ASPECTS OF NUTRIENT CYCLING IN SEMI ARID MALLEE AND MULGA COMMUNITIES

by

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STATEMENT

The work presented in this thesis is my own. Specific contributions by others have been referred to in the text and acknowledgements.

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ABSTRACT

A study was made of nutrient distribution and fluxes in mallee and mulga ecosystems to obtain an appreciation of the manner in which the woody plants have adapted to their infertile semi arid habitats. Emphasis was placed on utilisation and fluxes of nitrogen and phosphorus within these ecosystems.

Pool sizes of total phosphorus, 'available' phosphorus and total nitrogen within the communities exhibited remarkable similarities despite wide differences in geographical location and plant assemblages supported. There was a pronounced concentration of organic carbon, total nitrogen and 'available' phosphorus in the soil surface horizons.

High resilience within mallee communities was demonstrated by comparison of a fifteen year old regrowth community with an adjacent mature (c. 55 year old) stand. There were only small differences between both communities in nitrogen and phosphorus pool sizes in the vegetation, and in lignotuber biomass, leaf area index and the amount of leaf litter present on the soil surface. The above ground net primary productivity of the regrowth community (5406 kg/ha/yr) was more than twice that of the mature mallee (2379 kg/ha/yr).

The mulga community had high concentrations of nitrogen in both its living and dead tissues compared with mallee. This suggested that the Acacia/Rhizobium symbiosis was effective but there was apparently no build-up of total nitrogen within the soil profile.

There were considerable fluctuations in the pulses of litter and nutrients onto the floors of these woodland ecosystems. However litterfall from Eucalyptus spp. exhibited a distinct summer maximum whereas litterfall in mulga appeared to be largely independent of season and rainfall. Withdrawal of nitrogen and phosphorus prior to leaf abscission indicated conservation in the use of these elements.

There were striking similarities in the breakdown and decomposition rates of mallee and mulga leaves, despite higher extant nitrogen concentrations in the latter. Similarly within a particular community there was little variation in the decomposition rates on different microsites. The patterns of mineralisation and immobilization of nitrogen and phosphorus in decaying leaves, branches and bark were in broad agreement with similar studies carried out elsewhere in a range of vegetation types.

It was demonstrated that the widely accepted decay constant is an unstable value which changes as decomposition progresses. Derivation of this value by the assumption of 'steady-state' in mature semi arid shrub and woodland communities appears to be equally tenuous.

There was no suggestion of a specific xerophytic mycoflora being present on decomposing mallee and mulga leaves. The pattern of species colonization was consistent with that found elsewhere in Australia. A feature of the mycoflora was that only three species of Penicillium were

recorded on the mallee leaves and only one (at very low frequencies) was recorded on mulga litter.

Experiments were undertaken to observe whether any major advantages in phosphorus nutriton were possessed by trees and shrubs which would react in their favour when compared with native grasses. All species studied (Acacia aneura, Cassia nemophila and Eucalyptus socialis) were highly responsive to increasing concentration of nitrogen and phosphorus and there was a very strong nitrogen x phosphorus interaction recorded in sand culture. However growth rates and mean phosphorus absorption rates were much lower than those previously recorded for Australian semi arid grasses.

The relatively poor ground flora and the large volume of surface roots suggest both mallee and mulga communities operate on a tight extrinsic rather than intrinsic cycling of nutrients, although taken together the efficiency of both cycles could be high. In fact the nitrogen and phosphorus cycle times in the semi arid shrub/woodland ecosystems studied were quite comparable with those from more mesic environments. Furthermore it was shown that mulga grassland is much less efficient in utilisation of phosphorus than endemic woodlands and could also require much larger amounts of nitrogen per unit of dry matter than competing woody plants.

It was concluded that grasses possess initial advantages in the establishment phase, in these infertile semi arid ecosystems, through faster growth rates and mean

phosphrous absorption rates. In time, however, competing woody plants develop a much larger root system which assists in drought survival and nutrient absorption. Concomitantly, the more efficient use of the limited available nutrients results in dominance by the woody plants.

CHAPTER 1

Introduction

The presence of a dominant shrub or tree layer in many semi arid and arid regions is considered by Beadle (1951, 1960) and Whittaker and Woodwell (1972) to be a characteristic feature of the Australian vegetation distinguishing it from similar world homoclimates. The endemic woody plants of this zone often attain their highest densities in those areas with nutritionally impoverished soils (particularly red earths).

These considerations pose the questions - are woody plants better adapted to these soils than native grasses? and, if so why? By corollary, in the absence of ameliorative programmes is it futile to try to shift the balance of vegetation in favour of grass and herbage to benefit domestic stock? On inspection two factors would appear to react against the success of woody plants in these arid regions. First, woody plants are noted to be inefficient users of water and second, the soils on which they predominate may be extremely infertile (especially low in available phosphorus) - whereas data of El Ghonemy (1966) for Triodia pungens and Christie and Moorby (1975) for Thyridolepis mitchelliana suggest native grasses may be very well adapted to such conditions.

On the other hand woody plant tissues can be highly resistant to moisture stress (Slatyer 1960, Connor and Tunstall 1968) and the plants themselves may act as

nutrient "pumps" in infertile soils (Ebersohn and Lucas 1965). Also many researchers hold the view that, in arid zones with low leaching potentials, the products of rock decay must remain and accumulate in the soil to such an extent that there is no likelihood of nutrient shortage and limitations for vegetation production (Charley 1972). However Jackson (1957) has indicated that these soils may be as heterogeneous as those elsewhere, and that in a world view there are few generalisations about them that bear close scrutiny.

In the Australian arid zone most work on nutrient distribution and cycles has centred on salt bush communities (e.g. Beadle and Tchan 1955, Charley 1959, 1972, Charley and McGarity 1964, Charley and Cowling 1968, Cowling 1969, Jones, Hodgkinson and Rixon 1969). Such studies no doubt influenced Charley's (1972) observation that phosphorus has not been examined to any extent in shrub communities of arid lands, and that it is unlikely to be as significant in the control of plant production as nitrogen which is the nutrient most commonly in short supply where rainfall is low.

However data for two other arid zone communities, while limited, highlight the importance of phosphorus deficiencies over vast areas of the Australian pastoral ecosystem dominated by mallee and mulga vegetation (Figure 1.1). Coincidentally these are the areas in the arid and semi arid zones where management of woody plants often presents the greatest problem.

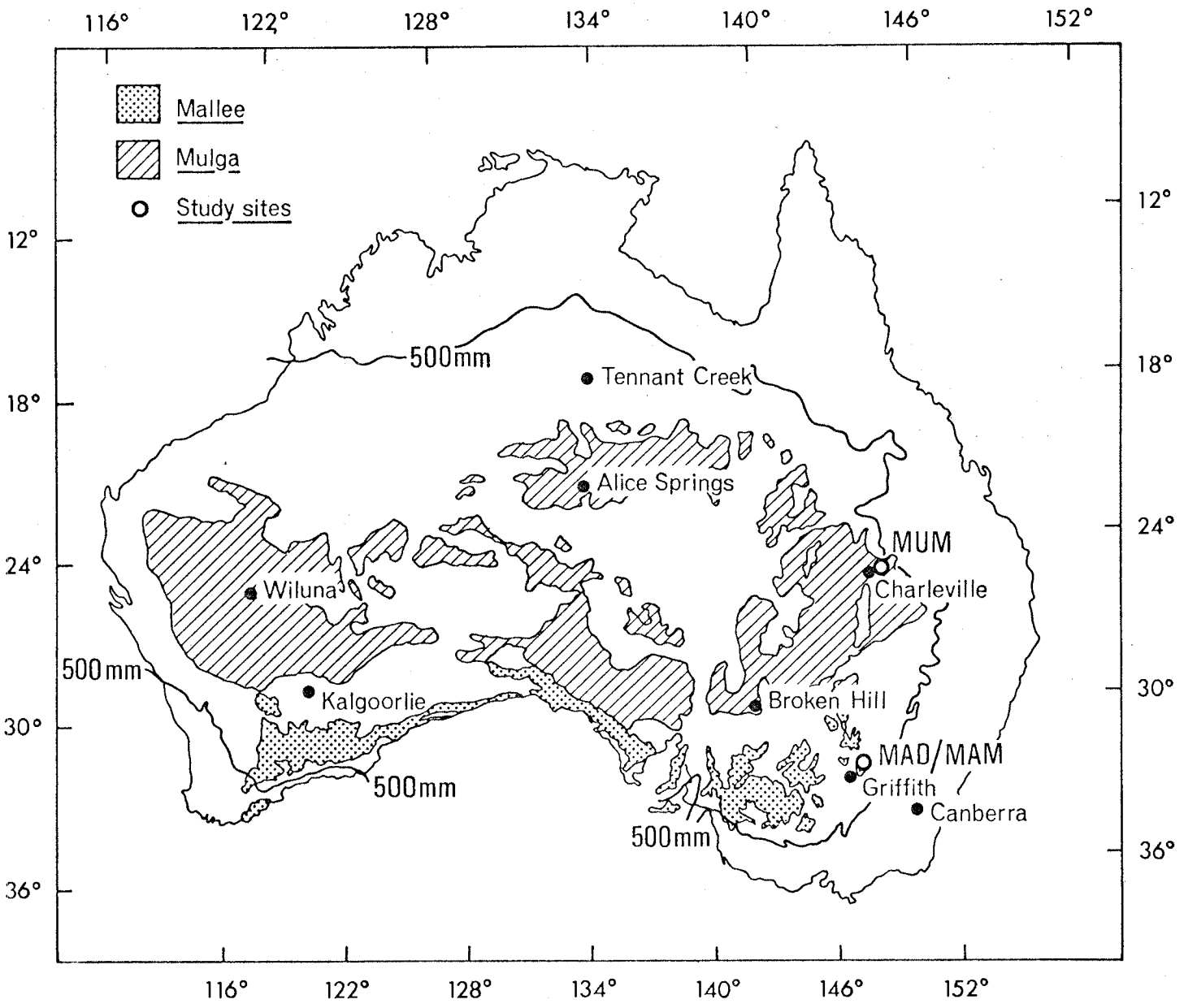


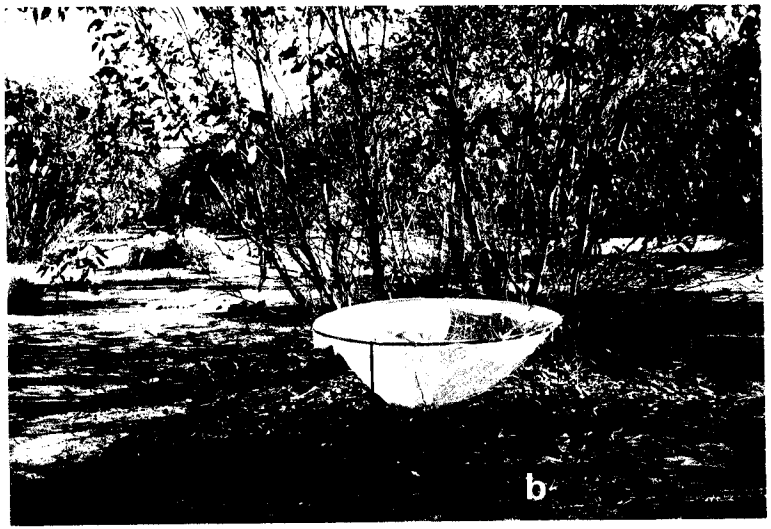
Figure 1.1
Distribution of mallee and mulga communities in Australia (after Carnahan 1976). Position of study sites and the 500 mm rainfall isohyet are also indicated.

The low level of available phosphorus in mulga soils has been shown by Jackson (1962), Winkworth (1964), Cowie (1968) and Dawson and Ahern (1973), while Christie (1975c) found that supply of phosphorus, not nitrogen, was limiting grass establishment on these soils. Deficiencies of phosphorus in mallee ecosystems have been demonstrated by El Ghonemy (1966) and Parsons (1968a). Parsons also found that mallee eucalypts were responsive to increasing levels of phosphorus nutrition.

The present study was undertaken to obtain a better appreciation of the soil-vegetation-nutrient interaction in these dry woodland ecosystems. In particular the project examines the efficiency with which nutrient capital available to the vegetation has been employed, and the manner in which nutrient homeostasis is maintained, in mallee and mulga ecosystems not grazed by domestic stock. Emphasis has been placed on the woody perennial component of the vegetation and on utilisation and fluxes of nitrogen and phosphorus within these ecosystems.

1.1 Description of field sites - Three communities were chosen for study:

1.1.1 Mature mallee (hereafter referred to as MAM) - a Eucalyptus socialis/E. dumosa community (Plate 1.a) with a prominent Melaleuca lanceolata understorey. It is situated 19 km E. of Rankins Springs, N.S.W. adjacent to



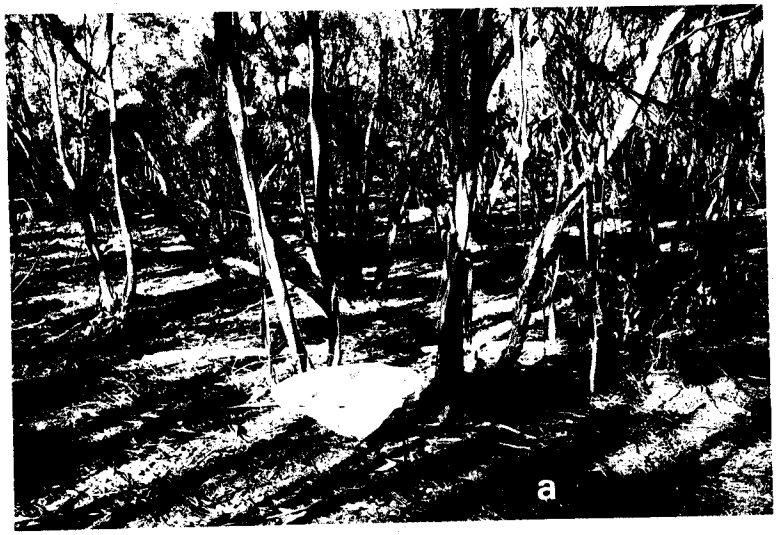


Plate 1 Mallee and mulga field sites

a. MAM

b. MAD

c. MUM

See text for details. Litter traps on each photograph are c.80 cm in diameter.

the Mid Western highway and on the property of Messrs R. and F. Sibraa (Lat. 33° 53' S., Long. 146° 30' E.).

1.1.2 Disturbed mallee (hereafter referred to as MAD) - A Eucalyptus socialis - E. gracilis - E. foecunda/ Triodia irritans/small shrub (Olearia sp., Beyeria sp.) community (Plate 1.b) situated c. 500 m west of MAM. It developed following tractor clearing and burning, but without fertilisation, of the original mallee vegetation in 1962.

1.1.3 Mature mulga (hereafter referred to as MUM) - an Acacia aneura/Eucalyptus populnea community (Plate 1.c) situated on the Charleville Experimental Reserve, Charleville, Queensland (Lat. 26° 25' S., Long. 146° 13' E.).

All three communities were protected from domestic stock during the course of the study but had been subjected previously to very light grazing pressure (< 1 sheep equivalent/10 ha). Layout of the study plots at each site was modelled on the suggestions of Newbould (1967). Three areas could be defined. A detailed study plot (100 m x 50 m for MAM, MUM; 100 m x 100 m for MAD) was surrounded by a 20 m buffer zone and aligned N-S-E-W. A 50 m zone surrounding this study plot and buffer was used for destructive sampling. Finally each of the previous areas were contained within similar vegetation types which acted

Table 1.1 Average climatic data for Charleville[+] and Griffith[xx]

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
(i) Charleville													
Rainfall (mm)	67	50	39	24	17	37	33	19	24	26	43	66	467
1973*	39	201	18	57	1	3	85	38	40	78	30	155	745
1974*	170	13	19	49	7	18	0	53	18	53	30	17	447
1975*	55	60	77	3	0	32	18	n.r.	n.r.	n.r.	n.r.	n.r.	n.r.
Evaporation (mm)	312	242	209	154	124	82	92	123	164	233	277	320	2333
Max.Temp. (^{o}C)	36.4	35.7	33.2	29.2	24.6	20.8	20.2	22.7	26.9	31.2	34.2	35.8	-
Min.Temp. (^{o}C)	21.5	21.2	18.4	13.2	8.4	5.8	4.5	5.7	9.4	14.3	18.0	20.3	-
(ii) Griffith													
Rainfall (mm)	28	28	42	35	34	35	32	38	29	46	30	30	407
1973*	36	46	39	19	7	33	66	59	19	88	60	48	520
1974*	29	71	16	224	9	14	34	47	81	114	21	2	662
1975*	7	0	5	19	16	15	32	n.r.	n.r.	n.r.	n.r.	n.r.	n.r.
Evaporation (mm)	279	236	206	114	66	46	48	74	124	175	234	269	1871
Max.Temp. (^{o}C)	33.3	32.1	29.3	23.9	19.4	15.8	15.0	17.1	20.9	24.4	28.2	31.2	-
Min.Temp. (^{o}C)	17.7	16.5	14.2	9.7	6.3	4.3	3.3	4.3	6.3	9.6	12.6	15.3	-
Av.Daily Global Solar Radiation (Langleys)	700	670	520	380	260	250	240	340	460	560	720	710	-

Table 1.1 (Continued)

* Data for the actual study sites - see text

n.r. = not recorded (study concluded)

[+]Source: Commonwealth Bureau of Meteorology (1956) "Climatic Averages, Australia"

[xx]Source: 'Meteorological Data 1931-1967' CSIRO Divison of Irrigation Research Griffith, New South Wales

as large external buffers. These latter areas comprised 80 ha for MAD, 25 ha for MAM and 800 ha for MUM respectively.

1.2 Climate - The climate of all sites is semi arid with a distinct summer (October-March) rainfall incidence for MUM (62.3%) and a more or less even summer-winter rainfall distribution for MAD/MAM (Table 1.1). The temperatures experienced at the mallee and mulga study sites are similar, even though they are some 800 km apart. Solar radiation levels are characteristically high for both areas (Hounam, 1963) but monthly data are available only for Griffith.

The climatic summaries presented in Table 1.1 are for the nearest detailed recording station to each site. The Charleville meteorological office is c. 2 km W. of the MUM site and Griffith is c. 95 km S.W. of MAD/MAM. Rainfall records presented for the study period were obtained from a pluviometer placed 100 m from the MUM plot and from a gauge situated at an adjacent homestead 1 km from the MAD/MAM plots.

1.3 Vegetation - General descriptions of mallee vegetation may be found in Beadle (1948) and Specht (1972). More detailed studies of mallee communities and their edaphic relationships in south eastern Australia are contained in theses (and papers arising therefrom) of El Ghonemy (1966), Parsons (1966), Holland (1967) and Noy-Meir (1970). For example see Parsons (1968a, 1969, 1970), Parsons and Rowan

Table 1.2 Species check list for MAD/MAM - October 1975

	Common name	Site
Asteraceae -		
Brachycome ciliaris		MAD
Helichrysum apiculatum	Yellow buttons	MAD
Helipterum jessenii		MAD/MAM
Minuria leptophylla	Minnie daisy	MAD
Olearia pimeleoides		MAD/MAM
Chenopodiaceae -		
Bassia diacantha	Grey copper burr	MAD
Euphorbiaceae -		
Beyeria opaca		MAD/MAM
Bertya cunninghamii		MAD/MAM
Lamiaceae -		
Prostanthera aspalathoides	Mint bush	MAD
Liliaceae -		
Dianella revoluta	Spreading flax lilly	MAD
Mimosaceae -		
Acacia brachybotrya		MAD
Acacia rigens		MAD
Myrtaceae -		
Eucalyptus dumosa	White mallee	MAM
Eucalyptus foecunda	Hooked mallee	MAD
Eucalyptus gracilis	Yorrel mallee	MAD
Eucalyptus socialis	Red mallee	MAD/MAM
Melaleuca lanceolata		MAM
Micromyrtus ciliata		MAD/MAM
Pittosporaceae -		
Billardiera cymosa	Dumplings	MAD
Poaceae -		
Danthonia caespitosa	White top	MAM
Danthonia eriantha		MAM
Danthonia setacea		MAM
Stipa variabilis	Variable spear grass	MAD/MAM
Triodia irritans var. *laxispicata*	Spinifex	MAD

Table 1.2 (Continued)

	Common name	Site
Santalaceae -		
Santalum acuminatum		MAD/MAM
Sapindaceae -		
Dodonaea cuneata	Hop bush	MAM
Thymelaeaceae -		
Pimelea dichotoma		MAD

(1968), Holland (1969a, b, c), Noy-Meir (1971, 1974). Mulga vegetation of south west Queensland has been described by Everist (1949), Holland and Moore (1962), Burrows and Beale (1969) and Boyland (1973, 1974). Edaphic relationships of mulga are presented by O'Hagan (1966), Cowie (1968), Christie (1970) and Dawson and Ahern (1973, 1974).

A check list of all vascular plants present on the plots was obtained for MAD/MAM in October 1975 and for MUM in July 1973. The lists (Tables 1.2, 1.3) are not necessarily exhaustive but are thought to include all of the perennials growing on the study areas. Staff of the Queensland Herbarium identified the MUM species and the National Herbarium in Sydney provided identification of all MAD/MAM plants. Authorities for botanical names are as accepted by those herbaria in 1973 and 1975 respectively.

A detailed description of the structure of the vegetation and soil nutrient status is presented in the following chapter.

Table 1.3 Species check list for MUM - July 1973

	Common name
Amaranthaceae -	
Ptilotus sp.	
Goodeniaceae -	
Goodenia sp.	
Mimosaceae -	
Acacia aneura	Mulga
Malvaceae -	
Abutilon sp.	Flannel weed
Hibiscus sp.	
Sida filiformis	
Myrtaceae -	
Eucalyptus populnea	Poplar box
Poaceae -	
Aristida jerichoensis	Jericho three-awn
Cymbopogon obtectus	Silky heads
Digitaria ammophila	Silky umbrella grass
Digitaria brownei	Silver spike grass
Digitaria diminuta	
Eragrostis eriopoda	Woollybutt
Eriachne helmsii	Woollybutt Wanderrie
Monochather paradoxa	Mulga oats
Thyridolepis mitchelliana	Mulga mitchell
Tripogon loliiformis	Five minute grass

CHAPTER 2
Biomass and nutrient distribution in mallee shrub and mulga woodlands

2.1 Introduction

The estimation of biomass and nutrient content in ecosystems dominated by woody plants provides a basis for the analysis of ecosystem function (Anderson 1971) and the determination of the efficiency with which the available resources have been employed. Many such estimates have been carried out in the northern hemisphere but few are recorded for southern hemisphere ecosystems (e.g. less than 3 per cent of the extensive bibliography provided by Rodin and Bazilevich (1967) refers to southern hemisphere studies).

Most work of this nature in Australia has been concerned with forest and shrub ecosystems in the higher rainfall areas (e.g. Attiwill 1966a, Forrest 1969, Specht 1969, Keay and Turton 1970). In communities dominated by woody plants in semi arid Australia biomass and nutrient distribution appear to have been studied together only in Acacia harpophylla (Moore, Russell and Coaldrake 1967), Atriplex vesicaria (Charley and Cowling 1968) and Eremophila gilesii (Burrows 1972). However studies of biomass alone have taken place in communities dominated by mallee (Holland 1969a), Atriplex spp. (Jones, Hodgkinson and Rixon 1969) and Acacia aneura (Burrows and Beale 1970, Pressland 1975). Work on the edaphic relationships of these communities has been carried out

by El Ghonemy (1966), Parsons (1969) and Noy-Meir (1971, 1974). Unfortunately the sites examined by the latter authors do not correspond with those on which biomass was determined, and extrapolation of results based on different sites and sampling times could be misleading.

The present study was undertaken in order to overcome this deficiency with respect to mallee and mulga communities. Both mallee and mulga are found on nutritionally impoverished soils and it is of considerable ecological significance to examine how these communities have utilised the nutrients available to them. To this end it is necessary to study biomass and nutrient distribution in some detail on the same site.

One mulga (MUM) and two mallee communities (MAD,MAM) were chosen for study. Descriptions of vegetation structure and some environmental parameters may be found in Chapter 1.

2.2 Methods

2.2.1 Principles

Seven basic steps can be distinguished in the estimation of biomass and nutrient content in multi-layered woodland ecosystems.

(i) soil analysis (bulk density and nutrient content)

(ii) stand analysis, non-destructive measurements

(iii) determination of the weight of surface litter and herbaceous understorey

(iv) determination of root biomass

(v) determination of standing crop relationships - destructive sampling of selected plants to obtain regressions between easily measured

independent parameters (e.g. stem circumference) and weight of various components of the biomass; derivation of 'mean' tree or shrub weights where necessary

(vi) nutrient analysis of sub-samples of plant tissues

(vii) calculation of stand biomass and nutrient content by means of independent stand parameters, predictions based on predetermined regressions, 'mean' weights and the stand table

The techniques utilised are well established but it was necessary to give particular consideration to the determination of plant biomass because of site differences in vegetation habit and structure. Estimation of forest biomass has been discussed in some detail by Ovington, Forrest and Armstrong (1967), Newbould (1967) and Whittaker and Woodwell (1971). The procedure most commonly employed is the use of regressions and stand tables (termed allometry in Europe and Japan (Kira and Shidei 1967) and dimensional analysis in North America (Whittaker and Woodwell 1968)). This approach has been used in Eucalyptus communities by Attiwill (1966a) and Holland (1969a).

For natural stands of varying size classes, the weight of a plant component usually can be plotted against some dimension (e.g. basal stem circumference) to give a straight line on double-log paper. Thus it has been expedient to calculate regressions as linear in the logarithms of the variables and to transform back to

arithmetic units by determining the antilogarithms for the expansion of the stand table to biomass (Baskerville 1972). However statistical aspects of the treatment are subject to question (Zar 1968, Hafley 1969, Baskerville 1972, Beauchamp and Olson 1973). In particular, a bias is introduced by simply taking antilogs of the previously transformed data because the geometric mean rather than the true mean of the estimated value is obtained (Munro 1974). This has resulted in a systematic underestimation of biomass whenever the logarithmic transformation has been used (Baskerville 1972).

Mathematical procedures which counteract this bias have been known for some time (e.g. Finney 1941) but rarely applied in ecological work (Baskerville 1972). In the present study the steps outlined by Beauchamp and Olson (1973) have been adopted and these are presented in Appendix 2.

Dimensional analysis , as outlined, is appropriate for tree and tall shrub vegetation. However, this method is limited where it is difficult to easily measure a suitable independent variable on which regressions may be based. This is particularly true of small, multi stemmed shrubs. In such vegetation the use of 'average' shrub techniques and stand enumeration seems unavoidable, unless the more labour intensive total harvest of shrubs is employed.

'Average tree' methods, and their attendant errors, have been discussed for forest application by Attiwill

(1966a) and Ovington, Forrest and Armstrong (1967). To minimise likely errors in the use of such techniques in shrub communities, it seems advisable to stratify populations into species size classes. 'Average' shrubs can then be selected within each size class as a basis for determination of stand biomass.

2.2.2 Procedures

(i) Soil analyses - The soil profile at each detailed study site was sampled to 1 m depth using a 5 cm diameter soil auger. Ten replicate samples were obtained from randomly stratified positions on the MAM and MUM plots and sub-divided into 0-2.5, 2.5-5, 5-10, 10-25, 25-50 and 50-100 cm depth fractions for subsequent chemical analyses. Similar depth intervals were sampled on the MAD site for 10 random intercanopy samples (2 sets of 5) and 10 samples (2 sets of 5) randomly placed beneath the eucalypt canopies.

Replicates were bulked, thoroughly mixed and sub samples analysed for pH, total P, available P, total N, exchangeable cations and organic C. The methods employed are detailed in Appendix 1.

Soil pits were dug on the MAD and MAM site for purposes of soil description. Samples were obtained for bulk density determinations from the face of these pits using a core of 4.35 cm internal diameter. Three replicate readings were obtained for each depth interval which had been sampled for chemical analysis. Soil bulk density figures for the MUM site were kindly provided by a

colleague, Mr A.J. Pressland, who had obtained the readings from the external buffer zone of this plot.

(ii) Stand analysis - Density of the vegetation at each site was determined in 1973 and again in 1975 by recording all woody perennial species (and Triodia irritans which occurred only on MAD) in 25 m x 2 m belt transects. These transects were randomly placed along the N-S axis and stratified to give a representative cover of the detailed study area. The MUM transects were permanently positioned but a new randomization was carried out for MAD and MAM in 1975. There was a minimum of 15 such transects for each site sampling period. Grass and herbaceous species, apart from T. irritans at the MAD site, were considered to be a minor and ephemeral component of the vegetation (total biomass<100 kg/ha - but see 2.3) and their density was not recorded.

Additional measurements were also obtained within each transect to permit better definition of community structure:-

MAD/MAM: Eucalyptus spp. - Following Holland (1967) the stem was taken as the basic unit of the mallee. The circumference of each stem within the belt was measured 30 cm above or along its axis from the base (Note: because of the spreading nature of stems growing under the mallee habit this is not necessarily 30 cm above ground level). The same flexible nylon tape was used for reading this parameter in 1973 and 1975. On each occasion the tape

was held firmly around the stem to give maximum readings repeatable to within 0.1 cm.

The number of stems per clump and the number of clumps per transect were also recorded. A clump was considered present if at least one of its stems occurred within the belt. On the MAD site an approximation of mean clump diameter was derived by averaging two diameter measurements taken at right angles to each other for each clump; each diameter was measured by placing a flexible tape horizontally through the centre of the clump and recording the distance between the two extreme vertical canopy projections (visually estimated) onto the tape.

It was possible to obtain a crude estimate of canopy cover per hectare using these clump diameter measurements and assuming circular canopies. However, by its nature, this figure is an overestimate as it does not take into account possible intermingling of the foliage of adjacent clumps. An improved estimate of canopy cover was, therefore, obtained by the stratified random placement of 31 x 30 m line transects in the detailed study area. The intercepts of the vertical projection of foliage onto these lines, as gauged by a straight 3 m rod, were used to determine percentage canopy cover of the mallee eucalypts.

Other shrubs and Triodia - Height class distribution was recorded for all other woody perennials within the belt transects. The class intervals chosen were < 0.5, >0.5-1, >1-1.5, >1.5-2, >2-3, >3 m tall. A similar classification scheme was used for T. irritans hummocks

which were divided into diameter classes of < 0.5, > 0.5-1, >1-1.5 m measured over the longest diagonal.

MUM: Acacia aneura and Eucalyptus populnea were the only woody perennials occurring on the MUM plot. The circumference of each stem (here measured 30 cm above the lowest ground level) was recorded as for the MAD/MAM plots. Repeated measurements on the same plant between 1973 and 1975 were ensured by attaching individually numbered aluminium tags to every stem.

(iii) Surface litter and herbaceous layer - Estimates of the surface litter layer were obtained at the commencement and conclusion of the study period i.e. when stem circumferences were recorded. Quadrats were placed in a stratified random fashion over the detailed study area of each plot and all litter lying above the surface soil and within the quadrats was collected. In addition any herbaceous plants rooted within the quadrats were harvested by cutting them off at ground level. The samples were placed in paper bags and brought back to the laboratory for sorting.

The number and size of quadrats varied between site and sampling period (see Table 2.5). This was largely dictated by consideration of the limited time available for sorting samples. The minimum quadrat size used was 25 cm x 25 cm and the minimum sample size employed was 30. In all cases the standard error of the mean value for the major nutrient pool (leaf litter) was less than 20 per cent.

Each litter sample was sorted into the following fractions: stem (> 1 cm diameter), twigs (< 1 cm), leaves*, herbaceous plants, bark, other species (i.e. other than Eucalyptus spp. for MAD/MAM and Acacia aneura for MUM), capsules (MAD/MAM), pods (MUM) and 'residue' (mostly fragmented leaf material - not retained by a 5 mm sieve). The sorted material was brushed free of soil particles as far as practicable and then dried to constant weight at 80°C. Subsamples were retained for chemical analysis.

(iv) Root biomass - The biomass of living roots was estimated at the final sampling period by coring for fine roots and excavation of stem butts and lignotubers.

Root cores, to a depth of 1 m, were taken with a 120 cm steel tube of 4.35 cm internal diameter. The cores (20 for MUM and 10 each for MAD/MAM) were positioned in a stratified random fashion over the detailed study site. A 1 m^2 area, containing the core position, was soaked with 100 litres of water in the 24 hour period prior to sampling. This facilitated sinking and extraction of the cores on the MUM site but was not carried out for MAD/MAM because the surface soil was moist from previous rain. However, at the latter sites it was

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*Throughout this thesis Acacia aneura phyllodes will be referred to as leaves for comparative purposes and the two terms will be used interchangeably

necessary to use a soil auger (5 cm outer diameter) to extract samples from the lower depths of the core. Where this was done appropriate adjustments were made in calculations of root biomass.

Each root core was sectioned into 20 cm lengths to give 5 depth intervals (0-20, 20-40, 40-60, 60-80 and 80-100 cm). The sections were placed in individually labelled bags and returned to the laboratory for root separation. Each section was soaked in 1 litre of tap water and then the roots were washed free of soil while being retained on a fine sieve. Because of the low clay content in these soils (< 22%) detergent was not added to the water to assist with soil dispersal. 'Live' root material (internally white and possessing some elasticity) only was collected. The roots were subsequently dried to constant weight at 80^{o}C and retained for chemical analysis.

Coring techniques provided an estimate of fine root biomass for the stands as a whole but it was impractical to separate the roots into different species fractions. However, a significant proportion of the total root biomass is found beneath the stem butts of the dominant plant species. To estimate this fraction excavation was necessary.

At the MUM site a fence line was being cleared through the external buffer area of the plot. It was possible to obtain more or less intact surface root samples from trees pushed over by a bulldozer for this purpose. Stem circumference was measured 30 cm above

'ground level' for each butt. The stem was then sawn off as close to 'ground level' as possible with a chain saw. The root butt with attached smaller roots (volume occupied c. 1 m diameter x 50 cm deep) was then taken back to the laboratory for washing with a water jet and drying to constant weight at 80°C. A subsample was kept for chemical analysis. Eight butts were sampled altogether corresponding to stem circumferences ranging from 17.3-61.5 cm. These data were used to establish a regression between stem circumference and root weight.

The estimate of lignotuber biomass for the mallee eucalypts (MAD/MAM sites) required alternative methods. During the final sampling hand excavation (volume sampled c. 1 m diameter x 40 cm deep) was carried out beneath eight selected clumps in both destructive study areas. Clumps were chosen to include a range of stem numbers, stem circumferences and Eucalyptus spp. in their composition. Prior to excavation the circumferences of individual stems on each clump were recorded (as detailed for stand analysis) and the stems were cut off from the lignotuber as close as practicable to ground level. The exposed root system was carefully brushed free of soil particles and the fresh weight recorded. A subsample was retained for determination of moisture content and nutrient analysis.

Hand excavation was also employed to obtain the weight of root butts of understorey shrub species on the MAD/MAM plots. In this case the same plants were excavated as were being sampled for aerial biomass. Shrubs covering

the range of species and size classes encountered were sampled. Shrubs chosen for harvest were considered 'average' for each species and particular size class. Fresh weights of the root material were recorded in the field and subsamples kept for analysis of moisture and nutrient content.

(v) Standing crop - Dimensional analysis was used to determine aerial biomass of mallee eucalypts (MAD/MAM) and mulga (MUM). The principle invoked is outlined in 2.2.1.

Regressions for determining standing crop were based on a maximum of 30 stems for MAD, 29 for MAM and 65 for MUM. The independent variable chosen for all regressions was stem circumference (measured 30 cm above ground for MUM and 30 cm from the stem base for MAD/MAM). Stems selected for harvest came from the destructive study area of the plots and were considered to be 'average' with respect to vigour, foliage cover etc. for their particular size class. The stems were chosen in a stratified fashion to include the range of circumferences previously found from the stand table. After the circumference was measured, the stem was cut off as close to ground level as practicable. To minimise loss of stem parts the fallen stem and associated leaves, fruits and branches were placed on canvas tarpaulins for subsequent sorting.

MAD/MAM: Prior to sorting, the height of each stem from base to tallest branch tip, and crown diameter, as

represented by horizontal projection of the leaves on the canvas, was recorded. Fresh weights of the following fractions were obtained - live stem (>4, >1-4, <1 cm diameter), dead stem, dead bark, leaves and capsules. A portion of each fraction was retained for determination of dry weight and nutrient analysis. The live stem portions were divided into wood and bark components before dry weight and nutrient content were determined.

Subsamples of the leaves collected from each stem were also retained for area determination. This was done with an integrating photometer (Lambda Instruments Corporation) on randomly chosen leaves (minimum of 30 per sample). These leaves were subsequently re-dried to constant weight and a weight/area ratio was derived.

MUM: Sample data from which biomass regressions were determined for mulga were kindly provided by a colleague, Mr A.J. Pressland, Charleville Pastoral Laboratory, Charleville (see Pressland 1975).

Because the trees felled by Pressland came from the external buffer zone of the MUM plot, and embraced the range of circumference sizes encountered in the MUM stand table, it was appropriate to utilise this data. However as he chose only well formed trees his data will tend to overestimate biomass on the MUM plot. To minimise this effect the data for the phyllode regression were augmented by a further 33 data sets utilised in the study of Burrows and Beale (1970). These latter samples were also obtained from the buffer zone of the MUM plot.

Furthermore, Pressland (1975) did not determine wood/bark ratios and his estimates did not employ the bias corrections indicated in Appendix 2. Both these deficiencies have been rectified in the present study.

An estimate of wood/bark ratio in mature mulga was obtained by felling an additional four trees in the destructive study area. Sixteen sub-samples of stem were taken from these trees for derivation of wood/bark ratio and nutrient content. Samples of the phyllodes from these trees were also retained for nutrient analysis.

The above ground biomass of shrubs on the MAD/MAM plots was derived from those previously selected for root biomass determination (see previous section). Fresh weight of the tops was obtained in the field and sub-samples kept for dry weight and chemical analysis.

Estimation of the aerial biomass of Eucalyptus populnea on the MUM plot involved a 'mean' tree approach. Mention of the advisability of using this method has been made earlier (section 2.2.1). However the lack of time and labour necessitated its use here.

Mean stem circumference (measured 30 cm above ground) of E. populnea trees on the MUM plot was 69 $\pm$ 11.2 cm (Table 2.4). A tree of circumference 68.3 cm was found in the destructive study area. The growth habit of this tree was visually assessed as being average for the stand and it was therefore selected for harvest.

Once felled the height and canopy diameter of the E. populnea tree was measured. It was then sorted into

live stem, dead stem, leaf and capsule fractions. The fresh weight of this material was recorded in the field and sub samples retained for dry weight and nutrient analysis.

(vi) Nutrient analysis - All plant fractions determined in the biomass study were analysed for nitrogen and phosphorus content. Methods of sample preparation and analysis are presented in Appendix 1.

(vii) Calculation of stand biomass and nutrient content - Each of the stand analysis transects (see (ii)) was treated as a quadrat for purposes of biomass estimation. By use of the appropriate regression (derived as in (v)) and the prediction program (LOGPRED - see Appendix 2) it was possible to estimate the weight of the dominant overstorey shrubs. Understorey shrub weights were estimated from the 'mean' weight for the particular size class and the number of shrubs present within that size class. Similar procedures were adopted for determining the weight of root butts (including lignotubers) within each transect.

Summation of weights of individual shrubs for each transect gave a transect total. These totals were summed for all transects on each plot and a transect mean determined. From this an estimate of shrub biomass per hectare was made. The weight of fine roots, surface litter and herbaceous understorey per hectare was obtained from the random core and quadrat samples previously detailed. 'Dead' soil organic matter was found by subtracting the core estimates of live roots from the organic C total derived from the soil analyses.

N and P concentrations varied considerably between and within various fractions of the biomass. Hence it was necessary to treat each compartment (e.g. bark, leaves, capsules, etc.) individually for determination of nutrient content, before single tree or shrub totals and subsequent transect totals could be derived. Similarly mean values of fine root, surface litter and herbaceous understorey fractions were multiplied by appropriate N and P concentrations.

Symbolically the steps involved in determining biomass and nutrient content may be represented by the following equations, using the notation methods of Sokal and Rohlf (1969) -

(a) Transect samples - weight of individual stems

(Eucalyptus spp. for MAD/MAM , Acacia aneura for MUM)

$$Sci = Wci + Bci + DWci + DBci + Lci + Fci \qquad (1)$$

where

Sci = weight (g) of individual stem i with circumference c
Wci = " " " wood in " " " " "
Bci = " " " bark " " " " " "
DWci = " " " dead wood in" " " " "
DBci = " " " dead bark in" " " " "
Lci = " " " leaf in " " " " "
Fci = " " " fruit in " " " " "

Wood and bark weights can be further fractionated for the MAD/MAM sites.

$$Wci = W\,(<1) + W\,(1\text{-}4) + W\,(>4) \qquad (2)$$

$$Bci = B\,(<1) + B\,(1\text{-}4) + B\,(>4) \qquad (3)$$

where B and W are bark and wood weights (g) for the respective size classes (<1, 1-4, >4 cm branch diameter) for stem i

with circumference c. The total aerial weight (kg) for stems per transect, S, is therefore

$$S = \sum^{n} Sci/1000 \qquad (4)$$

where n = number of individual stems in the transect. The total aerial weight (kg) of understorey shrubs per transect, H

$$H = \sum^{Sjk} Hsjk \qquad (5)$$

where Hsjk = 'mean' weight (kg) of each species for each size class

s = number of shrub species present

j = number of size classes

k = number of individuals in the size class

Weight of root butts (kg) per transect, R (MAD/MAM)

$$R = \sum^{p} Rp + \sum^{sjk} Rsjk \qquad (6)$$

where Rp = mean weight (kg) of root butts per Eucalyptus spp. clump

p = number of Eucalyptus spp. clumps per transect

Rsjk = mean root weight (kg) of each understorey species for each size class

s, j, k as for equation (5)

Weight of root butts (kg) per transect, R (MUM)

$$R = \sum^{n} Rci + \sum^{k} Rk \qquad (7)$$

where Rci = weight of individual root butt (kg) for stem i with circumference c

Rk = mean weight of Eucalyptus populnea root butt (kg)

n, k as for equations (4) and (5) respectively

(b) Random samples - weight of litter, L (kg/ha)

$$L = \sum^{f} Lf \qquad (8)$$

where Lf = weight of each litter fraction (kg/ha)

f = number of fractions

Weight of fine roots, W (kg/ha)

$$W = \sum^{v} Wv \qquad (9)$$

where Wv = weight of fine roots in each depth interval (kg/ha)

v = number of depth intervals (5 for all sites)

Hence, total above ground biomass, A (kg/ha)

$$A = L + G + 200 * \sum^{t} (S + H)/t \qquad (10)$$

where G = weight of herbaceous material (kg/ha)

t = number of 25 m x 2 m (1/200 ha) transects

S, H, L as before

Total below ground biomass, B (kg/ha)

$$B = 200 * \sum^{t} R/t + W \qquad (11)$$

To convert these values to nitrogen and phosphorus content per hectare it is necessary to reduce equations (10) and (11) to their simplest form and multiply every component by the nutrient concentration appropriate to it.

2.3 Results

Soil analyses for each site are presented in Table 2.1. Profile diagrams (Figures 2.1, 2.2) show the distribution of total nitrogen and phosphorus on an area basis. The MAD data are stratified between and under canopies (Table 2.1). To convert these figures to an area basis a 50% canopy cover at the time of sampling was assumed. This seems reasonable in this growing community where the canopy cover some 20 months beforehand was 42.5% (Table 2.2).

Figure 2.3 shows changes in stem circumference class distribution between 1973 and 1975 for MAD, MAM and MUM respectively. Similarly Tables 2.2, 2.3 and 2.4 illustrate changes in density and clump size of the woody perennials over the same time scale. These tables and Figure 2.3 provide the data on stand structure needed for biomass determination.

The weight of surface litter and its corresponding N and P content is shown in Tables 2.5 and 2.6 for MAD/MAM and MUM respectively. The tables give estimates for the litter present at the commencement and conclusion of the study period. However, due to the unusually large phyllode and pod fall during the first year of the MUM study an additional estimate of these components was obtained in July 1974 for that site.

Separate estimates of the biomass in the herbaceous layer (apart from Triodia irritans on MAD) were only determined for the MUM site in July 1974 and May 1975 (Table 2.7). At all other sites and sampling times this

Table 2.1 Soil properties at each detailed study site

Site	Depth (cm)	Bulk density (g/cc)	pH (1:5 H_2O)	Total P. (ppm)	Avail.P. (ppm) (acid)	Total N. (%)	Exchangeable cations (m.e. per 100 g)				Org.C. (%)	C/N ratio
							Ca	Mg	Na	K		
MUM	0-2.5	1.8	5.5	263	8	0.05	1.7	0.3	0.05	0.36	1.3	26
	2.5-5.0	1.6	5.4	230	4	0.06	0.9	0.1	0.05	0.29	1.0	17
	5.0-10	1.6	5.5	228	3	0.04	1.6	0.2	0.05	0.31	0.9	22
	10-25	1.6	5.0	223	3	0.04	1.6	0.2	0.05	0.29	0.8	20
	25-50	1.6	4.9	171	2	0.04	0.9	0.1	0.05	0.19	0.5	12
	50-100	1.6	5.2	168	2	0.02	1.2	0.2	0.05	0.16	0.4	20
MAM	0-2.5	1.49	6.4	388	6	0.18	10.3	4.4	0.23	1.24	2.9	16
	2.5-5.0	1.20	6.7	317	4	0.11	9.9	4.0	0.20	1.19	1.6	15
	5.0-10	1.20	6.7	300	3	0.07	9.8	4.0	0.20	1.14	0.8	11
	10-25	1.25	6.9	298	2	0.03	9.8	4.0	0.27	0.97	0.9	30
	25-50	1.50	7.0	238	2	0.04	7.8	4.5	0.36	0.85	0.7	17
	50-100	1.60	8.5	271	2	0.03	14.2	8.7	1.37	1.24	0.3	10

Table 2.1 (Continued)

Site	Depth (cm)	Bulk density (g/cc)	pH (1:5 H_2O	Total P. (ppm)	Avail.P. (ppm) (acid)	Total N. (%)	Exchangeable cations (m.e. per 100 g)				Org.C. (%)	C/N ratio
							Ca	Mg	Na	K		
MAD*	0-2.5	1.46	6.8	287	9	0.07	7.3	3.1	0.21	0.80	1.4	20
(inter-	2.5-5.0	1.44	6.7	263	6	0.06	7.0	3.1	0.12	0.80	0.9	15
canopy)	5.0-10	1.44	6.8	245	3	0.05	6.7	2.9	0.16	0.76	0.9	18
	10-25	1.52	6.9	225	2	0.03	5.9	2.8	0.31	0.71	0.7	23
	25-50	1.60	7.2	212	2	0.02	5.4	4.0	1.26	0.79	0.5	25
	50-100	1.60	8.0	197	2	0.02	14.3	9.3	4.15	1.57	0.4	20
MAD*	0-2.5	1.25	6.9	353	5	0.14	12.5	4.2	0.45	1.37	2.1	15
(under-	2.5-5.0	1.44	6.9	319	4	0.12	11.4	3.7	0.22	1.30	1.5	12
canopy)	5.0-10	1.44	7.2	260	2	0.07	10.5	3.3	0.24	1.15	1.0	14
	10-25	1.52	8.0	249	2	0.04	14.8	3.8	0.34	1.17	0.7	17
	25-50	1.60	8.6	218	2	0.04	15.8	4.5	1.06	1.08	0.5	12
	50-100	1.60	8.8	210	2	0.03	17.5	9.0	3.53	1.83	0.4	13

* Bulk density figures for MAD are means for 1 beneath and 1 between canopy profile for all sample depths except the surface 0-2.5 cm.

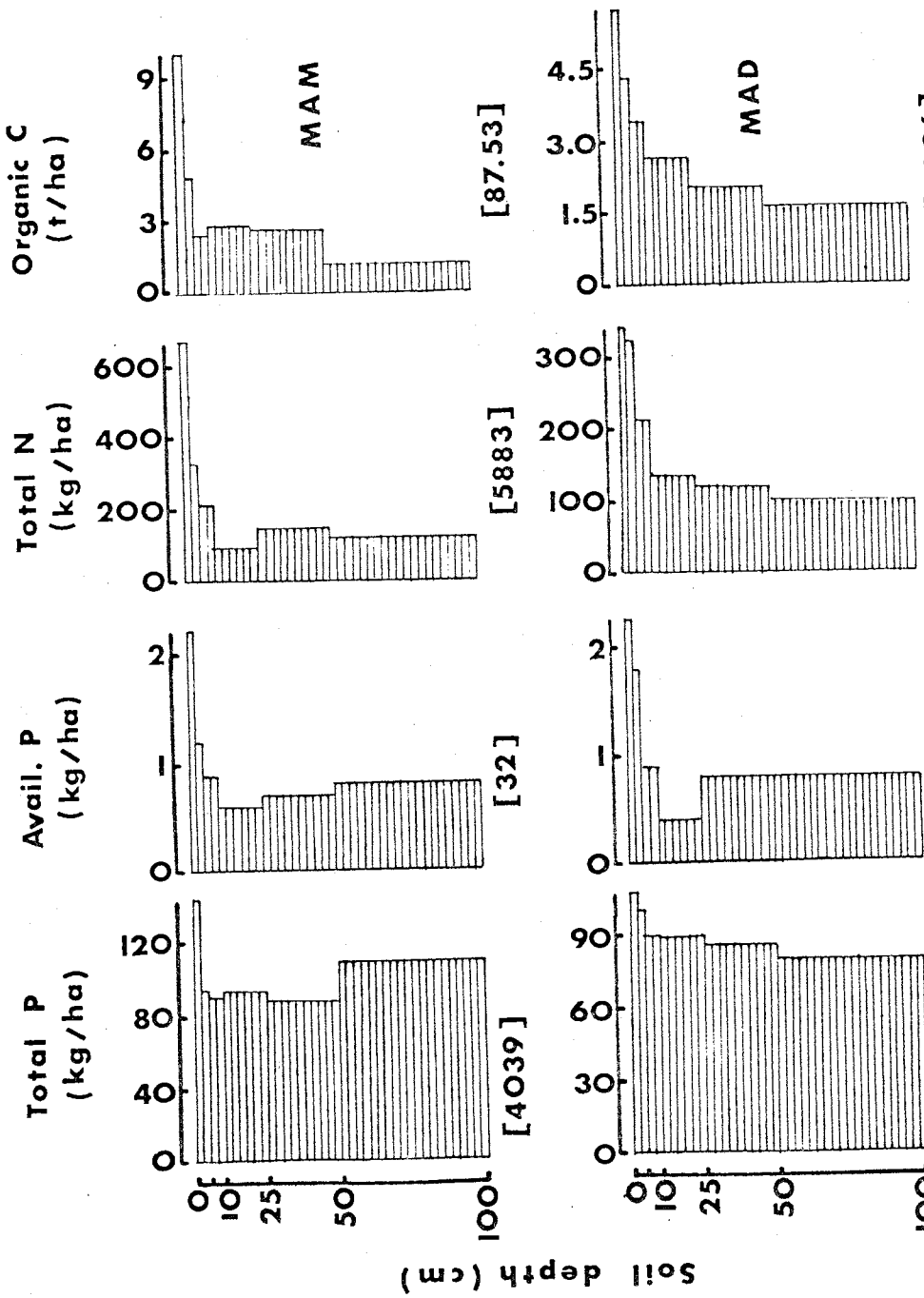


Figure 2.1 Soil profile diagrams for MAD and MAM sites. Note differences in horizontal scales. Samples were obtained from 0-2.5, 5-10, 10-25, 25-50 and 50-100 cm depth intervals but are averaged to 2.5 cm increments for comparative purposes. Organic carbon does not include biomass of lignotubers or root butts. Bracketed figures below each diagram are total amounts in profile to 1 m depth.

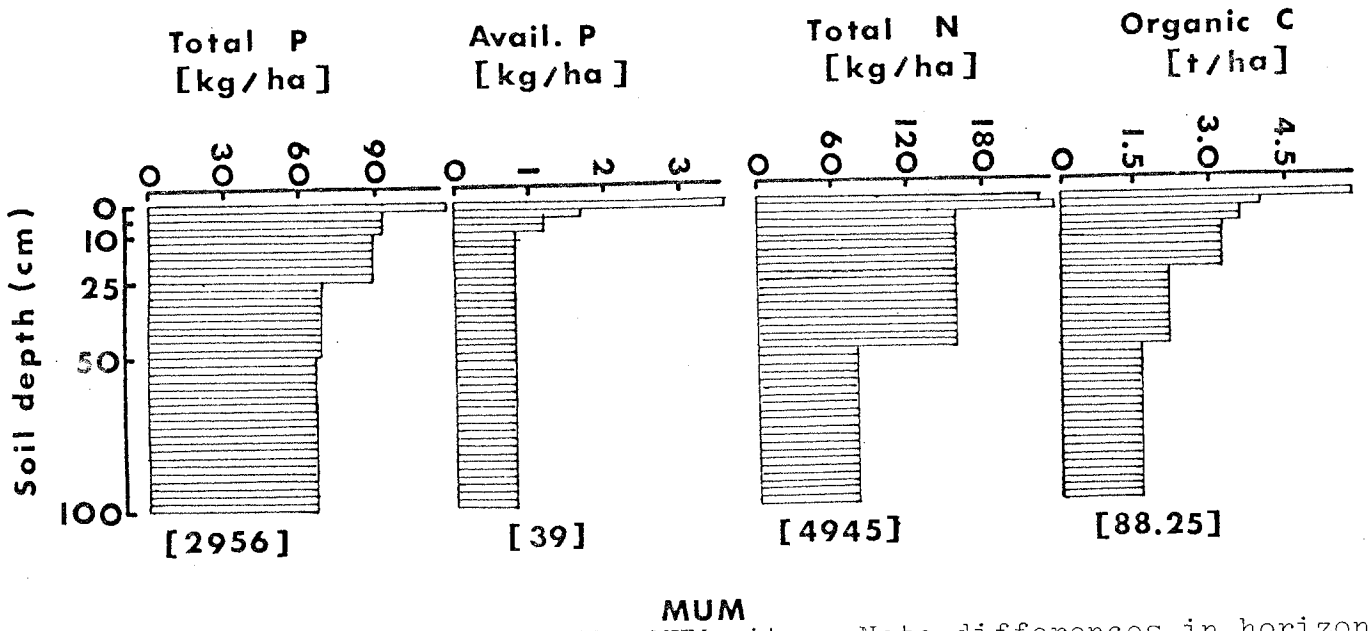


Figure 2.2 Soil profile diagrams for the MUM site. Note differences in horizontal scales. Samples were obtained from 0-2.5, 5-10, 10-25, 25-50 and 50-100 cm depth intervals but are averaged to 2.5 cm increments for comparative purposes. Organic carbon does not include biomass of lignotubers or root butts. Bracketed figures below each diagram are total amounts in profile to 1 m depth.

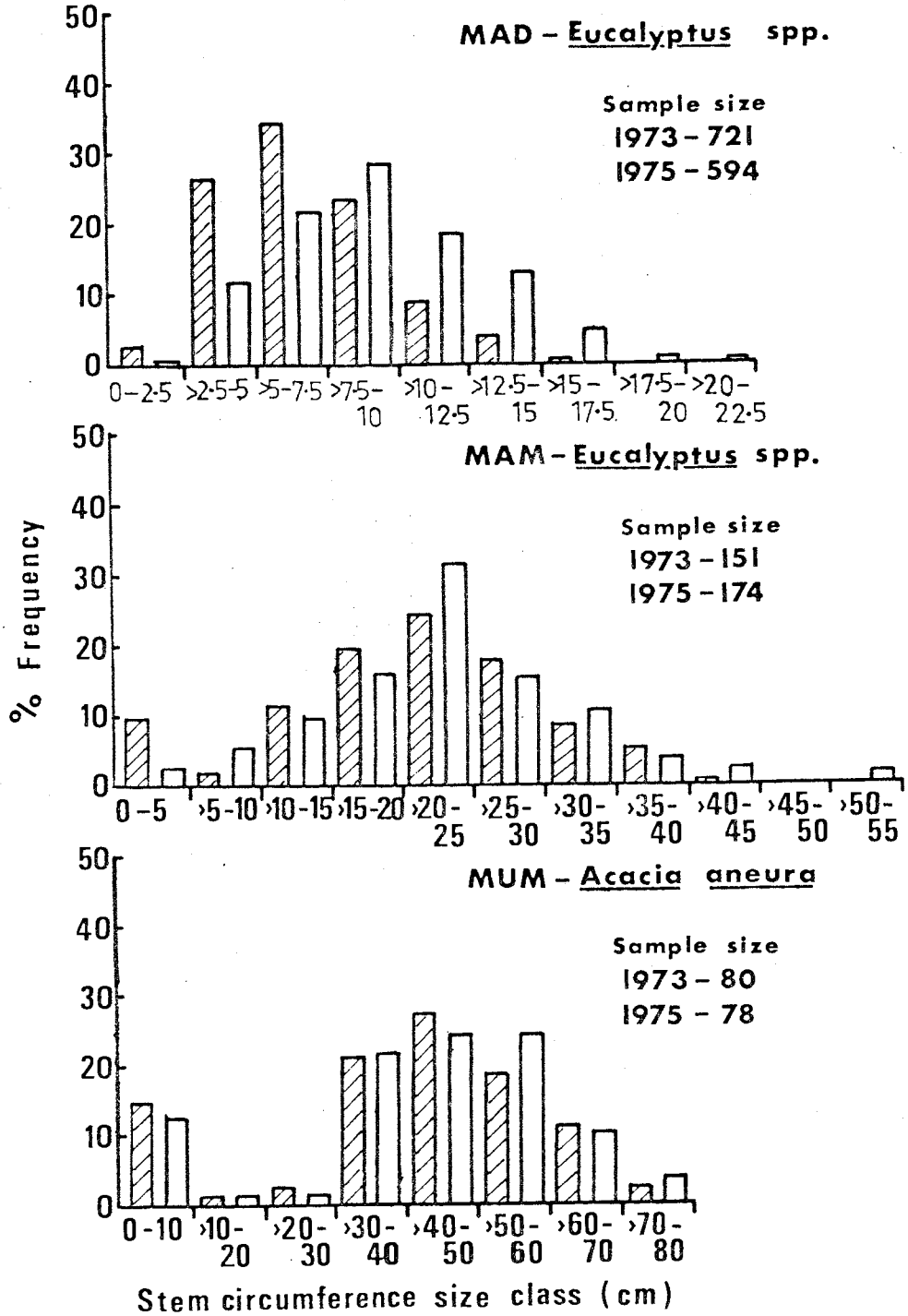


Figure 2.3 Frequency distributions for major components of MAD, MAM & MUM communities in 1973 (hatched) and 1975 (blank).

Table 2.2 Structural characteristics of the MAD site 1973/1975
(Means ± S.E. for 15 transects 25 m x 2 m)

a. *Eucalyptus* spp.

	E.socialis	*E.gracilis*	*E.foecunda*	Total
Density (Stem/ha):				
May 1973	6580 ± 660	3040 ± 700*		9620 ± 935
May 1975	5140 ± 820	2320 ± 520	420 ± 180	7880 ± 1182
May 1975 (dead stems)	920 ± 200	620 ± 180	80 ± 40	1620 ± 320
Stem circumference (live stems - cm):				
May 1973	7.0 ± 0.1	6.7 ± 0.2*		6.9 ± 0.1
May 1975	8.9 ± 0.2	9.9 ± 0.2	9.2 ± 0.5	9.2 ± 0.2
Basal area (live stems - m^2/ha):				
May 1973	2.6 ± 0.2	1.1 ± 0.2*		3.6 ± 0.3
May 1975	3.2 ± 0.5	1.8 ± 0.4	0.3 ± 0.1	5.3 ± 0.7
Stems/clump:				
May 1973	7.0 ± 0.4	6.3 ± 0.6*		6.8 ± 0.5
May 1975	6.1 ± 0.4	4.9 ± 0.5	4.3 ± 0.4	5.6 ± 0.3

Table 2.2 (Continued)

	E. socialis	E. gracilis	E. foecunda	Total
Canopy cover (%):				
May 1973 (ex mean clump diameter)	n.r.	n.r.	n.r.	50.0 ± 2.3
October 1973 (ex 31 line transects)	n.r.	n.r.	n.r.	42.5 ± 2.6

b. Other species

	Beyeria opaca	Olearia pimeleoides	Other shrubs	Triodia irritans
Density (plants/ha):				
May 1973	1320 ± 320	1000 ± 560	160 ± 60	180 ± 60
May 1975	1460 ± 320	1540 ± 460	620 ± 140	220 ± 60
Size class distribution (1975 data in parenthesis - %):				
0.5 m	40.4 (17.3)	78.7 (56.0)	75.0 (35.3)	23.1 (37.5)
0.5-1 m	53.5 (71.8)	18.7 (43.1)	16.7 (58.8)	53.8 (37.5)
1-1.5 m	6.1 (10.9)	2.6 (0.9)	8.3 (5.9)	23.1 (25.0)

* The E. gracilis and E. foecunda data were combined in this regrowth plot in 1973 because of the absence of identifying capsules on the plants.

n.r. = not recorded

Table 2.3 Structural characteristics of the MAM site 1973/1975
(means ± S.E. from 15 (1973) and 21 (1975) transects 25 m x 2 m)

a. *Eucalyptus* spp.*

	Density (stems/ha)	Stems/clump	Stem circumference (cm)	Basal area
May 1973	2054 ± 232	2.9 ± 0.3	21.0 ± 0.7	7.2 ± 0.8
May 1975	1660 ± 260	2.5 ± 0.2	22.6 ± 0.7	6.7 ± 1.0
May 1975 (dead stems)	250 ± 120	-	-	-

b. Other species

	Melaleuca lanceolata	*Olearia pimeleoides*	*Bertya cunninghamii*	Other shrubs
Density	(stems/ha)	(	plants/ha	)
May 1973	2940 ± 500	346 ± 132	300 ± 136	420 ± 100
May 1975	2480 ± 300	340 ± 120	180 ± 40	280 ± 60
Size class distribution - % (1973 data):				
0.5 m	0	80.8	26.1	62.5
0.5 - 1 m	0.4	11.5	39.1	31.3
1 - 1.5 m	19.8	7.7	4.3	6.2
1.5 - 2 m	0	0	0	0
2-3 m	65.8	0	30.4	0
3-4 m	14.0	0	0	0

* *E. socialis* and *E. dumosa* occurred on the plot but the data were combined for purposes of structural analyses.

Table 2.4 Structural characteristics of the MUM site 1973/1975
(means ± S.E. from 21 transects 25 m x 2 m)

	Density		Stem circumference	Basal area
	stems/ha	seedlings*/ha	(cm)	(m^2/ha)
a. *Acacia aneura*				
July 1973	762 ± 140	2704 ± 614	40.8 ± 2.2	10.1 ± 1.8
June 1975	742 ± 86	1562**	42.4 ± 2.1	10.4 ± 1.2
b. *Eucalyptus populnea*				
July 1973	104 ± 32	0	67.0 ± 10.9	4.0 ± 1.2
June 1975	104 ± 31	0	69.0 ± 11.2	4.1 ± 1.3

* An *Acacia aneura* seedling was defined as a plant which still had pinnate leaves present

**One seedling recorded in 40 quadrats 0.4 m x 0.4 m during litter sampling

Table 2.5 Surface litter and its N and P content on the MAD and MAM sites. Each parameter is presented ± S.E. (kg/ha)

Site	Date	Quadrat size	Number of Quadrats	Parameter	Total Litter	Stem (>1 cm diameter)	Twig (<1 cm diameter)	Leaf	Bark	Capsule	Other Species	Residue
MAD	April	1 m x	48	Dry weight	5982	1688	982	2290	210	12	32	770
	1973	0.5 m			±988	±430	±156	±456	±60	±4	±30	±160
	"	"	"	N	29.4	1.5	3.9	16.5	0.6	0.1	0.2	6.6
					±4.8	±0.4	±0.6	±3.3	±0.2	±0.02	±0.16	±1.4
	"	"	"	P	1.4	0.1	0.2	0.7	*	*	*	0.3
					±0.2	±0.02	±0.03	±0.1				±0.06
	April	0.25 m x	39	Dry weight	7562	1368	1584	2275	208	59	77	1976
	1975	0.25 m			±1238	±713	±272	±395	±64	±16	±42	±488
	"	"	"	N	43.5	1.2	7.7	17.9	0.6	0.2	0.3	15.5
					±7.1	±0.6	±1.3	±3.1	±0.2	±0.05	±0.2	±3.8
	"	"	"	P	2.6	0.1	0.5	1.1	*	*	*	1.0
					±0.4	±0.05	±0.1	±0.2				±0.2

Table 2.5 (Continued)

Site	Date	Quadrat size	Number of Quadrats	Parameter	Total Litter	Stem (>1 cm diameter)	Twig (<1 cm diameter)	Leaf	Bark	Capsule	Other Species	Residue
MAM	April	0.5 m x	30	Dry weight	9634	2348	1613	1946	1532	140	13	2042
	1973	0.5 m			±757	±404	±122	±136	±304	±24	±8	±191
		"	"	N	45.6	2.1	7.2	17.7	4.1	1.0	0.1	13.3
					±3.6	±0.4	±0.5	±1.2	±0.8	±0.2	±0.06	±1.2
		"	"	P	1.7	0.1	0.3	0.7	0.2	0.1	*	0.4
					±0.1	±0.02	±0.02	±0.05	0.04	0.01		±0.04
	April	0.25 m x	37	Dry weight	11372	1600	3283	2573	1024	320	12	2560
	1975	0.25 m			±1038	±832	±304	±155	±160	±48	±8	±256
	"	"	"	N	54.3	1.4	11.4	16.3	3.1	2.1	0.1	19.8
					±5.0	±0.7	±1.1	±1.0	±0.5	±0.3	±0.06	±2.0
	"	"	"	P	3.1	0.1	0.6	1.0	0.1	0.2	*	1.1
					±0.3	0.04	±0.06	±0.06	±0.02	±0.02		±0.1

*Specific value insignificant (< 50g/ha) but is included in total litter figure

Table 2.6 Surface litter and its N and P content on the MUM site.
Each parameter is presented ± S.E. (kg/ha)

Date	Quadrat	Number of Quadrats	Parameter	Total Litter	Stem (>1 cm diameter)	Twig (<1 cm diameter)	Phyllodes	Bark	Pod	Other species	Residue
July	0.4 m x	40	Dry weight	6949	3455	1061	831	352	138	267	880
1973	0.4 m			±1012	±911	±81	±72	±92	±14	±90	±56
			N	69.4	8.2	16.1	17.5	4.6	2.1	4.8	16.2
				±10.1	±2.2	±1.2	±1.5	±1.2	±0.2	±1.6	±1.1
			P	1.7	0.2	0.4	0.5	0.2	0.1	0.1	0.5
				±0.2	±0.04	±0.03	±0.04	±0.04	±0.01	±0.03	±0.03
July	0.4 m x	55	Dry weight	n.d.	n.d.	n.d.	2235	n.d.	195	330	n.d.
1974	0.4 m						±106		±13	±44	
			N	n.d.	n.d.	n.d.	46.6	n.d.	2.7	5.1	n.d.
							±2.2		±0.2	±0.7	
			P	n.d.	n.d.	n.d.	1.3	n.d.	0.1	0.1	n.d.
							±0.06		±0.01	±0.02	

Table 2.6 (Continued)

Date	Quadrat	Number of Quadrats	Parameter	Total Litter	Stem (>1 cm diameter)	Twig (<1 cm diameter)	Phyllodes	Bark	Pod	Other species	Residue
May	0.4 m x	40	Dry weight	13892	8428	1594	2032	94	19	731	994
1975	0.4 m			±5050	±5244	±244	±169	±25	±4	±200	±100
			N	109.5	20.1	21.4	38.4	0.6	0.3	11.3	17.4
				±39.8	±12.5	±3.3	±3.2	±0.2	±0.06	±3.1	±1.7
			P	3.2	0.4	0.4	1.5	*	*	0.3	0.6
				± 1.2	±0.2	±0.06	±0.1			±0.08	±0.06

n.d. = not determined

* Specific value insignificant (< 50 g/ha) but is included in the total litter figure.

component did not exceed 50 kg/ha and was therefore included in 'other species' of Tables 2.5 and 2.6.

Table 2.7 Above ground biomass of the herbaceous layer and its N and P content on the MUM site. Data presented ± S.E. (kg/ha)

	July 1974	May 1975
Dry weight	131.1 ± 29.3	131.2 ± 43.7
N	1.36 ± 0.30	1.36 ± 0.45
P	0.06 ± 0.01	0.06 ± 0.02

Weight of fine roots (< 5 mm diameter) and their N and P content at five depth intervals for the final harvest is given in Table 2.8. While the major portion of the roots extracted by the cores were less than 5 mm in diameter, this figure is an aid to definition only. On all sites some larger roots were encountered and they also contributed to the average values listed.

Tables 2.9 and 2.10 detail top and root biomass for understorey shrubs and Triodia on the MAD and MAM sites. These tables provide the data for 'mean shrub' estimates of biomass and nutrient content of the various species within each size class. Missing values in the table indicate that a specimen could not readily be found within the destructive study area or that the class was not represented in the stand table. Where a class is represented in the stand table but not in Table 2.9 the mean for all species is used in subsequent community estimates.

Table 2.8 Dry weight, N and P content of fine roots (< 5 mm diameter - see text) on MAD, MAM and MUM sites at final sampling (All values kg/ha ± S.E.)

Site	Parameter	Profile Depth				
		0-20 cm	20-40cm	40-60cm	60-80cm	80-100cm
MAD	Dry weight	1785 ± 416	1147 ± 241	1801 ± 1375	215 ± 59	208 ± 29
	N content	10.03 ± 2.34	4.21 ± 0.88	5.20 ± 3.97	1.03 ± 0.28	1.05 ± 0.14
	P content	0.54 ± 0.13	0.25 ± 0.05	0.37 ± 0.28	0.07 ± 0.02	0.06 ± 0.01
MAD	Dry weight	9159 ± 3105	3098 ± 1583	448 ± 81	324 ± 101	1165 ± 453
	N content	54.36 ± 18.43	16.61 ± 8.49	2.16 ± 0.39	1.86 ± 0.58	4.05 ± 2.53
	P content	3.06 ± 1.03	0.86 ± 0.44	0.12 ± 0.02	0.10 ± 0.03	0.24 ± 0.15
MUM	Dry weight	3485 ± 713	5217 ± 1736	885 ± 148	863 ± 182	1017 ± 222
	N content	47.41 ± 9.70	77.11 ± 25.66	14.12 ± 2.36	12.43 ± 2.62	13.52 ± 2.95
	P content	1.37 ± 0.28	1.49 ± 0.49	0.24 ± 0.04	0.26 ± 0.05	0.39 ± 0.08

Table 2.9 Dry weight, N and P content (g) of some 'mean shrubs' in various size classes on MAD/MAM sites.
Values are means for 3 plants in each size class unless otherwise stated.
The N and P values are multiplicands for community nutrient estimates and are therefore given to 2 and 3 significant figures respectively.

SPECIES	Height or Diameter Class											
	< 0.5 m						0.5 - 1.0 m					
	Rw	Tw	Rn	Tn	Rp	Tp	Rw	Tw	Rn	Tn	Rp	Tp
Acacia brachybotrya	7.0	86.0	0.04	0.89	0.002	0.03	28.0	373.0	0.15	3.81	0.008	0.115
Acacia rigens	8.0	85.0	0.04	0.91	0.002	0.02	15.0	93.0	0.08	1.00	0.004	0.029
Bertya cunninghamii	9.0*	51.0*	0.05	0.68	0.002	0.03	19.0*	164.0*	0.10	2.10	0.005	0.108
Beyeria opaca	3.0	11.0	0.03	0.13	0.001	0.006	11.0	102.0	0.09	1.24	0.003	0.052
Dodonaea cuneata	3.0	12.0	0.02	0.10	0.001	0.007	7.0	51.0	0.04	0.45	0.002	0.030
Micromyrtus ciliata	11.0*	59.0*	0.05	0.52	0.004	0.047	36.0	315.0	0.17	2.78	0.015	0.254
Olearia pimeleoides	13.0	43.0	0.06	0.36	0.003	0.021	20.0	71.0	0.09	0.58	0.005	0.035
Pimelea dichotoma	5.0	15.0	0.03	0.13	0.001	0.011	19.0	123.0	0.08	1.03	0.006	0.089
Prostanthere aspalathoides	6.0	20.0	0.03	0.22	0.002	0.013	10.0	75.0	0.05	0.83	0.003	0.051
Santalum acuminatum	n.d.	n.d.	-	-	-	-	n.d.	n.d.	-	-	-	-
Triodia irritans	n.d.	610.0	-	0.50	-	0.079	n.d.	1030	-	0.82	-	0.134

Table 2.9 (Continued)

	Height or Diameter Class											
	1.0 - 1.5 m						1.5 - 2.0 m					
SPECIES	Rw	Tw	Rn	Tn	Rp	Tp	Rw	Tw	Rn	Tn	Rp	Tp
Acacia brachybotrya	113.0	900.0	0.59	9.19	0.031	0.278	n.d.	n.d.	-	-	-	-
Acacia rigens	26.0	366.0	0.13	3.55	0.007	0.113	n.d.	n.d.	-	-	-	-
Bertya cunninghamii	77.0	774.0	0.40	9.93	0.021	0.510	219.0	2194.0	1.14	28.15	0.060	1.446
Beyeria opaca	115.0	603.0	0.99	6.39	0.028	0.278	n.d.	n.d.	-	-	-	-
Dodonaea cuneata	n.d.	n.d.	-	-	-	-	n.d.	n.d.	-	-	-	-
Micromyrtus ciliata	n.d.	n.d.	-	-	-	-	n.d.	n.d.	-	-	-	-
Olearia pimeleoides	50.0	248.0	0.22	1.83	0.013	0.109	n.d.	n.d.	-	-	-	-
Pimelea dichotoma	n.d.	n.d.	-	-	-	-	n.d.	n.d.	-	-	-	-
Prostanthere aspalathoides	n.d.	n.d.	-	-	-	-	n.d.	n.d.	-	-	-	-
Santalum acuminatum	90	785.0	0.47	8.63	0.025	0.526	210.0	1914.0	1.09	21.05	0.057	1.280
Triodia irritans	n.d.	3770.0	-	3.02	-	0.500	n.d.	-	-	-	-	-

* Data for one plant only
Rw = Dry weight of root butt, Rn = N content of root butt, Rp = P content of root butt
Tw = Dry weight above ground, Tn = N content above ground, Tp = P content above ground
n.d. = not determined

Table 2.10 Dry weight, N and P content of *Melaleuca lanceolata* on the MAM plot. Weights ± S.E. are means from 6 clumps with a total of 34 stems.

	1973	1975
Stems/ha**	2940 ± 500	2480 ± 300
Root butt/stem (g)	159 ± 59*	159 ± 59
Root butt (kg/ha)	467 ± 173	394 ± 146
Root N (kg/ha)	1.73 ± 0.65	1.46 ± 0.54
Root P (kg/ha)	0.07 ± 0.03	0.06 ± 0.02
Top weight/stem (g)	330 ± 188*	330 ± 188
Top weight (kg/ha)	970 ± 553	818 ± 466
Top N (kg/ha)	7.11 ± 4.05	6.00 ± 3.42
Top P (kg/ha)	0.34 ± 0.19	0.29 ± 0.16

* Mean root and top weights per stem and N and P concentrations assumed constant between years. Figures are actual for 1975

** Data from Table 2.3.

Lignotuber weights for MAD/MAM (Table 2.11) show considerable variation which is somewhat independent of stem numbers or their mean circumference. This could have resulted from some differences in the volume of soil sampled and the size of the tap root (which was cut off) at the base of the lignotuber. Two or three large horizontal roots extending outside the area sampled were also cut off from most of these lignotubers.

Table 2.11 Lignotuber weights beneath Eucalyptus clumps on MAD/MAM sites at final harvest. Volume of soil sampled c. 1 m^2 x 0.4 m deep.

Site	Species	# of stems	Mean stem circumference (cm)	Dry weight of lignotuber (kg)
MAM	E. dumosa	5	26.5	32.8
	" "	5	17.5	33.9
	" "	3	15.9	4.0
	" "	1	9.3	2.2
	E. socialis	4	17.5	33.5
	" "	3	19.4	23.1
	" "	1	10.1	0.4
	" "	1	21.1	2.2
MAD	E. socialis	6	8.2	6.1
	" "	7	7.1	2.2
	" "	12	13.0	23.1
	" "	2	9.6	2.5
	E. gracilis	5	9.2	7.4
	" "	10	10.5	9.4
	" "	9	8.1	6.8
	E. foecunda	13	2.8	15.4

The poor relationship existing between stem size and lignotuber weight ($r = 0.21$ for MAD, $r = 0.59$ for MAM) suggests that a 'mean tree' approach to community estimates of root biomass would be most appropriate for these sites . However for the single stemmed mulga trees a more positive relationship exists between stem size and weight of the

root butt (Table 2.12). The existence of this relationship permits estimation of the weight of root butt for each stem on the plot.

Table 2.12 Relation between stem circumference 30 cm above ground level and root butt weight in *Acacia aneura*

Stem circumference (cm) x	Dry weight of root butt (kg)
17.3	1.50
23.0	2.10
30.4	5.60
30.4	5.90
44.3	10.50
46.8	8.00
54.5	17.60
61.5	24.15

$\log_e y = 1.22 + 2.12 \log_e x \quad (R^2 = 0.95, P < 0.001)$

The weight of lignotuber attached to the 'mean' *Eucalyptus populnea* tree on the MUM site is estimated on the basis of 25% of the above ground stem biomass. Time was not available to actually excavate a *E.populnea* root system. The data concerning *E.populnea* must therefore be taken as an indicative guide only.

It is possible to estimate root biomass on each plot by combining plant density data (Tables 2.2-2.4) with the various root parameters present in Tables 2.9-2.12. These community values, with concomitant N and P contents, are shown in Table 2.13.

Table 2.13 Root biomass and N and P content in the roots at final harvest

	Dry Weight (kg/ha)	N (kg/ha)	P (kg/ha)
(i) MAM			
Eucalyptus spp. (Lignotubers)	13860	23.08	2.22
Melaleuca lanceolata (root butts)	467	1.73	0.07
Minor shrubs (root butts)	12	0.07	0.01
Fine roots	14194	79.04	4.38
Total	28533	103.92	6.67
(ii) MAD			
Eucalyptus spp. (Lignotubers)	15288	25.45	2.46
Understorey shrubs (root butts)	57	0.39	0.01
Fine roots	5156	21.52	1.29
Total	20501	47.36	3.76
(iii) MUM			
Acacia aneura (root butts)	8897	51.60	1.87
Eucalyptus populnea* (Lignotuber)	5078	7.76	0.56
Fine roots	11467	164.59	3.75
Total	25442	223.95	6.18

* Estimates based on 25% top weight and green wood analyses

Regressions required for the determination of standing biomass and nutrient content on the three sites are presented in Tables 2.14, 2.15, and 2.16. Each table shows the number of data sets (stems) on which the particular regression is based and includes the range of stem circumferences sampled. The tables also indicate the standard error of estimate for each regression. For logarithmic regression the antilog of this latter figure is the estimate of relative error (see Whittaker and Woodwell 1968, 1971). The variance of these regressions is the square of the standard error of estimate.

Space does not permit graphical presentation of all these regressions and appropriate confidence limits. However, to illustrate the type of data distribution found on each site the leaf regressions and the observed data and predicted values are plotted in Figures 2.4, 2.5, and 2.6. It should be noted that representative confidence limits are asymmetric about the predicted values.

The standing biomass and nutrient content of mallee eucalypts on the MAD and MAM sites and of mulga on the MUM site are given in Tables 2.17, 2.18 and 2.19 respectively. The data are the summarized output of the programme LOGPRED. Inputs for this programme are the regression data of Tables 2.14, 2.15 and 2.16 and stem circumferences for each particular quadrat sampling period. Altogether the circumferences of 1321 stems were measured in the MAD quadrats at the commencement and conclusion of the study.

Table 2.14 Regressions for mallee eucalypts on the MAD site. All regressions are logarithmic, $\log_e y = A + B \log_e x$. Stem circumference (x) is measured 30 cm from the base of the stem.

Regression on ln stem circumference, x (cm)

Dependent variable	# of data sets	Stem circum.range (cm)	Regression parameter A	B	R^2	Significance	Std.error of est.
Ln leaf weight,y (g)	30	1.8-23.2	0.8392	2.1884	0.939	***	0.382
Ln leaf N, y (g)	30	1.8-23.2	-3.8118	2.2008	0.927	***	0.425
Ln leaf P, y (g)	30	1.8-23.2	-6.6059	2.2471	0.921	***	0.452
Ln wood & bark,y (g)	30	1.8-23.2	1.4366	2.5661	0.993	***	0.151
Ln wood weight,y (g)	30	1.8-23.2	1.1721	2.5887	0.993	***	0.147
Ln wood N, y (g)	30	1.8-23.2	-4.7181	2.4735	0.991	***	0.165
Ln wood P, y (g)	30	1.8-23.2	-6.6438	2.2746	0.977	***	0.238
Ln bark weight,y (g)	30	1.8-23.2	-4.3421	2.4707	0.987	***	0.198
Ln bark N, y (g)	30	1.8-23.2	-5.8320	2.4201	0.986	***	0.200
Ln bark P, y (g)	30	1.8-23.2	-8.1786	2.2898	0.986	***	0.187
Ln capsule weight,y (g)	26	5.1-23.2	-6.5518	4.4611	0.652	***	1.469
Ln capsule N, y (g)	26	5.1-23.2	-10.2356	4.0197	0.727	***	1.110
Ln capsule P, y (g)	26	5.1-23.2	-11.3301	3.6649	0.771	***	0.902

Table 2.14 (Continued)

Regression on ln stem circumference, x (cm)

Dependent variable	# of data sets	Stem circum. range (cm)	Regression parameter A	B	R^2	Significance	Std.error of est.
Ln seed weight,y (g)	24	6.7-23.2	-7.6961	3.3173	0.695	***	0.860
Ln seed number, y	24	6.7-23.2	-0.4517	3.3171	0.696	***	0.859
Ln dead wood weight,y(g)	30	1.8-23.2	-0.1168	1.9767	0.642	***	1.017
Ln dead wood N,y (g)	30	1.8-23.2	-7.2339	2.5568	0.6335	***	1.338
Ln dead wood P,y (g)	24	5.2-23.2	-8.1941	1.6665	0.339	**	0.994
Ln dead bark weight,y (g)	24	5.2-23.2	-3.5051	2.8426	0.527	***	1.150
Ln dead bark N,y (g)	24	5.2-23.2	-9.7601	2.8142	0.536	***	1.118
Ln dead bark P,y (g)	24	5.2-23.2	-17.8203	4.9818	0.654	***	1.548
Ln total weight,y (g)	30	1.8-23.2	1.9943	2.478	0.991	***	0.165
Ln leaf area, y (m^2)	30	1.8-23.2	-4.9439	2.1510	0.939	***	0.376
Ln leaf number, y	30	1.8-23.2	2.7722	2.0356	0.930	***	0.383
Ln stem length, y (m)	30	1.8-23.2	-0.3543	0.6984	0.938	***	0.123
Ln canopy diameter,y (m)	30	1.8-23.2	-1.5665	0.6836	0.907	***	0.151

R^2 = coefficient of determination *** $P < 0.001$ ** $P < 0.01$

Table 2.15 Regressions for mallee eucalyptus on the MAM site. Regressions are in the forms: (linear) $y = a + b\,x$, and (logarithmic) $\log_e y = A + B \log_e x$. Stem circumference (x) is measured 30 cm from the base of the stem.

Regression on ln stem circumference, x (cm)

Dependent variable	# of data sets	Stem circum. range (cm)	Regression parameter A	B	R^2	Significance	Std.error of est.
Ln leaf weight,y (g)	29	2.5-55.2	2.6963	1.4296	0.877	***	0.349
Ln leaf N, y (g)	29	2.5-55.2	-1.9947	1.4524	0.888	***	0.336
Ln leaf P, y (g)	29	2.5-55.2	-4.7885	1.4013	0.871	***	0.351
Ln wood & bark,y (g)	29	2.5-55.2	2.0216	2.4321	0.978	***	0.240
Ln wood weight,y (g)	29	2.5-55.2	1.5967	2.5145	0.978	***	0.247
Ln wood N, y (g)	29	2.5-55.2	-3.8369	2.0860	0.975	***	0.217
Ln wood P, y (g)	29	2.5-55.2	-6.4481	1.9356	0.968	***	0.229
Ln bark weight, y (g)	29	2.5-55.2	1.2250	2.0719	0.963	***	0.265
Ln bark N, y (g)	29	2.5-55.2	-4.6218	2.0148	0.956	***	0.280
Ln bark P, y (g)	29	2.5-55.2	-7.6134	2.0636	0.961	***	0.270
Ln capsule weight,y (g)	25	2.5-55.2	-3.0683	2.8318	0.589	***	0.934
Ln capsule N, y (g)	25	12.4-55.2	-7.9475	2.8356	0.588	***	0.937
Ln capsule P, y (g)	25	12.4-55.2	-10.2069	2.8737	0.578	***	0.968

Table 2.15 (Continued)

Regression on ln stem circumference, x (cm)

Dependent variable	# of data sets	Stem circum. range (cm)	Regression parameter A	B	R^2	Significance	Std.error of est.
Ln seed weight, y (g)	25	12.4-55.2	-7.3759	2.8515	0.587	***	0.944
Ln seed number, y	25	12.4-55.2	-0.1319	2.8513	0.587	***	0.944
Ln dead bark weight,y(g)	29	2.5-55.2	-0.8396	1.9092	0.832	***	0.559
Ln dead bark N, y (g)	29	2.5-55.2	-6.8757	1.9107	0.834	***	0.555
Ln dead bark P, y (g)	29	2.5-55.2	-10.0764	1.8905	0.827	***	0.563
Ln total weight,y (kg)	29	2.5-55.2	-4.1671	2.2620	0.979	***	0.213
Ln leaf area, y (m^2)	26	2.5-55.2	-2.8642	1.3360	0.896	***	0.303
Ln leaf number, y	26	2.5-55.2	3.5786	1.6011	0.871	***	0.411
Ln stem length, y (m)	29	2.5-55.2	0.0353	0.6017	0.901	***	0.130
Ln canopy diameter,y (m)	29	2.5-55.2	-1.6509	0.7932	0.904	***	0.168
Linear regression on stem circumference, x (cm)							
Dead wood weight, y (g)	28	5.6-55.2	-695.61	85.755	0.634	***	736.7
Dead wood N, y (g)	28	5.6-55.2	-2.4978	0.30701	0.638	***	2.62
Dead wood P, y (g)	28	5.6-55.2	-0.1151	0.0142	0.630	***	0.123

R^2 = coefficient of determination *** = $P < 0.001$

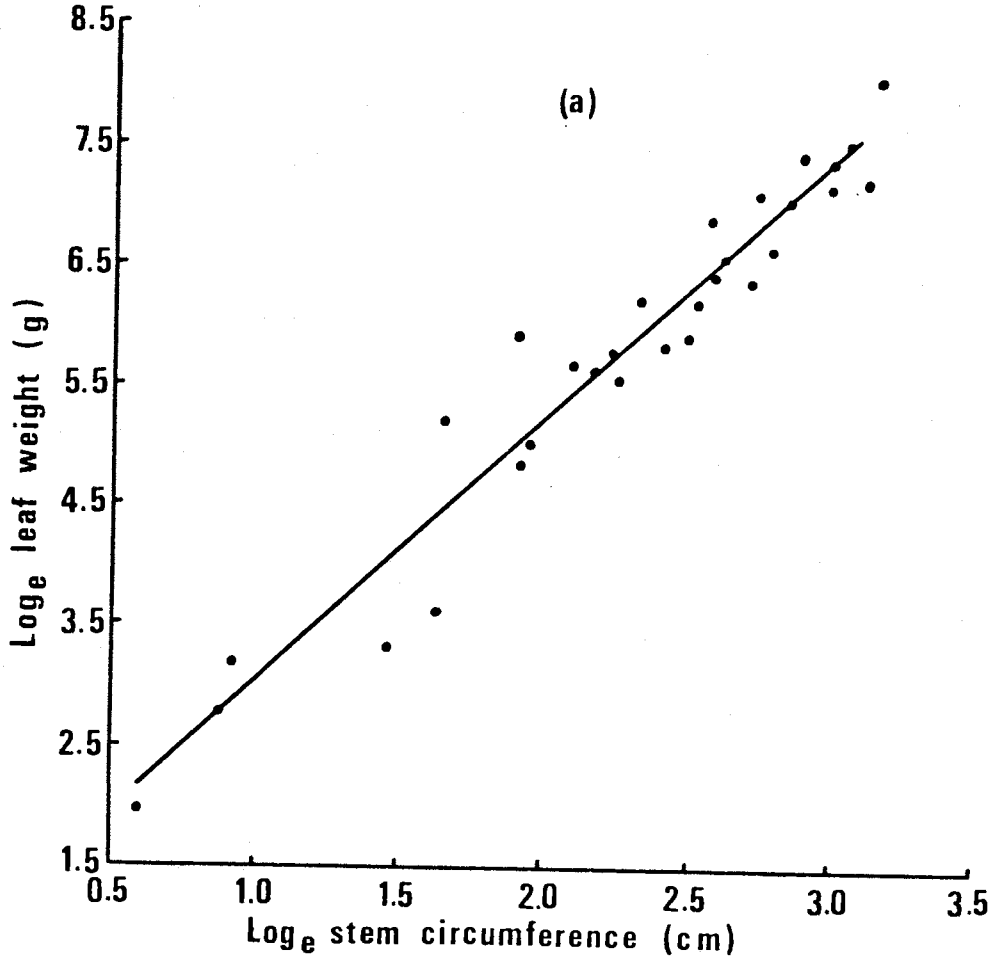
Table 2.16 Regressions for mulga on the MUM site. All regressions are logarithmic, $\log_e y = A + B \log_e x$. Stem circumference (x) is measured 30 cm above ground level.

Regression on ln stem circumference, x (cm)

Dependent variable	# of data sets	Stem circum. range (cm)	Regression parameter A	B	R^2	Significance	Std.error of est.
Ln phyllode weight,y(g)	65	1.8-86.0	1.9746	1.8568	0.958	***	0.381
Ln phyllode N, y (g)	65	1.8-86.0	-1.8959	1.8574	0.958	***	0.382
Ln phyllode P, y (g)	65	1.8-86.0	-4.9652	1.8711	0.957	***	0.391
Ln stem weight, y (kg)	32	1.8-86.0	-5.2193	2.3908	0.984	***	0.347
Ln wood weight, y (kg)	32	1.8-86.0	-5.4189	2.3901	0.984	***	0.347
Ln wood N, y (g)	32	1.8-86.0	-4.2607	2.3906	0.984	***	0.348
Ln wood P, y (g)	32	1.8-86.0	-8.3309	2.4094	0.985	***	0.346
Ln bark weight, y (kg)	32	1.8-86.0	-6.9297	2.3946	0.984	***	0.346
Ln bark N, y (g)	32	1.8-86.0	-4.2266	2.3975	0.985	***	0.344
Ln bark P, y (g)	32	1.8-86.0	-8.2557	2.3988	0.985	***	0.337
Ln height, y (m)	32	1.8-86.0	-0.8258	0.7301	0.940	***	0.212
Ln root butt weight,y(g)	8	17.3-61.5	1.2231	2.1214	0.953	***	0.225

R^2 = coefficient of determination *** = $P < 0.001$

Figure 2.4 Regression of stem circumference against leaf yield for the MAD plot (a) Log_e transformed values and regression line (b) Arithmetic plot of original and predicted values; indicative 95% confidence bars are shown for some predicted points.


(a)
8.5
7.5
6.5
5.5
4.5
3.5
2.5
1.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Log$_e$ leaf weight (g)
Log$_e$ stem circumference (cm)

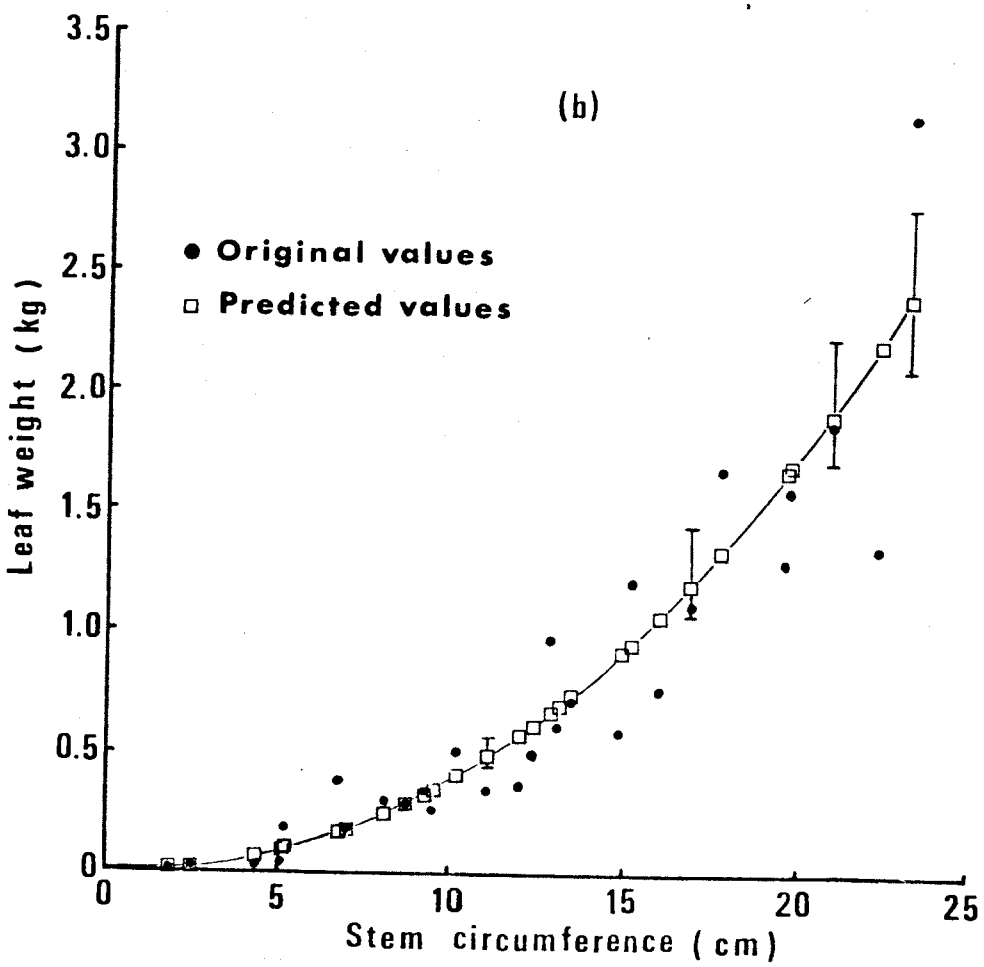

(b)
● Original values
□ Predicted values
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
0
5
10
15
20
25
Leaf weight (kg)
Stem circumference (cm)

Figure 2.5 Regression of stem circumference against leaf yield for the MAM plot (a) Log_e transformed values and regression line (b) Arithmetic plot of original and predicted values; indicative 95% confidence bars are shown for some predicted points.

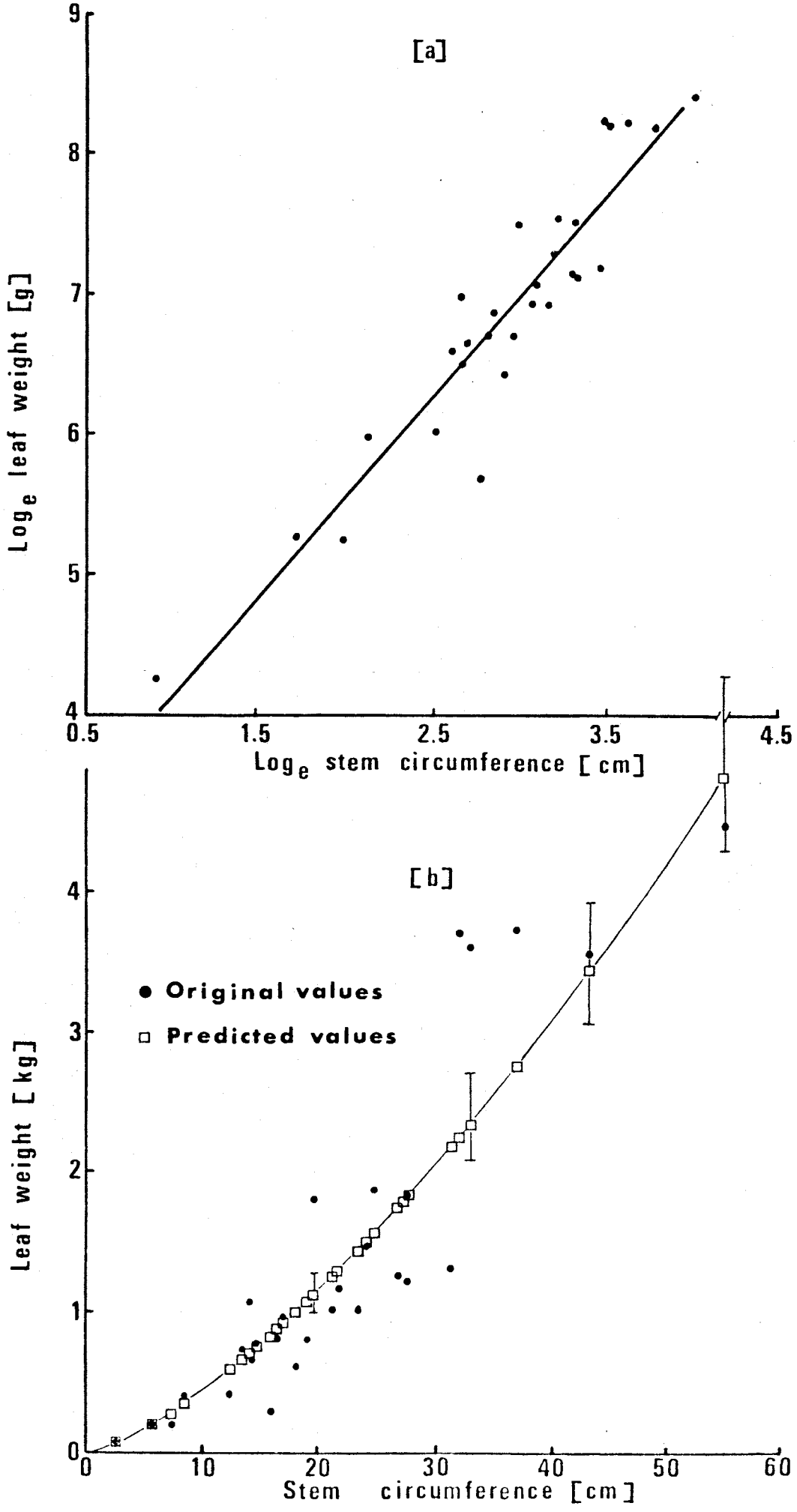
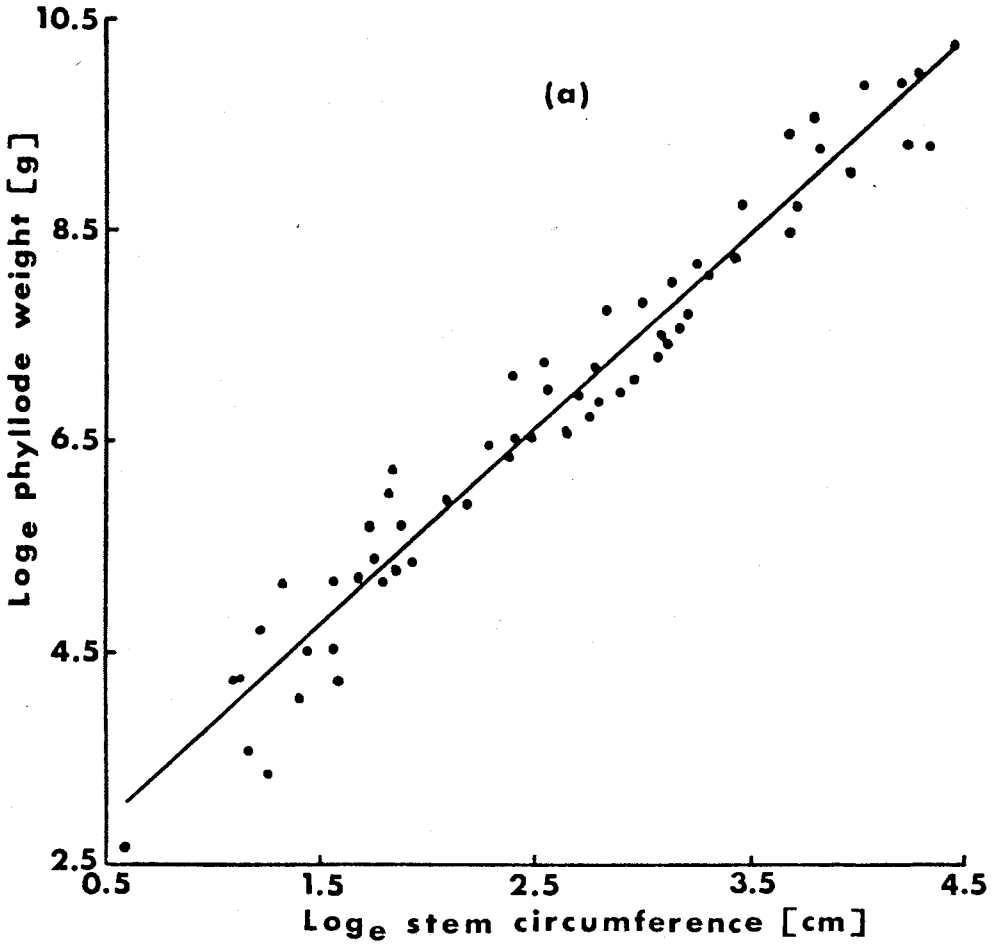

[a]
Log$_e$ leaf weight [g]
9
8
7
6
5
4
0.5
1.5
2.5
3.5
4.5
Log$_e$ stem circumference [cm]
[b]
Leaf weight [kg]
● Original values
□ Predicted values
4
3
2
1
0
0
10
20
30
40
50
60
Stem circumference [cm]

Figure 2.6 Regression of stem circumference against phyllode yield for the MUM plot (a) Log_e transformed values and regression line (b) Arithmetic plot of original and predicted values; indicative 95% confidence bars are shown for some predicted points.


(a)
10.5
8.5
6.5
4.5
2.5
Loge phyllode weight [g]
0.5
1.5
2.5
3.5
4.5
Loge stem circumference [cm]

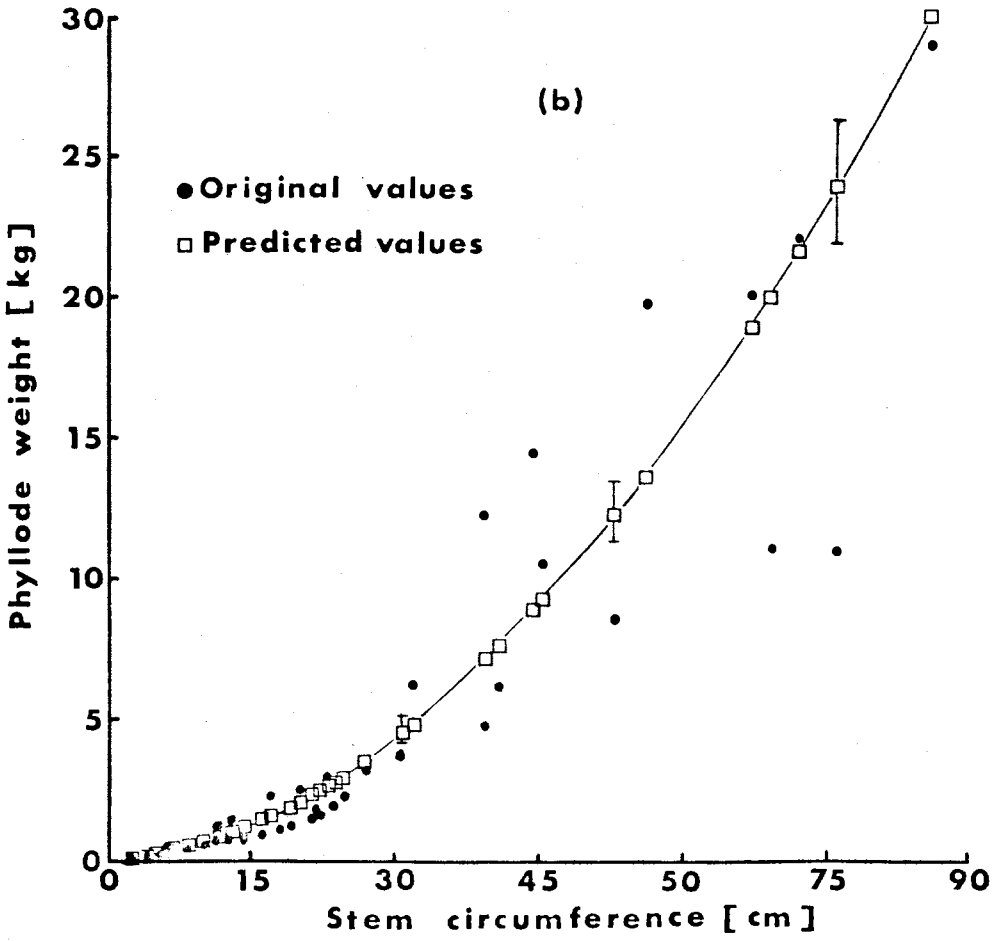

(b)
●Original values
□Predicted values
30
25
20
15
10
5
0
Phyllode weight [kg]
0
15
30
45
50
75
90
Stem circumference [cm]

Table 2.17 Standing biomass and nutrient content of mallee eucalypts on the MAD site. Data are means ± S.E. from 15 quadrats 25m x 2m.

Component	Sample Date	
	May 1973 (kg/ha)	April 1975 (kg/ha)
Leaf	1999 ± 204	3014 ± 191 **
Leaf N	19.9 ± 2.0	30.2 ± 1.9 **
Leaf P	1.36 ± 0.14	2.09 ± 0.13 **
Wood	6314 ± 690	10582 ± 739 ***
Wood N	13.6 ± 1.4	22.1 ± 1.5 ***
Wood P	1.30 ± 0.13	2.00 ± 0.13 ***
Bark	1513 ± 162	2459 ± 167 **
Bark N	4.0 ± 0.4	6.4 ± 0.4 **
Bark P	0.29 ± 0.03	0.44 ± 0.03 **
Dead Wood	738 ± 73	1052 ± 64 **
Dead Wood N	3.0 ± 0.3	5.0 ± 0.3 ***
Dead Wood P	0.10 ± 0.01	0.15 ± 0.01 **
Dead Bark	178 ± 22	333 ± 26 ***
Dead Bark N	0.31 ± 0.04	0.58 ± 0.04 ***
Dead Bark P	0.03 ± 0.004	0.08 ± 0.01 ***
Capsule	543 ± 85	1467 ± 159 ***
Capsule N	3.2 ± 0.5	7.7 ± 0.8 ***
Capsule P	0.38 ± 0.05	0.85 ± 0.08 ***
Total weight (by direct regression)	11290 ± 1209	18381 ± 1249 **
Total weight (by summation)	11286	18907
Total N (by summation)	44.0	71.9
Total P (by summation)	3.46	5.62

*** 1975 weight exceeds 1973 weight with $P < 0.001$

** 1975 weight exceeds 1973 weight with $P < 0.01$

Table 2.18 Standing biomass and nutrient content of mallee eucalypts on the MAM site. Data are means ± S.E. from 15 (1973) and 21 (1975) quadrats 25 m x 2 m.

Component	Sample Date	
	May 1973 (kg/ha)	April 1975 (kg/ha)
Leaf	2618 ± 296	2384 ± 353
Leaf N	25.7 ± 2.9	23.5 ± 3.5
Leaf P	1.34 ± 0.15	1.22 ± 0.18
Wood	29260 ± 3796	28750 ± 4566
Wood N	30.9 ± 3.8	29.4 ± 4.5
Wood P	1.39 ± 0.17	1.31 ± 0.20
Bark	4719 ± 577	4476 ± 683
Bark N	11.3 ± 1.4	10.7 ± 1.6
Bark P	0.7 ± 0.1	0.6 ± 0.1
Dead Wood	2324 ± 268	2107 ± 311
Dead Wood N	8.3 ± 0.9	7.5 ± 1.1
Dead Wood P	0.39 ± 0.04	0.35 ± 0.05
Dead Bark	394 ± 47	369 ± 56
Dead Bark N	0.9 ± 0.1	0.9 ± 0.1
Dead Bark P	0.04 ± 0.004	0.03 ± 0.005
Capsule	1144 ± 154	1147 ± 187
Capsule N	8.8 ± 1.2	8.8 ± 1.4
Capsule P	1.07 ± 0.15	1.08 ± 0.18
Total weight (by direct regression)	39639 ± 4972	38143 ± 5912
Total weight (by summation)	40459	39233
Total N (by summation)	86.1	80.9
Total P (by summation)	4.9	4.6

Table 2.19 Standing biomass and nutrient content of mulga on the MUM site. Data are means ± S.E. of 21 quadrats 25 m x 2 m.

Component	Sample Date	
	July 1973 (kg/ha)	May 1975 (kg/ha)
Phyllode[1]	7871 ± 1068	8043 ± 1091
Phyllode N[1]	164.4 ± 22.3	168.0 ± 22.8
Phyllode P[1]	8.15 ± 1.11	8.33 ± 1.13
Phyllode[2]	6821 ± 928	6972 ± 948
Phyllode N[2]	142.5 ± 19.4	145.7 ± 19.8
Phyllode P[2]	6.91 ± 0.94	7.06 ± 0.96
Stem (Wood & Bark)	41695 ± 5943	42837 ± 6098
Wood	34049 ± 4853	34982 ± 4980
Wood N	108.7 ± 15.5	111.7 ± 15.9
Wood P	1.97 ± 0.28	2.03 ± 0.29
Bark	7649 ± 1090	7858 ± 1119
Bark N	115.2 ± 16.4	118.4 ± 16.8
Bark P	2.11 ± 0.30	2.17 ± 0.31
Total (Phyllode[2] and Stem)	48516	49809
Total N	366.4	375.8
Total P	10.99	11.26

1 Regression from data of Pressland (1975) - 32 sample trees for regression.

2 Regression from combined data of Pressland (1975) and Burrows and Beale(1970)- 65 sample trees for regression.

Similarly, measurements were obtained on 365 stems from MAM quadrats and 158 from MUM. Thus the data summarized in Tables 2.17, 2.18, 2.19 and 2.20 are a condensation of some 46,000 individual predictions from the regressions and measured stem circumferences.

As a consequence of the destructive sampling necessary to establish stand regressions, it was convenient to obtain additional dimensional measurements for the MAD and MAM sites. These data (Table 2.20) provide further structural characteristics to those given in Tables 2.2 and 2.3. Another indirect result of this destructive sampling is the table of moisture contents for fractions of the mallee eucalypts (Table 2.21).

The standing biomass and N and P content of minor perennial species on each site are presented in Table 2.22. The Eucalyptus populnea sampled as a 'mean tree' on the MUM site had a circumference, measured 30 cm above ground level, of 68.3 cm, was 11.2 m tall and had a canopy diameter of 5.6 m.

The concentration of nitrogen and phosphorus in various fractions of the vegetation on each of the study sites may be calculated from those preceding tables in which biomass and nutrient contents are presented. In a study of this size (involving some 3500 separate N and P analyses) it is impractical to detail each individual tissue analysis. Furthermore it can often be misleading to compare tissue analyses without reference to the physiological status and weight of tissue involved.

Table 2.20 Some canopy characteristics for mallee eucalypts on the MAD and MAM sites.

Site	Canopy Parameter	Sample Date	
		May 1973	April 1975
MAD	Leaf area*(m^2/ha)	5663 ± 573	8454 ± 530
	L.A.I. (m^2/m^2)	0.57	0.85
	Mean stem length (m)	2.67 ± 0.24	3.27 ± 0.19
	Mean canopy diameter/stem(m)	0.77 ± 0.07	0.94 ± 0.06
MAM	Leaf number	$1.12 \times 10^7 \pm 1.30 \times 10^6$	$1.03 \times 10^7 \pm 1.54 \times 10^6$
	Leaf area*(m^2/ha)	7352 ± 824	6662 ± 985
	L.A.I. (m^2/m^2)	0.73	0.67
	Mean stem length (m)	6.42 ± 0.23	6.91 ± 0.20
	Mean canopy diameter/stem(m)	2.18 ± 0.09	2.38 ± 0.09

* Measured for one side only

Table 2.21 Moisture content of mallee eucalypts at final harvest. Moisture expressed as % oven dry basis ± S.E. for 20-30 samples. Lignotuber data is the mean of 2 samples only.

Fraction	MAD % moisture	MAM % moisture
Leaf	41.7 ± 1.3	42.0 ± 0.8
Stem >4 cm diameter	33.5 ± 0.7	29.6 ± 0.6
Stem 1-4 cm diameter	35.2 ± 0.6	32.7 ± 0.5
Stem <1 cm diameter	36.8 ± 1.0	36.3 ± 0.9
Capsule	43.8 ± 0.9	46.7 ± 0.8
Dead Wood	10.6 ± 0.3	10.6 ± 0.3
Dead Bark	8.8 ± 0.5	10.4 ± 0.7
Lignotuber	39.5	37.7

Table 2.22 Standing biomass and N and P content of minor perennial species on MAD, MAM and MUM sites. Data presented ± S.E. for MAD/MAM. Data based on 'mean tree' for MUM species. Sample size of 15 transects for MAD and for 1973 figures of MAM; 21 transects for remainder. All transects 25 m x 2 m.

Site	Component	Sample Date	
		May 1973 (kg/ha)	April 1975 (kg/ha)
MAD	Understorey shrubs	179.6 ± 61.8	315.0 ± 53.6
	Understorey shrubs N	1.6 ± 0.5	3.2 ± 0.5
	Understorey P	0.08 ± 0.03	0.15 ± 0.03
	Triodia irritans	271.0 ± 90.3	331.0 ± 145.4
	Triodia irritans N	0.2 ± 0.1	0.2 ± 0.1
	Triodia irritans P	0.03 ± 0.01	0.04 ± 0.02
MAM	Understorey shrubs*	151.6 ± 59.2	113.8 ± 44.4
	Understorey shrubs N	1.8 ± 0.7	1.3 ± 0.5
	Understorey shrubs P	0.10 ± 0.04	0.08 ± 0.03

		Sample Date	
		July 1973 (kg/ha)	May 1975 (kg/ha)
MUM	*Eucalyptus populnea*	19785+	20312
	Eucalyptus populnea N	44.1+	45.3
	Eucalyptus populnea P	2.94+	3.02

* Does not include *Melaleuca lanceolata* (see Table 2.10)

\+ Estimated from 1975 data and assuming same percentage change in biomass as occurred in associated *Acacia aneura*.

Table 2.23 Weighted mean concentrations of nitrogen and phosphorus in vegetative material on MAD and MAM sites at final sampling.

Fraction	Site			
	MAD		MAM	
	% Nitrogen	% Phosphorus	% Nitrogen	% Phosphorus
Above ground:				
Eucalyptus spp. - leaf	0.99	0.068	0.99	0.052
wood (> 4)*	0.13	0.007	0.07	0.002
wood (1-4)	0.17	0.013	0.10	0.004
wood (< 1)	0.20	0.025	0.23	0.016
bark (> 4)	0.22	0.013	0.24	0.014
bark (1-4)	0.25	0.017	0.25	0.014
bark (< 1)	0.31	0.021	0.27	0.015
capsule	0.76	0.098	0.77	0.092
dead wood	0.35	0.016	0.36	0.017
dead bark	0.18	0.005	0.24	0.009
Melaleuca lanceolata	-	-	0.73	0.035
Other shrubs	1.02	0.048	1.14	0.070
Triodia irritans	0.06	0.013	-	-
Total standing	0.39	0.030	0.22	0.012

Table 2.23 (Continued)

Fraction	MAD % Nitrogen	MAD % Phosphorus	MAM % Nitrogen	MAM % Phosphorus
Litter - leaf	0.79	0.047	0.63	0.041
wood	0.30	0.020	0.26	0.014
bark	0.29	0.013	0.31	0.012
capsule	0.42	0.034	0.67	0.052
minor shrubs	0.46	0.031	0.74	0.043
fragmented material	0.78	0.049	0.78	0.042
Total litter	0.55	0.028	0.48	0.027
Below ground:				
Eucalyptus spp. lignotubers	0.17	0.016	0.16	0.016
Understorey shrub root butts	0.70	0.017	0.38	0.015
Fine roots	0.42	0.025	0.56	0.031
Total root	0.23	0.018	0.36	0.023
Grand Total	0.34	0.024	0.31	0.018

* Wood and bark fractions are for >4, 1-4 and <1 cm diameter stems or branches respectively.

Table 2.24 Weighted mean concentrations of nitrogen and phosphorus in vegetative material on the MUM site at final sampling.

Fraction		Nitrogen (%)	Phosphorus (%)
Above ground:			
Acacia aneura -	phyllode	2.09	0.099
	bark	1.51	0.028
	wood	0.32	0.006
Eucalyptus populnea -	leaf	1.60	0.083
	wood	0.17	0.012
	dead wood	0.09	0.009
Grass and forbs		1.07	0.046
Total standing		0.60	0.020
Litter -	phyllode	1.89	0.072
	wood	0.41	0.008
	bark	0.64	0.015
	pod	1.51	0.051
	minor species	1.55	0.041
	fragmented material	1.75	0.060
Total litter		0.79	0.023
Below ground:			
Acacia aneura root butt		0.58	0.021
Fine roots		1.44	0.033
Total root*		0.88	0.024
Grand total*		0.69	0.022

* Includes an estimate for *E. populnea* lignotubers - see Table 2.27.

Nevertheless, on a community scale some comparisons of nutrient concentrations may be informative, so weighted mean data for MAD and MAM are presented in Table 2.23 and for MUM in Table 2.24.

Tables 2.25, 2.26 and 2.27 summarize community estimates of the distribution of organic matter, nitrogen and phosphorus within each ecosystem at the final sampling in 1975. As such these tables are a precis of the previous tables in this chapter. No estimates of sampling error are given in these summary tables as they have been presented earlier.

2.25 Organic matter, nitrogen and phosphorus distribution in a 15 year old mallee regrowth ecosystem (MAD site at final sampling).

Fraction	Organic matter (kg/ha)	Total N (kg/ha)	Total P (kg/ha)
(i) Above ground			
Eucalyptus spp.-Leaf	3014	30.2	2.09
Bark	2459	6.4	0.44
Wood	10582	22.1	2.00
Capsule	1467	7.7	0.85
Dead wood	1052	5.0	0.15
Dead bark	333	0.6	0.08
Understorey shrub	315	3.2	0.15
Triodia irritans	331	0.2	0.04
Total standing	19553	75.4	5.80
Litter - Leaf	2275	17.9	1.10
Wood	2952	8.9	0.60
Bark	208	0.6	0.05
Capsule	59	0.2	0.05
Understorey shrub	77	0.3	0.05
Residue	1976	13.3	0.40
Total litter	7547	41.2	2.10
Total above ground	27100	116.6	7.90
(ii) Below ground (1 m depth)			
Root - *Eucalyptus* spp. lignotubers	15288	25.4	2.46
Understorey shrub root butts	57	0.4	0.01
Fine roots	5156	21.5	1.29
Total root	20501	47.3	3.76
Soil*	79800	5074	3423 (32)**
Grand Total	127401	5238	3455

*Soil organic matter = organic C - weight fine roots
Soil N and P = soil N (or P) - weight of N (or P) in fine roots
Grand total is corrected as above. ** Bracketed quantity for soil P = 'available' P

Table 2.26 Organic matter, nitrogen and phosphorus distribution in a mature mallee ecosystem (MAM site at final sampling).

Fraction	Organic matter (kg/ha)	Total N (kg/ha)	Total P (kg/ha)
(i) Above ground			
Eucalyptus spp.-Leaf	2384	23.5	1.22
Bark	4475	10.7	0.63
Wood	28750	29.4	1.31
Capsule	1147	8.8	1.08
Dead wood	2107	7.5	0.35
Dead bark	369	0.9	0.03
Melaleuca lanceolata	818	6.0	0.29
Other shrubs	114	1.3	0.08
Total standing	40164	88.1	4.99
Litter - Leaf	2573	16.3	1.00
Wood	4883	12.8	0.70
Bark	1024	3.1	0.10
Capsule	320	2.1	0.20
Understorey shrub	12	0.1	0.01
Residue	2560	19.8	1.10
Total litter	11372	54.2	3.11
Total above ground	51536	142.3	8.10
(ii) Below ground (1 m depth)			
Root - *Eucalyptus* spp. lignotubers	13860	23.1	2.22
Understorey shrub root butts	479	1.8	0.07
Fine roots	14194	79.0	4.38
Total root	28533	103.9	6.67
Soil*	73336	5804	4035 (32)**
Grand Total	153405	6050	4050

* Soil organic matter = organic C - weight fine roots
Soil N and P = soil N (or P) - weight of N (or P) in fine roots
Grand total is corrected as above.
**Bracketed quantity for soil P = 'available' P.

Table 2.27 Organic matter, nitrogen and phosphorus distribution in a mature mulga ecosystem (MUM site at final sampling).

Fraction		Organic matter (kg/ha)	Total N (kg/ha)	Total P (kg/ha)
(i) Above ground				
Acacia aneura -	Phyllode	6972	145.7	7.06
	Bark	7858	118.4	2.17
	Wood	34982	111.7	2.03
Eucalyptus populnea -	Leaf	750	12.0	0.62
	Wood	18438	31.3	2.29
	Dead wood	1125	1.0	0.10
Grass and forbs		131	1.4	0.06
Total standing		70256	421.5	14.33
Litter -	Phyllode	2032	38.4	1.50
	Wood	10022	41.5	0.80
	Bark	94	0.6	0.05
	Pod	19	0.3	0.05
	Other species	731	11.3	0.30
	Residue	994	17.4	0.60
Total litter		13892	109.5	3.20
Total above ground		84148	531.0	17.53
(ii) Below ground (1 m depth)				
Root - *Acacia aneura* root butt		8897	51.6	1.87
Eucalyptus populnea lignotuber*		5078	7.8	0.56
Fine roots		11467	164.6	3.75
Total root		25442	224.0	6.18
Soil**		76780	4780	2950 (38.8)+
Grand Total		186370	5535	2974

* Estimate based on 25% top weight and green wood analysis
** Soil organic matter = organic C - weight fine roots
Soil N and P = soil N (or P) - weight of N or P in fine roots. Grand total is corrected as above.
\+ Bracketed quantity for soil P = 'available' P

2.4 Discussion

Soils on all sites are red earths having principal profile forms (Northcote 1965) of Gn 2.11 for MUM and Gn 2.13 for MAD/MAM. The soils are massive with an earthy fabric and exhibit little profile differentiation. The mallee soils have a thin surface crust formed by mosses and lichens (cf. Rogers 1972) and rounded ferruginous gravel is common in the MAD and MUM surface soils.

The MUM soils are characteristically acid to very acid throughout the profile while the MAD/MAM soils are generally neutral on the surface but become very alkaline at depth (Table 2.1). Concretionary lime can be found in the 50-100 cm interval on MAD/MAM. The presence of free lime is thought to be a feature of all soils supporting Eucalyptus socialis associations (Parsons 1968a).

Mean concentrations of total phosphorus for the 6 depth intervals sampled are 238 ppm for MAD intercanopy, 268 ppm for MAD understorey, 302 ppm for MAM and 214 for MUM. These low values are similar to the mean of 240 ppm reported for other Australian arid zone soils (Charley and Cowling 1968).

El Ghonemy (1966) suggested that sampling of soil properties in the mallee must take into account both radial variation away from clumps, as well as depth functions within the profile. On the basis of this observation soil samples for the MAD profile were stratified into beneath- and inter-canopy groups. Such stratification was not

considered necessary on the MAM site because of its much greater age and 'closed' canopy structure.

Differences are apparent between the canopy and inter-canopy zones of the MAD plot (Table 2.1) and confirm the necessity for stratification here. There appears to be an accumulation of exchangeable calcium and potassium as well as a predictable increase in organic matter and nitrogen beneath MAD canopies. Somewhat surprisingly there also seems to be an increase in total phosphorus under the canopy topsoil compared with intercanopy values. The extent of this chemical 'halo' (cf. Zinke 1962, Ebersohn and Lucas 1965) suggests that it has developed over a long time scale. This supports Holland's (1967) contention that mallee lignotubers could live for a considerable period during which the aerial biomass may regenerate several times following catastrophic events (e.g. fire).

'Available' phosphorus was extracted with 0.01 N H_2SO_4 (Appendix 1). Dawson and Ahern (1974) found a strong correlation between available P (acid extraction) and available P (bicarbonate extraction) for red earth soils. Generally the more alkaline a soil the lower the bicarbonate extractable P is in relation to acid extractable P. The available P values for the soils on all sites in the present study are extremely low and emphasize the importance P must have in the nutrition of these communities (see Chapter 6).

Total nitrogen and organic carbon concentrations in the soils are also very low but within the ranges reported for dryland soils elsewhere in Australia (Jackson 1962,

Charley and Cowling 1968). The wide C/N ratios (Table 2.1) may reflect to some extent the favourable growth conditions which prevailed during the course of this study. In such situations large amounts of the nitrogen reserves may be tied up in organic form, both in the soil organic matter and in the plant (Dawson and Ahern 1974). The low soil nitrogen levels in the MUM profile, which supports a leguminous tree woodland, is worthy of particular note. This phenomenon will be discussed in some detail at the conclusion of this chapter.

Profile diagrams (Figures 2.1, 2.2) illustrate the distribution of total P, 'available' P, total N and organic C within each study site. Because the diagrams represent weight rather than concentration of elements they are perhaps more meaningful presentations than similar data of Charley and Cowling (1968). Total pool sizes (indicated at the base of each diagram) show remarkable similarities despite wide differences in geographical location and vegetation supported. However, at this level of study there is no indication of short term requirements for vegetative production.

The distribution of elements in the top 10 cm of soil on each study site, as a percentage of the total amount in the top 50 and 100 cm respectively (Table 2.28) shows that total P is more or less equally distributed within the profile. On the other hand the data for available P, total N and organic C indicate a pronounced concentration in the surface soil. Charley (1972) observed that such data is

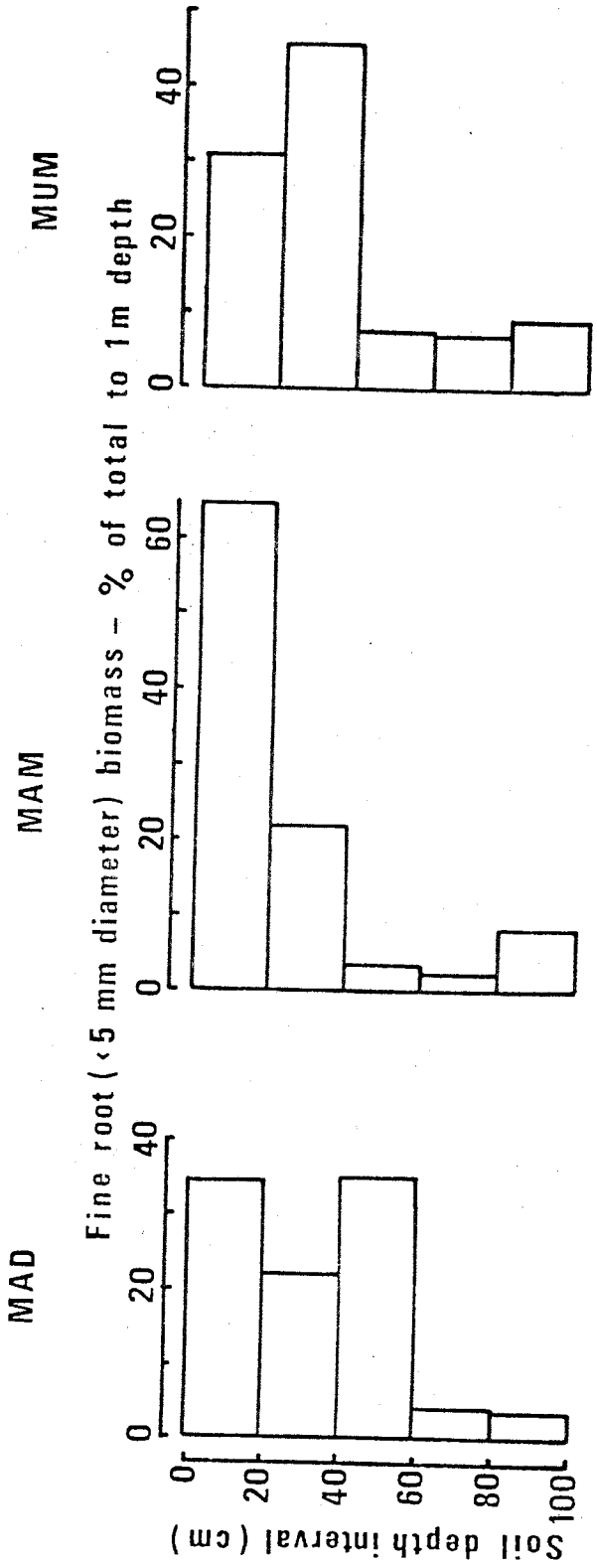


Figure 2.7 Distribution of fine roots (< 5 mm diameter) in the soil profile of each of the study sites.

difficult to interpret unless the effective 'biological' volume of soil is known. For all three systems studied there is good evidence that effective biological volume (as represented by feeder roots) is mostly situated in the top 50 cm of the profile (Figure 2.7).

Table 2.28 Distribution of elements in the top 10 cm of soil on each study site as a percentage of the total amount in profile depths of 50 and 100 cm respectively. Figures in brackets are the percentages that would be present if there was uniform distribution. Data for an Atriplex vesicaria soil profile (Charley and Cowling 1968) are included for comparison.

Site	Total soil depth (cm)	% soil element in top 10 cm			
		Total P	Avail.P	Total N	Org.C
MAD	100	11.6 (10)	18.0 (10)	21.5 (10)	20.0 (10)
MAM	100	10.4 (10)	16.4 (10)	24.1 (10)	23.3 (10)
MUM	100	13.0 (10)	19.6 (10)	15.9 (10)	19.3 (10)
MAD	50	21.4 (20)	35.6 (20)	35.4 (20)	32.1 (20)
MAM	50	22.4 (20)	32.7 (20)	40.8 (20)	32.1 (20)
MUM	50	24.4 (20)	47.5 (20)	23.5 (20)	30.3 (20)
Atriplex	45	21 (22.2)	-	27 (22.2)	38 (22.2)

These biologically induced vertical gradients are most pronounced for available P on the MUM site and total N on the MAM site. The consequences of profile truncation in these mature ecosystems are thus readily apparent. Any major distrubance in these communities which leads to wind and water erosion of the surface soil will severely reduce

the productivity and ability of plants to recolonize the site, through loss of essential nutrients already in limited supply (cf. Charley and Cowling 1968). Such effects have recently been noted for mulga areas of south west Queensland (Dawson and Boyland 1974). However, a comparison of MAD and MAM data (Table 2.28) suggests that where the surface soil remains intact there is a very high resilience in the nutrient pools, even following massive disturbance of the system. Thus, about 15 years following clearing and subsequent regeneration of the MAD site there is little difference in the total pool sizes (Figure 2.1) and distribution of essential nutrients in the soil profile compared with an adjacent undisturbed system (MAM).

Descriptions of the structural characteristics of the MAD, MAM and MUM communities (Tables 2.2, 2.3, 2.4 and 2.20) serve as a basis for biomass and subsidiary measurements in this and ensuing chapters. This tabulated data is largely self explanatory and will only be briefly discussed here.

The population (stems/ha) of the principal woody component decreased on all sites between 1973 and 1975 (Tables 2.2, 2.3, 2.4). This reflects the thinning out process in the regenerating MAD site and is a sign of post maturity in the MAD and MUM communities. Supporting evidence for this is given by the stem size class distributions (Figure 2.3). At the MAD site, mean stem circumference increased from 6.9 cm in 1973 to 9.2 cm in

1975 (Table 2.2). Increases in stem circumferences on the MAM and MUM sites, for similar time scales, were from 21.0 to 22.6 and 40.8 to 42.4 cm respectively (Tables 2.3, 2.4).

Only small changes occurred in the basal area of Eucalyptus spp. and Acacia aneura in the MAM and MUM plots over the period of observation. However, a significant increase ($P < 0.05$) in basal area of Eucalyptus spp. took place in the MAD stand, despite the decrease in overall stem density. There was also an increase in density in the understorey component in the MAD community (Table 2.2) in contrast to the apparent decline in the number of understorey shrubs in MAM (Table 2.3). These changes are not statistically significant but further highlight the differing status of the two mallee stands.

The leaf area indices determined for both mallee sites at the commencement and conclusion of the study period are of the same order (Table 2.20). It is noteworthy that the leaf area index for the MAD site at final sampling exceeded that for the MAM community at this time. However indices for both sites are much greater than the 0.15-0.20 reported for other mallee communities by Holland (1969b).

There are few estimates of ground litter accumulation in Australia's semi arid shrub/woodland communities. The most detail is provided by Moore, Russell and Coaldrake (1967) for a subtropical semi arid forest of brigalow (Acacia harpophylla). El Ghonemy (1966) presents leaf and bark data for a mallee community in south western New South Wales, but errors associated with his estimates are not

given. Litter accumulation in stands of Atriplex vesicaria (Charley and Cowling 1968) and Eremophila gilesii (Burrows 1972) has also been studied, although the physiognomy and biomass of the latter communities is quite different to that of the present study sites.

For the period of the current work there was an appreciable increase in the total amount of surface litter on all plots (Tables 2.5 and 2.6). This is thought to be largely due to the environmental conditions (especially above average rainfall) which were particularly favourable for growth (Table 1.1) and may also have promoted shedding of dead trunk wood.

The variance around mean values, in common with most litter estimates, is high. This could have masked likely significant trends for many fractions which may have been revealed with more intensive sampling. Because a considerable work load is involved in sorting litter samples time was not available for such intensive sampling here. Moreover, means of random samples of mallee litter will always tend towards high variance since deposition is greatest around the base of stems (El Ghonemy 1966).

Litter accumulation in the two mature stands for the present study (MAM, MUM) is much lower than the 75.5 t/ha reported for a mature brigalow ecosystem (Moore et al.1967).

Also the ratios of the weight of surface litter to total above ground biomass - 0.16, 0.22 and 0.29 for mulga, mallee (Tables 2.26, 2.27) and brigalow stands respectively suggest smaller proportionate litter build up on the former sites.

Leaf litter biomass on the MAD plots was largely unchanged at the commencement and conclusion of the study (Table 2.5). Such results were unexpected in this mallee regrowth community. Nevertheless leaf litter biomass on both MAD and MAM sites is almost identical, suggesting that equilibrium in terms of leaf litter input and turnover can occur within 15 years following disturbance of the mallee. These observations illustrate the stabilising influence that regrowth from lignotubers exerts on these ecosystems. The total leaf litter on the MAM plot (2000-2500 kg/ha) is far in excess of the 500 kg/ha which was reported for a nearby mallee stand of similar trunk wood biomass (El Ghonemy 1966).

In contrast to the MAD/MAM communities there was a highly significant ($P < 0.001$) difference in the leaf (phyllode) litter mat on the MUM plot between July 1973 and that present in July 1974 and May 1975 (Table 2.6). Defoliation in mulga is closely correlated with rainfall events (Wilcox 1960) and the above normal rainfall year of 1973 no doubt contributed to this marked increase in phyllode litter. In fact, between July 1973 and July 1974 there was 702 mm of rain on the MUM plot compared with a yearly average of 467 mm (Table 1.1).

Trends in nitrogen and phosphorus content of the surface litter follow that for its dry weight accumulation (Tables 2.5, 2.6). Major differences occur in the nitrogen content of the litter between MAD/MAM and MUM sites but phosphorus content (c. 3 kg/ha at final sampling) is very similar.

It is apparent even in these infertile semi arid ecosystems that leguminous dominants such as mulga have a marked effect on community nitrogen pools. This effect is not limited to leaf litter but is also most noticeable in the twig (< 1 cm diameter) litter of all sites. For example, at final sampling, 1584 kg/ha of twigs on the MAD site contain 7.7 kg/ha N and 0.5 kg/ha P. A comparable weight of twig litter (1594 kg/ha) on the MUM plot contains 21.4 kg/ha N and 0.4 kg/ha P (Tables 2.5, 2.6).

The estimates of root biomass and nutrient content made in the present study (Tables 2.8, 2.11, 2.12, 2.13) appear to be the first attempts to determine the amount of root material held in mallee and mulga ecosystems. However, other workers (e.g. Pressland 1975) have made estimates for individual plants. Because of the large effort involved in determining root biomass inadequate sampling is common. The present study suffers from this criticism but serves as a first approximation until more detailed work can be undertaken.

A comparison of root distribution within the top 100 cm of the soil profile (Figure 2.7) shows that at all sites feeder roots (< 5 mm diameter) are concentrated in the surface 40 cm. This effect is less pronounced on the MAD plot than in the mature MAM and MUM communities. The very high level of feeder roots in the top 20 cm of the MAM profile indicates a tight nutrient cycle dependent on continued input from litter and/or considerable competition

for moisture (particularly from light falls of rain) (e.g. Specht and Groves 1966). Both these effects are readily verified through edge effects in wheat fields where mallee shade lines have been retained. Wheat growing within two canopy widths of the mallee is commonly stunted and chlorotic when compared with the rest of the field.

The pattern of root distribution for mulga communities (Figure 2.7) is very similar to that found by Pressland (1975) beneath the extremities of single tree canopies. For all sites studied surface concentration of total roots would be accentuated if the respective lignotuber and root butt weights (Tables 2.11, 2.12) were added to fine root biomass.

Weight of individual lignotubers (Table 2.11) varies appreciably and appears to be more a function of the number rather than the mean size of stems supported. The small biomass of lignotubers supporting single stems (irrespective of circumference) on MAM suggests these may be seedling propagules. Specht (1972) considers that additional stems are produced when droughts or fires stimulate buried buds in the lignotuber.

The total weight of lignotubers on the MAD plot is very similar to that in the much older MAM stand (Table 2.13). While this difference can largely be related to differences in clump density, it does indicate that on a community level lignotuber biomass may remain 'stable', despite the wide fluctuations in the aerial biomass that results from disturbance. Chattaway (1958) found that year old Eucalyptus

seedlings, which formed lignotubers, could survive up to 26 complete defoliations before they died. However, while lignotuber biomass may remain constant, there is almost 3 times the weight of feeding roots on the MAM plot compared with that in MAD (Table 2.13).

Nitrogen and phosphorus contents of the root system on each site follow the pattern for root biomass (Tables 2.8, 2.13). Overall root weight is comparable for all sites (Table 2.13) so it is instructive to examine their nutrient contents in relation to each other if the values for MAD are taken as unity (Table 2.29).

Table 2.29 Ratios of biomass, nitrogen and phosphorus contents in the roots on MAD, MAM and MUM sites - based on values for MAD as unity

Root parameter	Site ratio		
	MAD	MAM:MAD	MUM:MAD
Biomass	1	1.4	1.2
N content	1	2.2	4.7
P content	1	1.8	1.6

Such comparisons must take into account edaphic factors (Table 2.1) but it is clear that the older stands retain greater amounts of nutrients in their root system than does the more actively growing MAD community. The very high ratio for nitrogen accumulation in the roots of MUM vegetation again emphasizes the effectiveness of symbiotic N fixation in these semi arid woodlands.

The problem of technique for estimating standing biomass in woodland ecosystems has been discussed extensively in recent literature (e.g. Ovington, Forrest and Armstrong 1967, Madgwick 1971, Nemeth 1973). Lately, the majority of workers have used regression techniques, probably as a result of the rising use of computers (Art and Marks 1971).

The general form of the regression relationship most often used is $\log_e y = A + B \log_e x$; where y = biomass, x = dimension (circumference, height etc.) and A and B are constants (Newbould 1967). This is the form mainly employed in the present study (Tables 2.14, 2.15, 2.16). The majority of the prediction equations shown in these tables have high coefficients of determination (R^2) and low errors.

The high coefficients of determination result from the wide range of stem sizes in the samples and because the dimensions used in prediction equations are highly correlated with one another. Nevertheless the use of highly correlated variables is quite appropriate for predictive purposes (Mead 1971).

Whittaker and Woodwell (1968) suggest that more useful expressions of dispersions of values from the regression lines are given as "estimates of relative error", E and e computed from the standard error of estimate (SEE). For a linear regression e is the SEE divided by the mean value of y; a value of 0.15 for e suggests an expected error range of $\pm$ 15%. In logarithmic regressions the SEE is itself a logarithm to be added or subtracted from log y; its antilog is consequently a factor (E) by which a given value of y

is to be divided or multiplied. A value for E of 1.20 thus indicates an expected error range from 1.20 y to y/1.20. However, Hughes (1971) points out that the size of the errors indicated by E should be viewed with caution, as E is a relative rather than an absolute estimate of error.

The problem of confidence limits for treatment of samples by logarithmic regressions is unsolved (Whittaker, Bormann, Likens and Siccama 1974). A detailed discussion may be found in Land (1972). In the present study (Appendix 2, Figures 2.4, 2.5, 2.6) Patterson's (1966) transformation has been used and, as already indicated, this is an approximate method only appropriate where the regression error mean square (variance) is < 1.

Tables 2.14, 2.15 and 2.16 give the SEE for all regressions. Since E is the antilog of SEE and the regression variance is the square of the SEE both these parameters may be computed from the tables if desired. In Table 2.15 mean y values for dead wood (weight, N and P content) are 1230, 4.38 and 0.21 respectively. These values are necessary for the determination of e in these linear regressions. The selection of linear regressions in the latter case was necessary because of the excessively high SEE associated with logarithmic regressions for dead wood.

Not unexpectedly there are also quite high SEE's in the logarithmic regressions for capsules, dead wood and dead bark on the MAD plot. However, as these components

make only minor contributions to the overall nutrient pool (Table 2.17), the logarithmic form was retained as the predictive equation here.

The regression techniques employed in the present study are similar in concept to those used for other mallee and mulga sites (Holland 1969a, Pressland 1975). As previously acknowledged, Pressland's raw data were a major contribution to the derivation of regressions for the MUM site of the current study.

In Holland's (1969a) work the independent variables were midpoints of age or basal circumference classes. This is thus a mean tree approach, stratified over a number of class sizes. Depending on the distribution of stems within each class, skewed above or below the midpoint, the prediction equation would therefore under or overestimate the true biomass. Given the nature of allometric stem growth it is likely that Holland's data underestimates the biomass of his plots (cf. Attiwell 1966a). This would be further accentuated for his Yara plot, where logarithmic regressions were used without applying the antilog correction mentioned earlier (section 2.2.1).

The direct regression of stem circumference against total above ground biomass gave an estimate for mallee eucalypts on the MAM plot of 38.143×10^3 kg/ha (Table 2.18). There were some 1660 stems/ha on the plot and the majority were aged between 45-65 years (based on basal ring count - see Holland 1969b). This biomass compares with Holland's

(1969a) for the 1360 stems/ha Yara plot, of similar composition, of 20.392 x 10^3 kg/ha. The mean age of the Yara stems was 35 years and the mean height of stems was 5.5 m (Holland 1969a, b).

It has already been suggested that Holland's biomass predictions could be underestimates. Since the Yara stand had some 300 fewer stems/ha, was at least 10-20 years younger and had a lower mean stem length to the MAM stand (6.9 m - Table 2.20) the biomass estimates for both communities seem to be of the same order. Further, the Yara estimates were for the drought years 1965-66.

This comparison of results is supported by the pattern observed in leaf area index - 0.20 for the Yara mallees (Holland 1969b) and 0.67 for those on MAM (Table 2.20). The more open nature of the vegetation, and perhaps lower fertility status, of Holland's Yara site vis-a-vis MAM is attested by the presence of Triodia irritans on the former (Holland 1969c) and its absence from the latter.

Estimates of standing biomass, nutrient content and canopy dimensions (Tables 2.17, 2.18, 2.19, 2.20) are based on the prediction equations of Tables 2.14, 2.15 and 2.16. These regressions are largely derived from 1975 samples and should strictly be applied only to stand predictions for that year. However, it seems reasonable to assume that these regressions are equally efficient as a description of the joint variation of stem basal circumference and dry weight, when they are applied to stems within the same size

range, from the same site and over a short time scale (2 years). Further, for the MAD/MAM sites in the present example, both sets of predictions are for identical physiological periods, i.e. at the conclusion of the summer growth cycle.

Holland (1969a) for mallee, Hughes (1971) for birch and Nemeth (1973) for loblolly and slash pine have previously adopted this approach of reapplying the same set of regressions to predict stem biomass changes over short periods of time. If errors do arise through the use of the same regressions over two or more sampling periods they are most likely to be in those components most responsive to climatic events, e.g. leaves and fruit.

(As an independent check of this argument consider the % canopy cover derived from mean clump diameters measured at the time of stand enumeration in 1973 (Table 2.2). This figure 50.0 $\pm$ 2.3% is within the range, 44.8 $\pm$ 8.5%, estimated from the regression predicted canopy diameter/stem and stand stem density for this time in 1973 (Tables 2.2, 2.20). Both these estimates do not take into account intermingling of canopies and are above the 'true' canopy cover of 42.5 $\pm$ 2.6% (Table 2.2)).

Significant differences between the standing biomass and nutrient content at the commencement and conclusion of the study period were only recorded for the MAD site (Tables 2.17, 2.18, 2.19). This result is not surprising as both MAM and MUM sites represent mature communities and

the indications of a fall in stem density (Table 2.3) and lower biomass (Table 2.18) suggest the MAM community may already be degenerate. Nevertheless little significance can be attached to this latter observation which could merely be due to sampling errors.

Differences in the manner in which stem circumference increments were monitored between the sites should be mentioned here. The MUM plots were 'permanent' in that stems measured for stem circumference in 1973 were tagged so that identical stems were measured again in 1975. This is standard forest mensuration practice. However, Holland (1967) reported that the period in which tagged diameters could be used on Eucalyptus socialis and E. dumosa was limited to 1-2 years, because they partially shed their bark in the summer months. It was therefore decided from the outset to take a new random sample of stems on MAD/MAM at the commencement and conclusion of the study.

The rapid growth in mallee eucalypts on the MAD site suggests that peak productivity, following disturbance, could be reached somewhere around 15 years after the event. An idealised comparison of MAD/MAM growth is made with that projected from the previous mallee studies (Specht 1966, Holland 1969a) in Figure 2.8. Considerable extrapolation was involved in producing this figure, but allowing for broad site, climate and stand differences some deductions can be made. It is apparent that mallee dominated by E. incrassata may have a faster initial growth rate, following disturbance, but a much lower peak biomass than

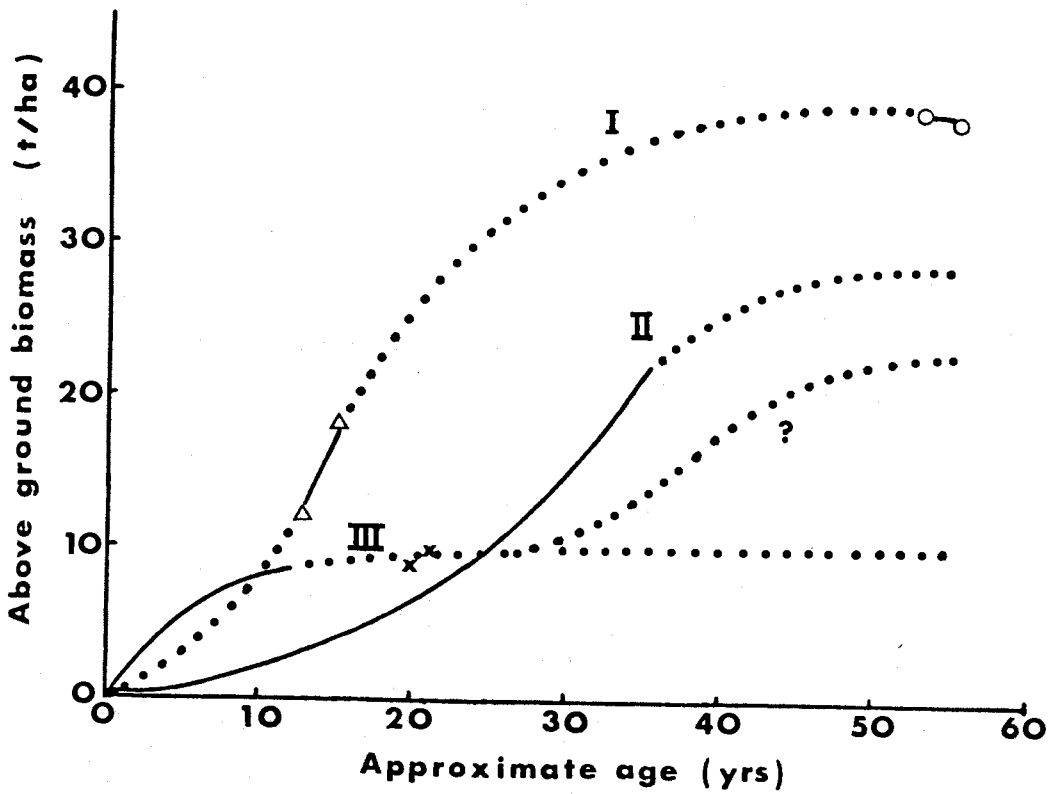


Figure 2.8 Postulated smoothed curves of changes in aerial biomass of mallee eucalypts.

I Data for MAD (Δ) and MAM (O) sites dominated by Eucalyptus socialis

II Data for E. socialis at Yara based on regression of Holland (1969a)

III Data for E. incrassata at Dark Island Soak from Specht (1966) and at Wyperfeld (X) from Holland (1969a)

Solid line indicates curve within range of known values.

Dotted line is postulated curve.

that in which E. socialis is dominant. These conclusions are supported by height measurements (Table 2.30).

Table 2.30 Age-height relationships in mallee eucalypts

Site	Species	Approx. age (yrs)	Height (m)	Reference
MAD	E. socialis	15	3.3	Table 2.20
Yara	"	36	5.6	Holland (1969a,b)
MAM	"	55	6.9	Table 2.20
Dark Island	E. incrassata	12	3-6	Specht (1966)

Moisture content of plant tissues in the MAD and MAM sites is remarkably similar (Table 2.21). Black (1952) has noted that moisture stored in the roots and lignotubers of E. socialis may be of great physiological importance. By combining data of Tables 2.13 and 2.21 it can be calculated that at the time of final sampling there was c.10 tonnes of water/ha held in the MAD lignotubers and c.8.4 tonnes of water/ha in those on the MAM site.

Standing biomass of minor perennial species on MAD, MAM and MUM sites is summarized in Table 2.22. This table is based on the data of Tables 2.9 and 2.10 and the stand table for each sample transect, enumerated at the beginning and end of the study. It is clear that these minor species, apart from Melaleuca lanceolata for MAM and Eucalyptus populnea for MUM contribute little to community biomass despite their overall density, which varies between 1000-

3500 shrubs/ha. The mean top weight of individual shrubs at final sampling on the MAD site was 87 g and that for the MAM shrubs was 142 g.

M. lanceolata (818 kg/ha) contributes about 2% of the total standing biomass on the MAM site and the contribution of all shrubs is only 2.3% (Table 2.26). By comparison, in the mallee-broombush association studied by Specht (1966), M. uncinata-Baeckea behrii contribute 20-30% of standing biomass within the community. A similar percentage of standing biomass is provided by E. populnea on the MUM site (Table 2.27) and it is apparent that this species should not be considered a 'minor' component of this mulga community.

There is a much higher concentration of nitrogen in MUM tissues (both living and dead) than in those of the MAD/MAM plots (Tables 2.23 and 2.24). The figures in these latter tables are means for all analyses of a particular tissue - but 'total' concentrations are obtained by division from previous tables in which total biomass, nitrogen and phosphorus contents are listed (cf. Woodwell, Whittaker and Houghton 1975). Of particular note is that high nitrogen levels on the MUM plot are found not only in phyllodes, but also in bark and wood tissue (Table 2.24). These nitrogen and phosphorus concentrations are comparable with those reports for Acacia harpophylla (Moore et al. 1967).

Eucalyptus populnea, the principal species associated with mulga, has much higher concentrations of nitrogen and

phosphorus in its tissues than the mallee eucalypts. This is predictable as E. populnea is a deep rooted species thought to act as a 'nutrient pump' in mulga communities (Ebersohn and Lucas 1965).

Not unexpectedly tissue nitrogen and phosphorus concentrations on the MAD and MAM sites are quite similar, especially with respect to nitrogen levels (Table 2.23). There is a general tendency for the MAD vegetation to exhibit higher phosphorus concentrations in its components, but this could be expected to decrease with community age, as more of the available portion of this element became 'locked up'.

A notable feature from the analyses is the consistency of nitrogen and phosphorus concentrations in leaf tissue - for the 29 MAM sample stems, ranging in circumference from 2.5 to 55.2 cm leaf nitrogen and phosphorus had coefficients of variation of 11.2% and 10.2% respectively (95% confidence limits for N = 0.99 $\pm$ 0.04% and for P = 0.052 $\pm$ 0.002%). Similarly, 30 MAD sample stems (circumference range 1.8-23.2 cm) had coefficients of variation for leaf nitrogen and phosphorus of 12.2% and 17.0% respectively (95% confidence limits for N = 0.99 $\pm$ 0.05% and for P = 0.068 $\pm$ 0.004%). The somewhat greater phosphorus variability on the latter site could have resulted from stems which were growing close to old burns following clearing of the original MAD community.

The consistency in nitrogen and phosphorus leaf tissue analysis for E. socialis has been previously observed by El Ghonemy (1966). The results reported here included a

wider range of mallee species viz. E. socialis, E. dumosa, E. gracilis and E. foecunda. Nevertheless, while the range of stem sizes sampled does suggest some physiological control, it is obvious that nutrient levels in the substrate could be a major influence also (cf. Russell 1961, Woodwell et al. 1975).

A feature of Tables 2.25, 2.26 and 2.27 is that estimates of root/shoot ratios on a community scale can be deduced. The ratios for MAD, MAM and MUM are 1.0, 0.7 and 0.4 respectively. Those estimates are restricted to 1 m soil depth and it is quite possible that the data for E. populnea lignotubers on the MUM site is considerably in error. Yet the ratios confirm, on a community level, that not all semi arid zone plants have high root/shoot ratios (Noy Meir 1973).

For some shrubs in semi arid Australia root/shoot ratios as low as 0.2-0.3 have been recorded (Jones and Hodgkinson 1969, Burrows 1972). However Anderson, Perry and Leigh (1972) question the physiological relevance of root/shoot ratios in which 'shoots' include stems, twigs and dead wood. They suggest that a better crude comparison would be that between the primary source of water loss (leaves) and the primary source of water gain (roots).

In the data on nutrient distribution presented in this chapter there has been a striking paradox which has so far not been discussed. This is the nexus of very low soil nitrogen on the MUM plot (Table 2.1) compared with very

high concentrations of N in the tissues (Table 2.24) and total N content of the biomass (Table 2.27).

Low soil N levels would suggest that the Acacia aneura - Rhizobium symbiosis is quite ineffective. Indeed the experience of many field workers is that it is very difficult to locate nodules on mulga roots. However both Hannon (1956, 1958) and Bowen (1956) have commented on the seasonal formation and sloughing of nodules on some wild Australian legumes.

Mechanism by which legumes could contribute to the N status of soils include loss of plant parts, and excretion of fixed N. Bryan (1962) observed that at high temperatures and light intensities the C/N ratio in the plant remains sufficiently wide to preclude the possibility of excretion. Thus Garcia-Moya and McKell (1970) could find no evidence that leguminous desert shrubs were upgrading N status of soils when compared with nonleguminous shrubs.

Similarly for mulga the N status of the soil may remain low because almost all the N fixed remains 'locked' in plant tissue (O'Hagan 1966). The contribution of N to the soil in mulga communities may then be solely dependent on the loss of plant parts such as leaf litter and decaying roots. A contribution from decaying roots should ultimately lead in a stable community to a more equal distribution of N throughout the soil profile vis a vis a nonleguminous community (see Table 2.28).

Tables 2.25, 2.26 and 2.27 summarize the comprehensive data presented in this chapter with respect to organic matter, nitrogen and phosphorus distribution within the three ecosystems studied. When combined with stand definition (Tables 2.2, 2.3, 2.4 and 2.20) a firm reference base is provided for more detailed studies of nutrient cycling within the communities. This will be covered in ensuing chapters.

CHAPTER 3

Biomass and nutrient content of litter fall in mallee shrub and mulga woodlands.

3.1 Introduction

Most of the vegetative production in terrestrial ecosystems eventually becomes detritus (Wiegert and McGinnis 1975). This dead organic matter plays a major role in determining ecosystem structure and function. For example, detritus represents an energy source for heterotrophic organisms, a nutrient reservoir for intrasystem cycling and a regulatory factor influencing hydrology (Lang 1974). Further, the accumulation and characteristics of the litter layer are important with respect to the germination and establishment of both existing plants and potential invaders (Ashton and Macauley 1972, Chapman, Hibble and Rafarel 1975).

Litter fall has been measured in many woodlands (see Bray and Gorham 1964, Jordan 1971) but concomitant observations on its nutrient content are less prevalent (Webb, Tracey, Williams and Lance 1969). Many of these studies have been in relatively fertile ecosystems and in situations where there is quite rapid decomposition due to favourable environmental conditions and/or species types (e.g. deciduous plants). However, in ecosystems where available nutrients are present in limited quantities only and where the rate of decomposition is low, the litter layer becomes increasingly important in the overall nutrient

regime of the system (Chapman, Hibble and Rafarel 1975).

Specht and Brouwer (1975) have recently summarized results of leaf litter fall studies on Australian endemic plant communities. Of the twenty-two reports cited only two are concerned with semi arid or arid zone species. In these dryland areas fertility levels are often very low (Charley and Cowling 1968) and environmental conditions appear inimical to rapid decomposition.

The present study examines the dynamics of litter fall and its nitrogen and phosphorus content in mallee shrub and mulga woodlands in the Australian semiarid zone. Both community types are found on typically infertile soils particularly deficient in available phosphorus. Nitrogen inputs were examined because phosphorus deficiency is known to limit biological fixation mechanisms (Jackson 1962, Walker 1962, Beadle 1968) while the communities studied were dominated respectively by Eucalyptus spp. and the leguminous mulga.

The lack of precision in many estimates of litter fall has been commented on by Specht and Brouwer (1975). Sampling problems are exacerbated in semiarid communities which are characterised by non-random plant distributions and open canopies. Because of these factors some attention was paid to the statistics of sampling in the current work.

3.2 Methods

Litter fall was studied at three sites (MAD, MAM and MUM) and detailed descriptions of site position, floristics and structure can be found in Chapters 1 and 2.

Identical litter traps were positioned on each site. The traps were modelled on suggestions of Newbould (1967) and comprised terylene 'mosquito' mesh cones, 35 cm deep, attached to circular iron hoops of area 0.5 m^2. The hoops were mounted on three legs so as to be 40 cm above ground level when in position. Each cone was weighed down with 150 g of lead shot.

The traps were placed on the detailed study area of each plot. There were initially 27 traps on the MAM site and 40 each on the MAD and MUM sites but this was increased to 52 on the MAD plot and 37 on MAM once the between trap variability became known, after the first collections. Every trap was permanently identified with a numbered tag.

MAM and MUM traps were positioned in a stratified random manner over the plots on the assumption that the canopy was 'closed'. This assumption was not valid for the MAD plot (Chapter 2) and it was necessary to identify two sampling areas between and beneath mallee clumps. It was observed that litter accumulation occurred directly beneath the canopies of the mallee clumps. Hence a greater sampling intensity was employed there than in the inter-canopy areas.

There were originally 10 inter-canopy and 30 beneath canopy traps on the MAD plot. This was subsequently increased

to 12 and 40 respectively. The traps, assigned to the two differing areas within the stand, were positioned in a stratified random manner over the plot. Subsequent community estimates of litter fall were corrected on the basis of inter-canopy traps sampling 57.5% and beneath canopy traps 42.5% of the total area. Possible wind directional effects on litter fall beneath the clumps were minimised by placing traps alternatively within the north, south, east and west face of the randomly sampled canopies.

All litter which fell into the traps at each site was collected at four weekly intervals throughout the duration of the study (c. 100 weeks). The litter was placed in paper bags appropriately identified with the site, trap number and date of collection. On return to the laboratory the contents of each bag were dried to constant weight at 80^{o} C and sorted into the following components:

For MAD/MAM - stem and twig, bark, leaf, capsules and flower parts, other species (other than Eucalyptus spp.) and insect frass.

For MUM - stem and twig, bark, phyllode, flower bud, pod, seed, other species (other than Acacia aneura) and insect frass.

The fractions were individually weighed to 0.01 g and then bulked for each collection date. The bulked components were thoroughly mixed and a subsample retained for N and P analysis (see Appendix 1 for methods).

3.3 Results and Discussion

3.3.1 Sampling statistics - Many of the litter fall estimates that have been reported in the literature are based on statistically dubious results. This is attributable to the wide temporal and spatial variation common in litter fall from most communities (Bray and Gorham 1964) and to the inadequate replication employed.

Estimates of litter fall in mallee communities have been made by Holland (1967) and in mulga by Wilcox (1960) and Beale (1972). Beale's study was the more intensive, involving some 10 traps in each of 7 replicated plots per treatment, but he does not report on the statistical aspects of his sampling which was done on an annual basis only. Holland (1967) placed 3 gravel sieves under canopies of Eucalyptus dumosa and E. socialis in order to study the pattern of litter fall, but he noted that this was inadequate for a statistically satisfactory survey.

In the present study the initial aims were to (i) if practical, determine litter fall on each plot with a 95% confidence interval equal to 10-20% of the mean,

(ii) to judge the efficiency of sampling on fluxes in leaf litter (as this was thought to be the major component of litter and nutrient input), and

(iii) to provide a guide to sampling intensity which may be required in future studies of litter fall in mallee and mulga ecosystems.

Greig-Smith (1964) discusses methods of determining the number of samples to be taken in ecological studies. Two important considerations are the degree of precision wanted and the time available to take and process the samples. Subjectively the number of samples required may be found by plotting the means of the first 5, 10, 20 ---- samples and judging when the mean has reached an acceptable stability. When an estimate of the population variance is known a more satisfactory technique is based on the formula given by Cochran (1953) and Kimmins (1973). Thus -

$$\text{Number of samples} = \frac{t^2 \times CV^2}{C^2} \qquad (3.1)$$

where CV = coefficient of variation of a preliminary sample

t = students t value for a desired confidence interval at a given probability level

C = desired confidence interval as a percentage of the mean

The number of traps chosen for sampling litter fall should be related to sample size, but Medwecka-Kornas (1971) suggested that for statistical reasons it should be a minimum of 25-30 per hectare. Because no data was available on the likely variability to be found in the present study of litter fall an initial sample intensity of 40 traps was selected for MAD and MUM sites and 27 for the MAM site. From previous studies it was expected that mulga litter fall would be greatest following significant rainfall events

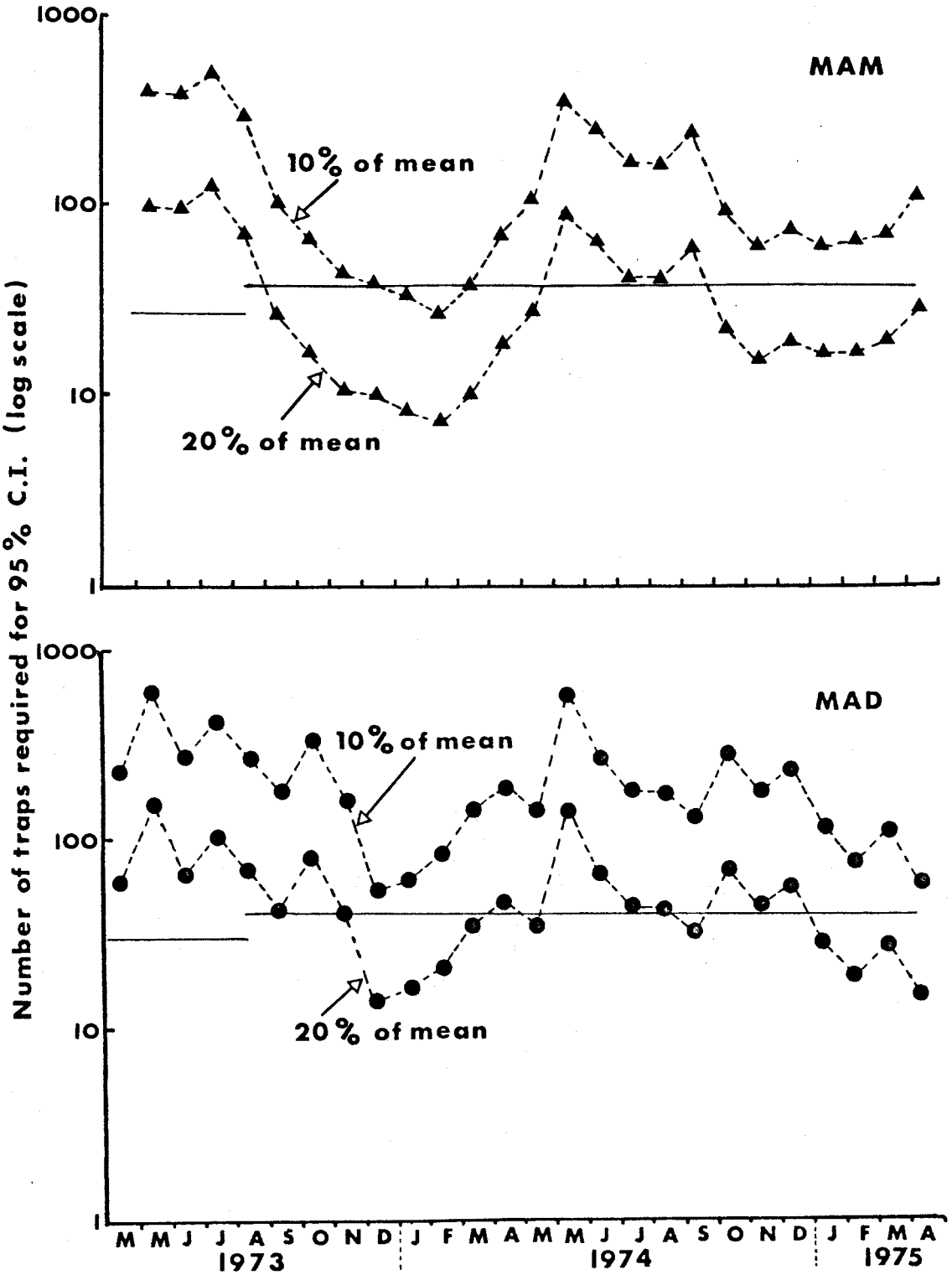


Figure 3.1 Number of litter traps required to estimate weight of Eucalyptus leaf litter fall (MAD/MAM plots) over all collection periods with a 95% confidence interval equal to 10 or 20% of the respective means. Solid lines show actual number of traps used. Calculations based on Equation 3.1 in text.

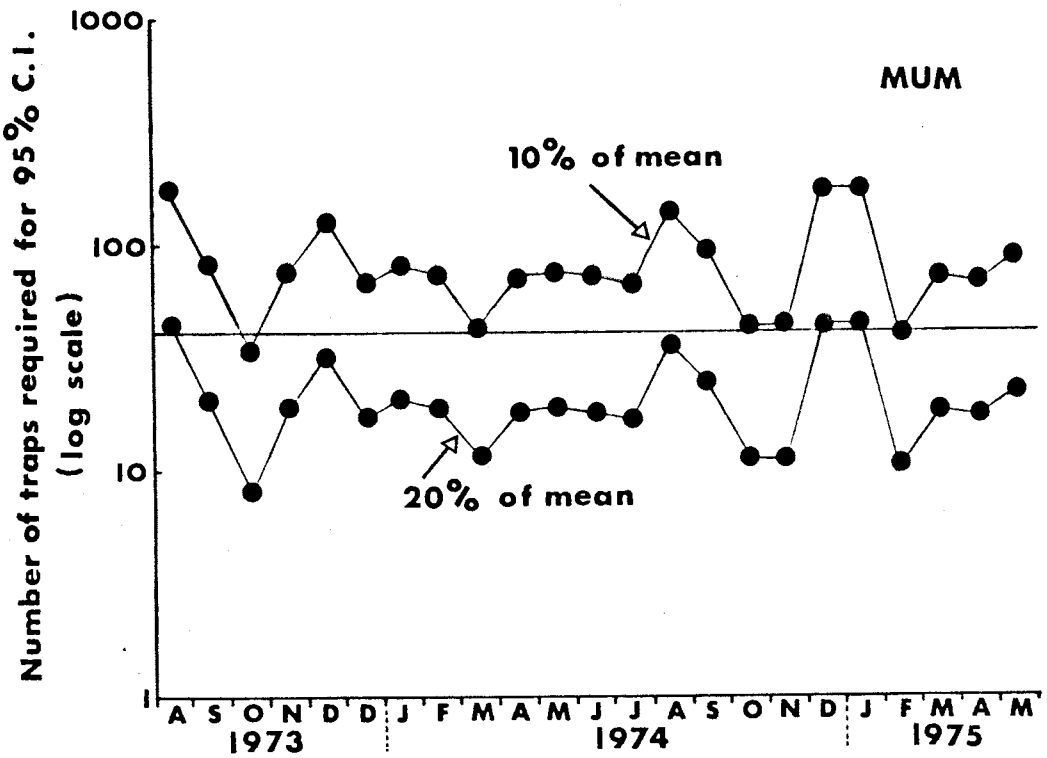


Figure 3.2 Number of litter traps required to estimate weight of phyllode litter fall (MUM plot) over all collection periods with a 95% confidence interval equal to 10 or 20% of the respective means.
Solid line shows actual number of traps used.
Calculations based on Equation 3.1 in text.

(Wilcox 1960, Slatyer 1974) and that maximum leaf fall from mallee eucalypts would occur during the late summer (Holland 1967).

The first few litter collections showed that the desired precision could be reached with the initial sampling intensity on the MUM plot (Figure 3.2) but that the variance for estimates of mallee litter was quite high during the winter months (Figure 3.1). Hence an additional 10 and 12 traps were placed on the MAM and MAD plots respectively. Subsequent collections showed that this sample number achieved the desired precision on the mallee sites although these collections also coincided with the period of maximum litter fall (see Figures 3.6, 3.7).

Following this period however, it was apparent during the winter collections of 1974 that the desired confidence interval could not be reached on the mallee plots without greatly increasing the number of traps. To test the effect of sample number on the estimate of mean leaf litter fall on all three sites a modification of Greig-Smith's (1964) graphical test was employed.

For these tests the collection showing maximum leaf litter fall (measured up till that period) was selected i.e. January 1974 for MAD/MAM and October 1973 for MUM. The weight of leaf litter collected in each of the 40 traps on the MUM plot and in the 40 traps placed beneath canopies on the MAD plot were tabulated according to trap identification. Similarly the weight of leaf litter collected from

each of the 37 MAM traps was listed. For each site these data were used to calculate mean leaf litter yields based on varying numbers of traps from 2, 3, 4, ----, 40. The appropriate trap yields used for these determinations were chosen randomly by computer and means (and coefficients of variation) calculated; this being repeated 50 times for the chosen number of traps. For each number of traps a plot was obtained for the maximum and minimum values obtained in this manner. This procedure offsets to some extent criticisms (Chapas 1969) that such presentations merely demonstrate the statistical theory that the variance of the mean of N sample individuals of a population is equal to $\frac{1}{N}$ times the variance of the parent population.

These graphs (Figures 3.3, 3.4) show the number of traps that would be required to obtain estimates of the mean within 5, 10 and 20% of the "true" mean (based on 40 traps for MAD/MUM and 37 for MAM). Graphs for other sample times revealed similar patterns. Thus, while Figure 3.1 showed that a substantially greater number of traps would be required to obtain the desired level of precision in the mallee during winter, Figure 3.3 suggests that the rate of improvement would be small for numbers of traps greater than 25-30.

Decreasing the size of these 0.5 m^2 traps, whilst increasing their number, was not appropriate as leaf collections during winter were already only 1-5 grams per trap. Thus at this time a smaller collection area per trap

Figure 3.3 Calculated maximum and minimum estimates of mean weight of leaf fall for numbers of randomly located traps ranging from 2 to 40 (MAD) and 2 to 37 (MAM). For each number of traps the two parameters were calculated 50 times selecting a new random distribution each time. The data points represent the extreme values obtained for the two parameters in this manner.

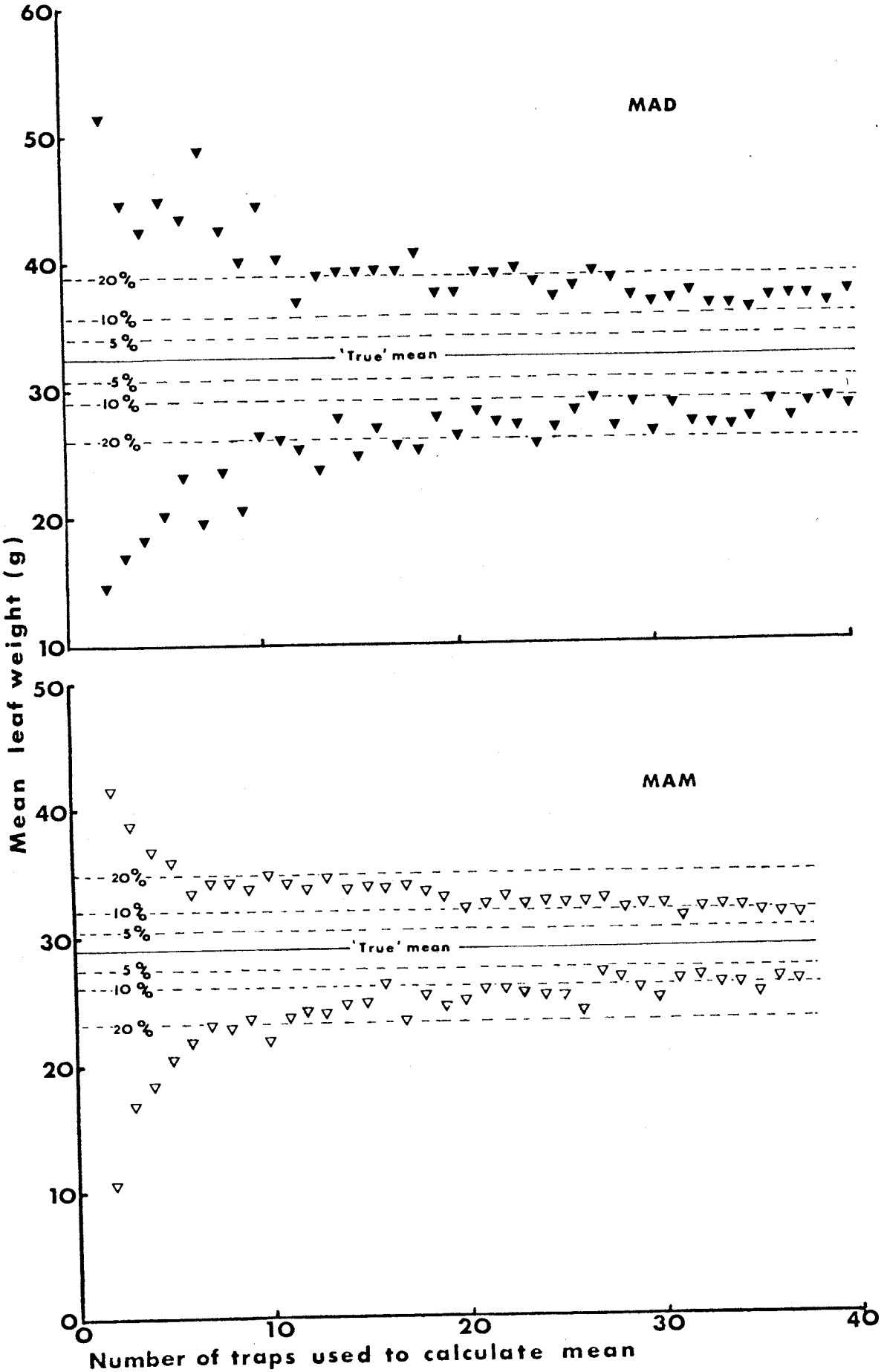
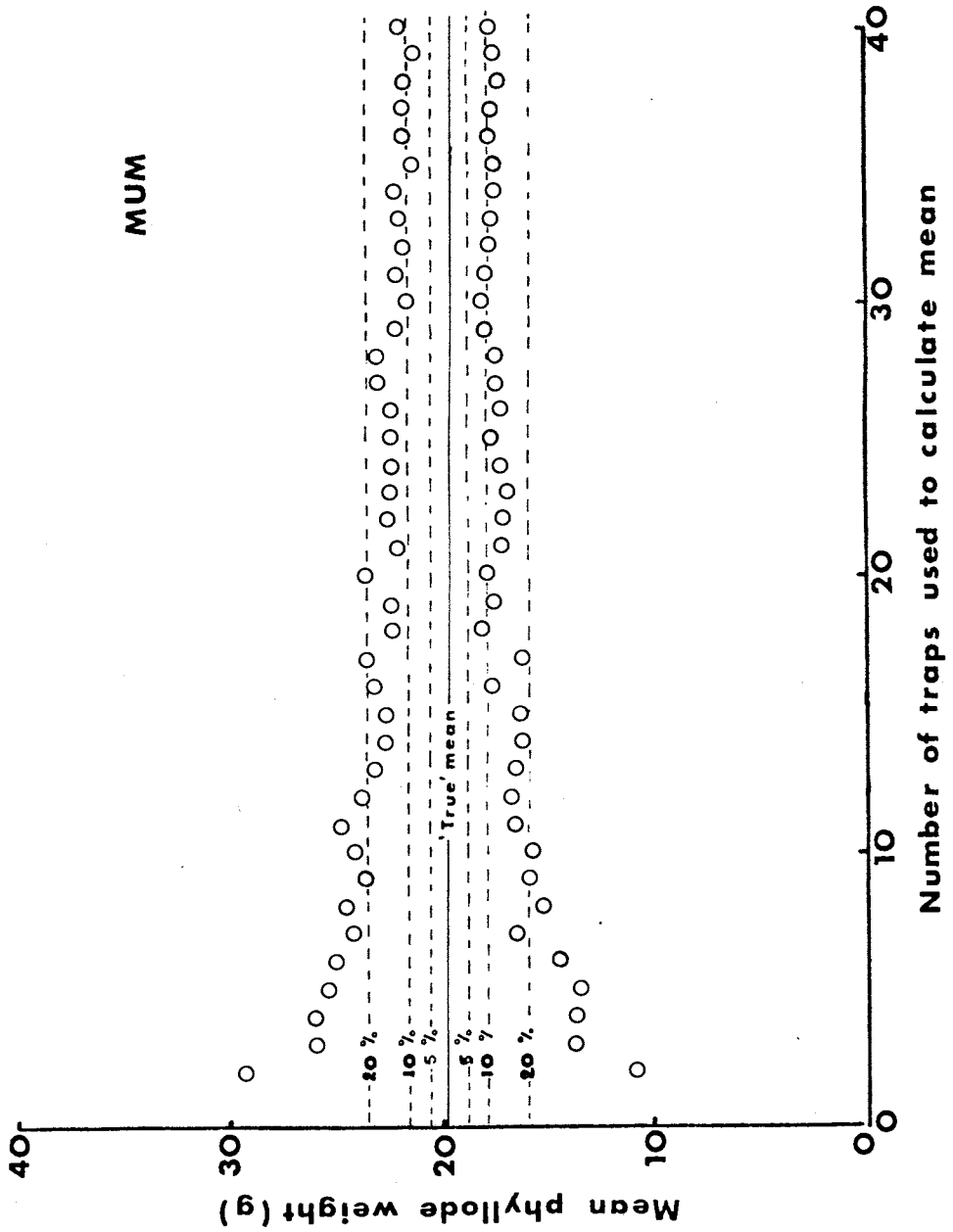

MAD
MAM
20%
10%
5%
'True' mean
-5%
-10%
-20%
Mean leaf weight (g)
Number of traps used to calculate mean
60
50
40
30
20
10
0
10
20
30
40

Figure 3.4 Calculated maximum and minimum estimates of mean weight of phyllode fall for numbers of randomly located traps ranging from 2 to 40 (MUM). For each number of traps the two parameters were calculated 50 times selecting a new random distribution each time. The data points represent the extreme values obtained for the two parameters in this manner.


MUM
Mean phyllode weight (g)
Number of traps used to calculate mean
'True' mean
20 %
10 %
5 %
5 %
10 %
20 %
0
10
20
30
40

would result in a greater number of empty traps. However a substantial increase in trap numbers was also impractical because of the major work load already involved in sorting the 127 trap collections every four weeks. Therefore it was decided to accept the wide standard errors associated with winter collections, particularly as the leaf collected during the five months May - September was only 10.2 and 7.6% of the annual total for MAD and MAM respectively.

It is clear from the data presented that substantial spatial and temporal variability occurs in litter fall within these communities. Because the traps were in 'fixed' positions spatial heterogeneity within sites is highlighted by examining, with a computer sorting routine, the relative order of traps in terms of the amount of leaf collected per sample date. This is shown for 7 collections on the MAM plot (Table 3.1) but similar results occurred for all sites and sampling periods.

In Table 3.1 the trap collecting the smallest amount of leaf litter was almost consistently trap 67 but there is little discernible pattern in the remaining order. The 'most typical' trap - that showing litter weights closest to the mean for each sample date - can be determined by regression analysis. On this site the regression of mean leaf yield for the 37 traps against leaf weight collected for each trap showed that trap 70, with a coefficient of determination (R^2) = 0.97, was most consistently the

Table 3.1 Trap position in order from smallest (1) to largest (37) amount of leaf in the trap for selected collections on the MAM plot.

Trap No.	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
Sample Date	Relative position in order of weight of leaf litter collected																	
19.9.73	16	12	6	8	19	21	2	10	33	31	29	11	3	28	15	17	20	32
17.10.73	4	9	25	6	13	8	2	23	32	35	27	20	26	37	33	36	31	5
14.11.73	2	24	30	18	3	8	12	14	36	37	33	34	35	25	15	26	9	4
12.12.73	37	20	33	16	12	5	32	31	36	22	26	23	28	15	3	21	11	10
13.1.73	29	27	26	24	7	11	8	23	28	25	33	31	20	21	3	22	30	5
6.2.73	35	23	28	11	18	6	9	22	30	32	26	37	33	29	4	19	13	10
6.3.73	14	33	24	31	10	22	3	28	36	13	12	21	9	15	18	30	29	6

Table 3.1 (Continued)

Trap No.	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Sample Date	Relative position in order of weight of leaf litter collected																		
19.9.73	22	23	30	4	18	9	13	26	5	25	14	7	34	24	36	27	1	37	35
17.10.73	12	28	24	7	18	1	19	16	17	34	15	3	21	14	10	22	29	30	11
14.11.73	19	31	17	11	16	1	7	32	21	28	23	20	29	27	10	5	13	6	22
12.12.73	13	24	30	7	6	1	4	35	8	34	25	17	27	9	19	2	29	14	18
13.1.73	16	36	37	19	13	1	4	35	15	18	34	12	32	6	9	2	14	17	10
6.2.73	17	20	32	12	25	1	7	16	14	15	34	24	36	5	3	2	27	21	8
6.3.73	5	37	35	11	20	1	7	17	23	27	32	25	19	8	2	4	34	26	16

closest to the mean. The identification of a trap which maintains a reasonably stable mean value is necessary if roving plot methods of estimating litter yield (see Will 1959, Attiwill 1966b, Kimmins 1973) are employed.

No realistic sampling procedure will adequately provide satisfactory accuracy and precision for all periods of the year. To illustrate this the number of traps required to sample leaf litter input on all three sites with 95% confidence limits equal to various percentages of the mean was calculated for periods of maximum and minimum recorded leaf litter production respectively (Figure 3.5). Such data may provide useful guidelines for further research into litter dynamics in these ecosystems.

Nevertheless if one is interested in the total annual pulse of litter and nutrients rather than four weekly fluxes it can be readily shown (Table 3.2) that this is attainable with acceptable precision. This table was derived by summation of the leaf litter fall in individual traps over a one year period. This was possible because the traps were permanently positioned and identified and each individual trap collection was labelled and identified as to its origin. Hence, since the overall interest of the current project was in yearly rather than daily or monthly fluxes it can be concluded that the sampling routine adopted was adequate for the purpose.

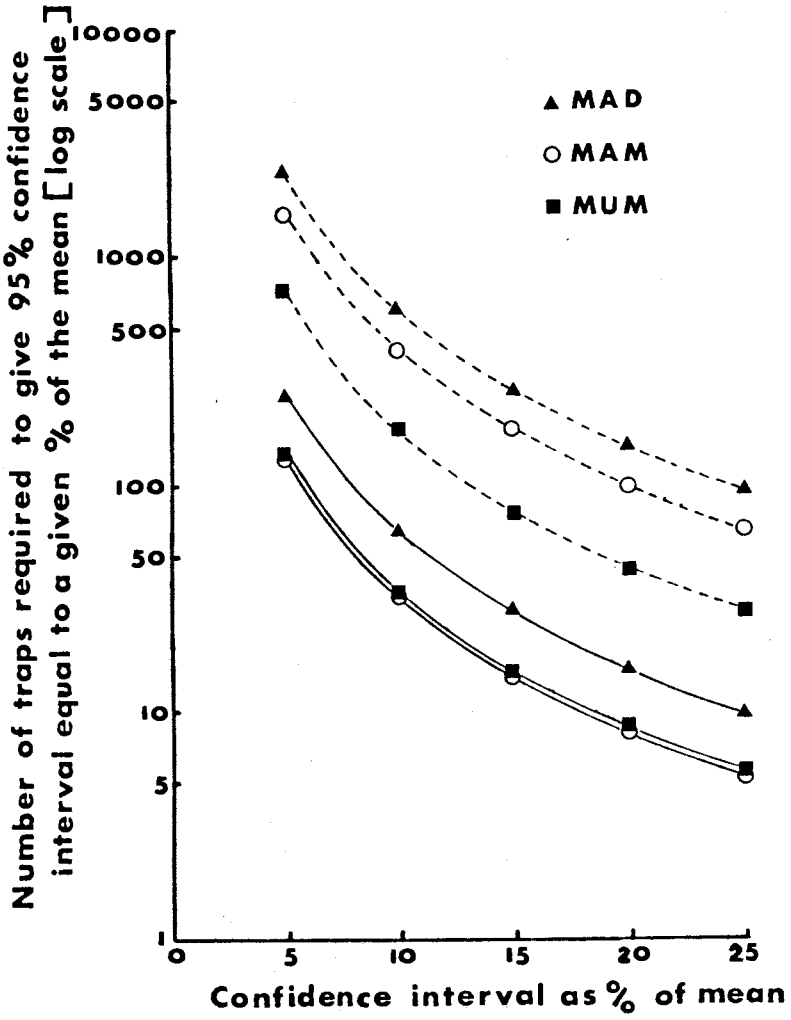


Figure 3.5 Number of 0.5 m^2 traps required to sample leaf litter input (on MAD, MAM and MUM plots) with the 95% confidence interval equal to various percentages of the mean. Solid and dashed lines are for periods of maximum and minimum leaf litter production respectively. Based on Equation 3.1 in text.

Table 3.2 Mean annual weight of leaf fall in individual traps on each site with associated standard errors and 95% confidence limits. Data obtained by summation of 4-weekly collections for individual traps for a 'standard' year.

	Site		
Component	MAD	MAM	MUM
# of traps	40*	37	40
Leaf (mean annual weight - g/trap)	118.04	102.37	70.04
Standard error	± 5.97	± 3.96	± 3.03
C.I. as % of mean	10.2	7.8	8.7

* Traps beneath canopy only considered.

C.I. = confidence interval ($P < 0.05$)

3.3.2 Litter production - The pattern of litter production on each site demonstrates the variability common to most litter fall estimates (Figures 3.6, 3.7, 3.8). The total rainfall for each collection period is shown rather than individual rainfall events as these could not be related to fluctuations in litter production within each sample period. Similarly, mean monthly maximum temperatures are shown to indicate likely seasonal effects. The temperature means are long term means and do not necessarily correspond to those actually recorded during the sampling period. However discrepancies from these

Figure 3.6 Four weekly litter production on the MAD plot - semi log scale. Total rainfall for each collection period is indicated. Maximum temperatures (°) are monthly means for Griffith plotted for collections which include >14 days of the particular month. Note - 2 collections obtained each May.

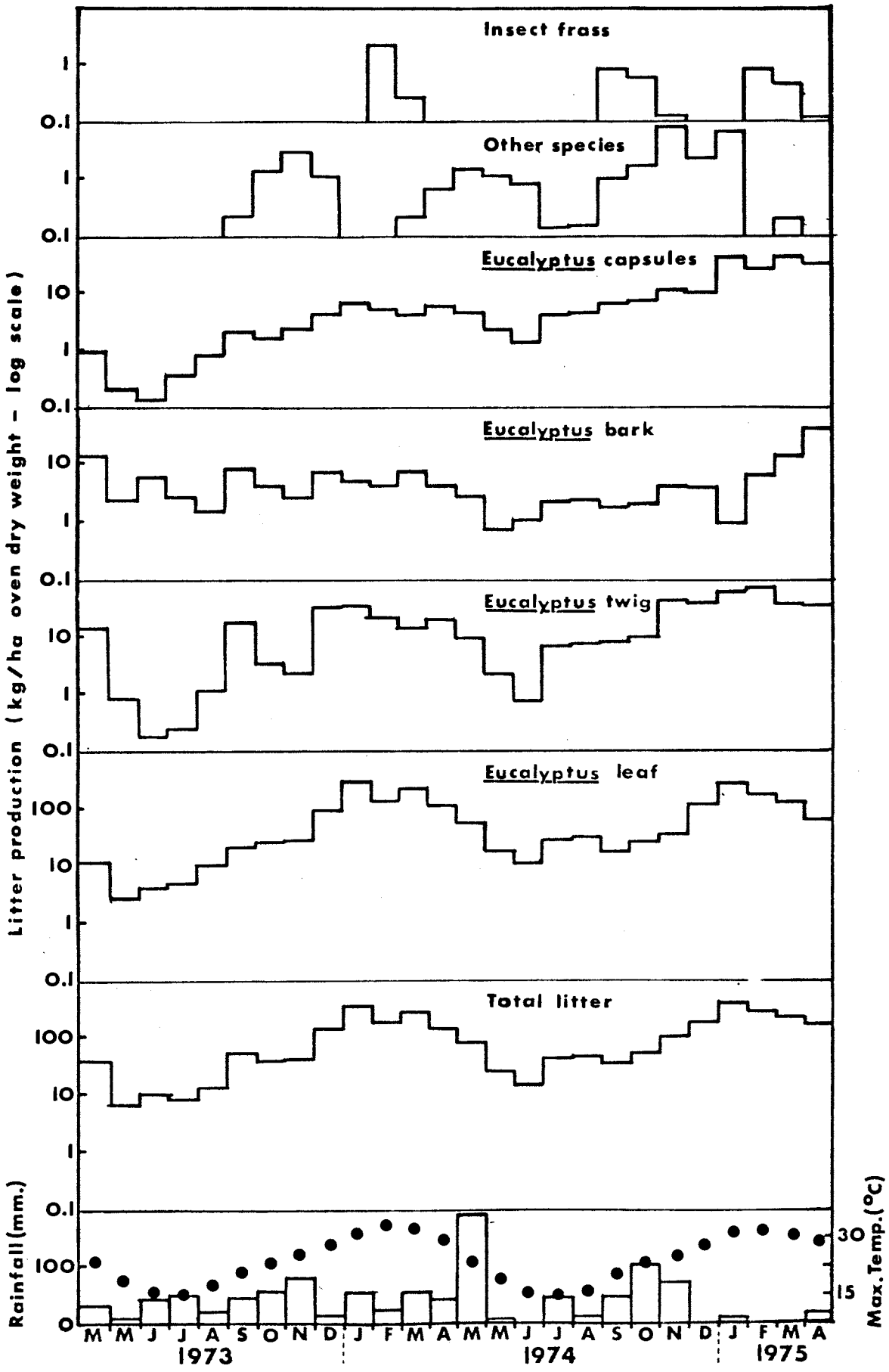

Insect frass
Other species
Eucalyptus capsules
Eucalyptus bark
Eucalyptus twig
Eucalyptus leaf
Total litter
Litter production (kg/ha oven dry weight - log scale)
Rainfall(mm.)
Max.Temp.(°C)
M M J J A S O N D J F M A M M J J A S O N D J F M A
1973
1974
1975

Figure 3.7 Four weekly litter production on the MAM plot - semi log scale. Total rainfall for each collection period is indicated. Maximum temperatures (°) are monthly means for Griffith plotted for collections which include >14 days of the particular month. Note: 2 collections were obtained in May 1974; the range in the vertical axes is variable for different fractions.

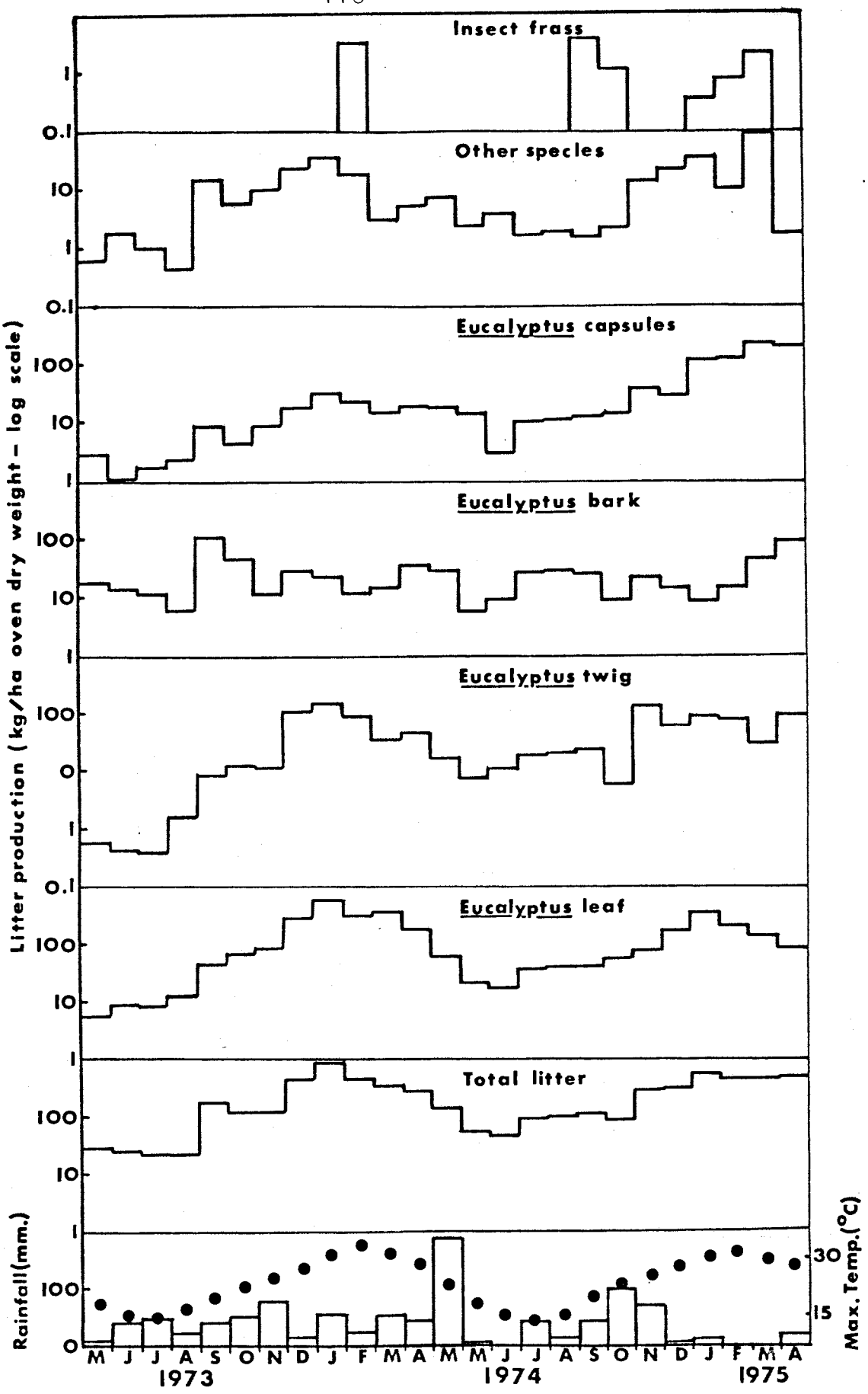
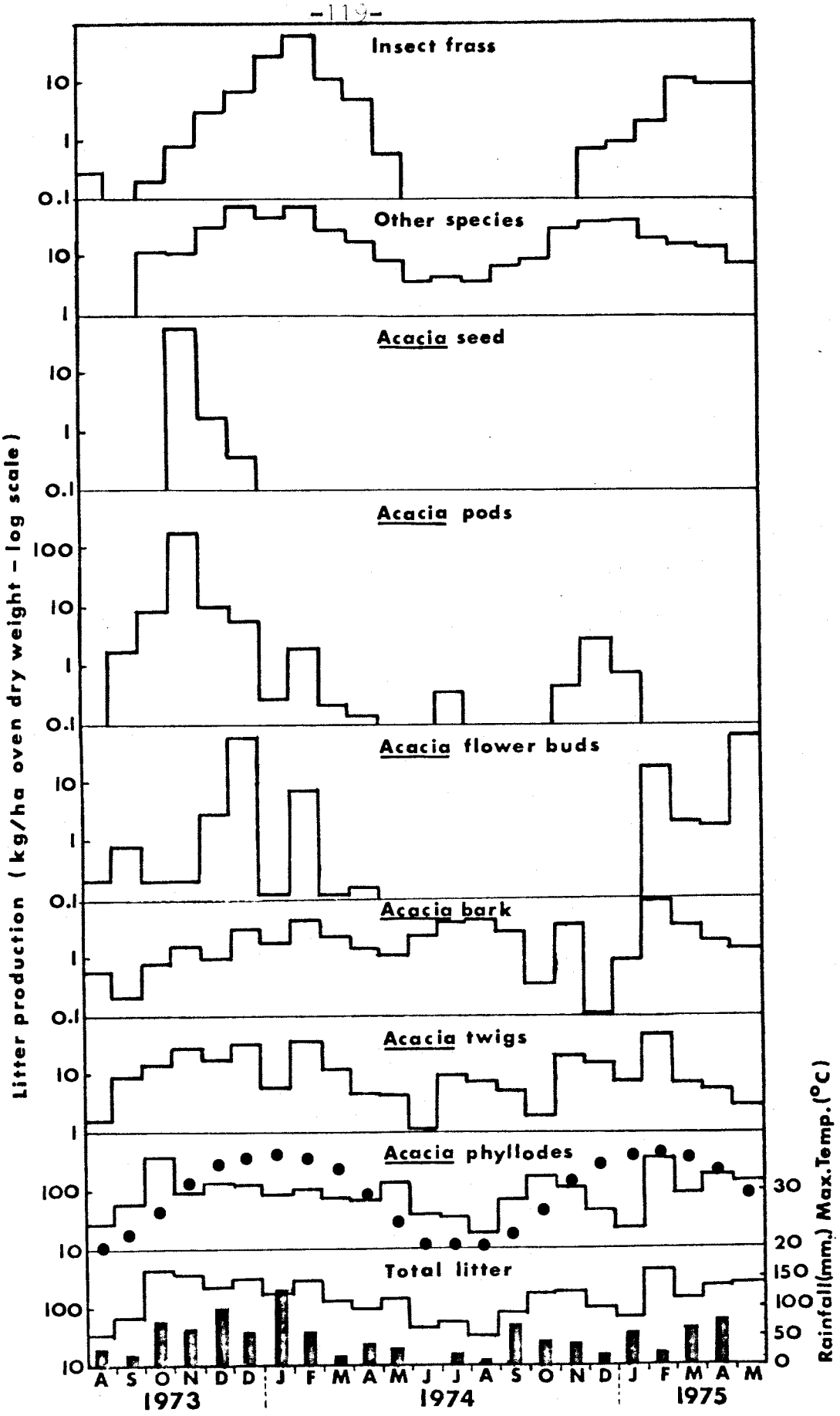

Insect frass
Other species
Eucalyptus capsules
Eucalyptus bark
Eucalyptus twig
Eucalyptus leaf
Total litter
Litter production (kg/ha oven dry weight – log scale)
Rainfall(mm.)
Max. Temp.(°C)
M J J A S O N D J F M A M M J J A S O N D J F M A
1973
1974
1975

Figure 3.8 Four weekly litter production on the MUM plot - semi log scale. Total rainfall (solid bars) and mean maximum temperatures (•) are also indicated for each collection period. Temperatures are mean monthly maxima for Charleville appropriate to each collection. Note: variable range in vertical axes; 2 collections were obtained in December 1973.


Insect frass
Other species
Acacia seed
Acacia pods
Acacia flower buds
Acacia bark
Acacia twigs
Acacia phyllodes
Total litter
Litter production (kg/ha oven dry weight – log scale)
Rainfall(mm.) Max.Temp.(°C)
A S O N D D J F M A M J J A S O N D J F M A M
1973
1974
1975

long term monthly means could be expected to be minimal in the present study.

In Figures 3.6 - 3.8 a logarithmic scale has been used on the vertical axes so that visual comparisons could be made of the pattern of litter fall within all litter fractions. Therefore caution has to be exercised in interpreting the figures since linear distances represent very different values for individual components.

It is apparent that litter production in the mallee (MAD/MAM) is distinctly seasonal with a pronounced mid-summer maximum (Figures 3.6, 3.7). The results are similar to those reported by Holland (1967) for Eucalyptus dumosa and E. socialis and appear fairly general for Eucalyptus spp. in south eastern Australia (cf. Attiwill 1968, Charley and Richards 1974, Ashton 1975a, Specht and Brouwer 1975). For the mulga site a distinct midsummer peak in litter production was also found for the 'other species' fraction (dominated by E. populnea) and this appears to have some influence on the pattern of total litter fall (Figure 3.8).

To test the effects of season (represented by mean monthly maximum temperature) and rainfall on litter production Pearson's product-moment correlation coefficients, r, were calculated for all sites between the former parameters and fractional litter weights as dependent variables (Table 3.3). The correlation coefficients confirm the existence of patterns observed from graphical representation.

Table 3.3 Product-moment correlation coefficients, r, for weights of selected litter fractions and total rainfall and mean maximum temperatures for the collection period.

Site	Dependent Variable	Independent Variables	
		Total rainfall for collection	Mean maximum temperature
MAD	Total litter weight	-0.19	0.84**
	Leaf litter weight	-0.13	0.79**
MAM	Total litter weight	-0.16	0.84**
	Leaf litter weight	-0.07	0.76**
	Capsule litter weight	-0.31	0.55**
MAD/MAM	Mean max. temperature	-0.06	-
MUM	Total litter weight	0.31	0.51*
	Phyllode litter weight	0.21	0.29
	Other species litter	0.38	0.74**
	Mean max. temperature	0.48*	-

* $P < 0.05$ ** $P < 0.01$

Surprisingly there is no significant correlation between phyllode fall in mulga and four weekly rainfall (cf. Wilcox 1960). This may have been due to the masking effect of recording litter deposition from total rainfall for the collection period, rather than that from individual rainfall events. Also this synchronized 'delay' in leaf drop following rain is most apparent in droughted woody perennials (Slatyer 1974) whereas the 1973 rainfall for Charleville was well above average (Chapter 1).

The patterns observed in litter fall are most pronounced for total litter and leaf fractions. Whilst twig fall in the mallee also exhibits a summer peak (Figures 3.6, 3.7) this is less evident for bark litter which tends to fall more uniformly throughout the year. The bark component forms a much greater proportion of total litter in the mallee than it does in the mulga community (Figures 3.6, 3.7, 3.8, Tables 3.4, 3.5).

Deposition of capsules on each mallee plot was far greater in the summer of 1974/75 than it was in 1973/74 (Figures 3.6, 3.7). Such a trend was not unexpected on MAD because more stems reached reproductive size during this period. However the similar pattern on the MAM plot shows that seasonal factors, as well as physiological age of stems, are also important in capsule production (cf. Ashton 1975b).

The observations on flower bud, pod and seed litter yield in Acacia aneura (Figure 3.8) support earlier findings

by Davies (1968, 1973) which showed mulga could flower in any month of the year, but fruit was only set after summer rain and only matured if good winter rain fell. Thus the good flowering (represented by flower bud drop) on the MUM site in December 1973 failed to yield seed the following November although aborted seed pods were produced. However the seed production on this site in November - December 1973 was 63.6 kg/ha which far exceeds the previous best seed production reported from mulga (11.45 kg/ha - Burrows 1973).

Estimates of insect frass falling on each site are approximate only and may greatly underestimate frass production, especially in the mallee. To be retained in the traps frass had to have a high fibre content and be large enough to be caught in the 'mosquito mesh'. In practice this meant that mallee insect frass was derived from sawfly (HYMENOPTERA:PERGIDAE) larvae and that recorded on the MUM site was from migrating spur throated locusts (Austracris guttulosa). Many other herbivorous insects were observed on the mallee - particularly leaf beetles (Chrysomelidae).

The MUM plot appeared to act as a shelter and resting place for migrating locusts in the summers of 1973/74 and 1974/75. There is little evidence of insect browsing on mulga phyllodes and only minimal damage was noted on phyllodes collected in the litter of this study. Since the grass production on MUM was very small (Chapter 2), it was

unlikely to sustain such large locust populations, so that the frass collected on the plot appears to be a definite input into the system. The grassed runways and approaches to the nearby Charleville aerodrome seem to have been an attraction to the locusts sheltering here.

A quantitative assessment of litter fall and its nitrogen and phosphorus content for the entire study period (Tables 3.4, 3.5) shows the dominant input on all plots is from leaf litter. In the mature mulga (MUM site) and the mallee regrowth stand (MAD site) leaf litter made up 64-68% of total litter fall. This is considerably above the 51.3% contribution leaf litter made to total litter deposition on the mature mallee (MAM) site. This latter figure is comparable to the 47.4% recorded by Holland (1967) in his mallee plot at Yara and also similar to that reported for E. obliqua (54% - Attiwell 1968) and E. regnans forests (c. 50% - Ashton 1975a). The accumulated data from these various studies indicate that leaf litter fall in mature Eucalyptus communities makes a lower contribution to total litter fall than the 60-76% reported for northern hemisphere species (Bray and Gorham 1964).

In the drought year 1965/66 twig and bark litter comprised c. 46% of all Eucalyptus litter on the mallee plot studied by Holland (1967) at Yara. This is about double the proportion which these fractions contributed to litter fall in the two mallee sites of the present study.

Table 3.4 Weight, nitrogen and phosphorus content of litter fall on MAD and MAM plots summed for all collections. Figures in parenthesis are the % of total litter fall.

Site	Parameter	Total Litter	Eucalyptus Leaf	Eucalyptus Twig	Eucalyptus Bark	Eucalyptus Capsule*	Other Species	Insect Frass
MAD (740 days)	Weight (kg/ha)	3030.4	2056.8	529.0	165.2	242.1	31.8	5.5
			(67.9)	(17.4)	(5.4)	(8.0)	(1.0)	(0.2)
	N (g/ha)	16062	12495	1623	453	1106	342	43
			(77.8)	(10.1)	(2.8)	(6.9)	(2.1)	(0.3)
	P (g/ha)	961	727	88	15	109	19	2
			(75.7)	(9.1)	(1.6)	(11.4)	(2.0)	(0.2)
MAM (712 days)	Weight (kg/ha)	6164.1	3167.9	1036.4	657.7	947.7	342.8	11.6
			(51.3)	(16.8)	(10.7)	(15.4)	(5.6)	(0.2)
	N (g/ha)	31243	17953	3354	2223	4421	3190	102
			(57.5)	(10.7)	(7.1)	(14.1)	(10.2)	(0.3)
	P (g/ha)	1497	725	136	63	391	178	4
			(48.4)	(9.1)	(4.2)	(26.1)	(11.9)	(0.3)

* Includes flower buds and opercula

Table 3.5 Weight, nitrogen and phosphorus content of litter fall on the MUM plot summed for all collections (661 days). Figures in parenthesis are the % of total litter fall.

Parameter	Total litter	*Acacia* phyllode	*Acacia* twig	*Acacia* bark	*Acacia* flower bud	*Acacia* pod	*Acacia* seed	Other species	Insect frass
Weight (kg/ha)	4099.4	2639.3 (64.4)	304.4 (7.4)	55.1 (1.3)	158.1 (3.9)	228.0 (5.6)	63.6 (1.6)	488.6 (11.9)	155.5 (3.8)
N (g/ha)	64667	41911 (65.0)	4143 (6.4)	586 (0.9)	3521 (5.5)	2955 (4.6)	1952 (3.0)	6490 (10.1)	2908 (4.5)
P (g/ha)	2068	1107 (53.6)	100 (4.8)	17 (0.8)	183 (8.8)	133 (6.4)	141 (6.8)	267 (12.9)	120 (5.8)

As noted previously twig and bark litter are a much smaller component of litter fall on the MUM plot than are similar fractions on MAD/MAM.

The contribution of reproductive structures to litter fall will be greatly dependent on the frequency of heavy fruiting years (Ashton 1975a). In the present work such structures comprised 8.0, 15.4 and 11.1% of total litter fall on MAD, MAM and MUM respectively. These proportions are in broad agreement with the data for tree species (Bray and Gorham 1964) and the arid zone shrub Eremophila gilesii (Burrows 1972). However they are greatly in excess of the 0.2 - 0.6% reported for Eucalyptus regnans (Ashton 1975a).

In keeping with their small biomass (Chapter 2) minor species contribute little to litter fall on the MAD site. For all study plots, litter originating below the height of the traps (40 cm) would naturally be excluded from the present estimates. Proportionately this effect would be greatest with the minor shrubs on the MAD plots, but in terms of community litter fall it could be regarded as negligible.

3.3.3 Nutrient return - Fluxes in nitrogen and phosphorus inputs via litter fall onto these woodland floors reflect similar patterns to the weight dynamics of each litter fraction (Figures 3.9, 3.10, 3.11, 3.12, 3.13, 3.14). But it is also clear that some components of the litter fall are insignificant pathways for community nitrogen and phosphorus movement (e.g. insect frass and other species on

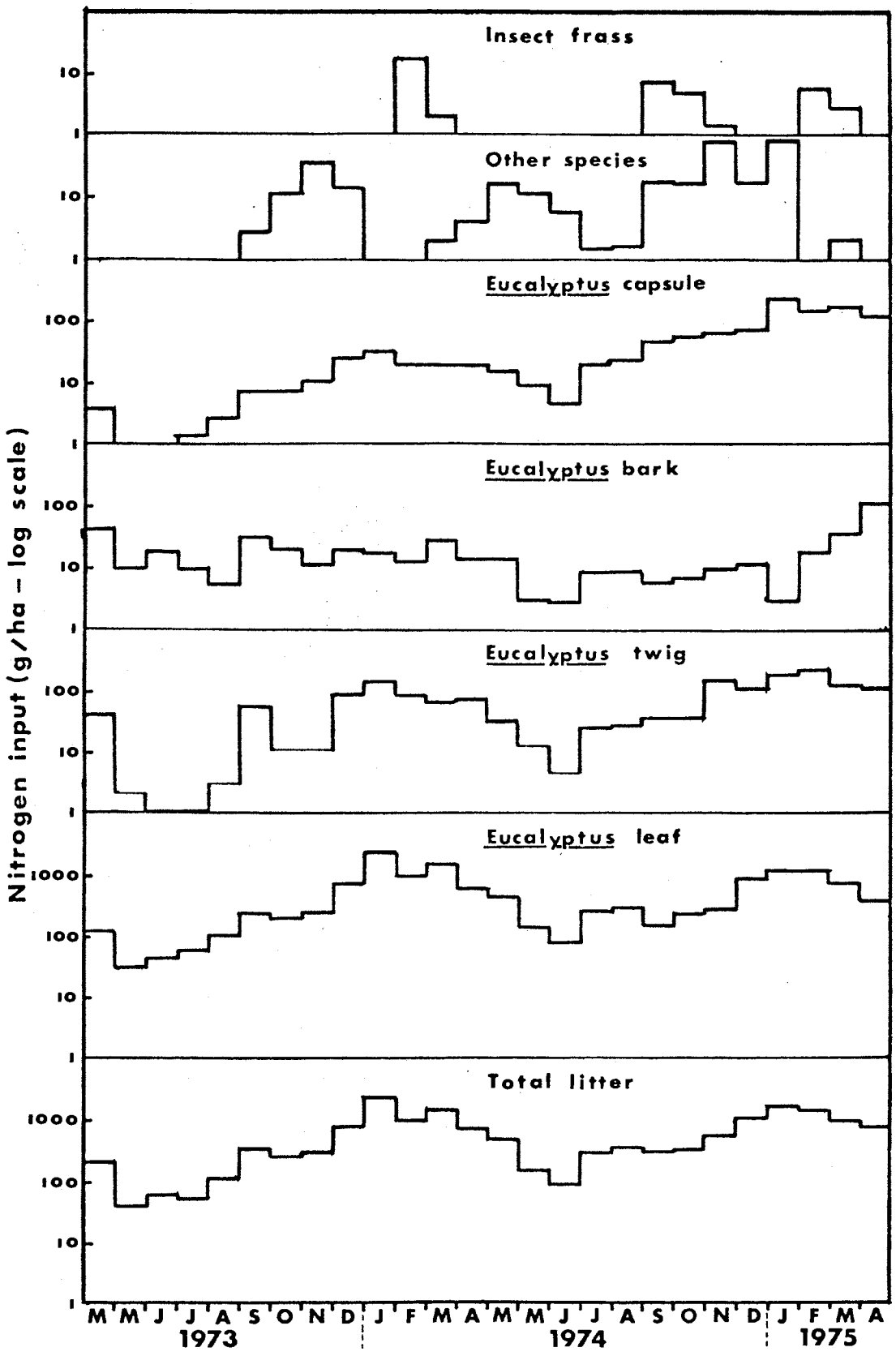


Figure 3.9 Pattern of nitrogen input through various litter fractions into the soil/litter pool (MAD plot) - semi log scale. Data based on four weekly collections with two collections obtained each May.

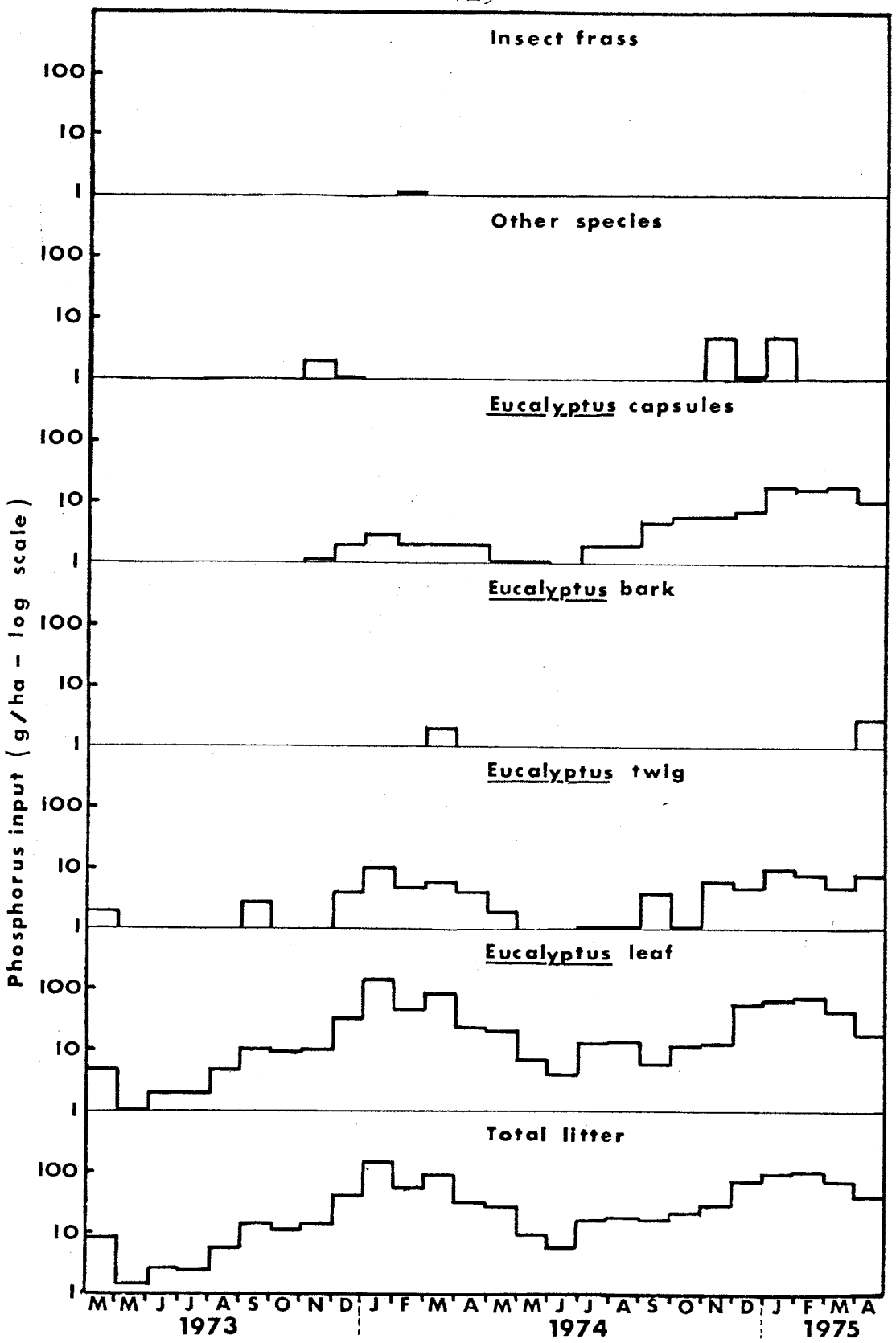


Figure 3.10 Pattern of phosphorus input through various litter fractions into the soil/litter pool (MAD plot) - semi log scale. Data are based on four weekly collections with two collections obtained each May.

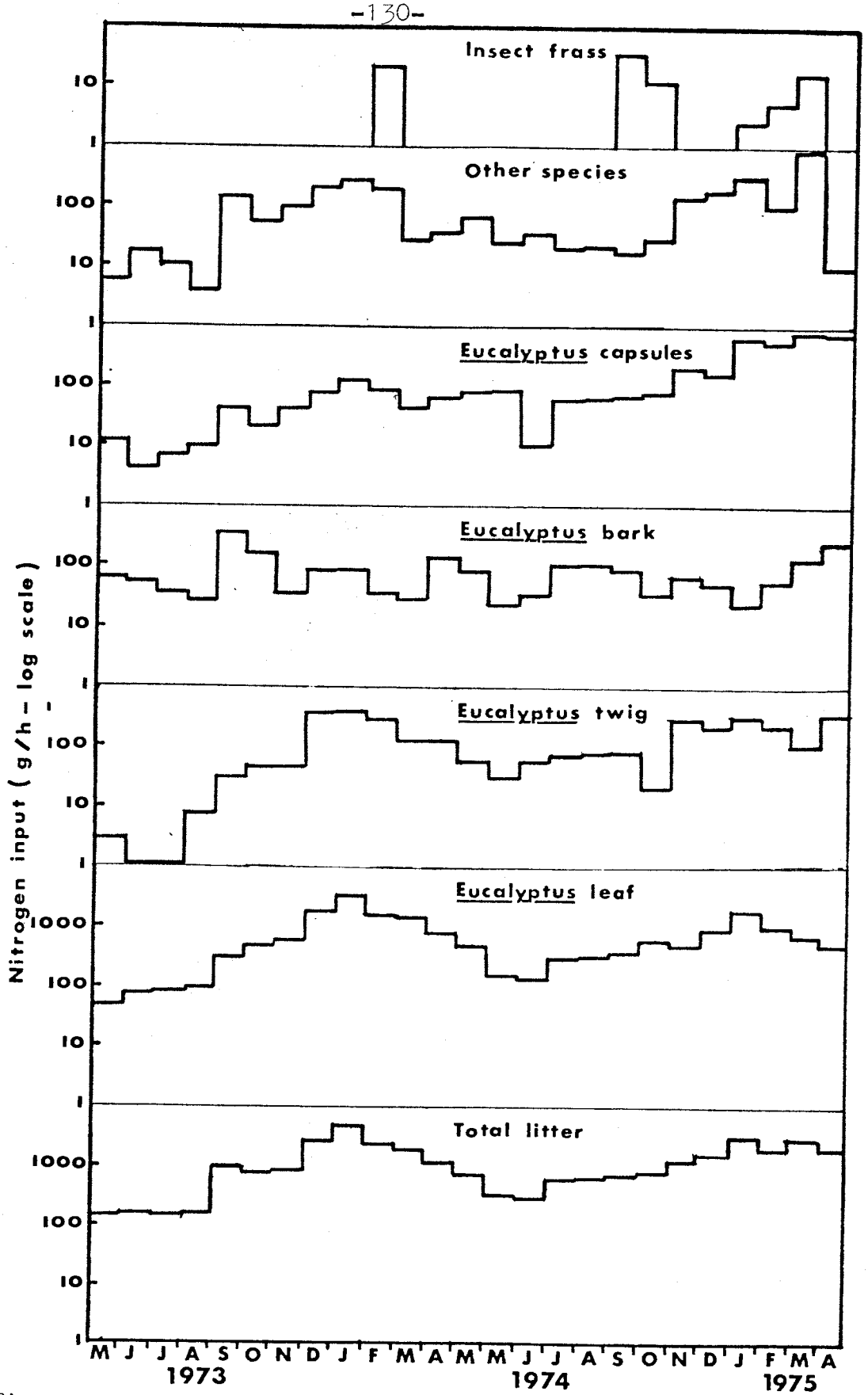


Figure 3.11 Pattern of nitrogen input through various litter fractions into the soil/litter pool (MAM plot) - semi log scale. Data are based on four weekly collections with two collections obtained in May 1974.

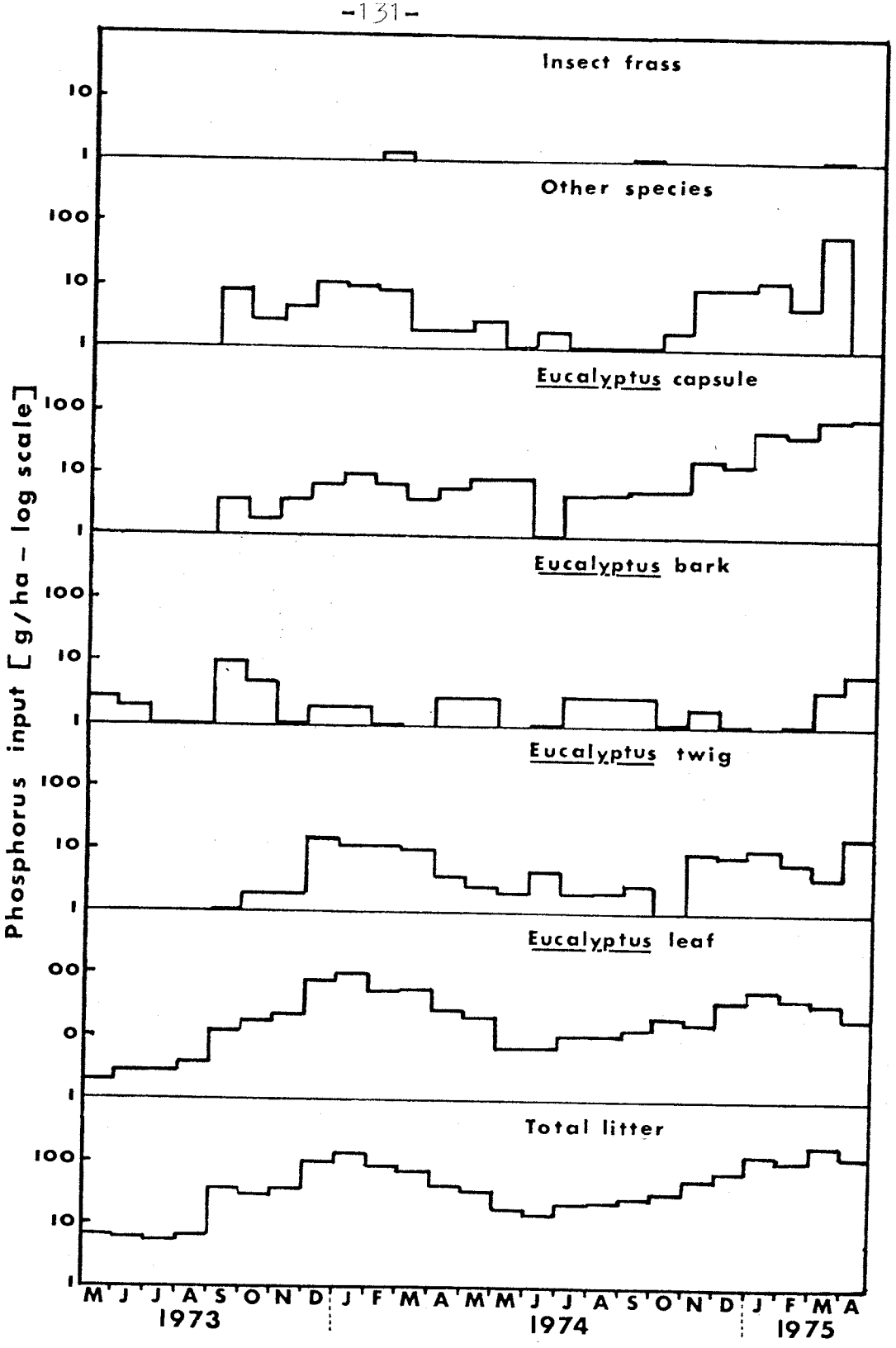


Figure 3.12 Pattern of phosphorus input through various litter fractions into the soil/litter pool (MAM plot) - semi log scale. Data are based on four weekly litter collections with two collections obtained in May 1974.

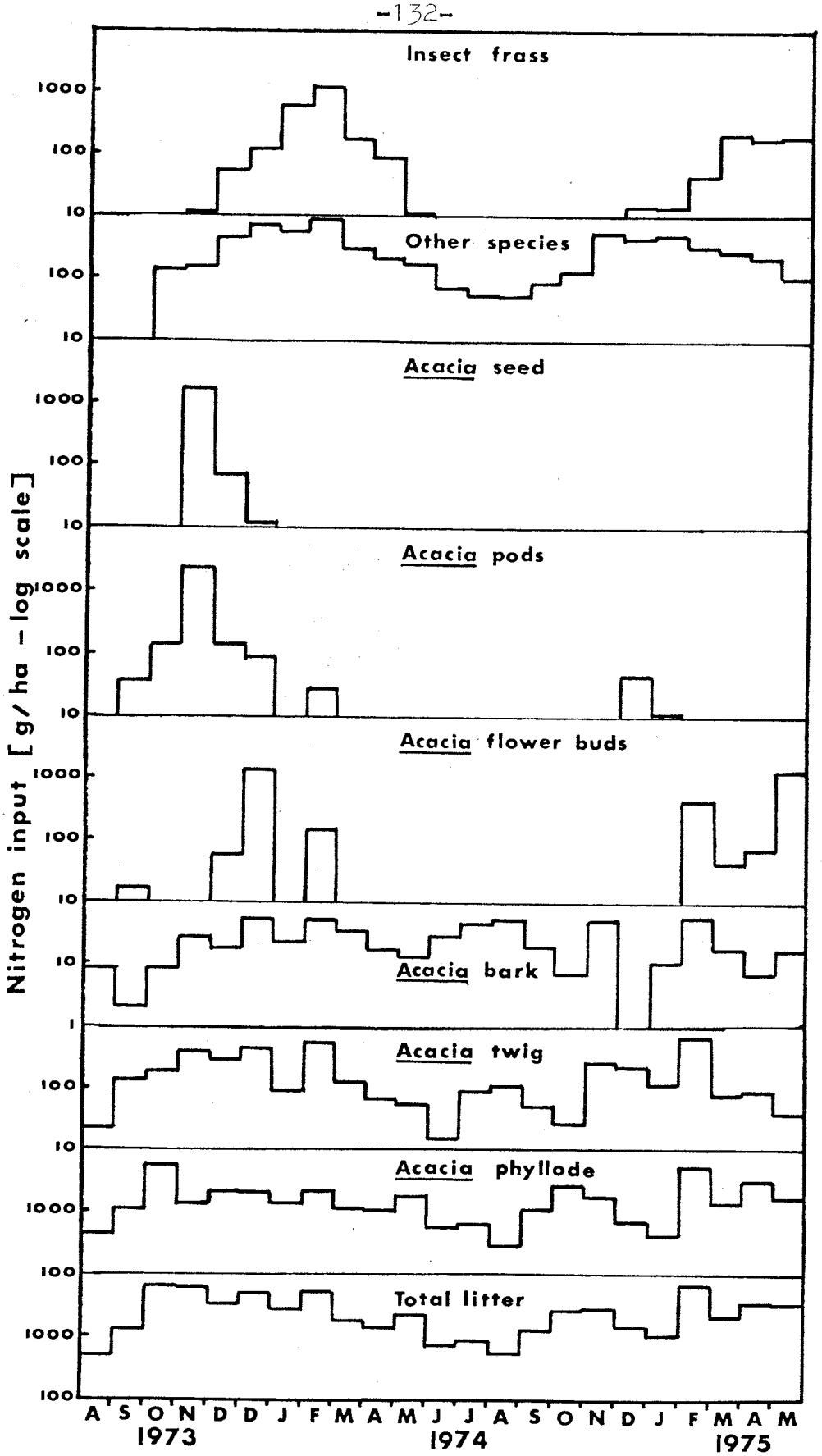


Figure 3.13 Pattern of nitrogen input through various litter fractions into the soil/litter (MUM plot) - semi log scale. Data are based on four weekly collections with two collections in December 1973 and a five week collection at the end of 1974. Note: variable range in vertical axes.

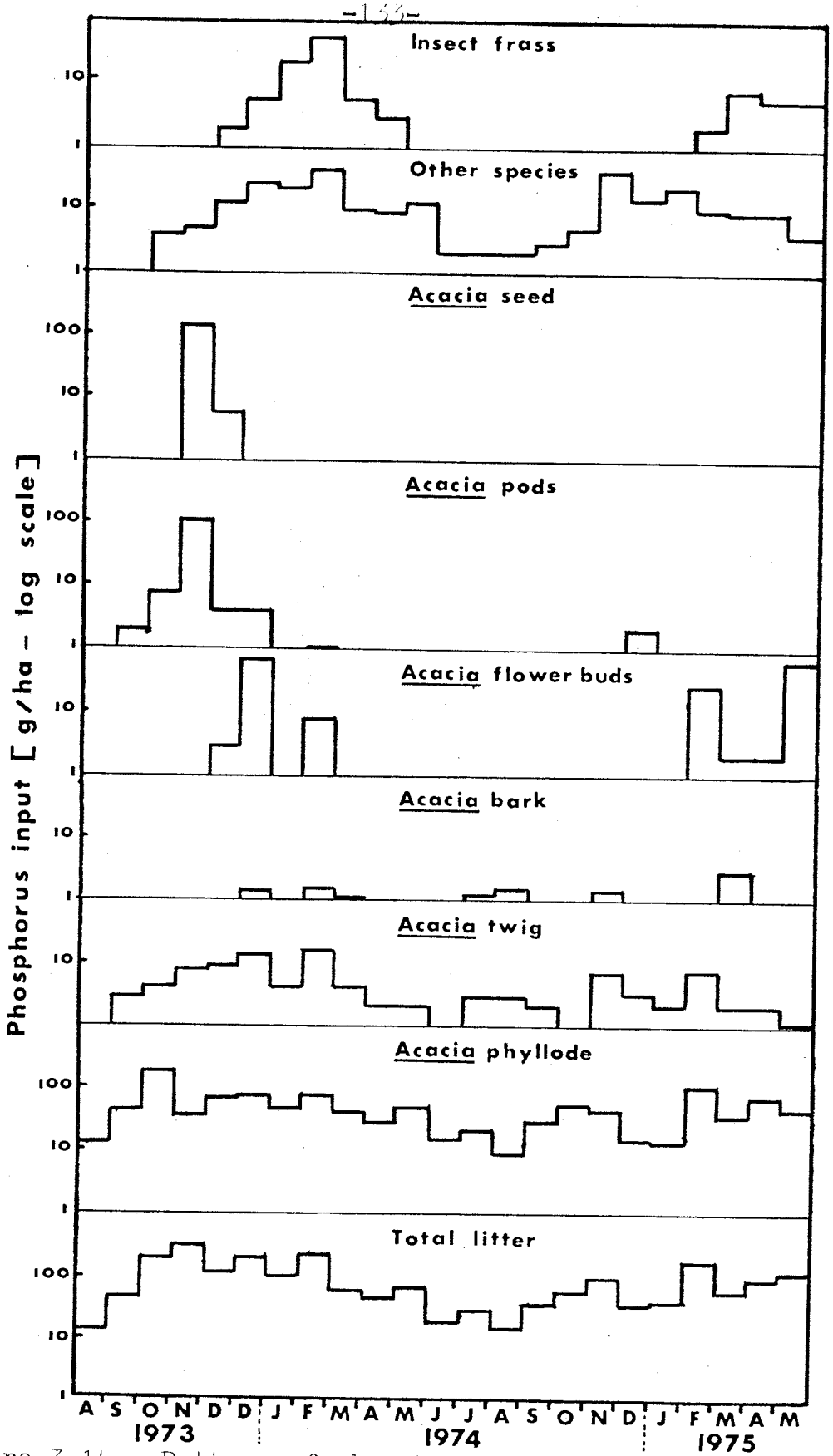


Figure 3.14 Pattern of phosphorus input through various litter fractions into the soil/litter pool (MUM plot) - semi log scale. Data are based on four weekly collections with two collections in December 1973 and a five week collection at the end of 1974.

MAD), while others (e.g. reproductive structures) are of greater importance than their overall weight suggests (Tables 3.4, 3.5). For example, 26.1 and 22.0% of all phosphorus returned in litter is contained within reproductive structure on the MAM and MUM plots respectively while their biomass is only 15.4% and 11.1% of the total respectively.

While leaves make similar contributions to total litter fall on MAD and MUM plots these proportions are appreciably different when nitrogen and phosphorus inputs are considered (Tables 3.4, 3.5). The concentrations of these elements in freshly fallen leaf litter are very consistent throughout the year (Tables 3.6, 3.7). Similar results were obtained in the subtropical forests studied by Webb, Tracey, Williams and Lance (1969). This led these authors to conclude that a single set of mineral analyses of litter taken over a short period should comprise a satisfactory sample for a single year. However such a procedure could be misleading if all litter is combined for analyses (e.g. Spain 1973) as the wide variation in contributions by reproductive structures may result in appreciable under-or over-estimates.

Not unexpectedly nitrogen and phosphorus percentages are most variable in wood and bark tissue. In keeping with the results obtained for live tissue (Chapter 2) these elements are found in much greater concentrations in twig

Table 3.6 Concentrations of nitrogen and phosphorus in components of litter fall on the MAD and MAM plots. Values are means, standard errors (S.E.) and coefficients of variation (C.V.) of all collections for each site.

Site	Statistic	Eucalyptus Leaf		Eucalyptus Twig		Eucalyptus Bark		Eucalyptus Capsule		Other Species		Insect Frass	
		N %	P %	N %	P %	N %	P %	N %	P %	N %	P %	N %	P %
MAD	Mean	0.72	0.038	0.34	0.020	0.31	0.011	0.44	0.046	1.00	0.060	0.79	0.044
	S.E.	0.03	0.002	0.02	0.002	0.01	0.001	0.02	0.003	0.07	0.005	0.06	0.004
	C.V.%	23.7	20.5	22.4	56.4	17.6	47.4	26.2	33.8	29.9	32.0	23.6	26.7
MAM	Mean	0.67	0.029	0.36	0.018	0.34	0.010	0.47	0.041	1.00	0.055	0.87	0.044
	S.E.	0.04	0.002	0.02	0.002	0.01	0.001	0.02	0.002	0.05	0.005	0.08	0.007
	C.V.%	26.3	29.9	20.4	60.7	17.6	34.5	18.4	21.3	19.9	41.0	19.8	35.6

and bark fall on the MUM plot than for similar fractions on MAD/MAM.

Table 3.7 Concentrations of nitrogen and phosphorus in components of litter fall on the MUM plot. Values are means, standard errors (S.E.) and coefficients of variation (C.V.) of all collections for the study period.

Component		Mean (%)	S.E. of mean	C.V. (%)
Acacia phyllode	N	1.64	0.03	10.2
" "	P	0.045	0.002	26.4
Acacia twig	N	1.34	0.04	14.8
" "	P	0.037	0.003	35.0
Acacia bark	N	1.20	0.15	47.0
" "	P	0.031	0.003	39.8
Acacia flower bud	N	2.11	0.05	8.0
" " "	P	0.102	0.006	19.6
Acacia pod	N	1.43	0.09	23.0
" "	P	0.067	0.008	46.0
Acacia seed	N	3.14	0.45	25.0
" "	P	0.213	0.057	46.7
Other species	N	1.45	0.06	20.3
" "	P	0.060	0.006	49.9
Insect frass	N	1.79	0.07	14.1
" "	P	0.067	0.005	28.6

Daily pulses of litter fall and nitrogen and phosphorus input on all sites (Table 3.8) demonstrate the extreme variability observed throughout this study. The maximum rate of litter production on all sites is greater than

that reported for three forest communities in the New England National Park (Charley and Richards 1974), although data for the latter studies only related to 11 months of measurement.

Table 3.8 Daily pulses of litter fall and its nitrogen and phosphorus content into mallee and mulga ecosystems. Minimum (or maximum) rates of litter, nitrogen and phosphorus input do not necessarily correspond to the same collection period.

Parameter	Site		
	MAD	MAM	MUM
Number of litter collections	26	25	23
Mean collection period (days)	28.5	28.5	28.7
Mean rate of litter production (kg/ha/day)	4.09	8.66	6.20
Minimum rate	0.24	1.05	1.22
Maximum rate	13.19	26.79	16.68
Mean rate of nitrogen input (g/ha/day)	21.7	44.1	97.5
Minimum rate	1.4	4.7	17.9
Maximum rate	77.3	131.3	259.5
Mean rate of phosphorus input (g/ha/day)	1.3	2.1	3.1
Minimum rate	0.05	0.2	0.5
Maximum rate	5.1	7.2	5.8

The mean rate of litter fall on the MUM site (6.2 kg/ha/day) is intermediate to that produced in the two mallee stands (Table 3.8). Yet nitrogen input via

litter on MUM is two and four times that on the MAM and MAD sites respectively. The three sites are more similar with respect to phosphorus inputs probably reflecting a 'tighter' cycling of this element.

Bray and Gorham (1964) found that intrinsic losses of about 20% occur in the dry weight of tree leaves before abscission. Concomitant losses in nutrient content are also common (Burrows 1972). Because woody plants rely to a great extent upon the internal cycling of nutrients on soils of low nutrient status (Specht and Groves 1966) it was desirable to examine leaf withdrawal in the nutrient poor communities of the present study.

Three methods of sampling were employed. On all plots leaves were sampled from particular stems, which contained obviously senescent and green material and which could be reached from ground level. To minimise leaf size effects the area of green and dead leaves was determined with an integrating photometer (LAMBDA INSTRUMENTS) and the ratio of leaf weight to leaf area expressed as g/cm^2 (Table 3.9).

On the MAD/MAM plots stems containing some dead crown leaves were observed among those stems harvested for biomass estimates (Chapter 2). In these cases paired collections of dead and green leaves were obtained. The final method of comparison involved mean estimates of nitrogen and phosphorus concentrations in green leaves obtained for biomass predictions and the mean percentage of these elements in the litter fall collections. Both of the

Table 3.9 Withdrawal of nitrogen and phosphorus from mallee eucalypt leaves (MAD/MAM) and mulga phyllodes (MUM) prior to abscission.
Concentration loss = $100 - \left(\frac{\text{concentration in dead leaves}}{\text{concentration in green leaves}} \times 100 \right)$

Site	Leaf Status	Leaf Weight Ratio (g/cm^2)	N (ppm)	P (ppm)	% Weight Loss per Unit Area			% Concentration Loss	
					Dry Weight	N	P	N	P
MAD	Green[1]	0.0378	11719	657					
	Dead[1](n.a.)	0.0328	9462	471	13.2	29.9	37.8	19.3	28.2
	Green[2]		9228	726					
	Dead[2](n.a.)		6385	470	n.d.	(39.9)*	(43.8)	30.8	35.3
	Green[3]		9923	681					
	Dead[3](a)		7201	380	n.d.	(37.0)	(51.6)	27.4	44.2
MAM	Green[1]	0.0327	9475	450					
	Dead[1](n.a.)	0.0249	7132	412	23.8	42.6	31.2	24.7	9.2
	Green[2]		9306	518					
	Dead[2](n.a.)		5773	306	n.d.	(52.7)	(54.9)	38.0	41.0
	Green[3]		9871	518					
	Dead[3](a)		6708	290	n.d.	(48.1)	(57.3)	32.1	44.0

Table 3.9 (Continued)

Site	Leaf Status	Leaf Weight Ratio (g/cm^2)	N (ppm)	P (ppm)	% Weight Loss per Unit Area: Dry Weight	% Weight Loss per Unit Area: N	% Weight Loss per Unit Area: P	% Concentration Loss: N	% Concentration Loss: P
MUM	Green[1]	0.0356	18750	692					
	Dead[1](n.a.)	0.0340	18064	556	4.6	8.9	23.2	3.7	19.7
	Green[3]		20898	1034					
	Dead[3](a)		16379	454	n.d.	(25.2)	(58.1)	21.6	56.1

[1] Leaves from lateral branches that could be reached from the ground.

[2] Leaves from crown of sample trees harvested for regression analysis (Chapter 2).

[3] Green leaf data are means of all regression sample trees, dead leaf data are means of all litter trap samples collected throughout the study.

n.a. not abscissed
a. abscissed
n.d. not determined

* Bracketed estimates are derived assuming similar weight losses to that occurring in leaves from lateral branches.

latter data sets gave means from large numbers of samples and variations in mean leaf area could be expected to be very small.

The results of this study (Table 3.9) show that consideration should be given to the way withdrawal of nutrients from leaves is estimated. It is expedient to measure such withdrawal on the basis of concentration changes (e.g. Ashton 1975a) but the present data indicate that this may lead to appreciable underestimates. Losses in dry weight in mallee eucalypt leaves prior to abscission (Table 3.9) are similar to the general figure of 20% quoted by Bray and Gorham (1964) but much higher than that observed for mulga leaves in this study. It should be noted that these weight changes are between green leaves and 'dead' leaves which have not abscissed. The dead mulga leaves sampled in the latter category were pale green in colour and may have been senescent rather than 'dead'. In any event physiological processes leading to abscission of mulga leaves appear to be most rapid following significant rainfall events (Wilcox 1960) and it is likely that much greater weight losses occur in this period.

It seems reasonable to assume that the observed weight loss in senescent leaves on each site would apply equally to those situations where weight loss was not determined (Table 3.9). If this leads to errors these are most likely to be by way of underestimates, especially for mulga. On this basis the percentage weight loss per

unit area (or withdrawal) of nitrogen and phosphorus from leaves prior to abscission can be derived. Also since method three of Table 3.9 involves the largest number of samples (c. 30 for green and 23 for dead leaves) and the dead leaves have actually abscissed it is probable that these values most closely represent 'true' withdrawal.

Thus phosphorus withdrawal based on method 3 seems similar on all sites (50-60%) but nitrogen withdrawal is most pronounced in mature mallee (48.1%) and is considerably lower in mulga (25.2%). Clearly the leguminous mulga does not rely on a tight internal cycling of nitrogen to maintain its requirements for that element.

By way of contrast the data of Ashton (1975a) indicates appreciable withdrawal of nitrogen (66.6%) from E. regnans leaves. This figure is derived from tissue analysis only but is still much greater than that recorded for the mallee eucalypts. However phosphorus withdrawal by E. regnans is similar to that found in the present study.

3.4 Conclusions

In this study the distinctly seasonal nature of total litter fall in Eucalyptus spp. is contrasted with litter fall from Acacia aneura which appears to be independent of season and rainfall. Nevertheless much of the litter fall seems dependent on growth processes, and environmental conditions which change plant tissue production therefore indirectly affect litter deposition (Bray and Gorham 1964).

Because of the extreme variability of litter inputs it is not practical to obtain statistically satisfactory estimates of litter fall for each four weekly collection period throughout the year. However for periods of maximum fall and for yearly totals satisfactory accuracy and precision may be attained. The precision reached in this study is comparable with the 80% confidence interval equal to 10% of the mean sought for leaf litter estimates by Johnson and Risser (1974) and within the range obtained by Spain (1973) for New South Wales conifer forest.

Withdrawal of nitrogen and phosphorus prior to leaf abscission indicates conservation in the use of these nutrients, especially phosphorus, on all sites. However the withdrawal of those elements does not appear to be as great as one would suppose for such infertile ecosystems. Beadle (1968) concluded from his studies of Australian xeromorphs that withdrawal of nutrients, even phosphorus,

from their leaves was not so markedly different from rainforest leaves that it could be regarded as a special adaptation leading to significant phosphate economy. In the present study Acacia aneura in particular appears to have a limited intrinsic nitrogen cycle. The relatively poor ground flora (both in terms of species diversity and biomass - Chapters 1, 2) and the large volume of surface roots (Chapter 2) suggest both mallee and mulga communities operate on a tight extrinsic rather than intrinsic cycling of nutrients, although taken together the efficiency of both cycles could be high.

There are considerable fluctuations in the pulses of litter and nutrients on to the floors of these woodland ecosystems. These fluctuations must affect subsequent processes of decomposition, mineralization and immobilization. Some of these aspects will be discussed in the following two chapters.

CHAPTER 4

Breakdown, decomposition and nutrient loss from litter components in mallee shrub and mulga woodlands

4.1 Introduction

Whittaker (1970) and Odum (1971) estimate that from 70 to 90 per cent of terrestrial net primary production in natural ecosystems is ultimately utilized by decomposers. Litter fall and litter decomposition also account for a substantial portion of internal nutrient cycling in terrestrial ecosystems. Annual nutrient uptake of a plant may come partly from external sources e.g. in rainfall or fertilizers, but if the nutrient stock is held mainly in organic material, whether living or dead, the stability of the ecosystem must depend on the long term balance between growth and litter mineralization (Satchell 1974). Further, the rate at which nutrients and energy pass through the soil-litter subsystem regulates the productivity of the whole system (Witkamp and van der Drift 1961) and this control function is particularly important in soils with low nutrient capital such as are common in Australia (Charley and Richards 1974).

Studies of litter decomposition in Australian woodland and forest communities have been largely confined to the higher rainfall areas of the south-east (e.g. McColl 1966, Attiwill 1968, Wood 1970, Ashton 1975a, Macauley 1975). There have been no community based studies of decomposition in semi arid shrub or woodland communities, although Charley and Cowling (1968) and Burrows (1972) indirectly

arrived at decomposition times for litter of Atriplex vesicaria and Eremophila gilesii respectively.

The present study examines the breakdown*, decomposition and nitrogen and phosphorus turnover in litter of mallee and mulga communities. Both communities are found on typically infertile soils particularly deficient in available phosphorus (Chapter 2). A detailed study of litter fall (Chapter 3) has estimated the nutrient transfer from mallee and mulga vegetation to organic debris; however, the decomposition of organic debris must be elucidated before one can quantify the transfer of nutrients back to the soil solution to initiate recycling. Furthermore, a number of authors (e.g. Waksman and Gerretson 1931, Witkamp 1966, Williams and Gray 1974) have suggested that the nitrogen content and particularly the carbon/nitrogen ratio of plant material is a critical factor determining

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* The term "breakdown" is used sensu stricto to describe the fragmentation and comminution of the leaf, bark or wood macrostructure while "decomposition" refers to the catabolic degradation of the tissue constituents by soil organisms (see Anderson 1973a). However general usage of "decomposition" implies both breakdown and decomposition per se, and it is in this sense that it is used in this thesis when it is not juxtaposed with breakdown.

its decomposition by soil organisms. As the nitrogen concentration in mulga phyllode litter is about 2.5 times that found in mallee leaf litter (Chapter 3), a comparison of decomposition rates in both mallee and mulga ecosystems would test the generality of this hypothesis.

4.2 Methods

Litter decomposition was studied in mallee (MAD/MAM) and mulga (MUM) communities and detailed descriptions of the sites, their structure, floristics and environment, are given in Chapters 1 and 2. The major emphasis of the present work was on the study of leaf decomposition, since the major proportion of litter fall in mallee and mulga communities arises from leaves (Chapter 3). However the decomposition of branch pieces was also monitored in both communities as well as bark decomposition in the mallee.

4.2.1 Leaf decomposition - The litter bag technique (Gilbert and Bocock 1958, Macauley 1975) was used in this study. Criticisms of the technique have been raised - for example, that it underestimates "true total decomposition" because it prevents leaf consumption by larger arthropods, earthworms and invertebrates(Witkamp and Olson 1963); that it maintains the micro-environmental characteristics of the surface litter layers and does not follow the breakdown and decomposition pattern of a typical leaf litter year class

(Anderson 1973a); and that significant spillage inaccuracies may arise, particularly when the litter becomes fragmented and finely divided (Sufling and Smith 1974).

One advantage of the litter bag technique is that it maintains the physical and chemical identity of the material under study. This is important where nutrient fluxes are being followed. Furthermore, while the criticisms of the technique are valid, they suggest to some extent compensating errors which may not greatly mask the "true" pattern of decomposition.

Litter bags used in this study differed between mallee and mulga sites; the objective being to use the largest mesh size which would retain the decomposing leaves yet allow movement of at least the smaller soil fauna. In the mallee site terylene mesh bags (40 x 25 cm) of mesh size 5 x 4 mm were used to confine the leaves. On the mulga study area fibre glass bags (30 x 30 cm) and mesh size (2 x 2 mm) were employed.

A feature of semi arid mallee and mulga vegetation is that litter mats tend to build up around the base of plants with the wide interstices often consisting of a bare soil surface. This suggested that different microenvironmental effects could influence litter decomposition within the communities. To test this hypothesis it was decided to secure the litter bags for both communities in each of three possible microsites viz. on 'young' litter mats arising from regrowth vegetation, on the soil surface and on a mature litter mat beneath a well developed stand.

Each of these microsites would in turn be subjected to different rates, amounts and nutrient contents of organic matter input. For the mallee this was achieved by positioning bags on litter beneath the canopies of the MAD site (LD), on the soil surface of the intercanopy area of the MAD site (LG) and on the litter mat of the MAM site (LM). For the mulga plot an area of regrowth (1956 germination) 200 m from the MUM study area provided a 'young' litter mat (D) while bags were also positioned on the soil surface (G) and mature litter mats within the MUM site itself (M).

At the time of commencement of this decomposition study the between plant variability of nitrogen and phosphorus concentration within freshly fallen litter was unknown (see Chapter 3). To provide uniform material to place in the litter bags mature green leaves were therefore harvested from a single plant from the respective mallee and mulga sites. The mallee leaves chosen were from Eucalyptus socialis since it was the dominant mallee species. Leaves for each study area were bulked, thoroughly mixed and air dried. Subsamples were retained for determination of oven dry weight* and nutrient analysis. Mallee leaf decomposition was studied only on MAD/MAM and mulga phyllode decomposition studied only on MUM.

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* Samples dried to constant weight at 80° C

Leaf 'litter' placed in each bag was weighed to within 0.01 g and was equivalent to about two thirds of the annual deposition from the canopy. The amount of litter enclosed approximated the natural spatial distribution of leaf litter existing in the communities (cf. Reader and Stewart 1972). Thus on an oven dry basis c. 8 g (80 g/m^2) of mallee leaf was accurately weighed into the mallee bags. Similarly c. 7.4 g (82g/m^2) of mulga phyllodes was placed in the mulga litter bags. Each bag was identified with individually labelled embossed tape and sealed with terylene stitching.

The bags were positioned in randomly placed plots on each microsite (treatment) in May and July 1973 for mallee and mulga study areas respectively. A plot consisted of six bags. The leaves in each bag were separated as far as possible to minimise overlap before the bags were secured in place.

Six randomly chosen bags were collected from each microsite at 4-weekly intervals, although an initial 2 week decomposition sample was also obtained from the mallee study.

A total of 22 collections was made from both mallee and mulga communities (i.e. 22 collections x 3 microsites x 6 bags per microsite = 396 bags collected from each study area).

To minimise contamination and loss of fragmented material each sample collected was carefully raised from

the litter surface and placed in clean polythene bags for transport to the laboratory for processing. In the laboratory the leaf material was removed from the mesh, brushed free of clinging soil and the fresh weight recorded. Subsamples were retained for determination of oven dry weight, chemical composition and identification of fungal colonizers (see Chapter 5).

4.2.2 Bark decomposition - Similar procedures to those adopted with leaf litter bags were followed to record bark decomposition in the mallee.

The bark used was obtained from E. socialis clumps on the MAM site in April 1973. It was hanging beneath aerial branches and was presumed to have decorticated the previous summer. The collected bark was cut into strips c. 30 cm long, bulked, thoroughly mixed and air dried. Subsamples were kept for determination of oven dry weight and nutrient content.

Approximately 11 g of bark (accurately weighed to 0.01 g) was placed in each of the bark litter bags, which were identical with those employed in the mallee leaf study. Similarly the bark samples were randomly positioned in plots of 6 bags on 3 microsite areas viz. on litter beneath canopies of the MAD site (BD), on the soil surface of the intercanopy area of the MAD site (BG) and on the litter mat of the MAM site (BM).

Six randomly chosen bags were collected from each microsite at about 8-weekly intervals commencing May 1973.

A total of 12 collections was made altogether (i.e. 12 collections x 3 microsites x 6 bags per microsite = 216 bags). On return to the laboratory bark samples were brushed free of soil particles, dried to constant weight at 80° C and weighed. Representative subsamples were retained for nutrient analysis.

4.2.3 Branch decomposition - Standing dead branches were collected from both mallee and mulga destructive study areas. The samples were brought back to the laboratory where they were sectioned into 25 cm lengths, dried to constant weight at 80° C, weighed and labelled with an aluminium tag attached with wire. Small subsamples were bulked for subsequent nitrogen and phosphorus analysis. Dead bark was still attached to each branch piece which was between 2-3 cm in diameter and had an initial weight of 50-200 g.

Mallee branch pieces were divided into two equal groups which were randomly positioned on the MAD and MAM plots respectively. Mulga branch pieces were randomly placed on the MUM plot. Each sample was laid flat on the litter or soil surface and fixed in position by attaching the label wire to a 15 cm nail driven into the ground.

Randomly selected branch pieces (8 per collection on MUM, 3 per collection on MAD and MAM) were gathered at 3-6 month intervals throughout the course of the study. The samples were initially positioned in the field in June and

July 1973 for MAD/MAM and MUM respectively. There were a total of 6 collections for MUM and 7 for MAD/MAM. The collected branch pieces were placed in plastic bags for transport to the laboratory where they were dried to constant weight at 80° C, weighed and subsamples taken for nutrient analysis.

4.3 Results and Discussion

4.3.1 Leaf litter - The dry weight loss of leaf litter in mallee and mulga study areas is shown in Figures 4.1 and 4.2 respectively. The pattern of leaf breakdown and decomposition is similar in both community types. There was a rapid loss of weight in the first four to eight weeks following placement of the leaves in the field and a more gradual decline thereafter. This effect, which is thought to be associated with leaching losses, has been observed in other leaf decomposition studies (Bocock 1963, Gosz et al 1973). In fact, average weight losses during the first 12 weeks decomposition on both sites are very similar to those reported for Eucalyptus regnans leaf litter (Ashton 1975a).

It is apparent from Figures 4.1 (a) and 4.2 (a) that between bag variability is quite high, as evidenced by indicative 95% confidence bars as decomposition progressed. This variability has masked comparisons of microsites

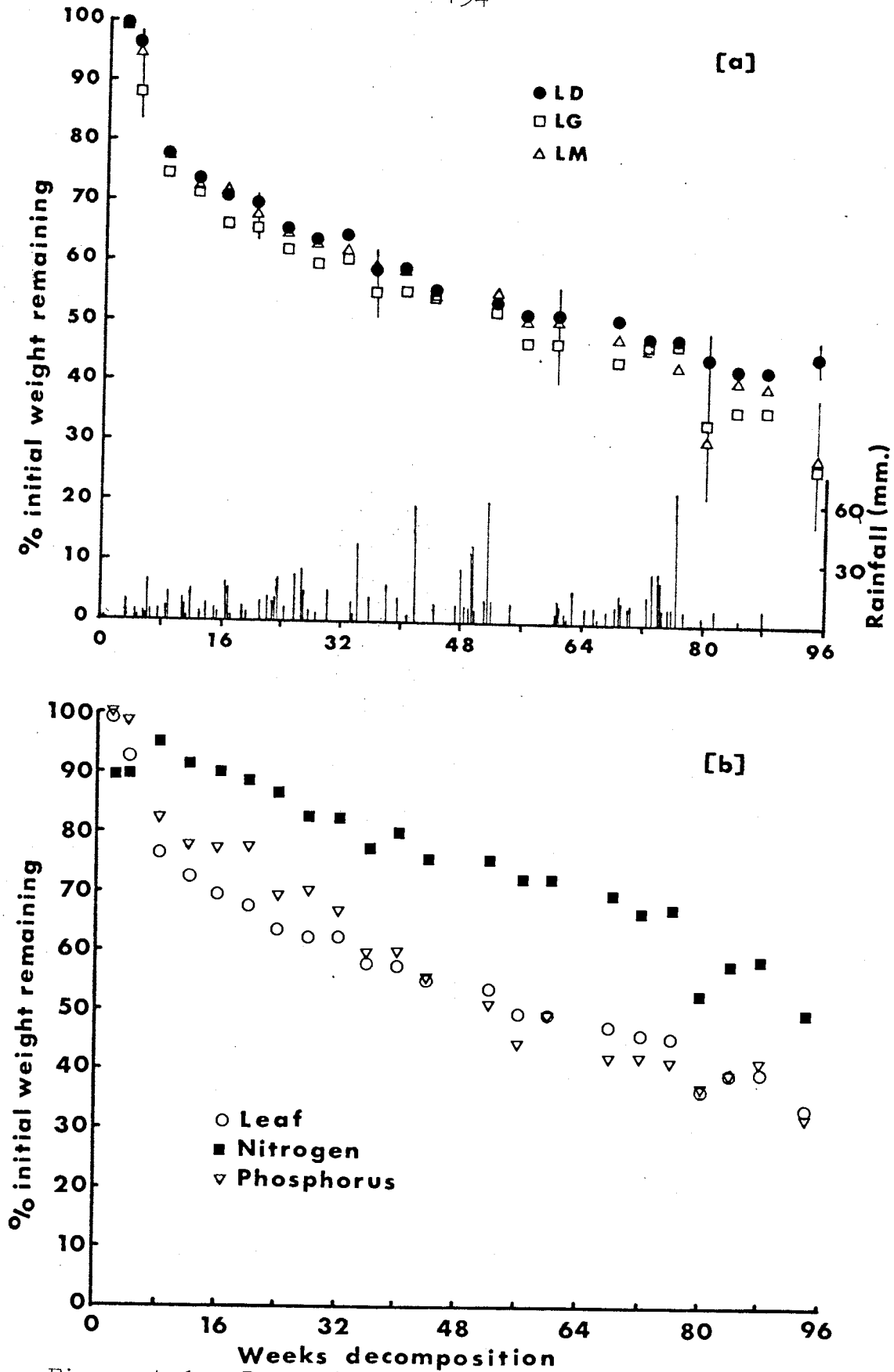


Figure 4.1 Percentage initial dry weight (a) and percentage initial weight of nitrogen and phosphorus (b) remaining in decomposing mallee leaves with time. See text for description of microsites (LD, LG, LM). Indicative 95% confidence bars are shown for some points. Rainfall during the period of study is also indicated.

within individual collection periods, although there is a general trend for the leaves placed on regrowth litter mats (LD and D) to lose weight at a slower rate than on the other microsites studied.

Much of the bag weight variability is thought to be due to loss of fragmented material from the litter bags (cf. Suffling and Smith 1974) and this effect became more pronounced as decomposition time increased. The effect was most noticeable for the mulga litter bags even though these were of finer mesh size than those used in the mallee study. The veins of mallee leaves were more resistant to decomposition than the inter-venal tissue and this helped to maintain the structure of the decomposing leaves on the mallee site.

For some collection periods and microsites there were apparent absolute increases in the mean weight of litter bag contents compared with the previous collection. Similar absolute increases in the weight of decomposing leaves were recorded in the litter bag study of Gosz et al (1973). These authors attributed the gains to contamination by current litter fall and/or an increase in the population of decomposing heterotrophs. In the present work contaminating material was commonly a different colour to that of the decomposing leaves and was removed before the leaf weight was recorded. Further, while increases in the heterotroph population may have partly contributed to observed weight gains, it is likely that fragmentation losses,

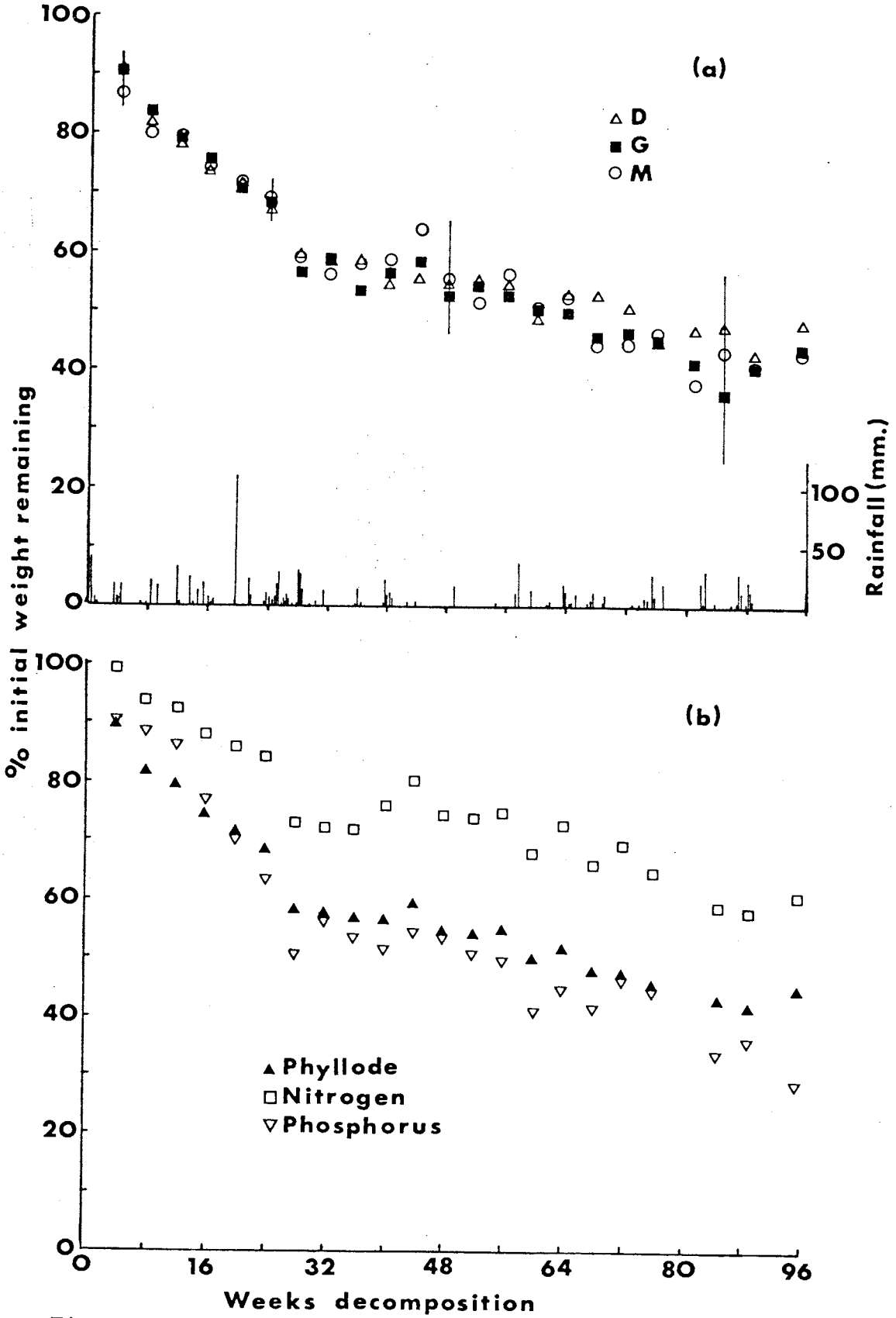


Figure 4.2 Percentage initial dry weight (a) and percentage initial weight of nitrogen and phosphorus (b) remaining in decomposing mulga phyllodes with time. See text for description of microsites (D, G, M). Indicative 95% confidence bars are shown for some points. Rainfall during the period of study is also indicated.

Table 4.1 Leaf decomposition regression parameters. Regressions are in the form $\log_e Y = a + bX$ where Y = % leaf remaining and X = decomposition time (weeks). See text for description of sites.

Site	Intercept (a)	Intercept (%)	Regression coefficient (b)	S.E. of b	Significance of regression	R^2
Mallee						
LD	4.4513	85.7	-0.0081	0.0006	$P < 0.001$	0.90
LG	4.4664	87.0	-0.0111	0.0007	$P < 0.001$	0.93
LM	4.5034	90.3	-0.0107	0.0007	$P < 0.001$	0.92
LG + LM combined	4.4847	88.6	-0.0109	0.0006	$P < 0.001$	0.93
Mulga						
D	4.1143	82.4	-0.0073	0.0006	$P < 0.001$	0.86
G	4.4467	85.3	-0.0085	0.0006	$P < 0.001$	0.90
M	4.4497	85.6	-0.0089	0.0006	$P < 0.001$	0.91
D + G + M combined	4.4351	84.4	-0.0082	0.0005	$P < 0.001$	0.91

as outlined previously, are the major reasons for this inconsistency.

The effect of microsite on decomposition in each study area may be compared by fitting regressions to weight losses of litter over the period of all collections. This approach detects the trends which may be masked between individual collections by the sampling errors previously outlined. The regressions (Table 4.1) are based on the assumption that there were constant fractional weight losses from the litter (i.e. a constant negative slope) estimated by the regression coefficient (b) for the natural logarithm of weight remaining in the bags as a function of time (Jenny et al 1949, Olson 1963) i.e.

$$\log_e \frac{Wt}{Wo} = a - bt$$

where Wt = weight remaining in the bag at time t

Wo = initial weight of material placed in the bag

t = decomposition time (weeks)

The assumptions underlying this model of decomposition will be examined later on in the discussion.

Differences in the rate of decomposition between microsites were examined by comparison of the respective microsite regression coefficients (Table 4.1), using the method of Steel and Torrie (1960). For the mallee site there was no significant difference between the rate of decomposition in leaves placed on bare ground (LG) and mature litter (LM) but both groups decomposed significantly faster ($P < 0.01$) than those placed on a regrowth litter mat (LD). Concomitant

microenvironmental data was not collected in this litter study but the litter mat of the MAD site had built up around the base of clumps so that LD litter bags were perched well above ground level. This contributed to an overall drier environment for litter bags here than for corresponding bags placed on the soil surface or on the MAM litter mat. On the other hand greater temperature extremes would have been experienced by the litter placed on the open soil surface of these red earth soils (Burrows 1973) but this did not seem to lead to faster decomposition rates for the LG litter compared with that placed beneath the canopy of the mature mallee shrub land (LM bags). Also there are indications that soil microfauna remain active even throughout the hottest months in the mallee (Greenslade and Greenslade 1973). A further possible effect could be that the species composition of fungal decomposers present on the LD litter was different to that prevailing in litter placed on the soil surface or mature litter mat. This possibility will be examined in Chapter 5.

Comparison of the slopes of the regressions for the mulga microsites (Table 4.1) showed no significant differences in the rates of decomposition. There was no great difference in the depth of litter mats in the D and M treatments here. Also, the regrowth area on which the D litter bags were placed was surrounded by mature mulga woodland so the proximity of litter types could have minimised differences between sites in the range of

decomposer organisms present. Furthermore, to obtain sufficient 'soil surface' (G) microsites it was necessary to rake back the existing litter mat within the MUM community to position some of the bags. Taken together these observations suggested that for the mulga community there were few real differences in the environment of each of the microsites and it is therefore not surprising that rates of decomposition were similar on them.

Since there were no significant differences in the D,G or M treatments it is permissible to combine these treatments to obtain a common regression line. Similarly the LG and LM treatments can be combined for the mallee site. Comparison of the decomposition rates of these overall regressions (D + G + M vs LG + LM) show a slightly greater decomposition rate for mallee leaves compared with mulga phyllodes ($P < 0.05$). However it must be emphasized that this similarity could be purely coincidental, given the widely different geographical location of the mallee and mulga communities studied. Climatic variability is of obvious importance and the different rainfall incidences for each site collection period are shown in Figures 4.1a and 4.2a. Moreover greater losses of fragmented material could have been expected from the larger mesh size of the mallee litter bags. Nevertheless this possible source of error was well appreciated throughout the study, and particular care was taken to minimise such losses at each collection.

Table 4.2 Mean concentration ± S.E. for nitrogen and phosphorus in mallee leaves after various periods of decomposition. Leaves were placed in position (0 time) on 3rd May, 1973. Sample Size = 6 for both elements. See text for description of treatments LD, LG, LM.

Elapsed time (weeks)	LD		LG		LM	
	N (ppm)	P (ppm)	N (ppm)	P (ppm)	N (ppm)	P (ppm)
0	10157 ± 141	529 ± 10	10157 ± 141	529 ± 10	10157 ± 141	529 ± 10
2	9116 ± 182	573 ± 12	9067 ± 251	502 ± 32	9348 ± 228	539 ± 22
4	9500 ± 289	560 ± 6	10527 ± 242	577 ± 13	9489 ± 156	553 ± 9
8	12238 ± 273	553 ± 16	13215 ± 252	576 ± 14	12545 ± 229	579 ± 16
12	12751 ± 132	576 ± 11	13339 ± 221	572 ± 11	12590 ± 869	567 ± 39
16	12764 ± 271	579 ± 8	13462 ± 477	575 ± 20	13217 ± 238	612 ± 16
20	13114 ± 180	633 ± 18	13661 ± 204	594 ± 13	13579 ± 272	623 ± 17
24	13867 ± 225	599 ± 20	14324 ± 232	533 ± 19	13424 ± 203	584 ± 21
28	13731 ± 407	631 ± 17	13539 ± 329	546 ± 15	12275 ± 594	584 ± 14
32	13245 ± 250	603 ± 25	13172 ± 316	518 ± 24	13912 ± 528	573 ± 8
36	13305 ± 501	557 ± 29	14238 ± 301	545 ± 15	13227 ± 407	533 ± 9
40	13565 ± 267	547 ± 16	14241 ± 289	528 ± 14	14664 ± 331	580 ± 14

Table 4.2 (Continued)

Elapsed time (weeks)	LD		LG		LM	
	N (ppm)	P (ppm)	N (ppm)	P (ppm)	N (ppm)	P (ppm)
44	13970 ± 341	567 ± 27	13777 ± 480	517 ± 15	14024 ± 190	523 ± 11
52	14566 ± 303	523 ± 6	14093 ± 473	459 ± 21	14102 ± 309	524 ± 11
56	15208 ± 462	520 ± 24	14061 ± 413	428 ± 23	14827 ± 203	459 ± 22
60	15321 ± 415	564 ± 12	14987 ± 275	489 ± 10	14281 ± 252	520 ± 16
68	14887 ± 326	493 ± 13	13973 ± 374	414 ± 10	15348 ± 293	480 ± 8
72	14729 ± 255	509 ± 17	13978 ± 452	447 ± 12	14634 ± 423	483 ± 6
76	14902 ± 174	497 ± 12	16050 ± 726	477 ± 0	15483 ± 794	673 ±141
80	15200 ± 444	514 ± 17	15164 ± 257	500 ± 9	13939 ± 388	464 ± 17
84	14672 ± 487	538 ± 27	14646 ± 222	513 ± 8	14798 ± 282	531 ± 19
88	15137 ± 156	588 ± 25	15271 ± 466	510 ± 29	15237 ± 316	561 ± 14
96	15473 ± 126	517 ± 20	15624 ± 567	552 ± 19	13321 ± 469	433 ± 33

Table 4.3 Mean concentration ± S.E. for nitrogen and phosphorus in mulga phyllodes after various periods of decomposition. Phyllodes were placed in position (0 time) on 13th July 1973. Sample size = 6 for both elements. See text for description of treatments D, G and M.

Elapsed time (weeks)	D		G		M	
	N (ppm)	P (ppm)	N (ppm)	P (ppm)	N (ppm)	P (ppm)
0	24100 ± 455	968 ± 32	24100 ± 455	968 ± 32	24100 ± 455	968 ± 32
4	26745 ± 522	948 ± 38	27326 ± 567	1024 ± 24	25988 ± 591	950 ± 30
8	27368 ± 508	1042 ± 31	27930 ± 293	1066 ± 22	27737 ± 282	1061 ± 23
12	28081 ± 459	1101 ± 25	27943 ± 303	1034 ± 25	28400 ± 226	1042 ± 13
16	28407 ± 481	1025 ± 26	28227 ± 295	984 ± 27	28831 ± 351	1002 ± 22
20	28733 ± 502	951 ± 28	28513 ± 286	935 ± 25	29262 ± 503	962 ± 27
24	29591 ± 561	898 ± 14	28798 ± 236	886 ± 23	29693 ±1005	923 ± 34
28	30091 ± 839	914 ± 36	28789 ± 250	736 ± 22	31126 ± 794	879 ± 42
32	30976 ± 985	1035 ± 38	28925 ± 665	817 ± 36	30756 ±1058	948 ± 18
36	32515 ±1158	959 ± 41	28116 ±1062	777 ± 44	31021 ±1671	1008 ± 21
40	34352 ± 471	953 ± 41	30801 ± 443	797 ± 26	33329 ± 494	906 ± 15
44	33473 ± 389	1008 ± 42	30504 ± 545	816 ± 26	33888 ± 512	942 ± 35
48	34309 ± 270	860 ± 137	32320 ± 583	903 ± 21	33117 ± 591	977 ± 40

Table 4.3 (Continued)

Elapsed time (weeks)	D		G		M	
	N	P	N	P	N	P
52	33530 ± 281	927 ± 30	31622 ± 393	811 ± 9	33958 ± 706	980 ± 17
56	33968 ± 356	961 ± 39	31251 ± 211	785 ± 42	34020 ± 614	880 ± 30
60	35270 ± 315	839 ± 13	31874 ± 672	754 ± 15	30490 ±2547	787 ± 65
64	34867 ± 415	845 ± 9	31358 ± 462	764 ± 26	35512 ± 504	930 ± 17
68	34935 ± 715	842 ± 35	31320 ± 536	792 ± 41	32965 ±1619	923 ± 26
72	36353 ± 468	985 ± 32	32472 ± 854	849 ± 30	36538 ± 406	1026 ± 32
77	35285 ± 244	1027 ± 61	32884 ± 549	877 ± 18	35053 ± 132	995 ± 11
81	35500 ± 487	889 ± 31	32396 ± 204	754 ± 30	35106 ± 680	921 ± 23
85	35306 ± 574	730 ± 24	30882 ±1457	732 ± 68	34234 ± 767	831 ± 17
89	33686 ± 741	799 ± 19	32295 ± 377	784 ± 19	33879 ±1153	899 ± 35
95	31620 ± 625	611 ± 43	29327 ± 523	525 ± 20	35170 ±1251	668 ± 11

Since the nitrogen content in mulga phyllode litter is about 2.5 times that found in mallee leaf litter (Chapter 3) it could be expected that mulga phyllodes would decompose more readily than mallee leaves (cf. Witkamp 1966, Williams and Gray 1974). However Handley (1961) and Davies (1971) point out that nitrogen may become unavailable in highly stable and decomposition resistant protein - phenol complexes in leaves; the degree of such complexing is much greater on soils which are poor in nitrogen and phosphorus (Davies, Coulson and Lewis 1964).

Mineralization or immobilization of nutrients from organic matter is reported to be governed primarily by soil heterotroph requirements (Gosz et al 1973) and it is generally accepted that plant litter with a carbon/nitrogen ratio greater than about 25:1 exerts a nitrogen demand on the soil and causes immobilization of nitrogen (Mulder, Lie and Woldendorp 1969). The nitrogen concentration in litter commonly rises as decomposition proceeds (Gosz et al 1973, Anderson 1973b, Macauley 1975). Thus in the present study mallee leaves contained c. 10 000 ppm N when initially placed out and c. 15 000 ppm after some 96 weeks decomposition time (Table 4.2). Similarly N concentration increased in mulga phyllodes from 24 100 ppm to c. 33 000 ppm after 95 weeks decomposition (Table 4.3).

Depending on overall rate of breakdown increases in nitrogen concentration may or may not result in net gains of nitrogen in decaying leaves (Gosz et al 1973, Anderson

1973b). The precise manner in which additional nitrogen is incorporated into the leaves is not known but most likely it is bound by micro-organisms. Most fungal hyphae contains 3 - 5 % dry weight of nitrogen (Harley 1971) so fungal immobilisation of nitrogen and/or fungal translocation of exogenous nitrogen sources into the leaves may be involved (Anderson 1973b). In the present study absolute increases of nitrogen were not recorded but the rate of loss of nitrogen from both mallee and mulga leaves was much less than total dry weight or phosphorus loss (Figures 4.1b and 4.2b).

Daubenmire and Prusso (1963) found poor correlations between decomposition rates and nitrogen content of litter. Moreover, additions of nitrogen from precipitation, frass and other exogenous sources did not increase the rate of decomposition in litter of oak (Bocock 1963) or beech (Anderson 1973b) in the first year after litter fall (but see Sorensen 1974). Daubenmire and Prusso (1963) suggested that a number of other factors may locally dominate chemical properties of leaves including temperature and moisture conditions, the physical structure of the tissues, the presence of toxic compounds in the litter and trace elements neglected in conventional analytical procedures. Thus Gosz et al (1973) found that apart from the C:N ratio, many other element ratios e.g. N:P, C:K affected decomposition rates.

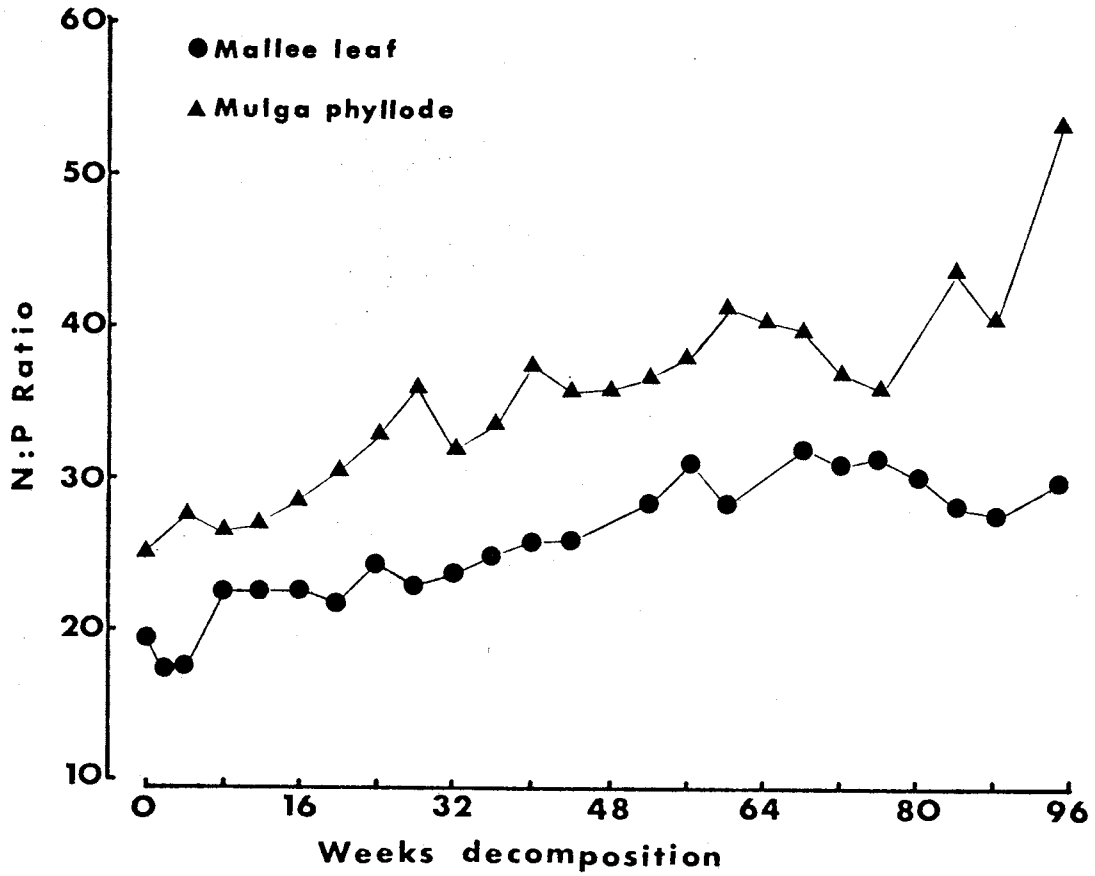


Figure 4.3 Changes in the nitrogen:phosphorus ratio with time in decomposing mallee leaves and mulga phyllodes

Table 4.4 Wood decomposition in mallee and mulga communities

Weeks decomposition	% original weight ± S.E. Mallee	Mulga	% original N and P content Mallee N	Mallee P	Mulga N	Mulga P
0	100	100	100	100	100	100
12	97.7 ± 0.2	99.0 ± 0.4	85.3	64.7	69.7	66.0
24	96.7 ± 0.1	98.1 ± 0.6	72.7	64.0	68.6	66.8
48	93.7 ± 0.3	97.0 ± 0.5	68.5	60.3	66.5	67.2
60	92.3 ± 1.4	96.7 ± 0.9	66.2	58.7	72.3	65.1
72	90.7 ± 1.1	97.0 ± 0.2	79.3	60.1	80.9	63.3
85	n.r.	94.8 ± 0.8	n.r.	n.r.	n.r.	n.r.
88	90.4 ± 1.7	n.r.	74.5	58.7	n.r.	n.r.
108	89.9 ± 4.2	n.r.	87.5	58.4	n.r.	n.r.

n.r. = not recorded

Both mallee and mulga leaves exhibited widening N:P ratios with time (Figure 4.3) and this may indicate that phosphorus supply could also be limiting decomposition rates in these infertile systems. Nevertheless the fact that dry weight and phosphorus weight losses were highly correlated ($r = 0.94$ for mallee, $P < 0.01$; $r = 0.98$ for mulga, $P < 0.01$) suggests that there was no unusual demand for this element by the heterotrophs. Attiwill (1968) and Macauley (1975) also found that phosphorus loss closely followed the loss of dry matter throughout decomposition in Eucalyptus obliqua and E. pauciflora respectively.

4.3.2 Branch decomposition - Both mallee and mulga branch pieces decayed at very slow rates during this study. After 108 and 95 weeks decomposition mallee and mulga branches were 89.9 and 94.8 per cent of their original dry weight respectively (Table 4.4). However it is clear that the period of observation was too short to reach any definite conclusion concerning total turnover times. Decay of wood may be expected to be slow initially because of high C:N and reduced surface:volume ratios. Nevertheless in both mallee and mulga there was an initial loss in nitrogen concentration observed after the first 12 weeks decomposition and at no time during the study did nitrogen concentrations regain their initial levels (1 021 ppm for mallee and 3 385 ppm for mulga). Similar results were recorded for phosphorus concentrations which were initially

77 and 75 ppm for mallee and mulga respectively.

Gosz et al (1973) recorded increased nitrogen concentrations in their study of branch decomposition in the Hubbard Brook ecosystem, but the increases were very small compared with those found in decaying leaves. Losses in element concentrations during the first few months of decomposition are most likely due to leaching (cf. Bocock 1963). However in tissue having wide C:N ratios some gains in nitrogen concentration could be expected as decomposition progressed. In the present study it is thought that fragmentation of bark, and the resulting physical removal of this 'nitrogen rich' material, has tended to reduce the concentration of nitrogen in the remaining tissue.

Nitrogen fixation has been demonstrated in decaying wood of chestnut (Cornaby and Waide 1973) and many other northern hemisphere forest species (Sharp 1975). However the decline in nitrogen concentration recorded in the present study of branch decay suggests that fixation is unlikely to be important in wood decomposition in Australian semi arid ecosystems.

Losses of phosphorus from decaying branches were significantly higher than overall dry weight losses. Attiwill (1968) attributed similar results in E. obliqua to leaching, but the physical loss of bark would also have been important in this case. Any portion removed physically would, however, be related to the deteriorating process of decomposition.

Table 4.5 Bark decomposition in mallee communities - BD, bark placed on regrowth litter on MAD site; BG, bark placed on soil surface between clumps on MAD site; BM, bark placed on litter mats of mature mallee community, MAM site.

Weeks decomposition	% original weight ± S.E.*			% original N and P content*					
	BD	BG	BM	BD		BG		BM	
				N	P	N	P	N	P
0	100	100	100	100	100	100	100	100	100
4	92.6±1.3	92.8±1.7	93.6±1.5	112.5	90.8	113.4	96.4	116.1	75.3
8	90.2±0.7	91.6±1.0	90.5±0.7	92.1	44.2	93.2	53.9	107.5	287.0
16	89.1±1.4	90.4±2.3	88.1±2.4	90.4	87.3	115.5	111.7	95.3	86.4
24	89.1±0.7	87.9±1.0	89.2±1.0	92.5	66.3	153.5	127.5	114.1	115.5
32	84.4±0.9	83.0±0.9	85.6±2.2	136.5	157.1	137.1	146.4	140.9	131.0
40	82.0±1.0	78.9±1.3	81.7±3.0	152.4	193.0	142.2	170.3	127.3	158.5
48	80.2±1.3	76.2±1.0	78.0±1.9	126.5	184.1	153.8	206.2	140.9	169.8
56	78.8±1.3	79.5±1.4	76.3±2.4	134.4	173.1	158.4	205.8	132.4	148.0
64	77.0±1.8	78.0±2.5	77.3±1.2	127.0	175.2	190.9	284.6	140.9	147.0
72	76.0±2.2	73.1±2.9	74.1±1.7	137.2	156.4	145.1	197.9	152.7	178.8
80	73.5±0.7	70.8±3.6	69.9±2.4	144.8	183.1	149.3	185.9	152.8	205.5
92	65.3±3.5	57.4±5.1	70.0±1.4	119.4	130.5	123.2	179.9	148.2	151.0

* Each value is the mean of 6 replicates

At the outset of this study it was thought that termites would play a major role in decomposing the branch pieces. Lee (personal communication) suggests that wood feeding termites are directly responsible for the decomposition of at least 40% of the wood that falls in dry sclerophyll forest in South Australia. In both mallee and mulga communities termites did attack several of the branch pieces, and some samples recovered towards the end of the study had lost from 50-60% of their original weight. However most pieces had escaped active colonization over the period examined and this is most likely related to the small branch size (25 cm long), which presented only a small surface area in direct contact with the soil.

4.3.3 Mallee bark decomposition - Mallee bark decomposed at a much faster rate than corresponding branch pieces (Tables 4.4, 4.5). Individual bark strips were 3-5 cm wide and only 1-2 mm thick and this resulted in very favourable surface:volume ratios for decomposition.

There was no significant difference in the rate of decomposition of bark placed on differing microsites when this was tested by the slopes of regression lines (Table 4.6). The regressions were established on the assumption of exponential decay over the period of observation, as earlier described for leaf decomposition. The appropriateness of the model is shown by the closeness of the intercepts of the regressions to the theoretical value of 100%.

Table 4.6 Bark decomposition regression parameters. Regressions are in the form $\log_e Y = a + bX$ where Y = % leaf remaining and X = decomposition time (weeks). See text for description of microsites.

Microsite	Intercept	Intercept (%)	Regression coefficient (b)	S.E. of b	Significance of regression	R^2
BD	4.5618	95.7	-0.0036	0.0002	$P < 0.001$	0.95
BG	4.5586	97.2	-0.0045	0.0004	$P < 0.001$	0.89
BM	4.5586	95.4	-0.0036	0.0002	$P < 0.001$	0.96

Table 4.7 Mean concentration ± S.E. for nitrogen and phosphorus in mallee bark after various periods of decomposition. Bark was placed in position (0 time) on 30th May, 1973. Sample size = 6 for both elements. See text for description of treatments BD, BG and BM.

Elapsed time (weeks)	BD		BG		BM	
	N (ppm)	P (ppm)	N (ppm)	P (ppm)	N (ppm)	P (ppm)
0	1410 ± 31	51 ± 1	1410 ± 31	51 ± 1	1410 ± 31	51 ± 1
4	1712 ± 54	49 ± 1	1721 ± 86	53 ± 4	1748 ±127	41 ± 5
8	1440 ± 60	25 ± 0.5	1434 ± 36	30 ± 4	1619 ±159	49 ± 1
16	1430 ± 50	50 ± 1	1801 ± 75	63 ±	1525 ±138	50 ± 2
24	1464 ± 79	37 ± 5	2463 ±124	73 ±11	1803 ± 98	66 ± 2
32	2282 ±133	94 ±15	2329 ± 92	90 ± 5	2320 ± 85	77 ± 4
40	2620 ±142	119 ± 7	2541 ±108	110 ± 6	2197 ± 81	99 ± 5
48	2223 ± 52	117 ±10	2845 ±121	138 ±12	2546 ± 77	111 ± 1
56	2405 ±138	112 ±16	2809 ± 91	132 ± 8	2448 ±128	99 ± 8
64	2324 ± 74	116 ±13	3448 ±231	185 ±15	2571 ±153	97 ±12
72	2546 ±174	105 ±16	2796 ±158	138 ±18	2905 ±206	123 ±18
80	2777 ±107	126 ±14	2975 ±184	134 ±14	3083 ±251	151 ±20
92	2578 ± 76	102 ±11	3029 ±192	160 ±21	2984 ±136	110 ±10

A feature of this bark decomposition study was the increase recorded in concentration and absolute amounts of nitrogen and phosphorus as decomposition proceeded (Tables 4.5, 4.7). There was about a two to three fold increase in nitrogen and phosphorus concentration in bark tissue over the 92-week study period (Table 4.7). Much of the absolute increase in nitrogen and phosphorus is thought to arise from that contained in fungal strands. Decaying bark pieces were often dotted with masses of white fungal hyphae which were firmly attached to the bark and thus not removed prior to final dry weight determination. The non-uniformity of this colonization contributed to variability of nitrogen and phosphorus levels between successive samples (Tables 4.5, 4.7). Bark destroying fungi apparently have a very efficient mechanism for nitrogen metabolism and conservation (Kaarik 1974). It is clear that in the present study these fungi were able to draw upon exogenous nitrogen and phosphorus sources as an aid to the catabolic degradation of the bark. Nevertheless it should be emphasized that the initial amounts of nitrogen and phosphorus in the bark tissue were very small, so correspondingly small importation into or onto the tissue would greatly increase the absolute amount present.

4.3.4 Kinetics of decomposition - The assumption of steady-state in the dynamics of the litter layer can sometimes justifiably be made, and methods of analysis described by Jenny, Gessel and Bingham (1949) and Olson (1963) may be

employed. Criticisms of a number of other assumptions that are necessary have been detailed (Minderman 1968) but this approach can still provide a useful and valuable starting point for analysis and discussion (Chapman, Hibble and Rafarel 1975).

If the woodland floor is in steady-state then pool size of the litter layer should remain relatively constant from year to year since input and output would be equal. Decomposition constants can be calculated from

(1) $k = L/M$

where L is annual input and M is the standing crop of litter.

Deviations from steady-state conditions are caused by seasonal and annual variations in leaf litter input, large pulse inputs of falling trees and branches, and environmental constraints on decomposer activity (Lang 1974).

Almost all mathematical treatments describing turnover of plant litter or its nutrient content utilize the first order decay equation:

(2) $-\frac{dC}{dt} = kC$

where C is the concentration of the material undergoing change, t is time and k a proportionality (or decomposition) constant and $\frac{dC}{dt}$ denotes the velocity of the reaction.

On integrating between limits of concentration at time O and t

$$-\int_{Co}^{Ct} \frac{dC}{C} = K \int_{o}^{t} dt$$

i.e. $Ct = Co\ e^{-kt}$

$\therefore$ $-\log_e Ct + \log_e Co = kt$

$\therefore$ $k = t^{-1} \log_e Co/Ct$

Thus, time taken for half initial amount (Co/2) to decompose

$$t_{0.5} = (\log_e 2)/k$$
$$= 0.693/k$$

Similarly, time for 95% to decompose

$$t_{0.95} = (\log_e 20)/k$$
$$\doteq 3/k$$

If exponential decay is also assumed under steady-state conditions the k values for a particular tissue should be similar whether determined from input/ground litter crop (Method 1) or the first order decay equation (Method 2). These values are shown in Tables 4.8 and 4.9 for leaf decomposition on the MAM and MUM sites respectively. (Values for Table 4.9 include data from the regrowth microsites but this will only marginally affect the comparison, as decay rates on all microsites were very similar - Table 4.1).

It will be observed that k values determined from the first order decay equation vary considerably, particularly over the first few months of decomposition (Table 4.9). This largely reflects the rapid decay associated with early leaching losses and more degradable substrate components e.g. the lower carbohydrates. The data suggest that caution

Table 4.8 Decay constant for mallee and mulga leaves determined from the rate of annual litter fall/mean ground litter crop (Method 1 - see text).

Parameter	Site			
	MAM	Reference	MUM	Reference
Leaf fall (kg/ha)	3167.9	(Table 3.4)	2639.3	(Table 3.5)
Period recorded (days)	712	(")	661	(")
Annual mean (L) (kg/ha/yr)	1583.9		1457.4	
Initial leaf litter (kg/ha)	1946+2042*	(Table 2.5)	831+880	(Table 2.6)
Final leaf litter (kg/ha)	2573+2560*	(")	2032+994	(")
Mean leaf litter (M) (kg/ha)	4560.5		2368.5	

$k_{(MAM)} = L/M$

$= 1583.9/4560.5$

$= \underline{0.35}$

$k_{(MUM)} = L/M$

$= 1457.5/2368.5$

$= \underline{0.61}$

*Residue is included in leaf litter estimates because it mainly comprised leaf fragments (Chapter 2).

should be exercised in using k values, determined from only a few months observations, in decomposition models. Turnover rates could be greatly overestimated in these situations.

For the present data k values derived by Method 2 appear to stabilise for both mallee and mulga leaves after about 52 weeks decomposition (Table 4.9). Thus, for purposes of comparing Method 1 and Method 2, k values for periods of greater than 52 weeks decomposition only will be considered. While the values are in broad agreement, especially for Mulga (Tables 4.8, 4.9), it appears that, even after a period of 95 weeks observation, k values, determined from litter bag studies, could still overestimate decay rates in mallee leaves. This is supported by the considerably larger amount of leaf litter 'residue' measured for the MAM site (Table 4.8), which suggests that comminuted mallee leaf material may be quite resistant to decay, e.g. containing condensed or polymerized polyphenols (c f. Minderman 1968). By way of contrast a k value of 0.85 (Method 1) may be derived from the data of Ashton (1975a) for Eucalyptus regnans leaves suggesting quite rapid turnover in that species.

Minderman (1968) demonstrated that the accumulation of organic matter on, and in, the soil cannot be calculated on the basis of a known annual addition and a fixed decomposition figure of the litter. He considered it

Table 4.9 Decay constant and estimated time required for the loss of one half and 95% of the original dry weight for mulga and mallee leaves. Values are based on the mean dry weight remaining over all microsites for each community sampling period (Method 2 - see text).

Weeks decomposition	Mallee			Mulga		
	Decay constant (k)	Time parameter (years) Half-time (0.693/k)	95% (3/k)	Decay constant (k)	Time parameter (years) Half-time (0.693/k)	95% (3/k)
2	0.22	3.1	13.6	n.a.	n.a.	n.a.
4	0.96	0.7	3.1	1.47	0.5	2.0
8	1.74	0.4	1.7	1.33	0.5	2.2
12	1.42	0.5	2.1	1.01	0.7	3.0
16	1.34	0.5	2.2	0.96	0.7	3.1
20	1.02	0.7	2.9	0.87	0.8	3.4
24	0.97	0.7	3.1	0.83	0.8	3.6
28	0.89	0.8	3.4	1.05	0.7	2.8
32	0.77	0.9	3.9	0.89	0.8	3.4
36	0.79	0.9	3.8	0.82	0.8	3.6
40	0.72	1.0	4.2	0.74	0.9	4.0
44	0.71	1.0	4.2	0.61	1.1	4.9
48	n.a.	n.a.	n.a.	0.66	1.1	4.5
52	0.62	1.1	4.8	0.62	1.1	4.8
56	0.65	1.1	4.6	0.56	1.2	5.3

Table 4.9 (Continued)

Weeks decomposition	Mallee			Mulga		
	Decay constant (k)	Time parameter (years) Half-time (0.693/k)	95% (3/k)	Decay constant (k)	Time parameter (years) Half-time (0.693/k)	95% (3/k)
60	0.61	1.1	4.9	0.60	1.2	5.0
64	n.a.	n.a.	n.a.	0.54	1.3	5.5
68	0.57	1.2	5.3	0.57	1.2	5.3
72	0.56	1.2	5.3	0.54	1.3	5.5
76	0.54	1.3	5.5	n.a.	n.a.	n.a.
77	n.a.	n.a.	n.a.	0.54	1.3	5.5
80	0.66	1.1	4.5	n.a.	n.a.	n.a.
81	n.a.	n.a.	n.a.	0.56	1.2	5.3
84	0.57	1.2	5.3	n.a.	n.a.	n.a.
85	n.a.	n.a.	n.a.	0.53	1.3	5.9
88	0.55	1.3	5.4	0.51	1.4	5.9
95	0.61	1.1	4.9	0.43	1.6	7.0

n.a. = not available

necessary to first know the behaviour of the separate chemical constituents of the litter and their speed of disappearing, before the decomposition of the total litter mass could finally be calculated. The observed discrepancies between k values determined by Methods 1 or 2 in the present study should be viewed within the perspection of Minderman's observations. Had the litter bag study continued for a longer period of time it is likely that the derived k values would have been in closer agreement, due to the greater proportion of recalcitrant compounds in the remaining leaf material in the bags. Nevertheless the k values determined by Method 1 (Table 4.8) assume steady state conditions, while it is clearly evident from initial and final leaf litter values that this assumption was not tenable, especially for the MUM site. Therefore most of the inferences suggested in this discussion are based on Method 2 k values, since a greater degree of control was exercised in their determination.

Estimates of half-time (0.693/k) and time for 95% decomposition (3/k) indicate that mallee and mulga leaves may take from 5-7 years to decay completely (Table 4.9). These estimates emphasize likely errors which may arise if k values, used to determine such time parameters, are based on short periods of observation. Nevertheless the time parameters themselves are extrapolations outside the period of measurement of a particular k, and therefore assume the same decay model will apply throughout the

whole decomposition period. Such extrapolation errors are well appreciated in regression theory (Draper and Smith 1966), while Minderman (1968) has shown that complete decomposition of a substrate follows a curve that corresponds to that constructed by summation of a number of exponential functions.

Table 4.10 Decay constant and estimated time required for the loss of one half and 95% of the original dry weight for mallee bark. Values are based on the mean dry weight remaining over all microsites for each sampling period.

Weeks decomposition	Decay constant (k)	Time parameters (years) Half-time (0.693/k)	95% (3/k)
4	0.94	0.7	3.0
8	0.63	1.1	4.8
16	0.37	1.9	8.1
24	0.26	2.7	11.5
32	0.28	2.5	10.7
40	0.27	2.6	11.1
48	0.27	2.6	11.1
56	0.23	3.0	13.0
64	0.21	3.3	14.3
72	0.21	3.3	14.3
80	0.22	3.1	13.6
92	0.25	2.8	12.0

Similar constraints apply to the estimation of decay constants and time parameters for mallee bark (Table 4.10). The data show similar variability in these parameters to that exhibited by decomposing leaves. However stability

in the decay constant appears after only about 24 weeks of bark decomposition. Not unexpectedly, this indicates that the bark is composed of decay resistant material and has correspondingly larger turnover times vis a vis mallee leaves.

4.4 Conclusions

This study suggests that there are striking similarities in the breakdown and decomposition rates of mallee and mulga leaves, despite higher extant nitrogen concentrations in the latter. Similarly within a particular community there appears to be little variation in the decomposition rates exhibited in different micro-sites. Taken together these observations indicate that macro-environmental conditions (e.g. rainfall frequency) may locally dominate decomposition rates in these semi-arid ecosystems. Thus, it may appear feasible to construct a universal model of leaf decay for Australian semi arid woodlands. However, it has been conclusively demonstrated that the widely accepted decay constant is in fact an unstable value which changes as decomposition progresses. Assumptions such as "the loss of dry weight after the first month estimates the rate of decomposition" (Gosz et al 1973) are therefore untenable in these situations.

The patterns of mineralization and immobilization of nitrogen and phosphorus in decaying leaves, branches and bark are in broad agreement with similar studies carried

out elsewhere in a range of vegetation types. Generally nitrogen concentrations rise with increasing decomposition time and this may also lead to absolute weight increases of the element in the substrate. Phosphorus concentration and consequently absolute amounts of phosphorus tend to fall in conjunction with weight losses in the organic matter. Although exceptions to these generalities occurred in both branch and bark decomposition studies, these could be explained by the nature of the particular substrate and experimental material.

Whether steady-state conditions can be assumed to exist within the litter component of mallee and mulga ecosystems depends very much on the scale at which the system is being examined. On a community basis small scale variations will cancel out and an overall situation approaching steady-state may be detected. However the interaction between biochemical properties, microflora, soil fauna and other biotic and abiotic components of the soil environment would seem critical in determining the accumulation rate and steady-state conditions of the litter layer. One cannot but agree with Anderson (1973b) that "it is unlikely that the study of any of these factors in isolation from the others will provide a method of predicting the breakdown and decomposition rate of soil organic matter".

CHAPTER 5
Fungal succession on decomposing mallee and mulga leaves

5.1 Introduction

Litter fall is of great importance in the nutrient cycle of forest ecosystems and there have been many investigations on the decomposition of litter in woodlands (See Chapter 4). Witkamp (1971a) notes that litter decomposition and nutrient loss are a complex interaction of biotic factors (e.g. micro-organisms, soil fauna, chemical content of the litter) and abiotic factors (e.g. temperature, moisture). Micro-organisms and soil fauna are synergistic in their litter decomposition roles because feeding upon litter by soil animals enhances decomposition rate and stimulates growth of microbial populations in litter (Macfayden 1963, Witkamp and Crossley 1966).

At least eighty per cent of chemical breakdown of plant material is generally believed to be a result of fungal and bacterial metabolism (Witkamp 1971b, Jensen 1974). In the New England National Park, New South Wales, fungal mycelium was the main contributor to total microbial biomass, accounting for eighty to ninety per cent of the combined fresh weight of bacteria, fungal and actinomycete spores and vegetative fungal hyphae (Charley and Richards 1974). Bacteria and actinomycetes are more sensitive to periods of drought than fungi, and since bacteria and actinomycetes have optimal development in neutral or alkaline conditions fungi tend to dominate in acid soils

(Steubing 1970). The surface soils of the MAD, MAM and MUM sites are characteristically acid in reaction (Chapter 2) so that it is likely that the mycoflora provide the dominant metabolic pathway for leaf decomposition in these semi arid ecosystems.

Because of their possession of hyphae the fungi are especially important in the breakdown of leaf litter (Harley 1971). The hyphal structure along with the production of extracellular enzymes allow the fungi to spread and penetrate deep into the substrate on which they develop. The data presented in this chapter compare and contrast mycoflora isolated from decomposing leaves in mallee and mulga ecosystems. There have been some studies of the soil fauna in these systems (e.g. Watson and Gay 1970, Watson, Lendon and Low 1973, Greenslade and Greenslade 1973, Greenslade 1975 pers.comm.) but so far as the writer is aware this is the first report of the mycoflora present. As such the work is essentially descriptive and incomplete in nature, but it should provide a basis for future studies of functional and biochemical relationships within such litter layers.

5.2 Methods

5.2.1 Technique - Fungal succession on decomposing mallee and mulga leaves was followed on material collected during the course of the litter bag study detailed in Chapter 4. That chapter should be consulted for descriptions

of the study sites, and method of placement and collection of the leaves.

Three randomly chosen sections of leaves (representing petiole, apex and central portion of the lamina) from each of the six replicate bags were placed in a flask labelled for each microsite. The bulked leaf sections were surface washed in a 1% detergent ('Teepol') solution (seven changes) and glass distilled water (eight changes). Approximately 0.5 cm x 0.5 cm pieces were cut from sixteen of the leaf sections and plated, four per petri dish, on malt extract agar (Raper and Thom 1949). The remaining portion was then surface sterilized with 0.1% mercuric chloride solution (Kendrick and Burges 1962), washed in sterile water and plated as for the surface washed material.

After about five days incubation at room temperature the presence of fungal colonies on each leaf piece was recorded and hyphal tips or conidia from unrecognizable colonies transferred to agar slants. After incubation the slant cultures were sorted into entities (presumptive species) and representative isolates of each entity were retained for later identification or matching with entities collected elsewhere. Subsequently, it was not possible to induce all these entities to sporulate nor was it possible to fully identify all the sporulating cultures, although various culture media were used and several specialists consulted.

The identical procedure was adopted for processing mallee and mulga samples. In general the mallee samples

were plated within twenty four hours of collection in the field and the mulga samples within forty eight hours. Mulga samples were air freighted to Canberra for processing. If samples had to be held overnight they were stored within sealed polythene bags in a refrigerator.

The relative merits and shortcomings of the procedure adopted and of the selectivity of the media used for isolation have been discussed by a number of workers (Christensen 1969, Witkamp 1971b, Steubing 1970). Whatever method is used year-round sampling (adopted in this study) is likely to improve the accuracy of the result obtained (Witkamp 1966). It is perhaps sufficient to state that the technique was considered the most convenient and suitable with the time and personnel available. Furthermore, because it involved identical procedures, the current work is directly comparable with the work of Macauley and Thrower (1966). This latter study is the only Australian report previously published on fungal succession on decomposing leaves.

5.2.2 Analysis - Two methods of recording frequency of individual species and mycofloral groups were adopted. For the mulga microsites:- % species frequency (SW or SS) for each sample data and microsite =

$$\frac{\text{Number of isolations of the species from SW (or SS) leaves}}{\text{Total number of all isolations from SW (or SS) leaves}} \times 100$$

where, SW = surface washed and SS = surface sterilized.

This method conforms with most other representations of species frequency in studies of mycoflora (e.g. Christensen et al 1962, Widden and Parkinson 1975). However, to permit stricter comparisons of the mallee (Eucalyptus socialis) data with that obtained by Macauley and Thrower (1966) for E. regnans their method of recording relative percentage frequency of isolates was adopted for the mallee study, and for the major groups occurring on mulga leaves.

i.e. RFSW or RFSS (of a species) =

$$\frac{\text{Number of isolations of the species from SW (or SS) leaves}}{\text{Total number of all isolations from both SW and SS leaves}} \times 100$$

where, RFSW = relative percentage frequency of individual species as surface inhabitants and RFSS = relative percentage frequency of internal colonisers.

The frequency analyses described enable presentation of the results as frequency histograms (see Macauley and Thrower 1966). However, the data collected may also be analysed by multivariate methods. For the purposes of this thesis only limited examination of the data was possible using these techniques. The methods chosen were two classification routines DIVINFRE (Mayo 1972) and CENTPERC (Dale, Lance and Albrecht 1971) available on the CSIRO computer network.

DIVINFRE is a modification of the program DIVINF (Lance and Williams 1968) which performs a monothetic

divisive classification, using an information statistic on binary (presence/absence) data.

Given a population of n individuals* defined by s binary attributes (species), such that the jth attribute is present in aj individuals, an information content of the population, I, is defined such that

$$I = sn \log n - \sum_{j=1}^{s} [aj \log aj + (n-aj) \log (n-aj)]$$

If a population (i) is divided into two groups (g) and (h) an information-fall, $\Delta I_{(gh,\ i)} = I_i - I_g - I_h$

The population is dichotomised on each attribute in turn, the I for each division calculated, and division effected on that attribute for which ΔI is maximum. Misclassifications can occur in divisive procedures due to (i) chance occurrences of an attribute on which a division is made and (ii) formation of a heterogeneous 'residual' group whose only common feature is that all members lack all division attributes. DIVINFRE includes a polythetic re-allocation procedure designed to overcome these defects.

Only species comprising greater than five per cent of all isolates (SW + SS) recorded for each community were

---

* For both mallee and mulga sites an individual was the summation of the presence/absence data from the 16 leaf pieces for each surface washed treatment per microsite and sample date. Thus there were 13 samples dates x 3 microsites = 39 individuals for mulga and 19 sample dates x 3 microsites = 57 individuals for mallee leaves.

used in the analysis. This was to minimise possible overemphasis of the importance of quantitatively very rare forms, which could have been ephemeral constituents of the soil mycoflora. (Note: Penicillium spinulosum was excluded from the analysis although subsequent identification of unknown Penicillia isolates showed that this species should also have been included.)

The relationship of the groups formed by the DIVINFRE procedure were examined using the agglomerative classification program CENTPERC. This programme uses the same information statistic as DIVINFRE, but in this case n is the number of individuals in the group in question and this is not necessarily constant. The most efficient route through the hierarchy is obtained by fusing those two individuals or groups which, on fusion, produce the smallest increase in I (Dale, Lance and Albrecht 1971).

This increase (ΔI or I-gain) is defined as

$$\Delta I\ (ij,k) = I_{(k)} - I_{(i)} - I_{(j)}$$

5.3 Results and Discussion

The succession of mycoflora on decomposing leaves was followed for 94 weeks for the mallee and 80 weeks for the mulga sites. Records of fungal colonies present on agar-plated samples were obtained on 13 separate occasions for mulga and 19 for mallee. The time between recordings varied from 2 to 12 weeks, the longer intervals occurring towards the end of the study when changes in the mycoflora composition were minimal.

Table 5.1 Species of fungi recorded on decomposing leaves of mallee

COELOMYCETES

- *Bartalinia robillardoides* Tassi
- *Ceuthospora innumera* Massee
- ? *Diplodia* sp.
- *Harknessia uromycoides* (Speg.) Speg.
- *Microsphaeropsis* (?) *callista*
- *Pestalotia* sp.
- *Piggotia substellata* Cooke
- *Truncatella* sp.
- Unidentified (14)

MONILIALES (excluding *Penicillium* spp.)

- *Alternaria alternata* Fr. (Keissler)
- *Alternaria* sp.
- *Aspergillus japonicus* Saito
- *Aureobasidium pullulans* (de Bary) Arn.
- *Botrytis cinerea* Pers. ex. Fr.
- *Cladosporium oxysporum* (Berk. and Curt.)
- *Cladosporium* sp.
- ? *Dactylaria* sp.
- *Epicoccum nigrum* Link
- *Fusarium* spp. (2)
- *Trichoderma koningii* Oud. aggr.
- *Trichoderma viride* Pers. ex. S.F. Gray aggr.
- *Trichoderma* spp. (2)
- *Verticicladium trifidium* Preuss.
- Unidentified (19)

PENICILLIA

- *Penicillium canescens* Sopp.
- *Penicillium piscarium* Westling
- *Penicillium spinulosum* Thom

PHYCOMYCETES

- *Cunninghamella echinulata* Thaxter
- *Monoblepharis* sp.

Table 5.1 (Continued)

Mortierella rammaniana (Möller) Linnem.
Mucor hiemalis Wehmer f *hiemalis*
**Mucor hiemalis* var. A
**Mucor hiemalis* var. B
**Mucor* sp. (Fits Schipper's *Mucor* sp. 2)
Rhizopus (?) *chinensis* Saito
Rhizopus stolonifer (Ehrenb. ex Fr.) Vuill.
Unidentified (3)

BASIDIOMYCETES
Unidentified (3)

* Do not fit *M. hiemalis* f *hiemalis* (Schipper 1973)

Table 5.2 Species of fungi recorded on decomposing phyllodes of mulga

COELOMYCETES

Bartalinia sp.
Coniothyrium (?) *acaciae* Trotter
Coniothyrium sp.
Haplosporella sp. 1
Haplosporella sp. 2
Harknessia sp.
Microdiplodia microsporella (Sacc.) Allesch.
Truncatella sp.
Unidentified (20)

MONILIALES

Alternaria alternata
Aspergillus japonicus
Aureobasidium pullulans
Cladosporium cladosporoides (Frensen) de Vries
Cladosporium oxysporum
Cladosporium sp.
Cochliobolus spicifer Nelson
Curvularia eragrostidis (P. Henn.) J.A. Meyer
? *Curvularia* state of *Cochliobolus lunatus* Nelson and Haasis
Curvularia lunata var. *aeria* (Batista, Lina and Vasconcelos) M.B. Ellis
Curvularia pallescens Boedijn
Curvularia trifolii (Kauffm.) Boedijn
Drechslera australiensis (Bugnicourt) Subram. and Jain ex M.B. Ellis
Drechslera (?) *frumentacei* (Mitra) M.B.Ellis comb.nov.
Drechslera hawaiiensis (Bugnicourt) Subram. and Jain ex M.B. Ellis
Epicoccum nigrum
Fusarium oxysporum Schlecht, emend. Snyder and Hansen
Fusarium spp. (11 unidentified to species)
Helminthosporium sp. 1

Table 5.2 (Continued)

Nigrospora sphaerica (Sacc.) Mason
Pithomyces chartarum (Berk. and Curt.)
Trichoderma koningii
Trichoderma viride
Trichoderma sp.
Unidentified (22)

PENICILLIA

Penicillium piscarium

PHYCOMYCETES

Mucor genevensis Lendner
Mucor hiemalis Wehmer f hiemalis
(?) *Rhizopus chinensis*

BASIDIOMYCETES

Unidentified (2)

Table 5.3 Species and presumptive species on decomposing mallee and mulga leaves

1. Common to both mallee and mulga

Aspergillus niger
Alternaria alternata
Aureobasidium pullulans
Cladosporium oxysporum
Epicoccum nigrum
Penicillium piscarium
Trichoderma koningii
Trichoderma viride
Mucor hiemalis f *hiemalis*
Rhizopus (?) *chinensis*

2. Recorded only on mallee

Bartalinia robillardoides
Botrytis cinerea
Ceuthospora innumera
Cunninghamella echinulata
Harknessia uromycoides
Microsphaeropsis (?) *callista*
Mortierella rammaniana
Mucor hiemalis var A
Mucor hiemalis var B
Penicillium canescens
Penicillium spinulosum
Piggotia substellata
Rhizopus stolonifer
Verticicladium trifidium

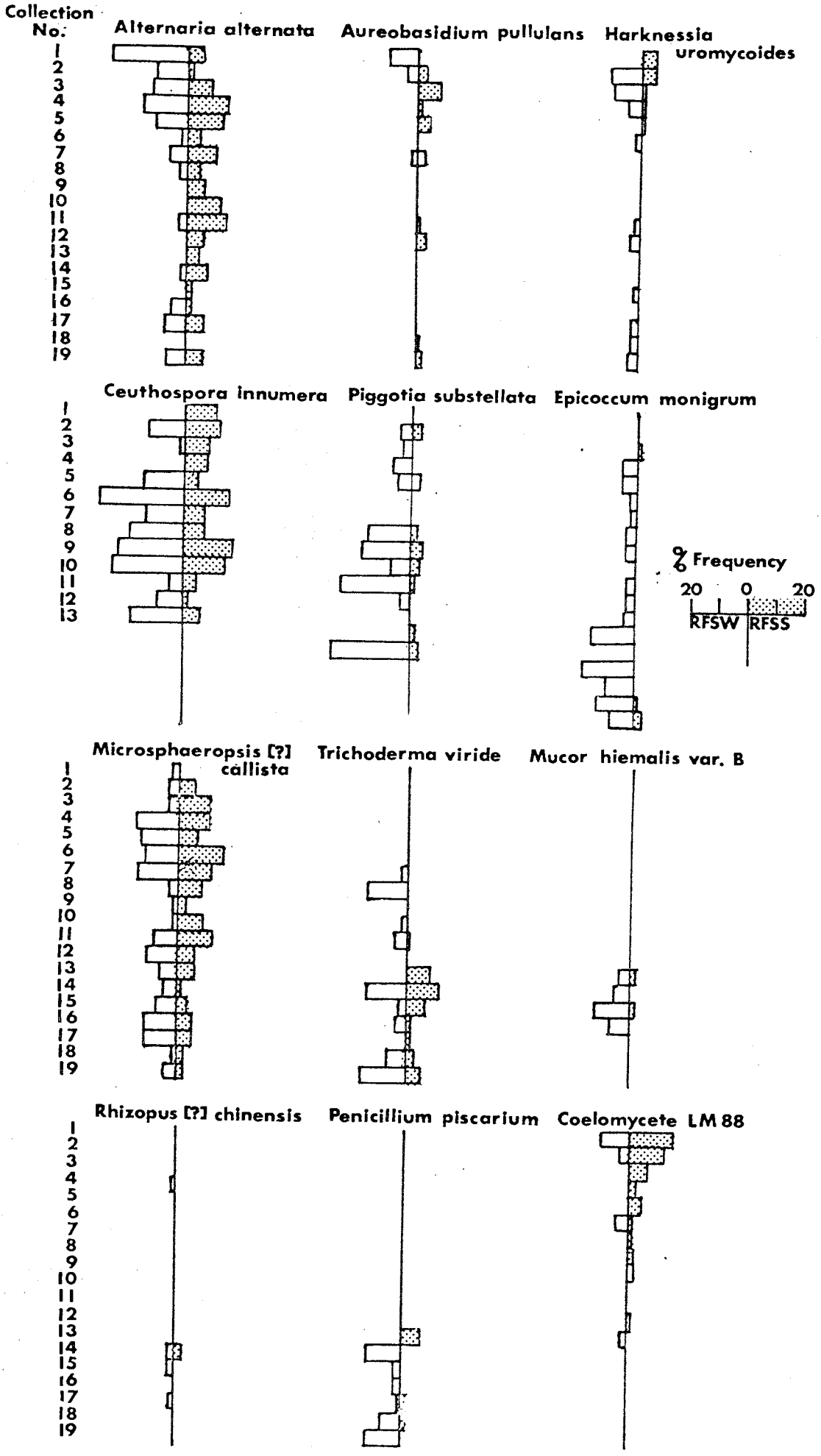
3. Recorded only on mulga

Cladosporium cladosporoides
Cochliobolus spicifer
Coniothyrium (?) *acaciae*

Table 5.3 (Continued)

Curvularia (?) *eragrostidis*
? *Curvularia* state of *Cochliobolus lunatus*
Curvularia lunata var. *aeria*
Curvularia pallescens
Curvularia trifolii
Drechslera australiensis
Drechslera (?) *frumentacei*
Drechslera hawaiiensis
Fusarium oxysporum
Nigrospora sphaerica
Pithomyces chartarum
Mucor genevensis
Microdiplodia microsporella

Figure 5.1 Mallee LD site. Relative percentage frequency of individual mycoflora species as surface inhabitants (RFSW) and internal colonizers (RFSS) of leaves of Eucalyptus socialis during decomposition. Species plotted are those comprising greater than 5 per cent of all mallee isolates. See text for methods of calculation.


Collection No:
Alternaria alternata
Aureobasidium pullulans
Harknessia uromycoides
Ceuthospora innumera
Piggotia substellata
Epicoccum monigrum
% Frequency
20 0 20
RFSW RFSS
Microsphaeropsis [?] callista
Trichoderma viride
Mucor hiemalis var. B
Rhizopus [?] chinensis
Penicillium piscarium
Coelomycete LM 88

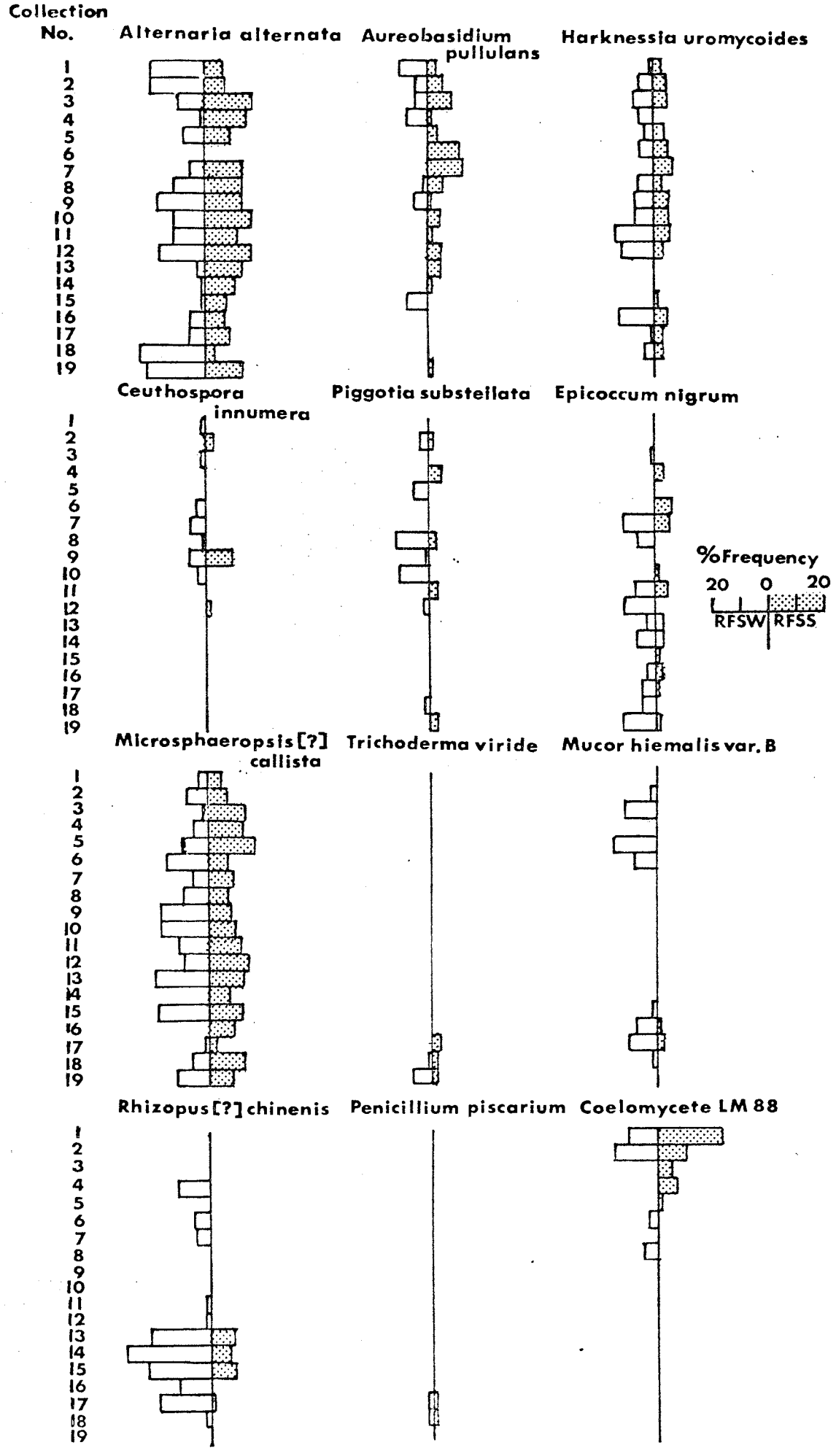


Figure 5.2 Mallee LG site. Conventions as in Figure 5.1

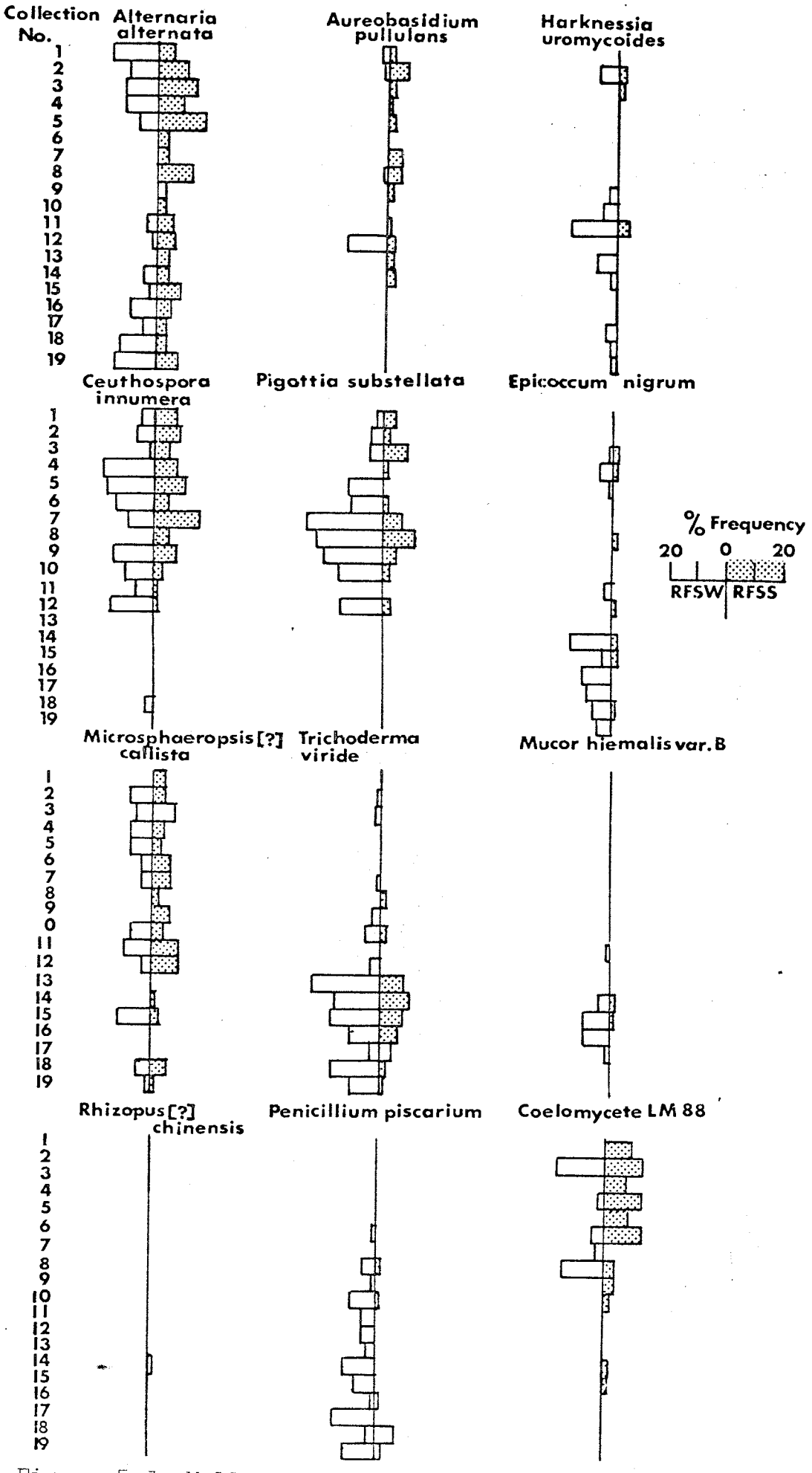


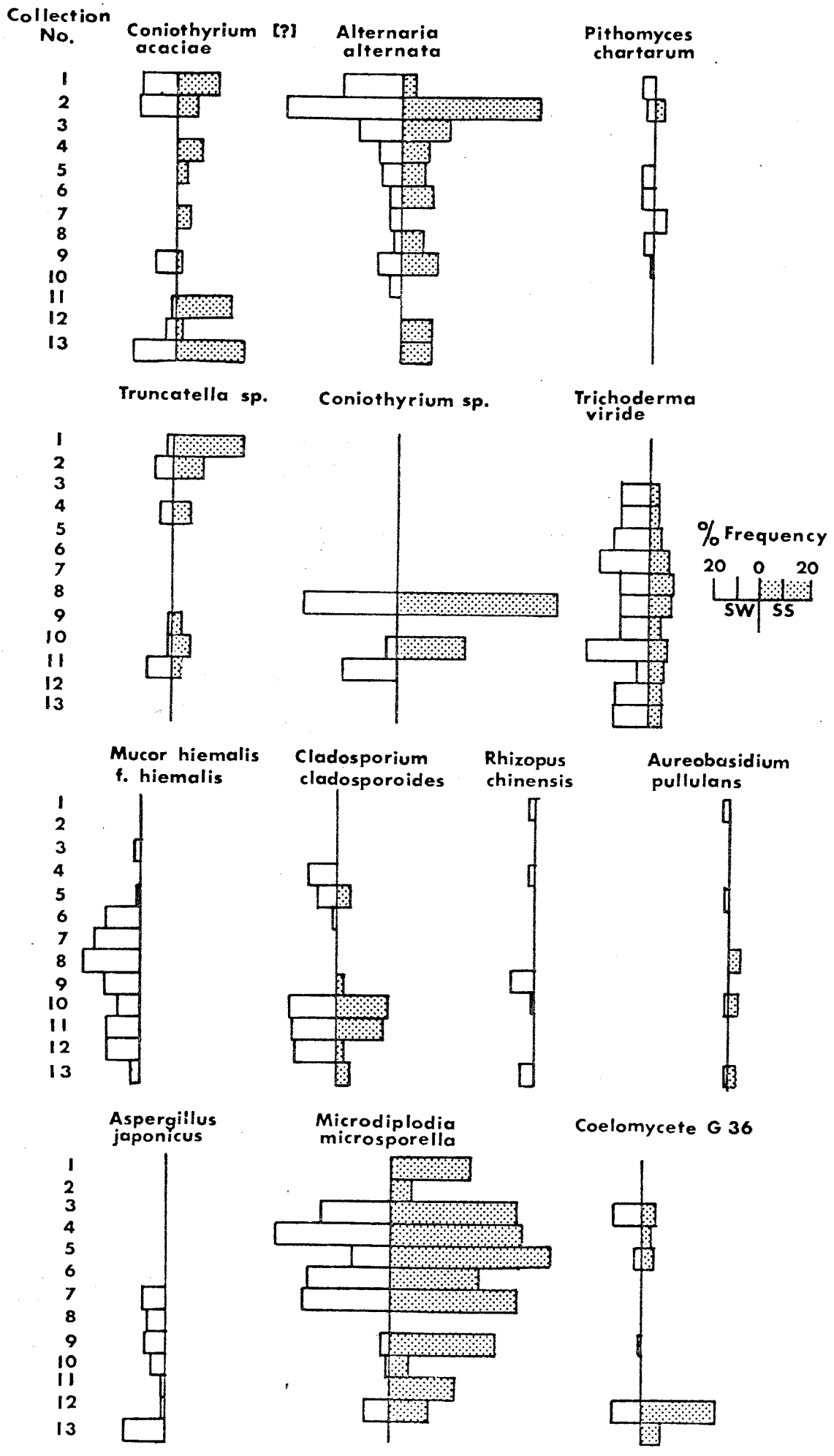
Figure 5.3 Mallee LM site. Conventions as in Figure 5.1

Over the entire study a total of 6453 entities were recorded on the plated leaf pieces. There were 2155 and 1496 colony entities recorded on surface washed and surface sterilized mallee leaf pieces respectively. Similarly 1693 and 1109 entities were observed on surface washed and surface sterilized mulga leaf samples. Subsequent cross checking incubation on agar slants and identification resulted in the delineation of 112 species, presumptive species or unidentified entities which were recorded over the entire study period for mallee, and 90 for mulga (Table 5.1, 5.2). At the species level it was possible to identify 10 species common to both sites while 14 were recorded only on the mallee and a further 16 recorded only on mulga leaves (Table 5.3).

Progressive changes in the frequency of individual species of mycoflora decomposing mallee and mulga leaves are shown in Figures 5.1 - 5.6. The species plotted are those comprising greater than 5 per cent of all isolates (SW + SS) recorded for each community type (i.e. 12 for mallee and 13 for mulga). They are thus the same species as used in the multivariate analysis and have been selected for identical reasons (see Methods).

For the mallee all species, defined as above, are common to each microsite (Figures 5.1 - 5.3). The frequency diagrams suggest that the succession of mycoflora is similar on all microsites, although the patterns for the LG site are somewhat different from LD and LM

Figure 5.4 Mulga D site. Percentage frequency of individual mycoflora species as surface inhabitants (SW) and internal colonizers (SS) of phyllodes of Acacia aneura during decomposition. Species plotted are those comprising greater than 5 per cent of all mulga isolates. See text for methods of calculation.


Collection No.
Coniothyrium acaciae [?]
Alternaria alternata
Pithomyces chartarum
Truncatella sp.
Coniothyrium sp.
Trichoderma viride
% Frequency
20 0 20
SW SS
Mucor hiemalis f. hiemalis
Cladosporium cladosporoides
Rhizopus chinensis
Aureobasidium pullulans
Aspergillus japonicus
Microdiplodia microsporella
Coelomycete G 36
1
2
3
4
5
6
7
8
9
10
11
12
13

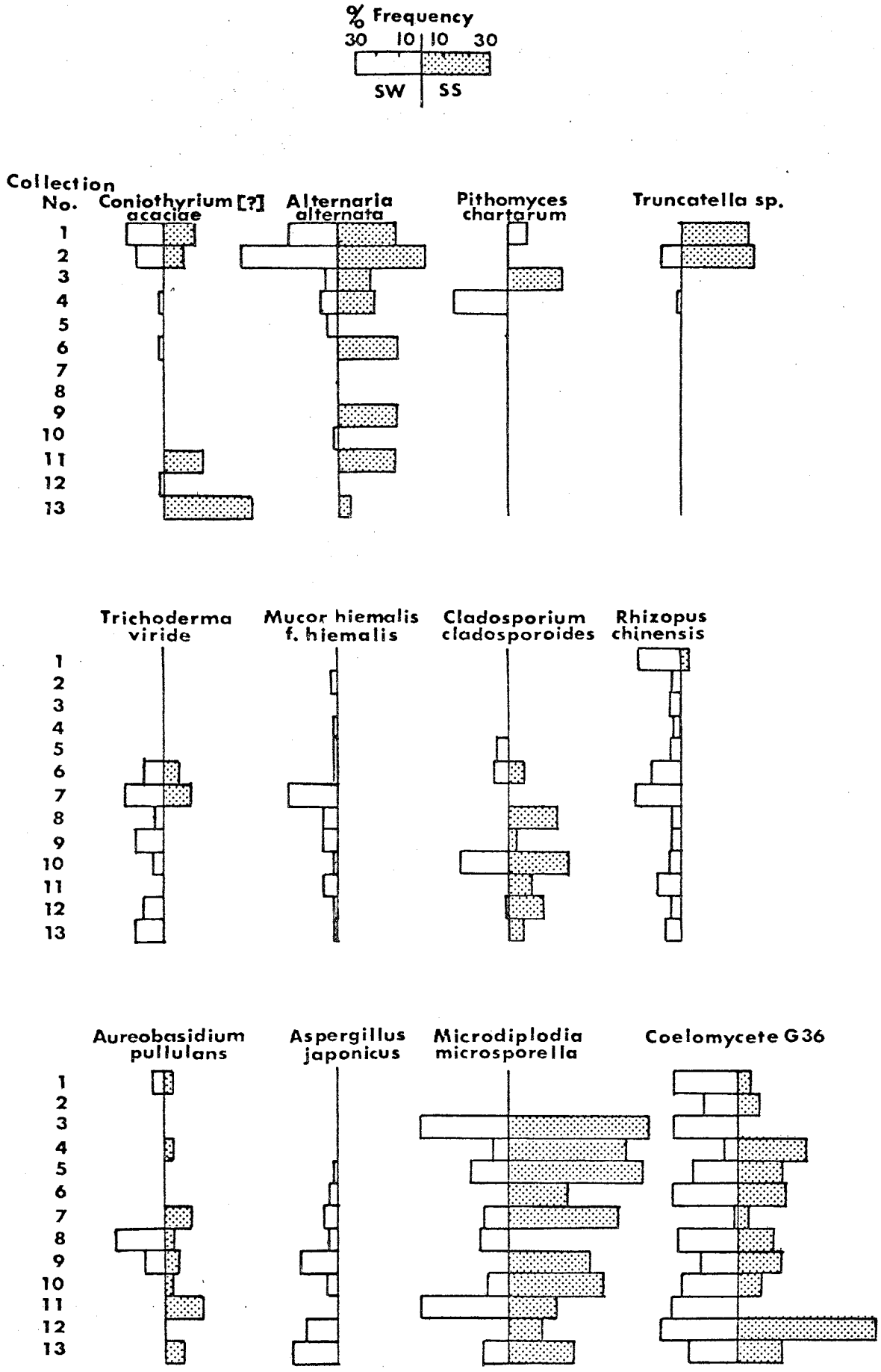


Figure 5.5 Mulga G site. Conventions as in Figure 5.4

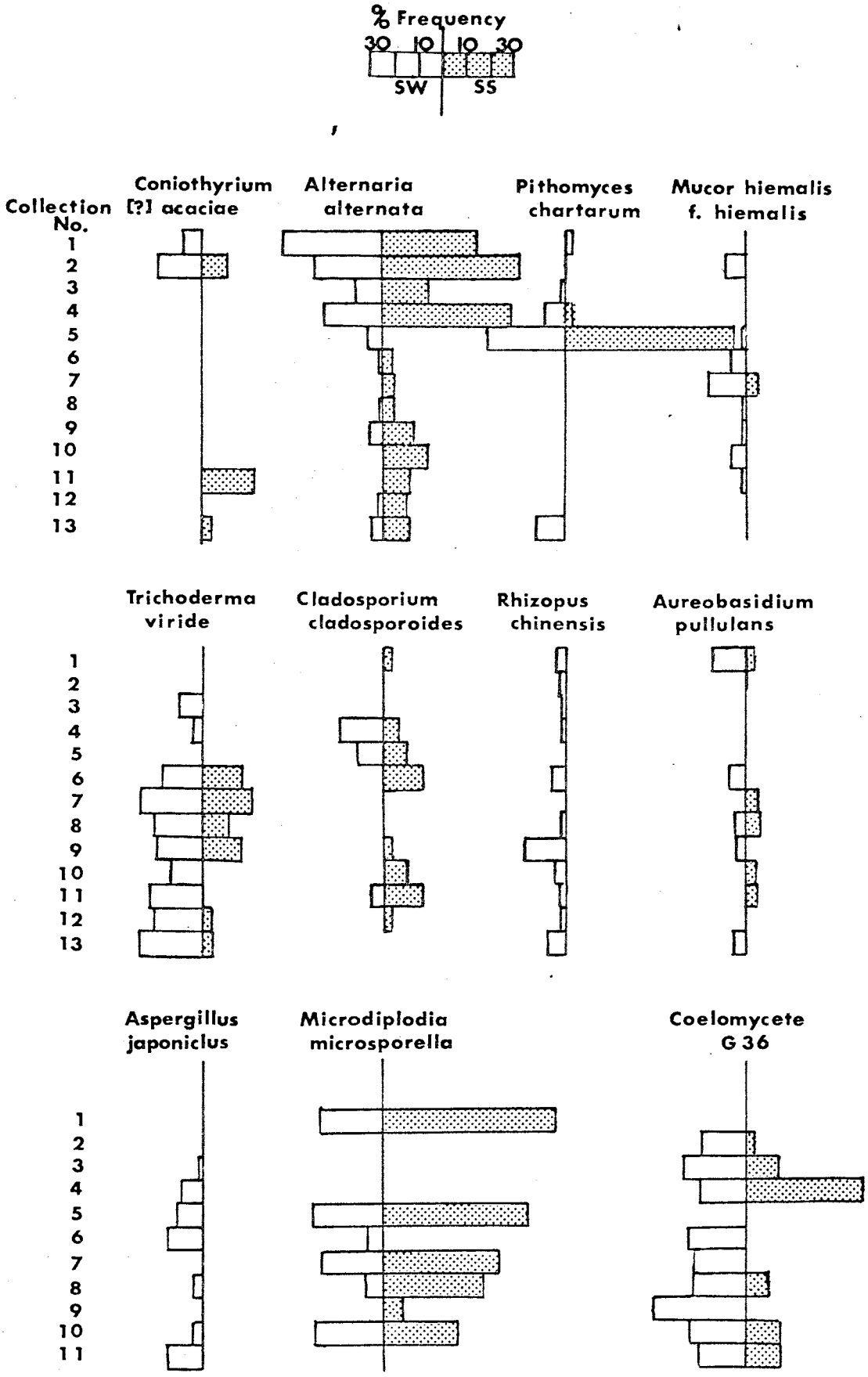


Figure 5.6 Mulga M site. Conventions as in Figure 5.4

positions - this is particularly noticeable with respect to Ceuthospora innumera, Penicillium piscarium, Trichoderma viride, Mucor hiemalis and Rhizopus (?) chinensis. It was shown previously that the rate of decomposition of LD leaves was significantly different from LG and LM leaves (Chapter 4). Such differences do not appear to be related to mycoflora colonization patterns. Rather it seems that the mycoflora composition reflects the substrate on which the litter bags were placed (c f. Witkamp 1966). Thus C. innumera is quite common in the early stages of colonization of LD and LM leaves but occurs only infrequently on the LG leaves. On the other hand the soil fungus, R. chinensis, tends to dominate as decomposition progresses on the LG leaves but is virtually absent from the LD and LM leaf litter.

The data for the isolates shown in Figures 5.1 - 5.3 indicate that all are capable of surface and internal colonization of the leaves. However some species e.g. Epicoccum nigrum and P. piscarium appear to be principally surface colonizers while others, such as Alternaria alternata and Coelomycete LM88* are largely internal

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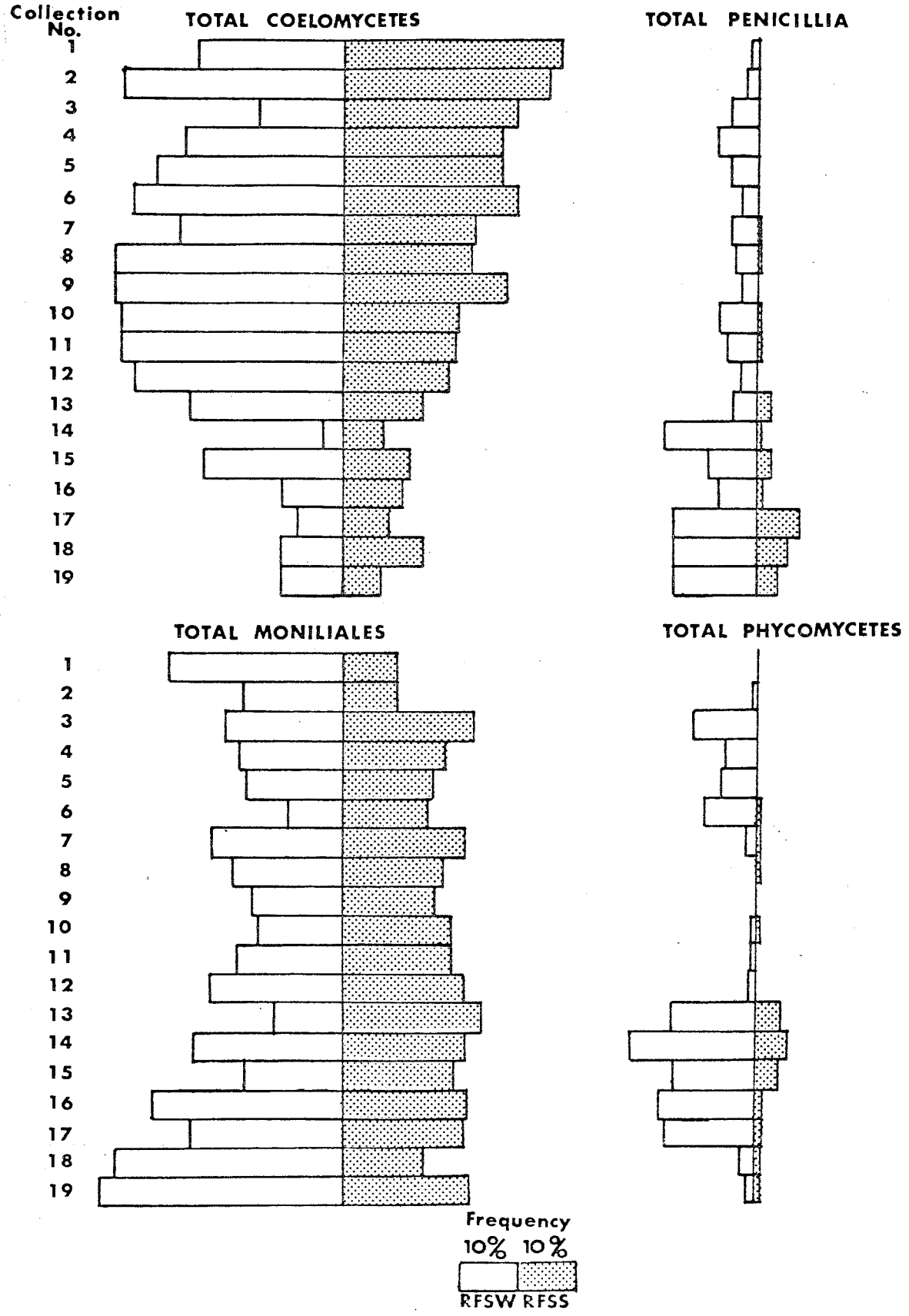
* Coelomycete LM88 - This is a common isolate which it was not possible to identify.

Figure 5.7 Relative percentage frequency of major groups of fungi as surface inhabitants (RFSW) and internal colonizers (RFSS) of leaves of Eucalyptus socialis during decomposition. See text for method of calculation.


Collection No.
TOTAL COELOMYCETES
TOTAL PENICILLIA
TOTAL MONILIALES
TOTAL PHYCOMYCETES
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
Frequency
10% 10%
RFSW RFSS

colonizers. A broader perspective of the colonizing pattern is given by combining the observations on all isolates when they are placed in their respective mycoflora groups (Figure 5.7). Note: the few Basidiomycete isolates are excluded from both mallee and mulga analyses because of their infrequent occurrence on the plates - further, the agar medium used does not favour the growth of this group although they no doubt contribute substantially to leaf decomposition, particularly in the later stages (Hudson 1968).

The pattern of fungal succession is clearly shown by this major grouping (Figure 5.7). The data are very similar to that shown by Macauley and Thrower (1966) for Eucalyptus regnans leaves. Coelomycetes are the primary colonizers on both surface and internal leaf tissues. Moniliales occur as codominants throughout all stages of decomposition, while the Penicillia and Mucorales (Phycomycetes) become more prominent as decomposition proceeds. It is notable that the Penicillia and Mucorales are mainly surface colonizers which is in substantial agreement with the results of Macauley and Thrower (1966).

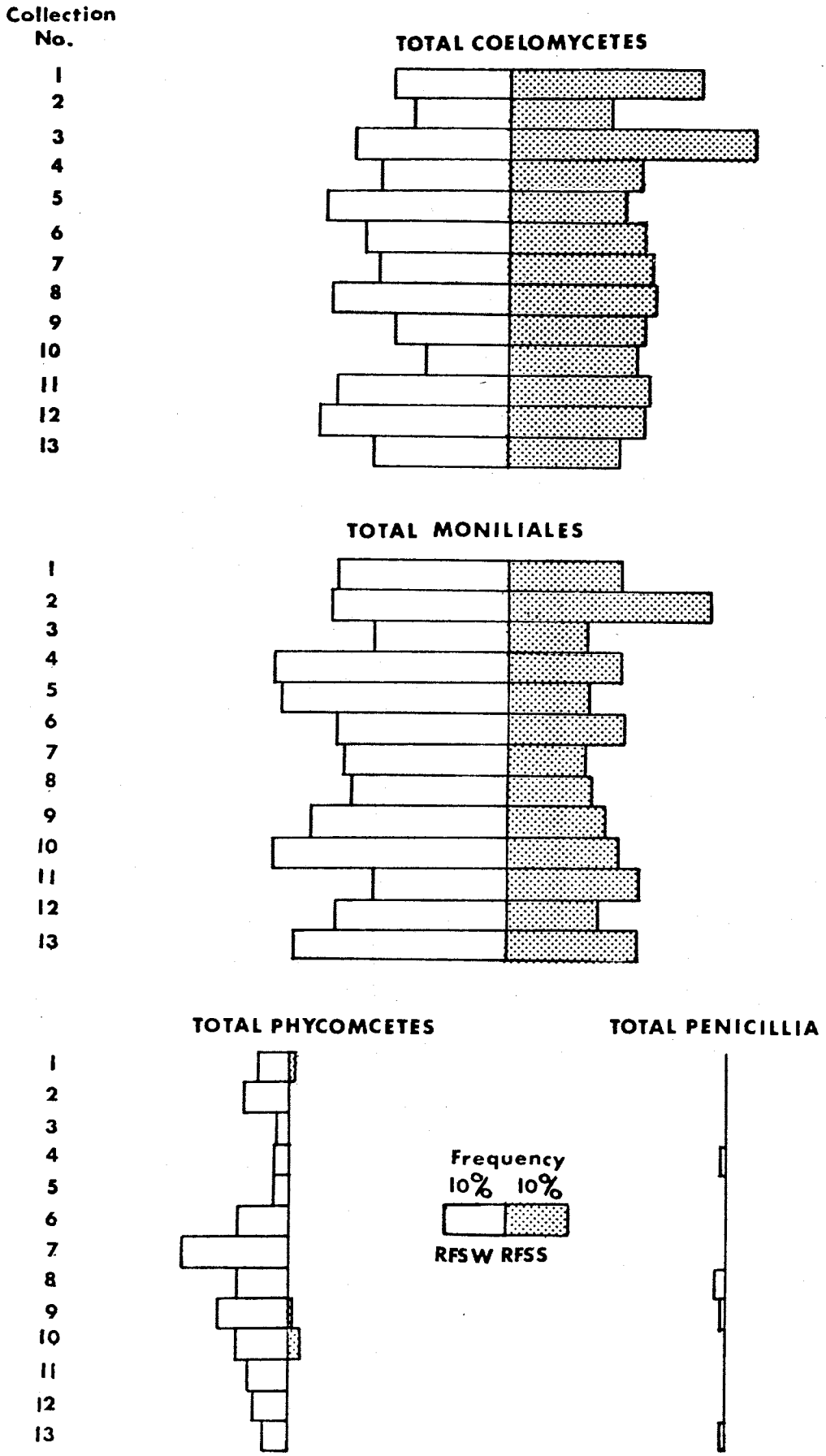
Of the species comprising greater than 5 per cent of all isolates from mulga leaves (Figures 5.4 - 5.6), all except Truncatella sp. and Coniothyrium sp. were common to each microsite (D, G, M). Truncatella did not appear in the isolates from leaves placed on the mature litter (M site), while Coniothyrium sp. was only recorded on the

D site. This probably resulted from intense competition from other isolates during incubation of the plates, rather than absences of the species per se. Apart from these two species there are no obvious microsite differences in the pattern of colonization by the most common mycofloral species. This observation is in keeping with the similarity of decomposition rates evidenced on D, G and M microsites (Chapter 4).

As in the mallee isolates some of the mulga species appear to be predominantly surface colonizers (Aspergillus japonicus, Mucor hiemalis f. hiemalis and Rhizopus (?) chinensis) while others dominate in the internal leaf tissue (Alternaria alternata, Microdiplodia microsporella). There is likewise a tendency for some species to occur early in the succession while others appear only after the leaves have been decomposing for some time. However when the species are combined into major groups (Figure 5.8) it is very clear that the distinct successional pattern evident for mallee (Figure 5.7) and Eucalyptus regnans (Macauley and Thrower 1966) is not shown here. It is suggested that this is related to the stage of decomposition at the conclusion of the observations. A longer period of observation may have revealed the expected pattern more closely.

A noteworthy feature of the mycoflora composition on decomposing mulga leaves was the prevalence of dematiaceous species of the genera Curvularia, Drechslera,

Figure 5.8 Relative percentage frequency of major groups of fungi as surface inhabitants (RFSW) and interral colonizers (RFSS) of phyllodes of Acacia aneura during decomposition. See text for method of calculation.


Collection No.
TOTAL COELOMYCETES
1
2
3
4
5
6
7
8
9
10
11
12
13
TOTAL MONILIALES
TOTAL PHYCOMCETES
TOTAL PENICILLIA
Frequency
10% 10%
RFSW RFSS

Helminthosporium and Nigrospora in the mulga litter compared with the mallee. The presence of Curvularia and Nigrospora is interesting in light of the observations of Hudson (1968) on the increased occurrence of these genera in the tropics. Of further note was the very infrequent recording of Penicillia on the mulga leaves. Only one entity, P. piscarium was recorded in very low frequencies (Figure 5.8), whereas for the mallee while only three species were recorded their frequency of occurrence was much greater (Figure 5.7). It is not clear why the Penicillia are so poorly represented in the mulga samples. Soil dilution plates were taken from several soil samples collected randomly from the soil surface (0-2 cm) on the MUM plot. The resulting counts gave a ratio of Fusarium:Penicillium:Aspergillus:Trichoderma of 10:5:2:1 which indicates a reasonable level of Penicillium abundance in the soil. Competition from other species, especially surface colonizers, has probably prevented Penicillium reaching its usual prominence in such studies (e.g. Macauley and Thrower 1966, Frankland 1966).

The traditional approach for examining fungal succession has been through the use of frequency diagrams as presented in the current study and elsewhere (Kendrick

and Burges 1962, Macauley and Thrower 1966). In microbial research the concept of utilizing computers for analysis of bacterial taxonomic data was first introduced by Sneath (1957). However while numerical classification methods have since received wide acceptance (Sneath and Sokal 1973, Clifford and Stephenson 1975) there are still very few reports of their use in studies of mycofloral populations. This is surprising as fungal populations commonly exhibit pronounced heterogeneity (vide Figures 5.1-5.6) and thus seem highly appropriate for analysis by multivariate techniques.

Perhaps the reluctance of fungal ecologists to use multivariate methods has been because of the well known limitations of the isolation plate technique as a means of determining fungal populations. Yet one of the prime purposes of classification is to simplify the spatial and temporal complexities of the data obtained. Employment of binary (presence/absence) data represents one of several stages in simplification (Frenkel and Harrison 1974), while the increase in effort expended in collecting and analysing numerical data is not always justified by the end results (Greig-Smith 1971).

The utility of multivariate classification routines in condensing the present succession data was examined using the CSIRO classification programmes DIVINFRE and CENTPERC. Since the latter shows the intergroup relationships of the former, results for CENTPERC only are given

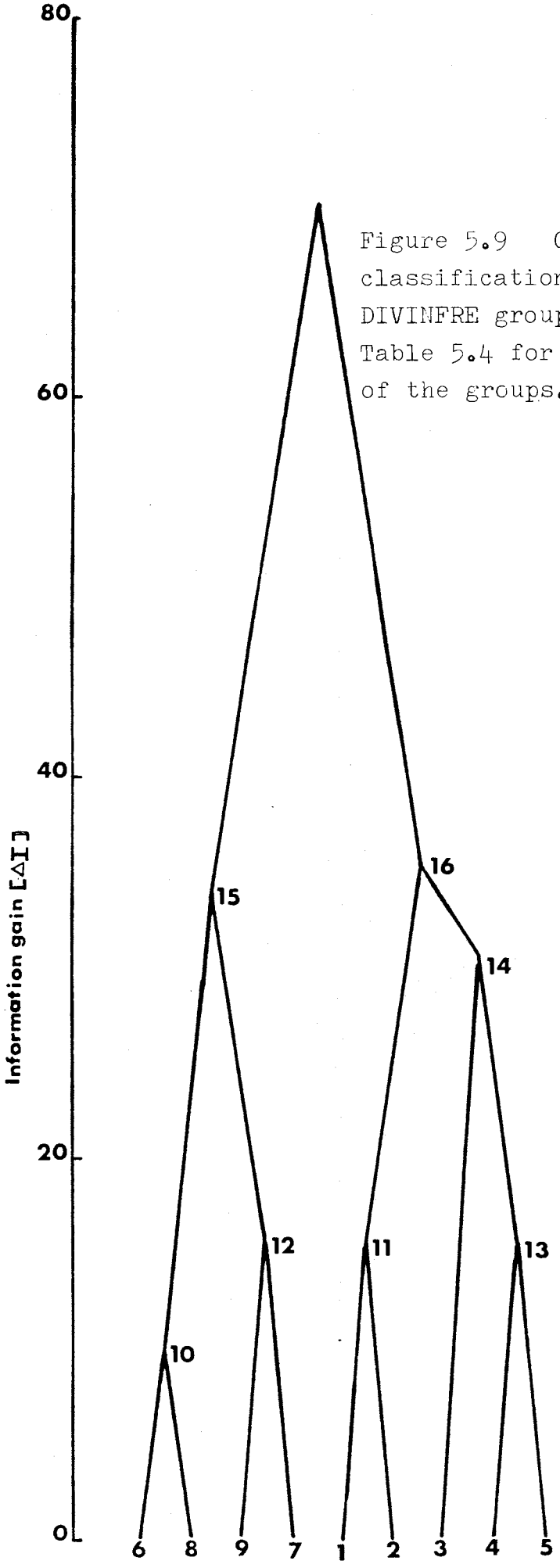


Figure 5.9 CENTPERC classification of mallee DIVINFRE groups. See Table 5.4 for composition of the groups.

here (Figures 5.9-5.10). Further the results from the classifications of the surface washed collections only will be discussed as the analyses for the surface sterilized samples led to similar conclusions concerning the method.

The relationship of the DIVINFRE defined groups with each other is indicated by the divisional branches of the CENTPERC hierarchy (Figures 5.9, 5.10). The smaller the information gain (ΔI) on fusion, the closer the groups are to each other (Dale, Lance and Albrecht 1971). It should be noted that the position of the groups along the horizontal axis is not significant as each group can be rotated 180^{o} about its fusion point (Sneath and Sokal 1973).

As detailed in methods the classifications were carried out on collection times and microsites and their efficacy may best be judged on the resultant grouping of these parameters (Tables 5.4, 5.5). The data suggest that there are no major differences in the mycoflora of the three microsites in the mallee community (Table 5.4), although Group 3 contains eight of the nineteen LM members. None of the mallee groups are site specific, however, and since the classification is based on presence/absence data this is not an unexpected result. For each microsite the decomposition bags were randomly positioned over the entire study area (Chapter 4). This would have also increased the probability of a common mycoflora being present on the leaves, even though the number of individuals of a particular species could have been very small on any one

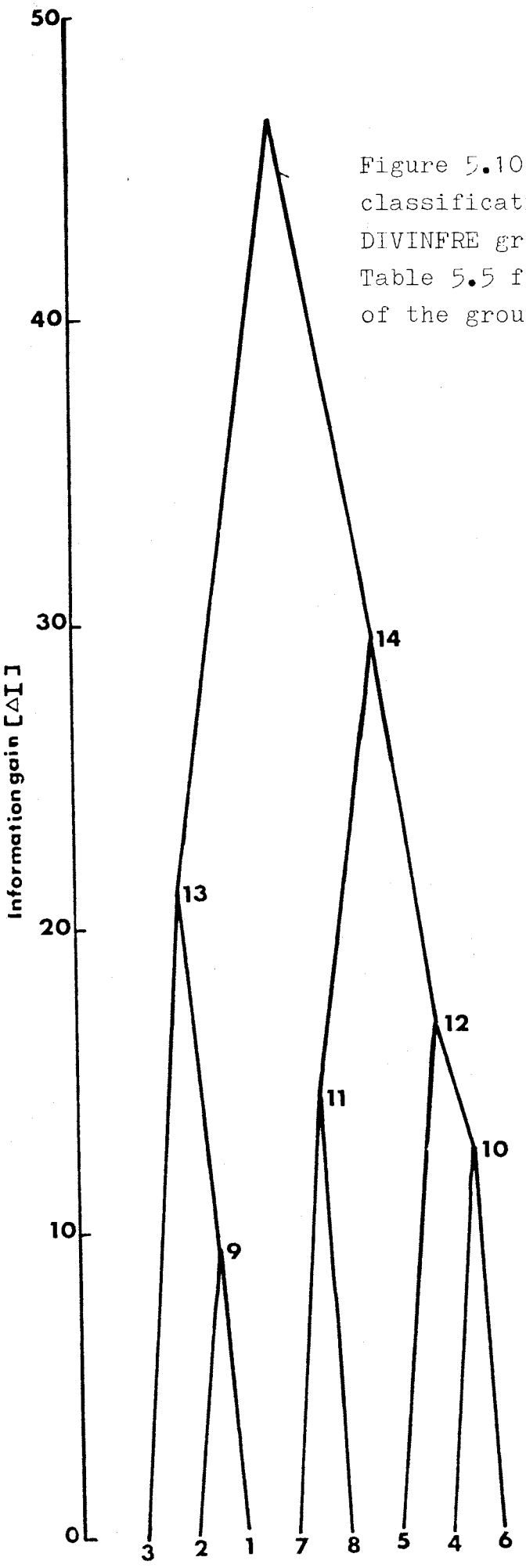


Figure 5.10 CENTPERC classification of mulga DIVINFRE groups. See Table 5.5 for composition of the groups.

microsite. Macauley and Thrower (1966) minimised such spatial variability by confining the naturally-fallen litter in layers at individual microsites at four weekly intervals and recording the fungi present in each layer at the conclusion of the study period.

The mallee classification (Figure 5.9, Table 5.4) suggests that there is a definite mycofloral sequence on the decomposing leaves. The collection numbers for the members of a particular DIVINFRE group were averaged and each group identified sequentially based on this 'mean collection time'. Thus members of Group 1 represented the shortest period of decomposition and Group 9 the longest. This approach minimises 'noise' within a particular group. For example, although Group 1 contains one member (LG15) representative of the fifteenth collection period its mean collection number was only 5.2 (Table 5.4). A comparison of the CENTPERC relationships (Figure 5.9) reveals a distinct dichotomy between those groups representing earlier stages of decomposition (1-5) compared with the later stages (6-9).

The classification of the mulga data (Figures 5.10, Table 5.5) gave similar results to that observed in the mallee. However, there is some suggestion of a distinctive mycoflora on the D microsite as DIVINFRE Group 6 contains ten of the thirteen collections obtained from the latter site (Table 5.5). Again there is clear evidence of a successional sequence and this is supported by the fusion of the groups in the CENTPERC hierarchy (Figure 5.10).

Table 5.4 Mallee DIVINFRE group members. LD, LG, LM represent microsites on which leaves were placed (see Chapter 4). Numbers following microsite symbols represent collection number (19 collections altogether).

DIVINFRE group	Group members	Mean collection number for group members
1	LD1	5.2
	LG2, LG3, LG5, LG15	
2	LD2, LD3	5.4
	LG1, LG4, LG6, LGG, LG8, LG10	
3	LD10	7.2
	LM1, LM2, LM6, LM7, LM8, LM10, LM12	
4	LD5, LDG, LD9, LD12, LD13	8.1
	LM4, LM5, LM11	
5	LD7, LD8, LD11	9.6
	LG19	
	LM3	
6	LD4	10.3
	LG7, LG11, LG13, LG14	
7	LD14, LD16	15.7
	LG18	
	LM14, LM15, LM16, LM17	
8	LD17	16.7
	LG16, LG17	
9	LD18, LD19	17.4
	LM13, LM18, LM19	

Table 5.5 Mulga DIVINFRE group members. D. G and M represent microsites on which leaves were placed (see Chapter 4). Numbers following microsite symbols represent collection number (13 collections altogether).

DIVINFRE group	Group members	Mean collection number for group members
1	D1	1
	G1	
	M1	
2	D2	2.5
	G2, G4	
	M2	
3	D4	3.5
	G3	
	M3, M4	
4	G5	5
	M5	
5	G6, G12	9
6	D3, D5, D6, D7	
	D8, D9, D10, D11,	
	D12, D13	7.9
	G10	
	M7, M9, M11	
7	G9	9.6
	M6, M8, M12, M13	
8	G7, G8, G11, G13	9.8
	M10	

This result was not nearly so apparent from the frequency diagrams (Figures 5.4-5.6, 5.8) indicating that the classification approach is more sensitive to subtle changes in mycoflora composition as decomposition proceeds.

Both methods of grouping the mycoflora population of mallee and mulga leaves (frequency diagrams or classification) have thus given similar results. There is no conclusive evidence that microsite differences in mycoflora exist in either community type, although the DIVINFRE grouping suggests the D mycoflora in mulga, and perhaps the LM in mallee, are of different composition to their corresponding microsites. However data on numbers or biomass of individual fungal species (not available in the current work) would be needed to quantify such differences. Since the LD and LG microsites were adjacent to each other in the MAD regrowth community and the G and M sites were juxtaposed in the mature mulga woodland (see Chapter 4) the data do indicate possible distinctions in the mycoflora based on community age. This in itself would merely be a broader reflection of the successional pattern clearly shown to pertain. Overall the classifications have tended to point out more subtle differences in the mycoflora populations otherwise not apparent from the frequency diagrams. Moreover where there is ready access to appropriate computer programmes it is far less time consuming to use the classification approach than the latter method. Nevertheless the general utility of

numerical classification in studying mycoflora succession would appear to be dependent on whether individual species or major groups are of primary interest.

It has been traditional to consider fungal succession on plant material as being started by colonization by 'sugar fungi' which require soluble carbon sources (Harley 1971). These were supposed to be followed by cellulose decomposers followed by lignin decomposers. However the succession on leaves and litter frequently omits the 'sugar fungi' (Pugh 1974) and the traditional sequence seems to have little basis in fact under natural conditions, where plant materials are concerned (Hudson 1968). These conclusions are supported by results in the present study where Coelomycetes and some Moniliales appear as principal components of the initial litter fungi (Figures 5.7, 5.8) whereas these are then replaced by members of the Mucorales and Penicillium ('sugar fungi'). Macauley and Thrower (1966) found that Eucalyptus regnans leaves lost their entire ethanol-soluble fraction within four weeks of exposure in the field and it is likely that the rapid initial weight losses in mallee and mulga leaves (Chapter 4) reflected similar changes. Nevertheless the decomposition of tree leaves is not a process which is entirely confined to the litter layer on the forest floor. In fact leaves are exposed to attack from micro-organisms and animals during their whole life, senescence and death (Jensen 1974).

Griffin (1972) observed that in general terms the mycoflora of different soils, even of greatly different geographical areas, are striking for their similarity rather than dissimilarity. This observation is supported by the mycoflora of mallee and mulga communities, which support quite differing plant assemblages in addition to being some 1200 km apart. A corollary of Griffin's observation is that there is no evidence for any selection of a xerophytic mycoflora in arid zones, despite the fact that species of Penicillium and particularly of Aspergillus are extreme xerophiles, able to grow at lower moisture levels than other fungi (Pugh 1974). However, Pentland (1967) suggests that microhabitats may be more variable in a drier soil than a wet one because there is less movement of water soluble products in the drier soil. Furthermore, Griffin (1972) notes that the survival of micro-organisms mainly as spores, is important, for by dormancy they are able to survive periods that are inclement for physical or chemical reasons.

There are two major difficulties in estimating the ecological roles of fungi: firstly, that of determining what species occur in any ecological substrate and their state of vegetative activity; and secondly, that of predicting from a study of fungi in culture, what they may be doing ecologically (Harley 1971). In the present study concomitant measures of dry weight losses, nitrogen and phosphorus content of the substrate and incident

rainfall (Chapter 4) were obtained for each period over which the mycoflora were isolated. It is clear from a consideration of the data of this and the preceding chapter that observed changes in the mycofloral succession in both mallee and mulga could be correlated with some of the measured substrate variables e.g. frequency of Coelomycetes and phosphorus content. However, correlation and causation are not necessarily the same. Therefore, in view of the complex of factors that mediate succession (Macauley and Thrower 1966, Griffin 1972), it could be misleading to relate the observed mycoflora populations to the few substrate variables measured.

5.4 Conclusions

This study has shown clearly that a succession of mycoflora species occur on decomposing mallee and mulga leaves. The pattern of species colonization is consistent with that found elsewhere in Australia (c f. Macauley and Thrower 1966). This is of the general order Coelomycetes ⟶ Moniliales ⟶ Mucorales/Penicillia. Differences were recorded between the major community types - notably the presence of species of Curvularia and Drechslera and the very infrequent occurrence of Penicillia in mulga - but there were few detectable differences in the pattern of colonization within microsites on each community. Species differences were noted between and within communities but a number of species (e.g. Mucor hiemalis, Trichoderma

viride) appear to be ubiquitous on decomposing leaves in Australia and elsewhere. There is no suggestion of a specific xerophytic mycoflora present on mallee and mulga.

As there have been very few studies of mycofloral successions on decomposing leaves in Australia it is not surprising that a significant number of isolates (all of minor occurrence) could not be positively identified within the time available. Nevertheless the comprehensive check list provided considerably extends present knowledge of the mycoflora in the Australian semi arid region.

Classical frequency methods and modern computer classification strategies were employed in the analysis of the data. The results confirm the applicability of multivariate analysis as a method of simplifying complex successional data. As is usually the case the classifications raised as many questions as were answered. For example what parameters (environmental, biochemical) lead to distinctions between the D and G/M sites in mulga? While some environmental data were available it was not thought advisable to compare these in a diagnostic fashion (see Lance, Milne and Williams 1968) as the data were clearly correlated with the stage of decomposition of the leaves (Chapter 4). An experimental approach similar to that adopted by Macauley and Thrower (1966) would be more appropriate to delineation of such relationships, but this was beyond the scope of the present study. The classical method of examining frequency diagrams led to substantially

the same conclusions as those reached with numerical classification, although more subtle differences in microsites and successions were not so evident. Nevertheless the frequency diagrams did give a better perspective on the place of individual species in the successional sequences and for this reason examining the data by both approaches was advantageous.

CHAPTER 6

Responses of mallee and mulga to nitrogen and phosphorus nutrition

6.1 Introduction

Numerous descriptive accounts of the flora of eastern Australia have been recorded but only a few studies have been directed towards understanding the relationship between vegetation and environment (Florence and Crocker 1962, Beadle 1968, Christie and Moorby 1975). Most Australian soils have very low phosphate levels (Wild 1958) and soils from the arid and semi arid regions are no exception (Charley and Cowling 1968). Eucalypt species have an ability to tolerate very low levels of phosphorus (Specht and Groves 1966, McColl and Humphreys 1967, Beadle 1968, Parsons 1968a) but seedlings growing on several forest soils of low phosphorus status have responded strongly to phosphate application (Beadle 1962, Cromer 1972).

A feature of Australian semi arid and arid vegetation is that it is often dominated by trees and shrubs, whereas similar world homoclimates support grass communities (Beadle 1951, 1960, Whittaker and Woodwell 1972). Semi arid mallee and mulga communities are typical examples. Both are found on characteristically infertile soils (Chapter 2) and it is of considerable ecological interest to observe the nutritional response (particularly to phosphorus) of the woody plants growing in these communities.

Gerloff (1963) suggests that native plants occurring on infertile soils may not only have the capacity to survive and grow in such areas, but may have adapted to them in having a slow growth rate and a low yield response, relative to faster growing species, as the nutrient supply increases. This type of response was demonstrated by Christie and Moorby (1975) for the grass, Thyridolepis mitchelliana, a species widespread throughout the mulga region. There is some evidence, however, that the growth of mulga (O'Hagan 1966) and red mallee (Parsons 1968a) may improve under increased nutrient supply.

The present study compares the phosphorus nutrition of mulga (Acacia aneura) and red mallee (Eucalyptus socialis). Cassia nemophila var. nemophila (formerly C. eremophila) was included in pot experiments since this was a woody plant common to both community types (Beadle 1948, Burrows and Beale 1969). One of the objectives of the work was to examine whether these woody plants possessed any characteristics in seedling phosphorus nutrition which could be advantageous when compared with grasses. It was also hoped that the study of seedling nutrition of E. socialis would further elucidate the problem of seedling regeneration in eucalypt communities. For example Attiwill (1972) suggests that the level of 'available' soil phosphorus under mature eucalypt forest is limiting to the growth of seedlings, whereas Florence and Crocker (1962) for E. pilularis, and Ashton and Macauley (1972) for

E. regnans, consider the micro-organisms of the forest litter may be directly antagonistic to seedling growth.

6.2 Methods

The phosphorus nutrition of A. aneura, E. socialis and C. nemophila was examined in two sand culture experiments (Experiments 1 and 2). Field trials were also carried out in A. aneura and E. socialis regrowth communities to gauge foliar nutrient responses to applied nitrogen, phosphorus and calcium (Experiment 3).

6.2.1 Phosphorus rate experiment (Experiment 1) - Seeds were scarified where necessary and then pre-germinated in petri dishes at staggered intervals so that seedlings of similar stages of development could be sown. On germination, seedlings were transferred to sand culture and maintained with distilled water only. They were planted out in 15 cm drained plastic pots four days before the first treatments were applied (24.3.74). At this time the seedlings had developed one to two pair of leaves and were selected for uniformity to leave one seedling per pot. Because of the short term nature of the study both the leguminous species were not inoculated with Rhizobia.

The culture medium comprised fine (c. 0.5 mm diameter) washed quartz sand (Australian Glass Manufacturing Co.). At no time during the course of the experiment were water

or nutrients added in excess of that required to bring the moisture content of the sand to field capacity.

Table 6.1 Composition of basal nutrient solution for P rate experiment

Total applied (mls/pot)	Stock solution
1.2	M Ca $(NO_3)_2$
3.6	0.5 M KNO_3
0.6	M Mg SO_4
0.3	Chelated Fe*
0.3	Trace elements+

* Chelated Fe was prepared according to the method described by Jacobsen (1951)

\+ Trace elements were prepared as per Hewitt (1966)

The design of the experiment was a randomized block (3 species x 4 phosphorus levels x 5 replicates). The phosphorus treatments, applied as NaH_2PO_4, were as follows:

P_1 0.03 mg P/pot (equivalent to 0.017 kg P/ha)

P_2 0.31 mg P/pot (equivalent to 0.175 kg P/ha)

P_3 3.10 mg P/pot (equivalent to 1.75 kg P/ha)

P_4 31.0 mg P/pot (equivalent to 17.5 kg P/ha)

Each pot received the identical basal nutrient solution (Table 6.1). The nutrients were applied at weekly intervals

for 10 weeks from the commencement of the experiment. Basal nutrients were given at the rate of 1/30 the total for the first five weeks and at the rate of 1/6 the total for the final five weeks. The increased rate of application over the latter half of the experiment was in order to overcome pronounced nitrogen deficiency or imbalance symptoms which developed in the P_4 treatments of A. aneura and C. nemophila.

The phosphorus treatments were applied at the rate of 1/10 the total at each weekly interval. Subsequent examination of uptake at the lowest rate of applied phosphorus suggested that demand would not have exceeded the supply of the element, especially as final phosphorus levels in the plant only approximated initial seed reserves for all species. Weekly nutrient applications were made in 50 ml of water. At all other times the pots were maintained at field capacity by daily applications of distilled water.

The experiment was run in a glasshouse at the CSIRO Black Mountain complex in which day/night temperature was maintained at 24/18° C. Pots were re-randomized twice weekly. The pots were harvested 12 days after the final application of nutrients on 6.6.74. The total growth period from the first nutrient application was 82 days. The following data were recorded: shoot weight, root weight, leaf number and stem height. The material from the replicates for each nutrient x species treatment was

bulked for chemical analysis of shoot and root. Determination of percentage nitrogen and phosphorus in shoots and roots was carried out as detailed in Appendix 1.

6.2.2 Phosphorus x nitrogen rate experiment (Experiment 2)- This trial was carried out as a result of imbalance observed in Experiment 1 and because it was thought nitrogen deficiency could have masked trends in the legumes. The procedures adopted were similar to the former study except that two seedlings were established in each pot, demineralized water (conductivity $< 2 \times 10^{-6}$ mhos) was used to maintain the pots at field capacity and the experiment was conducted in the Research School of Biological Sciences glasshouse (25/20^{o} C, day/night temperatures).

A factorial design was employed (3 species x 2 nitrogen levels x 3 phosphorus levels). There were six replicates of each treatment set out in six randomized blocks. Re-randomization was carried out within blocks twice weekly and between blocks at fortnightly intervals during the course of the study.

Treatments were applied as follows:

Nitrogen: N_1 5 mg N/pot (equivalent to 2.8 kg N/ha)

N_2 50 mg N/pot (equivalent to 28 kg N/ha)

The solutions were applied as $NaNO_3$ and NH_4NO_3 to supply nitrogen in the nitrate and ammonium forms in the ratio 9:1. This ionic balance was chosen since Moore and Keraitis (1971) found many eucalypt species performed better in sand culture when both ammonium and nitrate were present

in the nutrient solutions.

Phosphorus: This was applied as NaH_2PO_4

P_1 0.3 mg P/pot (equivalent to 0.175 kg P/ha)

P_2 1.0 mg P/pot (equivalent to 0.525 kg P/ha)

P_3 3.0 mg P/pot (equivalent to 1.75 kg P/ha)

Each pot received the identical basal nutrient solution comprising

0.8 ml/pot M Ca Cl_2

1.2 ml/pot 0.5 M K_2SO_4

0.4 ml/pot M $MgSO_4$

0.2 ml/pot chelated Fe

0.2 ml/pot trace elements

made up as for Experiment 1. The total amount of basal nutrients applied was less than in the phosphorus rate trial but the method of application ensured more equitable distribution throughout the growth period. The treatment and basal nutrients were applied at $^1/_{10}$ the total amount per pot in 50 ml demineralized water at weekly intervals for 10 weeks. The initial nutrient application was on the 25.10.74 and the pots were harvested on the 8.1.75 (Growth period, 75 days). Leaf area of the harvested seedlings was obtained with an integrating photometer (LAMBDA Instruments). Other seedling parameters were measured as detailed for the previous experiment.

6.2.3 Field nutrient responses (Experiment 3) - Foliar analysis was employed to gauge the nutrient response of E. socialis and A. aneura regrowth to applied nitrogen,

phosphorus and calcium. Dense uniform stands of mallee and mulga regrowth were located on topographically flat ground adjacent to the MAD and MUM sites respectively. The mallee regrowth was c. 10 years old and the mulga c. 15 years old. Both stands were less than 2.5 m in height and the apical foliage could be easily sampled.

Nitrogen, phosphorus and calcium were applied to each species in a 3^3 factorial design, with three replications laid out in three randomized blocks. The nutrients were placed on a 2.5 m x 2.5 m area surrounding the base of individual E. socialis clumps or A. aneura stems. Plots were positioned by establishing a 10 m x 5 m grid over each block and applying the appropriate treatment to the nearest uniform clump or stem adjacent to the intersections of the grid lines. Individual treatment levels for the mallee site were as follows:

Nitrogen - 0, 80 and 400 g $NH_4 NO_3$ per plot (N_0,N_1,N_2)

Phosphorus-0, 80 and 400 g NaH_2PO_4 per plot (P_0,P_1,P_2)

Calcium - 0, 80 and 800 g $CaCO_3$ per plot (Ca_0,Ca_1,Ca_2)

(Note: 80 g/plot is equivalent to 128 kg/ha
400 g/plot is equivalent to 640 kg/ha
800 g/plot is equivalent to 1280 kg/ha)

Identical rates and nutrients were applied to the mulga site except that the more soluble $CaCl_2$ was used in place of $CaCO_3$. The highest rates of calcium application were determined from a liming curve for mulga soil (Christie unpublished data) and were estimated to increase soil pH

(surface 20 cm) from 5-6.8. The treatments were applied to mallee regrowth on 30th September 1973 and to the mulga plots on 30th December 1973. Application times were chosen to correspond with the period when leaf growth was most likely to occur.

Leaves were harvested from the mallee plots at 6 and 16 week intervals following nutrient application. At the first harvest the leaves were collected from two positions in the canopy (i) 'apical' leaves (current season growth) and (ii) 'mature' leaves (1-2 year old). Fifty leaves in each class were chosen from random positions in the canopy and they were selected from more than one stem in the clump. The leaves from each replicate and canopy position were placed in individually labelled paper bags for return to the laboratory for analysis. Nitrogen and phosphorus contents were determined on the ground bulk sample of the fifty leaves from each replicate position. Similar procedures were adopted for the second harvest when only apical leaves were collected.

Only one harvest was obtained from the mulga trial 12 weeks after nutrient application. Both apical and mature phyllode classes were collected from each replicate and the samples were analysed as for the mallee material.

6.2.4 Growth analysis - Values for relative growth rate (R_W) and net assimilation rate (E_A) are defined by the expressions (Watson 1952)

$$R_W = \frac{1}{W} \cdot \frac{dW}{dt} \qquad (1)$$

and $$E_A = \frac{1}{A} \cdot \frac{dW}{dt} \qquad (2)$$

where W is total plant dry weight (g), A is leaf area (dm^2) and t is time in days (or weeks for E_A).

Estimates of the leaf area ratio (F_A) may be obtained from the relationship

$$F_A = 7 \times R_W/E_A \qquad (3)$$

Over finite time intervals ($t_2 - t_1$) average values for R_W and E_A may be calculated

$$\overline{R}_W = (\log_e W_2 - \log_e W_1) / (t_2 - t_1) \qquad (4)$$

$$\overline{E}_A = \frac{(\log_e A_1 - \log_e A_2)}{(A_1 - A_2)} \times \frac{(W_1 - W_2)}{(t_2 - t_1)} \qquad (5)$$

Similar relationships can be defined to describe the instantaneous absorption rate (I_M) of mineral elements per unit weight of roots (Williams 1948). Hence

$$I_M = \frac{1}{R} \cdot \frac{dM}{dt} \qquad (6)$$

where R is the dry weight of roots and M is weight of mineral taken up at time t. Average absorption rates ($\overline{I}_M$) are thus given by

$$\overline{I}_M = \frac{(\log_e R_2 - \log R_1)}{(R_2 - R_1)} \times \frac{(M_2 - M_1)}{(t_2 - t_1)} \qquad (7)$$

For equations (5) and (7) to be valid linear relationships must be assumed between the parameters over the time period considered. This is not always the case

(e.g. Radford 1967). It was assumed linear relationships existed between dry weight, phosphorus uptake and leaf area on time as this study was carried out only over seedling growth stages. It is most likely that this assumption would have been correct for nutrient non-limiting concentrations, but not so for the nutrient limiting situations. However, as the objective was to examine comparative differences in species response these mean rates were calculated to obtain some estimate of relative differences in species behaviour.

6.2.5 Statistical analysis - Analyses of variance (ANOVA) of the data were confined to the major growth parameters measured. The phosphorus rate trial was analysed by an ANOVA programme written in BASIC for the Research School of Biological Sciences NOVA computer. The factorial experiments (N x P rate study and field nutrient response trial) were analysed using the GENSTAT library available on the CSIRO computer network. Abbreviated listing of these ANOVA results are presented in Appendix 3.

6.3 Results and Discussion

6.3.1 Experiment 1 (Phosphorus rate experiment) - All species responded strongly to increased phosphorus concentrations in the nutrient solution (Table 6.2). However there was a decline in yield between the P_3 and P_4 treatments and this was associated with signs of nutrient

Table 6.2 Growth characteristics at the end of the experimental period (Phosphorus rate experiment)

Parameter	Species	Nutrient treatment				Diff. for significance*	
		P_1	P_2	P_3	P_4	$P < 0.05$	$P < 0.01$
Total dry weight (g)	E.socialis	0.0392	0.0426	0.3111	0.2956	0.0563	0.0738
	A.aneura	0.0774	0.0846	0.2417	0.1943	0.1231	0.1613
	C.nemophila	0.1270	0.1473	0.2772	0.2615	0.1431	N.S.
Dry weight shoot (g)	E.socialis	0.0218	0.0241	0.2101	0.2025	0.0450	0.0603
	A.aneura	0.0465	0.527	0.1691	0.1488	0.0993	0.1302
	C.nemophila	0.0506	0.655	0.1339	0.1528	0.0764	0.1031
Dry weight roots (g)	E.socialis	0.0174	0.0184	0.1009	0.0931	0.0376	0.0492
	A. aneura	0.0309	0.0319	0.0726	0.0455	0.0265	0.0348
	C.nemophila	0.0763	0.0818	0.1433	0.1087	N.S.	N.S.
Relative yield (% max)	E.socialis	12.6	13.7	100.0	95.0		
	A.aneura	32.0	35.0	100.0	80.4		
	C.nemophila	45.8	53.1	100.0	94.3		

Table 6.2 (Continued)

Parameter	Species	Nutrient treatment			
		P_1	P_2	P_3	P_4
Average relative growth rate $\overline{RW}$ (g/g/day)	E.socialis	0.026	0.027	0.052	0.051
	A.aneura	0.023	0.024	0.037	0.034
	C.nemophila	0.021	0.022	0.030	0.029
Shoot/root ratio	E.socialis	1.25	1.31	2.08	2.17
	A.aneura	1.50	1.65	2.33	3.27
	C.nemophila	0.66	0.80	0.93	1.40
#Leaves	E.socialis	9	11	28	25
	A.aneura	4	4	6	7
	C.nemophila	6	6	14	18

* Tukey's test - Snedecor (1956) p. 251

imbalance in each species, particularly E. socialis. In this species patchy red discolorations first appeared at the leaf tip and then developed along the leaf margins of the P_4 treatments. The most pronounced symptoms occurred in what were the most vigorous E. socialis seedlings some 2-3 weeks before the final harvest. Earlier Jacobs (1955) and Moore and Keraitis (1971) observed that Eucalyptus seedlings are sensitive to high concentrations of nutrients, although actual concentrations are not stated. The high foliar phosphorus concentrations (Table 6.3) suggest that luxury consumption of phosphorus may have led to phosphorus toxicity as well as nutrient imbalance in the P_4 treatments. Specht and Groves (1966) found a tendency towards chlorosis of the upper half of the older leaves in E. baxteri at applied phosphorus levels of 3 mg P/plant, but this was not observed in E. socialis in the present study. As stated in the methods section Acacia and Cassia displayed marked chlorosis in all treatments by the fifth week of the experiment but this was overcome in both species by increasing the level of basal nutrients.

Increasing phosphorus concentrations were accompanied by an increase in the shoot/root ratio in all species and an increase in the number of leaves. The shoot/root ratio of E. socialis and A. aneura was similar but was much less for C. nemophila at all nutrient concentrations (Table 6.2). C. nemophila also had lower relative growth rates than mallee and mulga at all concentrations. The most likely reason for this is the lower amount of photosynthetic

Table 6.3 Nutrient uptake at the end of the experimental period (Phosphorus rate experiment). Values are means of 5 replicates for *E. socialis* and *A. aneura* and 4 replicates for *C. nemophila*

Parameter	Species	Nutrient treatment			
		P_1	P_2	P_3	P_4
Applied P(mg)*	All	0.03	0.31	3.10	31.00
Applied N(mg)*	All	58.8	58.8	58.8	58.8
% N in shoot	*E.socialis*	1.91	1.86	1.72	1.62
	A.aneura	1.91	2.18	3.33	4.21
	C.nemophila	2.18	2.18	2.80	3.66
% N in root	*E.socialis*	0.69	0.57	0.60	0.61
	A.aneura	1.65	1.56	1.72	1.75
	C.nemophila	1.08	1.22	1.12	1.22
Total N shoot (mg)	*E.socialis*	0.417	0.447	3.614	3.281
	A.aneura	0.997	1.148	5.630	6.260
	C.nemophila	1.102	1.428	3.755	5.589
Total N root (mg)	*E.socialis*	0.120	0.105	0.603	0.564
	A.aneura	0.509	0.497	1.251	0.797
	C.nemophila	0.823	0.998	1.599	1.325
N shoot/ N root	*E.socialis*	3.47	4.26	5.99	5.82
	A.aneura	1.74	2.31	4.50	7.85
	C.nemophila	1.34	1.43	2.35	4.22
% P in shoot	*E.socialis*	0.04	0.03	0.23	2.97
	A.aneura	0.04	0.05	0.16	0.55
	C.nemophila	0.06	0.06	0.11	0.67
% P in root	*E.socialis*	0.02	0.02	0.09	1.03
	A.aneura	0.05	0.04	0.08	0.74
	C.nemophila	0.05	0.04	0.06	0.76
Total P shoot (mg)	*E.socialis*	0.010	0.008	0.479	6.032
	A.aneura	0.020	0.025	0.270	0.819
	C.nemophila	0.029	0.036	0.149	1.018

Table 6.3 (Continued)

Parameter	Species	Nutrient treatment			
		P_1	P_2	P_3	P_4
Total P root (mg)	E.socialis	0.004	0.004	0.091	0.958
	A.aneura	0.016	0.013	0.056	0.338
	C.nemophila	0.037	0.033	0.085	0.830
P shoot/ P root	E.socialis	2.50	2.00	5.26	6.30
	A.aneura	1.25	1.92	4.82	2.42
	C.nemophila	0.78	1.09	1.75	1.23

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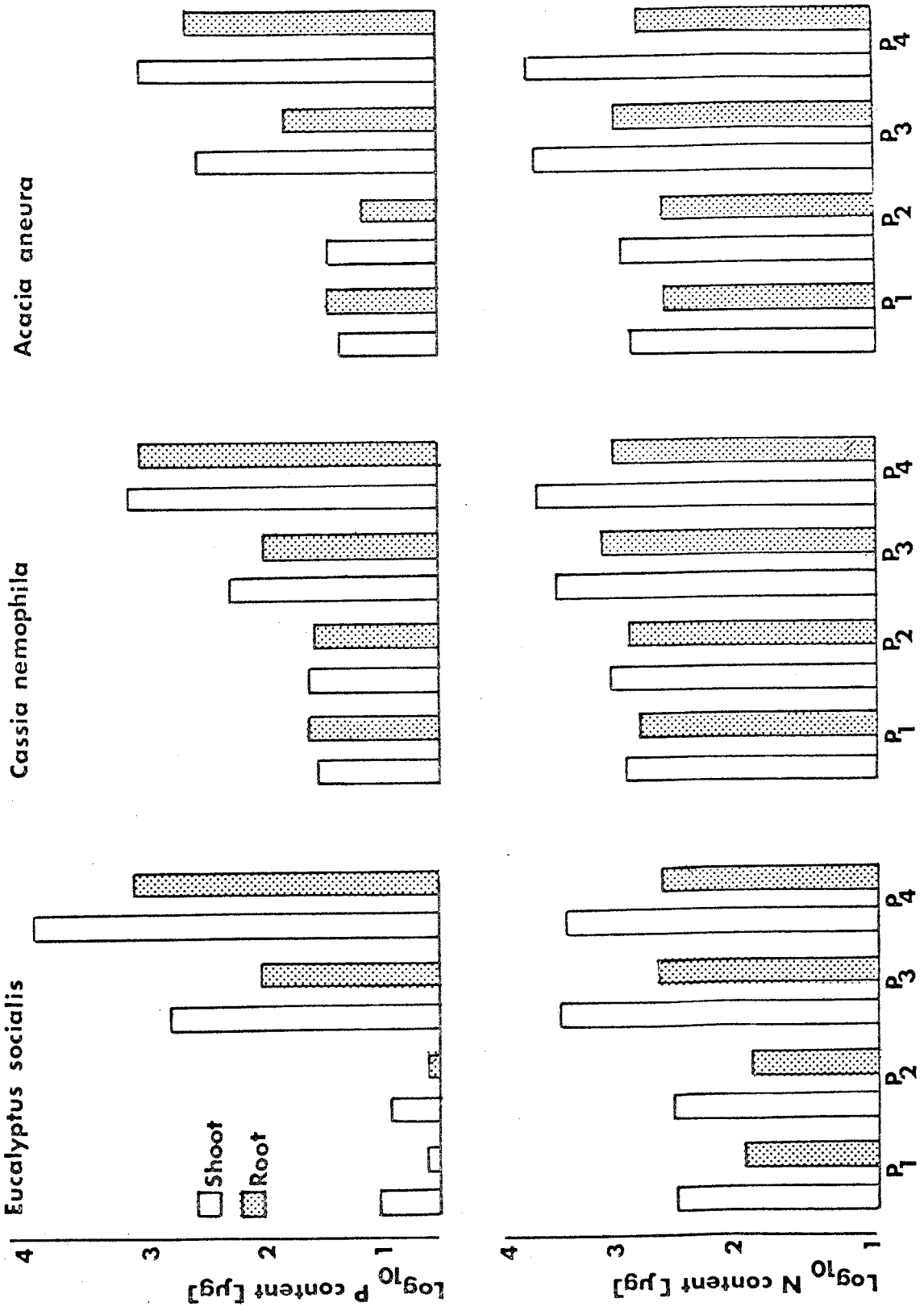
* Does not include seed reserves:

E.socialis	0.031 mg N, 0.008 mg P
A.aneura	0.477 mg N, 0.050 mg P
C.nemophila	0.516 mg N, 0.063 mg P

Figure 6.1 Uptake of nitrogen and phosphorus in seedlings of *Eucalyptus socialis*, *Acacia aneura* and *Cassia nemophila* grown in sand culture.
See text for description of treatments (Experiment 1)


Eucalyptus socialis
Cassia nemophila
Acacia aneura
Shoot
Root
log10 P content [µg]
log10 N content [µg]
4
3
2
1
P1
P2
P3
P4

surface in C. nemophila which is reflected in low leaf area ratios, not determined in the preliminary trial but which can be inferred from Table 6.6. The higher relative yields of Cassia in the P_1 and P_2 treatments compared with mallee and mulga (Table 6.2) also appear to be a reflection of the slower growth rates in the former species.

Several workers (e.g. Bradshaw et al 1964, van den Driessche and Wareing 1966, Parsons 1968b) have shown that many species on infertile sites have inherently slow growth rates. The seedling growth rate of all three woody species in the present study was extremely low (Tables 6.2, 6.5) - the values being much smaller than that recorded for mulga grass (Thyridolepis mitchelliana) by Christie and Moorby (1975) which exhibited relative growth rates of c. 0.1 g/g/day at the lowest solution concentrations (0.003 ppm phosphorus).

Nutrient concentrations in the plant tissues follow expected trends. Tissues of the leguminous species (A. aneura and C. nemophila) exhibit much higher nitrogen concentrations than occur in E. socialis (Table 6.3), especially in the P_3 and P_4 treatments. In each species the nitrogen concentration in the roots is fairly constant for all treatments so it appears that movement to the tops could be restricted by inadequate phosphorus levels. This is supported by the data for absolute uptake (Table 6.3, Figure 6.1). On the other hand the proportion of phosphorus distributed between shoot and root is greater for E. socialis

than for A. aneura and C. nemophila at all levels of applied phosphorus. This is indicated by the P shoot/P root ratios (Table 6.3) although the distribution of dry matter between shoots and roots needs also to be considered with this data. The phosphorus concentration in the shoot of E. socialis for the P_4 treatment (2.97 % P) is extremely high, but concomitantly high concentrations in the root contributed to similar P shoot/P root ratios in both P_3 and P_4 treatments (Table 6.3). Thus under these experimental conditions E. socialis appears to be much more efficient with respect to phosphorus transport than either A. aneura or C. nemophila.

It should be noted that this result was obtained in the absence of mycorrhizal inoculation of the E. socialis roots (c f. Malajczuk, McComb and Loneragan 1975). However recent work by Mulette, Hannon and Elliott (1974) and Ashford, Lee and Chilvers (1975) suggests that the beneficial role of mycorrhizal associations in eucalypts will only be evident from longer term experiments than those of the present study.

In the second pot study (Experiment 2) the nitrogen and phosphorus levels were varied concurrently. The phosphorus levels chosen (0.3, 1.0 and 3.0 mg/pot) covered the most responsive range of the preliminary trial (Experiment 1). The results (Tables 6.4, 6.5, 6.6, Figures 6.2, 6.3, 6.4) are similar to those obtained in the preliminary study. However statistical analysis of main

Table 6.4 Growth characteristics at the end of the experimental period (N x P rate study - Experiment 2)

Parameter	Species	Nutrient treatment N_1P_1	N_2P_1	N_1P_2	N_2P_2	N_1P_3	N_2P_3
Total dry weight (g)	E. socialis	0.0675	0.0680	0.1536	0.1592	0.1716	1.4487
	A. aneura	0.1242	0.1668	0.1280	0.2778	0.1551	0.8705
	C. nemophila	0.1980	0.2488	0.2259	0.3349	0.2205	0.7867
Dry weight shoots (g)	E. socialis	0.0375	0.0349	0.0733	0.0902	0.0740	0.9485
	A. aneura	0.0594	0.0903	0.0620	0.1534	0.0877	0.5390
	C. nemophila	0.0763	0.1118	0.0935	0.1463	0.875	0.4246
Dry weight roots (g)	E. socialis	0.0300	0.0331	0.0803	0.0690	0.976	0.5002
	A. aneura	0.0648	0.0765	0.0660	0.1244	0.0674	0.3315
	C. nemophila	0.1216	0.1370	0.1324	0.1886	0.1330	0.3621

Table 6.4 (Continued)

Parameter	Species	Nutrient treatment					
		N_1P_1	N_2P_1	N_1P_2	N_2P_2	N_1P_3	N_2P_3
Shoot/root ratio	E. socialis	1.25	1.05	0.91	1.31	0.76	1.89
	A. aneura	0.92	1.18	0.94	1.23	1.30	1.64
	C. nemophila	0.62	0.81	0.70	0.78	0.64	1.08
Leaf area (cm^2)	E. socialis	1.64	1.61	3.66	4.26	3.85	49.04
	A. aneura	2.74	4.69	2.63	7.02	2.72	21.05
	C. nemophila	2.59	3.52	2.66	4.57	2.74	11.03

effects is limited by the very strong nitrogen x phosphorus interaction ($P < 0.001$) observed in all species (Appendix 3). This interaction response has been found to be almost universal in *Eucalyptus* (Cromer 1972) and has been previously demonstrated in pot studies with *E. socialis* (Parsons 1968a). There were greater absolute yields of dry matter in the second study than in the phosphorus rate experiment (compare similar treatments of Tables 6.2,6.4) although both trials involved similar growth intervals. This is attributed to the fact that plants in the latter experiment were growing under higher levels of irradiance compared with Experiment 1.

The measurement of leaf areas in Experiment 2 permitted calculations of average net assimilation rates and leaf area ratios to be made. These growth responses in *E. socialis* and *A. aneura* are very similar (Tables 6.5, 6.6). However *C. nemophila* had higher net assimilation rates than the other species, but as in the first experiment it also exhibited slower growth rates at all nutrient concentrations. The slow growth rate is associated with lower leaf area ratios; the growth responses of *C. nemophila* are similar to those found in Mitchell grass by Christie (1975b). Shoot/root ratios of *C. nemophila* were also consistently lower than *E. socialis* and *A. aneura* at all nutrient concentrations. While these characteristics result in reduced capacity for growth under favourable conditions, they could be of considerable adaptive significance in periods of moisture stress.

Table 6.5 Influence of nitrogen and phosphorus supply on average relative growth rate ($\overline{R}_W$) average net assimilation rate ($\overline{E}_A$), and average leaf area ratio ($\overline{F}_A$) of *E. socialis*, *A. aneura* and *C. nemophila*.
See text for explanation of treatments and assumptions underlying the analysis (Experiment 2).

	Treatment					
	N_1P_1	N_2P_1	N_1P_2	N_2P_2	N_1P_3	N_2P_3
(i) $\overline{R}_W$ (g/g/day)						
E. socialis	0.036	0.036	0.047	0.048	0.049	0.077
A. aneura	0.032	0.035	0.032	0.042	0.035	0.058
C. nemophila	0.029	0.032	0.030	0.036	0.030	0.047
(ii) $\overline{E}_A$ ($g/dm^2/wk$)						
E. socialis	0.074	0.076	0.103	0.096	0.112	0.141
A. aneura	0.063	0.062	0.067	0.083	0.081	0.124
C. nemophila	0.089	0.096	0.101	0.114	0.097	0.159
(iii) $\overline{F}_A$ (dm^2/g)						
E. socialis	3.40* (2.43)**	3.31 (2.37)	3.19 (2.38)	3.50 (2.68)	3.06 (2.24)	3.82 (3.39)
A. aneura	3.55 (2.21)	3.95 (2.81)	3.34 (2.05)	3.54 (2.53)	3.02 (1.75)	3.27 (2.42)
C. nemophila	2.28 (1.31)	2.33 (1.41)	2.08 (1.18)	2.21 (1.36)	2.16 (1.24)	2.07 (1.40)

* From $\overline{F}_A = 7 \times (\overline{R}_W/\overline{E}_A)$ ** From $F_A = \frac{\text{leaf area } (dm^2)}{\text{total plant weight}(g)}$ both measured at final harvest

Table 6.6 Nutrient uptake at the end of the experimental period (N x P rate experiment). See text for description of treatments.

Parameter	Species	Nutrient treatment					
		N_1P_1	N_2P_1	N_1P_2	N_2P_2	N_1P_3	N_2P_3
Total N applied (mg)	All	5	50	5	50	5	50
Total P applied (mg)	All	0.31	0.31	1.03	1.03	3.10	3.10
% N in shoot	E. socialis	1.61	2.46	1.45	2.12	1.18	1.86
	A. aneura	0.98	2.15	1.07	2.01	1.28	2.60
	C. nemophila	1.14	1.92	1.00	2.06	1.09	2.58
% N in root	E. socialis	0.82	0.93	0.69	1.08	0.60	0.84
	A. aneura	1.39	2.31	1.40	2.27	1.37	2.19
	C. nemophila	0.99	1.83	0.90	1.59	0.96	1.97
Total N shoot (mg)	E. socialis	0.606	0.860	1.061	1.917	0.871	17.650
	A. aneura	0.581	1.946	0.664	3.079	1.120	14.021
	C. nemophila	0.867	2.149	0.932	3.014	0.953	10.953
Total N root (mg)	E. socialis	0.309	0.308	0.510	0.978	0.590	7.929
	A. aneura	0.902	1.765	0.926	2.820	0.921	7.267
	C. nemophila	1.199	2.514	1.188	2.994	1.285	7.147

Table 6.6 (Continued)

Parameter	Species	Nutrient treatment					
		N_1P_1	N_2P_1	N_1P_2	N_2P_2	N_1P_3	N_2P_3
N shoot/ N root	E. socialis	1.96	2.79	2.08	1.96	1.48	2.23
	A. aneura	0.59	1.10	0.72	1.09	1.22	1.93
	C. nemophila	0.72	0.85	0.78	1.01	0.74	1.53
% P in shoot	E. socialis	0.04	0.04	0.12	0.07	0.28	0.07
	A. aneura	0.07	0.05	0.12	0.06	0.23	0.10
	C. nemophila	0.07	0.05	0.10	0.05	0.24	0.11
% P in root	E. socialis	0.04	0.03	0.07	0.05	0.24	0.06
	A. aneura	0.06	0.05	0.09	0.06	0.19	0.10
	C. nemophila	0.06	0.05	0.08	0.07	0.17	0.08
Total P shoot (mg)	E. socialis	0.015	0.015	0.090	0.063	0.212	0.666
	A. aneura	0.041	0.042	0.074	0.100	0.202	0.546
	C. nemophila	0.052	0.051	0.093	0.080	0.207	0.451
Total P root (mg)	E. socialis	0.012	0.009	0.054	0.049	0.236	0.566
	A. aneura	0.038	0.037	0.063	0.081	0.131	0.335
	C. nemophila	0.073	0.073	0.104	0.124	0.232	0.293
P shoot/ P root	E. socialis	1.25	1.67	1.67	1.29	0.90	1.18
	A. aneura	1.08	1.13	1.17	1.23	1.54	1.63
	C. nemophila	0.71	0.70	0.89	0.65	0.89	1.54

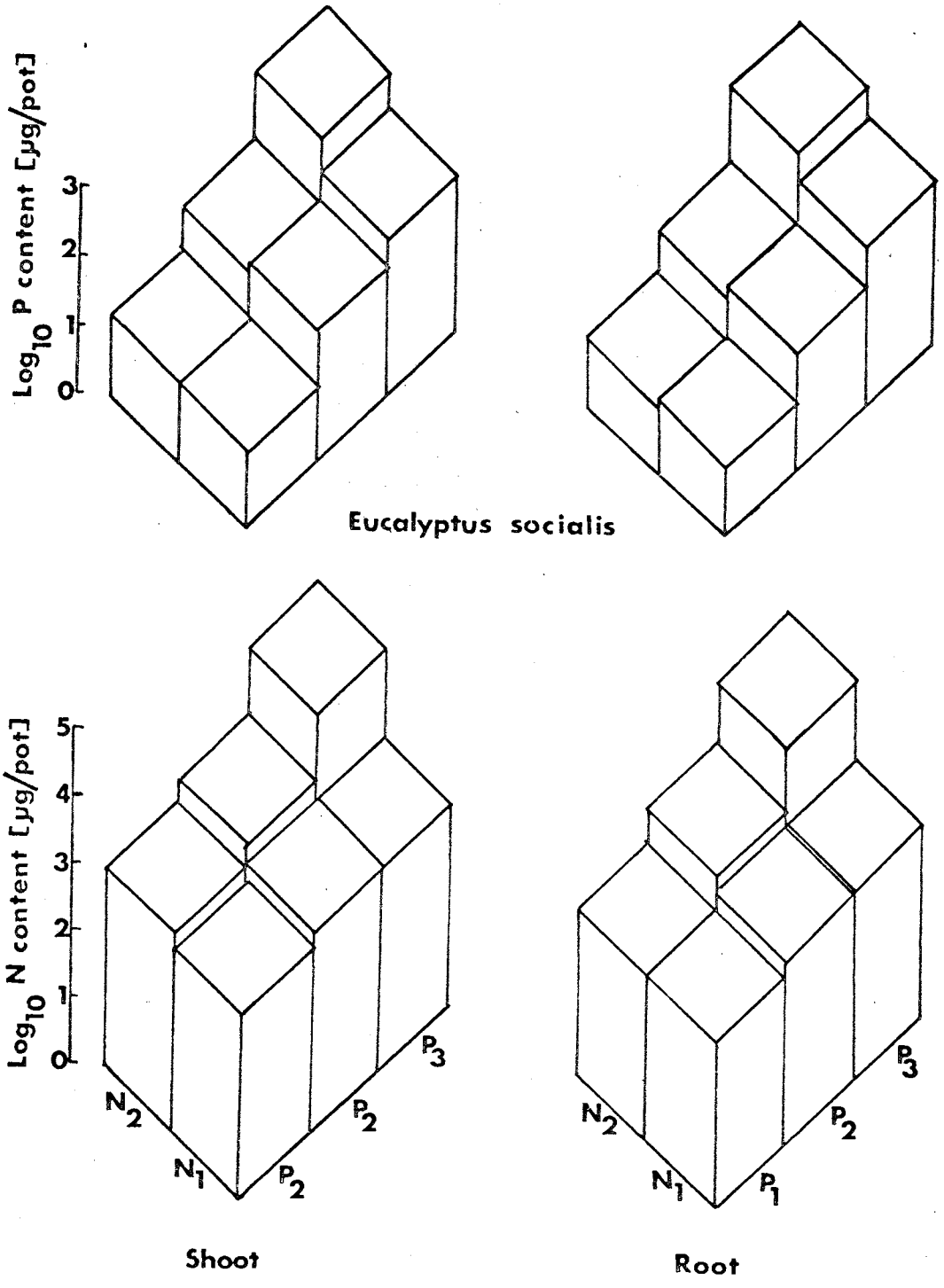


Figure 6.2 Uptake of nitrogen and phosphorus in seedlings of Eucalyptus socialis grown in sand culture. See text for description of treatments (Experiment 2).

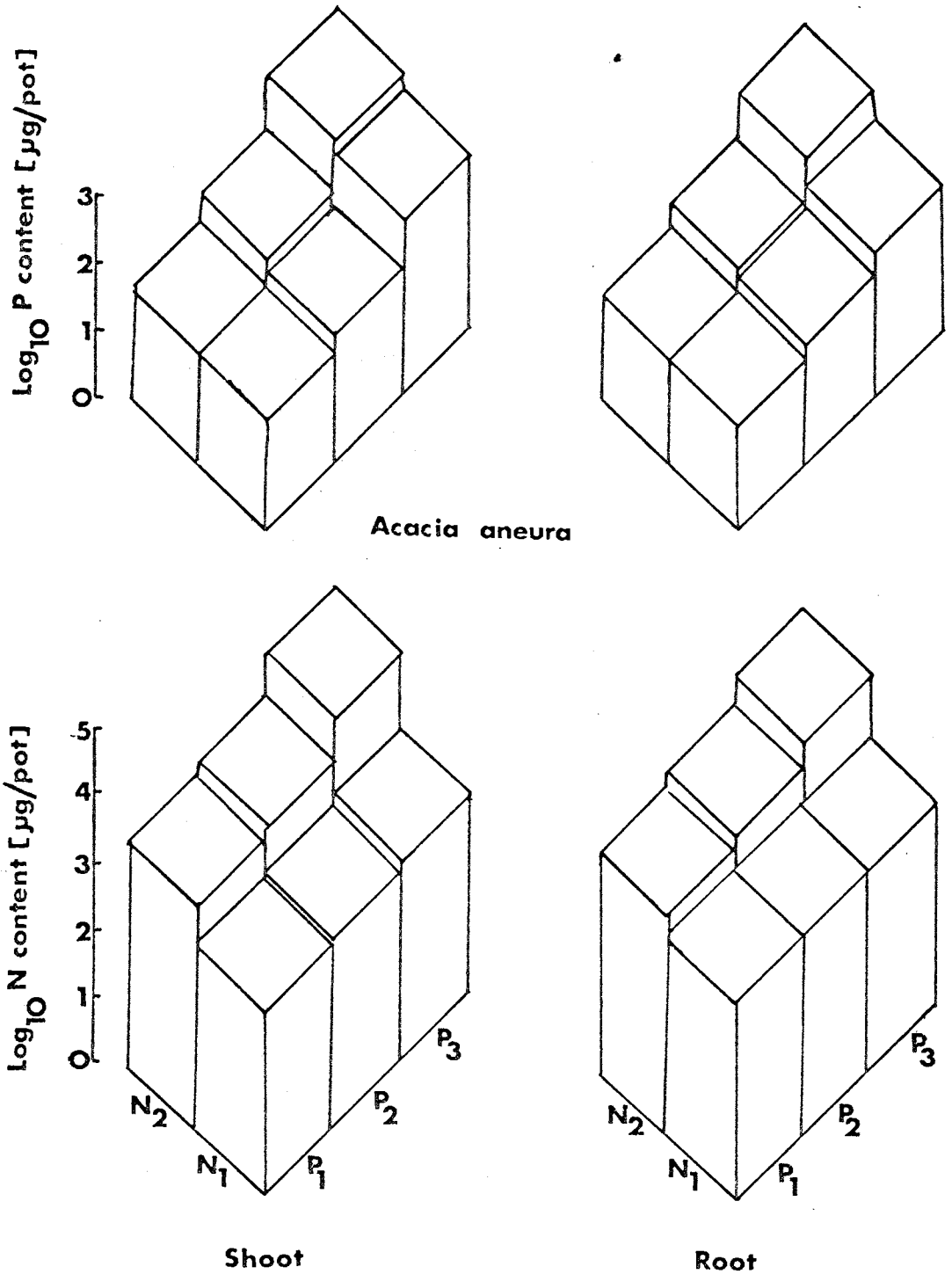


Figure 6.3 Uptake of nitrogen and phosphorus in seedlings of Acacia aneura grown in sand culture.
See text for description of treatments (Experiment 2).

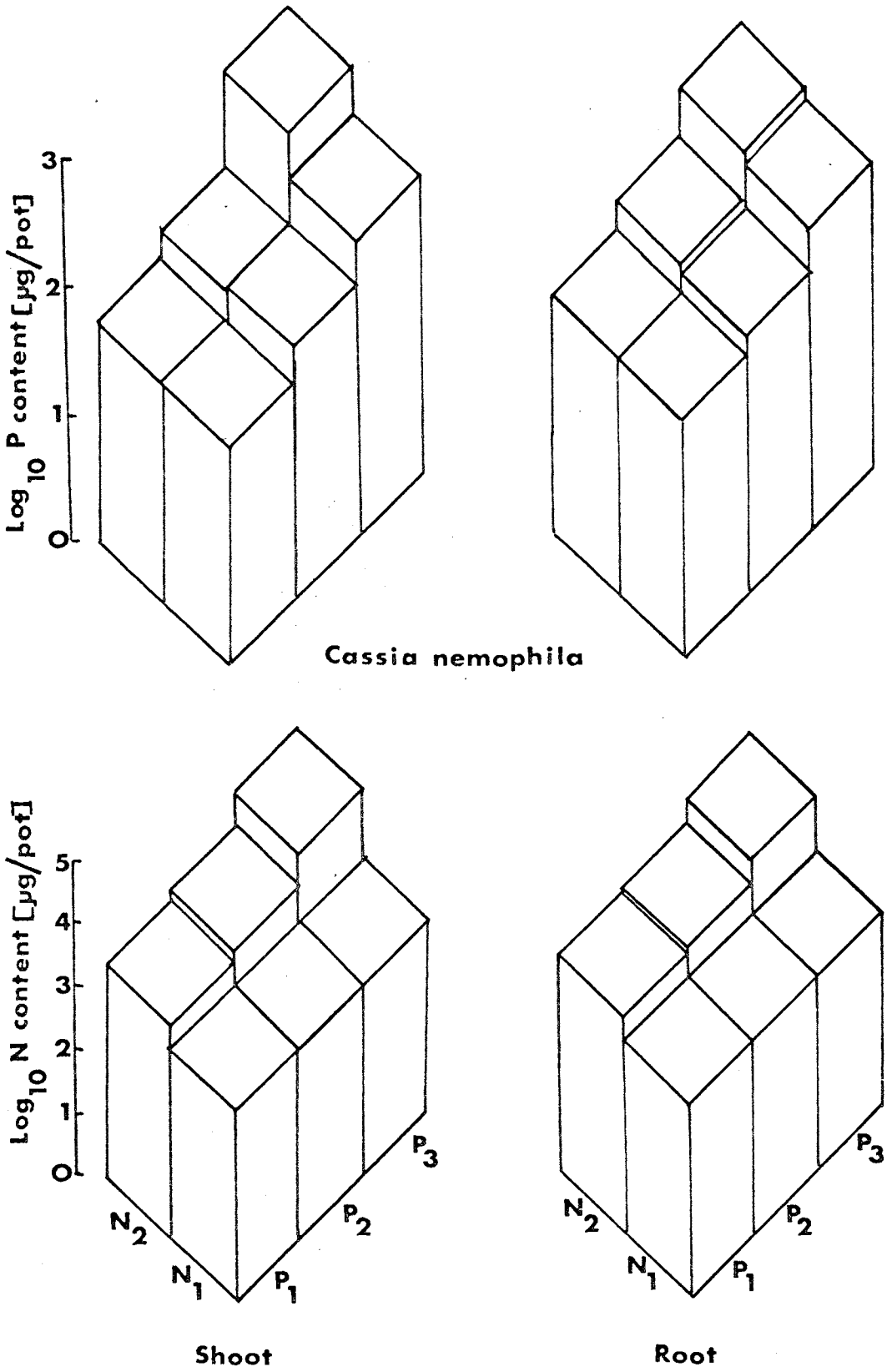


Figure 6.4 Uptake of nitrogen and phosphorus in seedlings of Cassia nemophila grown in sand culture. See text for description of treatments (Experiment 2).

In Experiment 2 there is a more equitable distribution of phosphorus between shoots and roots (Table 6.6, Figures 6.2, 6.3, 6.4) when compared with the responses in the phosphorus rate experiment (Table 6.3). In the latter experiment E. socialis appeared to be the most efficient in transporting substrate phosphorus at all nutrient levels. Nevertheless such comparisons are only valid, sensu stricto, if allowance is made for the differential effect of shoot/root ratio. A more direct method of measuring the efficiency of phosphorus uptake is through calculation of mean absorption rates (Table 6.7). The data reinforce the observations from Experiment 1 which suggest that E.socialis is more efficient at absorbing substrate phosphorus at all nutrient concentrations than are A. aneura and C. nemophila. Since the roots of E. socialis were much finer than in the latter species this may have simply resulted from a larger (and perhaps more permeable) absorbing surface than from any intrinsic physiological mechanism per se.

Table 6.7 Influence of nitrogen and phosphorus supply on mean absorption rates ($\overline{Ip}$) of phosphorus in E.socialis, A.aneura and C.nemophila. See text for explanation of treatments and assumptions underlying the analysis (Experiment 2).

	Treatment					
	N_1P_1	N_2P_1	N_1P_2	N_2P_2	N_1P_3	N_2P_3
	$\overline{Ip}$ (ug/g/day)					
E.socialis	20.7	16.6	73.3	62.7	205.8	162.2
A.aneura	15.8	14.0	46.7	44.8	79.8	136.8
C.nemophila	16.7	15.1	33.9	28.0	94.6	84.6

The results of Experiments 1 and 2 suggest that these woody plants possess no intrinsic advantage in terms of nutrient uptake and transport when compared with that shown by native grasses (Christie and Moorby 1975). The dominance of woody plants on infertile semi arid soils must therefore be explained in terms of other mechanisms. Williams and Shafter (1955) found that if nutrients and water are deficient then the organ closest to the source grows at the expense of the plant part furtherest away. Root extension rates were not measured in the present work, but Christie (1975a) found mulga grass (Thyridolepis mitchelliana) exhibited seminal root extension rates within the range 0.4 - 2.4 cm/day in solution phosphorus concentrations of 0.003 to 3.0 ppm. On the other hand Burrows (1971) found that the shrub, Eremophila gilesii, had mean root extension rates of 2.5 cm/day and maximum rates of 5.6 cm/day when grown in mulga soil maintained at field capacity. Hence the limited data suggest that seedling woody plants growing under low external phosphorus concentration may possess greater abilities to penetrate into the soil compared with native grass seedlings during the establishment phase. If this has general application to the Australian semi arid flora it could also be highly significant in periods of moisture stress.

Foliar analysis is a well established method used to assist diagnosis of mineral requirements for maintaining productivity in agriculture and horticulture. Its most successful application in forested ecosystems appears to

be in plantations where competition and age variables are minimised (van den Driessche 1974). In Australia, foliar phosphorus levels have been found to satisfactorily indicate the necessity for addition of phosphorus fertilizer to slash pine (Pinus elliotti) and loblolly pine (P. taeda) grown in phosphorus deficient soil (Bevege and Richards 1972). In view of these observations it is not unreasonable to expect that foliar analysis could assist in the diagnosis of possible nutrient deficiencies in uniformly dense and even aged mallee and mulga regrowth.

The field nutrient responses to applied nitrogen and phosphorus as measured by foliar analysis (Tables 6.8,6.9) were not as pronounced as may have been expected from the pot studies (Experiments 1 and 2) but root distribution patterns could have been substantially different in these established plants. In particular there was no evidence for a strong nitrogen x phosphorus interaction from the applied nutrients (Appendix 3). Many factors could mediate these results e.g. nutrient status of plant and soil, solubility of the applied nutrients, environmental conditions before and after application, redistribution of nutrients within the plant, time of sampling etc. Nevertheless the foliar analysis did indicate that both A. aneura and E. socialis would absorb significant levels of applied nitrogen and phosphorus in their natural habitats. The relationships between foliar nutrient concentrations and growth were not determined, however, so that the results must be looked

Table 6.8 Foliar responses in *E. socialis* to applied nitrogen, phosphorus and calcium. Main effects and standard errors of differences of means (S.E.D.). Each treatment main effect is the mean of 27 replicates. See text for description of treatments and Appendix 3 for ANOVA tables.

Treatment	First harvest (6 weeks)				Second harvest (16 weeks)	
	Apical leaves		Mature leaves		Apical leaves	
	N(%)	P(%)	N(%)	P(%)	N(%)	P(%)
N_0	1.65	0.196	1.19	0.073	1.35	0.101
N_1	1.72	0.195	1.19	0.070	1.38	0.100
N_2	1.81	0.199	1.24	0.071	1.47	0.103
S.E.D.	0.062	0.007	0.037	0.003	0.041	0.004
P_0	1.71	0.190	1.19	0.069	1.39	0.096
P_1	1.73	0.194	1.19	0.070	1.41	0.101
P_2	1.74	0.205	1.23	0.070	1.40	0.107
S.E.D.	0.062	0.007	0.037	0.003	0.041	0.004
Ca_0	1.72	0.200	1.22	0.074	1.41	0.103
Ca_1	1.72	0.194	1.21	0.071	1.44	0.105
Ca_2	1.74	0.195	1.19	0.070	1.35	0.096
S.E.D.	0.062	0.007	0.037	0.003	0.041	0.004

Table 6.9 Foliar responses in A. aneura to applied nitrogen, phosphorus and calcium. Main effects and standard errors of differences of means (S.E.D.). Each treatment main effect is the mean of 27 replicates. See text for description of treatments and Appendix 3 for ANOVA tables.

Treatment	Apical phyllodes		Mature phyllodes	
	N(%)	p(%)	N(%)	P(%)
N_0	2.41	0.099	2.22	0.077
N_1	2.55	0.106	2.36	0.081
N_2	2.57	0.110	2.40	0.079
S.E.D.	0.072	0.003	0.056	0.003
P_0	2.51	0.098	2.30	0.076
P_1	2.51	0.103	2.29	0.077
P_2	2.51	0.113	2.39	0.085
S.E.D.	0.072	0.003	0.056	0.003
Ca_0	2.51	0.105	2.34	0.079
Ca_1	2.51	0.105	2.31	0.079
Ca_2	2.51	0.105	2.33	0.080
S.E.D.	0.072	0.003	0.056	0.003

upon as diagnostic in terms of response rather than predictive (c f. van der Driessche 1974).

Calcium was included in these field trials since it is known to be important in the nutrition of E. socialis (Parsons 1968a) and in the legume/Rhizobium symbiosis (Epstein 1972), as well as generally enhancing the uptake of other ions (Viets 1944). However, no pronounced effects of calcium fertilization were recorded by the foliar analyses. There was some evidence ($P < 0.05$) for improved phosphorus uptake in mulga phyllodes in the presence of added calcium. This effect is not surprising in view of the low pH and small contribution made by calcium to the exchange complex in mulga soils (Chapter 2).

6.4 Conclusions

The experiments outlined in this study were essentially exploratory in nature - their principal objective being to observe whether any major advantages in phosphorus nutrition were possessed by trees and shrubs which would react in their favour when compared with native grasses. All species studied were highly responsive (in growth and nutrient uptake) to increasing concentration of nitrogen and phosphorus and there was a very strong nitrogen x phosphorus interaction recorded in sand culture. There was further evidence from foliar analysis of field trials that E. socialis and A. aneura would absorb applied nitrogen and phosphorus in their natural habitats. These results are in keeping

with the observations of Beadle (1962) and Cromer (1972) for other Australian native plant communities.

Features of E. socialis, A. aneura and C. nemophila were their extremely low growth rates and mean phosphorus absorption rates. The values recorded were generally highest for E. socialis but in all cases were much lower than those found for Australian semi arid grasses (Christie and Moorby 1975) even at phosphorus concentrations which were low enough to simulate natural soil solution levels (Christie 1974). Thus, there does not appear to be any intrinsic nutritional advantage which would account for the dominance of these woody plants when compared with grasses in their infertile semi arid habitats. Rather it is suggested that the woody plants may have greater ability to survive periods of moisture stress, and in the seedling phase this could manifest itself through greater root extension rates.

Attiwill (1972) maintains that the absence of eucalypt seedlings in mature forests is related to the low levels of 'available' phosphorus in the surface soil, although Parsons (1968c) found soil chemical factors were unimportant in controlling the germination of mallee eucalypts. The current results show that low phosphorus concentrations limited the growth of E. socialis but under the experimental conditions growth was not prevented in absolute terms. It is therefore likely that a combination of nutritional and micro-organism effects (e.g. Ashton and Macauley 1972)

prevent the widespread occurrence of seedlings in mature mallee communities - especially since the organisms known to cause death of E. regnans seedlings (Ceuthospora innumera and Piggotia substellata - Ashton and Macauley 1972) have been shown to be prevalent in mallee stands (Chapter 5).

CHAPTER 7

Synthesis and conclusions

In this final chapter results detailed in the preceding pages are integrated in the form of nitrogen and phosphorus budgets for mallee and mulga ecosystems and consideration is given to the nutritional adaptation of these communities to their infertile semi arid habitats.

There appears to be no published work on nutrient fluxes in Australian semi arid shrub and woodland communities, apart from the essentially static descriptions given for Atriplex vesicaria (Charley and Cowling 1968, Charley 1972) and Eremophila gilesii (Burrows 1972). In fact there have been few published nutrient cycles for Australian ecosystems generally which is surprising in view of the low fertility status of Australian soils (e.g. Jackson 1957, Wild 1958).

The limiting factor for plant growth in semi arid zones is usually water, but there is increasing evidence that second order nutrient limitations occur at some sites and times (Charley and Cowling 1968, Charley 1972, Noy-Meir 1974). In these situations it is probably less common for a single element to impose a definitive limit on the ecosystem than for more complex interactions to occur (Pomeroy 1970).

Mineral dynamics in arid regions are usually inferred from standing crop biomass, growth rate and litter turnover data (West 1976) and this approach is used in the present

study. Hydrologic based input - output studies such as those of Hubbard Brook (e.g. Likens and Bormann 1972) are not feasible in drier areas. However partial cycles of nitrogen and phosphorus can be constructed for mallee and mulga ecosystems based on data on annual rainfall (Chapter 1), productivity and nutrient distribution (Chapter 2) and nutrient fluxes out of the canopy (Chapter 3), if the following assumptions are made:-

(i) biomass regressions, 'mean tree/shrub' estimates and tissue nutrient concentrations obtained for each site in 1975 are equally applicable to 1973 recordings of independent variables, and minor tree or shrub classes, at the same site

(ii) root production is related to aerial biomass production (see Nihlgard 1972) as

$\Delta R = R.\Delta X/X$ where ΔR = root production
R = root biomass
ΔX = total above ground production
X = total above ground biomass

(iii) loss of nutrients in root litter is analogously related as (ii)

(iv) functional root and soil depth is 1 m

(v) concentrations of nutrients in rainfall at each site approximate mean values given by Hutton (1962) for nitrogen and Attiwill (1966b) for phosphorus, and

(vi) insect frass falling on the mallee sites results from consumption of mallee leaves with a digestibility of 51%*; insect frass falling on the MUM site is an input

*Based on two successive feeding experiments with sawfly larvae giving a digestibility for E.socialis leaves of 50.9 $\pm$ 2.4%.

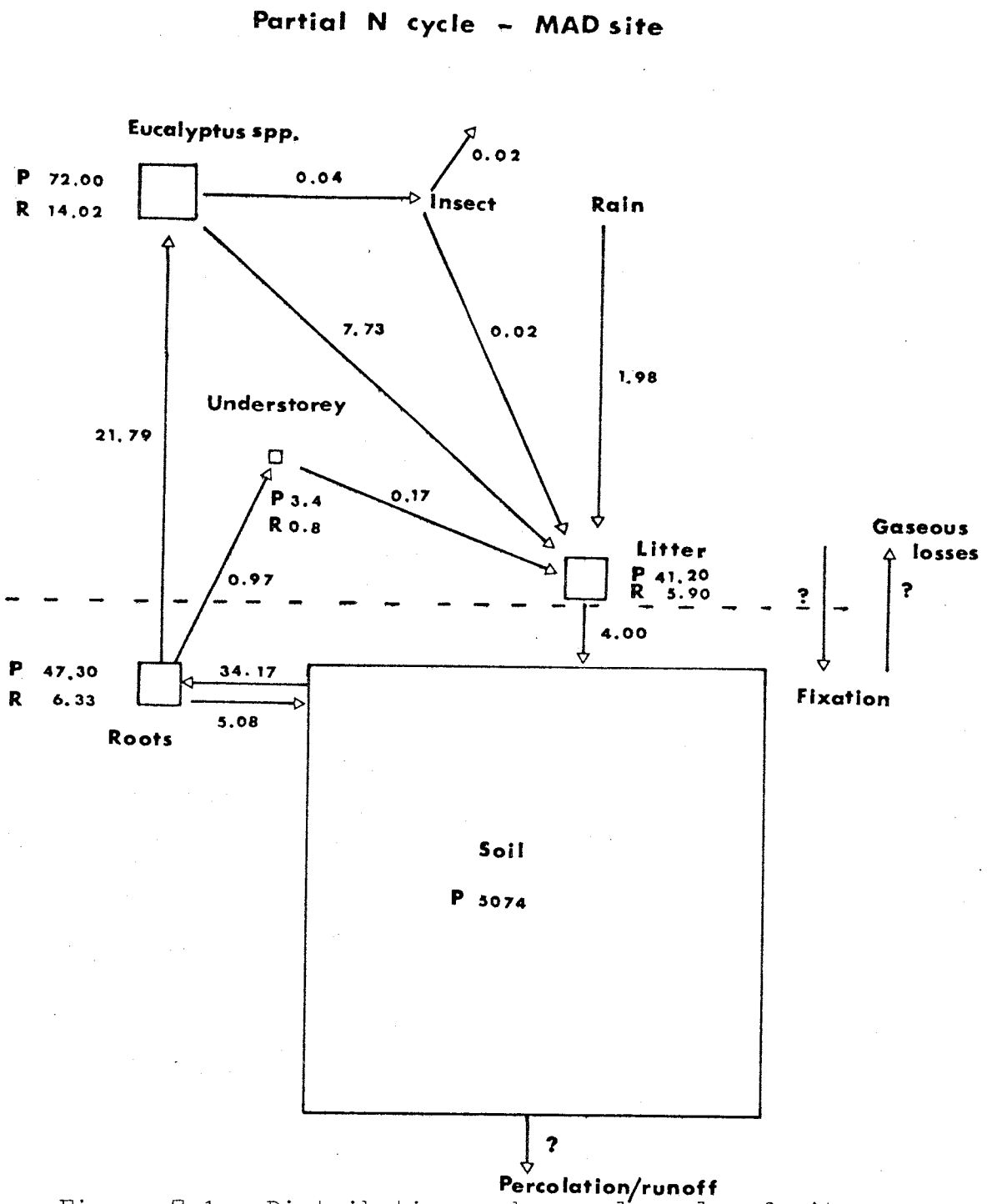


Figure 7.1 Distribution and annual cycle of nitrogen in a mallee regrowth ecosystem (MAD site). Compartmental pool sizes (P - kg/ha) and annual retention (R = annual gain or loss by compartments, kg/ha/yr) are indicated. Yearly fluxes (kg/ha/yr) are shown beside directional lines. All compartmental boxes are drawn to the same scale to indicate pool sizes. Roots and soil were sampled to 1 m depth.

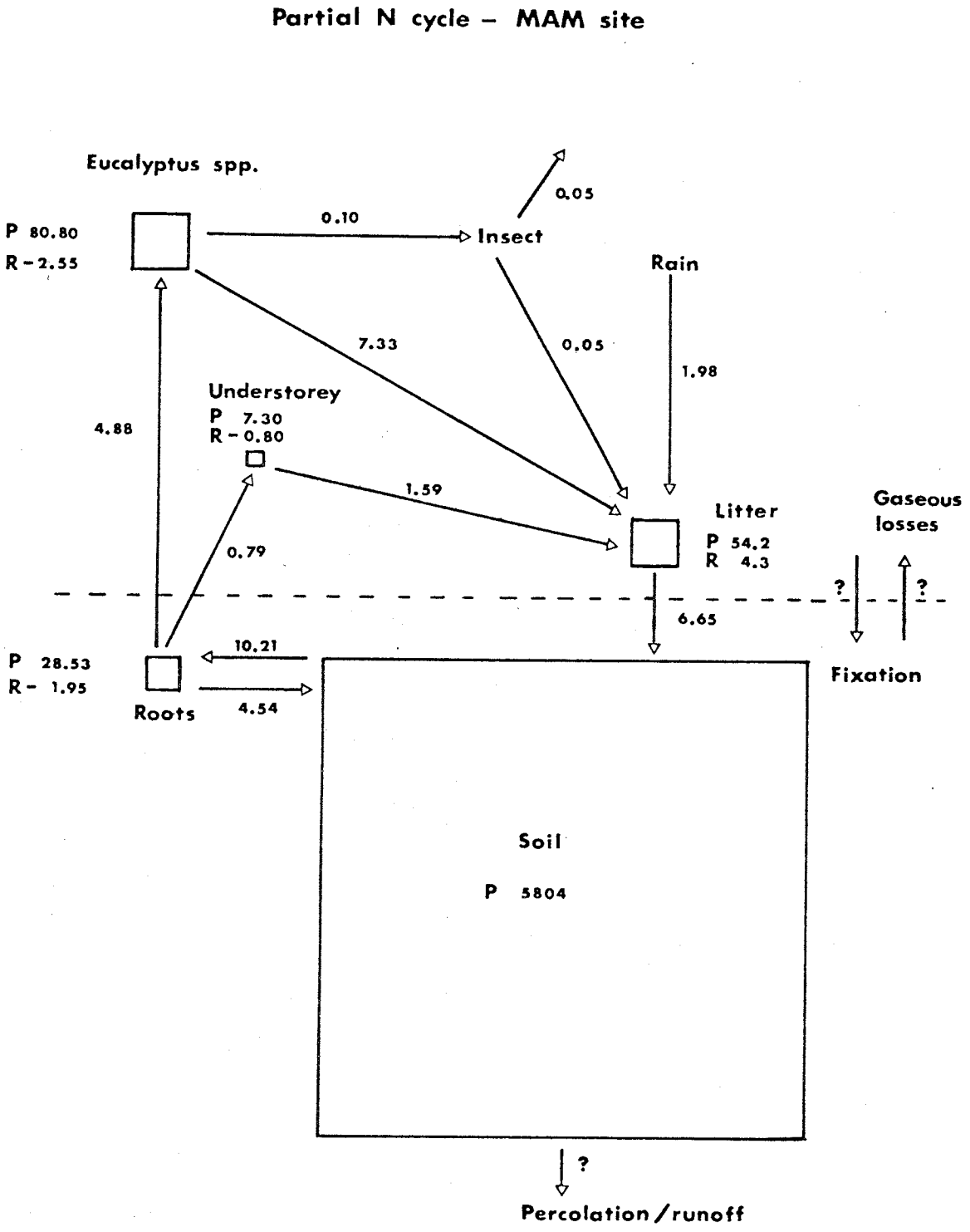


Figure 7.2 Distribution and annual cycle of nitrogen in a mature mallee ecosystem (MAM site). Conventions as in Figure 7.1

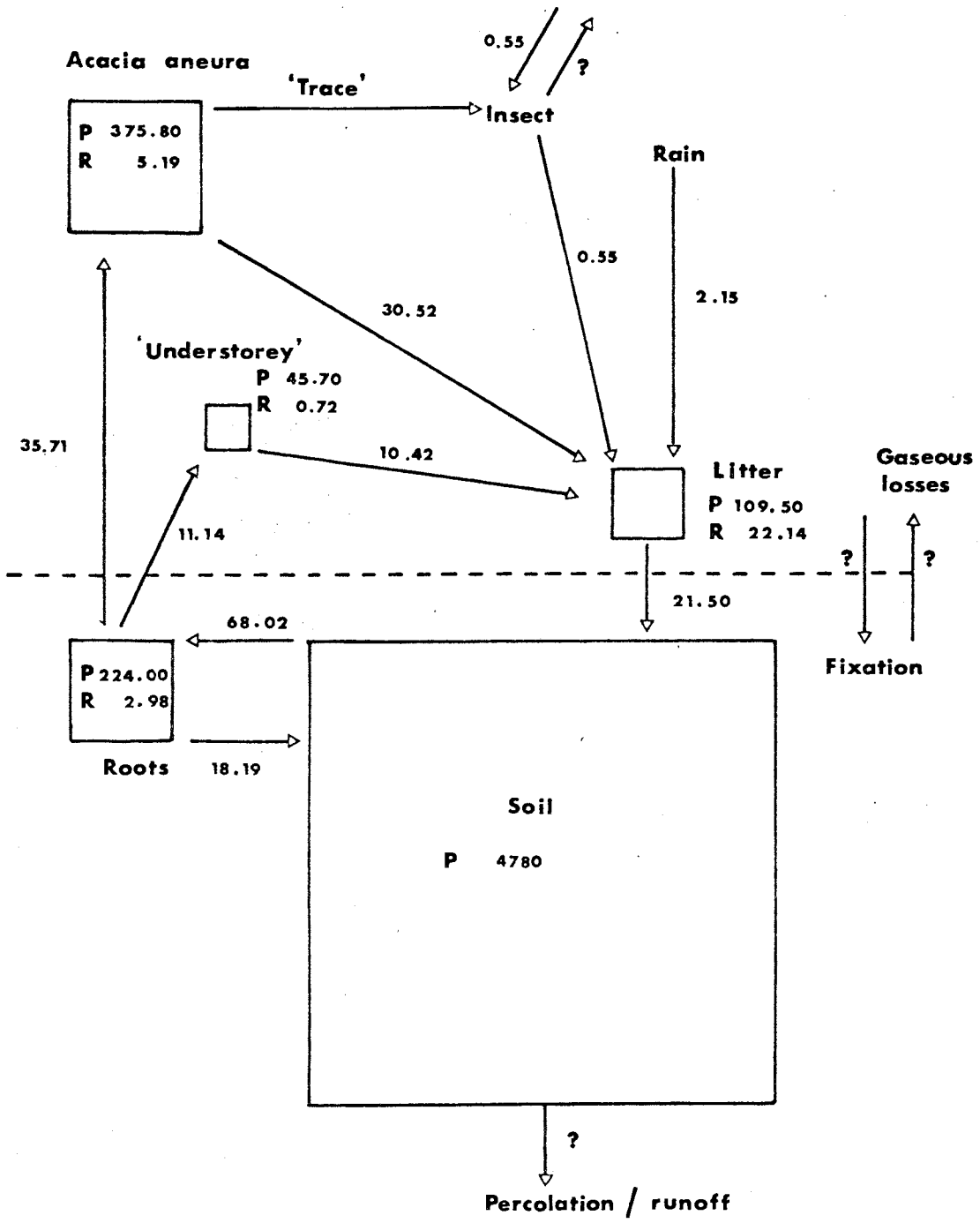


Figure 7.3 Distribution and annual cycle of nitrogen in a mature mulga ecosystem (MUM site). Conventions as in Figure 7.1

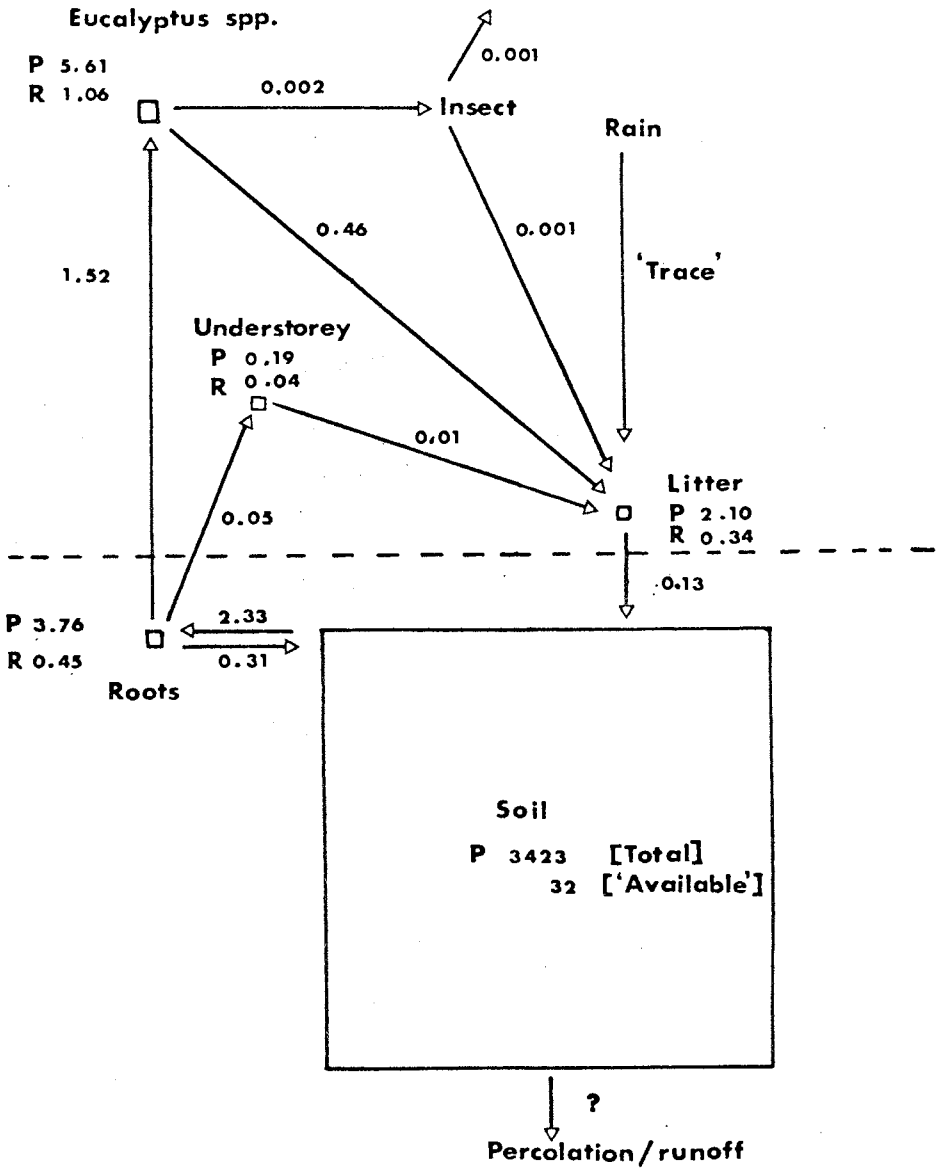


Figure 7.4 Distribution and annual cycle of phosphorus in a mallee regrowth ecosystem (MAD site). Conventions as in Figure 7.1

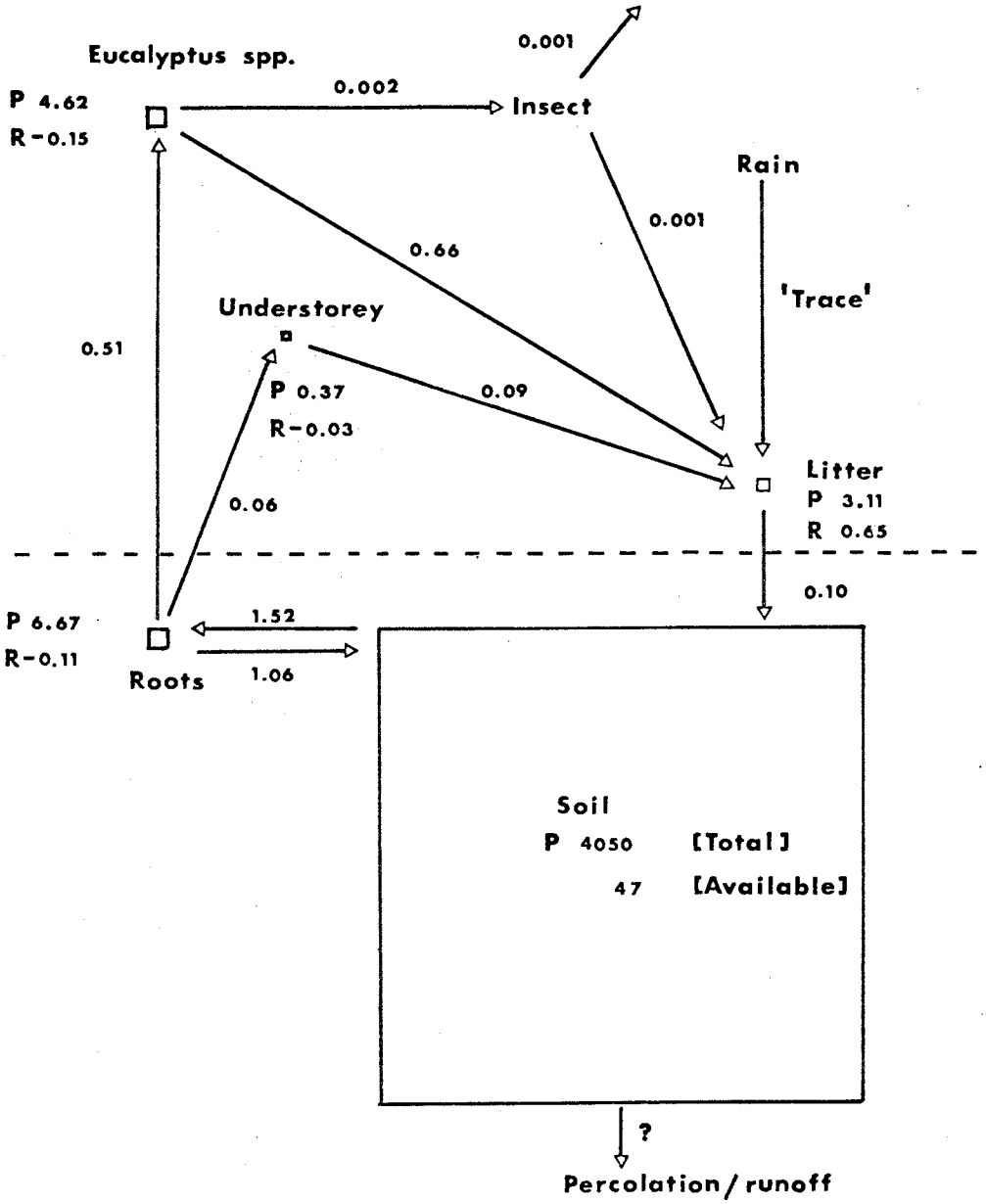


Figure 7.5 Distribution and annual cycle of phosphorus in a mature mallee ecosystem (MAM site). Conventions as in Figure 7.1

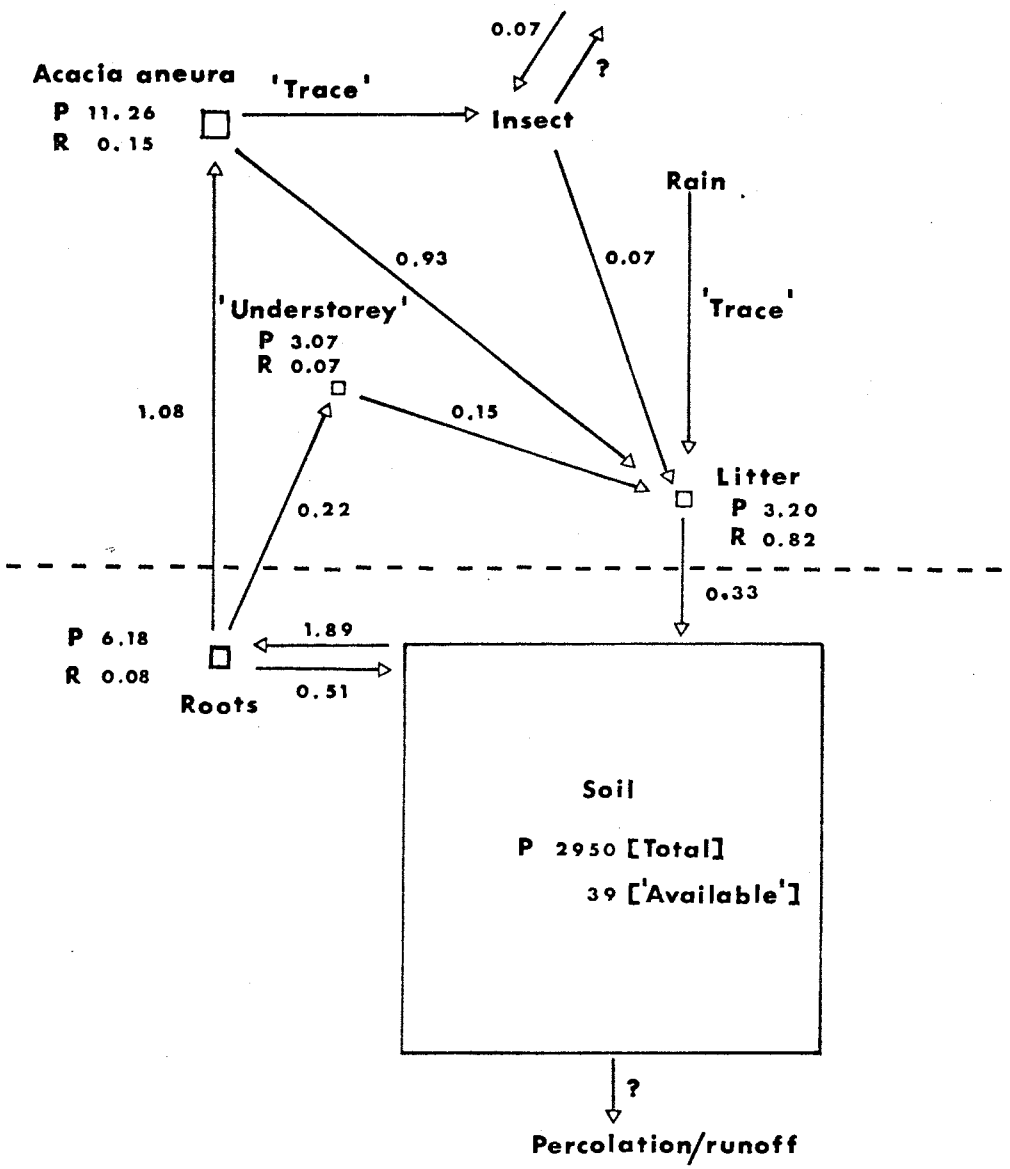


Figure 7.6 Distribution and annual cycle of phosphorus in a mature mulga ecosystem (MUM site). Conventions as in Figure 7.1

into the system.

The partial nitrogen and phosphorus cycles for MAD, MAM and MUM sites (Figures 7.1 - 7.6) show total transfer between compartments for an 'average' year of the measurement period, but actual pool sizes are those pertaining at the conclusion of the study (see Tables 2.25, 2.26, 2.27). Particular attention has been given throughout this thesis to the statistics of sampling and reference should be made to the appropriate chapter from which the data were obtained for an indication of the likely errors associated with these cycles.

The nutrient pool sizes are indicated by boxes drawn to the same scale on all diagrams (Figures 7.1 - 7.6) so that visual comparisons may be made within and between sites. Nitrogen and phosphorus pools are on the whole very similar for both mallee (MAD/MAM) communities. This highlights the strong resilience in mallee ecosystems following perturbation and is further exemplified by

(i) the similar lignotuber biomass between 15 year old MAD regeneration and the mature (c. 55 year old) MAM site (Tables 2.25, 2.26)

(ii) leaf litter biomass on both MAD and MAM sites being almost identical (Tables 2.25, 2.26), and

(iii) the similar leaf area index exhibited on both sites (Table 2.20)

The possession of regenerative capacity from lignotubers clearly exerts a marked stabilising influence on these semi arid communities. The similarity in nitrogen and phosphorus

pools in the young and mature mallee stands suggests that there is a rapid uptake after which the community requirement (at least for mobile elements) is largely met by recycling. It follows that if a nutrient is non-limiting during the rapid uptake phase then it is unlikely to be deficient during the remainder of growth.

Table 7.1 Biomass and net primary production (P_n) in mallee and mulga communities.

Site	Biomass (kg/ha)			P_n above ground (kg/ha/yr)
	Total	Root	Above ground	
MAD	40054	20501	19553	5406
MAM	68697	28533	40164	2379
MUM	95698	25442	70256	3328

Immature stands often have a net primary production (P_n) more than twice that of mature stands (Johnson and Risser 1974) and annual P_n can be expected to decrease as the stand matures (Rodin and Bazilevich 1967). These observations are confirmed by comparison of the P_n of the MAD and MAM sites (Table 7.1). Calculations of above-ground P_n in this table are based on biomass increment + litter fall + plant loss by consumer organisms (see Newbould 1967). The values are likely to be significant underestimates for both mallee sites as consumption by beetles (Chrysomelidae) was ignored because the frass was not amenable to collection (Chapter 3).

Table 7.2 Nutrient ratios (NR) for Australian semi arid woodlands and shrublands. NR = ratio of nutrients in vegetation to nutrients in vegetation + soil (expressed as a percentage).

Ecosystem	Site	C*	N	P(total)	P('available')
Mallee[1]	MAD	37.3	3.1	0.3	26.7
Mallee[1]	MAM	52.2	4.1	0.4	31.6
Mulga[1]	MUM	58.8	13.6	0.8	37.9
Brigalow[2]	Meandarra	51.0	14.0	2.2	49.0
Eremophila[3]	Charleville	17.3	2.4	0.3	5.7
Atriplex[4]	Broken Hill	8.1	1.1	0.1	NA

* Carbon was estimated as 44% of vegetation dry matter for all sites (Washburn 1927)

1 Present study - soil depth 1 m

2 Russell, Moore and Coaldrake (1967) - soil depth 90 cm (Note: the values quoted for total P in Table 5 of this paper appear to be in error by a factor of 10 and have been corrected for the present calculations)

3 Burrows (1972) - soil depth 45 cm

4 Charley and Cowling (1968) - soil depth 45 cm

NA = not available

Soil nitrogen and phosphorus pools are lower in the mulga ecosystem (Figures 7.3, 7.6) than in mallee communities (Figure 7.1, 7.2, 7.4, 7.5). However the MUM community has greater proportions of the total pool of these nutrients (particularly nitrogen) bound in organic matter than the mallee sites (Table 7.2). The close correspondence between mulga (Acacia aneura) and brigalow (A. harpophylla) in the utilization of nitrogen is particularly noteworthy. It has been previously observed (Chapters 2, 3) that mulga has much higher nitrogen concentrations in all its tissues than mallee communities of comparable biomass. Hence it seems reasonable to infer that an efficient legume/Rhizobium symbiosis is in operation even though nodules are difficult to detect in the field. Despite these observations there is little evidence for build up of nitrogen in mulga soils (Chapter 2). The following factors could contribute towards this:-

(i) low clay content in the soil (Chapter 2) leading to low levels of fixed ammonium and clay interlayer organic material (Charley and Cowling 1968).

(ii) gaseous losses of nitrogen through volatilization of ammonia and denitrification which are promoted by high temperature, amongst other factors (MacGregor 1972, West 1976).

(iii) low levels of phosphorus influencing the degree of nitrogen accumulation through limitation of biological fixation mechanisms (Walker 1962) and deficiencies of

phosphorus retarding transformation of nitrogen from the organic to the inorganic pool (see Cowling 1969, Charley 1972).

Cycling times for elements in ecosystems are influenced by rates of element uptake, release by plants and comminution and decomposition of litter. These rates and direction of flows are shown for the present study in Figures 7.1 - 7.6. Jordan and Kline (1972) define the cycle time of an element as the sum of turnover times for each compartment, where

$$\text{Turnover time (yrs)} = \frac{\text{mean yearly quantity of element in the compartment}}{\text{mean yearly quantity of element leaving the compartment}}$$

It is apparent that this definition assumes 'steady state' conditions and the validity of such assumptions for mulga and mallee litter layers have been discussed earlier (Chapter 4). Nevertheless, although a long term study of the decomposition process and litter fall is required, before complete accumulation budgets and process models can be drawn up, it is instructive to examine the data even for a two year sampling period (Table 7.3). For the present study total nitrogen and phosphorus pools in the soil are ignored since these are largely meaningless representations of what is 'available' to plants. Data for subtropical humid oak and cool temperate Douglas fir ecosystems are included in Table 7.3 to give a wider perspection to the results.

It may be concluded from these data that

Table 7.3 Compartmental turnover times and cycling times for nitrogen and phosphorus in mallee and mulga communities. See text for method of calculation.

(i) Nitrogen

Site	Compartmental turnover time (yrs)				Total cycle time (yrs)	Total minus soil cycle time (yrs)
	Roots	Tops	Litter	Soil		
MAD	1.7	9.5	10.3	?	?	21.5
MAM	2.8	8.9	8.1	?	?	19.8
MUM	3.4	9.2	5.1	?	?	17.7
Subtropical oak[1]	1.6	13.5	1.3	?	?	16.4
Douglas fir[2]	?	20.0	35.0	?	?	(55.0)**

(ii) Phosphorus

MAD	2.0	12.3	16.1	13.7*	44.1	30.4
MAM	4.1	6.6	30.8	30.9*	72.4	41.5
MUM	3.4	13.3	9.7	20.6*	47.0	26.4
Subtropical oak[1]	2.0	10.1	1.0	?	?	13.1
Douglas fir[2]	?	66.0	25.0	?	?	(91.0)**

1 From data of Johnson and Risser (1974)

2 From data of Cole, Gessel and Dice (1967)

* Based on 'available' phosphorus in soil

** Bracketed quantities are minimum values since root turnover was not available

(i) nitrogen and phosphorus cycle times in the semi arid shrub/woodland communities studied are comparable with those for more mesic environments (c f. West 1976) except for litter.

(ii) leguminous mulga vegetation (MUM) has a similar cycle time for nitrogen as the mature mallee eucalypt community, and

(iii) there is a more conservative use of phosphorus leading to slower turnover times (at least for evergreens) of this element compared with nitrogen usage.

The apparent anomalous result for phosphorus turnover in MAM tops and litter, compared with similar MAD compartments,is attributed to the MAM community starting to degenerate. This is shown by negative phosphorus and nitrogen retention in MAM tops (Figures 7.2, 7.5) as well as other indications discussed in Chapter 2 - and the concomitant large pulse of phosphorus in organic material onto the litter compartment during the period of measurement. This has contributed to the seemingly long turnover time calculated for phosphorus in the litter layer (Table 7.3).

Nutrient pulses through understorey species are not insignificant pathways (Figures 7.1 - 7.6) especially through Eucalyptus populnea on the MUM site, but it is unlikely that removal of these associated species from the communities would unduly affect the stability of nutrient cycles in the present MAD, MAM and MUM ecosystems. Bakuzis (1969) claims that the efficient recycling of minerals in forest systems may in part account for the rather low

nutrient requirements of forests as compared with agriculture. The efficiency of utilization of nitrogen and phosphorus in mallee and mulga ecosystems may be determined by dividing the annual weight of nutrients taken up into the tops (see Figures 7.1 - 7.6) by the annual above ground net primary production (Table 7.1). The results (Table 7.4) show clearly that the ecosystems studied are highly efficient in their utilization of phosphorus and, apart from the MUM site, in nitrogen utilization as well. The inefficient use of nitrogen in the mulga communities confirms earlier observations and again points to the apparent effectiveness of the mulga/ Rhizobium symbiosis without which mulga could obviously not sustain its productivity. It is also evident (Table 7.4) that mulga grassland is much less efficient in utilization of phosphorus than endemic woody plants and could also require much larger amounts of nitrogen per unit of dry matter than competing woody plants.

Adaptive success implies that an organism uses the environment advantageously for its physiological needs and that it copes with those features of the environment inimical to it (Epstein 1972). There can be little doubt that mallee and mulga communities have successfully adapted to their infertile semi arid habitats. This may not be surprising, however, in view of Slatyer's (1973) conclusions that - (i) woody plants will tend to dominate terrestrial ecosystems except where mechanical features of the

environment become of over-riding importance

(ii) shrubs will tend to dominate, rather than trees, as the environment becomes more severe, either physically (heat, cold, drought) or chemically (soil fertility) so that the physiologically more efficient life form of the shrub is needed for persistence.

Table 7.4 Amount of mineral nutrients (g) transported to tops for each 1 kg/ha net primary production above ground.

Ecosystem	N (g/kg)	P (g/kg)
MAD	4.2	0.29
MAM	2.4	0.24
MUM	14.1	0.39
Mulga Grassland*	18.2	0.83
European forests**	4.4 - 7.7	0.33 - 0.66
Field crops **	11.0 - 53.4	2.2 - 3.3

* Unpublished data of E.K. Christie - based on 6 week growing season during 1973/74 summer. Plot c. 700 m W. of MUM site.

** From Bakuzis (1969) based on data of Ehwald (1957)

The principal advantage woody plants have over grasses in stress environments appears to be their longevity. Firstly, this enables them to avoid the need for frequently recurring conditions favourable for regeneration from seed (Slatyer 1973) and secondly, established woody plants appear to be more efficient than grasses at utilizing nutrients under infertile conditions (Table 7.4). Obviously longevity is also a property of perennial grasses (although on a

shorter time scale) so further distinctions need to be drawn.

From studies in nutrient culture it appears that roots of endemic grass seedlings are more efficient at absorbing phosphorus than roots of mallee, mulga and Cassia seedlings (Christie and Moorby 1975, Chapter 6). However there is some evidence (Jones and Hodgkinson 1969, Burrows 1971) that root extension rates of endemic woody plants could be appreciably faster than those exhibited by native grasses (Christie 1975a). When this is associated with physiological resistance to moisture stress (e.g. as in mulga, Slatyer 1960) woody plant seedlings would seem better equipped to survive drought than perennial grass seedlings. If this is also coupled with less grazing pressure from herbivores there is a competitive advantage for the woody plant seedling in infertile semi arid environments.

Further, it has been shown that established mallee and mulga communities possess between 5000 - 10000 kg/ha of fine roots to 1 m depth (Tables 2.25 - 2.27) compared with 1000 - 12000 kg/ha for a mulga grassland (Christie pers. comm.). This indicates that regenerating woody plants develop a greater biomass of 'feeding' roots than competing grasses. In phosphorus deficient soils this greater root mass should result in a larger absorbing surface and greater volume of soil explored by woody plants compared with grasses; and this may well compensate for the poorer phosphorus absorbing efficiency of woody plant roots. Subsequently the woody plant requires far less phosphorus

uptake to produce 1 kg of dry matter than competing grasses (Table 7.4) and dominance is complete.

The preceding discussion helps to explain, in part, the widespread distribution of woody plants in the Australian semi arid zone (c.f. Beadle 1951, 1960, Whittaker and Woodwell 1972). Nevertheless it is clear that the restricted nature of this study (limited to nitrogen and phosphorus distribution and fluxes), and the above average rainfall experienced during the period of field experimentation (Table 1.1) may have greatly influenced its conclusions. Whether these conclusions have true generality remains to be tested in other woody communities and under differing environmental conditions.

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APPENDIX I

Analytical Methods

1. Soil - All soil analyses reported in this study were kindly carried out by the Agricultural Chemical Laboratory, Queensland Department of Primary Industries, Brisbane. Methods employed were as follows:

(i) Sample preparation - All samples were dried at 40° C in a forced draught oven. The samples were then ground to < 2 mm and all determinations were carried out on this soil. The results are reported on an air dry basis.

(ii) pH - A 1:5 soil/de-ionized water suspension was shaken for one hour and pH determined on the suspension using a glass electrode and saturated calomel reference.

(iii) Total N - The Kjeldahl method with copper catalyst was used.

(iv) Total P - A modification of the Beckwith and Little (1963) method was used. The soil (4 g) was ashed with magnesium acetate for one hour at 500-550° C then extracted with boiling HCl for 4 hours. Phosphorus was measured calorimetrically by the method of Murphy and Riley (1962).

(v) 'Available' P - Acid extractable P was determined by the Kerr and von Stieglitz (1938) method and readings carried out using an Auto Analyser technique.

(vi) Exchangeable cations - Samples were divided into two categories for analysis. Samples with an electrical conductivity > 0.3 mmho/cm were given a pre-wash treatment with 60% aqueous ethanol to remove soluble cations (Loveday, Beatty and Norris 1972). Five grams

of soil were shaken for 1 hour in 100 ml of molar aqueous ammonium chloride (pH 7.0) filtered and leached with a further 100 ml. Cations were determined on the leachate, Na and K by flame photometer, and Ca and Mg, after suitable dilution with strontium chloride solution, on an atomic absorption spectrophotometer.

(viii) Organic carbon - The wet combustion method of Walkley and Black (1934) was used on a finely ground soil sample. The reduced chromic ion (Cr^{+++}) was read calorimetrically (Sims and Haby 1971). Results reported are uncorrected Walkley and Black values.

More detail of the methods employed may be found in Ahern (1974).

2. Plant -

(i) Sample preparation - All plant material was dried to constant weight at 80^{o} C as soon as practicable on return to the Laboratory. Large samples were successively 'quartered' until a representative sample suitable for grinding was obtained. All samples, apart from wood and green bark, were then ground in a Culatti micromill to pass through a 0.5 mm sieve. Shavings of wood and bark samples were obtained by random drilling holes in the material using a 15 mm stainless steel drill. These shavings were subsequently ground as above. All ground material was stored in individually labelled air tight jars at c. 20^{o} C prior to analysis.

(ii) Analysis - Total N and P were determined using a modified Kjeldahl technique (Williams and Twine 1967) with 200 g K_2SO_4 in the digestion mixture, and a Technicon Auto Analyser (Williams and Twine 1967).

Note: The time factor and facilities available restricted analyses to total N and P. However samples of the ground plant material have been retained for cation analyses at the conclusion of this Ph.D. course. This will permit wider interpretation of the results which may arise from the present study.

APPENDIX 2

Corrections for bias in predictions based on lognormal regression

The procedure to be followed is an abbreviated version of that to be found in Beauchamp and Olson (1973).

Consider the random variable Z such that $Y = \ln Z$ is normally distributed with mean $E(Y) = \beta_0 + \beta_1 x$ which is a linear function of an independent non-random variable x, and with variance σ^2. From a sample of n observations on Z, desire minimum variance unbiased estimates of the mean and variance of the distribution of Z. If z_i represents the corresponding observed value of Z for $i = 1,2,\ldots,n$, then by using properties of the lognormal distribution

$$E(z_i) = \exp(\beta_0 + \beta_1 x_i + \sigma^2/2)$$

and $$\text{Var}(z_i) = (\exp(\sigma^2)-1)\exp(2\beta_0 + 2\beta_1 x_i + \sigma^2)$$

Let $\hat{\beta}_0$ and $\hat{\beta}_1$ be the maximum likelihood estimates of the parameters β_0 and β_1, respectively, obtained from the $n(x_i, y_i)$ pairs of observations transformed so that $y_i = \ln z_i$. Then the predicted value $\hat{y} = \hat{\beta}_0 + \hat{\beta}_1 x$ is normally distributed with mean $\beta_0 + \beta_1 x$ and variance $\sigma^2\phi/n$ where

$$\phi = \sum_{i=1}^{n} (x_i - x)^2 / \sum_{i=1}^{n} (x_i - \bar{x})^2$$

A good approximation to the unbiased estimator of E(Z) through terms of order $1/n^2$ is given by

$$E(Z) = \exp(\hat{\beta}_0 + \hat{\beta}_1 x + \sigma^2/2) \{ 1 - \sigma^2(2\phi + \hat{\sigma}^2)/4n + \sigma^2)^2 [(\hat{\sigma}^2)^2 + 2(16/3 + 2\phi)\hat{\sigma}^2 + 4\phi^2 + 16\phi]/32n^2 \} \qquad (1)$$

where $\hat{\sigma}^2 = \sum_{i=1}^{n} (y_i - \hat{y}_i)^2 / (n - 2)$

Confidence interval (C.I.) estimates for the mean of Z are discussed by Land (1972). In the present study

Patterson's transformation (Patterson 1966) is utilized -

$$C.I. = \exp(\mu_a + \hat{\sigma}^2/2) \qquad (2)$$

where $\mu_a = \hat{\mu} + t_{n-1(a)} \pm (\hat{\sigma}^2/n)^{\frac{1}{2}}$

μ = predicted value (in logarithms)

t = students t value

a = appropriate probability level

and $\hat{\sigma}^2$ = variance of the logarithmic regression

These confidence limits are asymmetric about the transformed mean but the asymmetry is in a direction which accounts for the skewness of the original units. Pattersons transformation is most appropriate where $\hat{\sigma}^2$ is small (e.g. <1).

A computer programme, REGPLOT, was written in BASIC to enable derivation of the logarithmic regression (by least squares) and plotting of the regression and original values in logarithmic and arithmetic units. The input values for this program were stem circumference (independent variable) and leaf, wood, bark etc. weight or nutrient content (dependent variables). The corollary program (LOGPRED), also written in BASIC, enabled prediction of dependent variables $\pm$ 95% C.I. for given values of the independent variables. These predictions are based on equations (1) and (2) respectively.

REGPLOT is similar to other regression and plotting routines and, being somewhat machine dependent, is not listed here. A listing of LOGPRED follows.

PROGRAM "LOGPRED"

```
10   DIM K(1500)
20   OPEN FILE(2,3), "MUMSTEM"
30   DIM G(25)
40   DIM R$(10)
50   REM PROGRAM "LOGPRED"
60   REM THIS PROGRAM ACCEPTS INPUT FROM A FILE CREATED BY
70   REM THE CORROLARY PROGRAM "REGPLOT" WHICH ESTABLISHES BY
80   REM LEAST SQUARES THE LOGNORMAL REGRESSION BETWEEN
90   REM THE INDEPENDENT VARIABLE (STEM CIRCUMFERENCE) AND
100  REM DEPENDENT VARIABLES SUCH AS WOOD WEIGHT,BARK WEIGHT
110  REM LEAF WEIGHT ETC.
120  PRINT "***PREDICTIONS FROM LOGNORMAL REGRESSION***"
130  PRINT
140  OPEN FILE(1,3), "ASCENTA"
150  REM INPUT REGRESSION PARAMETERS FROM REGPLOT
160  REM ALL VALUES EXCEPT N ARE IN NATURAL LOGS
170  READ FILE(1),A,B,Z,N,S
180  PRINT "INTERCEPT= ", A;
190  PRINT "SLOPE= ", B;
200  PRINT "RESIDUAL STANDARD DEVIATION= ", Z
210  PRINT "WHITTAKER E ="; EXP(Z)
220  PRINT " OF DATA SETS= ", N
230  PRINT "SS DEVIATIONS OF X = ", S
240  PRINT
250  LET N1=N-2
260  PRINT "T VALUE"; N1" D.F.=";
270  INPUT T
280  INPUT "SMALLEST APPLICABLE STEM= ", F
290  LET X=0
300  PRINT
310  INPUT "  OF QUADRATS = ", M
320  PRINT
330  PRINT, "1973 DATA"
340  PRINT
```

```
350  GOTO 0390
360  PRINT
370  LET M=21
380  PRINT, "1975 DATA"
390  PRINT,,"95% CONFIDENCE LIMITS"
400  PRINT "X VALUE", "PREDICTED Y", "LOW", "HIGH"
410  PRINT
420  IF X=-88 THEN GOTO 0480
430  DIM U(N)
440  REM INPUT X VALUES FROM REGPLOT
450  FOR I=1 TO N
460  READ FILE(1), U(I)
470  NEXT I
480  REM NOW HAVE ALL DATA NECESSARY TO PREDICT A
490  REM VALUE FOR A DEPENDENT VARIABLE FOR A
500  REM GIVEN STEM CIRCUMFERENCE
510  LET C=1
520  LET R1=0
530  LET R2=0
540  FOR I=1 TO 1500
550  READ FILE(2), K(I)
560  IF EOF(2) THEN GOTO 0870
580  IF K(I)=-99 THEN GOTO 0790
590  LET X=K(I)
600  IF K(I)=-88 THEN GOTO 0880
605  IF K(I)<F THEN GOTO 0860
610  LET D=A+B*LOG(X)
620  LET Y=EXP(D+Z^2/2)
630  FOR J=1 TO N
640  LET P1= U(J)-LOG(X)^2
650  LET P2=P2+P1
660  NEXT J
670  LET P3=P2/S
680  LET B1=Z^4*(Z^4+2*Z^2*(16/3+2*P3)+4*P3^2+16*P3)/(32*N*N)
690  LET Y=Y*(1-Z^2*(2*P3+Z^2)/(4*N)+B1)
```

```
700  LET Y2=Y1+Y2
710  LET D1=D+T*(Z^2/N)^.5
720  LET D2=D-T*(Z^2/N)^.5
730  LET H=EXP(D1+Z^2/2)
740  LET L=EXP(D2+Z^2/2)
750  LET P2=0
760  LET R$="######.###"
770  PRINT USING R$,X,Y1,L,H
780  IF X -99 THEN GOTO 0860
790  PRINT
800  PRINT "QUADRAT TOTAL= "; Y2
810  LET G(C)=Y2
820  LET C=C+1
830  PRINT
840  LET Y2=0
850  LET P2=0
860  NEXT I
870  CLOSE
880  PRINT
890  FOR C=1 TO M
900  LET R1=R1+G(C)
910  LET R2=R2+G(C)^2
920  NEXT C
930  LET R3=R1/M
940  LET R4=SQR(  (R2-R1*R1/M)/(M*(M-1)))
950  PRINT "QUADRAT MEAN", "STANDARD ERROR"
960  PRINT R3, R4
970  PRINT "AMT. PER HECTARE"
980  PRINT R3*200" + OR - ";R4*200
990  IF K(I) =-88 THEN GOTO 0360
1000 CHAIN "REGPLOT2" THEN GOTO 0280
```

APPENDIX 3

ANOVA tables for nutrition experiments (Chapter 6)

1) ANOVA of P rate pot trial (Experiment 1)

Eucalyptus socialis

(i) Total weight

Source	DF	SS	MS	F value
Treats	3	0.3449	0.1150	123.95 ***
Reps	4	0.0024	0.0006	0.65
Error	12	0.0113	0.0009	
Total	19	0.3585		

(ii) Top weight

Treats	3	0.1682	0.0561	90.02 ***
Reps	4	0.0021	0.0005	0.83
Error	12	0.0075	0.0006	
Total	19	0.1778		

(iii) Root weight

Treats	3	0.0314	0.0105	28.89 ***
Reps	4	0.0024	0.0006	1.65
Error	12	0.0043	0.0004	
Total	19	0.0382		

(iv) Root/shoot

Treats	3	0.4702	0.1567	4.59 *
Reps	4	0.3337	0.0834	2.44
Error	12	0.4099	0.0342	
Total	19	1.2138		

Acacia aneura

(i) Total weight

Treats	3	0.0995	0.0332	7.64 **
Reps	4	0.2588	0.0065	1.49
Error	12	0.0521	0.0043	
Total	19	0.1775		

(ii) Top weight

Treats	3	0.0609	0.0203	7.15 **
Reps	4	0.0142	0.0036	1.25
Error	12	0.0341	0.0028	
Total	19	0.1092		

(iii)Root weight				
Treats	3	0.0056	0.0019	10.24 **
Reps	4	0.0019	0.0005	2.63
Error	12	0.0022	0.0002	
Total	19	0.0098		
(iv) Root/shoot				
Treats	3	0.3810	0.1270	21.52 ***
Reps	4	0.0062	0.0015	0.26
Error	12	0.0708	0.0059	
Total	19	0.4580		
Cassia nemophila				
(i) Total weight				
Treats	3	0.0711	0.0237	5.64 *
Reps	3	0.0027	0.0009	0.21
Error	9	0.0038	0.0042	
Total	15	0.1115		
(ii) Top weight				
Treats	3	0.0302	0.0101	8.38 **
Reps	3	0.0003	0.0001	0.08
Error	9	0.0108	0.0012	
Total	15	0.0413		
(iii)Root weight				
Treats	3	0.0112	0.0037	2.91
Reps	3	0.0020	0.0007	0.52
Error	9	0.0116	0.0013	
Total	15			
(iv) Root/shoot				
Treats	3	1.3315	0.4438	6.17 *
Reps	3	0.3351	0.1117	1.55
Error	9	0.6468	0.0719	
Total	15	2.3134		

2) ANOVA of NxP rate pot trials (Experiment 2)

Eucalyptus socialis

(i) Top weight

Source	DF	SS	MS	F value	
Blocks	5	0.0683	0.0137	1.094	
Plots					
N	1	0.7903	0.7903	63.296	***
P	2	1.6487	0.8243	66.024	***
NxP	2	1.5049	0.7525	60.267	***
Residual	25	0.3121	0.0125		
Total	30	4.2561	0.1419		
Grand total	35	4.3244			

(ii) Root weight

Source	DF	SS	MS	F value	
Blocks	5	0.0056	0.0011	0.984	
Plots					
N	1	0.1553	0.1553	135.520	***
P	2	0.4950	0.2475	215.944	***
NxP	2	0.3308	0.1654	144.300	***
Residual	25	0.0286	0.0011		
Total	30	1.0098	0.0357		
Grand total	35	1.0154			

(iii) Leaf area

Source	DF	SS	MS	F value	
Blocks	5	158.2	31.64	1.105	
Plots					
N	1	2095.0	2095.0	73.170	***
P	2	4507.9	2254.0	78.721	***
NxP	2	4034.7	2017.4	70.457	***
Residual	25	715.8	28.6		
Total	30	11353.5	378.4		
Grand total	35	11511.7			

Acacia aneura

(i) Top weight

Source	DF	SS	MS	F value	
Blocks	5	0.0089	0.0018	1.062	
Plots					
N	1	0.3590	0.3590	213.037	***
P	2	0.3570	0.1785	105.919	***

NxP	2	0.3512	0.1755	104.197 ***
Residual	25	0.0421	0.0017	
Total	30	1.1093	0.0370	
Grand total	35	1.1182		
(ii) Root weight				
Blocks	5	0.0052	0.0010	1.273
Plots				
N	1	0.1118	0.1118	135.298 ***
P	2	0.1122	0.0561	67.933 ***
NxP	2	0.1082	0.0541	65.468 ***
Residual	25	0.0207	0.0008	
Total	30	0.3528	0.0118	
Grand total	35	0.3581		
(iii)Leaf area				
Blocks	5	5.1	1.0	0.813
Plots				
N	1	609.3	609.3	481.153 ***
P	2	470.9	235.4	185.931 ***
NxP	2	468.6	234.3	185.050 ***
Residual	25	31.6	1.3	
Total	30	1580.4	52.7	
Grand total	35	1585.6		
<u>Cassia nemophila</u>				
(i) Top weight				
Blocks	5	0.0181	0.0036	0.819
Plots				
N	1	0.1800	0.1800	40.645 ***
P	2	0.1805	0.0903	20.378 ***
NxP	2	0.1709	0.0854	19.291 ***
Residual	25	0.1107	0.0044	
Total	30	0.6422	0.0214	
Grand total	35	0.6603		
(ii) Root weight				
Blocks	5	0.0142	0.0028	1.894
Plots				
N	1	0.0905	0.0905	60.381 ***

P	2	0.0901	0.0450	30.074 ***
NxP	2	0.0772	0.0386	25.769 ***
Residual	25	0.0374	0.0015	
Total	30	0.2952	0.0098	
Grand total	35	0.3094		

(iii)Leaf area

Blocks	5	8.9	1.80	0.988
Plots				
N	1	123.9	123.90	68.097 ***
P	2	102.8	51.40	28.258 ***
NxP	2	96.0	47.99	26.381 ***
Residual	25	45.5	1.82	
Total	30	368.1	12.27	
Grand total	35	377.1		

3) Abbreviated ANOVA of field NxPxCa rate trials (Experiment 3)

(i) Mulga

		mature phyllodes		apical phyllodes	
		P(ppm)	N(ppm)	P(ppm)	N(ppm)
	DF	'F'	'F'	'F'	'F'
Blocks	2	2.551	5.261 **	0.050	0.117
Plots					
N	2	0.713	5.165 **	5.098 **	2.718
P	2	4.687 *	2.076	9.890 ***	0.008
Ca	2	0.035	0.101	0.004	0.007
NxP	4	1.363	0.404	0.555	0.014
NxCa	4	1.753	2.996	3.273 *	1.180
PxCa	4	0.778	1.848	2.989 *	2.210
NxPxCa	8	0.965	0.911	1.542	0.429
Residual	52				
Total	78				
Grand total	80				

(ii) Mallee

		First harvest (6 weeks)				Second harvest (16 weeks)		
		Mature leaves		Apical leaves		Apical leaves		
		P(ppm)	N(ppm)	P(ppm)	N(ppm)	P(ppm)	N(ppm)	
	DF	'F'	'F'	'F'	'F'	'F'	'F'	
Blocks	2	0.542	2.337	0.880	0.437	0.505	2.07	
Plots								
N	2	0.464	1.159	0.149	3.251*	0.328	5.151	**
P	2	2.714	0.781	2.147	0.102	4.057*	0.151	
Ca	2	0.959	0.338	0.284	0.069	2.897	3.062	
NxP	4	2.332	1.331	1.182	0.479	0.356	0.424	
NxCa	4	0.719	0.540	1.463	2.259	0.208	0.717	
PxCa	4	0.617	1.309	1.050	1.358	0.917	1.218	
NxPxCa	8	0.620	0.502	0.897	0.479	0.435	0.553	
Residual	52							
Total	78							
Grand total	80							

* P < 0.05 ** P < 0.01 *** P < 0.001