_2 (O'Connell et al. 1979). The C:N ratio of finely comminuted litter (60) is in the range from 40 to 60 considered to be common for forests by various authors quoted by Keeney (1980). However, the rate of mineralization of N, expressed as a percentage of total N, is reported to be extremely low for materials with C:N ratios above about 40 (Keeney 1980).

Leaching of jarrah forest litter, which removes about 27% of the dry weight, could affect its decomposition rate in several ways. Firstly the nutritional quality of the litter may be decreased by removal of inorganic nutrient elements, particularly K, and soluble carbohydrates. Secondly removal of polyphenolic constituents (tannins), which are known to inhibit the activity of some organisms (Edwards et al. 1970; Swift et al. 1979), may increase the decomposition rate of the litter. It has been estimated that freshly fallen jarrah and marri litter contain about 7% polyphenols on a dry weight basis (Hingston 1963), but to date the effect of leaching these compounds from litter on its decomposability has not been reported.

Litter Organisms and Decomposition Rates

The key role of soil invertebrates in the breakdown of litter is widely recognised (Edwards et al. 1970) but relatively few studies have been made in the jarrah forest ecosystem. Is this because the rate of decomposition is so slow that quantitatively it appears unimportant? Perhaps the scope for managing decomposition rates through processes involving invertebrates is too restricted? A preliminary investigation of litter fauna made by McNamara (1955) and subsequent studies by Springett (1976, 1979) have been concerned with the effects of burning on invertebrate numbers and species present. Feeding experiments by Springett (1979) using the common millipede (Podykipus sp.) and litter from Eucalyptus, Banksia and Bossiaea species allow some estimates to be made of daily consumption of litter under favourable conditions. These data, together with population estimates and estimates of the periods when conditions would be favourable, allowed Springett to calculate that the input of finely divided faecal material to the soil would probably be between 10 and 180 kg ha^{-1} yr^{-1} (for faecal material with 0.35% N this is equivalent to 0.035 to 0.63 kg N ha^{-1} yr^{-1}), the amount depending on a number of environmental conditions. Koch and Majer (1980) have recently identified groups of decomposer and predator invertebrates at jarrah forest sites. They relate the species richness and abundance to soil type, fire history and climatic pattern.

O'Connell and Menagé (pers. comm.) have conducted a series of litter-bag studies to determine the decomposition of litter through comminution by invertebrates, leaching and catabolism at several jarrah forest sites. The litter in their nylon mesh bags appeared to be largely physically intact after two winter-spring periods (18 months) on the forest floor. There was an average of 45% loss in dry weight, but much of this was due to leaching of soluble components rather than comminution. The rates of N loss

(b) Relationship between Properties.
Linear regression Y = b + mX

Y	X	b	m	r*	Significance
Potentially mineralizable N ($\mu g\ g^{-1}$)	N-flush Anaerobic incubation N ($\mu g\ g^{-1}$)	4.60	6.02	0.98	$p < .001$
	Biomass-C ($\mu g\ g^{-1}$)	-2.36	0.50	0.86	$p < .001$
	Total N(%)	32.5	503	0.64	$p < .05$
	Organic C (%)	1.25	31.21	0.96	$p < .001$
	Lipid-P ($\mu g\ g^{-1}$)	4.99	88.6	0.90	$p < .001$
Biomass-C ($\mu g\ g^{-1}$)	Lipid-P ($\mu g\ g^{-1}$)	37.6	148	0.88	$p < .001$

* r is the correlation coefficient.

Table 1. a) Soil characteristics relating to nitrogen availability, Cobiac Forest Block

Soil Type	Depth (cm)	N (%)	C (%)	Ratio C/N	1. Potentially Mineralizable N ($\mu g\ g^{-1}$)	2. Biomass C ($\mu g\ g^{-1}$)	3. Flush N-Mineralization (Anaerboic Incubation) ($\mu g\ g^{-1}$)	4. Lipid Phosphate ($\mu g\ g^{-1}$)
Yellow Sand	0-10	.062	2.12	34	57	262	5.8	.80
(<2mm fraction)	10-20	.042	1.26	30	45	106	7.8	.52
	20-30	.032	0.90	28	41	84	7.2	.32
Fine Yellow	0-10	.070	2.94	42	73	128	9.3	.92
	10-20	.030	1.00	33	37	60	3.5	.32
	20-30	.025	0.82	33	36	50	5.0	.27
Yellow Gravel	0-10	.131	5.95	45	216	368	33.8	1.91
(<2mm fraction)	10-20	.055	2.25	41	75	150	15.5	.52
	20-30	.040	1.65	41	64	102	9.4	.32
Orange Earth	0-10	.263	5.77	22	165	266	26.2	1.89
(<2mm fraction)	10-20	.163	2.33	14	68	188	11.0	1.02
	20-30	.132	1.85	14	38	118	8.3	.84

Notes
1. Incubation procedure (Stanford *et al.* 1974)
2. Method of Jenkinson and Powlson (1976)
3. Method of Waring and Bremner (1964)
4. Method of White *et al.* (1979)

from the bags was very low, only 8% of the original weight of N was lost from jarrah litter and 3% from marri litter in 18 months. Interpretation of the study is complicated to some extent by a gain of N in the first year, possibly due to invasion of the bags by micro-organisms and fungi, and by N added through N_2 fixation. Litter-bag studies have been criticized because completely natural conditions cannot be reproduced (Witkamp and Olsen 1963; Anderson 1973). However, they allow a first estimate of decomposition and nutrient losses from litter, provided they are carefully interpreted. The studies show that the quantity of N transferred from the litter bags to the soil was at least 2 kg ha^{-1} in the 18 month period. This indicates the very slow transfer of N from the litter layer to the soil. N accumulated in litter at the surface of the soil, i.e. not incorporated, is in a position where a considerable proportion of it may be lost from the ecosystem during prescribed burning or wildfires.

Soil N and Mineralization in the Jarrah Forest

Reports of mineralization of N in jarrah forest soils are not available in the literature to the present time. Recently, however, estimates have been made of the seasonal variation of mineral N and the net mineralization of N at 12 sites on gravelly (15 to 70% ferruginous gravel) sites near Dwellingup. These showed generally low concentrations of ammonium (1.1 to 3.3 μg N g^{-1} in the surface 5 cm of soil) and lower concentrations of nitrate (0.2 to 0.5 μg N g^{-1}). Experiments to estimate net mineralization of N on undisturbed cores in the field and in the laboratory indicated very low values. The coefficient of variation was high but estimates after 4 weeks' field incubation gave mean net mineralization of about 1 μg N g^{-1} soil (0-5 cm in depth). Cores returned to the laboratory gave mean net mineralization of about 1 μg N g^{-1} soil after two weeks incubation at 25°C. These values are on a whole soil and oven dry basis, where some of the soils contained up to 70% ferruginous gravel.

Examination of samples from three depths in four common soils in the jarrah forest using a variety of techniques gave the results shown in Table 1.

Correlations between potentially mineralizable nitrogen (Stanford et al. 1974) and mineralizable nitrogen estimated by anaerobic incubation (Waring and Bremner 1964) seems likely to be useful since the former technique takes longer to determine and is more involved than the latter.

The other correlations are in general agreement with data obtained for other soils. This lends weight to the evolving ideas about nitrogen mineralization processes. Modelling procedures taking into account the effects of soil moisture and temperature such as those suggested by Stanford and others show promise for providing an understanding of nitrogen availability in forest systems.

CONCLUSIONS

Managing the N in soils and litter in a natural ecosystem such as the jarrah forest presents a complex set of problems. Recent concepts of the decomposer sub-system for litter and soils help to provide the kind of framework needed to understand the cycling of N. Modelling techniques incorporating environmental variables and the characteristics of soil N are useful for determining N mineralization and providing a better basis for considering N availability than was available previously. However, given the constraints of a dry-sclerophyll eucalypt forest with low productivity growing in a region with a Mediterranean climate, the practical problems of manipulating the decomposition of litter, conservation of N and controlling mineralization of N provide a challenge for managers of the forest resource.

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FACTORS AFFECTING NITROGEN MINERALIZATION IN AN ACID SANDY FOREST SOIL

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ABSTRACT

Nitrogen mineralization was studied in acid sandy forest soil using incubation at 35°C for a total of 19 weeks. Factors affecting N mineralization included soil OM, soil mixing and liming. Soil OM has the major effect on the mineralization potential (N_o) and rate. Soil mixing alters the rate of mineralization. Liming or practices which reduce soil acidity will result in a change of mineralized N from NH_4 to NO_3, if pH is stabilized above 4.5.

INTRODUCTION

Soil N mineralization has been subject to extensive investigation over the last 30 years. Such studies were motivated by the need for rapid and reliable methods of assessing soil N availability. The most reliable were those involving incubation techniques (Bremner 1965). Stanford and co-workers (1955, 1972, 1973, 1974) developed incubation techniques for assessing and indexing a large range of agronomic soils according to their ability to mineralize N. Their methods have been used to assess the impact of organic amendments to soils (Epstein et al. 1978; Timm et al. 1980) and to gauge the relative effects of disturbances at site preparation for slash pine reforestation (Burger 1979). Most researchers have confined themselves to relatively fine textured agronomic soils; in fact, Verstraeten, Vlassak, and co-workers, in a series of studies (1969, 1970a, 1970b, 1972) using incubation techniques, found that agronomic soils should be handled separately from forest soils for regression analysis between water-soluble carbon and mineralized N. They also found that sandy soils did not behave in the same way as loamy or clayey soils with respect to mineralization of nitrogen. One clear difference between sandy podzolic soils (Spodosols) and clay rich soils is the nature of the cation-exchange complex. Sandy soils rely heavily on organic matter to supply exchange capacity with the clay complex providing this in finer textured soils.

This paper describes the impact of soil organic matter, soil mixing and soil liming procedures on nitrogen mineralization in an acid sandy forest soil.

MATERIALS AND METHODS

These experiments were conducted on soil commonly supporting slash pine (Pinus elliottii Engelm) in central Florida, U.S.A. The climate was sub-tropical with a mean annual temperature close to 21°C. The mean temperatures for the hottest month (July) are 33°C maximum and 22°C minimum; the corresponding temperatures in the coldest month (January) are 21.5°C and 12°C. Mean annual soil temperature at 50 cm is 23°C (hyperthemic).

Wauchula sand (Ultic Haplaquod, humus podsol, U_c 2.20) was sampled using PVC tubing 4.5 cm in diameter by driving sharpened tubes into the litter and surface soil. Intact cores taken in this fashion were paired with samples which had been mixed and sieved to homogenize the soil, and the soil then repacked into the PVC sampler.

The leaching solution used was 0.01 M $CaCl_2$ and it was found that 400 ml of solution was necessary to leach a soil column 15 cm x 4.5 cm. Ten core pairs were leached in this fashion, then incubated for five periods up to 40 days at 30°C, with a final leaching made after 131 days. NH_4-N and NO_3-N were determined on the leachates by steam distillation (Bremner 1965).

Soil organic matter (Walkley-Black) was determined for each soil core and values obtained used in regressions of cumulative NH_4-N mineralized.

When measured in 0.01 M $CaCl_2$, the solution used for the removal of mineralized N from the soil, the average soil pH fell by over 1.1 units compared with pH measured in water. In an attempt to counteract this salt effect on soil pH, $Ca(OH)_2$ was mixed with the soil. The average amount of $Ca(OH)_2$ required to raise and maintain the average soil pH from 3.2 to 4.3 was estimated to be 1.00 meq/100 g soil by titrating soil samples with $Ca(OH)_2$ in a 1:2 suspension of leaching solution. Four replicate cores from a soil sample were prepared without lime to compare effects of liming on N mineralization over time.

RESULTS

Unless the soil was limed NO_3-N was at the level of detection and was ignored.

Effects of Soil Organic Matter

From the first leachings the amount of NH_4-N mineralized and rate of mineralization varied from core to core. Figure 1 shows this core variation. Table 1 includes OM analyses for 18 cores and the cumulative NH_4-N at day 131. The linear relationship between cum. NH_4-N and soil OM% is clearly demonstrated in Figure 2.

Stanford and Smith (1972) demonstrated a linear relationship between cum. NH_4 and $\sqrt{Time}$ for many soils. The same relationship was true for this acid forest soil and the slopes of the regression cum. NH_4-N vs $\sqrt{Time}$ for each core indicated the mineralization rate for each core. In turn, when the slopes of these individual regressions were regressed against core OM% it was plain that OM% controlled rate of mineralization (Figure 3).

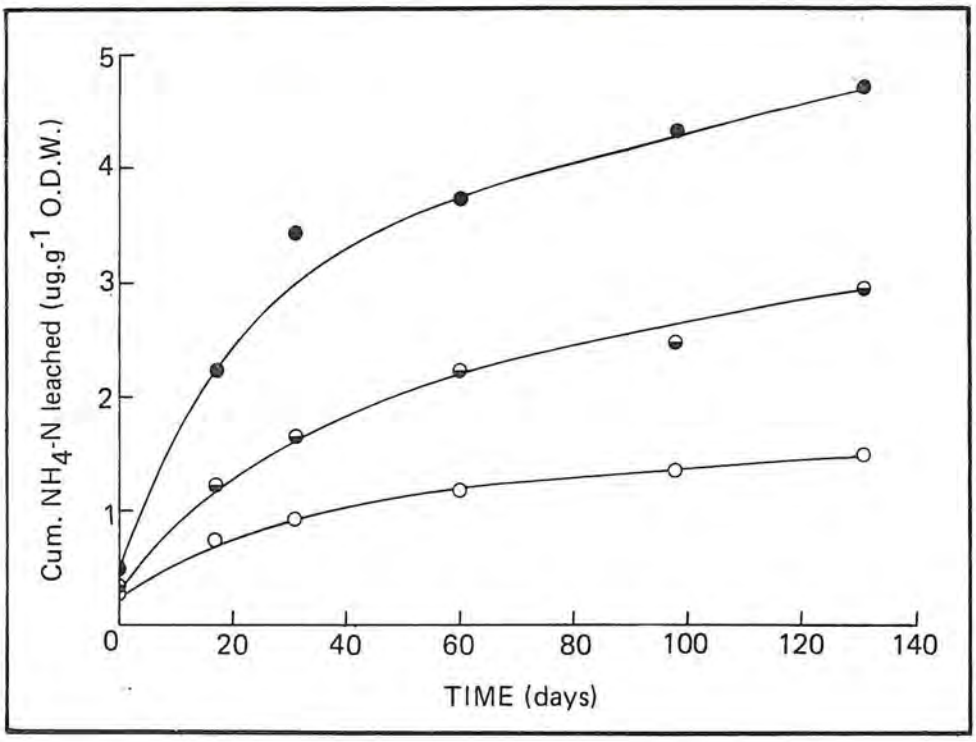

Fig. 1. Cum. NH_4-N leached from three different soil cores during 131 days.

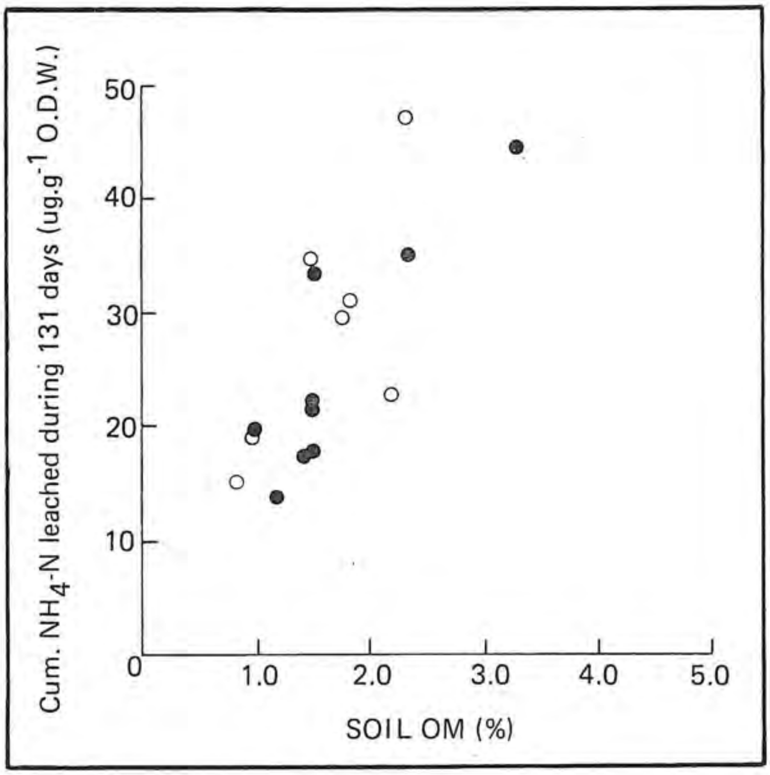

Fig. 2. Cum. NH_4-N leached during 131 days for intact (O) and homogenized (●) soil cores versus soil OM%.

Table 1. Cum. NH_4-N at Day 131 and Soil O.M.

Core No.	Code	Soil OM%	Cum NH_4-N ug g^{-1} O.D.W.	Code	Soil OM%	Cum NH_4-N ug g^{-1} O.D.W.
1	I	1.49	34.6	H	1.53	33.2
2	I	1.22	21.3	H	1.00	19.8
3	I	2.32	47.0	H	3.29	44.5
4	I	1.84	31.0	H	1.51	21.6
6	I	2.17	22.7	H	1.51	22.3
7	I	1.77	29.5	H	1.42	17.4
8	I	0.97	19.1	H	1.19	13.7
9	I	1.37	21.9	H	2.35	35.2
10	I	0.84	15.0	H	1.51	17.8

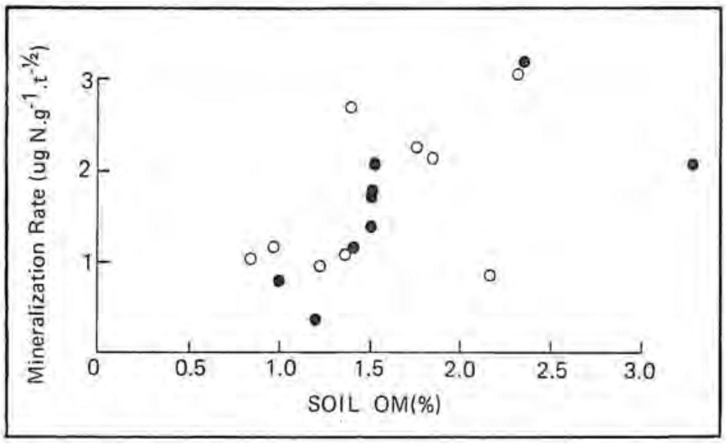

Fig. 3. Rate of mineralization for varying OM.

Intact vs Homogenized Soil Cores

On first inspection (Figure 2) there appeared to be little difference between intact and homogenized soil cores. When a reciprocal plot of cum. NH_4-N against time is made (Stanford and Smith 1972) the following relationship was demonstrated.

$$\frac{1}{N_t} = \frac{1}{N_o} + \frac{b}{t}$$

where N_t = ug N.g^{-1} O.D.W. soil mineralized during specific time t;

b = slope; and

N_o = N mineralization potential.

Linear regression coefficients were calculated for the above relationship and r values were generally around 0.98 for separate cores whether intact or homogenized.

Cum. NH_4-N was adjusted for core OM% and the coefficients N_o and b compared from regressions of all intact cores and all homogenized cores (Table 2).

Table 2. Regression coefficients for the relationship $\frac{1}{N_t} = \frac{1}{N_o} + \frac{b}{t}$

	$\frac{1}{N_o}$	N_o	b	r
Intact Cores	0.053	18.9	0.143	0.79
Homogenized Cores	0.063	15.8	0.229	0.64

Mineralization potential (N_o) did not differ greatly between core types, but mineralization rates were clearly different.

Effect of Liming

By keeping the soil pH from dropping below field levels, N mineralization in limed cores was expected to be enhanced. However, no significant change was observed in total amounts of mineralized N in soils from virgin and disturbed forest sites. Liming caused a 7% decrease in mineralized N from an intensively prepared site which was opposite to the expected result. Although liming had little effect on deamination and ammonification, nitrification was very sensitive to soil pH in this forest soil. NH_4-N and NO_3-N leached from soil columns during the final period were paired and plotted with soil pH values (Figure 4). A threshold value of around 4.5 was shown to be critical for nitrification. There was no nitrification below this pH but above this pH nearly all N was in the NO_3-N form. The critical pH, at which nitrification can begin, is about one unit lower than generally reported for agricultural soils.

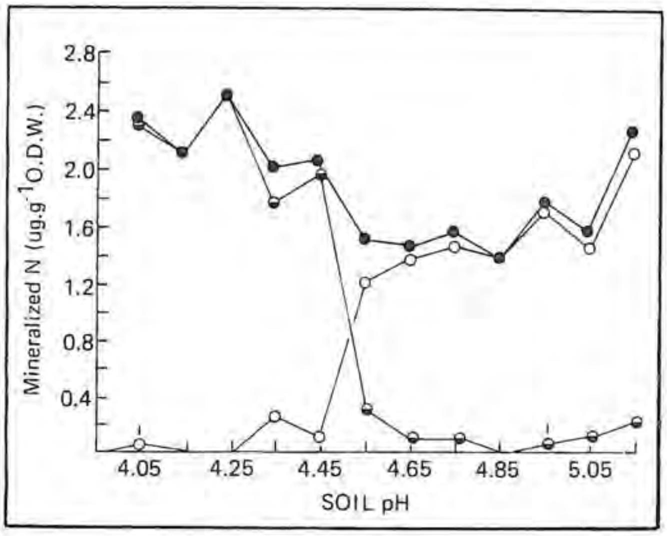

Fig. 4. The effect of soil pH on nitrification.

DISCUSSION

Incubation techniques used by Stanford et al. (1955, 1972, 1973, 1974) when applied to an acid forest soil revealed the strong influence of soil OM% on N mineralization. A similar contribution of soil OM% to this process was mentioned by Stanford* for agricultural soils. However, we believe that although the influence of OM% on cation exchange capacity was well known for acid sandy soils, the high correlations obtained in these studies for the effect of OM% on N mineralization were not fully appreciated. Once the effect of OM% is recognised and its overriding influence accounted for, then the effects of manipulations such as soil mixing and liming can be better analysed and interpreted. Disturbance of an acid sandy soil does not appear to result in a shift from NH_4-N to NO_3-N as might be expected from other forest soils considered by Vitousek and Melillo (1979). Soil conditions which favour ammonification and not nitrification can then be thought to

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* Stanford, G. (1980). Personal communication during discussions held at this workshop.

enhance N conservation as NO_3-N is subject to additional and/or more rapid pathways of loss from the soil. Liming can be thought of as a chemical disturbance with the potential to shift the form of mineralized N from NH_4-N to NO_3-N in forest soils as in agricultural applications.

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NITROGEN CYCLING IN KARRI (*Eucalyptus diversicolor* F. Muell.) FOREST LITTER

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INTRODUCTION

Litter production and decomposition play a major role in the transfer of energy and nutrients in forest ecosystems (Bray & Gorham 1964). In this paper we report on the N content of litter fall, the pools of N in components of forest floor litter and the rate of release of N from decomposing litter in pole stand karri (*Eucalyptus diversicolor* F. Muell.) forest.

The study area, located in Big Brook forest 6 km north west of Pemberton, W.A., has previously been described by Hingston *et al*. (1979). The site contains a karri pole stand overstorey aged approximately 40 years and a diverse understorey dominated by *Bossiaea laidlawiana* Tovey and Morris with smaller amounts of *Trymalium spathulatum* (Labill.) Ostf., *Acacia urophylla* Benth. and *Casuarina decussata* Benth. A cool prescribed fire burnt through the area in 1970-71.

LITTER FALL

Seven litter trays (area 0.372 m^2) were randomly located within the 50x50 m study plot. Litter was collected monthly for 2 years during 1977 and 1978, sorted into 12 litter components, weighed and analysed for N (Table 1).

The pole stand overstorey contributes about 80% of annual litter fall weight compared to 20% from understorey stratum. However, the concentration of N in litter originating from the understorey is relatively high in comparison with that from the karri overstorey. This is particularly so for the legume plants - for example B. laidlawiana leaf litter contains N at levels more than 3 times that found in eucalypt leaf litter. Therefore, although the weight of litter from the understorey is considerably smaller than from the overstorey, the weight of N returned to the forest floor annually by the two strata are approximately the same.

Table 1. Weight (ka ha^{-1} $year^{-1}$), nitrogen concentration (%) and nitrogen content (kg ha^{-1} $year^{-1}$) of components of annual litter fall in a 40 year old karri pole stand.

Litter Component		Litter weight (kg ha^{-1} $year^{-1}$)	N concentration (%)	N content (kg ha^{-1} $year^{-1}$)
Overstorey	Karri leaf	2698	0.61	16.3
	Karri twigs	1739	0.28	4.9
	Karri bark	744	0.27	2.0
	Karri fruit	200	0.24	0.5
Understorey	*B. laidawiana* leaf	797	2.02	16.1
	T. spathulatum leaf	227	0.76	1.7
	A. urophylla leaf	43	1.47	0.6
	Other understorey leaf	80	1.00	0.8
	A. urophylla seed pods	7	0.76	0.1
	B. laidlawiana seed pods	36	0.68	0.2
	B. laidlawiana flowers	36	2.26	0.8
Unidentified litter fragments		543	0.94	5.1
Total litter		7150	0.70	49.1

The leaf fraction of litterfall contributes about half of the total litter weight and, because it is relatively rich in N compared with other major litter components, it accounts for almost three quarters of the annual accession of N to the forest floor. More than half of the leaf litter N (54%) originates from the understorey plants, the major contributor being B. laidlawiana.

FOREST FLOOR LITTER

Forest floor litter was collected from 18 quadrats (0.5 x 0.5 m) within the study area. Samples were dried, sorted into four components (karri leaf, karri twig, karri bark and a fine litter fraction <1 cm) and analysed for N.

In the 9 years since the site was last burnt over 30.8 t ha^{-1} (SEM 2.2 t ha^{-1}) of forest floor litter accumulated (Table 2). Approximately half of this consists of fine material <1 cm. Major contributors to the fine litter component are understorey leaves, particularly B. laidlawiana, and fragmented eucalypt leaves. Compared with the twig, bark and karri leaf fractions the N concentration in fine litter is relatively high. More than 70% of the forest floor litter N pool is contained within the fine litter. Twigs, which account for about one third of the forest floor litter weight contain 15% of the litter N while karri leaves and bark each contain about 8% of the litter N.

Table 2. Weight (t ha^{-1}), nitrogen concentration (%) and nitrogen content (kg ha^{-1}) of components of forest floor litter in 40 year old karri pole stand.

Litter component	Litter weight (t ha^{-1})	N concentration (%)	N content (kg ha^{-1})
Karri leaf	2.67	0.78	20.9
Twigs	9.97	0.39	38.4
Bark	3.75	0.53	19.9
Fine litter < 1 cm	14.41	1.17	169.0
Total litter	30.80	0.81	248.2

LITTER DECOMPOSITION

Freshly fallen litter was collected on nets during the peak period of litter fall, sorted into components and placed in 25 cm x 25 cm mesh bags (1.4 mm aperture). Thirty two bags of each litter type (15 g/bag) were placed in the forest in April 1977. At intervals throughout the following two winters sets of bags (4/litter type) were returned to the laboratory, dried, cleaned, weighed and analysed for N.

Loss of dry weight increased in the order karri twig < karri leaf ≅ B. laidlawiana leaf < T. spathulatum leaf (Fig. 1). Leaves of T. spathulatum were reduced to half their original weight after 6 months on the forest floor, whereas both karri and B. laidlawiana leaves required 18 months to reach this stage of decomposition. Weight loss from karri twigs was slow and approximately linear, about 5% of the original weight being lost in each 6 month period.

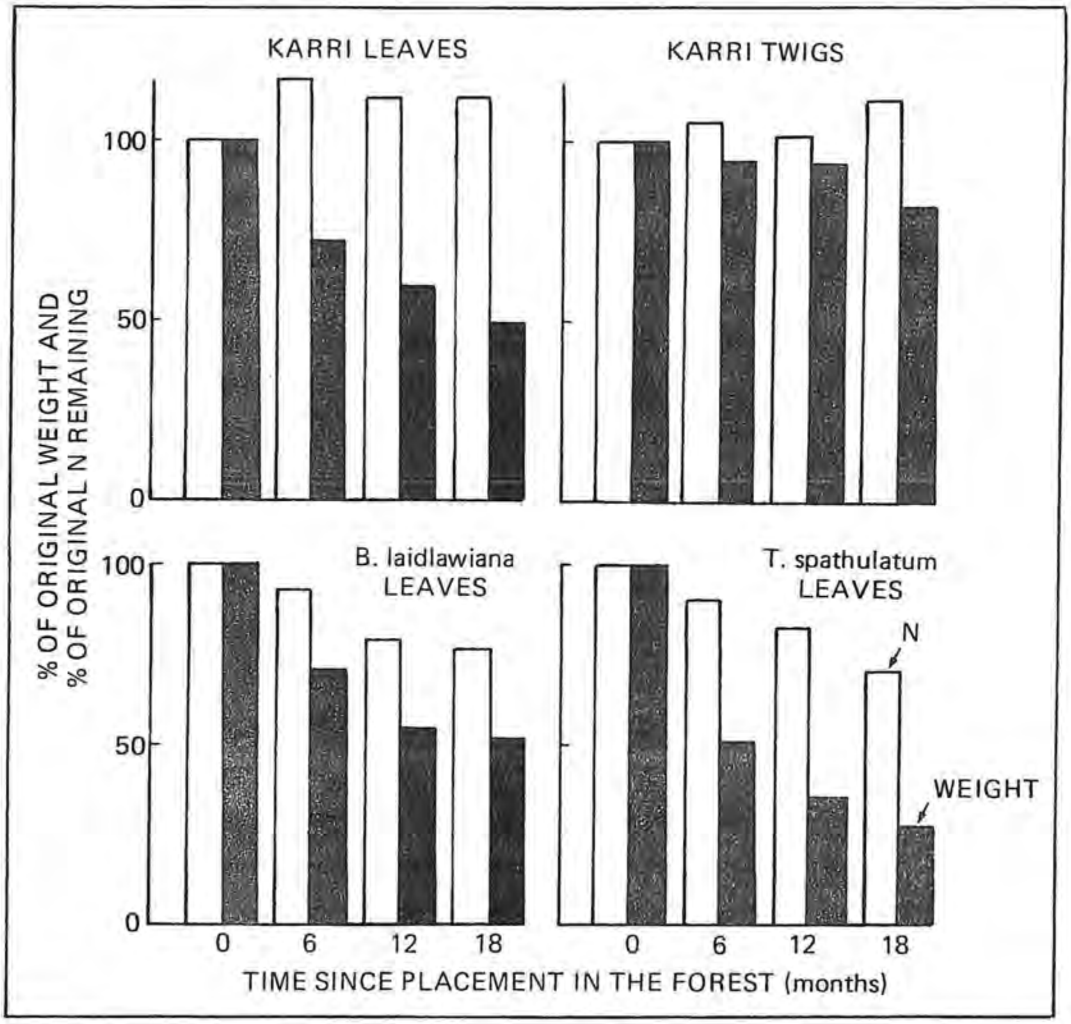

Fig. 1. Percentage of the original dry weight (shaded area) and amount of nitrogen remaining in mesh bags containing karri forest litter after 6, 12 and 18 months on the forest floor.

Changes in N content during decomposition differed between overstorey and understorey litter components. In the bags containing karri leaf and karri twig litter there was an increase in weight of N during the period of the experiment. In contrast, *B. laidlawiana* and *T. spathulatum* leaf litter each showed a net loss of N 6, 12 and 18 months after placement in the forest. However, even for the understorey leaf litter, loss of N was slower than loss of dry weight.

DISCUSSION

Our data indicates the importance of the understorey stratum in nitrogen cycling in karri forest. Although understorey accounts for only approximately 5% of the above ground biomass on this site (Hingston et al. 1979) it constributes 20% of the annual litter fall and about half the annual return of N to the forest floor. Leaf material, which is the most rapidly decomposed major litter component, contains almost three quarters of the N returned annually to the forest floor and more than half this N is in leaf litter from the understorey. Release of N from forest floor litter appears to be primarily associated with understorey components, at least in the first two winters following litter fall.

In addition, a greater proportion of the N in the legume biomass may be available for external cycling through litter fall than is the N in the eucalypt biomass. Much of the foliar N in karri appears to be redistributed, or biochemically cycled (Switzer and Nelson 1972) prior to litterfall. Comparison of N concentrations in mature green leaves and leaf litter of karri suggests that about half the N is withdrawn prior to abscission. A smaller proportion of the foliar N of the legumes B. laidlawiana and A. urophylla appears to be withdrawn before litterfall.

In the 9 years since the study site was burnt 30.8 t ha^{-1} of forest floor litter accumulated. Assuming steady state conditions, this corresponds to a litter half life of 3 years (Olson 1963). Half life of N in litter is longer since loss of N is slower than dry weight loss resulting in a relative enrichment of N in forest floor litter compared to fresh litter (Tables 1 and 2).

During the first 3 years following burning there are probably only small inputs of understorey litter to the forest floor because in this period the understorey is at an early stage of development. Thus, total N inputs in litter fall during the 9 year post fire period are probably 350-370 kg ha^{-1}. Nitrogen is released slowly from the decomposing litter and approximately 70% (248 kg ha^{-1}) of the litter fall N remains in the forest floor nine years after burning. This represents a substantial pool of N, approximately equal to the N contained in the above ground biomass (Hingston *et al*. 1979). A considerable proportion of the forest floor N is likely to be released to the atmosphere during burning (Debell and Ralston 1970) - an important factor to consider when choosing the period between successive fire hazard reduction prescribed burns.

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SESSION 5.

Basic Biological Processes

(c) Nitrogen Cycling and Losses

THE CYCLE OF NITROGEN IN FORESTS

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INTRODUCTION

Much is now known of the cycle of nitrogen in forests (Fig. 1 from Weetman 1961) although surprisingly little work has been done in Australian forests. In general, gains of N in rainwater and by fixation exceed the losses from the undisturbed forest so that steady rates of accumulation of N up to 10 kg ha^{-1} $year^{-1}$ (e.g. Gessel et al. 1973) are generally found although rates as high as 70 kg ha^{-1} $year^{-1}$ (e.g. in loblolly pine, Switzer et al. 1968) have been recorded.

The amounts of N cycling in forests may be large relative to the demands for new growth. Switzer et al. (1968) showed that, for 20-year-old loblolly pine, the total demand for growth and replacement was 70 kg ha^{-1} $year^{-1}$. Biochemical cycling within the stand supplied 32 kg ha^{-1}, or 46% of the demand. Biogeochemical cycling accounted for 30 kg ha^{-1}. New growth accounted for the remaining 8 kg ha^{-1}, or only 11% of the total N in the annual cycle.

This paper is concerned with aspects of this large annual cycle of N in forests. We discuss first the mineralization process in forest soils, the process by which organic N again becomes available to plants. Secondly we discuss the significance of N_2-fixation to N cycling in Australian forests. Finally, we discuss both processes in relation to reported losses of N from forests following clearfelling.

NITROGEN TRANSFORMATIONS IN FOREST SOILS

While the amount of N in the litter layers and in the soil is very large (Fig. 1), only a small amount, less than 5% of the soil N, is in inorganic forms. The organic N is mineralized in the process of ammonification by heterotrophic microorganisms.

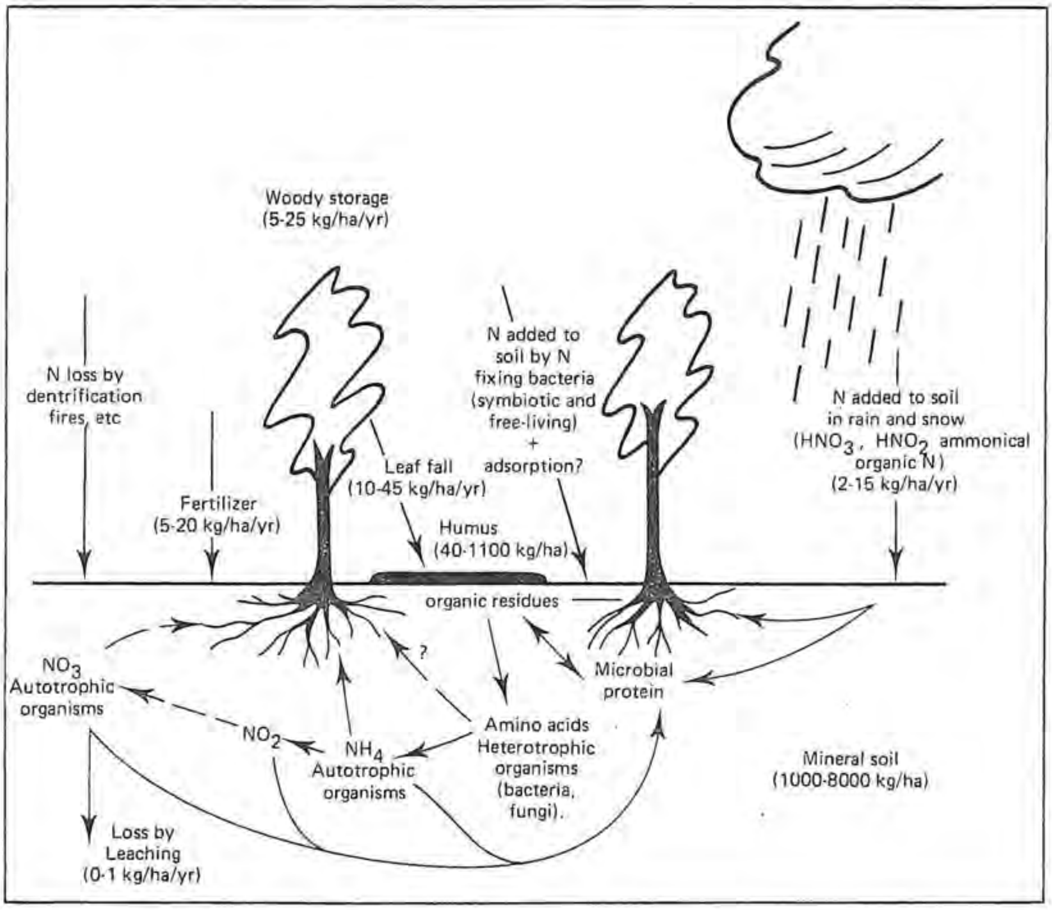

Fig. 1. The nitrogen cycle in temperate forest stands. (from Weetman, 1961)

In Jansson's (1958) classic paper, the high N content of microbial protoplasm (5-12% N) is maintained by a "continuous internal cycle" of NH_4^+ uptake. If the plant root is to feed on NH_4^+, it must do so in competition with immobilization of NH_4^+ by the heterotrophs and Jansson showed that the heterotrophs are better competitors than the autotrophs. Nitrification by autotrophic bacteria is therefore competitively minimized when the heterotrophs are presented with abundant energy in an environment where N is scarce. In such a situation, the ability of the autotrophic plant to compete successfully must be dependent on mycorrhizae; by this association, the autotrophic plant becomes heterotrophic for N when the N is present as NH_4^+. The NH_4^+ - nitrogen may be formed into glutamine in the fungus and the glutamine moves from fungus to root. Raven et al. (1978) suggest that the symbiont, in assimilating "non-pH-perturbing" glutamine, may also get rid of the excess H^+ which would otherwise accumulate in the plant cell.

In the mature temperate forest, litter fall is of the order of 3-5 x 10^3 kg ha^{-1} $year^{-1}$ and in tropical forest, as high as 10 x 10^3 kg ha^{-1} $year^{-1}$. Litter fall in temperate forests has a C/N ratio of the order of 70 or more. Applications of these amounts of high C/N litter to an agricultural soil would lead to nitrogen deficiency, yet the first detailed study of forest nutrient cycles (Ebermayer 1876) showed that the continuous removal of forest litter resulted in a decrease in forest growth.

Our studies have concentrated on the pattern of mineralization in forest soils and on the presence and inducibility of the enzyme nitrate reductase in the roots and leaves of forest trees. The simple hypothesis of the first study is that we expect forest soils to be ammonifying because of the large annual input of litter with a high C/N ratio. The hypothesis of the second study is that nitrate reductase activity (NRA) should be a good measure of the extent to which the tree is feeding on NO_3^- - nitrogen and hence, the extent to which mineralization in the forst soil has proceeded to nitrification.

The results are as expected:

(a) Soils under *Eucalyptus obliqua* forest and under *Pinus radiata* forest show little nitrification. Tree roots have only low NRA.

(b) Soils under thickets of *Acacia dealbata* are strong nitrifiers and the tree roots have high NRA.

(c) Soils supporting the most productive forest we have studied, *Eucalyptus regnans*, may show considerable nitrification. NRA is significant, but not to the same extent as in *A. dealbata*.

Following destruction of the previous rotation and establishment of the new crop (by fire and natural regeneration for the eucalypts, by clearing and planting for the pine) all the soils had probably become nitrifiers. Subsequent patterns of growth have determined whether mineralization in the mature forest stops at NH_4^+ nitrogen or proceeds to NO_3^- nitrogen. We have also added N at rates up to 1000 kg ha^{-1} to a mature pine forest which had developed a strongly ammonifying soil. These additions have reduced the C/N ratio to a level where N mineralization proceeds to NO_3^- nitrogen. NRA has been induced in the roots of the trees which were previously taking up only NH_4^+ - nitrogen.

From these studies we have formed the working hypothesis that most temperate forest soils will be ammonifiers; nitrification will result, however, under conditions favouring high productivity where an initial large pool of soil N is turned over rapidly. The hypothesis is supported by the work of Youngberg (1978) in Douglas-fir: "Although there appeared to be some factors other than total N content influencing N availability, the results show that the materials with the highest sustained N mobilization rates come from the highest site-quality Douglas-fir types". The measurement of appreciable nitrification in tropical forests (Pfadenhauer 1979) also supports the hypothesis; very high turnover rate in tropical forest results in only small amounts of N held in litter in the forest floor (Table 1). If we assume a concentration of N in litter fall of 0.5% and a litter fall of 10×10^3 kg ha^{-1} $year^{-1}$, the amount of N in litter on the forest floor of the tropical forest indicates a turnover time of about one year. In contrast, if we assume a litter fall for boreal forest of 2×10^3 kg ha^{-1} $year^{-1}$, we calculate a turnover time for N in the forest floor (Table 1) of about 70 years; we would expect the boreal forest soil to be strongly ammonifying.

Table 1. Distribution of nitrogen within major forest ecosystem components (from Pritchett 1979).

	N content (kg ha^{-1})		
Forest type	Living biomass	Forest floor	Mineral soil
Boreal	252	699	1 556
Loblolly pine	321	307	1 753
Tropical moist forest	2 016	35	4 592

INPUTS OF N TO FORESTS

Input of N to forest ecosystems occurs through rainfall and through biological fixation of N_2. We have measured an input in rainfall of about 2 kg ha^{-1} $year^{-1}$ to foothill forests in Gippsland, Victoria. This amount is relatively low (e.g. 6.2 kg ha^{-1} $year^{-1}$, Hollis et al. 1979; 6.5 kg ha^{-1}, Likens et al. 1978; and the range 2-15 kg ha^{-1} $year^{-1}$, Weetman 1961 (see Fig. 1)), even though our measurements were made on the southern slopes of the industrial Latrobe Valley.

We have also measured non-symbiotic N_2-fixation in soils and litters of Pinus radiata and Eucalyptus obliqua forests. Total rates of 1 to 2 ka ha^{-1} $year^{-1}$ are similar to those found in a number of other studies (e.g. Roskoski 1980). Higher rates observed in tropical forests and in some Douglas-fir forests are associated with phylloplane epiphytes.

Since the above inputs are generally only enough to balance losses from undisturbed forest ecosystems, it follows that significant accretion of N must be the result of symbiotic N_2-fixation. Native legumes, principally Acacia species, in these forests are abundant following severe disturbance such as clearfelling and burning, or wildfire, and remain so until canopy closure when they progressively die. In fact, acacias may be dominant in the early life of the forest and this is particularly true for many of the high-yielding, high-rainfall eucalypt forests. Rates of N_2-fixation by acacias of at least 20 kg N ha^{-1} $year^{-1}$ are feasible; Langkamp et al. (1979) measured 12 kg ha^{-1} $year^{-1}$ in a young stand of A. pellita on Groote Eylandt, north-western Australia. Rates of N_2-fixation by Alnus species (a non-legume, and in terms of N_2-fixation perhaps a northern hemisphere ecological equivalent to Acacia) range from 40-325 kg ha^{-1} $year^{-1}$ (Haines and DeBell 1979).

A conservative estimate of the net input of N to an Australian native forest may therefore be some 200 ka ha^{-1} over the first ten years. This accumulation is then slowly released to the soil as the Acacia stand dies and decomposes. The input of N at the beginning of the rotation has particular significance for management since the magnitude of the input may well be large enough to balance losses resulting from harvesting the previous rotation.

A GENERAL DISCUSSION

Much of the current interest in N in forests has emanated from the Hubbard Brook study (e.g. Likens et al. 1978) in which a substantial loss of N was demonstrated following clearfelling (and postfelling treatments including spraying with herbicides) of the forest (see Table 2). The pattern of N transformations in forest soils has, in particular, been the subject of speculation, with some workers (e.g. Vitousek et al. 1979) assigning various "strategies" to forests, none of which seems sufficient to "prevent or delay losses from relatively fertile sites". Some workers (e.g. Nakos 1977) have interpreted the lack of nitrification in mature forests as the inhibition of nitrifying organisms by the vegetation; clearfelling will remove the inhibitors, allow nitrifiers to develop, and the result will be a loss of NO_3^- nitrogen.

Table 2. Loss of nitrogen from forests (from Likens *et al.* 1978).

Origin of Loss	Amount of loss (kg ha^{-1})	
	Hubbard Brook (experimental)	Gale River (commercial clear-cut)
For first two years:		
Removed in streams	236	95
Removed in harvest	0	144
Total removed	236	239
For first ten years:		
Removed in streams	499	
Lost from adjacent forested ecosystem during ten years	43	

Clear-felling not only stops the accession of litter to the soil but provides, through better aeration and increased temperature of the soil, the right conditions for the accelerated decomposition of organic matter. According to our interpretation, after two or three years (or less if fire is used to reduce the debris remaining after logging) the C/N ratio will become low enough to allow nitrification. Since NO_3^- nitrogen is not held by the negatively-charged colloid, and since the vegetation at this pioneer stage is not sufficiently developed to cycle the N within the soil-plant system, N will be leached from the soil. Our interpretation accords fully with the work of Coats et al. (1976) in a conifer stand. As the stand approaches maturity, the C/N ratio increases so that the stand is dependent on both mycorrhizae and NH_4^+. The stand then begins to break up and becomes "leaky" in patches where nitrification is stimulated. Following clear-felling there is a lag-phase during which excess carbon is metabolized and following which NO_3^- nitrogen is released until forest growth again restores the demand for N. We may therefore think of the pattern of mineralization of N in a forest soil as variable in both time and space. It would seem that tree species make use of whichever form is available, but the lack of definitive work on this topic is serious.

The Hubbard Brook study has had the unfortunate result of focussing attention on the losses of N from forests (e.g. Raison 1980). Whether these losses are serious, ecologically or economically, depends on the ability of the organisms which fix N_2 to replace the loss. As we have seen, nodulated plants may be prominent, if not dominant, in the early years of forest growth.

Some estimates of the losses of N following harvesting of slash-pine have been provided by Hollis et al. (1979, see Table 3). The harvesting of tree stems accounts for a relatively small percentage of the N capital of the site. Even removal of all above-ground tree components results in a removal of only 15% of the total N reserves. The total loss of N by complete-tree harvesting followed by intensive site preparation is 550 kg ha^{-1}. Complete-tree harvesting removes 160 kg ha^{-1} in leaves and branchwood and 140 kg ha^{-1} in stems (Table 3) or 55% of the total loss.

Table 3. Estimates of annual cycling rates and of the nitrogen budget for a 20 year rotation of slash pine, south eastern United States (from Hollis *et al.* 1979).

	kg ha^{-1}	
Reserves		
Foliage and branches	160	
Stems	140	
Forest floor	225	
Mineral soil	1500	
Total N reserves at harvest		2050
After stem harvest		1885
After complete harvest and intensive site preparation		1500
Input		
Atmospheric	125	
N^2-fixation	112	
Total N input for 20 years		237
Losses		
Leaching	22	
Erosion and runoff	75	
Net N input over 20 years		140
Depletion per 20 year rotation		
Stem harvest		15%
Complete tree harvest and intensive site preparation		20%

Flinn *et al*. (1979) estimate that the combined losses of N from harvesting followed by a hot slash-burn in *Pinus radiata* forest in south-western Victoria amounted to 626 kg ha^{-1}. Again, a significant proportion (32% or 203 kg ha^{-1}) of the loss is due to the harvesting of the wood.

Raison (1980) has estimated absolute losses of N up to 2000 kg ha^{-1} in Tasmanian wet sclerophyll forests following harvesting and slash-burning. This estimate represents and extreme value from a forest with a duff layer of about 158 x 10^3 kg ha^{-1}, and in this situation the proportion of loss due to the removal of stems is small. The weight of the forest litter layers in south-eastern Australia is generally of the order of 20 x 10^3 kg ha^{-1} or less, and total combustion would result in losses of N of about 200 kg ha^{-1} or less.

It would seem that natural rates of N_2-fixation could easily balance this loss. The most general statement in support of the argument comes from a consideration of the natural regeneration of high-yielding eucalypts following the extensive and severe fires in Victoria in January 1939. Oxidation of organic matter to mineral soil and deeper, erosion, and loss of N through particulate matter, through volatilization, and through leaching undoubtedly led to a total loss of N in excess of the expectations from results of small, experimental fires. Evidence of any deficiency of N or of a decline in productivity of the forests resulting from the fires has never been documented.

Of all the elements, N is the one we can manage simply by biological means. Indeed, Australia leads the field in managing the N economy of agricultural crops. The fragmentary information we have on the ability of our native legumes to fix N_2 and on appropriate methods to manage this ability is a serious deficiency in forest research in Australia. Or is it a commentary on the happy chance that native forests tend to look after their own N economy? If the latter is appropriate, the former remains serious for softwood plantations unless economics permit us to replace harvesting losses with fertilizers.

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LOSSES OF NITROGEN TO THE ATMOSPHERE AS AFFECTED BY FOREST CONDITIONS AND MANAGEMENT PRACTICES

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INTRODUCTION

It is generally accepted that undisturbed forest ecosystems have nutrient cycles which are almost closed, and lose less nutrients, to the atmosphere or groundwater than other ecosystems. However, the equilibrium fluxes between the various components of an ecosystem established over long periods can be drastically altered by changes in management practices. Timber harvesting, for example, alters the amounts of residue returned to the soil and thus the extent of immobilization of nitrogen by soil microorganisms.

Any management or environmental change results in a new balance between the nitrogen pools within the system and accelerated losses of nitrogen to the environment may occur. Nitrogen can be lost to the atmosphere as ammonia, nitric oxide, nitrous oxide and dinitrogen, or to the groundwater by leaching of nitrate.

This paper will describe the processes involved in the emission of nitrogen gases from the soil, and the effect of some management practices on the rates of emission.

PROCESSES INVOLVED IN GASEOUS LOSSES OF NITROGEN

Most of the information concerning gaseous loss of nitrogen has been obtained from laboratory studies and little has come from field studies in either agricultural or forest ecosystems.

Ammonia volatilization

In a forest system, ammonia may have its source in the decomposition of soil organic matter or forest litter, rainfall, animal excreta or from additions of fertilizer, waste water or sewage sludge. Loss of ammonia from these sources is a complex process involving plant uptake, biological, chemical and physical factors in the soil, the meteorological conditions in the atmosphere.

Microorganisms are involved in the supply of ammonium ions by the decomposition of complex organic nitrogen compounds, by producing enzymes to hydrolyze urea, and in ammonium removal by immobilization (Clark and Paul 1970). The conversion of ammonium ions to ammonia and its loss to the atmosphere is governed by other biological reactions, including uptake by plants and nitrification, and by chemical and physical processes, some of which can be represented by the following equilibria:

$$\text{Adsorbed } NH_4^+ \rightleftharpoons NH_4^+ \text{ (in soil solution)} \rightleftharpoons H^+ + NH_3 \text{ (gas in solution)}$$
$$\rightleftharpoons NH_3 \text{ (gas, in soil air)} \rightleftharpoons NH_3 \text{ (gas, in canopy)}$$
$$\rightleftharpoons NH_3 \text{ (gas, in atmosphere)}$$

Thus volatilization of ammonia will occur when there is a difference in vapour pressure between the soil solution and air. This may follow the uptake of ammonia by the forest canopy or the removal of ammonia from the canopy by wind movement (Watkins et al. 1972). The solution vapour pressure is determined by the concentration of aqueous ammonia and temperature, whilst the aqueous ammonia concentration is a function of aqueous ammonium concentration, pH and temperature (Denmead et al. 1980).

At low pH values most of the ammoniacal nitrogen is present as ammonium ions, and the ammonia form only becomes important as the pH rises. Bates and Pinching (1950), for example, calculated that the percentages of unionized ammonia present at pH 6, 7, 8 and 9 are approximately 0.1, 1, 10 and 50 respectively. Thus there is little chance of ammonia being volatilized from undisturbed forest floors where the pH is usually low. If, however, the pH is altered by addition of urea fertilizer or lime, then volatilization of ammonia may become important (Mahendrappa and Ogden 1973).

In addition to the foregoing factors, there are many other factors, such as buffering capacity, cation exchange capacity, soil texture, reaction with clay minerals and organic matter, and water loss which will affect ammonia loss from soil (see, for example Freney et al. 1980).

Denitrification

It has been established that certain microorganisms in the absence of oxygen have the capacity to utilize nitrate as a terminal electron acceptor in their respiratory processes. This process of dissimilatory nitrate reduction is called biological denitrification, and results in the evolution of one or more of the gases, nitric oxide (NO), nitrous oxide (N_2O) or dinitrogen (N_2).

The rate and extent of denitrification in soil is governed by a number of factors including:

(i) nitrate concentration,
(ii) oxygen concentration and redox potential,
(iii) water content,
(iv) available organic carbon,
(v) pH, and
(vi) temperature (Broadbent and Clark 1965).

Oxygen decreases the rate of denitrification by microorganisms as it is a more efficient electron acceptor than nitrate. Redox potentials below approximately + 320 mV favour denitrification (Pearsall and Mortimer 1939). Related to these factors is the water content, as excess water inhibits the diffusion of oxygen. While denitrification can occur at very low moisture contents, it is usually most active at moisture contents above 60% of the maximum water-holding capacity (Bremner and Shaw 1958).

The availability of suitable energy sources is one of the most important factors determining denitrification rates in soil. An oxidisable substrate is required to furnish energy for growth of the denitrifying bacteria and to serve as a hydrogen donor for the denitrification process. In addition, the rate of organic matter decomposition markedly influences the oxygen level in the soil through respiration (Broadbent and Clark 1965). Denitrifying activity is greatest in the rhizosphere of plants and decreases rapidly in the first few millimeters away from the roots. This seems to be due to differences in availability of organic matter (Smith and Tiedje 1979).

The rate of denitrification is also markedly affected by pH. It is very slow in acid soils and most rapid at neutral or alkaline pH values (Bremner and Shaw 1958; Broadbent and Clark 1965). Low pH also influences the ratio of nitrous oxide to dinitrogen in the evolved gas.

Denitrification occurs at temperatures ranging from 0° to 75°C but the rate of reaction falls off dramatically below 5°C. Temperature also affects the ratio of nitrous oxide to dinitrogen in the evolved gas, with nitrous oxide being predominant at low temperatures and dinitrogen at high temperatures.

However, Wollum and Davey (1975) point out that denitrification has not been satisfactorily demonstrated in forest soils, and Henderson and Harris (1975) conclude that denitrification is probably not appreciable in an east Tennessee deciduous forest, where the soils are acid, well-drained and aerated, and have low nitrate contents. As nitrate levels seem to be typically low in most forest soils (Bengtson and Kilmer 1975; Ohta and Kumada 1978) it seems unlikely that denitrification will be a major loss mechanism unless the ecosystem is changed. This conclusion is also supported by the laboratory study of Nömmik and Thorin (1972) who found that little reduction of nitrate occurred in an acid raw humus soil from Sweden unless the pH was raised to 6 or 7.

Chemodenitrification

Chemodenitrification involves gaseous loss of dinitrogen, nitrous oxide and nitric oxide to the atmosphere through the instability of nitrite (Smith and Chalk 1980). It occurs primarily in soils where the first stages of the nitrification process are sufficiently retarded to permit the accumulation of nitrite as an intermediate in the transformation of ammonium to nitrate.

The reactions involved may include:

(i) chemical decomposition of nitrous acid at low pH,
(ii) reaction of nitrous acid with amino acids, ammonia or urea,
(iii) reaction of nitrous acid with soil organic matter or metallic cations (Broadbent and Clark 1965).

Generally these reactions require excessively high nitrite levels, low pH values, or concentrations of metallic cations not normally associated with most soil systems, and under normal conditions probably do not constitute an important loss mechanism (Wollum and Davey 1975). However, if urea is added to forest soils the potential exists for loss by this mechanism.

Nitrification

Nitrous oxide can also be formed under aerobic conditions during nitrification, i.e. during the oxidation of ammonium to nitrate (Yoshida and Alexander 1970; Bremner and Blackmer 1978; Freney et al. 1979), and be subsequently lost to the atmosphere. The acidity of the organic layer and soil in most forest ecosystems is not conducive to nitrification (Keeney 1980) with the result that nitrification rates in acid forest soils are usually low (Roberge and Knowles 1966; Crane 1972; Bengtson and Kilmer 1975; Bengtson 1979) and nitrifiers are found in extremely small numbers (Corke 1958). Most forest floors have very high carbon:nitrogen ratios (Keeney 1980) so that, initially at least, immobilization predominates over mineralization. This coupled with active plant uptake ensures that little ammonium is present to be nitrified. Rice and Pancholy (1973), on the other hand, suggest that nitrification is inhibited by tannins and tannin derivatives. However, the constant presence of nitrifiers suggests that nitrification must proceed in spite of the low pH, and possible presence of inhibitors though obviously at extremely slow rates. It seems that in natural forest environments nitrification does not contribute appreciably to the nitrogen cycle (Chase et al. 1968) and it is therefore unlikely that much nitrous oxide will be produced by this mechanism in unamended forest soils.

MANAGEMENT PRACTICES AND GASEOUS EMISSION

Fertilization

Many reports have indicated that nitrogen is a limiting factor for production in forests (e.g. Gessel 1968), and aerial fertilization with urea has often increased tree growth (Morrison and Foster 1977).

There have been few studies on ammonia loss from urea applications to forest soils and the results have varied widely. Losses have varied from as little as 3.5% to as much as 48% of the nitrogen applied (Acquaye and Cunningham 1965; Overrein 1968, 1969; Bernier et al. 1969; Volk 1970; Crane 1972; Carrier and Bernier 1972; Watkins et al. 1972; Nömmik 1973a; Mahendrappa and Ogden 1973; Morrison and Foster 1977; Terman 1980).

The size of the urea pellet seemed to influence the rate of volatilization of ammonia from forest soils (Crane 1972). The volatilization rate was retarded by increasing the urea pellet size, although the total loss was not affected (Nömmik 1973a,b; Watkins et al. 1972). This is probably caused by the slower dissolution rate of the larger pellet (Nömmik 1973b). Nömmik (1973b) also found that addition of phosphoric or boric acid to the large pellet urea greatly reduced the loss of ammonia to the atmosphere.

Nitrogen fertilization in the field markedly increased the nitrifying capacity of the majority of soils tested by Heilman (1974), whereas other workers have found no increase (e.g. Morrison and Foster 1977). He suggests that differences between field and laboratory incubation conditions may be at least partly responsible for this contradiction. Fertilization also increased the capability of those soils to nitrify subsequent nitrogen applications as well. This finding supports that of Roberge and Knowles (1966).

This suggests that soils treated with ammonium containing, or ammonium producing, fertilizers have the capacity to nitrify and thus produce nitrous oxide, which may be lost to the atmosphere. There is also the potential for any nitrate formed to be denitrified under favourable conditions. The potential would be even greater in forest seedling nurseries, where soils are usually limed to pH 5.5-6.0 (a range in which both nitrification and denitrification proceed more rapidly) and where high rates of soluble nitrogen are often applied to bare soil (Bengtson 1979).

Burning

Fire is an important management practice and is used, for example, to control levels of combustible fuel and wildfire hazards, to assist in site preparation and clearing, and for the control of understorey vegetation (Raison 1979).

Fire affects the nitrogen cycle directly by volatilization and oxidation of nitrogen in soil organic matter, and indirectly by altering the soil physical and chemical properties, which affects nitrogen transformations (Mroz et al. 1980; Wells 1971).

Large losses of nitrogen can occur during slash burning; Isaac and Hopkins (1937) reported a loss of 450 kg N ha^{-1} from a site after burning. De Bell and Ralston (1970) found that little ammonia was produced during burning of forest fuels and considered that most of the nitrogen was lost as dinitrogen. However, Crutzen et al. (1979) found that nitrous oxide and nitric oxide were also produced during forest fires, and calculated from relative NO_x/CO_2 emission ratios that essentially all bound nitrogen in the plant materials was volatilized as NO_x during combustion. They calculate the global NO_x emission from this source to fall within the range 20-100 x 10^{12}g N yr^{-1}, and the global N_2O emission to be of the order of 13 x 10^{12}g N_2O yr^{-1}.

Burning also affects the level of mineral nitrogen in soil (Mroz et al. 1980) and results in greater nitrification rates (Christensen 1973). Greater losses of fertilizer nitrogen by ammonia volatilization can also occur if urea or ammonium fertilizers are applied to recently burned areas (Raison and McGarity 1978). The resultant ash raises the surface soil pH, saturates surface soil exchange sites with basic cations and increases soil urease activity. The greater nitrification rates, increased nitrate levels and pH values after burning would increase the potential for nitrous oxide loss during nitrification, and nitrous oxide and dinitrogen loss during denitrification.

Clearfelling

The biological process of nitrification is often stimulated by clear cutting of forests (Fraser 1929; Popović 1975; Tamm 1979), and Hornbeck et al. (1975) found that complete forest clearing and strip cutting markedly increased the nitrate concentrations of stream waters in some northern hardwood areas of the U.S.A. They proposed four interrelated factors to account for the increase:

1. acceleration of the nitrification process;
2. exposure of the site to greater than normal amounts of heat and moisture, thereby accelerating decomposition processes in the soil;
3. blocking uptake by trees; and
4. acceleration of chemical weathering.

However, the removal of throughfall inputs to the soil by washing off impacted particulates and leaching from tree crowns (McColl 1977) may result in low nitrate concentrations in the soil solution (McColl 1978).

Clearfelling may result in anaerobic conditions due to higher soil water contents in the soil (McColl 1977) and from the sealing off of the soil profile during the downward movement of the wetting fronts (McColl 1978). Thus clearfelling may result in increased losses of nitrogen during nitrification and denitrification.

Miscellaneous Management Practices

While other practices, such as sludge disposal (Sidle and Kardos (1979), waste water disposal (Sopper 1975), recreational use (Monti and Mackintosh 1979), site preparation (Haines and Davey 1979) and agroforestry would be expected to affect the gaseous loss of nitrogen, no data are available on the effects of these practices.

Applications of liquid sludge and waste water may provide very high inputs of nitrogen into the forest system and, being associated with extra water, may well result in increased denitrification. In fact, the results presented by Sopper (1975) suggest that denitrification is important in a hardwood forest receiving waste water. In spite of doubling the nitrogen load, the nitrate concentration in the groundwater remained below 10 mg N/litre.

CONCLUSIONS

It is apparent from this brief review that the processes affecting the loss of ammonia, nitrous oxide, and dinitrogen to the atmosphere, are understood. While some data have been obtained on the rates and amount of ammonia volatilization in forest ecosystems, and the effect of some management practices on this process, there is virtually no information available on the loss of the other nitrogen gases from forest soils *in situ*.

Even the field work on ammonia volatilization is open to criticism because of the techniques employed to measure volatilization. Crane (1972) and Mahendrappa (1975) observed that the large variation in results may be due to the different techniques used for measuring absorption of ammonia.

Environmental conditions can have a marked effect on ammonia volatilization, and thus it is important that any method used to assess losses from the forest should not affect the environment above the soil. Some workers have used canopies over the soil with or without static acid traps to absorb volatilized ammonia. Such canopies may affect the temperature, moisture and wind speed over the soil and thus the rate of ammonia loss (see for example Crane 1972). The acid trap acts as a sink for ammonia in the air and sets up a strong concentration gradient which increases the volatilization rate. Other workers have hung acid washed filter papers in the air above the fertilized soil to measure volatilized ammonia but these suffer from the same deficiencies as the acid traps inside the canopies.

Even the ^{15}N recovery technique, which has been considered by some workers to be the most reliable method for assessing ammonia loss, has limitations. Ammonia loss is assessed as the difference between the added and recovered amounts of labelled nitrogen. Thus it can be affected by denitrification, leaching, experimental and sampling errors (Nömmik 1973a).

In addition, all of the field studies reported for ammonia volatilization were carried out at or near the soil surface. Ammonia lost from the surface may be absorbed by the forest canopy and thus not lost from the forest system (Mahendrappa 1975).

Techniques are now available for making field measurements on the emission of most of these gases (Freney and Denmead 1981), and it is to be hoped that forest research workers will use these methods to obtain reliable data on emission rates.

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LOSS OF NITROGEN FROM LITTER AND UNDERSTOREY SHRUBS DURING PRESCRIBED BURNING IN SUB-ALPINE EUCALYPT FORESTS*

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ABSTRACT

The loss of N resulting from prescribed burning of litter and Daviesia mimosoides, a leguminous understorey shrub, was measured in sub-alpine stands of E. pauciflora, E. dives - E. dalrympleana and E. delegatensis in the Brindabella Range, Australian Capital Territory.

The loss of N from litter was measured by comparing the mean amount of N contained in litterbeds on trays (0.12 m^2 in area) before and after an experimental low intensity (350-450 kW m^{-1}) prescribed burn. The shallow trays (2 cm lip) facilitated collection of the post-fire residue by separating it from the soil. Twenty trays were carefully loaded with in situ litter (excluding wood > 8 mm diam.) at each of two 20 x 20 m plots in each forest type two months prior to the fire. Ten trays, selected at random as the pre-fire samples were collected immediately before the fire while the remaining ten were collected within one hour of the fire passing.

Transfer of N from the understorey (to either the atmosphere or to the litter layer) was measured by comparing the N content of the understorey harvested from 4 m^2 areas before the burn, with that remaining after the fire.

The approximate total loss of N (in kg ha^{-1}) was 70-80 in E. pauciflora, 60-70 in E. dives - E. dalrympleana and 40 in E. delegatensis, while the loss of N from the understorey contributed about 24, 41 and 25% respectively to the total losses.

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Variation in the weight of litter consumption was the main reason for the difference between the sites in the loss of N from the litter layer. Over the range of litter consumptions measured (6.7 - 12.4 t ha^{-1}) there was a significant ($r = 0.92$ $P < 0.01$) linear relationship between the loss of N and the weight of litter burned. There was a loss of 5.3 ± 0.3 kg N for each tonne of litter consumed, and 85 ± 2% of the N contained in the litter burned was lost.

This data may allow the loss of litter N during prescribed burning to be predicted in other forests from a knowledge of the weight and N content of litter consumed.

MINERALISATION OF N IN SOILS OF CLEAR-FELLED AND BURNED COUPES IN SOUTHERN TASMANIA

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INTRODUCTION

In Tasmania, a range of forest types is clearfelled, and regenerated by slash burning and aerial sowing. Whilst the wellknown ash bed effect upon the growth of eucalypt seedlings is generally evident, the degree and duration of stimulation of growth varies widely with soil (and forest) type and intensity of the burn. The availability to plants of many elements increases after a burn and usually increases with increase in intensity of the burn. However, since forest sites differ greatly from one another, and since a variable and sometimes large proportion of the nitrogen in plant material and the surface layers of soil may be volatilized, it is not surprising that contradictory reports of the availability of N to plants after a burn appear in the literature.

In the coniferous boreal forest, where soil organic matter is concentrated in a discrete layer above the mineral soil, up to 90% of it may be consumed (Smith 1970), and Gagnon (1965) has reported acute N-deficiency in regeneration of black spruce on such sites following a hot fire. In the temperate coniferous rainforest of Washington, Grier and Cole (1971) found that only traces of organic and mineral N were released to the soil solution by burning. Other workers have noted enhanced production of ammonium and/or nitrate in the soil after slash burning (Fowells and Stephenson 1934; Viro 1974), and Jorgensen and Wells (1971) found an increase in the rate of fixation of N after prescribed burning. Detailed reviews of the effects of fire upon nitrogen in the soil have been given by Ahlgren and Ahlgren (1960) and Raison (1979). Gagnon (1965) noted that it is believed that each burn must be considered as a different problem and that no general conclusions should be drawn since soil conditions prevailing after a fire vary with the intensity of the fire, the nature of the soil parent material, and the site quality.

One objective of a study being conducted in Southern Tasmania is to determine the quantities and forms of mineral N produced in the soil of two contrasting forest types following clearfelling and slash burning.

FOREST TYPES

E. obliqua rainforest.

Tall mature E. obliqua with an understorey of Nothfagus cunninghamii, Atherosperma moschatum, Eucryphia lucida, Phyllocladus asplenifolius, Anodopetalum biglandulosum, Acacia melanoxylon, and a ground cover of ferns and mosses. The stands had not been burned for at least 200 years before felling.

The area is part of the east-facing side of the Picton Valley, where mean annual rainfall probably exceeds 150 cm. Soils are formed from dolerite and have developed krasnozen or brown mountain soil profiles. A thin (2-5 cm) horizon rich in organic matter overlies a heavy clay-loam B horizon. Around the bases of the large eucalypts accumulations of organic matter, derived mainly from bark, may exceed 50 cm in depth; elsewhere, discrete organic layers are thin or lacking.

E. obliqua/dry sclerophyll forest

Medium to low quality E. obliqua with E. amygdalina, E. viminalis, E. globulus, E. linearis, E. rubida, according to topographic position. Ground cover is sparse and consists of low shrubs, bracken and grass. The stands had been burned at intervals probably of less than 20 years.

The area is part of the Buckland Military training area and consists of broad ridges separated by steep valleys. Mean annual rainfall is about 85 cm. Soils are formed from dolerite and have developed yellow podzolic profiles. A thin (0-1 cm) horizon rich in organic matter overlies a sandy loam A horizon and a heavy clay loam B horizon.

METHODS

Sampling

In the Picton Valley four coupes have been selected; three had been burned respectively in March 1979, March 1978 and March 1976, and the fourth is an uncut control. In the Buckland area three coupes have been selected of which two were burned in March 1979 and March 1978, and the third is an uncut control. Within each area the coupes appear to be similar in soil, original forest type, aspect, slope, variety of micro-topography, and silvicultural treatment.

In each coupe, ten points were located so as to represent the range of topographic positions present (e.g. convex slope, concave slope, knoll, etc.), but excluding water-logged depressions.

Sampling commenced in April 1979 at the Picton Valley three weeks after the 1979 burn, and in the following August at the Buckland area, nearly five months after the burn. Twenty cores of soil, 3.5 cm wide x 10 cm deep, were collected from within a radius of 15 m of each point. The full range of micro-topography within that radius was sampled. The 20 cores were bulked to give a composite sample of micro-topographic variation for each point. Sampling has been repeated at intervals of four months.

At three points in each of the 1979 burn, 1978 burn, and uncut coupes in the Picton Valley a second series of samples was taken in which the 10 cm cores were subdivided into three components, 0-2 cm, 2-5 cm, and 5-10 cm. These components were bulked at each point.

Preparation and Analysis

Samples were dried at 30°C, rubbed through a 2 mm sieve, and stones and roots discarded. Fine organic material, including mosses and liver-worts, was passed through the sieve since it was deemed impractical to separate such material from the ash and mineral soil with which it was in intimate contact.

The following analyses were performed inter alia:

(i) Total C by electrometric titration and total N by steam distillation following CrO_3 digestion according to Anstett (1956).

(ii) Total P (Murphy and Riley 1962) following wet digestion according to Jackson (1958).

(iii) pH on a soil/water paste 1:2 W/V.

(iv) NH_4 and NO_3 nitrogen by microdiffusion after extraction with 2N KCl according to Bremner (1965). These determinations were made on subsamples before and after incubation. Both aerobic and anaerobic incubation was conducted.

(a) Aerobic incubation: 10 g of air-dry soil was moistened with 5 ml of water and incubated at 20°C for 14 days in ehrlenmeyer flasks sealed with parafilm to maintain constant moisture content.

(b) Anaerobic incubation: 10 g of air-dry soil and 25 ml of distilled water were incubated in a sealed tube at 20°C for 14 days).

RESULTS

Some total nutrient concentrations of the soils from the two areas are compared in Table 1. The Picton Valley soils contain about twice the concentrations of C and N found in the Buckland soils. Total C and N may have been diminished by the 1979 burn in the Picton Valley, and the N/P ratios indicate that, relative to P, in both the 1978 and 1976 burns the concentrations of N, one and three years after the burns were lower than that of the control.

In the Buckland coupes N/P ratios did not differ between burn and control.

Table 1. Total elemental concentrations in soils (0-10 cm).

Year of burn	C%	N%	P ppm	C/N	N/P
		Picton Valley			
1979*	5.4[a]	0.16[a]	149[a]	33.2	11.0[a]
1978*	7.1[a]	0.27[b]	218[a]	26.9	12.5[a]
1976*	7.2[a]	0.21[c]	173[a]	34.4	12.1[a]
Uncut**	6.8[a]	0.25[bc]	150[a]	28.8	16.4[b]
		Buckland Training Area			
1979**	2.8[b]	0.10[d]	93[b]	31.6	10.3[a]
1978**	2.7[b]	0.10[d]	125[ab]	26.6	8.3[a]
Uncut**	2.8[b]	0.10[d]	111[b]	26.4	9.3[a]

* Samples collected in April 1979.
** Samples collected in August 1979.

Three weeks after burning, the pH of the surface 0-10 cm of soil in the 1979 Picton burn was about 1.5 units higher than that of the control (Table 2). This difference diminished during the ensuing twelve months at which time all three burns were similar in soil pH and 0.6 units higher than control. Figures for the 0-2 cm, 2-5 cm and 5-10 cm layers are based upon only three samples in each coupe but show the expected gradients with depth (Table 3). In the Buckland coupes the differences in soil pH between burns and control are about 0.5 of a unit.

Table 2. pH of Soil 0–10 cm.

Year of burn	Date of Sampling				Mean C of V%
	April 1979	August 1979	Jan. 1980	May 1980	
		Picton Valley			
1979	6.04	5.90	5.49	5.44	8
1978	5.80	5.71	5.37	5.46	5
1976	5.48	5.64	5.36	5.31	8
Uncut	-	4.56	4.65	4.78	8
		Buckland Training Area			
1979	-	6.61	6.23	6.01	5
1978	-	6.69	6.06	6.06	5
Uncut	-	6.03	5.72	5.70	3

Table 3. pH of Soil in the Picton Valley.

Depth Interval (cm)	Date of Sampling					
	17.09.79	17.10.79	20.11.79	31.01.80	30.03.80	05.80
			March 1979 Burn			
0 – 2	6.74	6.66	6.49	6.31	6.27	6.13
2 – 5	5.13	5.14	5.10	5.12	5.27	5.25
5 – 10	4.71	4.87	4.87	4.92	4.87	5.02
			March 1978 Burn			
0 – 2	-	5.78	5.49	5.67	5.95	5.61
2 – 5	-	5.30	5.26	5.17	5.22	5.44
5 – 10	-	5.10	5.07	4.98	4.97	5.13
			Uncut			
0 – 2	-	-	-	-	-	4.43
2 – 5	-	-	-	-	-	4.60
5 – 10	-	-	-	-	-	4.79

The initial concentrations of ammonium and nitrate present in the soil and the amounts produced during both aerobic and anaerobic incubation are shown in Tables 4 and 5. For the Picton Valley soils, ammonium was the principal ionic species produced on all coupes; only in the 1978 burn was there an appreciable quantity of nitrate, although the difference from other coupes was significant ($P < 0.05$) only during the winter. The rate of production of ammonium did not vary significantly amongst dates of collection. Overall the amount of ammonium produced in the 1978 burn was significantly greater than that produced in the 1979 and 1976 burns: these latter did not differ significantly from the control.

In the Buckland coupes the amounts of ammonium produced during anaerobic incubation were nearly the same for burned coupes and control. Amounts were highest during the winter, and diminished significantly during the summer. In contrast to the Picton coupes, nitrate was the most important ionic species produced during aerobic incubation during the first one to two years. Ammonium is the principal species produced in soils of the uncut control, where nitrification appears to be negligible.

Table 4. Ammonium and nitrate (ppm N) in Picton Valley soils (0 - 10 cm).

Year	Date of Sampling: April 1979		Aug. 1978		Jan. 1980		May 1980		Mean C of V%	
	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-
	Initial Extraction									
1979	35.7	0.8	16.4	0.4	7.1	2.6	4.7	2.1	36	70
1978	23.3	4.3	17.6	3.0	8.6	3.2	9.6	2.2	35	48
1976	10.8	0.3	8.5	0.5	7.7	2.8	5.0	2.3	30	86
Uncut	-	-	6.2	1.1	14.7	3.1	10.1	2.2	38	38
	After Aerobic Incubation (Net)									
1979	46.8	1.1	33.8	1.6	36.4	1.1	41.7	1.3	41	167
1978	113.4	17.0	82.7	24.8	97.9	4.6	94.0	6.4	59	74
1976	37.7	3.4	27.5	8.3	55.5	2.3	40.3	0.8	61	159
Uncut	-	-	74.0	0.9	106.5	0.0	67.4	0.2	55	-
	After Anaerobic Incubation (Net)									
1979	51.4	-	73.5	-	43.7	-	62.8	-	34	-
1978	115.4	-	122.8	-	104.6	-	96.6	-	46	-
1976	52.0	-	58.4	-	76.7	-	56.8	-	39	-
Uncut	-	-	81.5	-	90.3	-	89.6	-	32	-

Table 5. Ammonium and nitrate (ppm N) in Buckland Training Area soils (0-10 cm).

Year of Burn	Date of Sampling: Aug. 1979		Feb. 1980		May 1980		Mean C of V%	
	NH_4^+	NO_3^-	NH_4^+	NO_3^-	NH_4^+	NO_3^-		
	Initial Extraction							
1979	7.3	1.6	3.9	2.8	3.8	2.3	41	63
1978	5.4	1.0	2.6	1.9	2.2	1.6	40	38
Uncut	3.8	0.4	2.4	1.8	3.4	1.6	34	47
	After Aerobic Incubation (Net)							
1979	-4.0	22.0	1.6	7.6	6.5	4.1	175	105
1978	-0.6	16.3	1.6	10.2	3.0	9.4	233	76
Uncut	13.7	1.3	22.3	0.8	13.3	0.5	95	159
	After Anaerobic Incubation (Net)							
1979	27.6	-	12.9	-	17.4	-	52	-
1978	29.5	-	14.9	-	14.1	-	49	-
Uncut	23.7	-	20.1	-	19.0	-	49	-

DISCUSSION

These preliminary data indicate several interesting aspects of N transformation in the soils that are being studied.

In the Picton Valley the amounts of fuel on the ground were enormous and very hot burns resulted; the pH of the soil surface was raised by at least 1.5 units. Yet the rate of mineralisation of N in soil of the burns does not appear to differ in any significant manner from that of the uncut control area. The lack of, or very low rate of, nitrification in the burned soils is surprising. This is so particularly when much less intense burns and smaller changes in pH of soils in the Buckland area appear to result in complete nitrification of ammonium for several months after a burn. Nitrifiers are evidently lacking in the Picton soils, and the implication is that very little mineral-N is likely to be leached from these soils despite the high rainfall.

The change of pH following a burn is marked in the top 2 cm of the Picton soil, is much less at the 2-5 cm depth, and is negligible at the 5-10 cm depth. Clearly, the soils are well buffered and/or are subject to little vertical leaching. The lowering of pH that occurs during the months after a burn is accompanied by a rapid proliferation of a succession of mosses that commences within two to three months of a burn and rapidly covers the entire burned surface. Eucalypt seedlings germinate soon after a burn but growth is very slow during the first year. Thereafter growth is rapid.

Very little consistent variation in rate of N mineralisation occurs in soil from either location collected at different seasons of the year. This may be because of the relatively equable climate of southern Tasmania, and contrasts with the situation found in more extreme climates.

With the method of sampling that was used, amounts of ammonium present initially, or produced during incubation (provided that they are more than trace amounts), are determined with coefficients of variation usually between 30% and 50%: for nitrate, the values are considerably higher. For pH, coefficients of variation are between 3% and 8%. With 10 plots per coupe, pH can be determined with considerable precision, but only fairly large differences in rate of mineralisation amongst coupes can be determined with $p < 0.05$ or better.

This study will be pursued in the Picton Valley on areas to be burned in 1981. Attention will be given especially to the changes that occur from immediately before to three months after a burn. Thereafter, it seems that changes occur only slowly. 'Baseline' conditions in uncut forest will continue to be monitored, but one imponderable at present is the answer to the question "What departures from baseline conditions are considered to be acceptable or unacceptable?"

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NITROGEN CYCLING WITHIN A 27-YEAR-OLD EUCALYPTUS GRANDIS STAND

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INTRODUCTION

Eucalyptus grandis Hill ex Maiden (flooded gum) plantations have been established on the north coast of New South Wales by both A.P.M. Forests Pty. Ltd. (Clarke 1975) and the Forestry Commission of N.S.W. because of the high productivity potential of the species. A cooperative study on *E. grandis* has been established between A.P.M. Forests Pty. Ltd., the Forestry Commission of N.S.W. (N.S.W.F.C.) and the University of New England to obtain information on the rate of organic matter production and nutrient turnover. Seven A.P.M. plantations ranging in age from 2 to 16 years were selected together with a N.S.W.F.C. 27-year-old stand. The development and distribution of biomass in this age series has been reported (Bradstock 1980). Stand productivity and nutrient turnover are being studied by ourselves while Dr. J. Charley from the University of New England is carrying out detailed studies on the soil component.

This present preliminary paper presents the distribution of nitrogen within the oldest stand (27 years of age) together with estimates of nitrogen turnover. This particular stand is of interest for several reasons which include the productivity of *E. grandis* and the future ecological development of these sites.

E. grandis is usually found on the more fertile soils of an area and usually within the relatively more moist situations. After a disturbance, such as fire, it can be a pioneering species growing rapidly to dominance above weeds on suitable sites. Growth plots indicate that, while productivity is high, after a particular stage the stand will suffer relatively high mortality and subsequent depression in basal area. There appears to be a relationship with soil fertility in that deaths occur earlier on poorer sites;

however, the process may start at about 30 years of age or may occur as late as 40 years of age (R. Horne, pers. comm.). While growth of the E. grandis continues, there is also development of the understorey trees which are often Acacia spp. in association with rainforest species. A rainforest ecosystem will probably be the final stage of development, assuming no further disturbance in the area.

The particular E. grandis stand chosen for this study was probably near both the time of maximum basal area and the point where the first "wave" of mortality occurs (R. Horne, pers. comm.) and hence near the maximum accumulation of nutrients. The rainforest understorey with a high component of Acacia spp. was also well developed at this stage.

SITE AND METHODS

The location of the plantation (Boyds Deviation) is within Conglomerate State Forest near Coffs Harbour in northern New South Wales. The area is subtropical with a predominantly summer rainfall pattern, the mean annual rainfall being 1760 mm. The mean annual maximum and minimum temperatures are 23.1°C and 13.6°C respectively (Climatic Averages 1975).

The plantation was established using tube stock in 1952 in a former rainforest gully burnt out by a wildfire in 1951. The soils were derived from Lower Permian sediments and have high to moderate fertility. Four growth plots in unthinned areas were established when the stand was 6-years-old and have been monitored to the present.

In 1978 a further plot was established adjacent to the growth plots to estimate biomass and sample soil and tissues for nutrient content. The methods employed were similar to those outlined in Turner et al. (1976).

RESULTS

The biomass and nitrogen contents of the stand together with preliminary estimates of net annual increases are given in Table 1. The aboveground tree component contained 434 kg ha^{-1} nitrogen of which 36% was contained within the crown. The net annual increase in nitrogen content was 13.5 kg ha^{-1} yr^{-1} of which 16.3% was accumulated within the crown.

Table 1. Biomass and nitrogen content of a 27-year-old *E. grandis* ecosystem at Boyds Deviation within Conglomerate S.F., N.S.W.

Component	Biomass*	Nett annual biomass increase**	Nitrogen content	Nett nitrogen content increase
	(kg ha^{-1})			
TREE				
– foliage	6 150	85	91	1.3
– branch	20 835	310	67	0.9
– bark	38 180	1 060	85	2.3
– sapwood	114 200	5 465	89	4.3
– heartwood	214 630	9 840	102	4.7
Total tree	393 995	16 760	434	13.5
UNDERSTOREY				
– foliage	3 090	200	47	3.0
– stem	38 045	2 595	137	9.3
– minor understorey	925	0	11	0.0
Total understorey	42 060	2 795	195	12.3
FOREST FLOOR				
– sticks/bark	7 315	n.s.	12	n.s.
– leaves	1 655	n.s.	6	n.s.
– other litter	2 320	n.s.	12	n.s.
– humus	16 795	n.s.	160	n.s.
Total forest floor	28 085	n.s.	190	n.s.
SOIL				
– 0 - 7.5 cm	-	-	1 785	-
– 7.5 - 22.5 cm	-	-	2 000	-
– 22.5 - 37.5 cm	-	-	1 455	-
Total	464 140	19 555	6 059	25.8

* Bradstock (1980)
** Preliminary estimates using five year growth data
n.s. No significant change.

The understorey contained 195 kg ha^{-1} nitrogen of which 94% was contained within the developing tree component composed mainly of Acacias but also including rainforest species. The nitrogen content of the understorey was 45% of the nitrogen content of the aboveground tree component. However the major proportion of this was within stems which are composed of bark and sapwood, rather than the low nitrogen concentration heartwood found in the E. grandis. For example, the sapwood and heartwood in E. grandis had nitrogen concentrations of 0.078% and 0.048% respectively while that in the understorey stemwood was 0.12%. The understorey was accumulating nitrogen at the rate of 12.3 kg ha^{-1} yr^{-1}, a quantity which was very similar to that within the aboveground tree component, even though the biomass accumulations were very different. The minor understorey had no net increases (this component actually was decreasing).

The forest floor contained 190 kg ha^{-1} nitrogen and appeared to be fairly constant in mass. The forest floors in the 15- and 16-year-old stands had 30,695 and 34,260 kg ha^{-1} organic matter respectively, while that in the 27-year-old stand was 28,085 kg ha^{-1} (Bradstock 1980). These were not significantly different from one another and thus the forest floor could be considered to be near equilibrium. It was noted that the major difference was that understorey litter tended to be lower in the 27-year-old stand (by 2,600 kg ha^{-1} from the 16-year-old stand) and this could mainly be the result of changes with age to more woody species as opposed to species such as lantana.

Nitrogen transfers within the system (with the exception of throughfall which was not available) have been estimated (Table 2). The total litterfall was 7035 kg ha^{-1} of which 30% was derived from the understorey component. The total litterfall returned 39.7 kg ha^{-1} nitrogen to the forest floor with a further 0.5 kg ha^{-1} returned from tree mortality. The stand had 24,895 kg ha^{-1} of currently produced organic matter of which 15,304 kg ha^{-1} was wood. An estimate of aboveground nitrogen uptake was determined by estimating the nitrogen content of the current tissues and subtracting from this, the nitrogen redistribution from litterfall and heartwood formation. Total wood production was estimated and the heartwood formation then calculated subsequently.

Table 2. Estimated nitrogen transfers for a 27-year-old *E. grandis* ecosystem at Boyds Deviation within Conglomerate S.F , N.S.W.

Transfer	Organic matter (kg ha^{-1} yr^{-1})	Nitrogen
INPUT (precipitation)		2.9
LITTERFALL		
– tree leaf	3 890	25.3
– tree other litter	1 035	3.7
– understorey	2 110	10.7
Total litterfall	7 035	39.7
TREE MORTALITY		
– stem wood	460	0.2
– stem bark	135	0.3
Total tree mortality	595	0.5
WITHIN VEGETATION		
– content of current tissue (tree and understorey)	24 895	105.8
– redistribution		
– tree leaf litter		32.0
– understorey leaf litter		13.3
– heartwood		2.9
Total redistribution		48.2
UPTAKE		57.6

DISCUSSION

The nutrient cycle compiled for this 27-year-old E. grandis stand has indicated that approximately 430 kg ha^{-1} nitrogen was accumulated within the major tree component. This is probably near a maximum since this stand will decline shortly in terms of basal area and biomass and the understorey component will increase in development. Further, the stand heartwood component which has a lower nitrogen content is assuming greater significance. Based on annual biomass increment levels, the actual annual uptake could be expected to be higher than this present stand would indicate (Figure 1). Compared with many tropical systems (Gessel et al. 1977), this ecosystem has a very high productivity, although much of this is within foliage and understorey components. The forest floor organic matter k factor was 0.2, which on the system of Olson (1963) represents a high turnover coupled with a very high litter production.

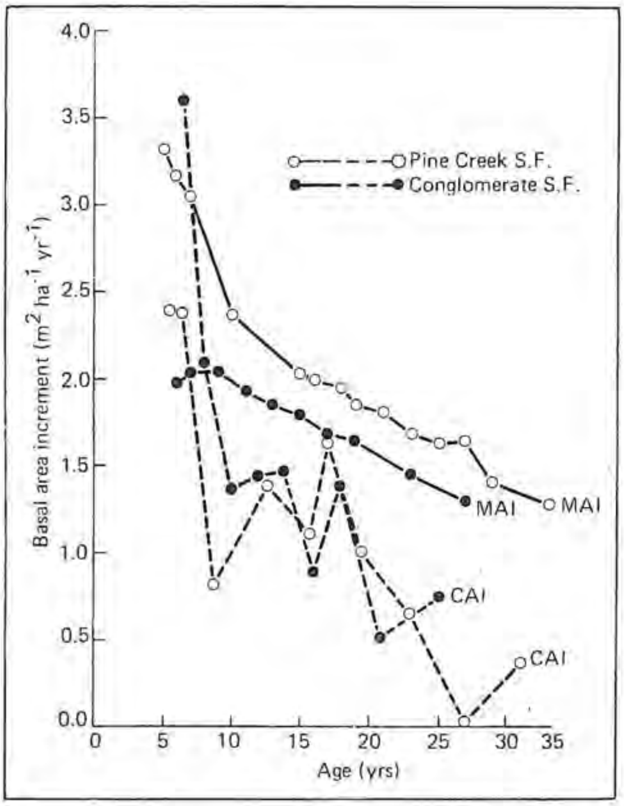

Fig. 1. Basal area mean annual and current annual increments for the study site (Conglomerate S.F.) and an older stand of similar structures (Pine Creek S.F.).

Several aspects need to be taken into account in relation to the developmental stages of this stand. Firstly, there is the role of the process of heartwood formation, the importance of which has been previously considered by Attiwill (1979) for E. obliqua. Within the sequence of E. grandis stands studied by Bradstock (1980), no heartwood was formed in stands younger than eight years of age. Some evidence suggests that the onset and rate of heartwood formation in these stands is related to soil fertility, especially phosphorus, but further work is required on this aspect. The rate of heartwood production was quite high in the early stages and then declined to about age 20 years, after which it appeared to have increased. Mortality had also increased at this time and in conjunction with this there had been the development of a significant component of woody understorey. The accumulation of nutrients within the system, together with the competition from the understorey possibly induced the higher heartwood formation and mortality. If one specific nutrient was to be related to this phenomenon, it would probably be phosphorus, but the high degree of redistribution of nitrogen would indicate this nutrient is also limiting. However <u>Acacia</u> species are a very well developed part of the understorey and a constant nitrogen input from this source could be expected.

In total, 40 kg ha^{-1} yr^{-1} of nitrogen was returned to the forest floor, 58 kg ha^{-1} yr^{-1} was taken up by the vegetation and there was a net increase of 26 kg ha^{-1} yr^{-1} in the vegetation. As it would be expected that uptake = loss + accumulation, there is a discrepancy of an uptake underestimation of 7.9 kg ha^{-1} yr^{-1}. This can be partly explained by not having taken into account the contribution to uptake by the 'other tree litterfall', the 0.5 kg ha^{-1} from tree mortality and approximately 4 kg ha^{-1} for minor understorey uptake (since data were insufficient). Therefore, a probable working estimate of uptake for this stand would have been approximately 60 kg ha^{-1} yr^{-1}.

The future development of this stand is of interest as the decline of the <u>E. grandis</u> will allow greater development of the rainforest species. The characteristics of the rainforest species indicate these species have very much higher nitrogen demands and considerably less internal redistribution, although annual uptake is lower because of the lower annual productivity of these stands. Comparative nutrient concentrations for some typical subtropical rainforest species (Table 3) indicate that if rainforest species are the final successional stage of the ecosystem, then a higher level of nitrogen availability will be required and hence the sources of nitrogen inputs will be critical.

Table 3. Mean nitrogen concentrations in various components of *E. grandis* and various subtropical Rainforest tree species (Turner *et al.* 1980).

Species	Component				Nitrogen decline from sapwood to heartwood (%)
	Foliage	Bark	Sapwood	Heartwood	
Eucalyptus grandis	1.47	0.22	0.08	0.05	38
Heritiera trifoliolata	1.89	0.48	0.31	0.11	65
Geissois benthamii	1.31	0.27	0.14	0.09	36
Doryphora sassafras	2.07	0.97	0.27	0.23	15
Cryptocarya erothroxylan	2.08	0.62	0.19	0.14	26
Ackama paniculata	1.62	0.32	0.12	0.08	33
Mean of Rainforest species	1.79	0.53	0.21	0.13	

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SESSION 6.
Nitrogen in Plantation Forestry

INTERACTIONS OF NITROGEN WITH OTHER NUTRIENTS IN CONIFEROUS STANDS

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INTRODUCTION

The term 'interaction' appears to be used in a variety of inadequately defined ways, all having different implications in forest management and nutrition. The use of the term 'interaction' relates to the method by which it is being assessed, and this may be by using a variety of ways including growth measurements in field experiments and/or chemical analysis. One poorly defined aspect derives from the inadequate descriptions of the nutrients being applied in fertilizer amendments such as an N x P interaction being ascribed despite phosphorus being applied as superphosphate. The various interaction definitions have been discussed here in relation to nitrogen nutrition and some possible explanations for various modes of action have been presented.

DEFINITIONS OF INTERACTIONS

Nitrogen fertilizers applied to a site react within the soil (Cole *et al*. 1974) and, after uptake, there will be some 'reaction' within the tree. Within the vegetative component of a forest ecosystem, an interaction of nitrogen with other nutrients must occur in order to obtain a response to applied nitrogen. That is, the applied form of inorganic-nitrogen has to be converted to metabolites and this involves nutrient interactions. These interactions may be monitored using a variety of parameters (for example, d.b.h. increment, changes in foliar biomass or litterfall, and/or variations in foliar organic and inorganic constitutents) and the manifestations of the interactions may take a variety of forms:

(a) No response apparent in the measured parameters - hence no actual response to added nitrogen, or the parameters being assessed are too insensitive or inappropriate.
(b) Response as expected - for example, when nitrogen and phosphorus are added simultaneously and the obtained result is the additive effect of nitrogen and phosphorus separately.
(c) Response above expected level - the response to two nutrients is more than the additive effect of the nutrients applied separately.
(d) Response below expected level - the obtained response is less than the additive effect of the added nutrients or less than the effect of either nutrient applied separately.

The 'response above expected level' is that which is usually cited as the interaction and is generally reported in terms of increased growth response, however the situation of a 'response below expected level' is also an interaction. All four of the above situations must be considered when ascertaining the most appropriate amendments for specific conditions. The interactions of responses (c) and (d) above can be described in terms of a nutrient A giving growth response X, a nutrient B giving growth response Y and nutrients (A + B) giving growth response (X + Y ± Z).

The types of interaction so far encountered include:

(i) Biochemical interactions
Biochemical interactions result from a fixed biochemical relationship between nitrogen and another nutrient. One example of this is the biochemical relationship between nitrogen and sulphur in amino acids and proteins. This is a close relationship and deficiencies of one nutrient have characteristics similar to or related to a deficiency of the other.

(ii) Empirical interactions
Empirical interactions relate to the growth increases obtained when nitrogen is added with other nutrients, particularly phosphorus and/or potassium, but when there is no obvious biochemical relationship between those nutrients. It

is termed 'empirical' because, whereas it has been measured in some circumstances, the fact of whether it will occur and the degree to which it will occur appear to be a trial and error process.

(iii) Developmental interactions

These interactions have been termed 'developmental' since they generally occur after the plants have started producing a high growth rate and may be the result of growth dilution effects. The effects are most obviously manifested as deformities, for example as a result of nitrogen induced trace element deficiencies such as copper and boron.

ASSESSMENT OF INTERACTIONS

On the basis of the above definitions, various interactions have been assessed in greater detail.

Nitrogen/sulphur Interactions

The precise biochemical relationships between sulphur and nitrogen in conifers have been previously discussed (Kelly and Lambert 1972; Lambert and Turner 1977; Turner *et al*. 1977; Turner and Lambert 1978; Turner 1979; Turner *et al*. 1979, 1980):

(i) There are insignificant concentrations of inorganic-nitrogen within conifer foliage, so that:

$$\text{Total-N} = \text{Organic-N},$$

however sulphur can be present as organic-sulphur and inorganic-sulphur, and therefore

$$\text{Total-S} = \text{Organic-S} + \text{Inorganic-S}$$

(ii) Nitrogen and sulphur are biochemically related (protein and amino acids) in conifer foliage:

$\frac{\text{Organic-S}}{\text{Organic-N}} \times 0.437 = 0.030$ (the relationship being on a gram atom basis and 0.437 is a conversion factor.

(iii) Sulphate-sulphur is accumulated in excess of that sulphur required to balance the nitrogen in protein formation and sulphate-sulphur is used as an indicator of foliage sulphur and nitrogen status. Since inorganic-nitrogen has not been found to accumulate, nitrogen uptake is limited if there is insufficient sulphur. A sulphur deficiency rating system for sulphur/nitrogen nutrition surveys has been established whereby P. radiata foliage with less than 80 ppm SO_4-sulphur is sulphur deficient, 80-200 ppm SO_4-sulphur is marginal to adequate, 200-400 ppm SO_4-sulphur is adequate to high and with 400 ppm+SO_4-sulphur there is sulphur excess. This rating system has been modified in relation to site productivity, but the same principles have been used. The sulphate-sulphur form of sulphur is that required for utilization by nitrogen in new growth (Figure 1).

(iv) Deficiency of sulphur leads to an accumulation of non-sulphur containing foliar amino acids, especially arginine. Deficiency of this nutrient may occur through the year or seasonally when additional demands are placed on sulphur reserves for growth (Figure 1).

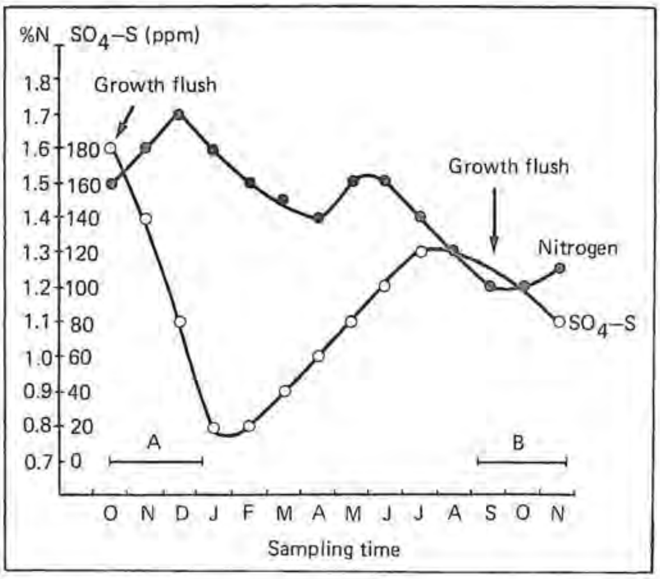

Fig. 1. Seasonal requirements of current foliage in P. radiata for sulphate-sulphur and nitrogen. (A is the period immediately after a growth flush when the needles are rapidly expanding. B is after a period when nutrients have been retranslocated to other new growth.)

(v) The non-sulphur containing amino acids are utilized by foliar fungal pathogens (for example, Diplodia and/or Dothistroma) as food sources allowing very rapid growth of these organisms. These fungi are thus the secondary cause of deformity or defoliation arising from the primary stress induced by nutrient deficiency.

(vi) Applications of nitrogenous fertilizers (urea or ammonium nitrate) lead to the utilization of sulphate-sulphur in order to form amino acids and proteins within the plant. While the theoretical utilization rate is 68 ppm SO_4-sulphur for every 0.1% N increase, calibration experiments with Douglas-fir have indicated that for an increase of 0.4% N (an increase giving a desired growth response), 400 ppm SO_4-sulphur was required. This latter larger requirement was partly due to increased needle expansion and retention.

(vii) Nitrogen fertilizer applications on sites with insufficient available sulphur result in induced sulphur deficiency with subsequent amino imbalances and increased fungal pathogen infection susceptibility. This has been reported in a fertilizer trial at Nundle State Forest. (Figure 2).

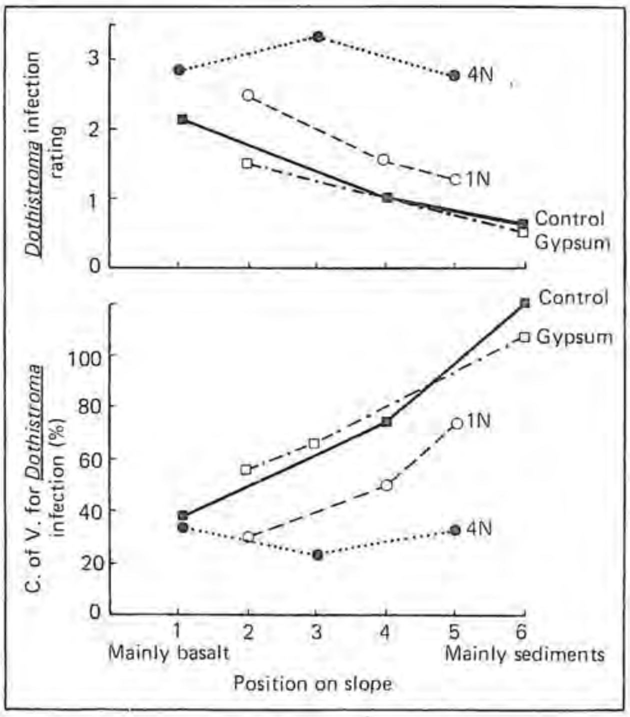

Fig. 2. Intensity and coefficient of variation of Dothistroma infection in relation to soil type for various treatments in a Radiata pine fertilizer trial on the northern tablelands, N.S.W.

(viii) Applications of nitrogen fertilizers to mature stands will result in interactions with sulphur in order to lead to a stem growth increase (e.g. basal area response), and hence growth responses will only be obtained when sufficient foliar sulphur is available. This was found to be the situation in a series of U.S. Pacific Northwest Douglas-fir stands. Areas with less than 400 ppm foliar sulphate-sulphur did not respond to nitrogen fertilizer while 80% of those with more than 400 ppm sulphuate-sulphur responded (Figure 3). Hence a growth response to nitrogen fertilizer (urea or ammonium nitrate) would be obtained when in excess of 400 ppm SO_4-sulphur was present, but if there was less than 400 ppm SO_4-sulphur, no response would be obtained. However, an N x S interaction would be noted if a nitrogen/sulphur fertilizer (ammonium sulphate) was applied.

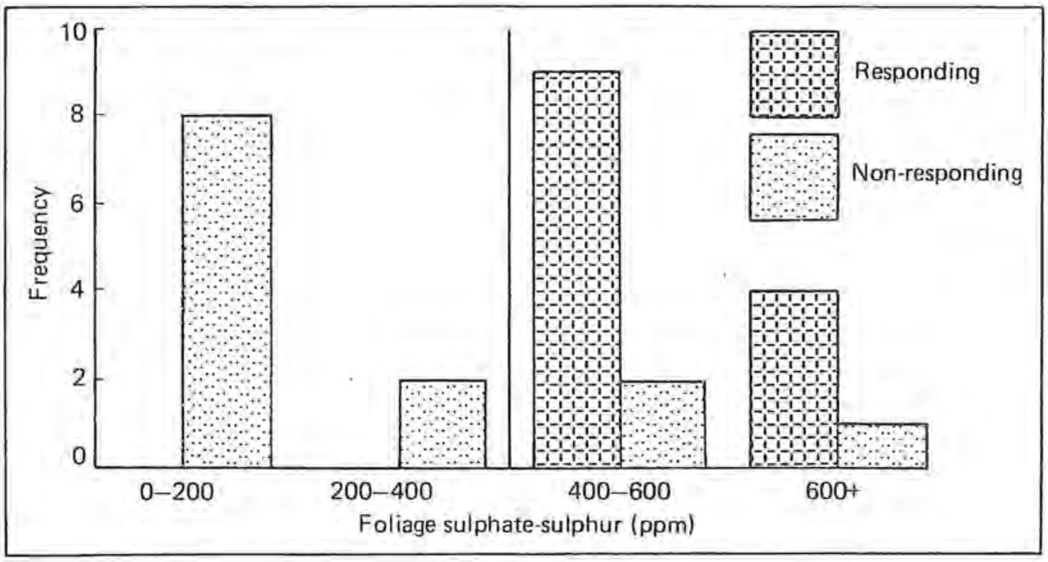

Fig. 3. Relationship between foliar sulphate-sulphur and response to urea applications in Douglas-fir for a series of Pacific Northwest Douglas-fir fertilizer installations.

Responses to ammonium nitrate and urea have been obtained on soil types with readily available sulphur or in geographical locations where sulphur inputs were adequate such as coastal locations or areas with high industrial inputs.

Nitrogen x Phosphorus and Nitrogen x Phosphorus x Potassium Interactions

The N x P or N x P x K type of empirical interaction has been reported for a variety of locations (Waring 1972; Neilsen and Crane 1977; Lambert and Turner 1978) and takes the following forms:

N fertilizer only applied - growth stimulus zero or depressed
P fertilizer only applied - growth stimulated
N + P fertilizers applied simultaneously - growth stimulated well beyond the additive effect of N and P separately.

The highest N x P responses have been reported either shortly after planting or in young stands, but results have been quite variable. A typical type of response has been shown in Figure 4.

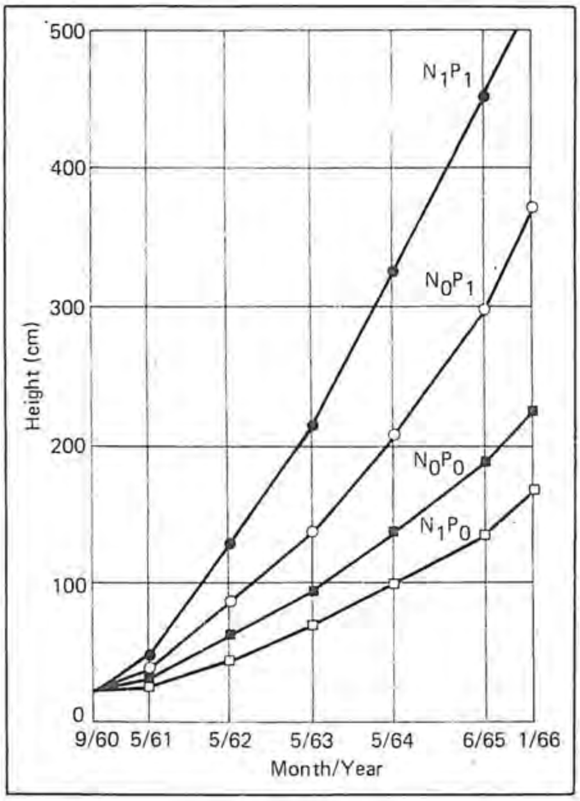

Fig. 4. Height growth (cm) at Belanglo State Forest for four different fertilizer regimes (Waring 1972).

Another trial, also involving four applied levels of both phosphorus and nitrogen (Table 1) has been reported by Neilsen and Crane (1977). These results suggest that an optimum balance of the applied nutrients is critical. Waring (1972) recommended that the nitrogen and phosphorus should be applied in fertilizers with nitrogen/phosphorus ratios of 0.9 to 2.0. When a quantity of nitrogen is applied which is excessive for the level of applied phosphorus, a depression in growth occurs and this is caused possibly by an intensification of the phosphorus deficiency (Waring 1972). A required balance of nitrogen and phosphorus has been stressed by Raupach et al. (1969) and in foliage this results in an optimum ratio of 10:1 (N:P). The fertilizers required to obtain this balance or ratio will vary from site to site depending upon the inherent fertility, phosphorus fixation capacity of the soil, the effect of interfering elements (for example, aluminium) and the moisture regime.

Table 1. Mean stem basal area response (cm^2/tree) for *P. radiata*, age 7 years, on land unit G2 (Tasmanian system), to four nitrogen and four phosphorus levels (Neilsen and Crane 1977).

Phosphorus treatments (superphosphate/tree)	Nitrogen treatment (urea)			
	N_0	N_1 (25 g $tree^{-1}$)	N_2 (50 g $tree^{-1}$)	N_3 (75 g $tree^{-1}$)
P_0	25	10	17	13
P_1 (62 g $tree^{-1}$)	28	38	32	39
P_2 (125 g $tree^{-1}$)	28	36	36	31
P_3 (187 g $tree^{-1}$)	27	47	37	28

The multiple interaction of N x P x K has been shown for example in Table 2 (Ellis et al. 1975). The treatments on Tasmanian land classes $M1_p$ and B_4 both gave significant N x P and N x P x K interactions while those on b_3 and B_{2b} produced an N x P effect but the addition of potassium had no significant effect on growth. In the cases of M1 and B_{2a} there was a significant N x P but potassium had a depressive effect. Based on height increments obtained in control plots, the responses did not appear to be related to site productivity.

Table 2. Response of *P. radiata* to fertilizer treatments (by land units). Response is expressed as the difference from the control height increment (mm) (Ellis *et al.* 1975).

Land unit	Fertilizer treatment*								Control height increment	Response %		
	Control	K	N	NK	P	PK	NP	NKP		NP/P[a]	NPK/P[b]	NPK/NP[c]
$M1_P$	0	15	45	65	375	325	1195	1310	105	220	220	10
M1	0	25	80	10	40	270	700	505	75	1650	1165	-28
B4	0	160	135	125	170	335	670	950	170	295	460	40
B3	0	65	-50	-100	595	675	1320	1370	530	1220	1300	4
B2a	0	-125	-290	-70	-65	-720	1250	1005	1400	2020	1646	-20
B2b	0	-435	-415	-385	55	80	555	530	1450	910	865	-5

*K = 170 kg ha^{-1} as KCl
N = 163 kg ha^{-1} N as urea
P = 83 kg ha^{-1} P as superphosphate
a ((NP - P)/P)%
b ((NPK - P)/P)%
c ((NPK - NP)/NP)%

The fertilizer forms predominantly used are urea or ammonium nitrate together with superphosphate and hence they include a mixture of phosphorus, nitrogen, calcium and sulphur. Experiments where phosphorus has been applied as low sulphur-containing ammonium phosphate in a low sulphur environment enable some analyses of the response to be made (Lambert and Turner 1978). On a site where sulphur was already reasonably adequate and enhanced by the sulphur in applied superphosphate, the 'traditional' N x P response has been obtained (Figure 5, site A). The nitrogen-only treatment utilized foliar sulphate-sulphur and the levels were maintained in the sulphur and N x P treatments. Site B was sulphur deficient and in this case the N x P treatment gave no additional response to phosphorus alone since the biochemical interaction resulted in growth limitation.

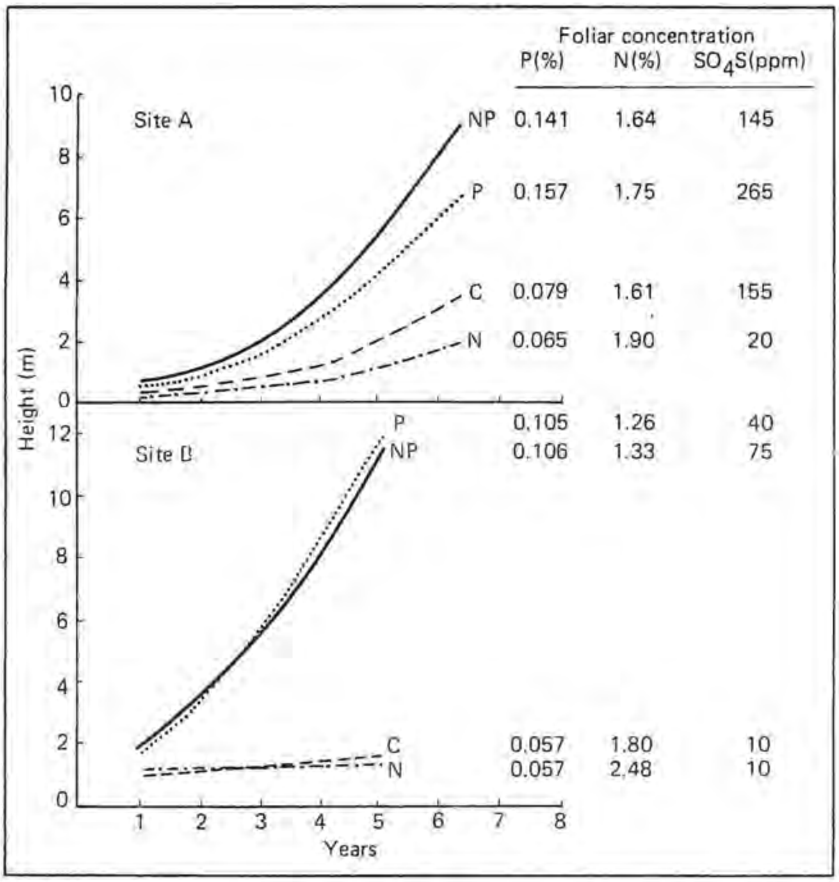

Fig. 5. Height growth (m) and foliar concentrations of P, N and SO_4-sulphur at two sites differing in their N x P response. Site A - adequate S, had a positive N x P response. Site B - deficient S, no N x P response.

There are minimal physiological data available on tree species with regard to nutrient regimes. Keller and Bucher-Wallin (1973) have reported data on photosynthesis for N x K and N x P interactions and found that with increasing nitrogen levels, photosynthesis increased (Table 3). Nitrogen in combination with increased potassium depressed photosynthesis while in combination with phosphorus the reverse was the case. Simultaneously, these same levels of nitrogen and phosphorus greatly increased transpiration rates (Table 4). Thus applications of N x P fertilizers would result in increased photosynthesis but also increased transpiration simultaneously. At higher nutrient levels, there may be such an imbalance of nutrients that increased transpiration rates will depress tree growth, i.e. induce water stress.

Table 3. Effect of nitrogen phosphorus and potassium supply on photosynthesis of spruce (Keller and Bucher-Wallin 1973).

N supply	K supply			P supply		
	K_1	K_2	K_4	P_1	P_2	P_4
			mg CO_2 g^{-1} ha^{-1}			
N_1	0.79	0.66	0.79	0.79	0.69	0.76
N_2	1.14	1.03	0.95	1.11	1.01	1.01
N_4	1.30	1.09	0.90	1.11	1.00	1.18

Table 4. Transpiration rate per plant of spruce at different nitrogen and phosphorus supplies (Keller and Bucher-Wallin 1973).

N supply	P supply		
	P_1	P_2	P_4
		g/hr	
N_1	5.5	5.9	6.4
N_2	7.3	8.4	8.5
N_4	10.1	9.8	9.9

Nitrogen/Copper Interactions

Copper deficiency is most often found on soils high in organic matter or on podzolic sands with organic matter in the surface horizons. The extent of complexing of copper by organic matter is high (Bloomfield and Sanders 1977) so that soils which have high total copper levels will have low copper availability. Applications of nitrogenous fertilizers (usually high levels of N x P x K fertilizers) have been found to induce copper deficiency in *P. radiata* in Victoria, South Australia, Queensland and New Zealand (N. Turvey, pers. comm.*, Ruiter 1969; Will 1972). Nitrogen fertilization has also induced copper deficiency in Douglas-fir in France (Bonneau 1973).

It is probable that copper deficiency induced by nitrogen fertilization is the result of the inability of roots to acquire sufficient copper from the soil to supply the enhanced growth rates. This is comparable to a dilution effect within the plant and it is probable that depressions of foliar copper levels occur in many stands after fertilization but the levels are not sufficiently depressed to cause deformities. Hopkins (1971) obtained increased growth responses (a positive N x Cu interaction) when copper was included in N x P x K fertilizers.

Nitrogen/Boron Interactions

Nitrogen/boron interactions are similar to those obtained for nitrogen/copper, in that applications of nitrogen have resulted in depressions in foliar boron concentrations. For example, in a cooperative *P. radiata* trial between A.P.M. Forests and the Forestry Commission of N.S.W. at Traralgon, Victoria, nitrogen fertilization resulted in a depression in foliar boron concentrations between 6-8 ppm which, because the initial foliar boron levels were 28 ppm, did not adversely affect tree growth.

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* Turvey, N. (1979). Copper deficiency in *Pinus radiata*; its extent and control in APMF plantations. APM Forests Research Report 2/79 (cited with author's permission).

A similar effect has occurred in various N.S.W P. radiata establishment trials (Dog Rocks State Forest) in that foliar boron levels were depressed from 14 to 7 ppm by N x P fertilizer applications, leading to tip dieback. Similar effects have been shown on a variety of other sites and these have become particularly severe in this past drought year. This relates to a climatic/boron concentration interation (M.J. Lambert pers. comm.) where drier climates have a higher critical level for boron than moister sites.

Two further aspects of the trend have been noted. In the Dog Rocks State Forest trial, soil mounding teatments were carried out to overcome drainage problems and these led to growth responses and subsequent tip death. This would lead to the conclusion that the effect of the N x P interaction affecting foliar boron concentrations is a growth dilution effect. This is not entirely supported by work in Douglas-fir where for the nitrogen treatments the three needle age classes showed declining boron concentrations with age (Figure 6) even though nitrogen was only applied one year previously (Turner 1979). Possibly the increased growth led to retranslocation of boron within the tree. The foliage analyses did not indicate a depression in concentration of any other trace elements (for example, iron and zinc) comparable to that in the case of boron.

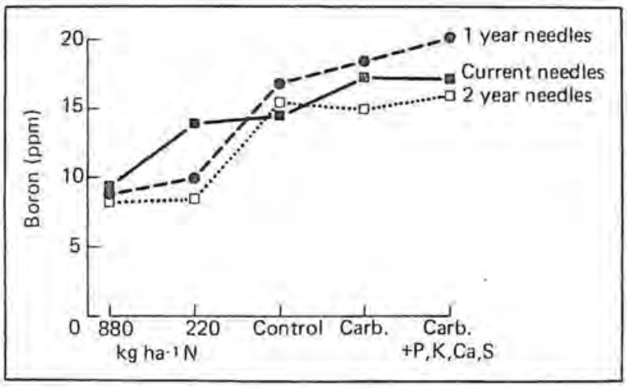

Fig. 6. The relationship between fertilized treatment, needle age and mean boron concentrations in Pacific Northwest Douglas-fir.

DISCUSSION

The data available on nutrient interactions within forest trees indicate that, to maintain a specific rate of growth, particular quantities of nutrients must be available and these are needed in specified proportions. That is, nutrients need to be added with regard to the 'law of the limiting' and simultaneously with regard to maintained balanced composition. In the case of excessive applications of nitrogen, growth will be suppressed or there may even be increased tree mortality. These aspects of the maintenance of correct nutrient balances have been discussed by various authors (for example, Baule and Fricker 1970) and in further detail for P. radiata by Truman and Lambert (this workshop).

As various responses can be obtained over a range of sites, at the practical level we need to consider soil reactions and formulation of fertilizer mixes and ratios appropriate to the particular site (especially considering trace element depressions).

At a more fundamental level, the effect of soil nutrient availability on tree nutrient regimes needs to be assessed both in young and mature trees, together with the effect of nutrient balances on growth, morphology and health of the tree. We know we can obtain growth responses in specific situations, but extrapolation to other sites is not particularly well understood.

The ratio and interaction on physiological processes such as photosynthesis, respiration and transpiration, and root development require further attention.

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NITROGEN FERTILIZATION AND *PINUS RADIATA*

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NITROGEN FERTILIZATION OF ESTABLISHING STANDS.

Nitrogen fertilization of establishing stands has become practice in the past decade in some areas. Among the forest services, New South Wales and Victoria do not use N on *P. radiata*, but South Australia, Western Australia and Tasmania do, as do the majority of the major forest companies. The prescriptions have proven to be very site specific, often requiring detailed research to differentiate between a nil or detrimental result, and a positive response. In some cases research has not resulted in a working prescription, and obtaining responses to N has often required more than a little defiance (of older policies), a green thumb, perseverance and perhaps 'faith'. In other cases, the decision not to use N is economically or politically determined. Occasionally the soil may have a surfeit of N.

On occasions, a prescription developed for one region and soil type has been applied to a different region or soil. The results have often been lethal and apart from the loss in stocking, fertilizer and money, these incidents have added to nitrogen's unreliable reputation.

Thus we have the situation in forestry today, where N is either loved or despised. If this appears an over-statement then it is true to say that nutrition is not as well understood by the managing foresters as by their professional counterparts in agriculture and horticulture. Forest soils and nutrition are not given high priority in Austraian teaching institutions, even today.

The major key to understanding nitrogen in forest ecosystems, and particularly with *P. radiata*, is an understanding of the 'N x P interaction'.

The pioneering work and first principles in this area were commenced in the 1950s by Hugh Waring in the Canberra region. The best summary of his work is Waring (1973). Waring found on the very P-deficient soils of Belanglo state forest (soils derived from Silurian 'Hawkesbury' sandstone), and the P-deficient soils around Canberra, that nitrogen applied alone as a soil fertilizer was detrimental to growth and caused trees to die or grow at rates less than that of the unfertilized controls. However phosphorus, when applied alone on these soils, resulted in a positive acceleration of growth, and nitrogen in combination with phosphorus resulted in a further acceleration. The N x P relationship is shown in Figure 1 (after Waring).

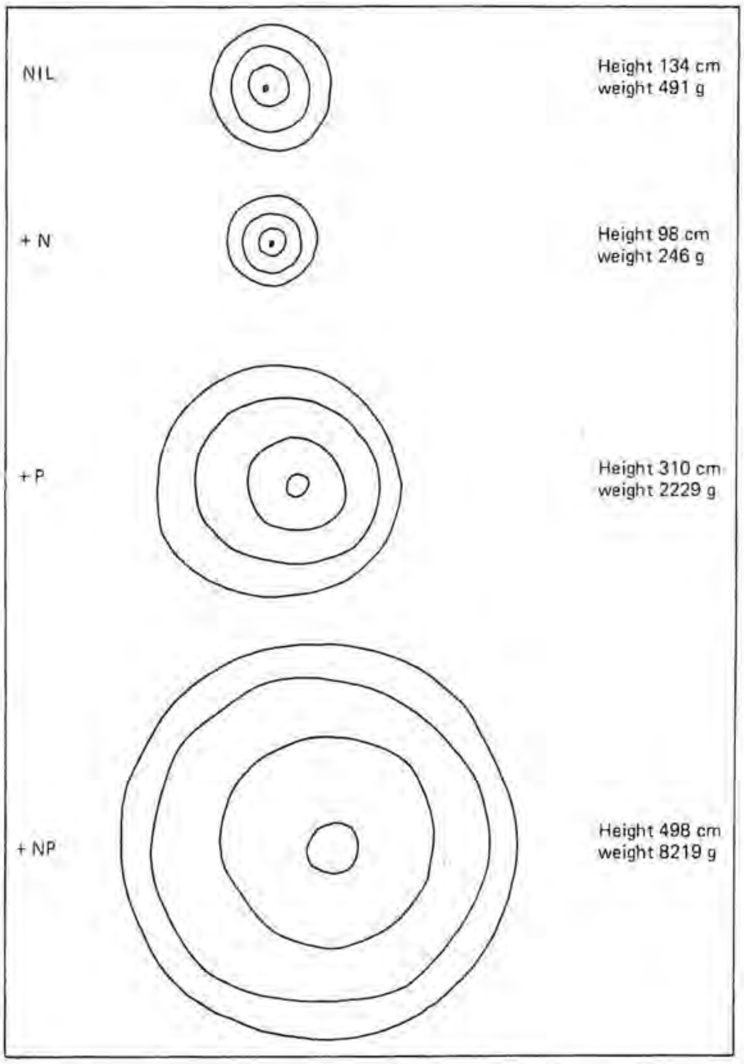

Fig. 1. Effect of N and P fertilization on *P. radiata* planted and fertilized Aug. 1960 Belanglo S.F., harvested Feb. 1964. Cross sections at 12" height of mean tree of treatment (after Waring 1973).

The NP relationship shows that it is essential to correct any P deficiency before nitrogen can be applied safely or for positive advantage. It is also essential to account for the fact that soils vary greatly in the degree of P fixation so that the N:P ratio in the fertilizer will need to be site-specific for each soil type. Inattention to these two basic principles is perhaps the most common fault in the use of N in forests.

On the sandy soils of southeast South Australia, where the phosphorus-fixing capacity is relatively low, an N:P fertilizer ratio of 11:2 is successful (Woods 1976). However this mixture is lethal on clay-loam soil of moderate P-fixing capacity. The N:P ratio in the foliage of P. radiata can have values in the range of 5-16. These ratios were determined for a large number of P. radiata forests in southeast Australia and in greenhouse pot trials by Raupach (1967). Using solution culture and an Ingesdadt approach it may be possible to approach these ratios. However on clay-loam soils in southern N.S.W. (Waring 1973) and in Tasmania (Neilsen and Crane 1977) the optimum N:P fertilizer ratio is in the range between 1:1 and 2:1.

Waring established that NP fertilization at planting could result in substantial gains in volume, and measured increases in growth 25 years later. Table 1 shows the gain obtainable by using N in addition to P as a starting fertilizer dose.

Table 1. Percentage response of various treatments over the control for basal area and volume (*P. radiata* planted 1963 at 2.5 x 2.5 m, Long Term Experiment 3, Belanglo, N.S.W., 1971 measurements), after Waring 1973.

Fertilizer and time of application	Percent response over control (nil)	
	Basal area	Volume
P 0 years (at planting)	100	235
P 2 years	73	161
P 4 years	58	118
NP 0 years (at planting)	156	376
NP 2 years	125	276
NP 4 years	77	137

Table 1 also shows the effect of delaying fertilizer. Delay of fertilizer until 4 years of age resulted in the halving of production at age 8 years.

Waring also showed that weed control was one of the largest interactants with nitrogen fertilizer, and this has subsequently been confirmed by most workers in the field. The control of herbaceous weeds is particularly important and Table 2 shows the drastic effect of NP fertilization in grasslands without controlling weeds. Nitrogen has the effect of enhancing the weeds which may then outcompete P. radiata for moisture and result in mortality and a negative response to fertilizer.

Table 2. Effect of NP fertilization and weedicide applied to *P. radiata* on a grassland site in the A.C.T. (W. Crane, unpublished data).

Treatment			Survival (%)	Vol. of live trees (cm^3)	Yield vol. (cm^3 10 tree $plot^{-1}$)
No fertilizer	No weedicide	(F_oW_o)	78	1.2	9
No fertilizer	Weedicide	(F_oW_1)	88	1.6	15
NP fertilized	No weedicide	(F_1W_o)	38	1.4	5
NP fertilized	Weedicide	(F_1W_1)	92	2.5	23

Similar negative responses can be obtained by interactions with browsing animals, or by an inappropriate fertilizer prescription for the specific types of soils, climate, seasonal conditions, physiological condition of the plants or by inappropriate placement of fertilizer. These interactants have contributed to the variable experiences obtained to N by forest research workers.

In South Australia Ruiter and his colleagues had little success with N through the 1960s (Ruiter 1974). However in the early 70s, Woods commenced a series of trials which showed that substantial responses could be obtained by paying attention to the timing and placement of fertilizer and weed control. Woods' work has subsequently been adopted and applied in the form of a 'maximum growth sequence (MGS)' where a 'complete mineral' NPK (11:2:5)/trace element mix is applied at six times during the first four years following planting. The MGS also includes cultivation and weed control. Approximately $500 000 was spent on nitrogenous fertilization by the Woods and Forests Department in 1979-80. The MGS has been partially adopted as a measure to alleviate 'second-rotation decline'.

However the MGS *in toto* supplies only approximately 250 kg N ha^{-1}, but the nitrogen required per rotation may be of the order of 600-800 kg ha^{-1}. Hence, even if the fertilizer added were used at 100% efficiency, the MGS supplies only 30-40% of the total 'replacement requirement' of the crop and only for 1/10th of a 40 year rotation. Additionally, fertilization efficiency seldom approaches 100% and may be as low as 10% (Nambiar and Woods 1979). Hence there appears to be a considerable and expensive problem in supplying N to *P. radiata* grown on the sandy loam soils in south-east South Australia and western Victoria.

Dargavil and Cromer (1979) found that substantial responses can be obtained to starter fertilizer on the sandy soils of Gippsland. Nitrogen resulted in an increased response over phosphorus alone and N is included in a complete macro (NPK) mix applied to all new plantations by APM in Gippsland. However, the energy costs and returns of N were found to be only marginal in favour of applying N.

In Tasmania, Neilsen and Crane (1977) also obtained responses to N fertilizer at planting - commencing in the early 60s. This work led to the routine use of an NP starter fertilizer (125 g superphosphate + 50 g urea) applied to all newly established *P. radiata*.

Hopkins (1971) in Western Australia also found that *P. radiata* could benefit from an initial starting dose of N, and currently 1500 ha of the total 1900 ha planted/year on the Donnybrook sunklands, the Hills, and the Coast are treated with an 18:18 NP mix.

In A.C.T., from 1975 through 1979, all new plantings (about 600 ha yr^{-1}) were fertilized with a 15:15:0 mix drilled into the ripping lines prior to planting. N fertilization has been abandoned in the A.C.T. in the past year, but its reintroduction is now being contemplated, together with a large-scale program of fertilizing established stands.

FERTILIZATION OF ESTABLISHED STANDS

In Australia there has been no development of the type of fertilization which has become popular in Scandinavia and North America, where coniferous stands of average or good health are fertilized at the time of thinning to produce additional growth of non-juvenile wood.

In 1972 fertilization of this type was applied to 155 000 ha of Scots pine and Norway spruce in Sweden using ammonium nitrate as a fertilizer (Holman 1972), and there is a continuing program of this scale. A typical fertilizer response is that reported by Moller (1971) in which an extra 12.5 m^3 ha^{-1} was added in five years following application of 100-120 kg N ha^{-1} to established Scots pine growing at a current increment of 4 m^3 ha^{-1} yr^{-1}.

In 1973, over 90 000 ha of established Douglas fir and Ponderosa pine forest were fertilized - mainly with urea - in the Pacific Northwest of the U.S.A. Atkinson and Morison (1975) have reported an average increase of 18% in two years following the application of 224 kg N ha^{-1}.

Both the Scandinavian and North American forests instanced above have growth rates of about 5 m^3 ha^{-1} yr^{-1} (Raupach 1967). However, in New Zealand, Chile, South Africa and Australia, there are considerable areas of coniferous forest (particularly of P. radiata) growing at rates of 15-30 m^3 ha^{-1} yr^{-1}. Only recently has attention been focused on the potential of increasing growth of these relatively fast-growing established stands by fertilization.

In the North Island of New Zealand, Woollons and Will (1975) measured total gains of between 36 m^3 ha^{-1} and 61 m^3 ha^{-1} in the seven years following fertilization with an NPK and trace element mixture applied to thinned 13-year-old P. radiata stands which had grown at 23 m^3 ha^{-1} yr^{-1} (MAI) on the yellow-brown pumice soils. The responses represented an increased increment of 7 m^3 ha^{-1} yr^{-1} and a 20% gain in volume over seven years. Mead and Gadgil (1978) showed that additional volumes of 93 m^3 ha^{-1} over a period of five years could also be obtained with P. radiata on less fertile P-deficient soils in the Nelson conservancy of New Zealand following fertilization with an NP mix. This response represented a 54% boost in CAI from 28 m^3 ha^{-1} yr^{-1} to 43 m^3 ha^{-1} yr^{-1}.

A program of research designed to investigate later-age fertilization of P. radiata was commenced in southern N.S.W. and in A.C.T. in 1976. The program is centred at the Canberra station of CSIRO Division of Forest Research and the first three field trials to determine the feasibility of increasing wood production of P radiata by fertilization were established at the Belanglo, Kowen and Uriarra plantations.

The plantations aged 16, 25 and 23 years respectively have been producing an average of 14 m^3 ha^{-1} total stem-wood per year, and were thinned before fertilizing from 1350 to 900 stems ha^{-1} by extraction of each third row.

Four years later the extra volume of wood resulting from fertilization was 17 m^3 ha^{-1} for all sites, and 24 m^3 ha^{-1} for the two sites in the A.C.T. This represented an acceleration of growth on the A.C.T. sites in the four-year period of 37%: 32% in 1976-77, 37% in 1977-78, 45% in 1978-79 and 34% in 1979-80. Eighty per cent of the increase was added to the largest one third of trees in the stands.

The increase in size of trees (volume) due to fertilization was about 8%. In the A.C.T. the largest one sixth of the trees increased in diameter (at breast height) by 2.1 cm, so that a tree of diameter 27.0 cm in 1976 was 30.7 cm in 1980 if unfertilized, and 32.8 cm if fertilized.

The increase obtained in volume and size of trees is shown in Figures 2 and 3.

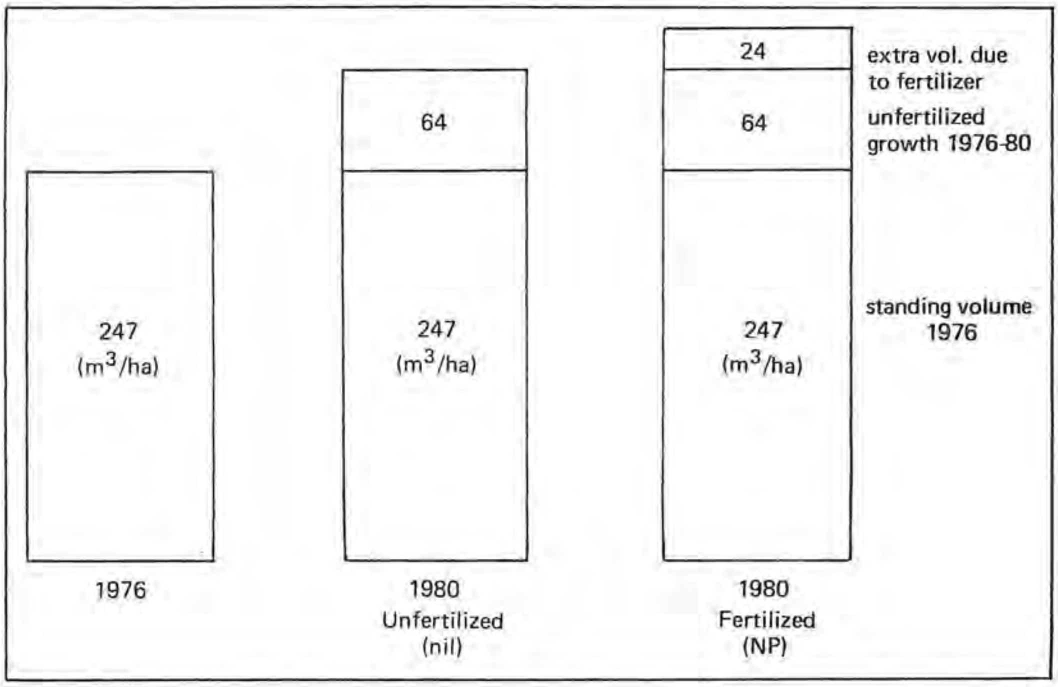

Fig. 2. Total standing volume (m^3/ha) in 1976 after thinning and before fertilization, and in 1980 with (NP), and without (nil) fertilization in the A.C.T.

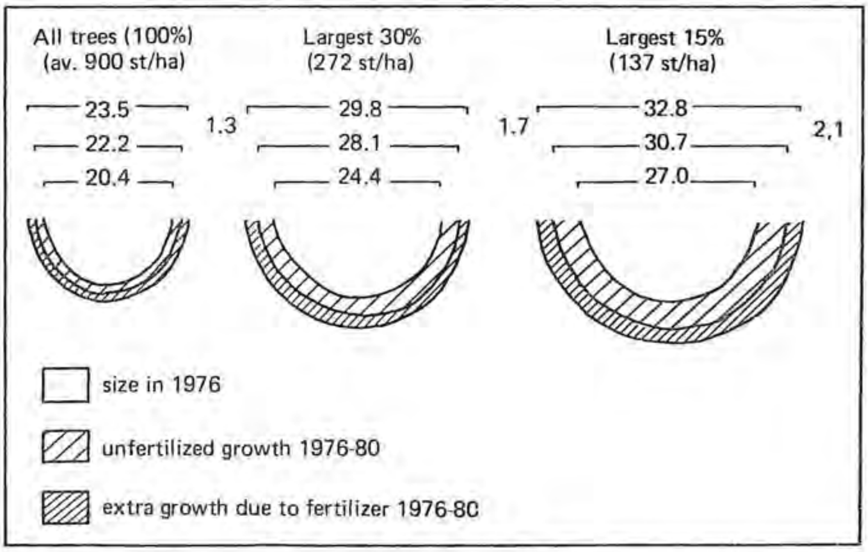

Fig. 3. Size (dbhob, cm) of trees before fertilizing in 1976, normal (unfertilized) increment, and additional increment due to NP fertilization in the period 1976-80 for different size classes of trees.

These experiments serve to illustrate the main questions concerning later-age N fertilization.

Firstly the magnitude of the total responses may be seriously under estimated because estimates were based only on measurement of diameter over bark at breast height (dbhob) and height. Any change in the taper or form of trees would not be accounted for by this method and work by Snowdon et al. (1980) and Whyte and Mead (1976) indicates that responses in the upper stem may be a major proportion of the total response. This point illustrates the first aspect of later-age fertilization; that of the challenge of measuring responses. Measurement of dbhob and height is insufficient. Several alternatives are: to climb individual trees and measure diameters along the bole, to destructively sample and use stem analyses, or to use an optical dendrometer or telerelascope.

Of the three trials, only two showed responses. The responses were directly proportional to both unfertilized growth rates, and to the foliar-N levels in the unfertilized trees. These relationships are shown in Figures 4a and 4b and this raises the question of diagnosis; in particular whether foliar analysis can be used to distinguish responsive from non-responsive stands? Some evidence to date would suggest that it can, although there is divergence of opinion on this subject. In New Zealand, Mead and Gadgil (1978) concluded that, if foliar N levels are higher than 1.4%, the chances of obtaining a response to N fertilizer were less than 20%. Boggie and Miller (1976) found that, for P. contorta, N concentrations in foliage varied considerably with season. This work indicates some of the dangers of ascribing absolute values for diagnosis. A calibration for each region, soil type and season would appear to be useful if foliar analysis is to be developed as a diagnostic tool. This area requires further fundamental research.

The trials also resulted in a similar relative fertilizer response (response as a proportion of unfertilized growth) in each size class of tree. This suggested that trees respond to fertilizer in direct proportion to their size and growth rates. Hence more wood will be added to faster growing larger trees by fertilization.

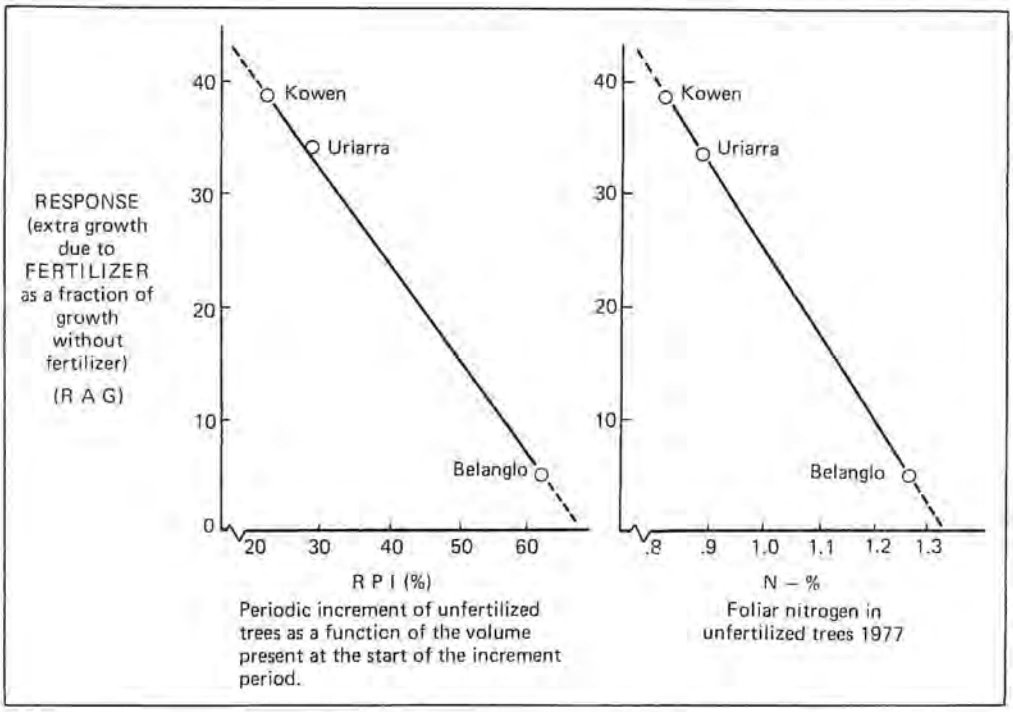

Fig. 4a. Relationship between fertilizer response and normal growth of unfertilized trees.

Fig. 4b. Relationship between fertilizer response and foliar-nitrogen in unfertilized trees.

There is no evidence to suggest that N fertilization increases photosynthetic efficiency. The current evidence suggests that N fertilization accelerates the replacement of green crown - if conditions of free growth are created (viz. by thinning). Evidence from New Zealand indicates that no response is obtained to N unless the stands are thinned to create conditions of free growth. This criteria may not be as rigid in Australia where stands are not completely limited by light alone. However it is likely that little worthwhile response will be possible without thinning.

The duration of responses is likely to be 5-7 years, based on evidence from Woollons and Will (1975) and Mead and Gadgil (1978). However H. Miller in Scotland has measured responses in Scots pine lasting 12-13 years and has shown that there is sufficient fertilizer N stored in the biomass in the first 4-5 years to positively affect growth up until 12 years. Miller et al. (1976) and Crane

(1980) have shown that N is translocated into older tissues (particularly foliage) laid down prior to the current year foliage at the time of fertilization. Hence the storage available for N is likely to be greater than that synthesized after fertilization.

However, the question of how much phosphorous or sulphur is required in conjunction with N to optimise N responses, and what diagnoses can be used to determine this, is not answered by these trials. The question of interacting nutrient is critical in determining the economics of later-age fertilization, and it is unlikely that any overseas research will provide the answers for the rather uniquely infertile forest soils of Australia.

John Turner has the task of approaching this subject next in this workshop. I do not envy his task as there is a dearth of data. Nonetheless it is true that (as was the case for the N x P interaction in N fertilization of establishing stands), the understanding of nutrient interactions,particularly N x P and N x S, is the key to understanding and developing N fertilization of P. radiata in Australia.

However, the main question is how are Australian P. radiata plantations to obtain N. I believe that the Australian softwood industry may soon face a nutritional crisis. Little emphasis has been given to this area of research and some current thinking is that the second rotational problem is 'solved'. I do not agree with such thinking.

There is currently very little nutritional philosophy or policy to replace nitrogen in harvested P. radiata crops, in Australia. As mentioned previously, professional training of foresters in the area of forest soils and nutrition is still not at a high level. This situation should be changed. Additionally, soils and nutrition should be ranked at least with genetics as a core area worthy of intensive research by the CSIRO Division of Forest Research. More research will be required before a satisfactory legume or nitrogen-fixing system is developed for P. radiata. Until this time (and unlike contemporary thinking and trends in agriculture) the most viable strategy of supplying N to P. radiata monocultures appears to be by fertilization in combination with a maximum effort to conserve the N resources currently on the site.

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LEGUME TRIALS IN WESTERN AUSTRALIAN PINE PLANTATIONS

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SUMMARY

The combination of pines and a legume understorey provides a rapid means of increasing the soil nitrogen status, and accumulation of 350 kg ha^{-1} of nitrogen have been recorded in some young W.A. pine plantations.

The preliminary data indicates that much of the increased soil nitrogen is held in the humic acid fraction of the soil.

INTRODUCTION

The combination of conifers and a legume understorey is a recent development in plantation forestry and many aspects of this work are still in the experimental stage. Some important aspects of this integration of agriculture and forestry have been discussed at a workshop organised by the CSIRO Division of Land Resources Management (Howes and Rummery, Eds. 1977). Another general view of this subject has been given by McKinnell and Batini (1978).

I do not propose to discuss the economic aspects of this form of forestry, but I would like to indicate how agroforestry can increase the amount of nitrogen in a plantation ecosystem.

EXPERIMENTAL

Composite surface soil (0-10 cm) samples were collected from three agroforestry trials in the Busselton Forest Division, 200 km S.S.W. of Perth. The areas were a series of paired plots, one half being the agroforestry trial and the adjacent area receiving normal plantation establishment treatment. The soils of these areas have been described by Smith (1951) and belong to the Mungite Soil Series. The experimental areas consist of widely spaced P. radiata with a sward of subterranean clover as a ground cover.

The fertilizer treatments for the two plots were:

(a) clover pasture; at establishment 500 kg ha^{-1} of super., copper, zinc, B. (8.4% P, 10.2% S, 0.33% Cu and 0.3% Zn) followed by an annual dressing of 100 kg ha^{-1} of the above fertilizer.

(b) routine plantation; 100 g/tree at planting of Agras No 1, (17.5% N, 7.6% P and 16.0% S) followed by a broadcast application at 3 years of 400 kg ha^{-1} of the Agras fertilizer. In addition, the young pines received a copper, manganese and zinc sulphate spray during the first year in the field.

The soil samples were analysed by standard laboratory procedures to estimate the build up of the soil organic matter by the clover sward.

RESULTS

The analytical data for the three areas is shown in Table 1. Statistical analysis of the organic carbon and nitrogen data showed that only the main effects due to the locality and clover were significant (Appendix 1).

These soils have a mean bulk density of 1600 kg ha^{-1} and using this figure it is a simple calculation to show that the nitrogen accumulation in the first 10cm of the three clover plots has amounted to:

Table 1. Jarrahwood agroforestry trials. Effect of clover on surface soil properties.

Location	No. of years under pasture	Clover	pH	T.S.S. %	O.C. %	N %	P – ppm Total	Bray	Olsen	CEC m.e.%
Chapman Lease	10	+	5.44	0.004	1.35	0.082	38	18	6.5	6.89
		-	5.52	0.003	1.43	0.060	6	0.6	1.0	8.84
No. 6 Road Agroforestry plot	5	+	6.30	0.006	1.32	0.066	67	12	1.5	9.36
		-	5.94	0.004	0.79	0.039	17	1.3	0.1	7.66
No. 7 Road Agroforestry plot	6	+	5.72	0.003	1.12	0.051	29	13	2.2	
		-	6.02	0.002	0.57	0.026	7	1.0	0.2	

Chapman Lease	352 kg ha^{-1}
No. 6 Road	432 kg ha^{-1}
No. 7 Road	400 kg ha^{-1}

In an attempt to determine if there is a change in the form of the soil nitrogen under the clover sward, two nitrogen availability indices were examined. These were extracted with (1) dilute sulphuric acid (Purvis and Leo 1961) and (2) the sulphuric acid potassium permanganate extractant suggested by Stanford and Smith (1978). The results are shown in Table 2 and this data indicate that there is some evidence of a decline in the percentage of nitrogen extracted by these reagents under the clover.

Table 2. Jarrahwood agroforestry trials. Nitrogen availability indices.

Location	Clover	Purvis and Leo		Stanford and Smith	
		N ppm	Percent of total N	N ppm	Percent of total N
Chapman Lease	+	59	7.2	36	4.4
	-	58	9.7	48	8.0
No. 6 Road	+	42	6.3	34	5.1
	-	45	11.6	41	10.6
No. 7 Road	+	67	13.1	49	9.6
	-	53	20.2	22	8.4
Means (all areas)	+		8.9		6.4
	-		13.8		9.0

Hydrolysis of the soil nitrogen by 6N hydrochloric acid showed very little difference in the percentage of nitrogen extracted by this method, viz.:

Clover	Percent of total N extracted by 6N HCl hydrolysis
+	67.2
-	70.2

Similarly, the amino acids released by this hydrolysis were very similar in both sets of soils:

Clover	Percent of total N extracted as amino acid nitrogen
+	68.0
-	68.2

Extraction of the soil organic nitrogen by alkaline sodium pyrophosphate (Kononova 1966) showed marked differences between the two sets of soils. The percentage of nitrogen extracted was similar for both, but it was clearly evident that the proportion of humic acid nitrogen was much higher under the clover (Table 3).

Table 3. Jarrahwood agroforestry trials. Organic nitrogen fractionation.

Clover	Percentage of total N extracted by alkaline pyrophosphate	Humic acid N as percentage of total N
+	43.0	14.1
-	43.0	8.1

DISCUSSION

It is evident that an agroforestry regime can cause a rapid (5 years) build up of soil nitrogen at a site and this technique could provide an important nutrient to some of our impoverished plantation soils.

This accumulation of nitrogen by legumes is not new work, as our colleagues in agriculture have used this technique to maintain and improve soil fertility for many years.

There is insufficient data at present to be able to comment definitely on the changes in the nature of the soil nitrogen, but the change in humic acid nitrogen is worthy of further investigation.

Moore (unpublished data) has indicated that P. radiata growing on clover trials at Jarrahwood appear much healthier and more vigorous than trees growing on non-clover areas and foliar nitrogen levels from one of these trials support this observation. This particular trial after 5 years under clover showed a foliar nitrogen level of 1.59% nitrogen, which is more than adequate for satisfactory pine growth.

There are of course silvicultural problems association with this plantation management technique and trials covering these aspects are currently being investigated.

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AGROFORESTRY UNDER 13 TO 18 YEAR OLD *PINUS RADIATA* AT WELLBUCKET, WESTERN AUSTRALIA

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ABSTRACT

Clover was established beneath 13 year old, high pruned, *Pinus radiata* which were thinned to 143 and 261 stems per hectare, and has now germinated for six years. The trees responded to thinning and fertilisation but were unable to fully utilise the site at the wider spacing. Higher soil nutrient levels are not yet reflected in the foliage. The tree crowns doubled in size in five years and the increase in shading caused a loss of pasture production. The pasture responded favourably to a further thinning of the pine to 70 stems per hectare.

INTRODUCTION

Agroforestry, the production of timber and agricultural products on the same land unit, is seen to be a land use with potential in parts of Western Australia where freehold farmland has been resumed for reforestation to reduce the salinity of groundwaters, and in the southwest of the State where there are extensive plantings of pine on repurchased farmland or former jarrah (*Eucalyptus marginata*) forest.

In an earlier paper (Anderson and Batini 1979), we indicated that successful establishment of clover under pines could be achieved and we presented data giving preliminary results of pasture and crop performance. The pasture has now germinated under the pine canopy for the sixth year in succession and this report updates the previous findings.

SITE DESCRIPTION

The site is located in the Darling Range 47 km east of Perth (latitude 32°S). The soil is a massive red earth, Gn 2.14 on the Northcote Key (Northcote 1971). The site is close to the 900 mm rainfall isohyet, but for most years of the trial the actual rainfall was considerably lower than this long term average.

In 1962 P. radiata seedlings were planted into a clover/grass pasture which had received regular dressings of plain superphosphate. The pines were planted at 1750 stems ha^{-1} in rows 2.75 m apart. In 1973 the trees were thinned to about 450 stems ha^{-1} leaving alternate rows. Zinc sulphate was applied in 1965 to correct obvious zinc deficiency symptoms. The trees were low pruned to a height of 2 m and the select 20% were subsequently pruned to a height of 4 m in 1975.

EXPERIMENTAL PLAN

In March 1975 two blocks with low (143 stems ha^{-1}) and two with medium (261 stems ha^{-1}) density were established. Each block was 40 x 33 m with buffers between and around these. The remaining trees averaged 20 cm in diameter (diameter at breast height over bark (dbhob)) and 13 m top height and were all pruned to 6 m to improve light penetration.

Six standard inventory plots were established in January 1977, two in each of the two thinning treatments and two in an adjacent, unthinned control. Following the spraying of volunteer annuals with a bipyridyl herbicide (0.1 kg active ion ha^{-1}) and cultivation, pasture was established by seeding with inoculated clover (8 kg ha^{-1}), and fertiliser (65 kg ha^{-1} P, 4.95 Cu, 2.25 Zn and 0.30 Mo) and light covering with harrow. Annual dressings of super, copper, zinc have been applied subsequently. In June 1979, the soils were analysed for total N, P, K, and organic Carbon and trees sampled for foliar N, P, K, Mn, Zn and Cu levels. The plots are grazed with sheep between June and January of each year. The medium and low density plots were thinned to 70 stems ha^{-1} in late January 1980.

RESULTS

Clovers

No establishment problems were encountered, and healthy pasture resulted. Detailed results have been presented for both cultivar and crop data (Anderson and Batini 1979). The pastures regenerated until 1978 without major problems. However, a substantial reduction in pasture in the denser plots during the 1979 season led to a decision to thin all plots in 1980 (Table 1). During 1980, pasture (particularly the clover component) regenerated well on the areas previously densely shaded.

Table 1. Pasture production at medium tree density (261 stems ha^{-1}) as a percentage of pasture production at low (143 stems ha^{-1}) tree density.

Year	1975	1976	1977	1978	1979	1980
Percentage	94	112	81	90	56	91

Trees

This was not a high quality P. radiata site (Mean Annual Increment to January 1977, 13 m^3 ha^{-1}) and was still showing some signs of zinc deficiency with thin crowns and some rosetting of needles. Plot statistics (1980) are presented in Table 2.

Table 2. Plot statistics for diameter, basal area, height and volume (January 1980).

Statistic	Thinned, fertilised, pastured 143 stems ha^{-1}	261 stems ha^{-1}	Control 313 stems ha^{-1}
Dbhob cm	28.7	26.7	26.0
BAOB m^2	8.4	12.3	17.0
Volume under bark			
to 6 cm crown m^3	62	91	122
to 23 cm crown m^3	25	27	35
Height mean m	18.9	19.1	18.2
top m	19.8	20.8	20.7

Table 3. Periodic mean annual increment (PMAI) for thinned and controlled plots for the period January 1977 to January 1980.

Statistic	Thinned, fertilised, pastured 143 stems ha^{-1}	261 stems ha^{-1}	Control 313 stems ha^{-1}
Dbhob cm	1.42	1.05	0.72
BAOB m^2	0.69	0.80	0.70
Volume under bark:			
to 6 cm crown m^3	7.8	9.9	10.2
to 23 cm crown m^3	6.6	7.2	7.6

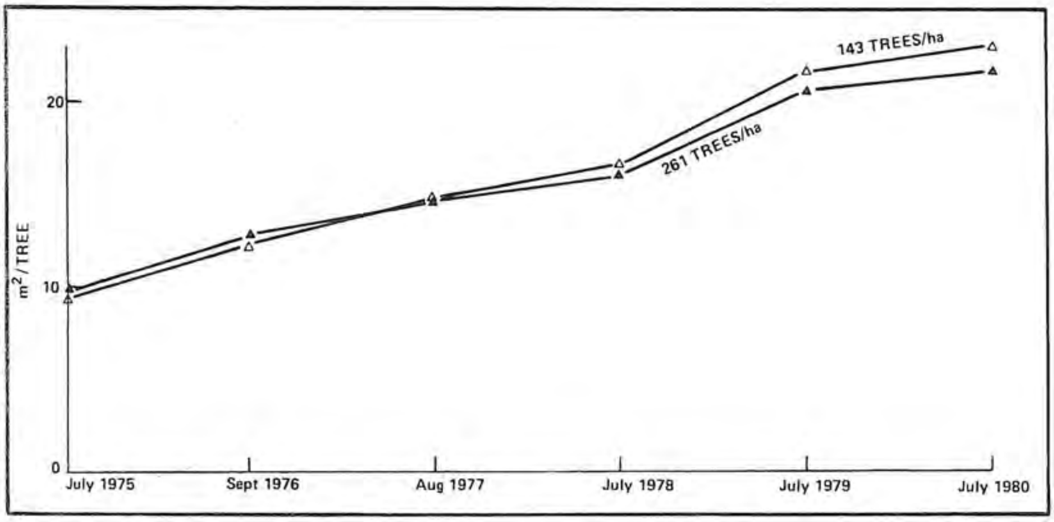

Fig. 1. Mean foliage basal area of 1962 planted P. radiata pruned to 6 m 1975.

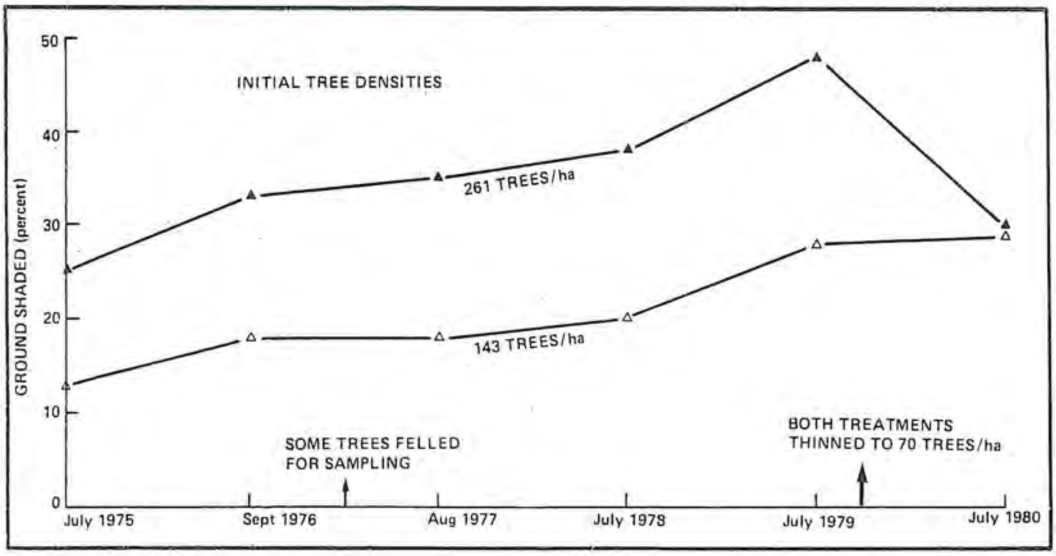

Fig. 2. Percent ground shaded by two 1962 plantings of P. radiata thinned and pruned to 6 m 1975.

The trees responded to thinning treatments, but volume production was decreased slightly, Table 3. The periodic Mean Annual Increment (to 6 cm crown) over this three year period (1/77 to 1/80) was 9.3 m^3 ha^{-1}. The crowns responded well to fertilisation and this was reflected in the needle colour, needle length and a greater retention of needles on the branches. Measurements of the growth of tree crowns indicated similar increases for both tree densities, the crowns doubling in size over 5 years (Fig. 1) with marked effects on the percentage area which was shaded (Fig. 2).

Although the stand was heavily thinned, less than 10% of the trees produced epicormic growth; these were not serious and could readily be pruned. Thinning in 1980 removed about 20 m^3 ha^{-1} of sawlog sized material (18 cm small end diameter), leaving behind about 40 m^3 ha^{-1} of sawlogs, and reduced the percentage area shaded to 29% over the whole site (Fig. 2).

Nutrition

Soil analyses for total N, P, K and organic Carbon showed higher levels ($P<0.001$) for all except K, and lower C:N ratios ($P<0.01$) in the thinned, pastured and fertilized treatments (Table 4). At the same sampling, foliar levels did not indicate an increased uptake of nutrients when expressed on a percentage basis.

Table 4. Soil analysis for total N, P, K and organic carbon, for thinned and control plots, from soil samples collected four years after the establishment of the trial (June 1979)

Soil Analysis	Thinned, fertilized, pastured 143 stems ha^{-1}	261 stems ha^{-1}	Control 313 stems ha^{-1}	Remarks
N %	0.194	0.188	0.112	***
P ppm	250	246	158	***
K m.e.%	0.92	1.04	0.94	n.s.
Organic carbon %	3.12	3.19	2.20	***
C:N ratio	16	17	20	**

Note: *** = Control different ($P < 0.001$)
** = Control different ($P < 0.01$)
n.s. = No significant difference.

Foliar levels of N, K, Zn and Cu exceed the levels considered as adequate for growth, but those for P and Mn are still below these levels (Table 5).

Table 5. Foliar analyses for N P, K, Mn, Cu and Zn, for thinned and control plots, from foliar samples collected four years after the establishment of the trial (June 1979)

—Soil Analysis	Thinned, fertilized, pastured 143 stems ha^{-1}	261 stems ha^{-1}	Control 313 stems ha^{-1}	Remarks
N %	1.49	1.46	1.53	1.2*
P ppm	0.093	0.094	0.119	0.12*
K %	0.92	0.70	1.06	0.4*
Mn ppm	20	29	32	30*
Zn ppm	18	21	25	14*
Cu ppm	6	7	7	4*

* adequate.

Sheep

The plots were grazed annually until most of the herbage and some of the burr has been consumed. Some camp damage and scratching at the base of trees occurred, partly exposing some of the larger roots. Apart from occasional fly strike, no symptoms of ill health in the sheep was observed. The carrying capacity was estimated at about 7 sheep ha^{-1}.

DISCUSSION

The trial is now in its sixth year with no apparent harmful effects on either the trees, the sheep or the pasture. The trees responded well to increased nutrition and to thinning, but were apparently unable to utilise the site fully, which would explain the greater volume production in the unthinned plots. The run of dry years probably contributed to the reduced PMAI (9 as against 13 m^3 ha^{-1}). Though the heavier thinning reduced total volume production slightly, diameter growth was improved substantially and the volume increment in the larger size classes was not affected as greatly.

The higher nutrient levels in the soil were not yet reflected in foliar levels in the needles, though the biomass in the crowns was substantially increased. Even so, the levels of P and Mn are still slightly below the generally accepted adequate levels for the growth of P. radiata. This reflects in part the high phosphate fixing capacity of these lateritic soils.

As the crowns increased in size and density and the trees grew taller the increase in shading began to seriously affect pasture production, especially in the denser plots. Two management choices were available - to prune the trees further, or to thin. We chose the latter and the pasture has responded favouraby to the increase in light. In the process about 20 m^3 of sawlogs were produced (worth about $400 royalty at current valuation). It was observed that pastures stayed greener for one to two weeks longer in Spring under the canopy and that when false breaks in the season occurred, the new germinants dessicated more slowly when under the trees.

Annual grazing by sheep reduced the pasture to less than 500 kg ha^{-1} by the end of December. When combined with pruning to 6 m this produced a pine stand most suited as a fire reduced buffer. The sheep tend to remain wetter when grazing under a canopy and greater care needs to be taken against damaging fly strike. No erosion was evident following logging, even after reasonably heavy opening rains. The greater exposure to sunlight caused sun-scald wounds to open on some trees, thereby reducing their market value. This factor could become a problem in hot exposed climates.

The trial indicates that the combination of agriculture and forestry has been sustainable for six years under pines aged from 13-18. After 5 years, thinning was necessary to maintain pasture production. The trial is too small to differentiate between the effects of pasture, fertiliser or of thinning alone on tree growth. Also for reliable measurements of grazing potential larger, replicated plots are necessary. A much larger trial to investigate these aspects more fully has been established in nearby compartments.

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MANAGEMENT OF NITROGEN IN THE P. RADIATA PLANTATIONS OF THE SOUTH EAST OF SOUTH AUSTRALIA

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ABSTRACT

In the early 1970's new silvicultural techniques for *P. radiata* were developed using nitrogen in complete fertilizer mixtures. An intensive silvicultural prescription of integrated fertlizer and weed control treatments known as the MAXIMUM GROWTH SEQUENCE is now applied to all second rotation plantings in the region. The treatments show promise of correcting the second rotation decline in productivity. Good responses are also being obtained in older stands to the same fertlizer formulae. The large scale (3 000 tonnes yr^{-1}) fertilizer programme is briefly described.

A study on N losses due to windrowing or broadcast slash burning of the clearfelled first rotation suggests a direct relation between organic matter N losses and the second rotation decline. An experiment is described in which all the litter and slash is retained *in situ* with the aim of reducing the total reliance on artificial N by maximum conservation of organic matter.

Soil and litter N losses due to a wildfire were measured. A trial is described in which sub clover has been seeded into the burnt area to replace N losses. N accumulation by the sub clover is being monitored.

PART 1

Fertilizer nitrogen work 1973-79

INTRODUCTION

Prior to 1975 nitrogenous fertilizers had not been used in general forest operations in the Region because research results had been conflicting. However, in 1972-73-74 Woods (1976) showed that recently planted trees did respond to N applied on the more infertile sands provided root damage by fertilizer salts was avoided. First of all it was shown that fertilizer N + P was better than P only, and then complete mineral (NPK + 5 trace elements) mixtures were better than N + P. Subsequently nitrogen has always been used in mixtures with P (sometimes K) and trace elements, but the dose rate is always specified on the N content of the fertilizer.

THE MAXIMUM GROWTH SEQUENCE SILVICULTURE

In 1973-74-75 Woods (1976) developed the RT8 Series of trials at Tantanoola Forest using integrated weed control and successive annual applications of the complete mineral fertilizer mixture on young stands in order to determine the maximum potential growth on the infertile sands when nutrients were not limiting. The total package of treatments terminates at canopy formation (age 5) and is known as the MAXIMUM GROWTH SEQUENCE (MGS). Because there had been an unresolved problem of significant decline of the order of 25-30% in second rotation (2R) growth rates in the Region (Keeves 1966), the MGS was applied in the RT8 Series of broadscale trials to both 1R and 2R sites.

The responses in foliar and biomass growth rates to the MGS have been consistent and sustained on both 1R and 2R sites.

These have been so promising that in 1976, in view of the long standing "2R problem", a policy decision was made to apply the MGS to all new 2R plantings in the Region, amounting to some

600 ha yr^{-1}. This policy still stands in 1980. The MGS applies a total of some 300 kg N ha^{-1} and other elements to the site in 6 dressings.

In 1976-77 the same complete mixtures were experimentally applied to unthrifty "yellow spindle" stands of 6 to 20 years of age with equally good results in foliar and volume responses.

THE FERTILIZER FORMULAE

The complete mineral formula was originally designed by the fertilizer company for plant growth (lawns) on deep sandhill sites, and therefore the ratios between the elements approximately corresponded to the ratios between the major elements in a green plant, i.e. it was a "hydroponic" formula. The NPK content of the mixture was 10.5, 1.6, 5.0% respectively (elemental).

However, the mixture gave problems in physical handling in the field. In 1978 two better granulated amended formulae were developed. Forest Mixture No. 1, with a total of 13 elements, carried on the "hydroponic" philosophy of the complete mineral mixture. Forest Mixture No. 2 eliminated K, Mn, Fe from the original formula because more recent foliar analyses indicated these elements were not limiting in the soils being treated.

In 1980 these two formulae have been still further modified to the following analyses:

	Elemental %									
	N	P	K	S	Mg	Cu	Zn	Mn	Mo	Co	Bo
Forest Mix No 3	9.2	2.9	6.5	17.5	.19	.25	.30	.04	.001	.0001	.002
Forest Mix No 4	13.8	2.2	-	19.4	-	.8	.75	-	.002	-	-

The formula to be used in the major operations in the immediate future will be FM/4. As the dose rate per tree or hectare is determined by the N content and the two formulae are roughly equivalent in price per tonne ex factory door it can be seen that treatment with FM/3 is 50% more expensive than FM/4.

All the N in both formulae is in the form of ammonium sulphate.

FOREST OPERATIONS

Currently four jobs are organised each year.

M.G.S. Spring

This is the main job of the year with a planned 1228 tonnes to be spread in spring 1980, in a combined exercise of part manual, agricultural VICON spreader, and aerial application. The first method covers the first three MGS treatments. The latter two methods cover the latter three MGS treatments where dose rates and coverage are more applicable to machine application.

M.G.S. Autumn

A small manual job which applies the only split treatment in the MGS at 10 months after planting.

Post Canopy 7 and 12 Year Old Plantations

These are unthrifty 1R and 2R plantations planted prior to the 1976 decision to apply the MGS to all 2R plantings. Owing to the above decision, and termination of 1R plantings on unfertile sites after 1974 due to no further ex scrub plantings, this work will phase out after 1981.

Applications are made in autumn either by agricultural tractors travelling the inter-row space or by aerial contract. Current work is ca. 900 tonnes yr^{-1}.

Post Thinning Applications

These are made in late spring by a high clearance agricultural tractor travelling the clearfelled outrow (spaced 6 rows apart) following the first thinning. The intervening "bay" of five rows is just the correct width to gain a good broadcast from the agricultural spreader mounted on the machine.

Currently ca. 1100 tonnes yr^{-1} this work will increase in the future because it is efficient and cheap spreading, and foliar and wood increment responses in the treated stands are very promising (see Fig. 3).

The application rate is 200 kg N ha^{-1} plus the other elements as supplied in the FM/4 formula.

Timing and Logistics

Ideally these works should apply fertilizer only in mid autumn or mid spring when there is adequate moisture and temperature for root uptake, i.e. avoiding the excessive leaching of winter. However, as the current programme is 3000 tonnes yr^{-1} the optimum season is "stretched" by the logistic problems associated with available man-power, vehicles, tractors and spreading equipment. As a result the spring programme usually extends from the end of August to early November. More research is needed on the efficiency of nutrient uptake relative to soil moisture and temperature in the Region.

Fig. 1 shows that the amount of elemental N applied in the Region by the Department has risen from nil in 1973 to 414 tonnes in 1979. It will probably level out at ca. 450 tonnes yr^{-1} in the immediate future. The total cost of the programme in 1979/80 was $525,000.

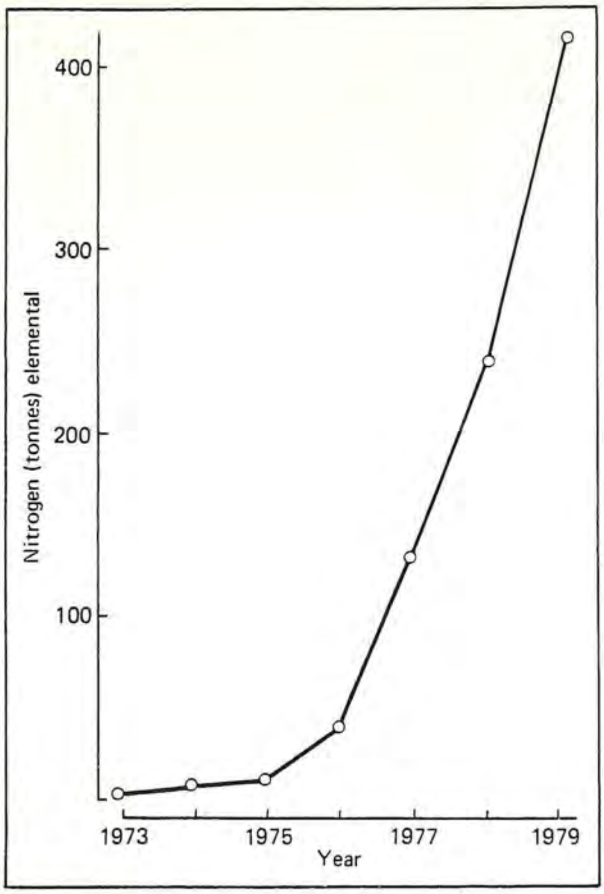

Fig. 1. Trends in fertilizer use - South east region.

RESPONSES

Treatment from Planting Time

Although a S.Q. class cannot be assigned to a plantation before age 9½ years (Lewis et al. - 1976), early growth trends of the MGS trials have been measured for B.A. to monitor current progress. Fig. 2 shows the trends in B.A. on RT8 (74)2 which is the first 2R plantation to have received the complete MGS silviculture, and is now 6 years of age.

The IR site quality was S.Q. IV which would have been expected to decline to S.Q. V/VI if it had received the standard pre-1974 silviculture. Fig. 2 growth trends suggest that the 2R stand will be at least S.Q. III, or about 2½ site class lift due to the MGS (approximately 55% lift in productivity).

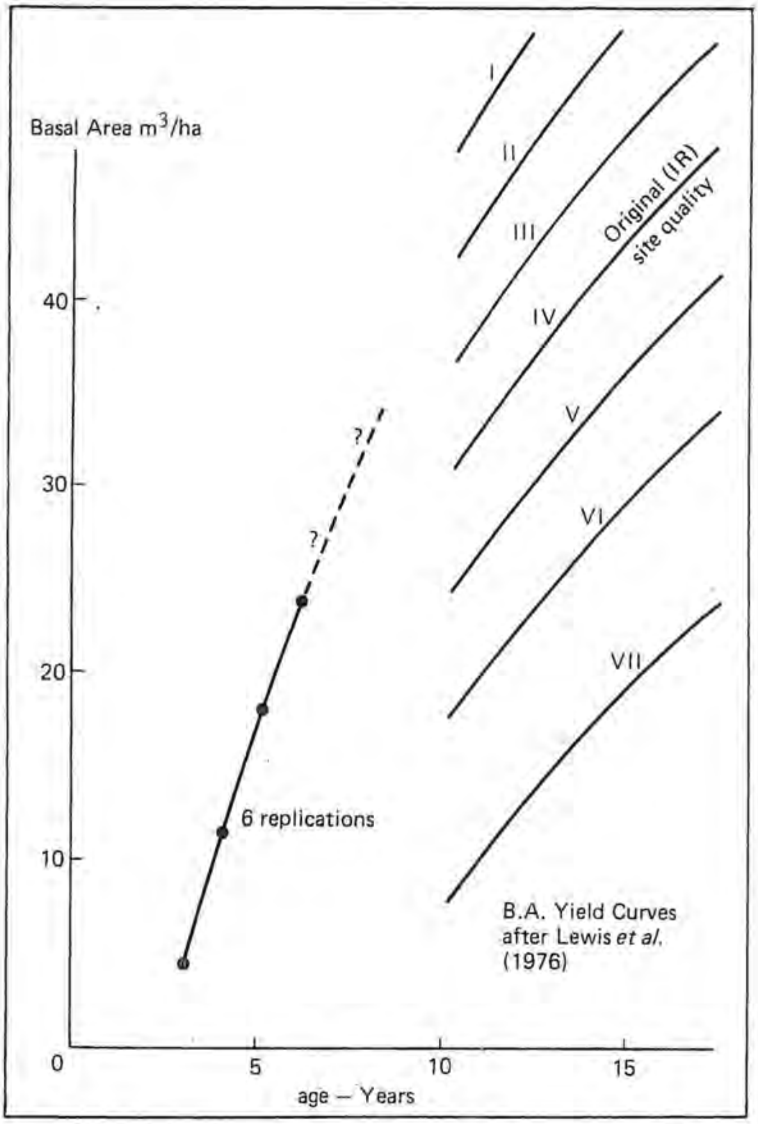

Fig. 2. RT8 (74) 2 - 2R site. B.A. response to M.G.S. silviculture.

These interim results are particularly pleasing as it was the first attempt at recovering the decline in productivity of a 2R site with an intensive weed control and fertilizer regime (the initial work started in the adjoining (2R) 1973 plantation but before the MGS fertilizer techniques had been fully developed).

Treatment at Mid-Rotation

Fig. 3 shows the annual volume increments obtained by stem analysis of co-dominant trees in a S.Q. V stand which had been first thinned at age 19 and fertilized at age 20 (RT19 - post T1 fertilizer trial). Two rates were applied viz. 150 and 300 kg N ha^{-1} as complete mixtures.

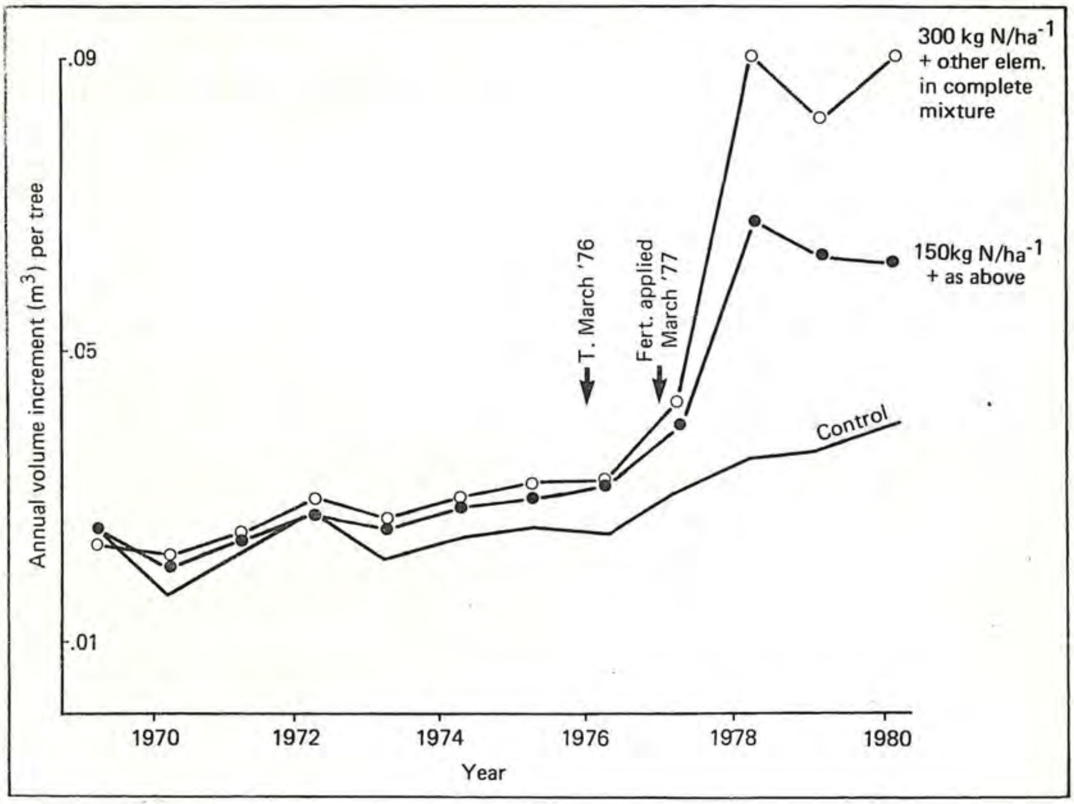

Fig. 3. RT19. Response in volume increment. Mean of two co-dominant trees/treatment.

Fig. 3 shows that volume responses have peaked in the first growing season following the treatment, that they are substantial and closely related to the quantity applied.

These results were in a 1R stand. Very recent B.A. measurements in a 2R, S.Q. VII stand treated at 25 years of age have shown a 113% increase in B.A. increment at 24 months after treatment with 220 kg N ha^{-1} applied in a complete mixture.

Height increment has also improved.

Volume increment should be at least doubled.

GENERAL

This section outlines a fertilizer programme in the South East Region which has grown from a very small start in 1973-75 to a large annual operation costing over half a million dollars. In terms of fertilizer material costs nitrogen, as ammonium sulphate, represents about 80% of the total material costs and is therefore the most important element in the mixtures applied (in a monetary sense not necessarily a biological sense).

Owing to the serious 2R problem of productivity decline and the general paucity of available new ground for P. radiata in the State the fertilizer programme has been pushed ahead concurrently with, rather than following, field research.

This deliberate and vigorous policy has involved some management risks but the interim results to date suggest that the initial targets will be easily achieved in both young and middle aged plantation. The optimistic note sounded by Woods (1977) on the potential to lift P. radiata productivity about 60% on the dry marginal soils in the South East Region has been strengthened rather than weakened by further data gained in the last three years.

Further research is needed on the long term fertilizer requirements to maintain these responses because it is most unlikely that one treatment will be adequate for the whole rotation. Part 2 will show how steps are being taken to reduce fertlizer requirements in the second rotation.

PART 2

Conservation of organic matter nitrogen from the first rotation

INTRODUCTION

A recent study by Woods (in press) of N losses due to second rotation (2R) site preparation suggests a direct correlation between the 2R decline in productivity in P. radiata stands in the South East region and total N losses (Fig. 4). There is probably a "non-nutrient" factor also involved but this is considered to be relatively minor in its effect (Sands et al. 1979).

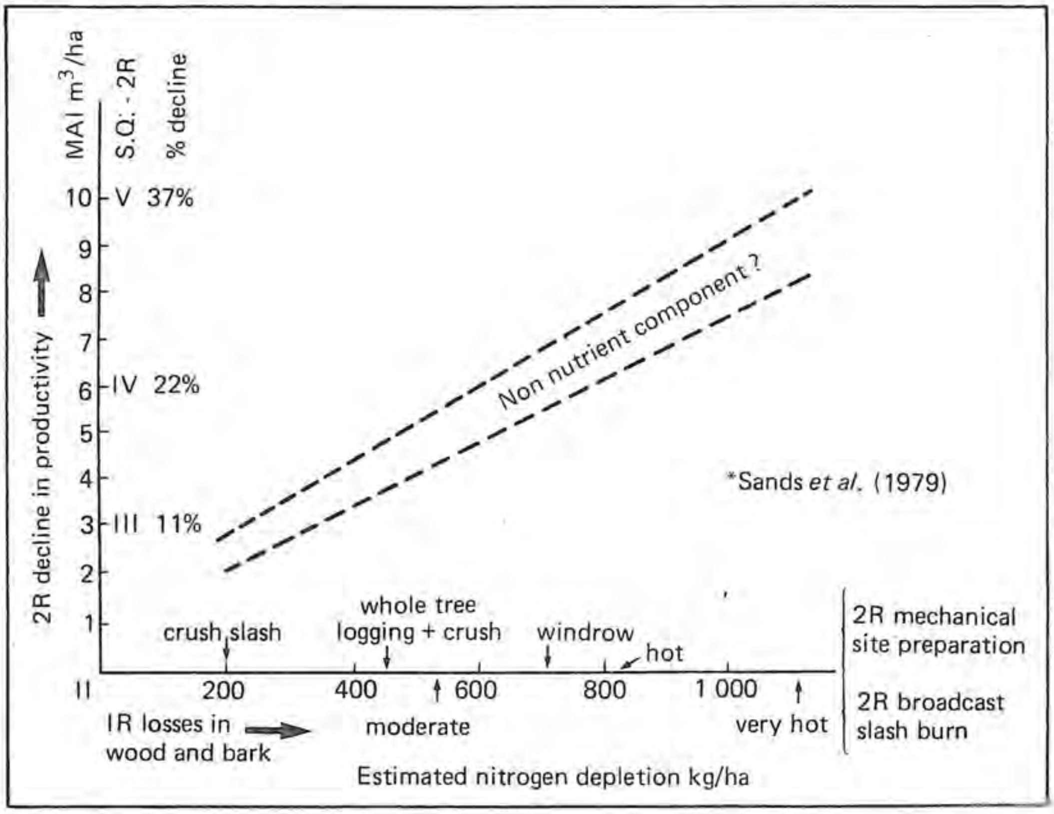

Fig. 4. Proposed correlation between N loss and 2R decline P. radiata SQII rotation 27 years.

Briefly a very hot broadcast slash burn will result in a drop in productivity of about three Site Classes (37% reduction), wind rowing of the slash about 1½ to 2 site classes (18 to 24%), and retention of the slash in situ about 1 site class or less. For a S.Q. II stand clear felled at 27 years of age the treatments described above were estimated to have caused losses in N of ca. 917, 516 and nil kg ha^{-1} respectively excluding losses to the sawmill in the form of wood and bark. There are concomittent losses of other nutrients but estimates are confined to N because, in terms of replacement costs, it is the most expensive element. Nitrogen forms a high percentage of the total nutrients in the biomass (50-60%) and percentage volatilisation losses of N in a fire are higher than for other elements.

Hot broadcast slash burns were the standard practice in South Australia for the first 27 years of 2R establishment. In the last 17 years windrowing has been the practice, but the recent study described above suggests there are still considerable N losses in windrowing. In N fertilizer replacement terms very hot burns and windrowing on a S.Q. II site would cost ca. \$600 and \$340/ha respectively (material and application). In terms of the forest fertilizer mixture No. 4 (Paper on South Australian fertilizer work - this seminar) replacement costs would be ca. \$1,200 and \$680 ha^{-1} respectively. It is more difficult to apply a dollar value to the organic matter losses with these operations. But it is well known that organic matter is a very important component in the light sandy soils of the Region (Sands et al. - 1979).

CONSERVATION OF ORGANIC MATTER AND N

It is clear from the foregoing that serious attempts must be made to conserve the maximum organic matter on 2R sites in the Region. While in the short term fertilizers via the M.G.S. schedules (Woods 1976) appear to be replacing the lost productivity, this must be considered only a stop gap while methods are devised to reduce organic matter losses to a minimum.

It is also clear that this can only be achieved by eliminating windrowing in favour of crushing the clearfelled slash in situ. The main obstacle to this in the past in the South East has been the unmerchantable log in tops, smashed pieces and deformities which can be very large pieces after clearfelling of 50 year old multi-thinned high S.Q. stands. Markets are now being developed for this material to be sold after chipping in a mobile chipper on site. The markets should be fully developed within 3-4 years.

The large stumps still remain somewhat of a problem but machines are being developed to recut these at ground level after the general clearfelling operation.

EXPERIMENTAL CONSERVATION OF ORGANIC MATTER

In order to gain a lead on the above general operations a trial RT29 has been estbalished at Penola Forest Reserve. One compartment has been windrowed and the adjoining compartment has been slash crushed in situ. The problem of waste log was solved by collecting all waste including tops (branches left on site) with a forwarder which dumped them off the site. The block was then crushed in the summer of 1980 by a D7 tractor towing a bladed roller which reduced all slash material to no more than 25 cm above ground. The planting lines were scalped by a small V bladed "snow plough". The blocks were planted in 1980.

Three levels of fertilizer are being applied - nil, 50% of the M.G.S. sequence and 100% M.G.S. With two types of site preparation (windrowing versus crushing in situ) this trial will be broadscale 3x2 factorial which should be, a good lead to the future 2R silviculture in the South East Region.

PART 3

Nitrogen losses due to a wildfire and replacement by a sub clover pasture

Nitrogen losses

A large wildfire which occurred at Myora Forest Reserve (Caroline Fire of February 2, 1979) in young and middle aged *P. radiata* plantation yielded the opportunity to measure N losses after fire, and also the opportunity to establish a trial to replace these losses by means of a sub clover pasture.

The Agriculture Department of South Australia has measured N losses from the litter and 0-30 cm of the soil profiles in three 10 year old *P. radiata* stands killed by the fire. Mean N losses were 89 kg ha^{-1} from the litter and 150 kg ha^{-1} from the soil profile. N loss from the crowns was estimated to be 120 kg ha^{-1} making a total loss of 359 kg ha^{-1} due to the fire itself. To this figure must be added the approximately 50 kg ha^{-1} of N in the wood and bark in the trees which are due to be bulldozed and swept into windrows. Total losses would thus be of the order of 410 kg ha^{-1} of N.

Nitrogen replacement by sub clover - RT 36

In autumn 1979 a surface seeding of sub clover at 10 kg ha^{-1} was applied with P, K and trace elements under the 10 year old burnt trees. Vigorous clover germination and development took place such that at 12 months soil analyses showed that a mean of 95 kg N ha^{-1} had been fixed. Thus N losses should be replaced within 4-5 years.

With the rising cost of N fertilizers and the risk of fertlizer N leaching losses in the sandy soils of the region there is little doubt that legumes will play a future part in the *P. radiata* forest systems in the Region.

This will take place in addition to the nutrient conservation measures outlined in this paper because not only do we aim to maintain 2R productivity but actually upgrade it above that of the first rotation.

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NITROGEN/SULPHUR UTILIZATION BY FAMILIES BY *P. RADIATA**

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ABSTRACT

Nutritional differences between families of *Pinus radiata* are discussed specifically for nitrogen and the interaction effects with phosphorus, sulphur and boron. Difference between families for nutrients exists but the method of propagation (grafts or cuttings) strongly affects the results. This may partly be an effect of incipient incompatability in the grafted stock. Foliar nutrient levels and differences of clone bank material could be related back to the location of the parent materials. The clone bank was on a moderately fertile soil. Clones for which the parent tree was on a much more fertile soil were generally low in foliar nutrients while the reverse was true for trees from poor sites. As the nutrient status affects the growth and appearance of trees this would be a critical factor in the final assessment of trees for breeding programmes. The seasonal growth patterns of different families were also discussed.

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* Paper presented at combined Forestry Council Research Working Groups I and III, Traralgon, February 1981.

THE USE OF DRIS INDICES TO DETERMINE THE BALANCE BETWEEN NITROGEN PHOSPHORUS AND SULPHUR IN *Pinus radiata* FOLIAGE

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SUMMARY

An investigation has been carried out into the possible use of the Diagnosis and Recommendation Integrated System (DRIS) in determining the balance between nitrogen, phosphorus and sulphur in the foliage of *Pinus radiata*.

It was found that both the ratio of total-nitrogen to total-sulphur and the difference between the nitrogen and sulphur DRIS indices provided a good estimate of the level of inorganic-sulphur required for normal growth. Where imbalances occurred, the nitrogen and sulphur indices did not take into account the possible limiting effect of phosphorus. This was overcome by the inclusion of the phosphorus index which enabled the order of requirement of the three elements to be determined and an estimate of the magnitude of any imbalance to be made.

It has been concluded that DRIS shows some merit, particularly with regard to the selection of remedial measures. The difficulties encountered when expanding the system to include other essential elements are mentioned.

INTRODUCTION

The Diagnosis and Recommendation Integrated System (DRIS) was first proposed by Beaufils (1971, 1973) as a means of detecting mineral imbalances in plants (corn and rubber). The system was fully described by Sumner (1977) who demonstrated its advantage over the critical value approach in predicting nutrient element deficiencies in corn. Briefly, DRIS utilises indices which measure the degree of nutrient balance and rank the order of requirements of nutrients by the plant. In many P. radiata plantations in N.S.W. there are multiple nutrient deficiencies and imbalances and in order to more efficiently diagnose these imbalances, the use of DRIS indices was investigated.

Ideally, all essential elements should be included (Sumner 1978) but the following in which only nitrogen, phosphorus and sulphur are considered will serve as an example of the method involved. The indices are calculated from the follwing equations:

$$\text{N index} = \frac{fN/P + fN/S}{2}$$

$$\text{P index} = \frac{fP/S - fN/P}{2}$$

$$\text{S index} = \frac{(fN/S + fP/S)}{2}$$

The method of calculation for one of the functions is:

$$fN/S = 100\left(\frac{N/S}{n/s} - 1\right) \times \frac{10}{CV} \text{ when } N/S > n/s$$

$$\text{or} \quad fN/S = 100\left(1 - \frac{n/s}{N/S}\right) \times \frac{10}{CV} \text{ when } N/S < n/s$$

The N/S ratio is the ratio of the two actual elements (in this example, (%) nitrogen and (%) sulphur) in the plant under investigation while n/s is the value of the 'norm' derived from the mean value of the N/S ratios for a population of the plants with relatively high yields. The coefficient of variation for this population is CV. The index with the greatest negative number denotes the element in shortest supply, while the greater the total of the indices irrespective of sign, the more pronounced is the deficiency of the element in shortest supply.

A preliminary investigation of the use of the DRIS system has been used to assess the relationships between phosphorus, nitrogen and sulphur in P. radiata foliage.

METHODS

DRIS indices for nitrogen, phosphorus and sulphur were determined using data obtained from an experiment in which the ash-bed effect on the growth of P. radiata in Sunny Corner State Forest has been studied. The study site and method of sampling have been described by Humphreys and Lambert (1975). Twelve trees, six on and six off the ash-bed were each sampled each winter during the period 1962 to 1970 and chemically analysed.

Using combined data available from chemical analyses of foliage from high site quality trees (> 26 m at 20 years of age) sampled in surveys at Bondi, Carabost and Nalbaugh State Forests, 'norms' were derived for phosphorus, nitrogen and sulphur. These norms were applied to the data from Sunny Corner State Forest to determine the DRIS indices. Those trees which had a total of the DRIS indices which was less than 10, were considered to have apparently balanced nutrition, and data from those trees were then used to estimate a more precise set of norms for the Sunny Corner trees. These latter norms had much reduced coefficients of variation and were used to recalculate the Sunny Corner DRIS indices. The two sets of calculated norms have been given in Table 1.

Table 1. Calculated norms and coefficients of variation

Ratio	Bondi, Nalbaugh, Carabost S.F.		Sunny Corner S.F.	
	norm	CV	norm	CV
n/p	9.3	25.4	10.2	13.6
n/s	12.4	8.8	12.4	4.6
p/s	1.28	21.4	1.23	10.9

The methods of foliar sample collection, preparation and chemical analysis were those reported by Lambert (1976a,b).

RESULTS

Ratios of elements, particularly those which are nutritionally related, have been used by many workers to study mineral imbalances, particularly in crops. However, while correlations between yield and these ratios have at times been found (for example, Westermann 1975), in other cases no such relationships were obtained (for example, Rasmussen et al. 1975). Sumner (1978) has pointed out that when, for example, the nitrogen/sulphur ratio is optimal, nitrogen and sulphur may both be adequate, excessive or deficient. Thus, if nitrogen and sulphur are adequate and all other factors are favourable, the maximum yield is possible, but if they are deficient or if they are excessive and some other element is limiting, then a lower yield than that expected will be obtained. A number of possibilities also exist if the nitrogen/ sulphur ratio is higher or lower than the optimum range but in these instances the maximum yield will not be obtained.

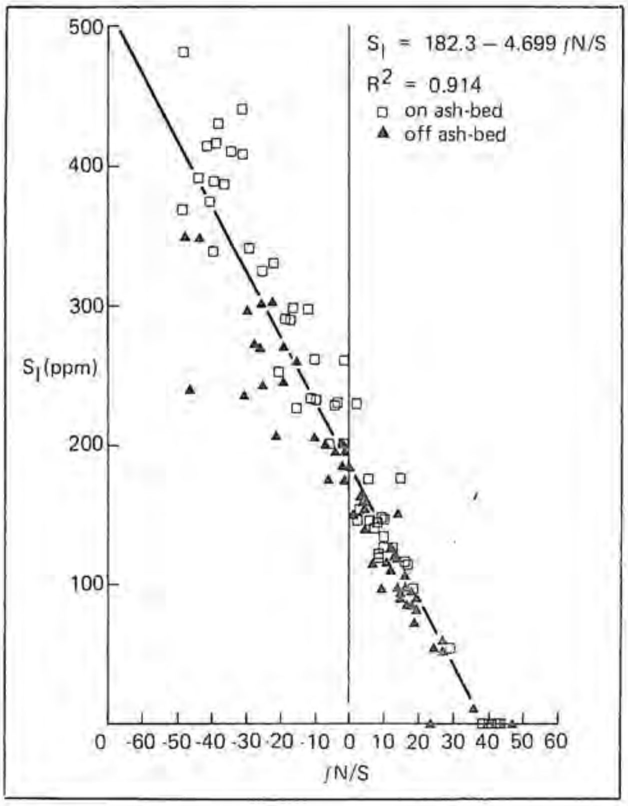

Fig. 1. The relationship between fN/S and foliar sulphate-sulphur (ppm) for P. radiata on and off ash-beds at Sunny Corner State Forest.

The relationship between fN/S and sulphate-sulphur is shown in Figure 1 where it can be seen that as fN/S approaches the optimum value (zero), the sulphate-sulphur concentration approaches 180 ppm, a concentration which agrees fairly well with the value proposed for sufficiency (Table 2).

Table 2. Deficiency and sufficiency sulphate-S levels in *P. radiata* foliage (Turner *et al.* 1977)

Sulphur status	SO_4–S (ppm)
Deficiency to incipient deficiency	0–80
Marginal to adequate	80–200
Adequate to high	200–400
High (possible N deficiency)	400+

The use of fN/S only provides a measure of the imbalance between the two elements and indicates that the higher the negative or positive value, the greater the likelihood that a response would be obtained to the application of nitrogen or sulphur fertilizers. However, it does not take into account the fact that the response may be limited by the insufficient availability of one or more other essential elements.

The relationship between the difference between the N and S DRIS indices and sulphate-sulphur (Figure 2) indicates that when the two elements are balanced, the sulphate-sulphur concentration is approximately that proposed for sufficiency (Table 2). When the nitrogen and sulphur indices are both positive and balanced, the phosphorus index is of course negative and therefore that is the element most limiting growth. On the other hand, when the nitrogen and sulphur indices are negative and balanced, the phosphorus index is positive, so that depending on the index total, a response to say ammonium sulphate may be expected. If the nitrogen and sulphur indices are not balanced, a response to either nitrogen or sulphur fertilizer application is indicated, but this will depend on the phosphorus index and the index total.

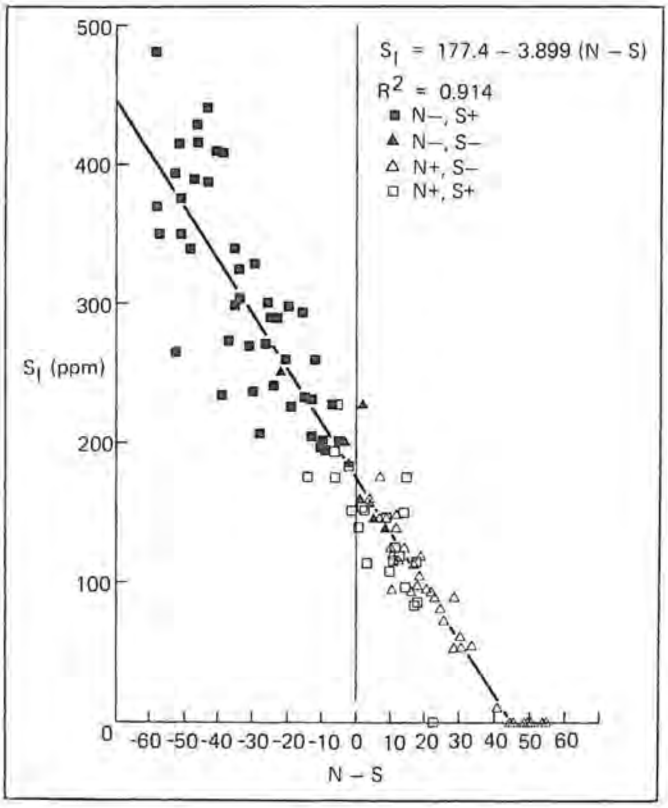

Fig. 2. Relationship of the difference between the nitrogen and sulphur DRIS indices (N-S), and foliar sulphate-sulphur for *P. radiata* on and off ash-beds at Sunny Corner State Forest.

Individual data for the 108 samplings were too numerous to present here, but some examples have been given (Table 3).

For the first example, the nitrogen and phosphorus concentrations are satisfactory (Will 1978) and sulphate-sulphur is near the optimum. The indices are well balanced and hence no corrective measures are indicated. Sample No. 12 is an example of gross imbalance. Foliage nitrogen is satisfactory but phosphorus and sulphur are below the critical values. Since the sulphate-sulphur level (10 ppm) is very low and phosphorus (0.116%) is only just below the marginal range of 0.12 - 0.14% (Will 1978), it could be assumed that there is a greater deficiency of sulphur than phosphorus. The DRIS indices, however, show that the reverse is the case. An example of this was provided by Sumner (1977) who reported an NPK experiment with corn, the foliage of which contained nitrogen and phosphorus levels below the critical values.

Table 3. Foliage concentrations and DRIS indices for nitrogen, phosphorus and sulphur at Sunny Corner S.F.

No.	Sample	Foliage concentration Total-N	Total-P (%)	Total-S	SO_4-S (ppm)	DRIS index N	P	S	Total	Order of requirement
1	2 on/1967	1.69	0.170	0.135	190	0	2	-2	4	S>N>P
2	2 off/1965	1.39	0.116	0.107	115	12	-13	1	26	P>S>N
3	2 off/1966	1.45	0.117	0.115	155	10	-18	8	36	P>S>N
4	2 off/1969	1.40	0.119	0.123	270	-4	-18	22	44	P>N>S
5	4 off/1963	1.46	0.121	0.110	100	15	-12	-3	30	P>S>N
6	4 off/1970	1.41	0.119	0.127	305	-7	-20	27	54	P>N>S
7	1 on/1967	1.27	0.165	0.103	160	-13	26	-14	53	S>N>P
8	1 on/1970	1.28	0.180	0.113	252	-26	30	-4	60	N>S>P
9	3 on/1963	1.65	0.171	0.128	150	3	6	-9	18	S>N>P
10	3 on/1966	1.65	0.177	0.143	300	-12	4	8	24	N>P>S
11	3 on/1970	1.62	0.172	0.144	330	-16	3	13	32	N>P>S
12	5 off/1963	1.69	0.116	0.117	10	34	-27	-7	68	P>S>N

The application of nitrogen alone at 280 kg ha^{-1} gave a lower grain yield than that with the application of 168 kg ha^{-1} even though the nitrogen level in the foliage was increased. The $N_{168}P_{25}$ treatment gave a marked increase in yield, but this was again reduced in the $N_{280}P_{25}$ plot. A response to nitrogen was only obtained when phosphorus was increased to 100 kg ha^{-1}. This experiment therefore showed that phosphorus was the more limiting element and this was correctly predicted by the DRIS indices.

Humphreys and Lambert (1965) showed that the ash-bed effect is associated with increased phosphorus availability, with resultant higher phosphorus levels in the foliage of the trees on the ash-beds. The latest data available to Humphreys and Lambert (1965) were those obtained from the 1963 sampling, but it can be seen (Table 3) that, during the ensuing years, the difference in the phosphorus levels was maintained and this is reflected in the DRIS indices. One trend apparent at all sampling sites was the change in the nitrogen/sulphur balance with the passage of time. For instance, examples 2 and 5 show that nitrogen is present in excess of sulphur and that a response could be expected after the application of superphosphate. However, in examples 4 and 6, the position with regard to nitrogen and sulphur is reversed so that at this stage superphosphate would tend to worsen the nitrogen to sulphur balance. As no fertilizers were applied during this study, it can only be assumed that the improvement in the sulphur status has been due to an input of sulphur emissions from Wallerawang Power Station. This station which became fully operational in 1962 is situated 25 km from Sunny Corner.

The DRIS indices shown in example No. 11 indicate that nitrogen is the limiting element although the nitrogen level in the foliage is well above the marginal range of 1.2 - 1.4% (Will 1978). If in a case such as this a response to nitrogen was obtained, it would show that nutrient balance is more important than foliage concentration in predicting optimum growth. Further investigation is required in order to clarify this point.

In summary, the use of DRIS indices appears to have some merit in determining the balance of nitrogen, phosphorus and sulphur in the foliage of P. radiata. The indices also appear to have some application in the choice of a fertilizer to correct a nutrient imbalance, particularly when two elements are limiting. A more balanced view would be obtained if the indices for all essential elements or at least those of the major elements were calculated. However our investigations have shown that this presents some difficulties in that the development of a general set of norms for P. radiata is not possible. For example, at Green Hills State Forest which is situated on soil derived from granite, the magnesium level in the foliage is nearly always less than calcium so that the ratio of magnesium to calcium is 0.81. At Bondi State Forest which is situated on soil derived from sedimentary rocks, the reverse is true and the ratio of these two elements is 1.05. However, provided sufficient relevant data are available, it should be possible to develop norms for each forest or perhaps each soil type.

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NITROGEN IN FOREST ECOSYSTEMS : ASSESSMENT AND SYNTHESIS

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INTRODUCTION

Nitrogen and Energy Budgets : State of the Art

Notwithstanding many years of effort, we appear to be still a long way from preparing meaningful energy and nitrogen budgets for forest ecosystems. (For that matter, the position may be no better for the majority of agricultural systems.) This is probably due not so much to lack of appropriate techniques but rather to a somewhat fragmentary research approach in an area which has not been seen to be of high priority. The prevailing attitude, at least up until now, has been 'nitrogen looks after itself' and funding agencies, aided and abetted by researchers themselves (through conscious or unconscious lack of interest) have correspondingly afforded scant support to a somewhat esoteric area of research; the pay-off in terms of benefits to forest management have been seen to be somewhat tenuous.

The current attitude, reflected in this meeting, appears to be that there is a problem of nitrogen supply and a running-down of the nitrogen resource in our forest ecosystems. In my opinion, insufficient work has been done to enable any forest manager to decide whether he has a nitrogen problem or any researcher to be unequivocal about the role of nitrogen in our varied forest ecosystems. Hence our research approach at this stage should be to more closely define the nitrogen economy of our forests. This will then enable us to decide whether any problems of immediate or long term supply exist; paying closer attention at this time to manipulation of legumes to increase nitrogen supply to forests on the a priori assumption that, because they are being burnt, logged, converted to plantations etc., their nitrogen economy is somehow in jeopardy, is to put the cart before the horse. Until the nitrogen economies of forests, including the influence of energy

Would love to do it this way if the research resources were available - facing this, I'm happy with having the cart before the horse (or without both).

flow through the system on nitrogen mineralisation and fixation are adequately defined, we cannot justify many of the assumptions we currently appear to hold. This is not to question the value of research into components of the system: e.g. the role of nodulated plants in nitrogen fixation, the rate of nitrogen immobilisation in developing communities, or the effects of management practices on nitrogen availability. Such studies at this stage should be seen as basic to our understanding of the nitrogen economy, rather than in an allegedly problem solving context.

Organisation of Research

The basic approach may be more difficult to sustain in seeking support from funding agencies, but we must be careful not to 'cry wolf' at this stage of our knowledge. There have been calls for integrated team research on 'important' forest ecosystems at this meeting; they will only be successful if funding agencies can be convinced that a real problem exists or has the potential to develop. This requires much more background data than would appear to be readily available at the present time. The problem is to attract funding for this essential basic work.

It is desirable to coordinate studies within a particular program (e.g. IBP), and also between programs. There is a need for communication between teams; at present, the level of awareness of activities is not very high (but has improved over the last couple of years since the Perth Ecosystem Symposium[1] and as a result of this meeting). There is the possibility of establishing task forces to tackle specific problems; these need to be organised across disciplinary and organisational boundaries. Such programs would need to be strategic, problem-oriented and of defined duration, and would embrace all the problems alluded to above.

Fixed duration does not preclude the long-term research so necessary in this area. Long term research however, demands that

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[1] 'Nutrient Cycling in Indigenous Forest Ecosystems' symposium. CSIRO Division of Land Resources Management/W.A. Forests Dept., Perth, May, 1977.

the relevant questions be addressed and appropriate methodology be employed; both these areas contain difficulties at the present time. Despite this, the essentiality of long term research must be recognised and attract not only the appropriate level of support, but the guarantee of continued support. This may require some radical change of philosophy in our research organisations as presently constituted.

NITROGEN IN AUSTRALIAN FOREST ECOSYSTEMS

Nitrogen Levels

What are adequate levels; levels for stand maintenance or to maximise production? There is a need for all nitrogen components to be evaluated; specific mention has been made of atmospheric accession, phyllosphere fixation (which may be more important in rainforests than in sclerophyll forests, but this is unknown), the below ground ecosystem (soil, roots, litter). There are difficulties in generalising and extrapolating (how far?) from the few available studies - general studies may be needed covering a range of forest types, but existing data should be evaluated before any further detailed studies are undertaken.

There is a need for an early warning system for determining nitrogen losses before deficiency symptoms are evident; however, there are difficulties in designing appropriate early warning systems for regular monitoring - what do we monitor; processes or pools or fluxes, direct indicators (nitrogen-mineralisation) or indirect indicators (soil respiration, tree growth)?

Sampling

We need to recognise spatial and temporal variability in studying processes and measuring pools and fluxes. Estimates of spatial variation established for particular variables for one forest type, while providing useful guides in designing further studies, should not be uncritically applied to forests of differing structure and typology. Different sampling intensities may be needed for spatial and temporal variation, as well as for different parameters. Sampling intensity adopted should also be considered in relation to the costs involved and the objectives to be achieved.

Atmospheric Accession.

A major problem is adequate methodology for sampling and estimation, particularly of dry deposition and rainfall inputs. This results in imprecise data with large and undefined variance whose significance is difficult to evaluate. Accurate (sensitive) and appropriate (i.e. effort expended in relation to relative significance of parameter to entire system) methods are required for estimation of these apparently small pools with large flux variance; their extreme variability (due to oceanic, terrestrial, agricultural and industrial sources) indicates that specific studies may be needed for particular forests; at this stage no generalisation on size or significance of these accession pools can be made. Methodology needs to take into account season of sampling, frequency, relation to rainfall events, etc.; standardisation of technique, while desirable, may not be the best strategy at this time because the ideal methodology has yet to be developed; rather, various methodologies should be evaluated so that consensus can be reached on the most appropriate methodology.

Direct uptake of atmospheric ammonium-nitrogen may be significant in forests because of their large canopy catchments - little is known of this and it deserves further study.

Gaseous Losses.

The significance of gaseous losses of nitrogen as di-nitrogen, ammonia and nitrogen oxides from forests is unknown. Denitrification may be significant in high rainfall, cool temperate forests during winter, or as a result of water-logging such as is often associated with wet weather utilisation. Ammonia losses could be associated with nitrogen fertilizer use, more particularly urea; losses might be minimised by consideration of fertilizer form, time of application, soil moisture, temperature and pH characteristics.

Nitrogen losses as a result of burning require quantification. The considerable variation among ecosystems is due to forest and fuel characteristics, season, periodicity and intensity of burning. Studies reporting losses from litter are of little value unless these variables are adequately defined. Terms such as wildfire and prescribed burning are meaningless in an ecological/functional context. Volatisation losses occur from partly burned litter and from scorched crowns - what is the nature of the non-volatiles retained, and to what extent do these substrates influence subsequent decomposition and mineralisation patterns? To what extent does burning lead to losses of soil nitrogen as distinct from litter nitrogen?

This area deserves closer attention to determine the extent to which gaseous losses occur in forests, and ways to minimise any losses via appropriate management techniques. While there may be some problems associated with methodology, the major hurdles have been overcome and application to the forest situation is now timely.

Fire and Disturbance.

Fire mineralises phosphorus and cations from litter and releases fixed phosphorus from heated soil. There may be a lag phase while nitrogen-fixing systems re-establish themselves; for this time vegetation may be in nitrogen/phosphorus imbalance - but excess phosphorus can be stored in roots, mycorrhizas, etc., e.g. as polyphosphate, until nitrogen availability rises to restore nitrogen/phosphorus balance. Fire-weeds also may play a significant role by immobilising phosphate and other nutrients mobilised by burning. There is a need to measure relative losses and gains following disturbances, and these might include biomass, nitrogen concentrations and contents of vegetation, fluxes of processes associated with nitrogen mineralisation, fixation and immobilisation.

Fauna and Fungi.

The importance of fauna requires quantification; their role as grazers (insects, macropods and arborial mammals) of regenerating legumes, other nitrogen-fixing species (e.g. Casuarina) and the forest canopy. This affects both the effectiveness of the nitrogen-fixing plants and the redistribution of nitrogen within the forest as frass. Fauna comminution and incorporation of litter through digging, turning and burying by mammals, birds, earthworms, insects must influence patterns of nitrogen mineralisation. The role of termites (and their associated nitrogen-fixing gut bacteria) in decomposing refractory organic matter and cellulose needs further investigation, particularly for forests and woodlands in seasonal climatic environments where other decomposers such as fungi and higher arthropods suffer severe constraints to their activity.

Fungi and animals interact, e.g. mycorrhizal fungi can be redistributed in the faeces of rodents and insects; rat-kangaroos feed on hypogeous mycorrhizal fungi and therefore have the potential to act as dispersal agents. Insects and small mammals graze on fruiting bodies of ectomycorrhizal basidiomycetes and also act as agents of spore dispersal, as do coprophagous insects feeding on the faeces of these animals. Dispersal also is a consequence of the litter incorporation activities alluded to above.

Fungi are rich in nitrogen and can utilise organic forms of nitrogen directly from litter and soil organic matter. Higher plants can do this also but are at a competitive disadvantage compared to the fungi. Hence plants with mycorrhizas may benefit directly by having access to this combined nitrogen as well as to mineralised nitrogen in the litter and soil. The role of fungi in mineralisation, and particularly in ammonification in our acid forest soils is worthy of closer study.

While it is difficult at this stage to envisage how it may be done, conscious management of fauna and fungi may be desirable, if benefits to the nitrogen economy of the forest as a whole as a result of their activities, can be demonstrated.

MANAGEMENT OF NITROGEN IN FORESTS

Production and Nitrogen Requirements

Is nitrogen a primary limiting nutrient for optimising production? Objectives of management need to be established for particular forests (e.g. softwood plantations for wood production, native forests for wood or for water etc.), before the question can be answered. Perhaps it would be better to rephrase the question as: Is nitrogen a limiting factor in the maintenance of that long term stability of forests upon which productivity ultimately depends? As the answer to this cannot be unequivocal, management of nitrogen must be conservative and cannot be ignored.

Nitrogen limitation can be primary or secondary; the latter is the more frequent situation with phosphorus the primary limiting nutrient. Interactions to be considered in managing the nitrogen economy are those between nitrogen and phosphorus; nitrogen, sulphur and water; effects of nitrogen on root/shoot ratio (through influences on wind stability); disease susceptibility or expression (e.g. nitrate-nitrogen can predispose trees to disease more readily than ammonium-nitrogen); inducement of other deficiencies (e.g. copper). Effects on crown characteristics - crown density, branch size and taper and wood properties - should be recognised and either exploited or avoided, if production of wood is the management goal.

Application of Fertilizer Nitrogen to Plantations

"Nitrogen is a difficult nutrient to manage". This statement to the meeting by a forest nutritionist possibly reflects the state of our knowledge and technology rather than any intrinsic problem associated with nitrogen. Agriculture and horticulture have managed nitrogen successfully, albeit with annual crops and orchards. Perhaps it is the attempt to transpose agricultural principles of fertilization to forest crops which has led to difficulties, due to a failure to recognise fundamental differences between agricultural crops and forests in the way in which their nitrogen economies are organised.

The stage of application of fertilizer nitrogen is important - nutrition in the first ten years of a plantation is critical if site potential is to be realised. Strategies involve fertilizer use in the establishment phase and at later ages (at or following canopy closure, following thinning etc.); economic analysis is essential to determine whether growth responses justify cost of application; this applies equally to later age and establishment fertilizing. The Maximum Growth Sequence (MGS) system is an interesting case in point. It is now the basis for softwood plantation fertilizing in the south-east of South Australia, and involves the intensive use of mixed fertilizers, with rates governed by the desired nitrogen regime, from establishment to canopy closure (about five years). It would appear that there is a need for the system to become more site specific and there is a need for an economic analysis justifying the high inputs across all sites that are involved. There are also the potential utilisation problems associated with the production of excess core wood which need to be considered in assessing the overall economics of the practice.

What is the fate of fertilizer-nitrogen? The form of nitrogen applied needs to be related to soil pH and the nature of labile soil nitrogen. Immobilisation or mineralisation may take place either in the litter or soil, and this has implications for effective uptake by trees. Hence the efficiency of nitrogen use will vary as to whether ammonium, nitrate or organic (e.g. urea) sources are employed, and the method of application which introduces quantity/intensity factors and concentration gradients (e.g. the use of broadcast, spot or annulus techniques); burial or surface application; use of slurries or mixes; use of protective coatings or delayed release techniques (e.g. sulphur coating, resin membrane pellets or plastic impregnation etc.).

It would appear that many tree species prefer ammonium to nitrate sources - this is logical in energy terms given that nitrate must be converted to ammonium on the pathway to amino acid and protein synthesis. The potential for ammonium toxicity however needs to be recognised, and this may relate as much to the broad edaphic environment of the forest as to its nitrogen mineralisation characteristics.

Conservation of Nitrogen

The organic matter is the pool governing the long term supply of nitrogen to the stand via mineralisation, and possibly even of di-nitrogen fixation. Conservation of organic matter, particularly at plantation establishment or re-establishment in subsequent rotations, is therefore a wise strategy, more particularly on coarse textured soils where cation exchange capacity is also dependent on the organic matter (e.g. various podzols).

Windrowing leads to re-distribution and loss of nitrogen as well as posing management problems associated with the uneven growth of the subsequent stand. Burning for protection purposes should be recognised as another management strategy leading to loss of nitrogen. This may be temporary, and be replaced by stimulation of nitrogen fixation, or may lead to permanent loss. While the need for burning may be incontestable from a management viewpoint, it should be monitored to determine its long term effects - supplementary nitrogen fertilizing may be necessary in some circumstances but this has yet to be demonstrated; there is a need for closer examination of the dynamics of nitrogen under prescribed burning regimes.

Conservation of organic matter therefore becomes important; deliberate management to conserve the organic matter pool (e.g. by adopting appropriate site preparation techniques, considering the timing and intensity of prescribed burning not only for protection purposes but as a means of mineralising the refractory litter components) requires much greater research inputs to establish the necessary data base, than are currently being committed.

Monitoring of Trees

Foliar analysis techniques as currently applied for monitoring nitrogen status of trees are not completely satisfactory, possibly due to the perenniality of target species and the interest in vegetative rather than reproductive growth. Closer attention needs to be paid to sampling techniques (time, position, foliage

age and maturity) and the calibration against biomass and other growth indices. Ratios of N to P, N to S should also be considered, particularly where burning is part of the management regime. An extension of the ratio approach is DRIS (Diagnosis and Recommendation Integrated System), and this is worthy of exploration as a possible means of overcoming some of the difficulties in interpretation of tissue analysis.

Environment

There are a number of aspects to the environmental influence of nitrogen. Eutrophication hazards are associated with leaching, particularly of nitrate-nitrogen, through sandy soils to ground water. Sources of nitrogen might be fertilizers or enhanced mineralisation following clear cutting or burning. There is also the potential for direct application of nitrogen to waterways where aerial fertilizing might be practised. A more subtle influence could develop as the result of a world-wide trend to apply nitrogen to forests and that is the energy and other environmental costs associated with fertilizer manufacture. While this may be small compared to agriculture, it nevertheless needs to be considered as a component in the overall environmental context. On a more positive note, the potential role and value of forests on suitable soils as sorption areas for nitrogen (and other nutrients) contained in urban/agricultural effluents should not be overlooked. Use of such effluents would have the two-fold role of supplying nitrogen to the forest and improving the quality of ground water. Before such technology can be confidently applied however, we need to know much more about the movement of nitrogen through our forest soils, their mineralisation and denitrification characteristics, and the effects of continuous high nitrogen additions on the vegetation, including maintenance of balance between nutrients.

Agroforestry

Major discussion in this area takes place in the context of exotic pine - legume pastures. Little discussion or awareness appears to be generated concerning the wider agri-silviculture alternatives as being conceived elsewhere in the world, e.g. Central America, East Asia or Africa. There appears to be an ambivalence of attitude here - is the (legume) pasture merely a means of promoting the nitrogen economy of the pines, with some benefits in terms of revenue from animal production, or can the system be managed to optimise both timber and animal production?

There is concern with such aspects as the fertilizer (other than nitrogen) inputs required, the nitrogen gained and available to the pines as a result, the time for which legumes (e.g. clover) may be required to enable tree establishment (alternatively, shading by trees and competition for moisture can influence pasture production and quality vis a vis the grazing animal), accelerated mineral cycling and the trace element economy of the mixed system. Moisture relationships also require consideration.

The alternatives of simultaneous or sequential use of the land for trees and pasture have hardly been considered in optimising productivity of the land both spatially and temporally.

Evaluation of sequential pine-pasture systems may be of significance in overcoming problems associated with continuous pine culture, problems associated not only with nutrient availability (particularly nitrogen), but soil physical characteristics and disease potential as well.

The economics of scale and practical management difficulties also need to be looked at from the view points of both the small farmer and the larger forest enterprise.

Economic Analysis

Modelling provides a conceptual framework through which research and management strategies for fertilization or legume establishment can be examined. Economic models cannot be generalised, but given the constraints and management parameters for a particular forest, sensitivity analysis can determine the extent to which nitrogen fertilization/legume establishment strategies are viable, and aid in the choice of alternative strategies. There are problems in establishing the appropriate cost structure to be used for such models, often depending on the nature of the forest operation (e.g. private enterprise or forest authority), but this does not negate the value of the approach.

NITROGEN FIXATION

Systems Survey

There is a need to identify and assess the relative importance of nitrogen fixing systems of major forest types, recognising that the contributors may be many but the individual contributions small. This introduces problems of methodology; appropriate techniques are probably available but translating them for field use, or developing indirect indices more amenable to field manipulation (e.g. acetylene-reduction assay for nitrogenase activity) requires further investigation.

Artefacts which are notoriously inherent in sample collection and preparation for incubation studies should be recognised and avoided by developing appropriate calibration techniques for the particular system under study.

As an adjunct to the study of symbiotic nitrogen fixers, the fate and function of symbiotic endophytes in the absence of the higher plant should also be considered, particularly in situations where management activities may temporarily alter or even eliminate the host.

Symbiotic-Nitrogen-Fixing Systems

The significance of symbiotic nitrogen-fixers, e.g. *Casuarina*, *Acacia*, the cycads is not known; there has been a suggestion that inputs may only satisfy requirements of the individual, and that the effectiveness of nitrogen-fixing systems may change during ontogeny but there is little data; levels of nitrogen in foliage of maturing individuals, e.g. of *Acacia*, may be of little value in assessing the potential of these species because of a general lack of knowledge of their nutritional physiology. An appreciation of nitrogen inputs is required, and the possible stimulation of their nitrogen-fixing systems via use of phosphorus, copper and molybdenum applications in native forests is a potential area for study. There is considerable scope for manipulating nitrogen inputs via introduced legumes and native nitrogen-fixing systems. There is also a need for information on effects of management (fire use, weed control, stand density manipulation, etc.) on understorey development and its nitrogen-fixing capabilities.

Role of Legumes

As legumes appear to be potentially large contributors to the nitrogen economy, some priority might be given to studies in this area. It has been pointed out that the current state of knowledge of legume-systems could be ranked as follows:

Agronomy Agroforestry *Pinus* plantation/legume Eucalypt forest

The questions for symbiotic nitrogen fixation in eucalypt forests appear to be: Do the legumes fix? If so, how much and when? (Influences of season, succession, ontogeny.) What is the rate of turnover of nitrogen fixed by legumes? What is the mechanism for transfer of fixed nitrogen to soil or other plants? (There has been some speculation on the role of fungal transfer via mycorrhizas.) What is their nett contribution over and above immediate internal requirements? i.e. How does the internal cycling of nitrogen vary among species? What is their drain on water and nutrients in the system, particularly nitrogen and phosphorus? (e.g. in Karri forest, it was reported that 50% of the nitrogen requirement of legumes was taken from the soil). That legumes respond to applied phosphorus is established; while this may be manipulated by management to increase their nitrogen-fixing capabilities (if this is shown to be desirable), it demonstrates that the phosphorus economy of these systems is also finely balanced. It is suggested that nitrogen and phosphorus applications to native forests should be made to examine the influence on development of understorey and overstorey as an aid to assessing ways of manipulating legumes via stand nutrition.

Rapid growth of legumes following fire or disturbance may be a consequence of higher nutrient availability (phosphorus from ash and release from soil organic matter, nitrogen from increased mineralisation). During this period they may not be particularly effective nitrogen fixers but constitute a source of immobilisation - this is not necessarily a bad thing, as nutrients are being returned to the organic pool. Can this suppression of nitrogen fixation under high soil nitrogen levels be overcome, and is this desirable anyway? We must also consider the pool of nitrogen in roots of legumes which is not lost in burning and the regeneration of acacias from existing root stocks as well as from seed (e.g. brigalow) - the regeneration from roots might be a more effective nitrogen-fixing system in overcoming the lag phase in redevelopment. Fire is an obvious management tool for manipulating legumes but more work is required on timing and intensity of burning to optimise legume development as a nitrogen-fixing system.

Legumes in Management

Are legumes better than mineral fertilizers as a source of nitrogen? Care should be taken in extrapolating experience with legumes on sands, and particularly high phosphorus sands (e.g. the New Zealand experience) to the more general situation of heavier textured low phosphorus soils. Phosphorus is critical to adequate legume growth; while this may be added to plantations to promote growth of trees as well, its application to stimulate legumes in native forests may result in weed invasion problems or undesirable changes in stand structure, e.g. from shrub woodland to grassy woodland.

Legumes may be promoted in native forests by burning, but germination, establishment and development requirements of target species should be investigated - some species will establish following site disturbance without burning. Species selection should also take into account the selection of appropriate symbionts and the matching of species to site and symbiont to maximise nitrogen fixation, where this is found to be desirable.

The form of legume should be appropriate to management - woody species may be undesirable in plantations due to access problems; competition for moisture, phosphate etc. needs to be assessed.

A subsidiary role of legumes is a consequence of their dynamic nature; consider their influence on nitrogen mineralisation in litter and soil, disease inhibition (e.g. *Acacia pulchella* inhibits *Phytophthora* activity in jarrah forest) and increased rate of litter decomposition. Maintenance of soil organic matter and mineralisation capacity is necessary to provide the milieu for mineralisation of legume-nitrogen to forms available to other components of the forests.

Free-living Nitrogen Fixation

The potential role of free-living nitrogen-fixers associated with soil, roots, litter and decaying dead wood should not be overlooked. They may be of significance in the early stages of stand development following massive perturbation (e.g. pole stage plantation development), and in mature forests with a wide variety of organic substrates and microhabitats. The potential role, particularly of the soil-based nitrogen fixers, where burning is regularly practised and where legume establishment may not be possible, should not be overlooked.

SOIL NITROGEN MINERALISATION

Measurement of Nitrogen Mineralisation

Incubation studies providing an estimate of mineralisation potential (N_o), can provide some qualitative indication in *in situ* mineralisation in certain soils, but not in others. Reasons for this might include:

(i) experimental artefacts due to soil disturbance, moisture/temperature/surface area relationships in samples and the presence of severed roots or removal of roots; even intact cores suffer from some of these defects.

(ii) eco-physiological influences on microbial activity due to seasonal variation in phenology of the forest, to root activity (including exudates), energy sources, leaf fall/litter incorporation, competitive effects with other organisms including fungi. The resulting heterogeneity is large and introduces formidable sampling problems for both incubation and *in situ* studies; there is probably no ideal solution to this; sampling schemes must compromise between inherent variability in the parameter being estimated, logistic constraints and the aim of the study.

Incubation studies however are valuable for comparing treatments and seasonal effects on N_o, but are less useful for determining mineralisation in the field, where actual fluxes are necessary for determining nitrogen budgets. Indirect methods of determining mineralisation via measurement of more easily determined and related parameters may hold some promise in this area, e.g. use of ^{15}N and carbon isotopes.

Standardisation of methodology is important if comparisons are to be made among various forest ecosystems; adoption of at least one standard technique (e.g. the Waring-Bremner anaerobic incubation technique might be appropriate) will be necessary if proposals to mount a broad comparative study of nitrogen mineralisation potential in Australian forest soils are taken up.

Factors Affecting Mineralisation

The utilisation of nitrogen in litter is influenced by the 'quality' of the litter which is related to vegetation diversity and species characteristics; these substrates influence litter and soil biota and provide the carbon components which act as energy sources for soil microbial processes. Hence quality of organic matter may influence not only the nitrogen mineralisation process itself; carbon components produced as a result of mineralisation may in turn influence the course of other nitrogen-cycle related soil processes.

The mineralisation of high C/N ratio litter can lead to competition for nitrogen between decomposers and autotrophs; this leads to questions of heterotrophic uptake of nitrogen as ammonium or amino acids by plants, and particularly by their mycorrhizas.

Mineralisation and nitrogen turnover are also influenced by the activity of soil fauna in burial and comminution of litter;

regular burning, by preventing development of a litter pack to the stage where active incorporation by soil fauna can take place, can therefore have a secondary effect apart from the more obvious one of nitrogen losses through volatilisation.

Plant waxes are resistant to insect activity and hence may protect litter from comminution by fauna; they can also confer hydrophobic characteristics to the soil and as a result might influence mineralisation patterns due to changed moisture characteristics (e.g. wettability of soil and litter). Other potential inhibitors of mineralisation such as polyphenols appear to play a somewhat ambiguous role.

Nutrient pulses to the forest floor result from the deposition of high-nutrient green litter such as scorched foliage following fires or green crowns during logging. Rates and patterns of mineralisation may be speeded up considerably thereby. This material is also low in extractives such as polyphenols compared to the senescent leaves of normal litterfall, which would further enhance rates of decomposition.

TREE AND STAND RESPONSE

Nutrient Balance

The large biomass of forests and perenniality of its dominant members permit the development of large storage pools for energy and nutrients which can buffer the ecosystem against perturbation. These pools need to be balanced; ratios such as C/N, N/P, N/S, P/S, C/P need to be optimised to ensure energy flow follows pathways which fulfil management objectives. Practices aimed at increasing nitrogen and carbon in the system should ensure that these balances are maintained; however we know very little about optimum nutrient ratios in forests and their influences on energy flow and nutrient cycling.

While the penalties of luxury applications of nitrogen in agriculture may not apply to forests and there may be long term benefits in terms of organic matter accumulation and nutrient cycling, it is important to ensure that deficiencies of other elements are not induced, particularly phosphorus and sulphur. Fertilizing with nitrogen should maintain the balance between nitrogen and phosphorus; phosphorus fertilizing may need to be initiated with nitrogen fertilizing depending on circumstances. Phosphorus availability in soil and the residual value of previously applied phosphorus should be determined prior to initiation of nitrogen fertilizing - definition of the phosphorus fixing properties of the soil can be helpful in this regard. the soil phosphorus status can then be taken into account in designing the most appropriate nitrogen fertilizer regime. There is also a need to consider trace element supply, particularly of copper and zinc when nitrogen fertilizing of plantations is being considered.

Sulphur, like nitrogen, can be lost by burning but is dependent on atmospheric accession for replacement; given the close links between nitrogen and sulphur in organic matter, programmes aimed at increasing nitrogen supply in forests should monitor stand sulphur status as a consequence; sulphur mineralisation needs to be studied along with soil nitrogen and leaching studies examining nitrate movement might with advantage be extended to incorporate sulphate as well. Sulphur, like nitrogen, can be lost by volatilisation during burning, but unlike nitrogen is probably returned in the soil surface (elsewhere) via precipitation.

Given the demonstrated links between sulphur deficiency and disease susceptibility, at least for Pinus species, there is a need to differentiate between health and stand growth in assessing nutritional requirements. Application of nitrogen can induce sulphur deficiency and raise foliage arginine levels. This amino-acid would appear to be a useful indicator of potential disease susceptibility, and should be monitored in any system where nitrogen fertilizer use is being considered, and where foliage sulphate levels are low.

Nitrogen fertilizing should also be considered in relation to potential water use, particularly where water yield from catchments is of concern. It has been suggested that water availability may define the upper level of productivity and nutrition the rate at which processes proceed to that end, but it may be better to regard water as one of the suite of nutrients and ensure appropriate balance between it and other nutrients, particularly nitrogen which can influence crown density and hence the transpiration surface.

A large body of knowledge now exists on nutrient requirements of pine, and a smaller body, none the less valuable, is available for eucalypts. This knowledge requires synthesizing in order to design much needed process studies on nutrient physiology of these two important genera, particularly in interpreting nutrient interactions, trace element requirements and the pattern of internal nutrient cycling. Integration within a land classification framework should also permit economy of effort in future research. Nutrients requiring most study would appear to be nitrogen, phosphorus, sulphur and to a lesser extent copper, zinc, potassium and calcium.

Wood Quality

It is generally recognised that, within normal silvicultural and economic limits, fertilizing does not present a potential problem with regard to wood quality. However, excessive use of nitrogen can lead to increased branch growth which may compromise the utilisation potential of logs from within the crown section of the tree. This may be exacerbated when nitrogen fertilizing is combined with heavy thinning, as is advocated in many pine plantation situations. There is also some controversy as to whether fertilizing influences tree taper, and the direction any influence might take. A more critical analysis is required in this area embracing species, stage of stand development, nature of fertilizer used, level of response expected (i.e. correction of deficiency or movement to a higher plane of production), interaction with site and silvicultural factors.

Measurement of Response

The parameters measured to determine response to fertilizing depend on the aim of management, e.g. application of nitrogen may increase biomass and reduce water yield; wood production involves a completely different set of criteria to maximising species diversity, water yield, recreational potential etc., i.e. there is a need to define clearly management criteria as distinct from biological criteria. Variables measured must also be related to the objective of the study which in itself should be clearly set in the appropriate scientific and silvicultural context. Yield curves predicting response may vary from normal; this is a reasonable expectation if the objective of the programme is to produce a different type of stand. Deviations from the norm need therefore to be established, but care is required in this approach to ensure that one is not merely measuring sampling error rather than real population differences.

Mensurational procedures for measuring tree and stand response in plantations are well developed but are less precise for mixed sized class native forests. This is an area where some research attention could be addressed, particularly if indices of long term response are to be sought based on short term measurements. Some fundamental work is required in this area if research efforts are to be expended in determining the production potential of native forests. Again, aims of management will dictate the most appropriate methodology to be adopted.

Intensity of Production

Socio-economic factors tend to determine the extent and direction of application of research results, e.g. research may indicate an appropriate direction in terms of intensive silviculture with site preparation, heavy commitment to fertilizers, use of legumes, etc.; or the move to later-age nitrogen fertilizing in order to increase production from existing stands. An alternative approach is to plant over larger areas, accepting a lower level of production from a more extensive operation with a lower input base. The latter has been the traditional approach to forestry in both plantations and native forests. The former is the approach currently in vogue. There is room for both, and both have their legitimate place given a particular environmental framework. However, no matter what the social context of the aim of management may be, maintenance of long term ecosystem stability (in the dynamic sense) should be the goal - this therefore involves consideration of optimising as distinct from maximising production. While this is particularly apposite to plantation forestry, it is equally relevant to native forest management. A better understanding of the nutrient economy of our forests, particularly of nitrogen, is essential if sustained productivity is to be achieved.