LITTER STUDIES

IN THE SOUTHERN FORESTS OF TASMANIA

by

CHARLES R.A. TURNBULL

Dip.Ag.Tech., W.A.

Submitted in partial fulfilment

of the requirements for the degree of

Master of Agricultural Science

UNIVERSITY OF TASMANIA

HOBART

December, 1982

(Conferred March 83)

U

Plate 1. View of the study area in the Lune River Valley
from Coal Hill.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University, and to the best of my knowledge contains no copy or paraphrase of material previously published or written by any other person except where due reference is made in the text of the thesis.

Charles R.A. Turnbull,
University of Tasmania,
Hobart.

December, 1982.

ACKNOWLEDGEMENTS

CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

APPENDIX A.

1. Basal area (B.A.) $m^2.ha.^{-1}$ and stem numbers per ha. per species. Site 1.

2. Basal area (B.A) $m^2.ha.^{-1}$ and stem numbers per ha. per species. Site 2.

3. Basal area (B.A.) $m^2.ha.^{-1}$ and stem numbers per ha. per species. Site 3.

4. Mean height and DBHob of selected dominants per site.

5. Height layering of understorey species.

6. Vegetation present on study sites.

7. Hastings Chalet meteorological data.

APPENDIX B.

APPENDIX C.

APPENDIX D.

Media and Reagents.

APPENDIX E. STATISTICAL ANALYSES.

ABSTRACT

Process oriented investigations of litter were made at Hastings, Southern Tasmania, of a range of forests characteristic of the region.

Accession. There was a marked seasonal pattern and correspondence of litterfall between sites over three annual cycles. Bimodality of litterfall was attributable to a peak period of leaf fall and a period of bark and twig fall. Leaf litterfall was significantly correlated with mean maximum temperature, and the secondary peak of bark and twig fall to periods of high wind and heavy rain. A relationship was found between the basal area of individual species and their annual rate of leaf accession. There was no significant difference in slope or intercept of regressions for individual sites, and the relationship existed for all species regardless of their taxonomic group, canopy exposure, or leaf structure and size classification. Annual accession rates were similar to forests of the world of corresponding latitude (ca. 5 t.ha.$^{-1}$).

Accumulation. Detailed descriptions were made of the litterbed characteristics of individual study sites, and techniques for improving determination of standing-crop values devised. Steady-state decay constants were derived, and a climatic index utilised to compare results of Australian litter studies.

Decomposition. The rates of decomposition of leaves of two eucalypt overstorey species, eight understorey species, and of two overstorey-understorey species mixtures were measured by litter bag techniques. Percentage loss of initial dry weight of leaves varied per species from 12.5 to 58.0 over the initial twelve months of field exposure. Species of higher leaf accession rate generally exhibited a faster rate of decomposition. There were no significant between-

species interactions monitored in leaf mixtures.

Litterbed microflora were demonstrated to be the primary decomposer agencies, with bacteria of initial importance to some species. Macroarthropods and invertebrates demonstrated no significant effects upon the decomposition rates of leaf species other than the eucalypts within the time sequence of the litter bag studies. The role of litter fauna is considered secondary to, and dependent upon, decomposition by other agencies.

A method of measuring the decomposition of naturally accumulating litter in the field was devised.

Temperature and moisture, as represented by a defined annual climatic index, 'I', were significantly related to annual litter accession and calculated annual decay constants, 'k', for a range of Australian litter studies. Litter macroclimate was thus the most important influence upon litter accumulation.

CHAPTER 1

GENERAL INTRODUCTION

1.1. BACKGROUND

Litter in the cool, temperate forests of Southern Tasmania does not form a deep litterbed despite the cool temperatures and wet conditions that prevail. It was assumed that efficient decomposer systems exist within the litterbed, and of these the invertebrates and microflora would be of greatest importance.

Observations of ground litter over a range of representative sites have shown that leaves of some litter component species e.g. *Pomaderris apetala*, Labill., appeared to decompose far more rapidly than others, e.g. *Phyllocladus aspleniifolius* (Labill.) Hook. The understorey species of these forests form a significant amount of the total basal area of the various stands, and it was hypothesised that the leaves of these species play an important role in the decomposition of the major leaf litter component, *Eucalyptus obliqua*, L'Herit.

Given that there are observable differences in leaf litter breakdown rates, then the intrinsic characteristics of the various leaf litter species must contribute to those differences viz. species of high phenolic content might be expected to resist decomposer attack, while those of high carbohydrate status might be rapidly colonised and decomposed.

Although the greater portion of leaf litter in the litterbed of these stands is from *E. obliqua*, an appreciable quantity originates from the understorey, and must contribute to the nutrient turn-over and mineralisation process.

1.2. OBJECTIVES

The objectives of these studies were to:

(a) quantify the litter system of a range of sites representative of the Southern Forests of Tasmania, and

(b) to test hypotheses related to the litter breakdown process.

1.3. APPROACH

Throughout the study emphasis was placed upon methodology, including the development and evaluation of new methods whilst information was obtained on litter accession, accumulation, and decomposition processes.

The systematic and sequential approach adopted is illustrated in the flow-chart of Fig. 1.1.

1.4. OUTLINE

Chapter 2 surveys pertinent literature under subject headings. Whereas many published reports exist of litter studies in the cool, temperate forests of the Northern Hemisphere, none have previously been made in those of Australia. Results of other Australian studies must be expected to differ from those reported in ensuing chapters, as they were conducted in the coolest of environments for production forestry in Australia, within stands of diverse tree flora, and with a- substantial difference in the degree and duration of extreme drying conditions than experienced in other areas of Australia.

A general description of the Southern Regrowth Forests is given in Chapter 3, and the reasons for selection of the four study sites are discussed. Site descriptive parameters are detailed and illustrated by tables and figures, e.g. plot size and topography, stand age, site index, inventory, health and floristics, plus descriptions

FIG. 1.1

FLOW-CHART OF APPROACH.

Site selection, preparation, description

| ACCESSION | ACCUMULATION | DECOMPOSITION |

Effect of: *METHODOLOGY*   *METHODOLOGY*   *Effects of:*

Species composition   Type of device   Standing crop ———— Leaf litter + twigs <1.0 cm   Litter bags   Species

Stand density   Species interaction

Basal area   Sample size   Litterbed characteristics   Woody material >1.0 cm   Double trap   Temperature

Temperature   Rainfall

Rainfall   Location   Depth   Decay constants   Time ——Leaf development

Wind   Fixed, roving   Stratum   Earthworm population   Enumeration   Field placement

Temperature   Microflora   Collection

Moisture   Invertebrates

Humus

Soil

Green canopy leaves ———— Freshly shed leaves ———— Decomposing leaves

3

of soil profiles. The general environment is described and meteor-
ological data from a neighbouring weather station detailed. Both the
site descriptive data and meteorological data are used in later chap-
ters to explain and account for individual aspects of the litter pro-
cesses.

As illustrated in the flow-chart (Fig. 1.1) there are 3 pro-
cesses central to any litter system: accession (input), accumulation,
and decomposition (output). These 3 processes and their inter-
relationships under steady-state conditions, i.e. where input equals
output, that exist in the floristic communities selected, are the main
topics of these studies.

Chapter 4 examines litter accession on the 4 study areas at
regular intervals over a period in excess of 3 years, during which
time the composition of accessing litter is detailed for the first 2
years. Seasonal and annual variation in litterfall are illustrated,
discussed, and compared with other forests of Australia. The compar-
ison includes decay constants for the various forests, where the con-
stants are calculated from values of accession and decomposition.

Methodology sections of Chapter 4 examine the efficacy of var-
ious trapping devices, and a cheaply produced, simply constructed
device that facilitated handling of litter catches is described.
Catches in fixed and roving devices within plots, and in devices at
differing levels within the floristic strata are compared.

Litter accumulation, or standing crop, is the subject of
Chapter 5. The methodology of field sampling, and laboratory process-
ing is examined with particular emphasis upon the problems associated
with the inclusion of inorganic matter.

A comparison is made between litter accumulation in these
forests and in other forests of Australia. The comparison includes

decay constants for the various forests, where the constants are calculated from values of accession and decomposition.

Chapter 5 also deals with litterbed characteristics viz. depth, pH of litter and humus layers, and estimates of litter perched on logs, across fallen limbs, and around stumps.

Decomposition studies are described in Chapter 6.

Litter bag techniques were selected as the most viable means of investigating rates of decomposition of the major overstorey and understorey species components of litterfall, and to determine whether species interactions existed in species mixes. A series of experiments were devised to investigate aspects of litter bag methodology, viz. selection of leaf material for inclusion, and time of bag placement in the field. Treatments with insecticide and fungicides were incorporated to determine the roles of invertebrates and microflora in the decomposition process. Individual experiments are detailed, and then discussed as a whole.

A double-trap system was developed and tested in an attempt to examine decomposition of undisturbed litter as it accessed on the forest floor. Problems and benefits associated with use of the system are discussed.

Rates of decomposition determined by experiment, and calculated decay constants are compared with values available for other forests.

Litter bags used in decomposition studies within tall, open forest and low scrub were used in an invertebrate survey of the two environments, results of which are detailed in Chapter 7. Extracted invertebrates at the different harvest dates were identified by Dr. J.L. Madden of this faculty, and were grouped according to major taxa. Preferences of groups for individual leaf species and their temporal array are used together with the results of treatment effects

within litter bags to assess the role of invertebrates in the decomposition process.

Chapter 7 also details results of an earthworm survey made in the litter, humus, and soil immediately beneath litter bags, at each harvest date, in tall, open forest, and the role of these organisms in leaf litter decomposition is discussed.

The role of litter microflora and litter properties that may affect their activity in the decomposition process are the subject of Chapter 8.

An enumeration of microflora inhabiting leaves of the canopy, litter surface, and litterbed was made in the spring of 1981 coincident with a period of active decomposition monitored by litter bag experiments. Methods of sampling, washing, filtration, dilution and plating, and results of counts are detailed and discussed.

The effects of leachates of selected species upon litterbed microflora were investigated and methodology and results are detailed, and the effects of the leachates on the growth of litterbed microflora are discussed. Comparative quantitative analyses were made of the carbohydrate and phenolic contents of the same leaf species used in the leachate investigations in an attempt to explain the basis of the observed results.

An overall discussion at the end of the Chapter defines the role of leaf litter microflora in the decomposition process.

Chapter 9 summarises the conclusions and discussions of the previous Chapters and emphasises the importance of climate to the 3 major litter processes.

CHAPTER 2

LITERATURE SURVEY OF SUBJECT AND METHODS

The various litter processes have been the subject of many reviews (Lutz and Chandler, 1946; Bray and Gorham, 1964; Rodin and Basilevic, 1968; Duvigneaud, 1974; Phillipson, 1971; Dickinson and Pugh, 1974; Leith and Whittaker; 1975, Bevege, 1978), most of the literature relates to studies conducted in the Northern hemisphere. These studies were concerned primarily with eucalypt forests and emphasis has been placed upon literature pertinent to such forests in Australia.

ACCESSION AND ACCUMULATION

In the context of these studies, accession is a measure of litter production, the organic debris shed by forest vegetation upon the soil surface.

Leith and Whittaker (1975) describe primary production as the very basis of the functioning of ecosystems. Net primary production of organic matter is the difference between gross primary production of photosynthetic plants and their respiration, and includes the amount of organic matter contributing to biomass increase, discarded from trees as litter, or lost from plant biomass through death of individuals, and which is consumed by heterotrophs (Attiwill, 1979). Litter accession is therefore an important component of net primary production.

Kittredge (1944) and Van Loon (1970) considered litterfall as an interesting index of ecosystem productivity generally related to the quantities of photosynthetic machinery in the system.

Ashton (1975) describes forest litter as an important stage in the cycle of habitat conservation, providing nutrient return and org-

anic matter replenishment, and supporting a wide variety of niches for fauna and microorganisms. Ashton and Macauley (1972) demonstrate litter to be of considerable significance to forest reproduction.

Charley and Richards (1974) remark that "the greater part of net primary production in forest ecosystems passes directly into the detritus food chain where mineralisation processes release organically bound nutrients for re-utilisation by the plant producers". They further state that the rates of energy and nutrient throughput in the soil-litter sub-system may be used as indices of total community function, and that the soil-litter sub-system is the 'gate' through which passes virtually all absorbed nutrients and much of the energy fixed by forests. Flow rate regulates the productivity of the whole system and this control function is of particular importance to soils of low nutrient capital such as are common in Australia (Charley and Richards, 1974).

Measurement

Medwecka-Kornaś (1971) summarised a number of methods for measuring litter accession based on the IBP Methodology leaflet of Ovington and Newbould, the IBP Handbook by Newbould (1967) and his own investigations at the Nature Conservation Research Centre, Krakow (Medwecka-Kornaś, 1967). Recommended definitions were -

(1) The term litter should be used for all ecosystems and should indicate all that material lying on the soil surface, which is mainly composed of dead plants or their shed organs.

(2) Litter present at a given moment in a definite area of an ecosystem may be considered as its biomass or 'standing crop' and may be expressed in weight per unit area $(kg.ha.^{-1})$.

(3) The amount of litter formed and shed by the ecosystem within a defined period should be called litter production, and expressed as $kg.ha.^{-1}an.^{-1}$.

(4) Decrease of the amount of litter in an ecosystem, caused by decay and mineralisation, animal consumption, wind transport, harvest by man etc. may generally be termed disappearance.

(5) Litter accumulation depends on the rate of production as well as on the rate of disappearance.

Fig. 2.1 is taken from Medwecka-Kornaś (1971) and illustrates a variety of litter traps described in literature by Newbould (1967), Ovington and Newbould (IBP Methodology Leaflet) and Ovington and Murray (1967). Recommended optimal sizes of trap openings were 1000-1250 cm^2, preferably circular to reduce edge effects, and with a minimum number of 25-30 ha.$^{-1}$, distributed randomly or to a defined system. The numbers and size of samples should be large enough to obtain an accuracy of 5% at 95% confidence limits (Ovington and Newbould, IBP Methodology Leaflet). Forest communities with the most discontinuous canopies possess the greatest variability in litterfall (Pressland, 1982, and Charley and Richards, 1974).

Information regarding the efficiency of various types of traps and the errors associated with litterfall and standing crop measurement in Australia is scarce, although specific aspects have been examined by Richards and Charley (1977), Pressland (1982) and Birk (1979a).

Frequency of collection depends upon the phenology of the ecosystem and methods adopted, but should be often enough to yield results representative of the whole year or total growing season, and be based on a minimum of 3 years duration (Medwecka-Kornaś, 1971).
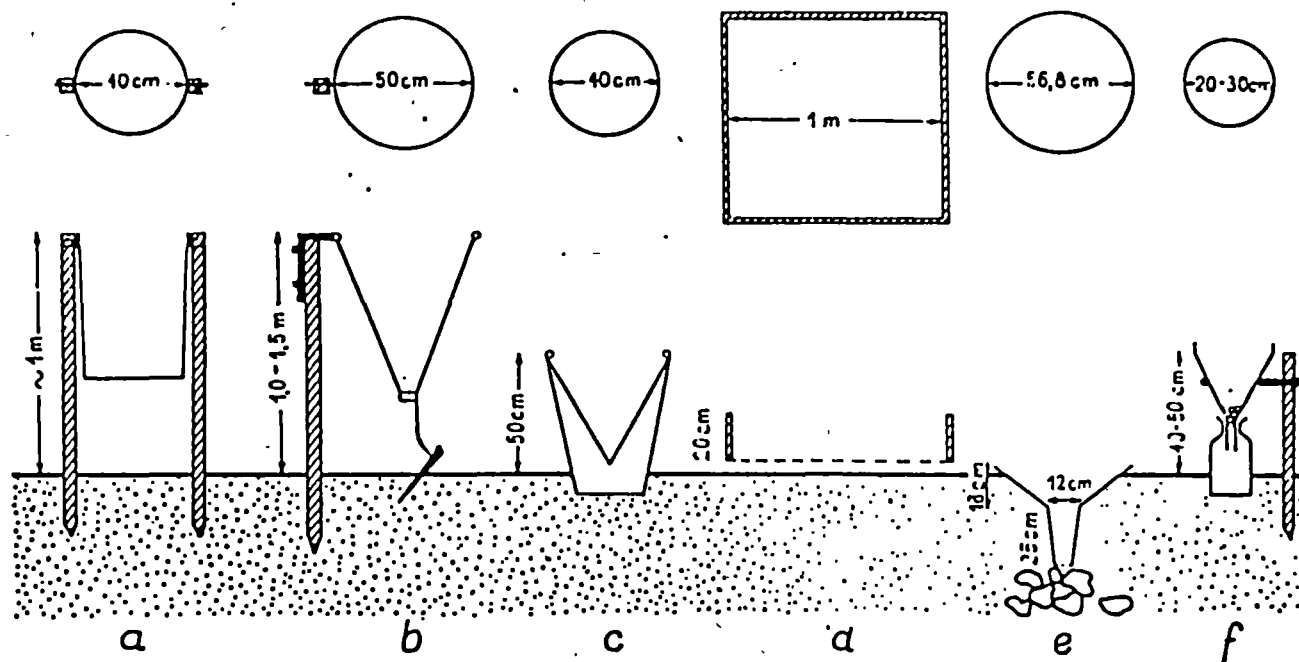
FIG. 2.1. Some types of litter traps: a - simple bag of sail cloth; b - bag of nylon mesh, cheesecloth, sail cloth, etc., suspended from the hoop and pegged (may be weighed) to prevent it blowing inside out; c - some receptacle like a plastic dustbin or bucket with a bag of terylene gauze inside; d - shallow trays with wooden boards and terylene or nylon net at the bottom; e - funnel of tinplate with screen at lower end, buried in the soil; the stone layer promotes water drainage; f - micro-litter trap consisting of polyethylene funnel with glass wool plug in lower part and outlet into polyethylene bottle. In upper part of the figure schemes of trap openings; below, their vertical cross-sections. Taken from Medwecka-Kornaś (1971).

Litter in trays loses weight due to leaching, microbial decomposition, and feeding by saprophagous animals (Kirita and Hozumi, 1969). They state that litterfall may be underestimated if the interval between 2 successive collections is too long, and proposed a mathematical model interpreting relations between weight loss of litter accumulating in trays, length of time interval between successive collections, and the extent of the resultant error of estimated litterfall rate and a correction factor to account for the loss. They remark that in cool, temperate forests correction may be of minor significance but is necessary in warm, temperate, evergreen forests such as those of S.W. Japan and trays should be emptied once a week, or a correction factor applied.

Trap placement is generally random, but Wilm's (1946) fixed and roving gauge technique has been used with success by Attiwill (1966a) in studies of nutrient cycling by rainwater, and by Attiwill *et al.* (1978) for studies of nutrient cycling in litterfall at 2 Victorian *E. obliqua* sites. In the 1978 studies, Attiwill *et al.* maintained 2 traps at each plot at permanent locations that were selected to avoid abnormality within the plot, and 3 traps were 'roved', i.e. moved to new, randomly selected, locations within each plot at the commencement of each collection period. Wilm's technique, following analysis of covariance, allowed the calculation of an expected value of the amount of litterfall for each period from a linear regression that used the average of the 2 fixed traps for each period as the independent variable.

Birk (1979a) and Walker (1981) compared spatial as well as temporal variability in both overstorey and understorey litterfall in Australian forests. Birk compared a Newbould (1967) type raised trap, a ground trap, and a stratified shrub trap in a mixed *Eucalyptus* and

Angophora community near Brisbane. Ground traps provided the most representative measurement of litterfall by collecting material from all layers of the vegetation. Shrub litter fell in localised concentrations under individual shrubs, and the stratified shrub trap was best suited for that measurement. Birk (1979a) also demonstrated that overstorey litterfall measurements are likely to be underestimated unless traps are placed in areas between, rather than under shrubs.

Many authors have neglected study of the understorey component in Australian litter studies, but there are works that indicate its importance (McColl, 1966; Ashton, 1975; Van Loon, 1977; O'Connell *et al.*, 1978; Attiwill *et al.*, 1978; and Birk, 1979a). The understorey litter component is important because it contributes very significant amounts to total nutrient return. Weights of nutrients contributed by wood and bark are of less importance than leaf material in nutrient cycling on a short term basis (Ashton, 1975; Attiwill *et al.*, 1978), and understorey leaves may also have important effects on rate of turnover of overstorey litter.

The proportion of understorey litter collected in eucalypt forests is high by world standards (Bray and Gorham, 1964) and studies in other ecosystems have shown a greater significance attributed to understorey and ground vegetation in forests than their relative proportion of plant or litter biomass suggests, generally because they tend to conserve nutrients (Scott, 1955; Ashton, 1975).

Estimates of 'standing crop' may be made in several ways viz. hand-sampling, raking, mechanical sampling (Medwecka-Kornaś, 1971) or by objective assessment techniques such as that of Sneeuwjagt (1973). Medwecka-Kornaś suggests the use of metal hoops to produce sample plots of similar size and number as litterfall traps. Hoops

are fixed in the ground and contained litter cut around and lifted out. All determinations should be on a defined dry-weight basis.

Sneeuwjagt's (1973) objective assessment was developed for measuring forest floor litter, sticks, and understorey shrub fuels in large areas of high value forests in West Australia. Scrub fuel weights are related to average cover density and top height of the scrub type. Litter quantities in W.A. forests can be estimated from records of past burning and forest canopy cover (Peet, 1971), but complications arise from trade cutting, incomplete burning, and insect infestation of tree crowns. Sneeuwjagt's technique established a close relationship between litter depth and fuel weight in 4 hardwood (*E. diversicolor*, *E. marginata*, *E. callophylla*, and *E. callophylla/E. marginata*) and 3 softwood forests (*P. radiata*, *P. pinaster*, and *Casuarina decussata* (*sic*.)).

Litter production

Litter production in forests of the world has been the subject of an extensive review by Bray and Gorham (1964), in which results from almost 300 stands are listed under four major headings based on four broad climatic zones: Arctic-Alpine, cool-temperate, warm temperate, and equatorial. Average litter production per zone was in the ratio of $1:3.5:5.5:10.9$ $t.ha.^{-1}an.^{-1}$ respectively, which was similar to their calculated ratios of bole production of $1:2.7:5.1:7.0$ for the same zones.

Effect of climate and latitude

Fig. 2.2 is taken from Bray and Gorham (1964) and illustrates the major role of temperature in controlling litter production, where total annual litterfall is plotted versus latitude. Fig. 2.3 is a similar plot using litter accession data from 28 Australian litter

FIG. 2.2.   ANNUAL PRODUCTION OF TOTAL LITTER IN RELATION
TO LATITUDE.
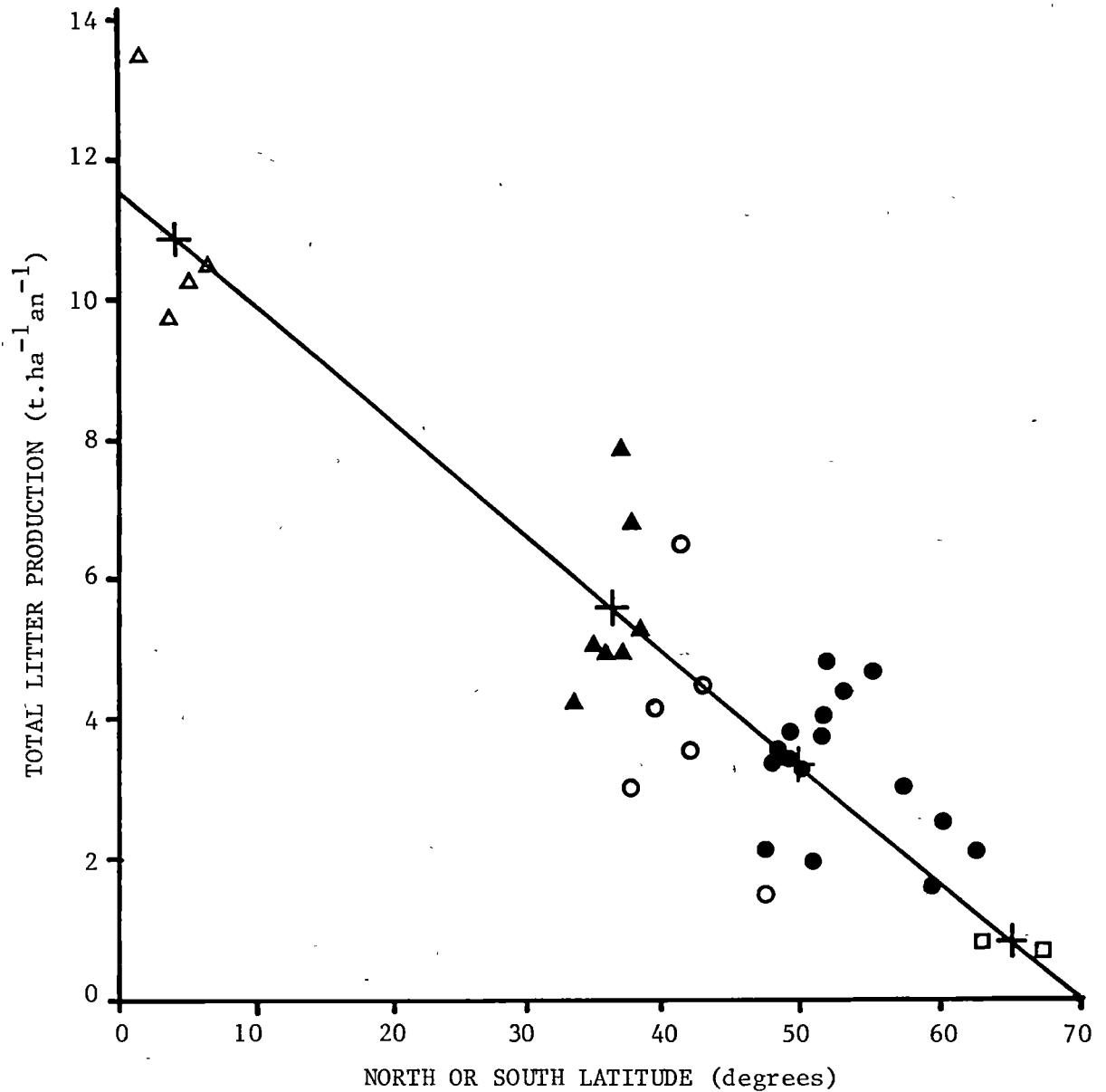
Open triangles – equatorial, solid triangles – warm temperate,
circles – cool temperate North American (open) and European
(closed), squares – Arctic Alpine.   Line fitted visually to
means for climatic zones, shown by large crosses.   One alpine
Californian stand is excluded.   (Taken from Bray and Gorham
1964, Fig.1, p.128).

FIG. 2.3.   ANNUAL PRODUCTION OF TOTAL LITTER IN RELATION
TO LATITUDE, AUSTRALIAN STUDIES.
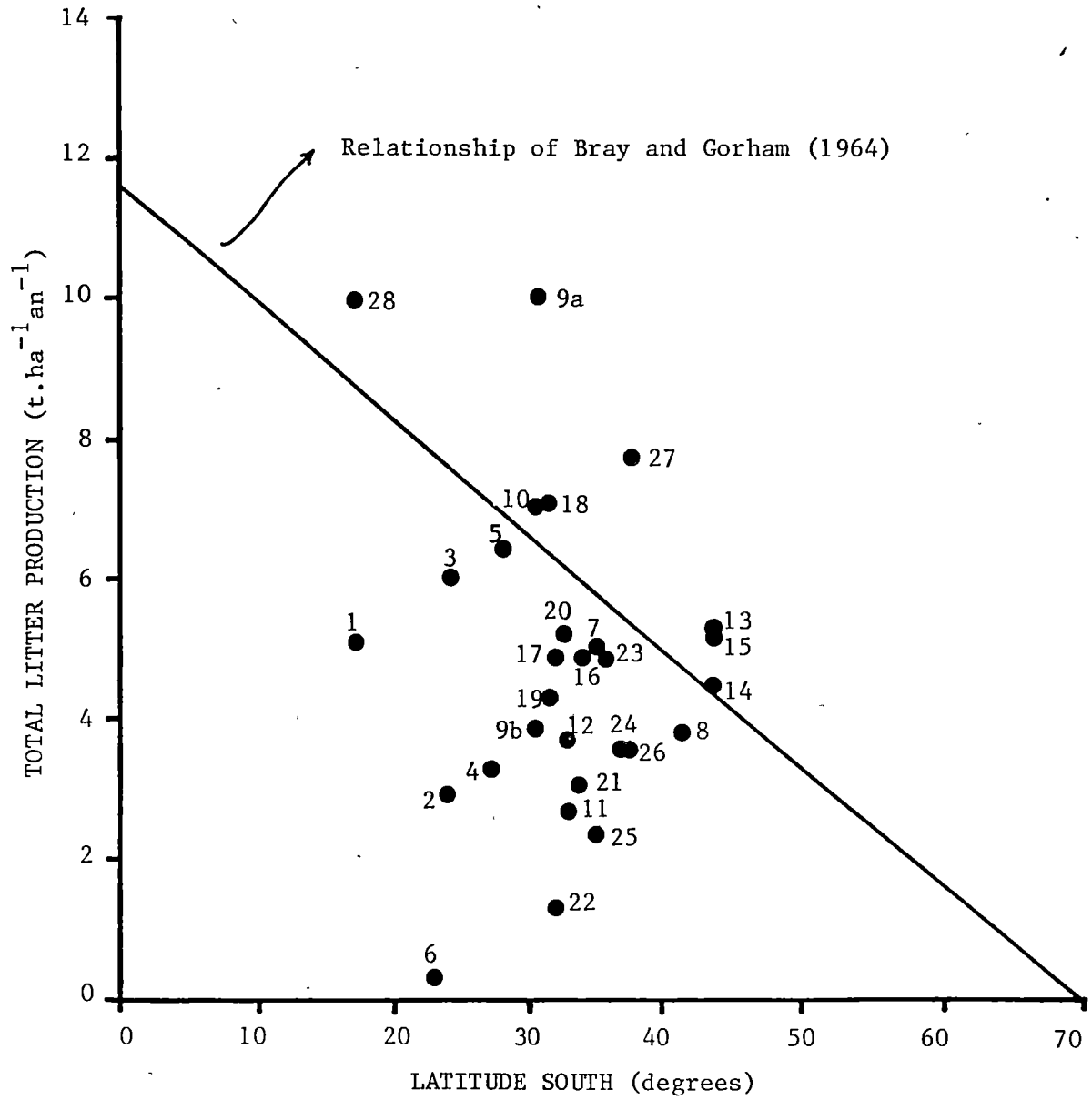
Legend. Fig.2.3.

1. Bailey (1976). Tropical, closed forest.

2. Nicholls (unpublished.) in Walker (1981). Grassy, open forest.

3. Walker (1981). Closed grassland.

4. Birk (1979a). *E. umbra/E. baileyana*.

5. Rogers and Westman (1977). *E. signata/E. umbra*.

6. Winkworth (1973). Woodland.

7. Hutchings and Oswald (1975).

8. Jackson (1968). Open-forest.

9. Richards and Charley (1977). *E. saligna/E. viminalis*.

10. Watson (1977). Temperate, closed forest.

11. Hatch (1955). *E. marginata*, open forest

12. Peet (1971). *E. marginata*, open forest.

13. These studies. Tall, open *E. obliqua*.

14. These studies. Tall, open *E. obliqua*.

15. These studies. Closed *Nothofagus* forest.

16. Maggs and Peason (1977). Dry sclerophyll scrub.

17. Nicholson and Love (1972). *E. pilularis*.

18. Van Loon (1970, 1977). *E. pilularis*.

19. Van Loon (1969). *E. pilularis*.

20. Fox *et al.* (1979). *E. pilularis/A. costata*.

21. Van Loon (1977). *E. sieberi*.

22. Leigh *et al.*. Shrub woodlands.

23. McColl (1966). *E. maculata*.

24. Park (1977). Alpine, open-forest.

25. Lee and Correll (1978). *E. obliqua/E. baxteri*.

26. Attiwill (1968). *E. obliqua*.

27. Ashton (1975). *E. regnans*.

28. Brasell *et al.* (1977). Tropical rainforest.

studies over a latitudinal range of 17° to 43°30'S. The range of temperature spanned by the illustration of Bray and Gorham (1964) is from below freezing to about 25°C. Associated with the higher temperature and longer growing season is the greater amount of insolation during the period of photosynthesis. Using maps of Black (1956), Bray and Gorham suggest that the total amount of solar radiation received during the growing season is roughly in the ratio 1:3:5 for extreme Arctic-Alpine, cool temperate, and equatorial sites.

Attiwill *et al.* (1978) in studies of *E. obliqua* litterfall at Mt. Disappointment, Victoria, demonstrated that at least part of the seasonal variation in litterfall was explained in terms of temperature with the relationship showing hysteresis. There were higher rates of litter production during the period of increasing temperature in the months from winter through spring to summer, and lower rates during the period of decreasing temperatures through autumn. At Stewart's Creek, Victoria, Attiwill *et al.* (1978) demonstrated the same trend in 1972/73 and 1973/74, but in 1971/72 and 1974/75 autumn falls exceeded those of spring. This difference was attributed to correlation with lower than average rainfall in the summer and autumn of 1971/72 and 1974/75, and Attiwill *et al.* suggested that the hysteresis pattern was typical of normal growth patterns, and the variation of differing years a reflection of increased stress through decreased water availability. The suggestion that litterfall appears to be the resultant of both growth and physiological stress is in agreement with Kozlowski (1976).

Lee and Correll (1978) working in *E. obliqua* forests in S.A. related litterfall with absolute maximum temperature and suggested that this parameter reflects seasonal variations, with the possibility

that death of leaves from thermal shock at high temperature is an important factor contributing to the seasonal variation.

Stand structure: basal area, density, canopy cover

Van Loon (1970) showed that the mean annual litterfall in stands of *E. pilularis* in N.S.W. was fairly closely related to basal area of the individual stands, and a similar relationship was demonstrated by Fox *et al*. (1979). Bray and Gorham (1964) cite the work of Bonnevie-Svendsen and Gjems (1957) in a series of Gymnosperm and Angiosperm stands in Norway where a distinct correlation existed between annual fall of leaf litter and stand basal area. Similar relationships were found by Crosby (1961) between total litterfall of *Pinus echinata* and stand basal area in Missouri, U.S.A.

Bray and Gorham (1964) found there was no relation between litterfall and stand density, and a similar finding was reported by Ashton (1975) in *E. regnans* stands in Victoria.

Hatch (1955) suggested relationships between litterfall in *E. marginata* in W.A. and canopy cover percent.

The amount of litter produced in a forest may be expected to depend on the amount of foliage held in the community. There is a logarithmic relationship between the foliage weight of some needle-leaved and some broad-leaved trees and tree stem diameter (Kittredge, 1944; Cable, 1958; Sattoo, 1962).

Attiwill (1962) established relationships between branch girth of *E. obliqua* in Victoria and the weight of leaves and branch wood, and later developed a set of allometric relationships betweeen tree diameter and the dry weights of components of individual tree crowns (Attiwill, 1966). There were no significant differences between relationships for sub-samples selected according to age, crown class, or site quality within the sample, and relationships did not change

over 22 years of measurement.

Specht (1970) defined projective foliage cover as an indirect measure of foliage quantity, and projected cover as defined by Carnahan (1976) was used by Walker (1981) to illustrate that, for data of many Australian litter studies, a curvilinear relationship exists between foliage cover and litter input.

Peet (1971) examined litter accumulation in jarrah and karri forests in W.A. and related it to years since previous burn and canopy cover measurements. Best estimators of jarrah litter weight were the number of years since fire and log.canopy cover per cent, and for karri, the square root of the number of years and canopy cover per cent. Quantity of litter in jarrah forest increases with each summer fall of leaves and twigs for at least 25 years, and in karri for at least 15 years (Hatch, 1955).

Windrun, rainfall, soil moisture and fertility

McColl (1966) related high falls of twigs and leaves during winter 1964 to high winds of a severe storm in July. Ashton (1975) found the fall of twigs and branch wood of *E. regnans* in Victoria to be greatly dependent on storm incidence, and found similar sporadic patterns of twig and branch fall for the understorey species *Acacia, Pomaderris, Cassinia,* and *Olearia* that was related to heavy storms and snow. Ashton (1975) also found fern frond accession to the forest floor to be irregular, partly due to lag between death and accession, and always related to heavy snow falls.

In *E. obliqua* forests at Stewart's Creek and at Mt. Disappointment, Victoria, green leaf and green branch fall with leaves intact showed little seasonal variation, and was considered primarily dependent on abrasion or wind damage in the tree crowns (Attiwill *et al.*, 1978).

A dry sclerophyll scrub community in the Sydney Metropolitan area demonstrated a significant multiple linear relation between litterfall, windrun and pan evaporation (Maggs and Pearson, 1977).

Pressland (1982) suggests that much of the difference in litterfall between years may be attributed to rainfall and soil moisture content. Leaf litterfall in a study of a mixed *Eucalyptus* dry sclerophyll forest in N.S.W. was positively correlated with temperature and solar radiation on 2 catchments. Leaf litterfall was correlated with mean maximum, minimum, and daily temperatures and there was little difference in their values for rising (winter to summer) or falling (summer to winter) temperatures. Soil moisture content was correlated with litterfall in summer ($r = 0.67$, $P<0.05$) at one study site (sandy) but not at the other (Mt. Duval).

Higher accumulation and litterfall were related to increased rainfall and higher mean monthly temperatures by Specht and Brouwer (1975) and Fox *et al.* (1979), and these climatic factors have been discussed on a world forest productivity basis by Bazilevic *et al.* (1971). The joint effect of heat and moisture are illustrated in Bazilevic *et al.* (1971), and they show that if the values of the radiation balance, R, do not exceed 40 $Kcal.cm^{-2}an.^{-1}$, productivity rises quickly following an increase in heat. However, under high values of R (>40 $Kcal.cm^{-2}an.^{-1}$) the productivity increment is predominantly influenced by moisture availability.

Bonnevie—Svendsen and Gjems (1957) reported higher litterfall on more fertile soils in Norway, and Bray and Gorham (1964) tabulated results of studies by European authors that demonstrated decreasing litterfall with decreasing site quality. O'Connel *et al.* (1978) demonstrated similar relationships where significant differences in *E. marginata/E. calophylla* litterfall occurred between sites of differing soils ranging from yellow sand to reddish gravel.

Fire

The role of forest litter in providing a habitat for soil fauna and flora has been emphasised by Witkamp (1966), Ashton (1975), Springett (1976), and Ashton and Macauley (1972), and in the provision of nutrients by many authors both overseas and in Australia (Hatch 1955; Scott 1955; Gilbert and Bocock, 1960; Bocock, 1963, 1964; King and Heath, 1967; Attiwill, 1968; Harley, 1971; Wood, 1974; Ashton, 1975; Rogers and Westman, 1977; O'Connell *et al.*, 1978; Lee and Correll, 1978; Feller, 1980; Specht, 1981).

Springett (1976) demonstrated that reduction of the litter layer by regular prescribed burning affected soil fauna both in population density and species diversity. These changes in turn may influence the rate of breakdown of litter accumulating subsequent to burning. Conversely, Peet (1965) describes fuel reduction burning in jarrah and karri forests of the Dwellingup region of W.A., and states it can promote an abundance of species of understorey shrubs and attractive habitat for fauna.

Although the relative importance of fire compared with other agents of decomposition will vary with forest type, fire frequency, and intensity, Birk (1979b) suggests that regular fires may substantially influence the long term turnover of biomass in Australian eucalypt forests. This view is shared by many other authors as exemplified by Jackson (1968) and Gilbert (1959). O'Connell *et al.* (1978) demonstrated that in common with other Australian native species (Specht and Groves, 1966; Attiwill, 1968) phosphorous is retained in the tree biomass of jarrah and marri in W.A. by up to 80 per cent. Intense burning that involves the scorching of tree crowns prevents translocation and hence increases the amount of phosphorous in subsequent litterfall. O'Connell *et al.* (1978) consider that modification of chemical composition of litter in this way may have profound

effects on the nutrient content and decomposition rate of forest floor litter, and hence on the recycling rate of nutrients.

Regardless of contrary views on the merits of prescribed burning, it has been described as one of the most dramatic changes in Australian forest management policy in recent years (Van Loon, 1970). Justification of the practice is to keep low quantities of fuel and thus reduce the chance of wildfire, and to enable control agencies to contain such fires should they occur. McArthur (1962, 1967) demonstrated that as fuel quantity doubles the fire intensity will increase fourfold. Van Loon (1977) has reported investigations, in the Blue Mountains Region of N.S.W., that were designed to survey fuel weights occurring on areas with different fire histories, and to examine the effects of repeated low intensity fire on the native vegetation.

Fox *et al.* (1979) tested the applicability of the modified exponential model for litter accumulation of Jenny *et al* (1949), and Olson (1963), for estimating time since the last fire, and for predicting the build-up of fuel. Their interest was related to effects of fire on mammal communities through removal of litter fauna (significant diet of insectivorous, marsupial mice), and they reported a linear increase in height of the ground vegetation with time since fire over a period of one to nine years. Litter accumulation demonstrated an exponential increase with time that closely followed Olson's (1963) model. These findings agreed with those of Van Loon (1970). Van Loon suggested that this does not reflect the growth rate of an individual species but can be regarded as the envelope produced as different species dominate the understorey.

Seasonal variation in litterfall

Although there is a marked seasonal influence on litterfall in

Australian forest communities (Hatch, 1955; McColl, 1966; Ashton, 1975; Specht and Brouwer, 1975; Maggs and Pearson, 1977; Rogers and Westman, 1977, 1981; Richards and Charley, 1977; Lee and Correll, 1978; Attiwill, 1978; Plowman, 1979; Fox *et al.*, 1979; Birk, 1979a; Pressland, 1982) several authors (Fox *et al.*, 1979; Birk, 1979b; Birk and Simpson, 1980) consider the continuous litterfall model of Olson (1963) better suited to Australian situations than his discrete litterfall model. In spite of seasonal fluctuation in litterfall, the accumulation of litter on the forest floor has been shown to vary little throughout the year (Van Loon, 1970). Fox *et al.* (1979) point out that although the use of Olson's (1963) exponential model with two parameters (steady state accumulation, X_{ss}, and rate of accumulation, k) that are functions of the annual litterfall is adequate for use in eucalypt forests, it should be recognised as a gross simplification of the multiplicity of factors which affect litter accumulation, and in particular where a constant value for k is assumed. Problems associated with the use of the exponential model have been discussed in detail by Birk (1979b) and Birk and Simpson (1980).

Ashton (1975) with *E. regnans*, and Attiwill *et al.* (1978) with *E. obliqua*, in Victoria, reported seasonal patterns of litterfall that were similar in many respects and that relate to the *E. obliqua* forests of these studies more closely than most other Australian litter studies.

E. regnans leaf fall was the major component of litterfall in Ashton's (1975) studies, with a very marked and regular seasonal distribution. Peak fall began in December some weeks after shoot growth commenced. There was major fall in summer with maximum in January, and summer fall constituted approximately half the annual amount. The ratio of January maximum to July minimum was about 9:1 for pole and mature stands, and 15:1 for spar trees. There were two peaks of bark

fall each year from autumn to spring, usually associated with high wind. Bark shed usually commenced on the small branches and was scattered widely, whereas strips of bark from the trunk tended to hang on branch axils, from points of decortication, and from the under-storey canopy for long periods. Much of the coarser bark tended to accumulate as "haloes" around the butts of the larger trees. A similar finding was reported by Charley and Richards (1974) in a lay-ered eucalypt forest in the New England National Park, N.S.W., and by McColl (1966) for *E. maculata* in N.S.W. In Ashton's (1975) studies twig and branch fall was conspicuous and highly variable in its dist-ribution. Wood and twig fall in *E. regnans* forests was higher than for many other forest types owing to the rapid ramification of shoots, a characteristic of the faster-growing eucalypts (Jacobs, 1955).

In general non-leaf litterfall of *E. regnans* (Ashton, 1975) was close to 40% of the total in all stands studied, a figure greater than that for other hardwoods in Australia, but similar to values cited for many angiosperms by Bray and Gorham (1964).

Attiwill *et al.* (1978) carried out a detailed seasonal analysis of the weight and nutrient content of the components of litterfall in *E. obliqua*, Victoria. About 50% of the total eucalypt litter fell during December to February with leaf fall approximately 75% of the total fall during this period.

Pressland (1982), working in dry sclerophyll forests in N.S.W., recorded low (2500-3750 kg.ha.$^{-1}$) annual litterfall rates by world standards (Bray and Gorham, 1964), but which were seasonal, and similar to other dry sclerophyll sites in Australia (Lee and Correll, 1978; Hatch, 1955; Birk, 1979a). Lee and Correll (1978) did not separate leaves from fine twigs, bark, and fruit, but excluding stick fall recorded 47.5% in summer, 22.8% in autumn, 11.1% in winter, and 18.6% in spring. No such seasonal pattern of fall was shown in these

S.A. *E. obliqua* forests, seasonal proportions being 24.5, 28.8, 26.0, and 20.7 respectively.

Leaf fall of understorey species in the *E. regnans* study of Ashton (1975) was variable, and depended on stand density, species composition, and maturity. Seasonality of the understorey leaf fall was chiefly January-March, particularly due to the behaviour of *Pomaderris* which shed 40% of its litter in summer and 15% in spring. A similar pattern occurred with *Prostanthera* and *Hedycarya*, whereas *Acacia dealbata* had a maximum fall in autumn, and *Olearia argophylla* a diffuse fall over most of the year. Leaf fall of *Pomaderris aspera* understorey in pole stage *E. regnans* was significantly less than in the 50 year old understorey of mature forest even though density of the contributing trees was greater (Ashton, 1975).

Van Loon (1970) reported two peaks of litterfall in *E. pilularis*, both occurring between October and January, the season of highest mean litterfall. Maximum-minimum ratios between 3-monthly periods were 7:1, and there was a 1.6 to 1.0 maximum-minimum ratio of variation between years of measurement over 4 study years. Bray and Gorham (1964) quote maximum-minimum ratio variations between years of measurement as high as 5:1.

Birk (1979a) measured significant temporal and spatial variations in annual litterfall from all layers of forest vegetation in mixed *Eucalyptus/Angophora* forest near Brisbane. Patterns of litterfall from overstorey and understorey species layers were strongly seasonal but out of phase. The understorey litter accession trend was bimodal and coincident with the bimodal curve of the photosynthetic index for evergreen perennial communities in the Brisbane area (Specht and Brouwer, 1975). Rogers and Westman (1981) in studies of growth rhythms and productivity of a coastal subtropical eucalypt forest at Stradbroke Island, 30 km from the study area of Specht and Brouwer

(1975), found a marked bimodal pattern of leaf fall in only one species, *E. umbra subsp. umbra*. The less marked bimodality of leaf fall was attributed to more moderate temperature fluctuations and greater summer moisture availability of the more coastal site. Leaf fall and leaf growth were roughly synchronous in the studies of Rogers and Westman (1981) although leaf initiation noticeably preceded leaf fall. The result was in accord with those of Specht and Brouwer (1975), and Birk (1979a) and suggest that perennial understorey species, like eucalypts (Jacobs, 1955) shed more litter during the period of active shoot growth.

Walker (1981) describes the causality of leaf fall as a complex interaction between a large number of factors, including drought, wind, fire, insect attack, phenology, plant growth and leaf longevity, and suggests that plant growth provides the most useful causal relationship, as most leaves fall during periods of new growth. This view is supported for eucalypts by Jacobs (1955), Birk (1979a), Ashton (1975), Rogers and Westman (1981), for *Nothofagus* by Howard (1973), and for mulga by Slatyer (1974) and Winkworth (1973). Walker (1981) stresses the equal importance of soil moisture status and temperature.

Litter components

Components of leaf fall and of the litter layer are summarised from the reported results of the authors of a range of Australian litter studies in Tables 2.1 and 2.2 respectively, and may be compared with data presented in Tables 2.3, 2.4, and 2.5 taken from pp118 and 119 of Bray and Gorham (1964) for a range of species, and climates of the world.

Minerals

Ashton (1975) measured the nutrient concentration of fallen litter in *E. regnans* stands in Victoria, and reported that analyses of

Table 7.1. Components (percent) of leaf fall; selected Australian litter studies.

Authority	Species/Community	Leaf	Non-leaf Bark	Twigs	Flower	Seed	Other
Maggs and Pearson (1977)	Dry sclerophyll scrub, N.S.W.	69		7.2	6.4	1.4	15.9
Lee and Correll (1978)	*E. obliqua/E. baxteri*, S.A.	81.5		18.5	-	-	-
Van Loon (1970)	*E. pilularis*, N.S.W.	51.5	13.2	27.9	-	-	7.4
Attiwill *et al.* (1978)	*E. obliqua*, N.S.W.	54	12	29	-	-	5
Florence (1961)	*E. pilularis*	51	13	32	-	-	4
Pressland (1982)	Dry sclerophyll *eucalyptus*, N.S.W.	49-67	7-14	-	-	-	11.9
Ashton (1975)	*E. regnans*, Vic.	47.1-53.5	14-18	21-27	-	-	-
"	Understorey	74.5-82.5	-	-	-	-	-
Birk (1979a)	*Eucalyptus/Angophora*	57-61	-	-	-	-	30
McColl (1966)	*E. maculata*, N.S.W. O/M	42.8	28.7	20.9	-	-	7.7
	P	47.2	41.5	7.3	-	-	3.9
	S	46.2	45.8	7.3	-	-	1.0
Hatch (1955)	*E. marginata*, W.A., O/M	47.4		27.3	-	-	25.2
	P	69.4		25.3	-	-	5.4
	S	60.0		28.2	-	-	11.9

O/M = Over-mature, virgin.

P = Pole.

S = Sapling.

Table 2.2.1.   Components (percent) of the litter layer in
                E. pilularis forest in N.S.W.

Authority	Species/Community		Leaf	Bark	Twigs
Van Loon (1977)	E. pilularis,	Blue Mts.	23	9	35
	"	Eden	24	8	35
	"	Kendall	27	6	35
	"	Taree	28	5	35
	"	Armidale	20	5	33
	"	Kempsey	20	8	25
	"	Bellangry	23	12	40

Table 2.2.2.   Components (percent and Kg ha^{-1}) of the litter layer in a
                Eucalyptus/Angophora community, Brisbane, Queensland.

Authority	Material type	%	Kg ha^{-1}
Birk (1979a)	Intact overstorey leaves	2.29	234.7
	Fragmented overstorey leaves	23.23	2,378.0
	Dead grass	8.85	905.9
	Small shrub leaves, mainly Pultenea	0.97	99.0
	Large shrub leaves, mainly Acacia	0.63	64.9
	Non-leaf litter	37.21	3,809.5
	Comminuted fraction	26.81	2,744.8
	Total	99.99	10,206.4

Table 2.3. Percentage of non-leaf material in forest
litter (from Bray and Gorham, 1964).

	Individual values	By author
All species	30	30
Angiosperms	30	31
Gymnosperms	29	27

Table 2.4. Percentage of non-leaf litter in different
climates[*] (from Bray and Gorham, 1964).

Climate	Gymnosperms	Angiosperms
Tropical	–	(33)
Warm temperate, Australia and New Zealand	(39)	42
Warm temperate, North America	37	23
Cool temperate	23	21
Arctic – alpine	(39)	21

[*] Figures in parentheses taken from single author's data.

Table 2.5. Detailed separation of litter components (from
Bray and Gorham, 1964).

Species	Percentage of total litter					
	Leaf	Fruit	Branch	Bark	Other[*]
Pinus	60	11	12	14	<1
Pinus	62	17		21	
Pinus	69	2	12	11	6
Picea	73	5	13	–	10
Picea – Betula	76	6		18	
Betula	71	–	12	<1	16
Quercus	75	<1	15	9	–
Eucalyptus	60	15[†]		25	

[*] Flowers, budscales, fragments, epiphytes, insects.
[†] Including buds.

leaf material indicated that *E. regnans* is relatively poor in nutrients compared with the leaf fall of many American forest trees (Kittredge, 1948). There was a considerable variation between leaf litter of different species, and a relative poverty of nutrient in *E. regnans* bark and twigs. The weight of nutrient returned in Ashton's (1975) Wallaby Creek studies was similar to that of *E. pilularis* in N.S.W. (Webb *et al.*, 1969), but 2-6 times as great as that of dry sclerophyll forests of *E. marginata* in W.A. (Wallace and Hatch, 1955), 1.3-2.3 times that of dry sclerophyll *E. obliqua* in Victoria (Attiwill, 1966b), and 2.5-5.5 times that of *E. obliqua* dry sclerophyll forests in S.A. (Lee and Correll, 1978).

Wood (1974) studied losses of mobile elements by leaching of *E. delegatensis* leaves in terylene mesh bags at 21 sites in south-east Australia, with a mean annual rainfall range of 508-1651 mm. He found potassium concentration decreased by 51-91% in coarse mesh bags, and by 27-84% in small mesh bags after 12 months field exposure, and that the decrease in concentration was positively related with rainfall (r = 0.55). Similar experiments of Wood (1974) at Mt. Kosciusko with leaves of *E. delegatensis* and *E. pauciflora* found decreases of 80-90% in potassium concentration after 3 months field exposure. Attiwill (1968) showed losses of 60% potassium and 80% sodium from leaves of *E. obliqua* after 6 months exposure, and Attiwill (1966a) demonstrated significant leaching by rainwater of nutrients, and of potassium in particular, from senescing parts in the canopy. Ashton (1975) observed that reduction of phosphorous, nitrogen, and potassium in fresh litterfall was pronounced due to probable withdrawal before abscission, although some leaching of K was considered likely to have taken place. Conversely, Ca and Mg increased during the maturation phase. In Ashton's studies the total Ca content of litter under pure *Pom-*

aderris aspera was 2-3 times as great as under *E. regnans*, and exchangeable calcium in the surface 7.5 cm of soil was 1.8 times as great. Differences in levels of exchangeable Ca between the two soils were apparent to depths of 15 cm.

Charley and Richards (1974) found the standing crop of total mineral nitrogen (NH_4-N + NH_3-N) content of 3 forest soils was at its lowest level (129 $mg.m^{-2}$) in late winter, and rose to its highest value (653 $mg.m^{-2}$) in late summer. These changes paralleled those for population densities of heterotrophic bacteria and fungi. Ammonium and nitrate fluctuation were of essentially similar seasonal trend.

Attiwill *et al.* (1978) in studies of *E. obliqua* litter in Victoria demonstrated by analysis of variance of litter nutrient concentrations that variations due to years and to the interactions of seasons and years were not significant, and each element varied significantly between seasons for at least two litter categories. In general, Ca, Mg, Na, and K were maximum in late summer to early autumn with P at that time minimal. Despite the seasonal or monthly differences in nutrient concentrations, the nutrient content of litterfall per unit time was dependent on the weight of litterfall per unit time i.e. 50% of total dead eucalypt litter in the studies of Attiwill *et al.* (1978) fell during the summer months and contained 40-60% of the total nutrients. Subordinate vegetation demonstrated greater nutrient levels than those in litter from the eucalypts, in agreement with the findings of Ashton (1975) and of O'Connell *et al.* (1978) who found levels of N and S in *Acacia pulchella* leaves in *E. marginata/E. callophylla* stands in W.A. to be more than twice the concentration of that in the eucalypts.

Lee and Correll (1978) measured nutrient concentrations in *E. obliqua* litter in S.A. over a 5 year period. Again, there was a clear

harmonic seasonal variation with N, P, Zn, Fe and Cu concentration at a minimum in late winter to spring when litterfall was at a minimum. Concentration of Ca, Mg, and Mn varied inversely. Seasonal effects of temperature could not be replaced by other meteorological factors but regressions were improved by addition of data for rainfall and the numbers of rainy days. K concentration did not correlate with that of other elements, but there was a negative correlation between the concentration of K and the number of rainy days. There was no seasonal trend in the nutrient content of sticks but over 5 years Ca, Mg, Zn, Mn, and Ca generally increased in concentration whilst N and P generally decreased. The ratios of nutrient concentrations in sticks compared with leafy material were 1/3 K, 1/2 N, P, Mg, Mn, 2/3 for Ca and Zn, and greater than 1 for Cu and Fe.

The annual litterfall and nutrient return for selected overseas and Australian hardwood forests are well illustrated by Table 2.6 below, taken from Attiwill *et al*. (1978). As discussed by those authors the concentration of P in litter of *E. obliqua* is clearly low by world standards, but is in agreement with data for other eucalypts.

The biogeochemical cycle in which approximately 70% of the P is redistributed within the biomass (Ashton, 1975; Attiwill *et al*., 1978; O'Connell *et al*., 1978) prior to litterfall is of major significance to eucalypts growing on soils which are low in P by world standards.

Biomass and nutrient distribution in *E. regnans* forest and a mixed *E. obliqua-E. dives* forest near Melbourne have been reported by Feller (1980), and have been reviewed for indigenous forest ecosystems by Bevege (1978). The aboveground living biomass ($t.ha^{-1}$) and its nutrient content ($kg.ha.^{-1}$) of Australian forest ecosystems, and the range of nutrient concentrations (%) found in living tissues of eucalypts growing in Australia are summarised in Tables 2.7 and 2.8 resp-

Table 2.6.   Annual litter fall and nutrient return for selected overseas and Australian hardwood forests. (Taken from Attiwill *et al.*, 1978).

Author	Forest	Annual litter fall (t ha^{-1})	Annual nutrient return (kg ha^{-1}) P	Ca	Mg	K
Overseas studies						
Carlisle *et al.* (1966)	Sessile oak, England	3.8	2.2	24	3.9	11
Chandler (1941)	North-eastern hardwoods, U.S.A.		3.7	74	10	15
Miller and Hurst (1957)	*Nothofagus truncata*, N.Z.	5.6	2.2	55	9	6
Nye (1961)	Moist tropical forest, Ghana	10.5	7.3	206	45	68
Remezov (1961)	Oak, Russia	3.8	4.6-12	55-96	7.7-13	14-34
Australian studies						
Hatch (1955)	*E. marginata*, W.A.	2.7	0.6	21	7.3	6.3
Webb *et al.* (1969)	Subtropical closed-forest, N.S.W.	7.3	10	133		41
	Warm temperate closed-forest, N.S.W.	4.5	2.1	43		9.3
	E. pilularis, N.S.W.	6.5	1.3	25		8.3
Ashton (1975)	*E. regnans* (mature) Vic.	7.8	1.9	49		7.5
Attiwill *et al.* (present study)	*E. obliqua*, Vic. Mt. Disappointment	3.6	1.0	21	8.3	5.5
	Stewart's Creek	5.5		30	9.4	8.9

33

ectively (taken from Feller, 1980).

DECOMPOSITION

Decomposition of tree leaves is not a problem which is entirely confined to the litter layer of the forest floor, as decay processes start from the moment leaves are formed, and they are exposed to attack by animals and micro-organisms during their whole life, senescence, and after death (Jensen, 1974).

The basic pattern of litter breakdown is the rapid disappearance of water soluble compounds, particularly sugars, followed by readily hydrolysed starches and proteins, then hemicelluloses and celluloses, and lastly lignin (Burges, 1965). All biologically synthesised compounds are subject to decomposition, but their rates of breakdown may vary considerably (Alexander, 1971). Decomposition is a combination of mechanical and chemical breakdown, with fauna mainly responsible for mechanical breakdown (Van der Drift, 1958; Witkamp, 1971) which improves conditions for microflora (Edwards and Heath, 1963), the main chemical breakdown agencies (Jensen, 1974).

Measurement of decomposition rate

The efficient recycling of mineralised nutrients that result from the decomposition of detritus, above and below ground, enables forests to sustain a higher productivity than most other natural terrestrial ecosystems (Witkamp and Ausmus, 1975). Hence the rate of litter decomposition is an important determinant of processes that affect forest ecosystem productivity through accumulation, nutrient cycling, soil organic matter content and consequent effects on soil structure, rooting environment, and water relations (Charley and Richards, 1974; Westman, 1978; Raison, 1980; Woods and Raison, 1982).

Reviews of techniques for studying the decomposition of litter

Table 2.7. Aboveground living biomass (t.ha^{-1}) and its nutrient content (Kg.ha^{-1}) of Australian eucalypt forest ecosystems. (Taken from Feller, 1980).

Forest	Biomass	N	P	K	Na	Mg	Ca	Reference
1. *E. regnans* (38 years old)	654.4	399	38	1389	138	192	849	This study
2. *E. regnans* (27 years old)	831.4	–	17	–	–	–	–	Ashton (1976a)
3. *E. obliqua-* *E. dives* (38 years old)	373.4	426	17	111	103	71	264	This study
4. *E. obliqua* (51 years old)	316	–	31	256	–	204	336	Attiwill (1964)
5. *E. sieberi* (27 years old)	928.6	–	14	–	–	–	–	Ashton (1976a)
6. Mixed dry* sclerophyll (unknown age)	175.6	395	–	–	–	–	–	Hannon (1958)
7. *E. signata-* *E. umbra* (unknown age)	103.6	456	18	192	169	77	344	Westerman & Rogers (1977a, 1977b)
8. *E. diversicolor* (37 years old)	262.6	473	27	296	82	211	1133	Hingston *et al.* (1979)
9. *E. diversicolor-* *E. calophylla* (unknown age)	304.8	449	31	424	125	344	1266	Hingston *et al.* (1979)

* Includes roots.

Table 2.8.   Range of nutrient concentrations (%) found in living tissues of eucalypts growing in Australia.   (Taken from Feller, 1980).

Component	N	P	K	Na	Mg	Ca	References
Stemwood	0.04–0.23	0.002–0.02	0.01–0.11	0.01–0.17	0.003–0.11	0.03–0.15	3,4,5,7,12,13
Stembark	0.17–0.92	0.005–0.05	0.07–1.60	0.07–0.21	0.04–0.32	0.38–3.21	1,3,6,9,12,13
Branches	0.16–0.40	0.005–0.04	0.01–0.31	0.03–0.14	0.001–0.33	0.10–0.81	3,6,12,13
Leaves	0.57–1.74	0.02–0.15	0.12–1.25	0.04–0.33	0.16–0.55	0.18–1.22	1,2,3,5,6,7,8,9,10,11,12,13
Roots	0.17–0.38	0.004–0.02	0.01–0.12	0.03–0.07	0.001–0.05	0.07–0.18	12

1. Ashton (1975a)
2. Ashton (1976a)
3. Attiwill (1964)
4. Bamber (1975)
5. Bevege (1978)
6. Cromer *et al.* (1975)
7. Hannon (1956)
8. Hatch (1955)
9. McColl & Humphreys (1967)
10. Nielsen & Palzer (1977)
11. O'Connell *et al.* (1978)
12. Westman & Rogers (1977)
13. Hingston *et al.* (1979)

in Northern Hemisphere forests have been published by Anderson and Macfadyen (1975), Dickinson and Pugh (1974), and Singh and Gupta (1977). Merits of various techniques and problems associated with their use in eucalypt forests have been discussed by Richards and Charley (1977), and reviewed by Woods and Raison (1982). These techniques study selected litter components by the use of

(a) mesh bags (McColl, 1966; Attiwill, 1968; Wood, 1974; Macauley, 1975; Rogers and Westman, 1977; Birk, 1979b),

(b) tethering devices (Birk, 1979b),

(c) undisturbed litterbeds by collection of litter leachate (Feller, 1978),

(d) calculation of the decomposition constant, k, based on the ratio of annual litterfall to accumulated litter (Hatch, 1955; Attiwill, 1968; Ashton, 1975; Rogers and Westman, 1977; Lee and Correll, 1978; Plowman, 1979, Birk, 1979b).

Singh and Gupta (1977) state that studies of selected leaf litter are difficult to carry out because it is impossible to obtain the full range of environmental factors that operate under natural conditions. They consider it suitable for studies of decomposition patterns in various plant species, the evaluation of changes in chemical composition, and the role of soil microbiota and soil animals.

Green, picked leaves have been used in many Australian litter decomposition studies (McColl, 1966; Wood, 1970, 1974; Macauley, 1975, 1979; Birk, 1979b). Use of such material has been criticised by Singh and Gupta (1977), Richards and Charley (1977) and Woods and Raison (1982) as the energy and nutrient status of green leaves differs from senescent leaves. High initial nutrient concentration promotes subsequent decomposition (Witkamp, 1966; Wood, 1970, 1974; Ashton, 1975;

Bunnell *et al.*, 1977). Davies (1971) showed that the tanning of leaf proteins during senescence rendered the senesced leaves less susceptible to attack by microorganisms.

Ideal study material should be represented by the bulk of the naturally shed material accessed to the forest floor, i.e. senesced leaves during the period of maximum litterfall (Woods and Raison, 1982), as only 9% of leaves that were trapped in *E. obliqua* forest by Attiwill *et al.* (1978) were green.

Litter bags

The use of litter bags has been criticised by many authors (Gilbert and Bocock, 1962; Witkamp and Olson, 1963; Anderson, 1973; Suffling and Smith, 1974), but they remain a simple and widely-used method of determining rates of litter decomposition in the field, and can be modified to exclude all or some groups of litter fauna, enabling assessment of the relative roles of litter fauna and microflora (Wood, 1971, 1974; Macauley, 1975).

Problems associated with litter bag usage are discussed in Chapter 6.

Tethered leaves

Tethered leaf techniques were developed by Witkamp and Olson (1963), and have been used in Queensland by Birk (1979b). This method maintains material under natural conditions but may result in overestimations due to particle loss (Singh and Gupta, 1977).

Litter leachate collection

Feller (1978) sampled litter leachate beneath eucalypt and exotic conifer stands in Victoria by intercepting water percolating through the litter pack above the mineral soil. Total nutrient content of the leachate was used to estimate above ground nutrient input,

less stemflow, to the soil. There was a seasonal pattern in cation concentration in the leachate with a peak in autumn caused by leaching of fresh litterfall in summer (Feller, 1978).

Nutrient input from decomposing litter can be determined if the throughfall contribution is measured separately and subtracted from the total nutrient input value (Woods and Raison, 1982).

Litterfall method: calculation of decomposition constant, 'k'

Under steady state conditions of accumulated litter, X_{ss}, on the forest floor, the decomposition constant, k, can be calculated from the equation,

$$k = \frac{L}{X_{ss}},$$ where L is the annual litter accession (Jenny *et al.*, 1949; Olson, 1963).

The method has been used extensively in Australian litter studies for determination of both decomposition and accumulation (Attiwill, 1968; Van Loon, 1970; Rogers and Westman, 1977; Lee and Correll, 1978; Fox *et al.*, 1979, Birk, 1979b; Walker, 1981), but there are many problems associated with its use (Birk and Simpson, 1980) as discussed in Chapter 5.

Respiration

Singh and Gupta (1977) state that soil respiration represents the sum total of all soil metabolic functions in which carbon dioxide is produced, and involves microbial, faunal, and root respiration, and chemical oxidation.

Field measurements are difficult to make because of the need to estimate the contribution made by live roots to total soil and litter respiration (Woods and Raison, 1982), and because of problems in estimating moisture fluctuation. Moisture has an important effect on respiration rates (Singh and Gupta, 1977).

Richards and Charley (1977) employed a laboratory technique that measured relationships between the carbon dioxide produced from a core of litter plus soil under optimum moisture levels, and used the relationships to calculate field respiration rates from changes in soil temperatures.

Factors affecting decomposition

There are four main groups of factors affecting litter decomposition:

Type of plant material,

Environmental conditions,

Litter and soil fauna, and

Microflora.

Type of plant material:

Significant differences have been reported in the rate of decomposition of Angiospermous litter (Bocock and Gilbert, 1957; Shanks and Olson, 1961; Heath *et al.*, 1966; Edwards, 1977). Gymnospermous litter generally decomposes less rapidly than that from the Angiosperms (Kendrick, 1959; Alison and Murphy, 1963; Witkamp and Olson, 1963; Gosz *et al.*, 1973) due to hardwood litter containing higher levels of the more mobile essential mineral elements, with less lignin and generally less ether soluble fraction than coniferous litter (Heath *et al.*, 1966).

Young leaves decay more rapidly than old, and leaves decay more rapidly than twigs and branches (Lang, 1974). Softer shade leaves decompose more rapidly than sun leaves (Heath *et al.*, 1966).

In general, the rate of decomposition is highest in material with maximum ash and N content, and minimum C/N ratio (Witkamp, 1966; Richards and Charley, 1977). Gosz *et al.* (1973) suggest that levels

of P may influence rates of mineralisation and immobilisation of other important nutrients. This may be of considerable importance to eucalypt litter studies, where P has been shown to be withdrawn from leaves prior to abscission by up to 80% (Ashton, 1975; Attiwill *et al.*, 1978; O'Connell *et al.*, 1978).

Olson and Crossley (1963) and Witkamp (1966) have shown that the differences in decomposition rate between different litter species are most prominent during the initial stages of decomposition, and species influence decreases as decay progresses.

Wood (1974) found leaves of *E. delegatensis* decomposed more slowly than leaves of many European broad-leaved species and compared data from Australian studies with data for studies in a range of species in England and Holland, where more than 90% of the original leaf dry weight was lost in the initial 12 months, viz.

E. obliqua,   49%   Attiwill (1968)

E. marginata,   38%   Hatch (1955)

E. maculata,   36%   McColl (1966)

E. pauciflora,   dry sclerophyll,   34%

                   wet sclerophyll,   43%

                   alpine herbfield, 45% (Wood, 1970)

E. delegatensis, dry sclerophyll,   41%

                   wet sclerophyll,   78% (Wood, 1974)

European broad-leaved species, >90% (Heath, Arnold and Edwards, 1966; Bocock *et al.*, 1960; Bocock, 1964; Witkamp and Van der Drift, 1961).

In Wood's (1974) studies correlations were obtained between the concentration of elements in large and small mesh bags and the weight lost with time, that indicated that leaf-feeding invertebrates preferentially consumed material having relatively low concentrations of Ca, and relatively high levels of P, N, and possibly Mg.

Environmental conditions:

Soil

Loub (1962) demonstrated soil microfloral population changes during the annual cycle, with weather conditions playing a large part in the determination of population level e.g. a marked reduction during summer months except for soils associated with wet conditions. It was considered that soil organic matter content, calcium carbonate, the S-T-V value (where S = total exchangeable metal ions, milliequiv. $100g.soil^{-1}$, T = cation exchange capacity, millliequiv. $100g.soil^{-1}$, and $V = \frac{S}{T} \times 100$ represents percent saturation) and acidity, were of greater significance in determining the nature and type of decomposition that occurs than the importance of moisture and temperature (Loub, 1962). Given similar climatic conditions, Loub reported a correlation between acidity and the increasing number of anaerobic organisms concerned with nitrogen fixation and cellulose decomposition.

In Australian studies McColl (1966) observed differing rates of decomposition of *E. maculata* leaves due to differing nutrient status of the soil. Wood (1974) in studies of the decomposition of *E. delegatensis* leaves at 21 sites in S.E. Australia showed microbial decomposition to have a positive linear correlation with soil organic carbon, and a negative linear correlation with soil pH. Total weight loss, and weight loss attributed to fauna showed significant quadratic relationships with soil pH.

Charley and Richards (1974) estimated microbial populations and biomass in 3 forest soils in N.S.W. Hyphal activity was estimated in the litter layer and the 0-7.5 cm soil layer, and bacterial populations concerned with N transformations in the mineral soil. Fungal populations were high relative to bacteria (10^4 and 10^5 propagules per

gm. oven-dry soil respectively). Population densities were lowest in late winter and early spring. Actinomycetes and bacteria were least abundant in microphyll mossy forest, and fungi in layered forest. Fungi and bacteria were best developed in grassy forest, and actinomycetes in layered forest.

In all 3 systems studied by Charley and Richards (1974) fungal mycelium was the main contributor to microbial biomass, and accounted for 80-90% of the combined fresh weight of bacteria, fungal and actinomycete spores, and vegetative fungal hyphae. In the 0-7.5 cm soil layer average total biomass throughout the year was 18.5 $g.m^{-2}$ in layered forest, 8.1 $g.m^{-2}$ in grassy forest, and 6.3 $g.m^{-2}$ in microphyll mossy forest. Higher microbial biomass in layered forest was consistent with the greater productivity of that ecosystem. Soil pH of 5.5 and 4.9 in grassy forest and microphyll mossy forest were considered the cause of lower levels of microbial growth than the layered forest with pH 6.0. The layered forest had a lower organic matter content that was consistent with a greater microbial mediated decomposition process.

Climate:

Franz (1962) reported that decomposition processes in soils of the U.S.S.R. slowed down in dry and frosty periods when the numbers of organisms were low, and increased in humid, warm weather, when numbers of organisms were high. Loub (1962) described a correlation between the numbers of decomposer organisms and the progress of decomposition.

In European forests, Olson and Crossley (1963) described a pattern of exponential decay that was influenced by seasonal variations which they attributed to changes in moisture and temperature. No such seasonal variation was recorded by Richards and Charley (1977) in Australian forests.

Richards and Charley (1977) have demonstrated decisive influences of temperature upon rates of litter disappearance, with significant relationships between temperature and decomposition.

Richards and Charley (1977) in studies of the temperature response pattern of ammonification of 3 forest soils showed an initial plateau between 10 and 20°C in the temperature response of grassy-forest and layered forest soils in the New England region of N.S.W. There was then a marked response to further temperature increase up to 45°-50°C, and inhibition beyond this level. Microphyll-mossy forest soil differed significantly, with no low-level plateau, but a linear response to increasing temperature from 5 to about 50°C, when inhibition occurred. Evidence from their experiments with pure cultures supported their view that the temperature responses of nitrogen mineralisation represented the combined activities of several organisms with distinctly different temperature optima. Microorganism population densities were lowest in late winter and early spring.

In Wood's (1974) most thorough investigation of eucalypt leaf (*E. delegatensis*) decomposition, and the rate and loss of nutrients in relation to environmental factors at 21 sites in S.E. Australia, there were significant relationships between temperature and rainfall and decomposition. Total loss in weight varied from 35-97%, loss in weight due to microbial activity plus leaching from 29-60%, and due to fauna from 4-59%. Microbial decomposition plus leaching resulted in positive linear correlations, decomposition increasing with increasing rainfall, but no relationship with temperature. In contrast, faunal decomposition, and total decomposition yielded significant quadratic relationships with mean and maximum temperature.

In America, Jenny *et al.* (1949) reported the combined effects of temperature and moisture were more prominent than the effect of

temperature alone. Witkamp (1963) found temperature and moisture to have a decisive influence upon microbial populations and litter breakdown, and Witkamp (1966) reported temperature to be the most important factor influencing the respiration rate of decomposing leaves.

Fauna:

The main contribution of animals is in the mechanical breakdown of litter, assisting the litter microorganisms to carry out chemical decomposition (Kevan, 1962; Van der Drift, 1958; Witkamp, 1971).

The relative importance of macroarthropod groups in litter breakdown in Northern Hemisphere deciduous forests is illustrated in Table 2.9 below, with data taken from Edwards (1974).

Table 2.9. Approximate consumption of litter by macroarthropods $(g.m^{-2})$

Average deciduous litterfall,	3000
Isopoda	73
Symphyla	60
Diploda	146
Isoptera	570
Diptera and Coleoptra	180
Total	1029

Hence from Edward's (1974) data it may be seen that approximately one third of total litterfall is consumed in these forests, and other groups e.g. earthworms, bacteria, and fungi must account for the rest of the turnover.

Van der Drift (1958) demonstrated that lumbricidae were most important in litter decomposition, with an effect three times as great as the smaller invertebrates e.g. Enchytracids, Collembola, and

dipterous larvae. Satchell (1967) reported that earthworms were able to remove more than total leaf fall in Northern hemisphere forests. Termites may take the place of earthworms in the tropics, Wood (1976), and Lee and Butler (1971) reported that termites consumed at least 40 percent of total wood fall in woodland in S.A.

Ashton (1975) demonstrated experimentally that earthworms and amphipods were responsible for rapid disintegration and removal of leaves from litter into the soil. Ashton recorded a mean earthworm population of 167 m^{-2}, amphipods (*Talitrus* spp.) of about 400 m^{-2}, and a wide variety of other soil animals in the litter of *E. regnans* forest in Victoria. Earthworms and amphipods feed and move about in the litter layers only when conditions in the litter layer and under-laying soil are moist, and temperatures moderate. Lee and Correll (1978), in their dry sclerophyll eucalypt litter studies in S.A. found populations to be low, and activity restricted by drought and high temperatures for 6 months of the year. The macrofauna were not so restricted by the lower temperature regimes and higher rainfall of *E. maculata* forests studied by McColl (1966), and *E. regnans* by Ashton (1975).

Fox *et al.* (1979) showed that there was a time lag of 3 to 4 years after fire in the establishment of a suitable microclimate for a decomposer fauna that was capable of keeping pace with the production of leaf litter in a *E. pilularis - Angophora costata* open forest community in N.S.W. The absolute, and relative importance of leaves diminished as more efficient leaf decomposition took place. Ashton (1975) reported similar shifts in leaf contribution both from litter-fall to litter accumulation, and within accumulating litter as a function of forest age in *E. regnans*.

In studies in microphyll-mossy forest (MMF), layered forest (LF), and grassy forest (GF) in N.S.W., Richards and Charley (1977)

extracted the fauna of soil and litter samples at 2-monthly intervals and sorted them into 10 major groups of invertebrates — mites, spiders and pseudoscorpions, adult beetles, adult flies, insect larvae, springtails, centipedes, millipedes, crustaceans, and earthworms. Lower (3.75-7.5 cm) soil samples contained a lesser variety of fauna than upper soil samples in all three ecosystems. LF soil contained 25% fewer major groups than MMF or GF soil. Mites were the most common animals in all three forests, followed by insect larvae and springtails. LF also contained far fewer large earthworms. Litter fauna were of comparable variety in the LF and MMF, whereas in the GF there were 40% fewer major groups isolated, and this was related to the less well developed litter system of the GF. Mites were again the most common group, followed in order by insect larvae and springtails. The GF litter differed from MMF and LF in that it lacked centipedes and millipedes.

An indication of the importance of litter and soil fauna to the breakdown of leaf material in particular may be seen in the work of Nef (1957) who showed that oribatid mites may increase the surface area of a pine needle up to 10,000 times.

Mycroflora:

The role of fungi in ecosystems has been discussed by Harley (1971), and the ecology of fungi on plant remains above the soil reviewed by Hudson (1968). Last and Deighton (1965) have reviewed the occurrence of fungi on leaf surfaces, and Preece and Dickinson (1971) the ecology of leaf surface microorganisms. The general biology of plant litter decomposition has been extensively covered by Dickinson and Pugh (1974).

Hudson (1968) discussed the succession of fungi on deciduous tree leaves and considered that there was a uniform pattern of colon-

isation. In the phylloplane leaves are initially colonised by a variety of host specific or restricted parasites followed by primary saprophytes that may be common to a variety of leaf species. These groups are Fungi Imperfecti or Ascomycetes, and after leaf shed other fungi from these groups appear in various sequences. In the decomposing litter *Penicillia, Mucorales,* and *Trichoderma* spp. occur together with Basidiomycetes.

Ruscoe (1971a, 1971b) studied the mycoflora of the phylloplane and internal tissues of *Nothofagus truncata* leaves in New Zealand, and of the forest soil. Mycoflora of the surface humus and mineral soil were similar and there was a general decrease in the amount of mycelium with increasing profile depth. Species with a 5% and greater frequency of occurrence in the humus and mineral soil horizons were *Penicillium spinulosum, Trichoderma viride, Aspergillus versicolor, Absidia spinosa, Acremonium sp., Tubercularia sp.* and *Mucor hiemalis.* Fifteen species of macrofungi were recorded, all Basidiomycetes except for the discomycete, *Helvella sp.*. There was an autumn flush of sporophores that continued through winter. During periods of early growth, maturity, senescence, and leaf death, Ruscoe (1971a) observed a peak of fungal activity in summer. Young leaves were colonised by internal parasites and discrete surface colonies soon after unfolding, with a succession of Fungi Imperfecti and ascomycetes. The components of succession were similar to Hudson's (1968) schema but appeared at different stages of leaf development (Ruscoe, 1971a).

Eicker (1973) studied fungi from the soil horizon and litter layer of *E. maculata* stands in Zululand. A total of 87 fungal species were isolated from leaf litter and soil of which 34 species (39%) were common to both. There were differences in the composition of the

fungal populations but a close agreement was suggested between myco-flora supported by the organic (litter) and mineralised (soil) horizons of the soil profile.

Macauley and Thrower (1966) studied the succession of fungi in leaf litter of *E. regnans*, and Macauley (1979) of *E. pauciflora*. The pattern of succession was similar, with initial colonisers species of Coelomycetes and Moniliales. In *E. pauciflora* increasing decomposition of leaves matched decreasing frequency of the Coelomycetes and increasing frequency of *Penicillium spp.* (that were excluded from the initial Moniliales) and Zygomycetes. The frequency of occurrence of the Moniliales was not related to that of the Coelomycetes in the *E. regnans* studies. There were individual species of fungi common to both eucalypt species as well as a similarity of pattern of succession of the major groups. The successional pattern was considered by Macauley (1979) to be in agreement with the general schema of Hudson (1968) as previously discussed.

CHAPTER 3

SELECTION AND DESCRIPTION OF STUDY SITES

3.1. GENERAL DESCRIPTION OF THE SOUTHERN REGROWTH FORESTS

The regrowth forests of Southern Tasmania are bordered by the Western slopes of the Picton River, Catamaran to the South, the Huon River to the North, and include Bruny Island and the Forestier and Tasman Peninsulas to the East (Fig. 3.1.1). These forests and their environment have been described by Podger *et al.* (1980). The terrain is hilly to mountainous and has a temperate-rainy climate (Köppen cfb) with appreciable summer and winter rainfall (Dick 1975). Detailed weather information is given in section 3.2.2 for Hastings Chalet, a meteorological station approximately 4 km to the East of the area selected for these investigations. Mean monthly maximum temperature at Hastings Chalet is approximately 21°C for January and approximately 11°C for July, with July mean minimum of ca. 3°C, and mean annual rainfall of ca. 1400 mm.

The predominant vegetation is tall-open forests (Specht 1970) of *E. obliqua* L'Herit. and *E. regnans* F. Muell. below elevations of 400m, and of *E. delegatensis* R.T. Baker and closed *Nothofagus cunninghamii* (Hook.) Oerst. forest above 400m, with their floristic composition depending upon the time since burning and their ecological position between shrub and rainforest communities. The frequency of fire has strongly influenced the mosaic of vegetation types in the region, and the eucalypt forests are believed to be fire disclimax to a reduced area of regional climax *Nothofagus – Atherosperma moschatum* Labill. rainforest (Jackson 1968). Wet shrub, heath, and hummock sedgeland communities occur on sites that are minerally impoverished or poorly drained.

FIG. 3.1.1.   GEOGRAPHICAL LOCATION OF THE SOUTHERN FORESTS
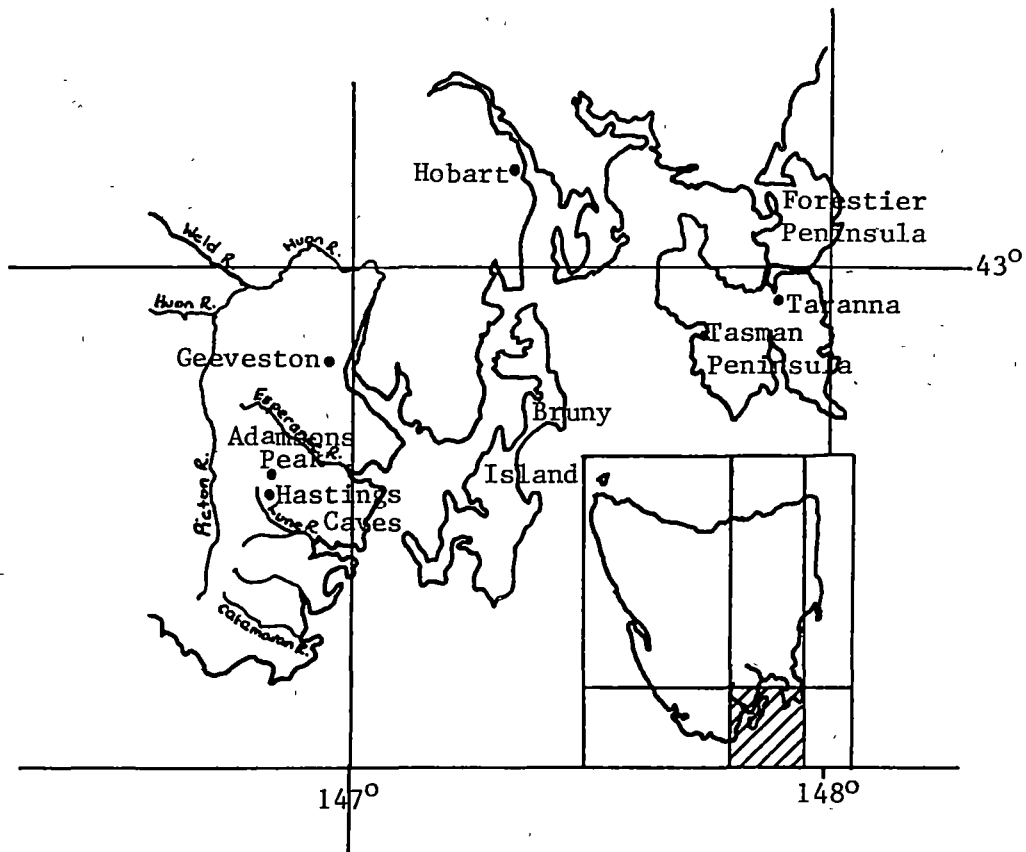
The original virgin forests of *E. obliqua* and *E. regnans* were over 80m tall and 400 years of age, but since settlement much of these forests have been cut-over, or clear cut and burnt for regeneration, resulting in large areas of even-aged stands of the same species. Hence the region is now characterised by discrete areas of virgin eucalypt forests, even-aged stands of eucalypt regrowth, multi-aged eucalypt stands, management areas of young eucalypt regeneration, tall and low scrub, heath, and small areas of virgin rainforest.

3.1.1. Selection of study sites

Four plot sites were selected along a 1.1 km transect (Fig. 3.1.2) based on a tramway running south-east from Hastings Caves Rd.[1] to a disused silica quarry on the Hogs Back[2], Lune River Plain. Site 1 was situated about 200m from Hastings Caves Road and was typical of economically productive, tall-open forest (Specht 1970) of *E. obliqua* regrowth regenerated from fire in 1915. Site 2 was a closed rainforest of predominantly *Nothofagus cunninghamii* with *Atherosperma moschatum*, c.300 years old with charcoal evidence of a light ground fire in 1920 that resulted in a sparse population of *E. obliqua* regrowth. Site 3 was representative of mixed-aged, tall-open *E. obliqua* regrowth forest and tall scrub, dating to a regeneration fire of 1915 and a 1940 low intensity wild fire from the adjacent Lune River Plain. Site 4 was established in low scrub with an overstorey of *E. nitida* Hook.f. and *E. obliqua* of the 1940 fire, and was situated between the tall-open eucalypt forest and the heath and hummmock sedgeland communities of the Lune River Plain. Vegetational and

1. Grid reference 878957) HUON SHEET, No.8211, 1:100,000
2. Grid reference 875945) Topographic Survey of Tasmanian
                           Lands Department

FIG. 3.1.2.   ILLUSTRATION OF VEGETATION TYPE CHANGES ALONG STUDY TRANSECT

| Tall open forest | Closed rain forest | Tall open forest | Tall open forest and tall scrub | Low scrub | Heath | Hummock sedgeland | Low scrub and heath |
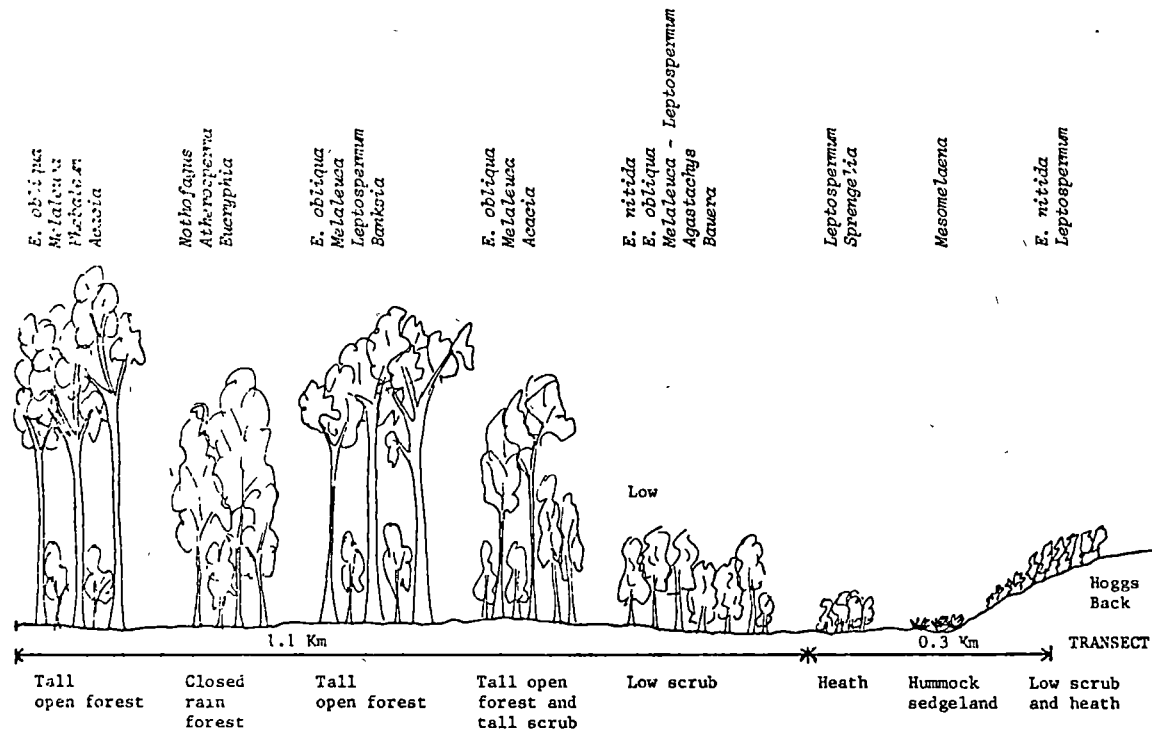
environmental characteristics of the 4 selected sites were expected to assist the testing of hypotheses regarding their litter processes.

3.1.2 Plot size and delineation

A 0.10 ha., 40 x 25m plot was established within a homogenous area at each site in November, 1978, avoiding inclusion of over-mature old growth eucalypt remnants of regeneration fires. Permanent boundary tracks were cut and the plot areas of Sites 1, 2 and 3 were divided into 40 sub-plots of 5 x 5m (Fig. 3.1.3), each being monumented in the SW corner with a permanent, numbered peg. Sub-division could not be carried out at Site 4 without destroying the nature and density of the ground cover, particularly of *Bauera ruboides* Andr.

3.1.3 Topography

Slope was measured by a Haga inclinometer as the mean percent slope of the whole plot, and the direction of slope was measured by prismatic compass to determine plot aspect.

Altitude was interpolated from the 20m contour intervals of the Tasmanian Lands Department 1:100,000 Topographic Survey Sheet No.8211 for Huon.

Measurements are listed in Table 3.1.1.

3.1.4 Stand age

The date of regeneration and wild-fires associated with each plot were obtained from the Lune and Hogs Back Management assessment data of the Tasmanian Forestry Commission, and confirmed by ring counts of a suitable understorey tree species e.g. *Pomaderris apetala* Labill. which produces distinctive annual rings, and is established concurrently with eucalypt in the first season following fire. The age and year of regeneration of each site are listed in Table 3.1.1.

FIG. 3.1.3.   PLOT LAYOUT

0.20 ha. Site Index
measurement plot

40m

5m

36 35 26 25 16 15 6 5

5m   25.4m   7 4

25m   8 3

                               9 2

40 31 30 21 20   10 1

Contour

0.10 ha. Study plot

Slope % and aspect of plot
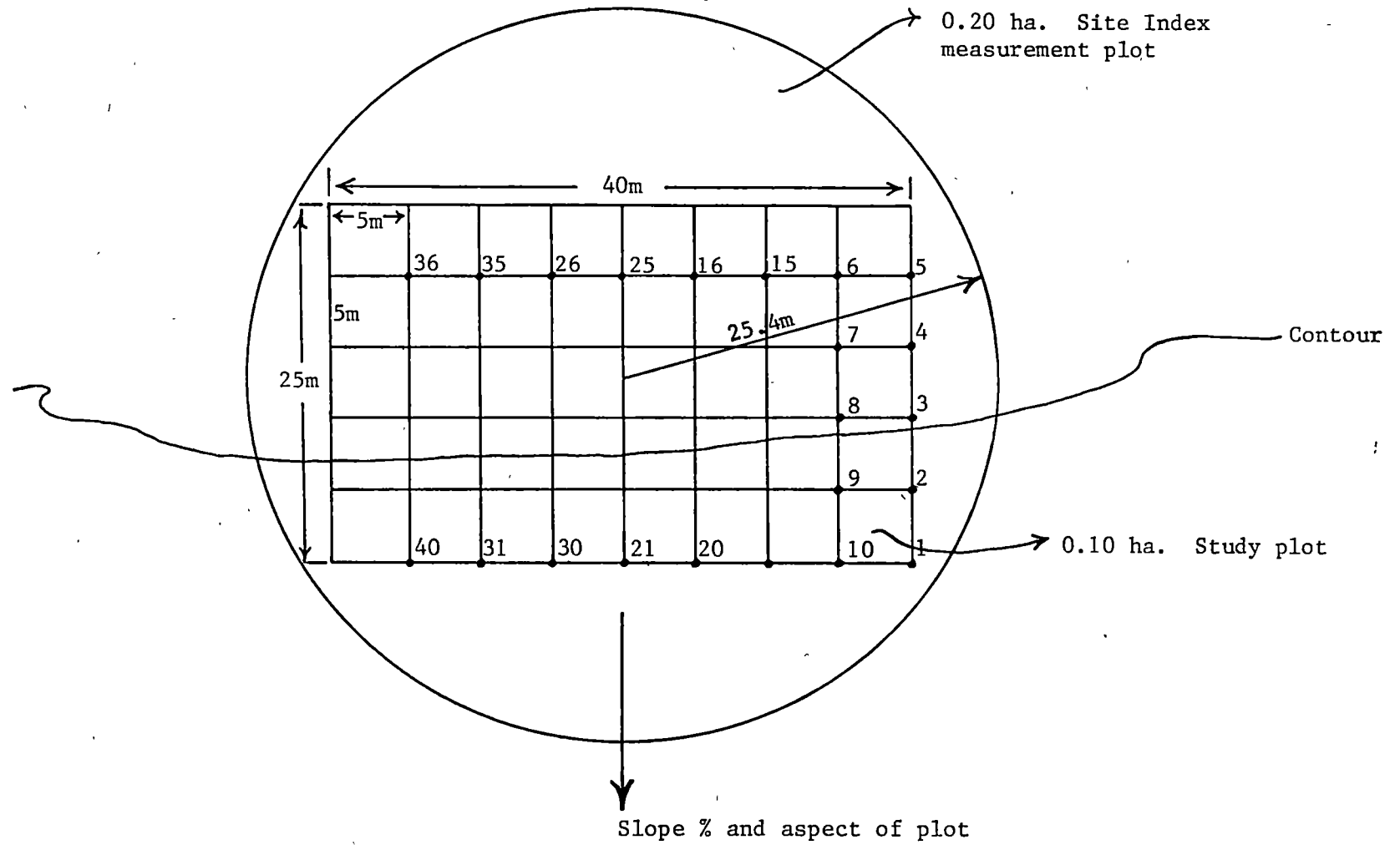
Table 3.1.1.   Stand characteristics, November, 1978.

Characteristic	Site 1	Site 2	Site 3	Site 4
Age (years	63	400/58[*]	63/38[*]	38
Year of regeneration	1915	Partial, 1920	1915/1940	1940
Site Index	30		27	18
Overstorey	*E. obliqua*	*Nothofagus* *Acacia* *Phyllocladus* *E. obliqua*	*E. obliqua*	*E. nitida* *E. obliqua*
No. live stems/ha				
- overstorey	950	60 (*E. obliqua*)	650	510
- understorey	5240	8370	8400	
Live basal area m^2/ha				
- overstorey	57.72	3.22 (*E. obliqua*)	32.38	12.94
- understorey	39.19	79.60	37.39	
M.D.H. (m) overstorey	33	23		
Ht. range of understorey	*Acacia* 18 *Tropocarpa* 2	*Melaleuca* 14 *Drimys* 3	*Leptospermum* 16 *Tropocarpa* 2	*Leptospermum* 6 *Bauera* 2
Slope %	8	2	4	2
Aspect, °T	132	180	180	180
Altitude (m.a.s.l.)	80	80	60	60

[*] Two ages from different fires.

56

3.1.5 Site index

The site index of a eucalypt stand is the mean dominant height of the stand in metres at age 50 years, and is derived by interpolating the 50 year intercept for data of current stand age and height from growth curves developed by the Tasmanian Forestry Commission (Lawrence 1978).

A circular plot of 25.4m radius (0.20 ha.) was established about the centre of each 0.10 ha. rectangular plot, and a Haga inclinometer and surveyors tape used to measure the height of the tallest two eucalypts within each quadrant of the circle (Fig. 3.1.3). Mean dominant height was calculated and site index interpolated. Results are listed per plot in Table 3.1.1.

3.1.6 Eucalypt and understorey inventory

Diameter breast height over bark (DBHob) was measured of every stem greater than 1.0 cm, of all species on Sites 1, 2, and 3. Dense ground cover (of *Bauera ruboides* in particular) prevented inventory at Site 4 as measurement would have trampled the vegetation of the site. It was intended that Site 4 inventory be measured immediately after completion of field studies, but was prevented by destruction of the site by wild-fire in 1981, after which the only measureable stems remaining were those of *E. obliqua*, *E. nitida*, and *Banksia marginata* Cav.

Diameter measurements were used to determine the basal area (B.A.), $m^2.ha.^{-1}$, per site of both overstorey and understorey species, and their relevant numbers of stems. Table 3.1.2 lists the total, live and dead B.A., and total, live, and dead numbers of stems per site of eucalypt and understorey species on a per hectare basis to two significant figures. Appendix A, Tables 1, 2, and 3 list the same data on a per species basis for Sites 1, 2, and 3 respectively.

Table 3.1.2.   Basal areas (B.A.), m^2ha^{-1}, and stem numbers
per ha, Sites 1, 2, and 3.

(All data expressed per ha to two significant
figures).

	Site 1	Site 2	Site 3
Total live B.A.	96.91	82.83	69.78
Total dead B.A.	13.58	5.74	6.68
Total B.A.	110.49	88.57	76.46
Total live stems	6190	8430	9050
Total dead stems	2750	1140	4390
Total stems	8940	9570	13440
Total live *eucalypt* B.A.	57.72	3.22	32.38
Total dead *eucalypt* B.A.	6.25	0.017	0.84
Total *eucalypt* B.A.	64.10	3.24	33.22
Total live understorey B.A.	39.19	79.60	37.39
Total dead understorey B.A.	7.34	5.73	5.85
Total understorey B.A.	46.52	85.33	43.24
Total live *eucalypt* stems	950	60	650
Total dead *eucalypt* stems	530	10	210
Total *eucalypt* stems	1470	70	860
Total live understorey stems	5240	8370	8400
Total dead understorey stems	2220	1130	4180
Total understorey stems	7460	9500	12580

Total live B.A. and total live numbers of stems of overstorey and understorey species are listed under stand characteristics in Table 3.1.1.

The mean height and DBHob of the 5 selected tallest trees on Sites 1, 3, and 4, and the 3 tallest trees on Site 2 are listed in Appendix A, Table 4. The average height of the understorey species per site are shown in Appendix A, Table 5 and illustrated in Fig. 3.1.4.

3.1.7 Vegetation description

Vegetation was surveyed at Sites 1, 2, and 3 and listed at Site 4 because of difficulties involved in non-destructive sampling.

All stems greater than 1.0 cm DBHob of all species were measured during eucalypt and understorey inventory at Sites 1, 2, and 3 for all 40 Sub-plots of each 0.10 ha. area. The presence of low understorey such as *Dicksonia antarctica* Labill. and *Ghania grandis* (Labill., ut *Scleria* sp., 1800) S.T. Blake, and of ground cover species and infrequent occurrences of epiphytic ferns and lianas were recorded per sub-plot and are listed in Appendix A, Table 6. A percent frequency value is listed per species calculated from the number of sub-plots upon which the species occurred and is illustrated in Fig. 3.1.5. Reference texts for identification were Curtis (1963, 1967), Curtis and Morris (1975), Galbraith (1977), Wakefield (1975), and Jones and Clemensha (1981). At Site 4 species are simply listed as present.

3.1.8 Stand health

A lethal dieback of *E. obliqua* and *E. regnans* was first observed in Tasmania's southern regrowth forests in 1964 (Bowling and McLeod, 1968) and has since become extensive and severe. Five euc-

HEIGHT (m)

FIG. 3.1.4.

MEAN HEIGHT OF UNDERSTOREY

A. melanoxylon
M. squarrosa,
P. squameri
E. lucida
A. moschatum
A. biglandulosum
P. bicolor
N. cunninghamii
C. nitida
A. glandulosus
P. aspleniifolius
D. lanceolata
T. disticha
C. glauca
O. argophylla
O. diversifolia
P. apetala
C. quadrifida
Leptospermum spp.
A. verticillata
B. marginata
B. rubioides
O. ellipticum
A. odorata
A. riccana
A. mucronata

SITE 4.
SITE 3.
SITE 2.
SITE 1.

09

% FRFQUFNCY

FIG. 3.1.5.

PERCENT FREQUENCY OF PRESENCE OF INDIVIDUAL SPECIES PER SITE

Site 1.

Site 2.

Site 3.

T. disticha
P. corinthoides
M. glauca (P)
S. incarcata (P)
F. straminea
A. moschatum
C. nitida (P)
B. marginata (P)
O. diversifolia
A. odorata (P)
P. drupacea
N. cunninghamii
H. flabellatum
D. antarctica
G. billardieri
B. nudum
B. wattsii
H. incisa
H. rugosula
P. esculentum (P)
S. tener
T. billardieri
L. deuferodensum (P)
G. dicarpa (P)
P. aspleniifolius
D. cyanocarpa (P)
G. grandis (P)
C. aristata
D. lanceolata
P. bicolor
B. longiflora
A. peduncularis
P. squameum (P)
P. apetala
O. ellipticum (P)
A. verticillata
A. melanoxylon
A. mucronata (P)
A. riceana (P)
A. biglandulosum
B. rubioides (P)
A. glandulosus
D. binata (P)
E. lucida
G. teucroides (P)
L. scoparium (P)
L. nitidum (P)
N. squarrosa (P)
M. squamea (P)
E. obliqua (P)
E. nitida (P)
P. gunnii
C. quadrifida
O. argophylla
C. glauca

20 40 60 80 100
20 40 60 80 100
20 40 60 80 100

I9

alypt dieback problems have been recorded in Tasmania (Felton, 1972), and their disease syndromes have been compared (Podger *et al.*, 1980). The disease is currently widespread in the southern forests and it is difficult to find areas of healthy forest except south of the Catamaran River, on Bruny Island, and on Tasman Peninsula.

Symptoms of regrowth dieback are:

(i)   appearance of epicormic shoots amongst the

main branches,

(ii)   foliage death and twig dieback in the primary

crown,

(iii) branch dieback,

(iv)   death of the epicormic component of the crown.

Dead leaves are shed within 12-18 months and fine twigs within 3 years hence the incidence of severe regrowth dieback may contribute to measured litter accession and accumulation with a concommitant effect upon calculated values for decay constants. To ensure that such contributions were not a part of the litter systems under study, all sites were assessed for dieback in November, 1978. The method of assessment (Anon., 1978) involved determination of the proportion of primary branches in crowns of dominant and codominant eucalypts that have died back from the branch terminal. Individual trees were inspected with field binoculars and counts made of the proportion of major branches affected. The mean value for all dominants of both classes was taken as the overall dieback rating of the stand. Suppressed and subdominant trees were excluded from assessment because of the difficulties associated with symptoms of suppression due to competition within a stand. Healthy stands were considered those with a dieback rating less than 20%, and severely affected stands those with an average value of 40% or more.

Mean dieback ratings of the stands involved at the 4 study sites were as follows:

Site 1, 33%

Site 2, 10% (3 eucalypts)

Site 3, 10%

Site 4, less than 10%

The severity of the disease had not increased at any of the sites by completion of field studies in 1982.

3.1.9 Soil descriptions

Soils of the southern forest region were classified by Nicolls and Dimmock (1965) according to the Great Soil Group Classification of Stephens (1962) mainly as yellow podzolics and grey-brown podzolics, with small areas of krasnozems and ground water podsols. All were acid, moderately to strongly leached, and relatively high in organic matter.

A series of 10 cm diameter holes (minimum of 6) were augered across each 0.10 ha. study site to a minimum depth of 1.5m, or to parent material, and the profile described after the method of Northcote (1971). Individual site classifications were:

Site 1, Dy 3.11

Site 2, Dy 3.11

Site 3, Dy 3.21

Site 4, Dy 2.21

This classification is in agreement with the duplex (Northcote, 1960) yellow podzolics of Nicolls and Dimmock (1965).

Samples taken from various depths, of changes in individual soil profiles, were mixed with distilled water in 1:5 ratio and electrometric determinations made of pH. Results are listed in Table 3.1.3. The soils of all sites were acidic, with values to 1 metre

depth ranging from 4.9 in the rainforest (Site 2) to 3.6 in the tall scrub (Site 4).

TABLE 3.1.3.   pH values at various profile depths per site.

Site	Depth (cm)	Material	pH	Munsell[1] colour
1	2-12	Sandy clay loam	4.3	10 yr 6/2
	12-90	Clay with mottle	4.3	10 yr 6/1
		ca.50%		10 yr 5/4
	90-150	Gley	6.0	5G 5/1
2	2-20	Fine sandy clay loam	4.7	10 yr 6/2
		Clay with 50% mottle	4.9	10 yr 6/1, 10 yr 5/4
		Gley	5.2	5G 5/1
3	2-25	Sandy loam	4.0	7.5 yr 3/2
		Clay, 50% + mottle	4.0	7.5 yr 5/4
4	2-10	Organic sandy loam	3.6	5 yr 3/2
		Sandy clay	4.3	10 yr 6/8

[1] Munsell Color Co. (1954)

3.2   ENVIRONMENT

3.2.1 General description

The study area is located at approximately 43° 24'S, 146° 20'E at an altitude of 80m above sea level, in the Lune River Valley, and is bordered by Adamsons Peak (1226m) to the North, Mt. Alexandra (920m) to the West, and Moonlight Ridge (1034m) to the South.

Meteorological records have been maintained since 1947 at Hastings Chalet, approximately 4 km to the East of the study area. Table 3.2.1 lists the mean monthly maximum and minimum temperature, rainfall and number of rain-days for Hastings Chalet during the period

Table 3.2.1.　　　　　　　　　　　Hastings Chalet:　meteorological data.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Mean monthly maximum temperature, °C	20.6	20.7	19.1	16.5	13.5	11.9	11.2	12.2	13.6	15.9	17.2	18.8
Mean monthly minimum temperature, °C	9.0	9.1	8.1	7.0	4.9	3.2	2.7	2.8	3.8	5.6	6.9	8.3
Mean monthly rain-fall (mm)	74.0	69.6	77.4	107.6	129.8	117.2	161.3	151.2	130.4	118.5	117.5	125.1
Mean monthly number of raindays*	13	12	14	19	20	18	22	21	20	20	18	17

1957-1979 (inclusive). Mean annual rainfall during the period was 1380 mm.

Predominant winds are westerlies, and from a comparison of wind-run data for neighbouring meteorological stations, the area is relatively sheltered.

3.2.2 Meteorological data, Hastings Chalet

Daily meteorological data for the Hastings Chalet were used to calculate the maximum and minimum, and the mean maximum and minimum temperature, total rainfall, and total evaporation, and the mean wind-run (km 24 hr^{-1}) per each 6 weekly litter sampling interval from the 6 weeks prior to 31.1.1979 through to 21.4.1982. All data are summarised in Appendix A, Table 7 together with the frequency percentage of days per sampling interval when maximum temperature equalled or exceeded 10, 15, 20, and 25°C. This maximum temperature regime is illustrated in Fig. 3.2.1.

Maximum and minimum, and mean maximum and mean minimum temperature per accession interval are illustrated in Fig. 3.2.2, and total rainfall and evaporation, and the mean wind-run per interval in Fig. 3.2.3. Records of evaporation and wind-run were commenced in the sampling interval ending on 30.7.1980.

3.2.3 Litter temperatures

'Grant' temperature recorders were established at Sites 1 and 4. Sites 1 and 3 were of comparable canopy cover and stand density, and hence litter temperatures measured at Site 1 could be expected to correspond to those of Site 3. At Site 4 the litter pack was shallow and the vegetative cover open. It was expected that litter temperatures at Site 4 would closely resemble the air temperatures measured at Hastings Chalet, but that litter temperatures of the eucalypt

FIG. 3.2.1.　　　ILLUSTRATION OF MAXIMUM TEMPERATURE REGIME
DURING THE STUDY PERIOD, HASTINGS CHALET

LEGEND

Percentage of days per
period. Max.T $\geq 25^{\circ}$C

Percentage of days per
period. Max.T $\geq 20^{\circ}$C

Percentage of days per
period. Max.T $\geq 15^{\circ}$C

Percentage of days per
period. Max.T $\geq 10^{\circ}$C

Percentage of days per
period. Max.T $< 10^{\circ}$C
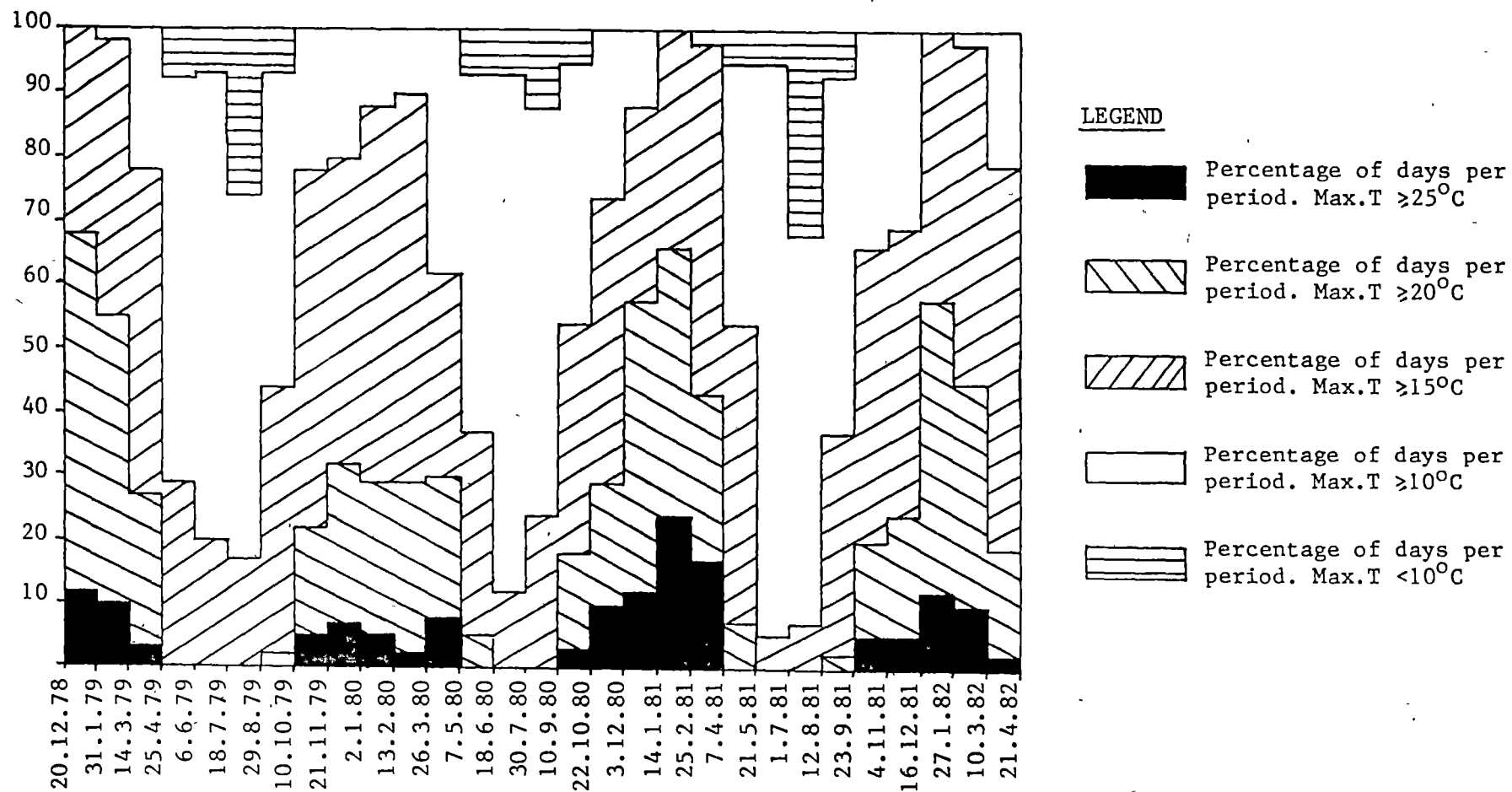
FIG. 3.2.2. MAXIMUM[1] AND MINIMUM[2], AND MEAN MAXIMUM[3] AND
MEAN MINIMUM[4] TEMPERATURE PER ACCESSION PERIOD
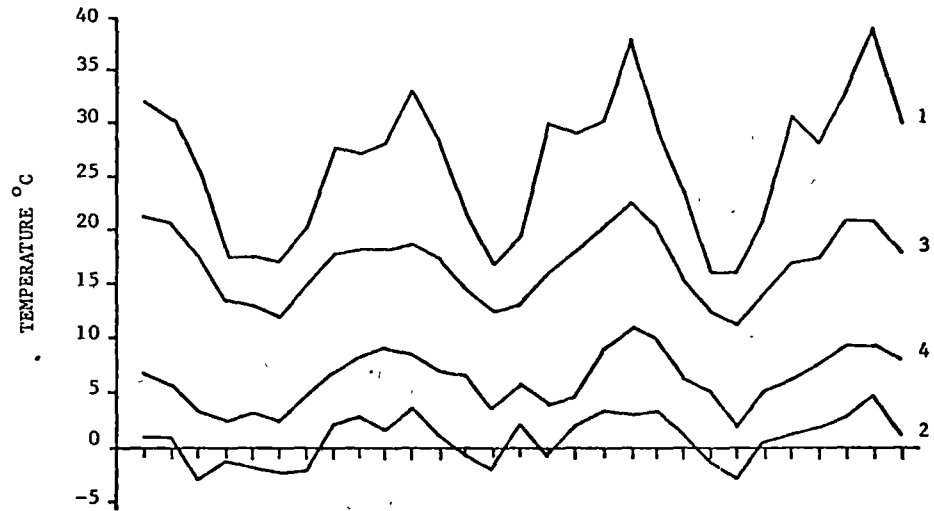
FIG. 3.2.3. TOTAL RAINFALL (mm), TOTAL EXAPORATION (mm) AND
MEAN WIND-RUN (Km.24hr)[-1] PER ACCESSION PERIOD

LEGEND

●————○ Total rainfall (mm)
▲————▲ Total evaporation (mm)
■————■ Mean wind-run (Km/24hr)
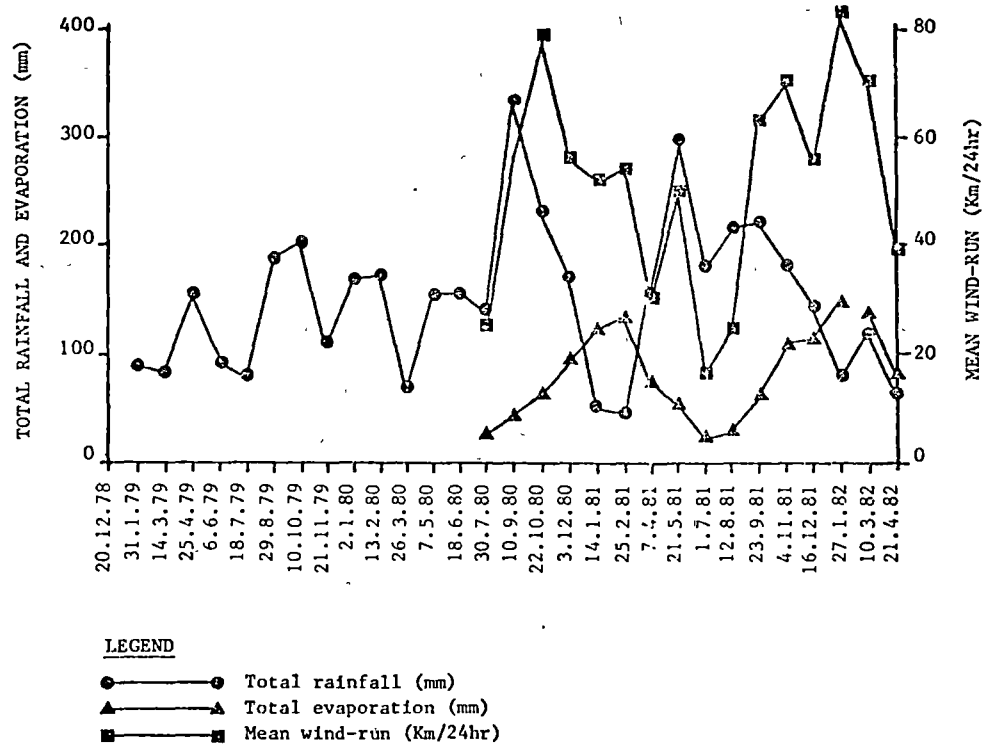
FIC. 3.2.4.   DAILY MAXIMUM TEMPERATURE OF LITTER ON SITE, AND OF THE
AIR AT HASTINGS CHALET.
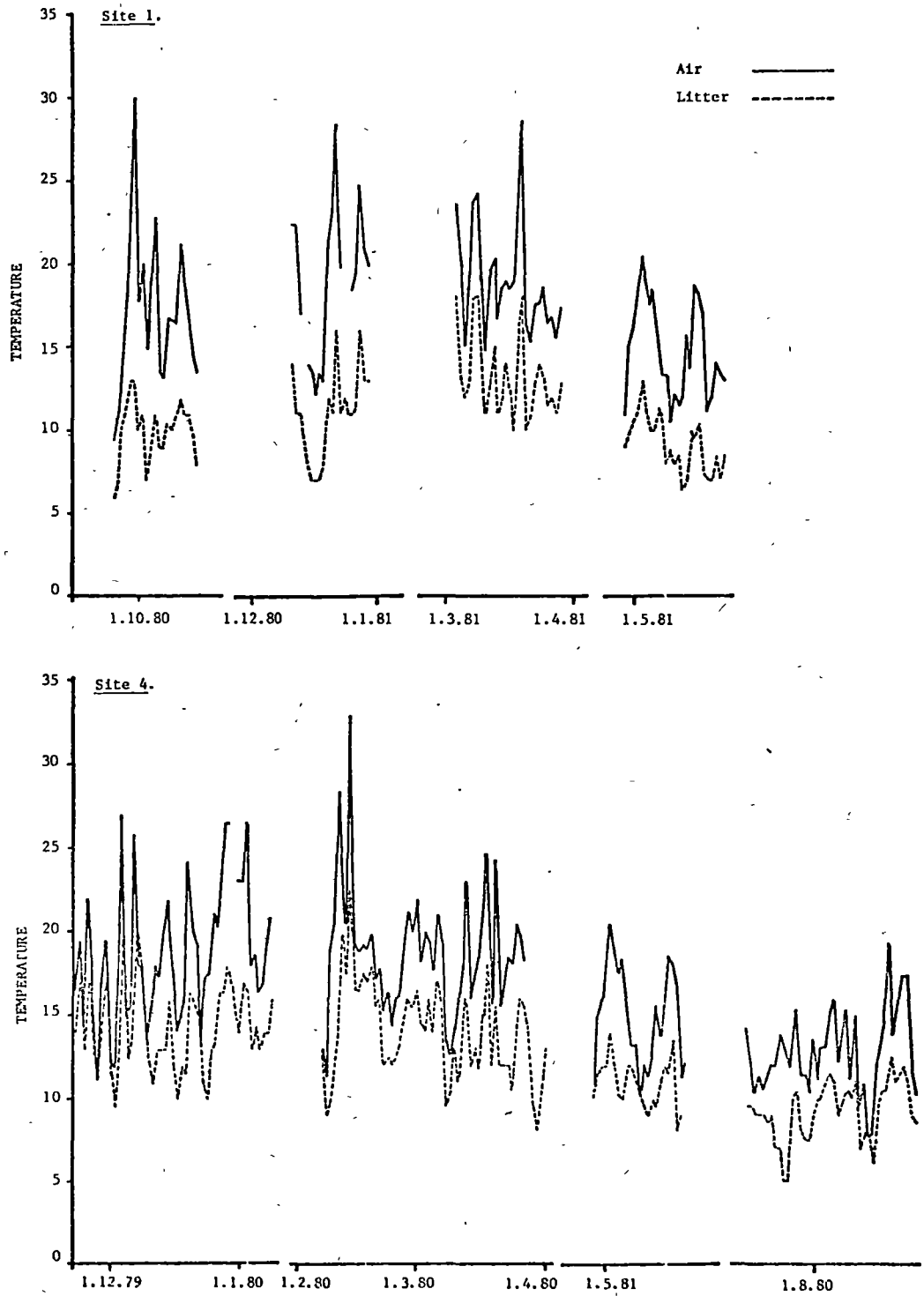
regrowth forest would be buffered with some lag in litter temperature response.

Fig. 3.2.4. illustrates the daily maximum litter temperature at each of the 2 sites and the corresponding daily maximum air temperature at Hastings Chalet. A marked correspondence was apparent between air and litter temperature at both sites although Site 1 fluctuated to a lesser degree.

Linear regression analyses of the 2 data sets were:

Site 1:

Periods of litter temperature recording:

$$25.9.80 - 15.10.80$$

$$11.12.80 - 30.12.80$$

$$3.3.81 - 3.12.81$$

$$28.4.81 - 22.5.81$$

litter temperature, $\bar{Y} = 10.76°C$, S.E.M. $= \pm0.287°C$

air temperature, $\bar{X} = 16.52°C$, S.E.M. $= \pm0.548°C$

and $Y = 5.7139 + 0.3055X$, $r = 0.583$, $n = 82$

The significance of the relationship was tested by the method of Neter and Wasserman (1974) using the equation

$$t_{n-2} = \frac{r_{12}\sqrt{n-2}}{1-r^2_{12}}$$

i.e. $t_{80} = 6.418$ which from Table III of Fisher and Yates (1963) indicated that $P<0.005$ for the correlation.

Site 4:

Periods of litter temperature recording:

$$21.11.79 - 9.1.80$$

$$7.2.80 - 1.4.80$$

$$28.4.80 - 18.5.81$$

$$16.7.80 - 25.8.80$$

litter temperature, $\bar{Y}$ = 13.71°C, S.E.M. = 0.256°C

air temperature, $\bar{X}$ = 17.93°C, S.E.M. = 0.370°C

$$Y = 4.3267 + 0.5236X$$

$$r = 0.757, \; n = 119$$

and $\quad t_{117}$ = 10.817 (P<0.005)

Results of the individual regressions are illustrated in Fig. 3.2.5.

Litter temperature responded immediately to changes in air temperature at both sites without a detectable lag, although Site 1 (closed) was buffered relative to Site 4 (open). The magnitude of temperature change was less at Site 3 relative to Site 4, e.g. air temperature of 16.5°C resulted in litter temperatures of 10.8°C and 13.0°C for Sites 3 and 4 respectively.

3.3 DISCUSSION

The Hastings area is representative of large areas of Tasmania's Southern Forests, and the four study sites selected were representative of the range of vegetation communities encountered. Deliberate selection of sites ranging from commercially productive tall-open eucalypt forests, closed rainforest, and commercially non-productive low scrub on the border of the Lune River Plain was made to enable testing of hypotheses regarding litter processes. The different species, and their expected differing accession, accumulation and decomposition rates within their different environments were intended to provide a comparison.

Regrowth dieback is currently widespread within these forests, and although one study site was assessed at 33% dieback as an overall stand health rating, this level was not considered high enough to exclude the site from the study, and the fact that the assessed health rating did not alter during the 3 year study period indicated that the

FIG. 3.2.5. RELATIONSHIPS OF DAILY MAXIMUM LITTER TEMPERATURES
AT SITES 1 AND 4 AND DAILY MAXIMUM AIR
TEMPERATURES AT HASTINGS CHALET.
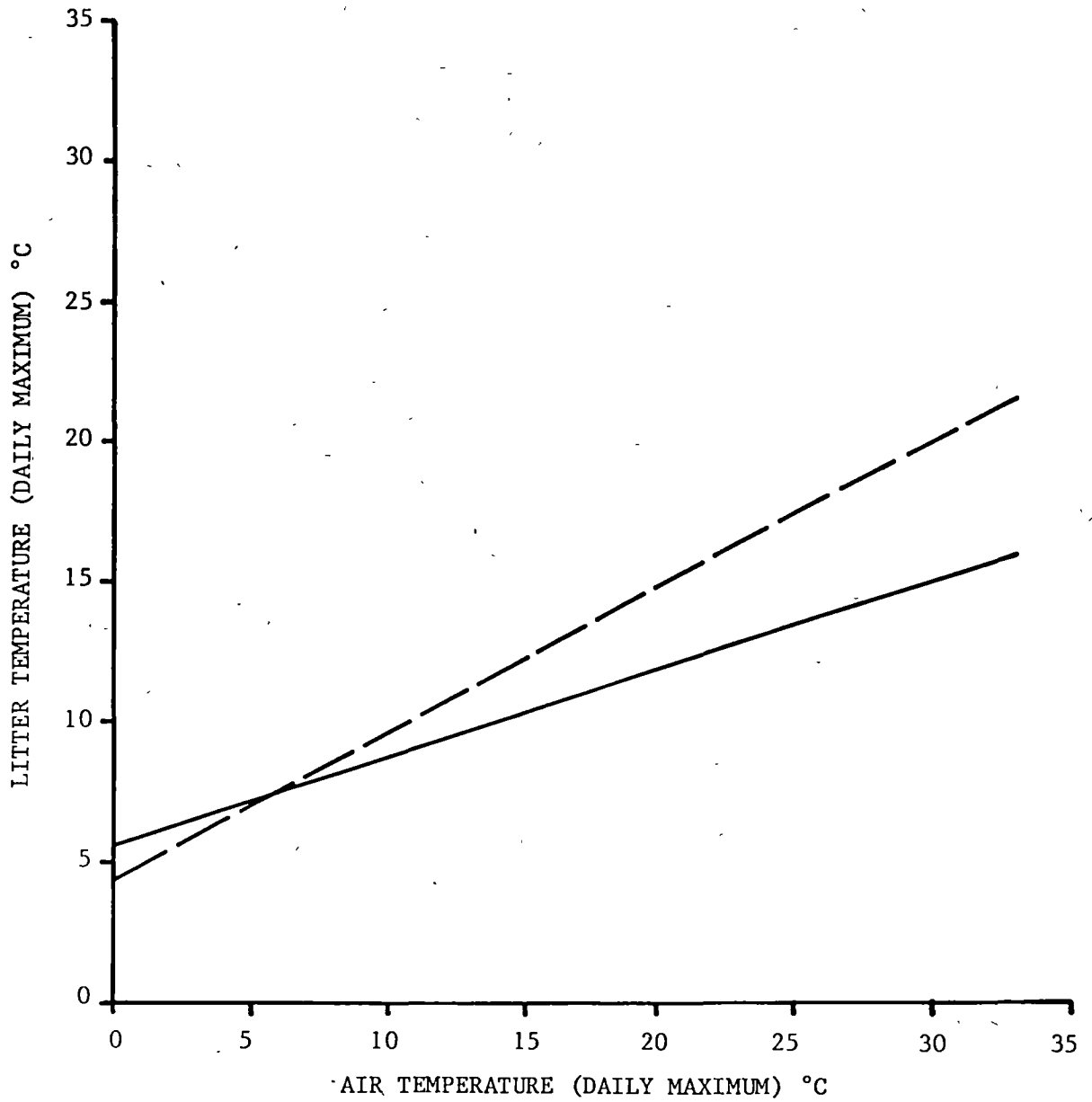
LEGEND

Site 1 ——————— $Y = 5.7139 + 0.30554 \cdot X$

Site 4 —— —— —— $Y = 4.3267 + 0.52364 \cdot X$

stand was not in a condition of active decline, and hence the disease would not have significantly affected litter processes, during the study interval. Much of the surrounding continuously inventoried forest has been assessed by the same method to be in an unhealthy but stable decline situation for the past 10 years.

There was little difference in altitude, and aspect of the four sites. All were on the major soil classification group for the region i.e. duplex yellow podzolics, and this, coupled with their uniform topography was considered consistent with the aim of studying litter processes of various vegetation types.

The range of eucalypt ($64 - 33m^2.ha.^{-1}$) and of understorey ($85 - 43 m^2.ha.^{-1}$) basal area and numbers of stems (13,440–8,940 per $ha.^{-1}$) of the various stands were intended to assist assessments of relationships between stand density, basal area, and litter accession. Differences in stand structure as illustrated by canopy closure, understorey height layering, and vegetation survey, were further characteristics of interest. These stand properties are discussed in relation to litter accession in Chapter 4.

Soil depth and drainage were determinant factors regarding site productivity as expressed by Site Index, and both depth and drainage decreased at Sites 3 and 4, as indicated from soil profile descriptions of augered holes and from the presence of *Leptospermum* species at these sites. A green gley was encountered below 1.5m at both Sites 1 and 2, which although indicative of waterlogging was considered to have little effect upon the root zone of the stands of these sites. Observation of wind-thrown eucalypts in the Southern Forests demonstrated a flat, circular "plate" of roots with few penetrating to a depth much greater than 1m. The presence of *Pomaderris apetala* Labill.

either within the plots or their surrounds at both Sites 1 and 2 is also indicative of a relatively fertile, well drained soil.

Section 3.2.2 lists details of temperature, rainfall, evaporation, and wind-run observations at Hastings Chalet, a meteorological station 4 km East of the study sites. These data are referred to in greater detail in Chapters 4 and 6, where the effects of environmental parameters are considered in relation to litter accession and decomposition. The differing temperature regimes experienced at Sites 1 and 4, as illustrated in Table 3.2.2, were expected to have an effect upon litter accession and decomposition rates, and upon decomposition agencies. The greater extremes of environment, primarily due to the lack of the buffering effect of understorey canopy closure at the open, low-scrub site, were evident during litter bag harvest in August, 1981. Bags at Site 1 were loose, easily harvested, and contained leaves were separable, whilst bags at Site 4 were covered in ice and both bag and contents frozen to the litterbed.

CHAPTER 4

. ACCESSION

4.1. INTRODUCTION

In ecology, litter has been described by Satchell (1974) as:

(i)   the layer of dead plant material present on the soil surface,

(ii)   dead plant materials which are not attached to a living plant.

Material type (i) is measured and discussed in Chapter 5 under "accumulation", and material type (ii) is measured and discussed in this Chapter under the heading "accession". Litter accession is defined as the amount of dead plant materials no longer attached to a living plant that arrives upon the forest floor in a given time interval, and may include material that is green and generally wind detached, naturally shed senesced material, and litter that may have been produced by either means but which has been perched within the canopies of differing vegetation strata.

Van Loon (1970) made the statement that "litterfall is an interesting index of ecosystem productivity as it is generally related to the quantity of photosynthetic machinery in the system". Attiwill *et al.* (1978) describe the production and fall of litter as a major pathway for both energy and nutrient transfer in forest ecosystems, and Ovington (1961) demonstrated that up to half the energy and carbon fixed annually in a forest was contributed to the forest floor as litterfall. Ashton (1975) stressed the importance of litter in the cycle for habitat conservation, the provision of nutrients, replenishment of organic matter, and support for a wide variety of niches for fauna and microorganisms. Ashton and Macauley (1972) demonstrated the importance of litter to forest reproduction.

The measure of litter accession is essential to a comprehension of the total litter process. · There are numerous descriptions of trapping devices and methods for sampling litter accession for Northern hemisphere deciduous and coniferous forest studies, and recommendations regarding trap size and type, and number per study area are made by Medweka-Kornaś (1971). There is little information available regarding the suitability of trapping devices and their site location for Australian forest types, although Birk (1979a) describes trapping devices designed to measure temporal and spatial variability in annual litter accession of overstorey and understorey vegetation in a mixed *Eucalyptus* and *Angophora* community in the Brisbane area.

Examples of varying layout, sampling interval, and trap type used in Australian studies of eucalypt forests are given in Hatch (1955), McColl (1966), Webb *et al.* (1968), Van Loon (1970), Ashton (1975), Lee and Butler (1977), Rogers and Westman (1977), Lee and Correll (1978) and Attiwill *et al.* (1978).

These accessional studies were intended to determine the seasonal and annual litter accession rate of both overstorey and understorey in four vegetation communities typical of Tasmania's Southern Forests, and to test hypotheses of relationships between litter accession and stand characteristics, and climatic variables. During sampling, various trapping systems were utilised and compared.

4.2. MATERIALS AND METHODS

4.2.1 *Trapping devices*

The tall, open, 63 year old *E. obliqua* regrowth stand of Site 1, the rainforest stand of Site 2, and the mixed aged (63/38 yr.) tall, open *E. obliqua* regrowth stand of Site 3 had a uniform cover of understorey that did not present sampling problems regarding spatial distribution. A ground cover of ca. 80 cm of *Blechnum wattsii* was

present at all 3 sites, uniformly distributed throughout Sites 1 and 2, but of patchy incidence at Site 3.

A number of problems were associated with sampling litter accession in the tall scrub vegetation community of Site 4. Situated between the low scrub/heath community of the Lune River Plain and the tall, open forest type of Site 3, the plot was open to predominant Westerly winds. The overstorey component of *E. nitida* and *E. obliqua* was scattered and not uniformly distributed over the area, and a dense tangled ground cover of *Bauera ruboides* was present over most of the plot to an average height of 2.1 m. The *Bauera* cover visually separated the vegetation into 2 strata, that of the overstorey and that contained within the *Bauera* layer. It was considered that a significant proportion of litterfall from the overstorey may be trapped and become "perched" in the *Bauera* layer, and that this may lead to erroneous measurement of the temporal characteristic of litter accession to the forest floor, as litter throughfall may become dependent upon disturbance of the *Bauera*, chiefly by wind.

Bins

Plastic refuse bins of 60l capacity, 50 cm in height and 48 cm in diameter, were used to manufacture litter traps as described by Newbould (1967). The open end of each bin was covered with nylon filament 'Sarlon' shadecloth (rated at 52% shade) with a mesh of 1 mm, in such a way that the cloth hung within the bin and could not be disturbed by wind. All bins were securely pinned with galvanised fencing-wire pegs to prevent their being knocked over by animals or light branch fall (Plate No. 2).

Plate No.2.   Standard bin.

Bin area was 1810 cm^2 which was greater than the minimum recommendation of IBP Handbook No.18 (Phillipson, 1971) and 10 bins were established at each 0.10 ha. site (recommended minimum number 20-30 ha.$^{-1}$).

Wilm (1946) described the improved sampling of rainwater throughfall in forest stands that is achieved by employing a number of fixed and roving rain gauges. The use of fixed and roving "stations" enable variations associated with both position and time to be sampled simultaneously, providing relatively precise average values for each area and period. Attiwill *et al.* (1978) employed this technique in the measurement of litterfall in *E. obliqua* forest in South Australia. At each of Sites 1, 2, and 3, three bins were randomly established at fixed (permanent) positions, and 7 bins were roved randomly about the plot immediately after each litter collection. Each site was divided into 40 subplots of 5 m^2 (Section 3.1.2) and sub-plot numbers were used to assign random locations of the roving bins by the Tables of Random Permutations of Green (1968).

Ground traps

Sampling beneath the *Bauera* of Site 4, and the *Blechnum* cover of Sites 1 and 2, required a more suitable device than the 50 cm high bin.

An inexpensive, simple to construct, and robust ground trap was manufactured from 26 gauge galvanised-iron sheet (Plate No. 3 and Fig. 4.2.1). A 10 cm deep outer rim was pop-rivetted together to form a circular, 48 cm diameter support for the trap, of the same area (1810 cm^2) as the standard bin device. 'Sarlon' shadecloth (52%) was placed over the rim and pushed downwards, internally, to a height of 5 cm and rivetted into place with an inner hoop made from a 2.5 cm wide strip of galvanised-iron of the same length and gauge as the outer rim. The

PLATE No.3.   GROUND TRAP TUCKED UNDER *BAUERA*

FIG. 4.2.1.   GROUND TRAP CONSTRUCTION
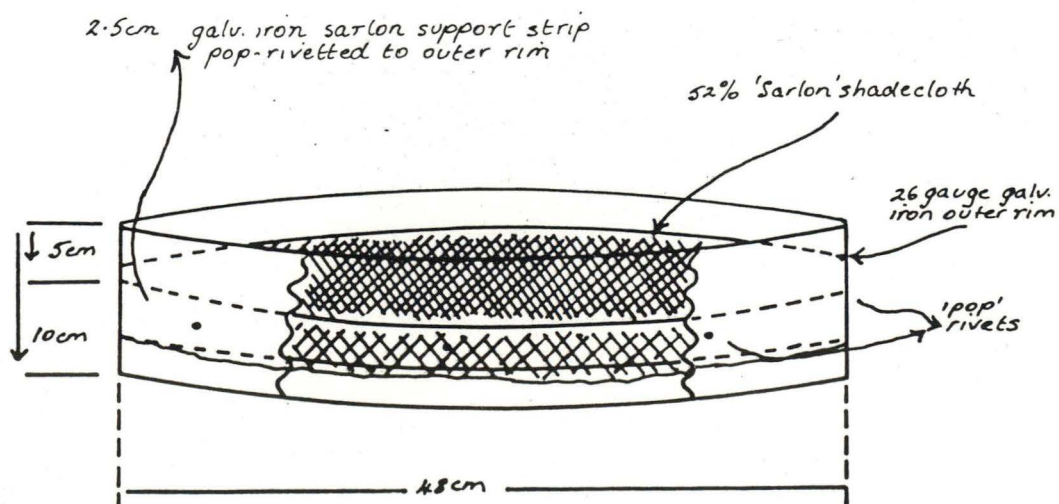
structure was inverted to form a circular trap that was pliable enough to be squeezed between vegetation stems and yet would retain its shape (and area) on positioning. It was essential to ensure that the mesh was not stretched into position by the inner retaining hoop, as this caused larger mesh to result that may have lost trapped material, and a trampoline effect that on testing bounced heavier materials viz. capsules and twigs, out of the trap.

Ten ground traps were randomly positioned in permanent locations at Site 2 for litter catch comparisons with the fixed and roving bins of that site. Ten were also located in permanent locations at Site 4.

Raised bins

A modification of the standard bin was used to sample the upper (overstorey) stratum at Site 4 (Plate No. 4 and Fig. 4.2.2).

A circular platform of 19 mm hardwood was glued and screwed to a 2.4 m length of 70 x 30 mm hardwood. A circular hardwood disc was bolted inside a standard bin to strengthen the plastic base, and the threaded ends of the bolts (3) left to protrude by 50 mm. Matching holes were drilled in the platform and used to attach the bin. The hardwood posts were driven into the ground at selected sampling positions until the platform height coincided with the height of the *Bauera* cover, and guyed against wind damage with light-gauge wire to surrounding overstorey stems. The bin opening was 50 cm above the lower vegetation stratum at all sampling positions.

Litter was collected by unbolting the bins from their platforms and handling in the standard manner.

Bin and ground trap location at Site 4 was of necessity different to the other sites. An accurately cut track was established on the 40 x 25 m plot perimeter. Use was made of an existing animal

Plate No.4.   Raised bin, Site 4.

FIG. 4.2.2.   RAISED BIN CONSTRUCTION

Sarlon mesh tied to bin

Holes for drainage

Bolts

70 x 30mm post

Bin base reinforcing

Bin platform

Layer of Bavera rubioides
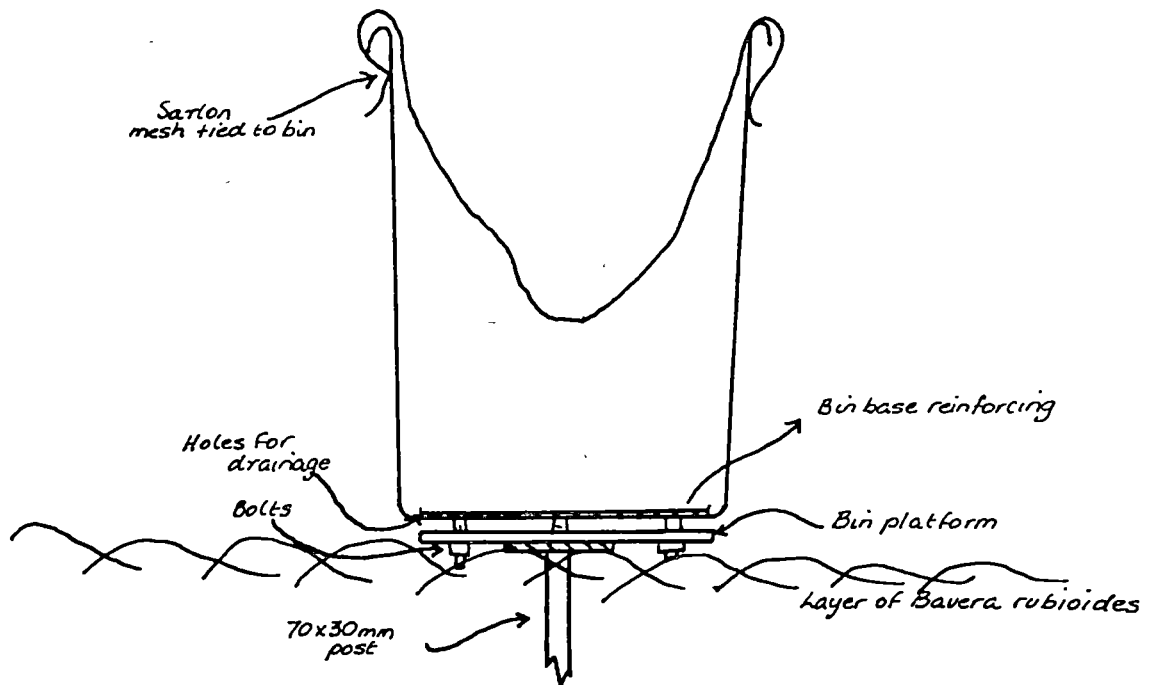
FIG. 4.2.3.   TRAP POSITIONS, SITE 4

animal track

40 m

25 m

corner pegs

_ _ _ _ Pushed track   _____ Cut track   .... Tunnel

O = Raised bin
G = Ground trap
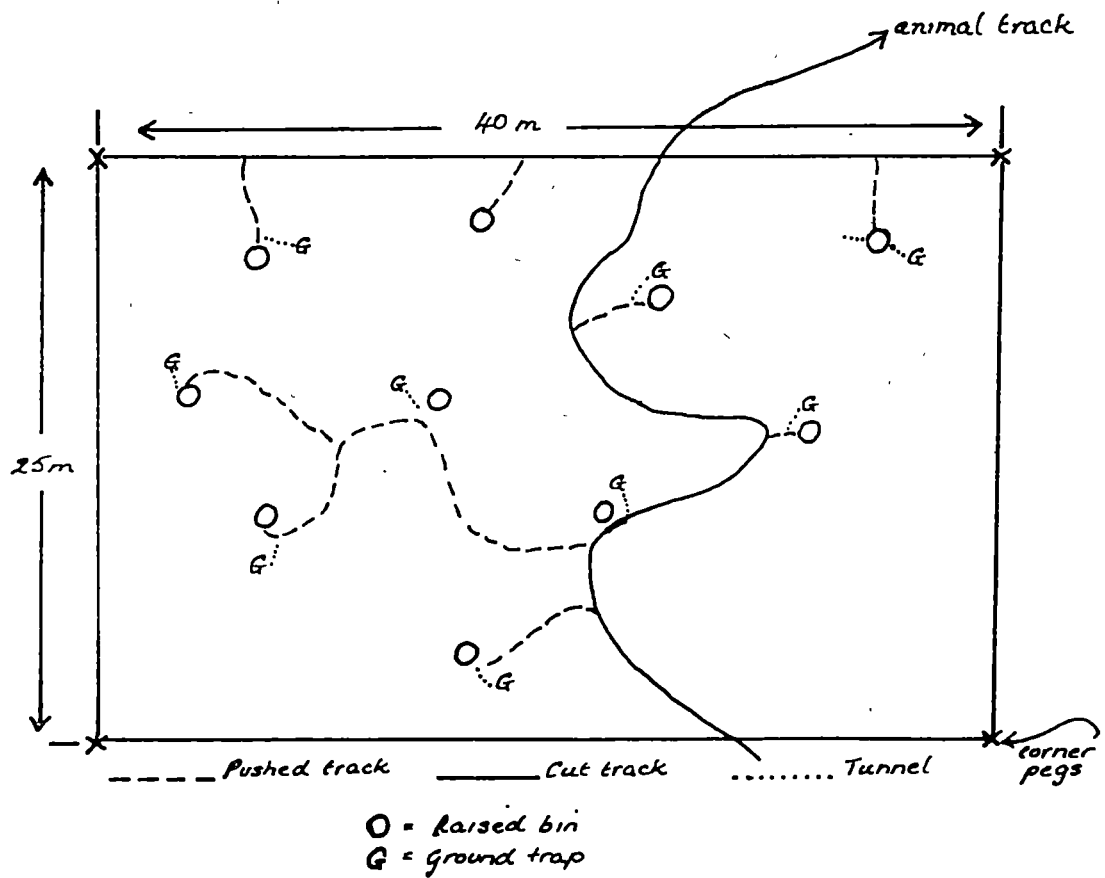
track that ran across the plot, and from this and the plot surround
narrow tracks were made to give access to permanently situated, raised
bin positions, with the *Bauera* pushed to one side rather than cut.
Ten raised bins were positioned in this manner (Fig. 4.2.3). Tunnels
were made along the ground through the *Bauera* to a position suitable
for the establishment of a ground trap of the same construction as
used at Site 2. No vegetation was cut, and all ground traps were
situated within 2 metres of each raised bin. This establishment pro-
cedure was designed to determine the "perching" effect of *Bauera* on
overstorey litterfall.

4.2.2 Sampling period and collection intervals

All trap devices (60) were sampled at 6 week intervals (42 days
exactly per interval) from the 20th December, 1978, until the 21st
April, 1982, at Sites 1, 2, and 3. Fire destroyed Site 4 in November,
1981, and sampling terminated at this site after 25 collection inter-
vals on November 4th, 1981.

4.2.3 Sorting of litter components

During the period 20.12.78 to 14.1.81 (18 collection intervals)
litter catches per device were sorted into the following 22 compon-
ents:

Leaves of: *E. obliqua*

      E. nitida

      Nothofagus cunninghamii

      Atherosperma moschatum

      Phyllocladus aspleniifolius

      Acacia melanoxylon

      Eucryphia lucida

      Phebaleum squameum

Banksia marginata

Pittosporum bicolor

Pomaderris apetala

Anodopetalum biglandulosum

Anopterus glandulosus

Drimys lanceolata

Olearia argophylla

Cenarrhenes nitida

Oxylobium elipticum

and

Miscellaneous leaves (viz. *Cyathodes, Leptospermum*)

Bark, and twigs <1.0 cm diameter

Floral parts, seeds, capsules, dust, and frass

Ferns and mosses

Grasses.

From the 14.1.81 to 21.4.82 (11 collection intervals) sorting was limited to a separation of eucalypt leaves from all other materials.

4.3. RESULTS

4.3.1 Temporal variation per species and material type.

Total litterfall (t.ha.$^{-1}$) per site during 29 contiguous 6 weekly intervals are compared in Fig. 4.3.1. There was a marked correspondence in the temporal pattern of litter accession between sites. The 1979/80 cycle of litterfall differed from those of 1980/81 and 1981/82 as the 2 latter cycles exhibited 2 distinct periods of peak litterfall, one in September/October, and the major peak in January/February. These peaks were coincident at all 4 sites in the 1980/81 cycle, and at Sites 1, 2, and 3 of the 1981/82 cycle (Site 4 destroyed). Peak litterfall occurred in February/March of the 1978/79

cycle with a minor peak at Site 3 in December. Least litterfall of each cycle at all sites occurred at the sampling times in the period May, June, July, August, with troughs in the July interval.

Considering the 1980 calendar year data for litter accession, the 18 week winter interval June, July, August, accounted for 13.7, 11.3, 10.0, and 15.2% of total annual accession at Sites 1, 2, 3, and 4 respectively. The peak fall period over 18 weeks in January, February, March accounted for 53.7, 47.1, 46.7, and 50.8% respectively, and the minor peak in October for 17.5, 25.4, 22.9, and 15.3%.

Average annual litterfall during the 3 years of measurement varied from:

Site 1, 5.060 to 5.638, mean 5.308 t.ha.$^{-1}$

Site 2, 4.058 to 5.074, mean 4.689 t.ha.$^{-1}$

Site 3, 4.412 to 5.502, mean 4.894 t.ha.$^{-1}$

Site 4, 1.952 to 2.174 (2 years) mean 2.063 t.ha.$^{-1}$

The pattern of litterfall was strongly seasonal, but appreciable amounts of litter fell throughout the year. The mimimum to maximum ratio of both total litterfall and total leaf fall varied between years of measurement viz. Table 4.3.3

Table 4.3.3   Minimum to maximum ratios of total and leaf litterfall.

| | 1979 | | 1980 | | 1981 | |
	Total	Leaf	Total	Leaf	Total	Leaf
Site 1	1:22.3	1:22.6	1:10.6	1: 7.2	1:11.4	–
Site 2	1: 9.4	1:16.7	1:12.1	1:10.0	1: 7.8	–
Site 3	1:17.4	1:18.6	1: 7.4	1: 5.0	1:10.3	–
Site 4	1:15.2	1:13.1	1: 6.4	1: 5.7	1:11.7	–

Ratios for both total and leaf litterfall were least in 1979, and there was considerable variation between the differing sites. Table 4.3.4 compares total and leaf litterfall ratios at the 4 sites on a seasonal basis, i.e. summer (January, February, March) accession to winter (June, July, August) accession. The data emphasise the seasonality of litterfall but variation in the ratios of both total and leaf litter accession existed between years of measurement, and between sites.

Table 4.3.4   Winter minimum to summer maximum ratios of total and leaf litter accession.

| | 1979 | | 1980 | | 1981 | |
	Total	Leaf	Total	Leaf	Total	Leaf
Site 1	1:5.0	1:11.0	1:5.8	1:6.1	1:8.6	—
Site 2	1:3.0	1: 4.7	1:6.2	1:5.5	1:5.3	—
Site 3	1:9.5	1:12.8	1:3.9	1:4.5	1:7.0	—
Site 4	1:8.0	1: 7.8	1:4.4	1:3.9	1:7.3	—

Accession $(t.ha.^{-1})$ per site of total litter, and the total leaf, understorey leaf, and bark plus twigs (<1.0 cm diameter) components of the total litter per sampling interval are listed in Table 4.3.1, and illustrated in Fig. 4.3.2, 4.3.3, 4.3.4, and 4.3.5 for Sites 1, 2, 3, and 4 respectively. Litter components were sorted during the 18 initial sampling intervals and only total litter yields are listed for intervals 19 to 29. Total annual yields per site of the major components of litter accession are summarised on the basis of yield $(t.ha.^{-1})$ and percentage of total litterfall in Table 4.3.2.

Table 4.3.1.   Accession of total litter, leaf litter, and bark and twigs (t.ha^{-1}) per sampling interval, and per annum.

Interval No.	Date	Site 1				Site 2				Site 3				Site 4			
		Total	Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	Understorey Leaf	Bark + Twigs
1	31.1.79	1.447	1.151	0.263	0.263	0.735	0.567	0.458	0.120	1.739	1.002	0.304	0.655	0.852	0.444	0.270	0.322
2	14.3	1.260	1.040	0.341	0.179	0.696	0.651	0.631	0.024	0.882	0.789	0.251	0.059	0.413	0.308	0.162	0.089
3	26.4	0.741	0.373	0.159	0.353	0.688	0.599	0.565	0.043	0.424	0.319	0.163	0.090	0.297	0.176	0.125	0.059
4	7.6	0.242	0.090	0.044	0.138	0.273	0.177	0.160	0.076	0.399	0.107	0.038	0.290	0.074	0.055	0.031	0.014
5	19.7	0.298	0.109	0.059	0.185	0.202	0.080	0.072	0.098	0.176	0.083	0.043	0.088	0.099	0.061	0.032	0.035
6	29.8	0.065	0.046	0.031	0.017	0.078	0.039	0.035	0.031	0.100	0.057	0.035	0.032	0.059	0.035	0.024	0.018
7	10.10	0.164	0.086	0.051	0.059	0.359	0.117	0.105	0.175	0.132	0.054	0.031	0.055	0.056	0.034	0.017	0.015
8	21.11	0.228	0.152	0.054	0.049	0.526	0.329	0.313	0.106	0.242	0.152	0.060	0.069	0.117	0.068	0.041	0.016
9	15.12.79	0.615	0.230	0.066	0.348	0.501	0.259	0.223	0.172	0.675	0.261	0.095	0.320	0.207	0.124	0.079	0.032
Total 1979		5.060	3.277	1.018	1.589	4.058	2.818	2.559	0.845	4.769	2.824	1.022	1.658	2.174	1.305	0.782	0.600
9	2.1.80	0.308	0.115	0.033	0.174	0.250	0.129	0.111	0.086	0.337	0.131	0.048	0.160	0.103	0.061	0.026	0.016
10	13.2	0.961	0.713	0.175	0.184	0.867	0.582	0.424	0.126	0.951	0.665	0.233	0.216	0.401	0.283	0.192	0.051
11	26.3	1.612	0.894	0.346	0.640	1.041	0.691	0.637	0.239	1.227	0.678	0.233	0.475	0.401	0.229	0.195	0.070
12	7.5	0.455	0.408	0.191	0.039	0.417	0.364	0.346	0.039	0.394	0.343	0.142	0.037	0.191	0.165	0.101	0.017
13	17.6	0.329	0.291	0.118	0.035	0.220	0.164	0.153	0.048	0.300	0.248	0.108	0.041	0.115	0.090	0.046	0.012
14	30.7	0.152	0.125	0.058	0.024	0.086	0.069	0.058	0.024	0.166	0.133	0.055	0.026	0.063	0.050	0.016	0.012
15	10.9	0.291	0.139	0.063	0.137	0.251	0.098	0.085	0.120	0.399	0.167	0.096	0.183	0.118	0.080	0.027	0.009
16	22.10	0.988	0.281	0.129	0.687	1.255	0.260	0.176	0.925	1.261	0.311	0.125	0.908	0.298	0.140	0.082	0.030
17	3.12	0.346	0.280	0.133	0.052	0.328	0.247	0.225	0.061	0.259	0.217	0.123	0.031	0.161	0.115	0.078	0.114
18	17.12.80	0.196	0.156	0.052	0.034	0.220	0.112	0.169	0.014	0.208	0.173	0.068	0.044	0.101	0.077	0.049	0.008
Total 1980		5.638	3.402	1.318	2.006	4.935	2.716	2.385	1.682	5.502	3.066	1.231	2.121	1.952	1.290	0.813	0.339

88

Table 4.3.1. Cont'd.

Interval No.	Date	Site 1				Site 2				Site 3				Site 4			
		Total	Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	Understorey Leaf	Bark + Twigs
18	14.1.81	0.392	0.321	0.103	0.069	0.440	0.224	0.339	0.027	0.416	0.347	0.137	0.022	0.201	0.155	0.098	0.016
19	25.2	1.518	*	*	*	0.971	*	*	*	1.144	*	*	*	0.421	*	*	*
20	7.4	0.842				0.857				0.615				0.304			
21	20.5	0.367				0.648				0.382				0.169			
22	1.7	0.141				0.223				0.142				0.063			
23	12.8	0.133				0.125				0.111				0.036			
24	23.9	0.874				0.738				0.724				0.155			
25	4.11	0.477				0.550				0.435				0.200			
26	15.12.81	0.483				0.522				0.443				††			
Total 1981		5.227				5.074				4.412							
27	27.1.82	0.978				0.735				0.912							
28	10.3	1.400				0.623				1.040							
29	21.4.82	0.430				0.530				0.372							

* Sorting of litterfall components discontinued.

†† Plot destroyed by fire.

FIG. 4.3.1.   TOTAL ACCESSION, TONNES/HA, AT 6 WEEK INTERVALS OF TIME
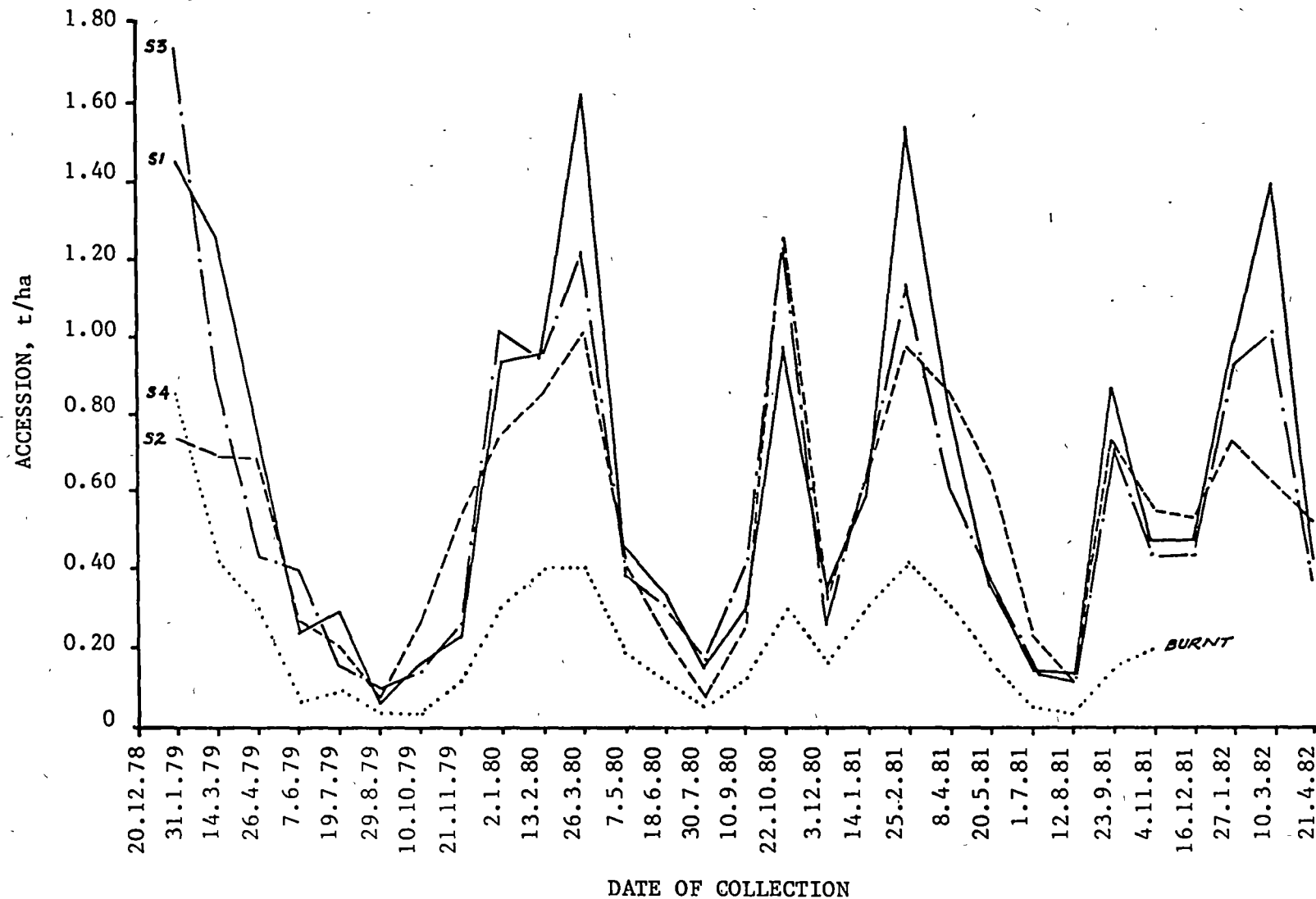
Table 4.3.2. Accession of major components as a percentage of total annual yield per site.

Year		Site 1					Site 2				
		Total	Leaf	E. obliqua Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	E. obliqua Leaf	Understorey Leaf	Bark +
1979	t.ha^{-1}	5.060	3.277	2.214	1.018	1.589	4.058	2.818	0.265	2.559	0.845
	%	100	64.8	43.7	20.1	31.4	100	69.4	.6.5	63.1	20.8
1980	t.ha^{-1}	5.638	3.402	2.103	1.318	2.006	4.935	2.716	0.415	2.385	1.682
	%	100	60.3	37.3	23.4	35.6	100	55.0	8.4	48.3	34.1

Year		Site 3					Site 4				
		Total	Leaf	E. obliqua Leaf	Understorey Leaf	Bark + Twigs	Total	Leaf	E. nitida+ E. obliqua Leaf	Understorey Leaf	Bark +
1979	t.ha^{-1}	4.769	2.824	1.800	1.022	1.658	2.174	1.307	0.524	0.782	0.600
	%	100	59.2	37.7	21.4	34.8	100	60.1	24.1	36.0	27.6
1980	t.ha^{-1}	5.502	3.066	1.833	1.231	2.121	1.952	1.330	0.517	0.813	0.339
	%	100	55.7	33.3	22.4	38.5	100	68.1	26.5	41.6	17.4

FIG. 4.3.2

ACCESSION OF TOTAL LITTER, LEAF LITTER, AND BARK + TWIGS (t.ha^{-1}) PER SAMPLING INTERVAL

FIG. 4.3.4

Site 1.

Site 3.
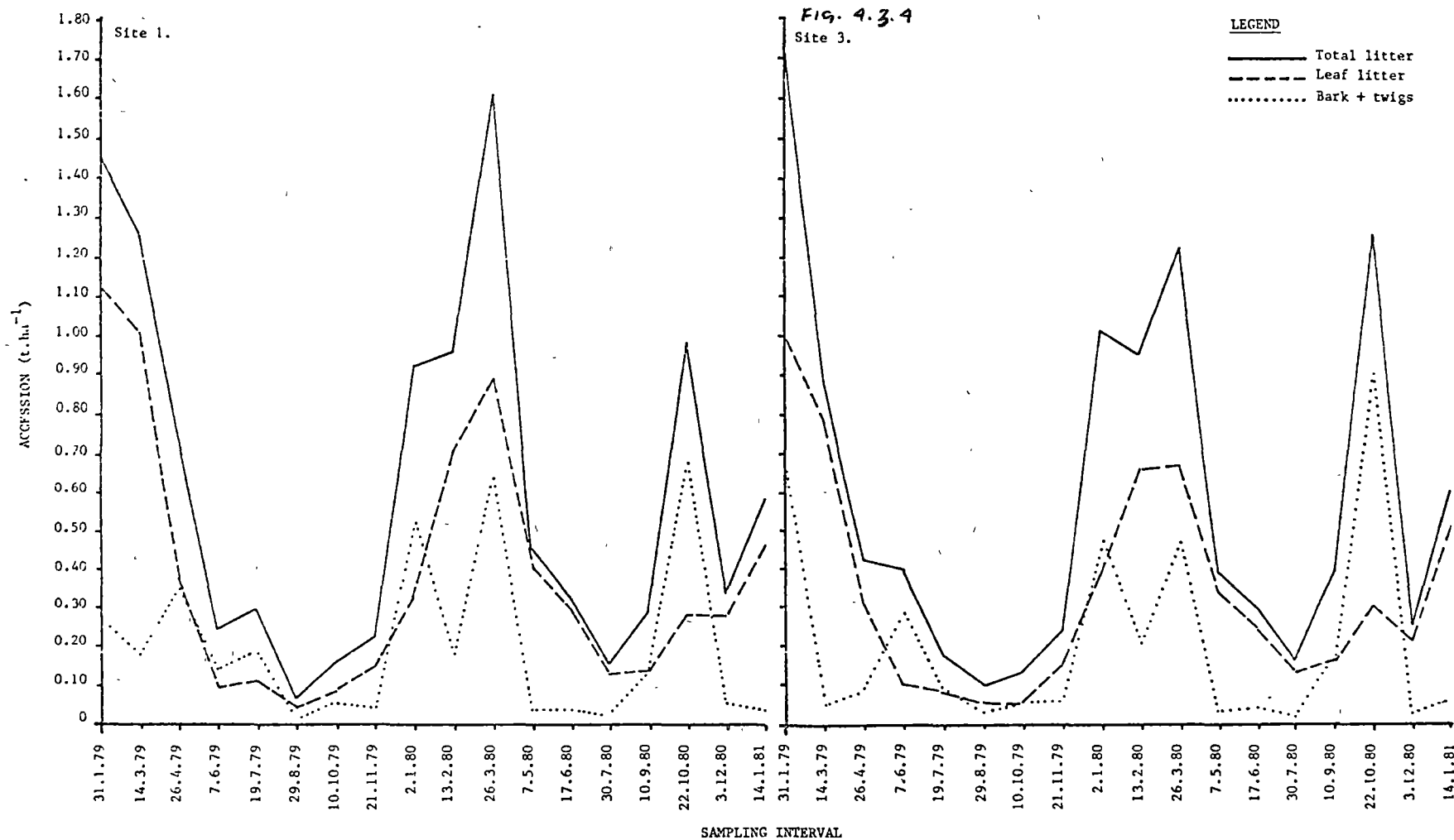
LEGEND

——— Total litter
– – – – Leaf litter
·········· Bark + twigs

FIG. 4.3.3 ACCESSION OF TOTAL LITTER, LEAF LITTER, AND BARK + TWIGS $(t.ha^{-1})$ PER SAMPLING INTERVAL

LEGEND
Total litter
Leaf litter
Bark + twigs

93
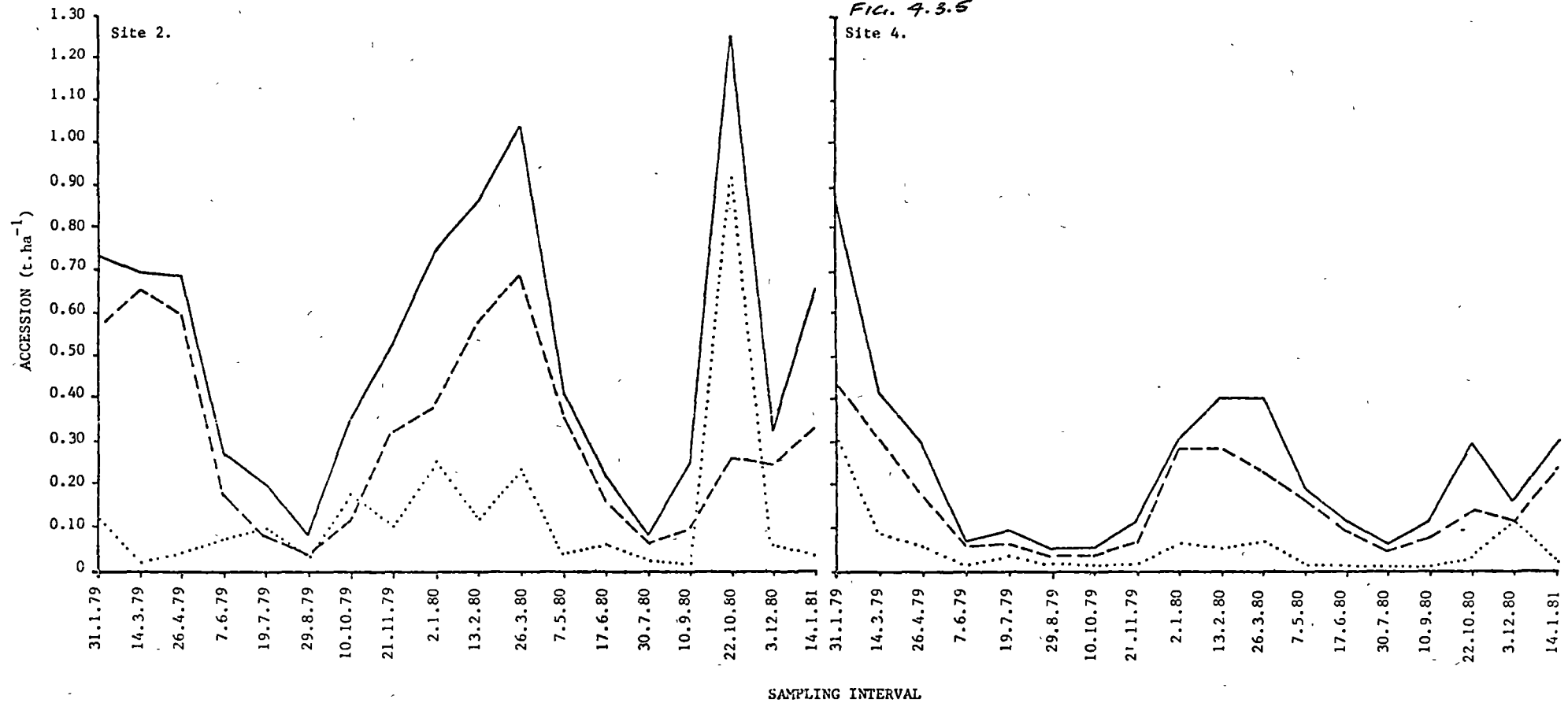
Leaves were the major component of litterfall at all sites during each year of measurement. *E. obliqua* leaves comprised the greater percentage of leaf fall at the eucalypt regrowth Sites 1 and 3. Understorey species contributed the major proportion of leaf fall at Sites 2 and 4, although it is difficult to compare understorey litterfall at Site 2 with the other sites. Species that are definably understorey at Sites 1 and 3 comprise elements of both the overstorey and understorey at Site 2, e.g. *Nothofagus cunninghamii, Eucryphia lucida, Acacia melanoxylon,* and *Phyllocladus aspleniifolius.*

Appendix Section B.1 to 6 details the total accession per interval of all sorted litter components per site. Data represent the total weight of litter (g) in 10 traps of total area 1.8098 m^2, for comparative purposes. Multiplication by a factor of 0.005525 transforms the data to yield in t.ha.$^{-1}$. Table 4.3.5 summarises the data on the basis of total annual yield (t.ha.$^{-1}$) for the 10 bin devices at Sites 1, 2, and 3, and the 10 ground traps at Site 4. Accession of selected major components of leaf litter at the individual sites are illustrated in Fig. 4.3.6, 4.3.7, 4.3.8, and 4.3.9. Individual trap data are available on tape at the University of Tasmania Computing Centre.

Results are discussed in Section 4.4.

4.3.2 Sampling

All litter yields were logarithmically transformed prior to analyses.

Fixed and roving bins

Litter yields in the 3 fixed bins and 3 randomly selected from the 7 roving bins of each of Sites 1, 2, and 3 were compared by analysis of variance. The analysis of variance table and a table of

Table 4.3.5. Annual accession of sorted litter components, (t.ha^{-1}) per site.

	1979[*]				1980[††]			
	Site 1	Site 2	Site 3	Site 4	Site 1	Site 2	Site 3	Site 4
Leaves of:								
E. obliqua	2.2135	0.2650	1.8003	0.0190	2.1031	0.4149	1.8327	0.0256
E. nitida	-	-	-	0.5046	-	-	-	0.4915
N. cunninghamii	0.0527	1.1729	0.0402	-	0.0546	0.9700	0.0176	-
A. moschatum	0.0019	0.0943	0.0002	-	0.0052	0.0944	0.0004	-
P. aspleniifolius	0.0003	0.1011	0.0003	-	0.0027	0.0697	0.0003	-
A. melanoxylon	0.1787	0.3064	0.0365	0.0006	0.2093	0.3808	0.0731	0.00002
E. lucida	0.0747	0.5718	0.0260	-	0.1644	0.5474	0.0337	-
P. squameum	0.3660	0.0203	0.3295	0.0047	0.4139	0.0281	0.4334	0.0159
B. marginata	-	-	0.0193	0.1638	-	-	0.0239	0.1848
P. bicolor	0.0032	0.0098	-	-	0.0017	0.0006	-	-
P. apetala	-	0.0349	-	-	0.0003	0.0689	-	-
A. biglandulosum	0.0381	0.0006	0.0174	-	0.0165	0.0030	0.0012	-
A. glandulosus	-	0.0650	0.0015	-	0.0023	0.0523	0.0011	-
D. lanceolata	-	0.0078	-	-	-	0.0025	0.0004	-
O. argophylla	-	0.0095	-	-	0.0030	0.0109	-	-
C. nitida	0.0005	0.0050	0.0022	0.00004	-	0.0035	0.0015	0.0017
O. ellipticum	-	-	-	0.0214	-	-	-	0.0417
Miscellaneous spp.	0.3469	0.1424	0.5487	0.6028	0.4243	0.1496	0.6420	0.5815
Dust-frass, floral parts	0.1943	0.3746	0.2866	0.2187	0.2243	0.4611	0.3370	0.2148
Bark and twigs	1.5890	0.8450	1.6580	0.6120	2.0060	1.6820	2.1210	0.3450
Ferns and mosses	0.00004	0.0201	0.0003	0.0231	0.0075	0.0110	0.00004	0.0174
Grasses	-	0.0004	0.0001	0.0152	0.0008	0.0006	0.0001	0.0151

[*] 1979, 20.12.1978 to 15.12.1979.
[††] 1980, 15.12.1979 to 17.12.1980.

FIG. 4.3.6/8.   RELATIVE ACCESSION OF LEAF LITTER COMPONENTS PER SAMPLING INTERVAL
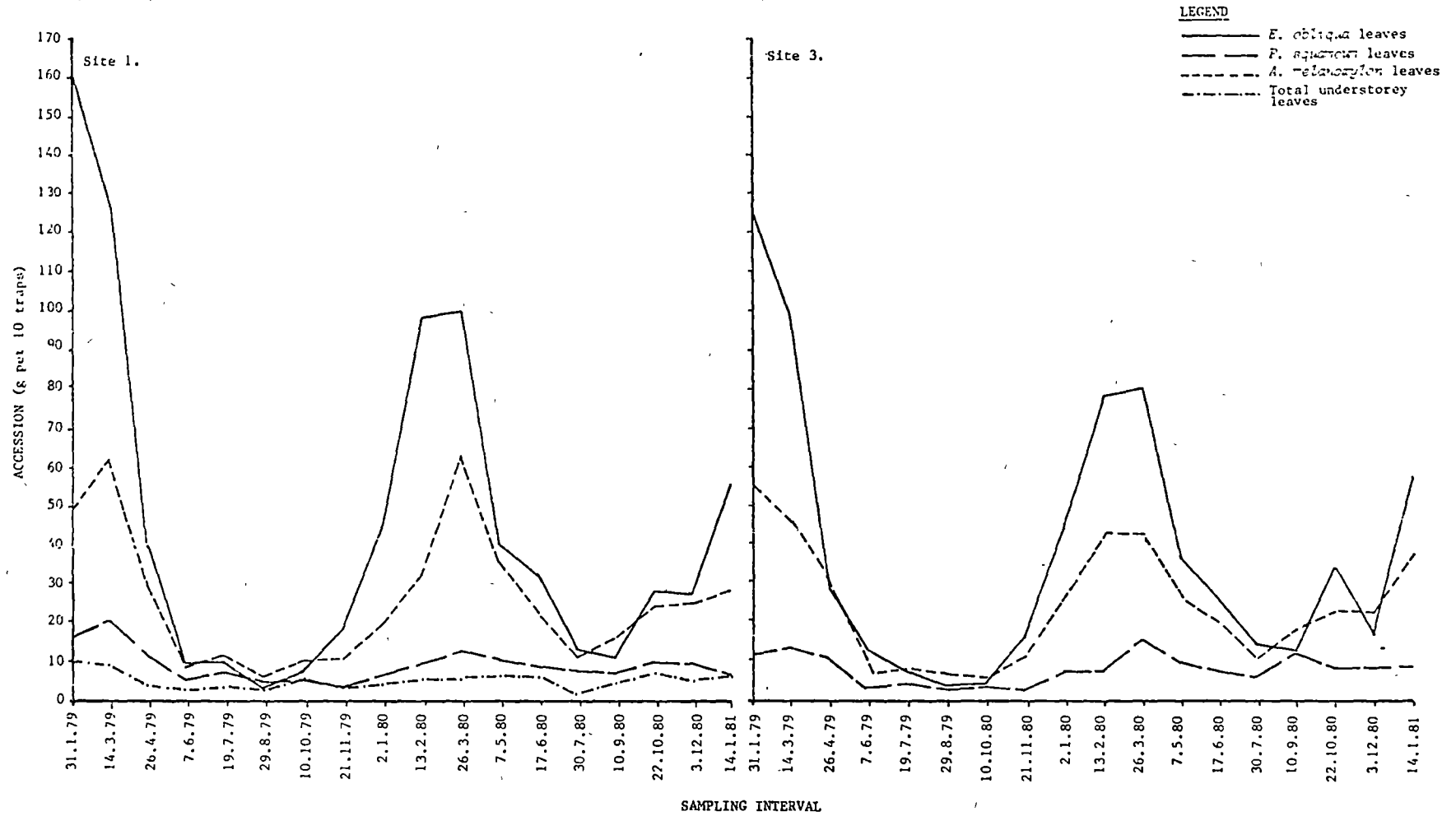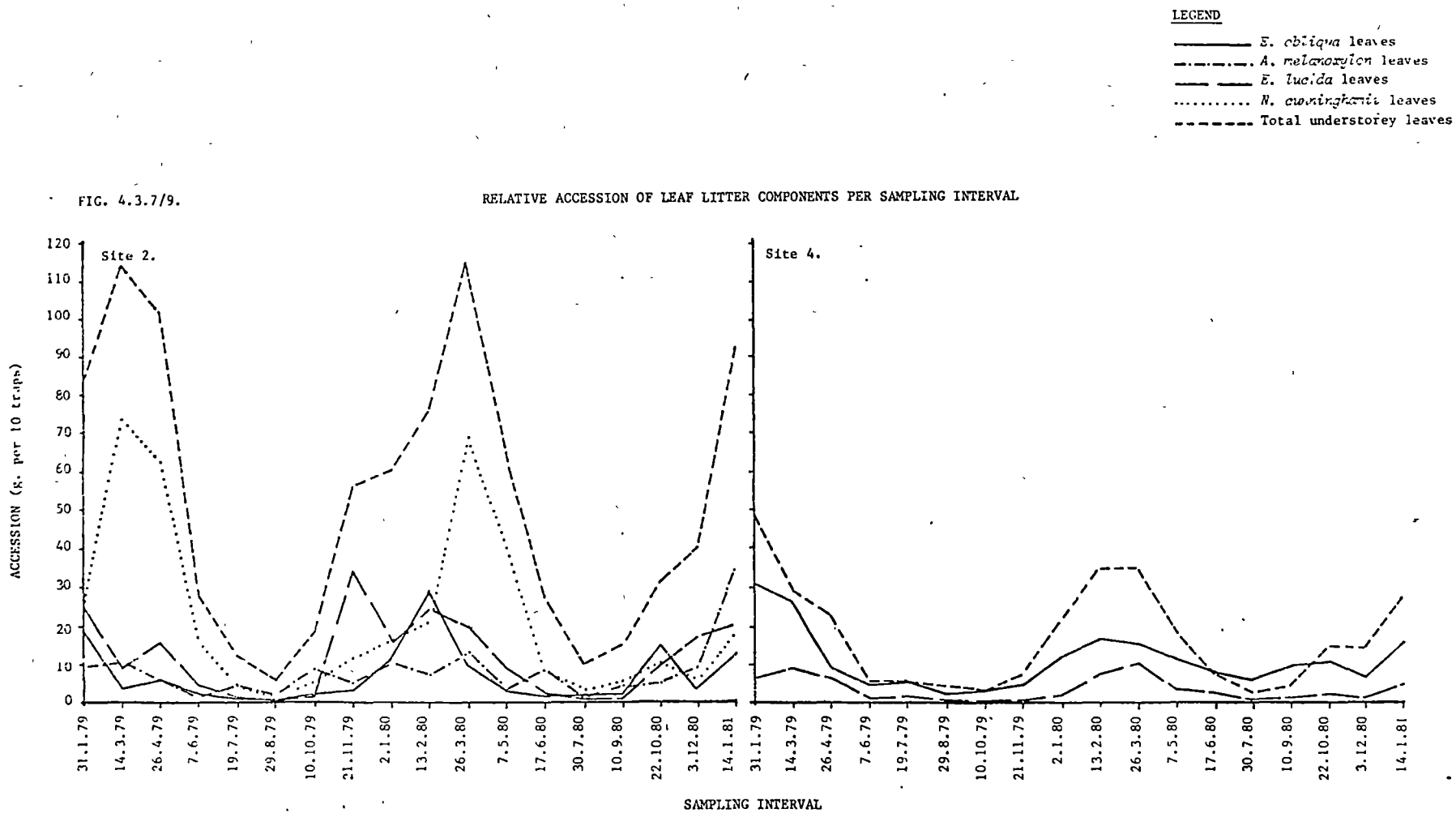
LEGEND
—————— E. obliqua leaves
—— —— P. aquaticum leaves
— — — — A. melanoxylon leaves
—·—··—··— Total understorey leaves

Site 1.

Site 3.

ACCESSION (g per 10 traps)

170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0

31.1.79
14.3.79
26.4.79
7.6.79
19.7.79
29.8.79
10.10.79
21.11.79
2.1.80
13.2.80
26.3.80
7.5.80
17.6.80
30.7.80
10.9.80
22.10.80
3.12.80
14.1.81

SAMPLING INTERVAL

FIG. 4.3.7/9.   RELATIVE ACCESSION OF LEAF LITTER COMPONENTS PER SAMPLING INTERVAL

back transformed log.mean yield per interaction are presented in Appendix, Statistical Analysis, 1. There was no significant difference between the trapped litter yields of the fixed or roving bins, for any of the 15 sampling intervals tested.

A non-orthogonal design analysis of variance was made of the litter catches in each of the 3 fixed devices in comparison with each of the 7 roving devices at Sites 1, 2, and 3 over 29 sampling intervals. There were significant differences between sites and between sampling intervals as expected. There was no significant difference between the litter catches of the fixed and roving devices, and there was no significant difference in the treatments x times interaction. The analysis of variance table is given in Appendix, Statistical Analysis, 2.

The standard deviation for a single device was 0.433 g and for the mean of any 10 devices was 0.137 g.

Bins and ground traps

Litter yields in the 10 bins and 10 ground traps of Site 2 were compared by analysis of variance. The analysis of variance table and a table of back transformed log.mean yield per interaction are presented in Appendix, Statistical Analysis, 3. There was no significant difference between the trapped litter yields of the bins or ground traps for any of the 15 sampling intervals tested.

Raised bins and ground traps

E. obliqua and *E. nitida* overstorey leaf litter yields in the 10 raised bins and 10 ground traps at Site 4 were compared by analysis of variance. The analysis of variance table and a table of back transformed log.mean yield per interaction are presented in Appendix, Statistical Analysis, 4. There was no significant difference between

the overstorey yields of the raised bins or ground traps for any of the 15 sampling intervals tested.

4.3.3 Relationship between live basal area, live numbers of stems and leaf litter accession of individual species.

The live basal area (B.A. m^2ha^{-1}) and annual leaf accession ($t.ha.^{-1}$) of all sorted leaf components (species) were multiplied by 10^4, (Table 4.3.6), and the regressions of individual sites compared by analysis of variance for common slope and intercept (Appendix, Statistical Analysis, 5).

There was a highly significant (P<0.001) correlation between log.BA of individual species and their respective annual leaf litter-fall during the year of BA measurement. There was no significant difference in slope or intercept of the regressions for individual sites. Regression equations per site, and the equation common to all sites, are given in Table 4.3.7 together with their regression coeff-icients. Fig. 4.3.10 illustrates the relationship.

The numbers of live stems per species at each site and their corresponding leaf accession (Table 4.3.8), and the regression lines of individual sites were compared by analysis of variance. There was a significant difference (P<0.05) between the individual regression lines, with a significant difference in the slopes (P<0.05) of the lines, and between their intercepts (P<0.01). Appendix, Statistical Analysis, 6, tables the tests for coincidence, common slope, common intercept, and regression coefficients for each site together with their standard errors and t-values.

4.3.4 Effect of climate upon litter accession

Ten climatic parameters (Appendix A, Table 7) were compared by multiple regression with log.total and log.leaf accession over 17 sampling intervals at all 4 sites. Parameters compared were,

Table 4.3.6. Log live basal area (m^2ha^{-1}) and log leaf accession ($t.ha^{-1}$) per annum.
All data x 10^4 prior to log transformation.

Species	Site 1		Site 2		Site 3	
	Log live BA	Log leaf fall	Log live BA	Log leaf fall	Log live BA	Log leaf fall
E. obliqua	5.7613	4.3451	4.5085	3.4232	5.5103	4.2553
P. squameun	5.1463	3.5636	3.6746	2.3075	5.0871	3.5179
A. melanoxylon	4.7774	3.2519	4.9041	3.4863	4.3071	2.5623
N. cunninghamii	4.5039	2.7210	5.5964	4.0693	3.9446	2.6042
E. lucida	4.1092	2.8733	5.1481	3.7572	3.7958	2.4150
A. moschatum	3.3232	1.2553	4.8080	2.9745	2.5119	0.3010
P. aspleniifolius	1.7782	0.4771	4.5984	3.0048	1.4150	0.4771
P. bicolor	3.7014	1.5185	3.0671	1.9912	-	-
A. glandulosus	∮	∮	4.2587	2.8129	3.1761	1.1761
A. biglandulosum	4.0563	2.5786	-	-	3.4434	2.2405
C. nitida	2.1553	0.7782	2.7701	1.6690	2.8591	1.3424
D. lanceolata	∮	∮	3.3073	1.8921	∮	∮
O. argophylla	-	-	3.3612	1.9777	-	-
B. marginata	-	-	-	-	3.9810	2.2856
P. apetela	-	-	3.9885	2.5428	-	-
M. squarrosa	∮	∮	∮	∮	∮	∮
Leptospermum spp.	∮	∮	-	-	∮	∮
A. verticillata	∮	∮	-	-	∮	∮
C. glauca	∮	∮	∮	∮	∮	∮
T. distidia	∮	∮	∮	∮	∮	∮
C. quadiifida	-	-	∮	∮	-	-
O. diversifolia	-	-	∮	∮	-	-
Miscellaneous leaves, ∮	5.1086	3.5403	4.5767	3.1544	5.3042	3.7393

∮; species bulked under "miscellaneous leaves".

Table 4.3.7. Regression equations. Log B.A. versus log leaf accession
per species, per site.

Site	Regression equation	n	r
1	Log Ye = -1.54098 + 0.98723 Log X	11	0.94865
2	Log Ye = -0.81301 + 0.86182 Log X	14	0.99054
3	Log Ye = -1.50710 + 0.99264 Log X	12	0.95988
Common	Log Ye = -1.37627 + 0.96973 Log X	37	0.96973

FIG. 4.3.10. Live basal area ($m^2.ha^{-1}$) and leaf litter accession ($kg.ha^{-1}an^{-1}$)

Site 1 ●

Site 2 ○

Site 3 ■

Log Y = -1.37627 + 0.96973 Log X
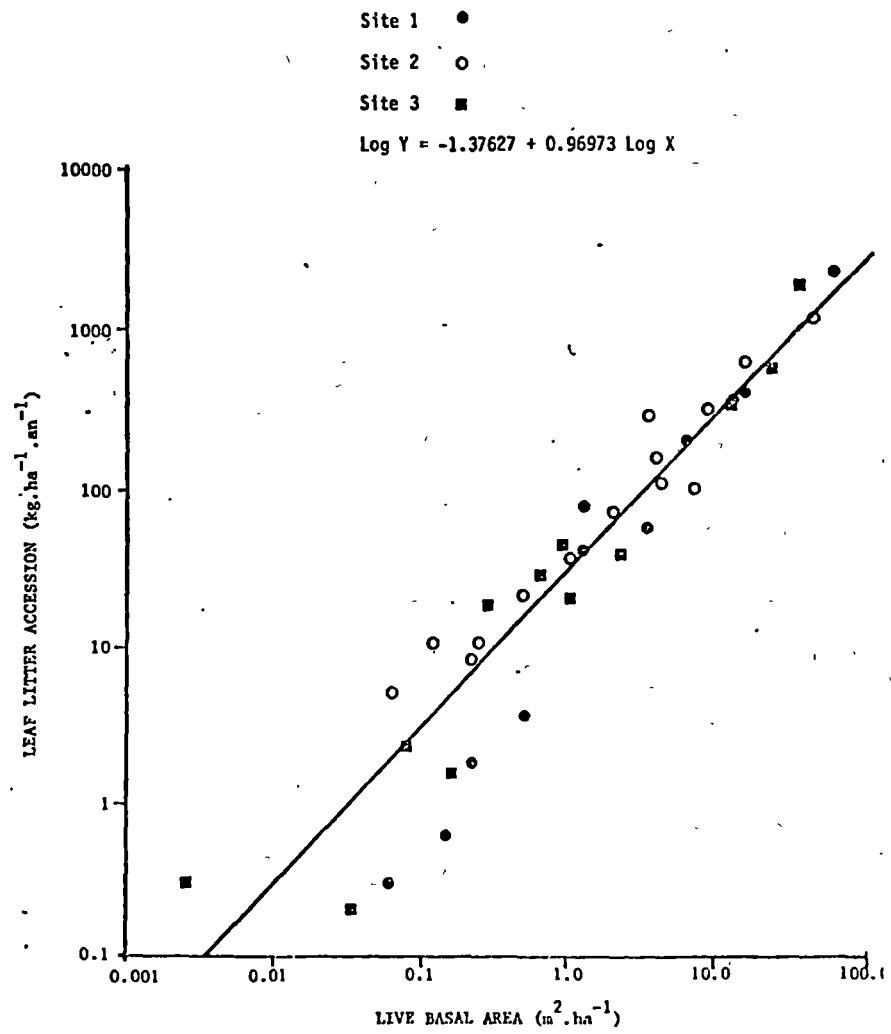
Table 4.3.8. Log live number of stems and log leaf accession $(t.ha^{-1}an^{-1})$.

Species	Site 1		Site 2		Site 3	
	Log No. stems	Log leaf fall	Log No. stems	Log leaf fall	Log No. stems	Log leaf fall
E. obliqua	2.9777	4.3451	1.7782	3.4232	2.8129	4.2553
P. squameum	3.3345	3.5636	1.9031	2.3075	3.5416	3.5179
A. melanoxylon	2.5911	3.2519	2.2304	3.4863	2.1139	2.5623
N. cunninghamii	2.2553	2.7210	2.9085	4.0693	2.3010	2.6042
E. lucida	2.6532	2.8733	3.3997	3.7572	2.5563	2.4150
A. moschatum	2.0414	1.2553	3.2480	2.9745	1.7782	0.3010
P. aspleniifolius	1.3010	0.4771	2.3222	3.0048	1.3010	0.4771
P. bicolor	1.9542	1.5185	1.9542	1.9912	–	–
A. glandulosus	∅	∅	3.1399	2.8129	2.3424	1.1761
A. biglandulosum	2.6335	2.5786	–	–	2.5315	2.2405
C. nitida	1.3010	0.7782	1.4771	1.6690	2.0792	1.3424
D. lanceolata	∅	∅	1.9031	1.8921	∅	∅
O. argophylla	–	–	1.0000	1.9777	–	–
B. marginata	–	–	–	–	1.4771	2.2856
P. apetala	–	–	1.8451	2.5428	–	–
M. squarrosa	∅	∅	∅	∅	∅	∅
Leptospermum spp.	∅	∅	–	–	∅	∅
A. verticillata	∅	∅	–	–	∅	∅
C. glauca	∅	∅	∅	∅	∅	∅
T. distidia	∅	∅	∅	∅	∅	∅
C. quadiifida	–	–	∅	∅	–	–
O. diversifolia	–	–	∅	∅	–	–
Miscellaneous, ∅	3.1004	3.5403	3.0645	3.1544	3.5353	3.7393

(i)   maximum temperature per interval

(ii)   minimum temperature per interval

(iii)   mean maximum temperature per interval

(iv)   mean mimimum temperature per interval

(v)   frequency percentage of days per interval when

        maximum temperature >10°C

(vi)   as per (v), but   >15°C

(vii)   as per (v), but   >20°C

(viii) as per (v), but   >25°C

(ix)   total rainfall per interval

(x)   mean windrun per interval (Geeveston).

There was a highly significant correlation between log.total and log.leaf litter accession and mean maximum temperature per sampling interval at each site. No further variance was explained by the addition of any other variable. The correlation matrix is presented in Table 4.3.9.

Transformation of mean maximum temperature per interval to logarithmic values improved correlation with the corresponding total and leaf litter accession values per site. The correlation was improved by the consideration of the leaf fraction of litter accession both with and without log transformation of the temperature data.

The regression lines for each site were tested for coincidence by analysis of variance and found to be significantly different. No significant differences between the regression lines were obtained by a test for common slope, therefore the intercepts differed. The tests for coincidence and common slope and table of regression coefficients, standard errors, and t-values are tabled in Appendix, Statistical Analysis, 7. Intercepts of the individual regressions were compared by the methods of Zar (1974) and no significant differences were

Table 4.3.9. Correlation matrix. Hastings Chalet meteorological data and log total and log leaf litter accession per sampling interval.

Meteorological parameter		Correlation coefficients											
		1	2	3	4	5	6	7	8	9	10	11	12
Maximum temperature	1	1.0000											
Minimum temperature	2	0.6618	1.0000										
Mean max. temperature	3	0.9323	0.5865	1.0000									
Mean min. temperature	4	0.7725	0.8498	0.6697	1.0000								
% days > 10°C	5	0.7412	0.5106	0.7995	0.6076	1.0000							
% days > 15°C	6	0.9249	0.5981	0.9848	0.6850	0.7816	1.0000						
% days > 20°C	7	0.8547	0.4842	0.9533	0.5435	0.6709	0.9033	1.0000					
% days > 25°C	8	0.7706	0.5374	0.8638	0.5473	0.6355	0.7937	0.9196	1.0000				
Total rainfall	9	-0.2474	-0.0153	-0.3710	0.0273	-0.3805	-0.3498	-0.3818	-0.2847	1.0000			
Mean windrun	10	0.4034	0.4862	0.2725	0.5339	0.1215	0.2989	0.2218	0.2308	0.5339	1.0000		
Log total litter	11	0.8659	0.5334	0.8402	0.6480	0.7247	0.8340	0.7824	0.5928	-0.2137	0.4581	1.0000	
Log leaf litter	12	0.8856	0.5758	0.9201	0.6991	0.7965	0.9036	0.8760	0.7167	-0.3349	0.2221	0.9224	1.0000

obtained between Sites 1, 2, and 3, but the intercept of the Site 4 regression differed significantly (P<0.05) from those of all other sites.

Table 4.3.10 lists the individual regression equations per site, and their correlation coefficients, r.

Fig. 4.3.11 illustrates the correspondence between leaf litter accession (kg.ha.$^{-1}$) and mean maximum temperature per sampling inter- val at the 4 study sites.

The accession of bark and twig litter (t.ha.$^{-1}$) at all sites were compared with mean maximum temperature and mean windrun (km.24hr^{-1}) per sampling interval by regression analysis and analysis of variance. Tests for coincidence, and regression coefficients, standard errors, and t-values are presented in Appendix, Statistical Analysis, 8 for mean maximum temperature correlation, and 9 for corr- elation with windrun.

Mean windrun, mean maximum temperature, and total rainfall per interval were logarithmically transformed and compared with log values of bark plus twig accession for the corresponding interval by multiple regression (Table 4.3.11). The correlation matrix and table of regression coefficients, standard errors, and t-values are given in Appendix, Statistical Analysis, 10.

Regression of bark + twig accession with windrun resulted in a correlation coefficient, r, of 0.501 which with the addition of log.total rain per interval improved to 0.64. There was no improve- ment in the percentage variance explained by the addition of mean maximum temperature per interval.

4.4. DISCUSSION

There was a marked correspondence in the temporal pattern of litter accession between sites that was maintained regardless of diff-

Table 4.3.10. Log mean maximum temperature versus log total, and log leaf accession per interval.

	Site	Regression equation	n	Correlation coefficient, r
Log leaf	1	Log Ye = -3.4444 + 4.8631 Log X	17	0.874
	2	Log Ye = -3.4547 + 4.8335 Log X	17	0.942
	3	Log Ye = -2.8619 + 4.3461 Log X	17	0.838
	4	Log Ye = -2.6979 + 3.9460 Log X	17	0.864
	Common	Log Ye = -3.1147 + 4.4972 Log X		
Log total	1	Log Ye = -2.5771 + 4.3299 Log X	17	0.820
	2	Log Ye = -2.1135 + 3.9117 Log X	17	0.833
	3	Log Ye = -1.7974 + 3.6712 Log X	17	0.731
	4	Log Ye = -2.6349 + 4.0436 Log X	17	0.867
	Common	Log Ye = -2.2807 + 3.9891 Log X		

108

FIG. 4.3.11. Leaf litter accession (kg.ha^{-1}) and mean maximum temperature (°C) per sampling interval.

Site 1 ●   Site 3 ■

Site 2 ○   Site 4 □

Mean maximum temperature °C ----------
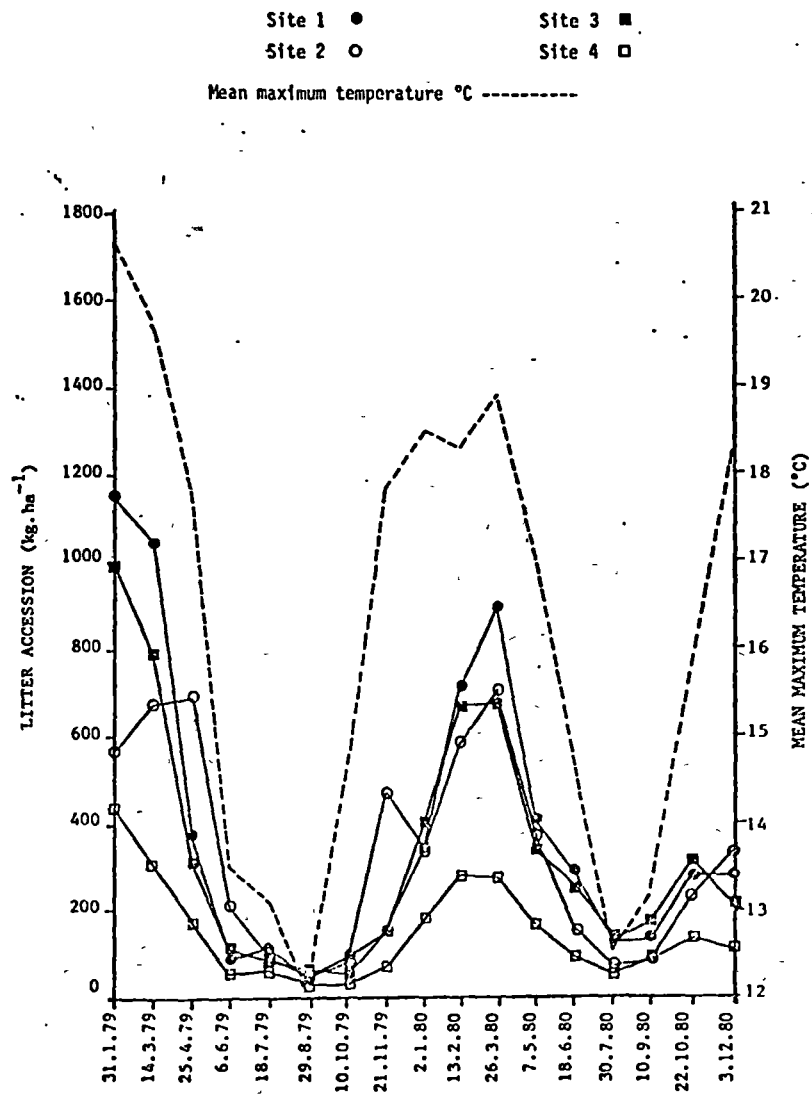
Table 4.3.11. Log bark + twig accession (t.ha^{-1}) and log mean
maximum temperature, and log mean windrun
per interval.

Log temperature	Log windrun	Log bark + twigs accession			
		Site 1	Site 2	Site 3	Site 4
1.316	2.201	2.420	2.879	2.816	2.508
1.295	2.064	2.253	1.380	1.771	1.949
1.250	2.019	2.548	1.633	1.954	1.771
1.130	1.951	2.140	1.881	2.462	1.146
1.117	2.065	2.267	1.991	1.944	1.544
1.083	2.087	1.230	1.491	1.505	1.255
1.167	2.166	1.756	2.243	1.740	1.176
1.250	2.125	1.690	2.025	1.839	1.204
1.267	2.301	2.718	2.408	2.681	1.819
1.263	2.225	2.265	2.100	2.334	1.708
1.277	2.146	2.806	2.378	2.677	1.845
1.233	1.996	1.591	1.591	1.568	1.230
1.164	1.997	1.544	1.681	1.613	1.079
1.097	1.927	1.380	1.380	1.415	1.079
1.121	2.278	2.137	2.079	2.262	0.954
1.199	2.322	2.837	2.966	2.958	1.477
1.255	2.179	1.716	1.785	1.491	2.057
1.314	2.066	2.013	1.613	1.820	1.380

erences in accessional patterns between individual annual cycles.

The litterfall cycles of 1980/81 and 1981/82 (Fig. 4.3.1) were strongly bimodal compared to the cycle of 1979/80. Birk (1979a) recorded a bimodal trend for the litter accession of understorey species in a mixed eucalypt forest in the Brisbane area, that was shown to coincide with the photosynthetic index of the same general area reported by Specht and Brouwer (1975).

Biomdality of litterfall in these studies is attributed to the bark plus twig component. Annual cycles of overstorey and understorey leaf accession (Figs. 4.3.2 to 4.3.9) are unimodal and strongly seasonal, with peak litterfall occurring during the summer months of January, February, March, and minimum falls in the winter months June, July, and August. This trend is in agreement with the seasonal variation in litterfall reported by many authors of Australian litter studies, e.g. Hatch (1955), Stoate (1958), McColl (1966), Webb *et al*. (1969), Van Loon (1970), Ashton (1975), Rogers and Westman (1977, 1981), and Walker (1979).

The secondary (lesser magnitude) peaks of total litterfall for the sampling intervals ending 22nd October, 1980, and 23rd September, 1981, were coincident with the highest mean windrun (km.24hr^{-1}) values measured during each annual cycle, i.e. 210.1 and 213.1 km.24hr^{-1} respectively. The 1979/80 cycle exhibited a secondary peak of total litterfall at Sites 1 and 3 (eucalypt regrowth stands) for the interval ending 2nd January, 1980, although the peaks were of minor significance compared with those of 1980/81 and 1981/82. This interval also coincided with the highest mean windrun value for that cycle (200.1 km.24hr^{-1}).

Litter components were not sorted during 1981/82, but the influence of the bark plus twig component upon the total litterfall

pattern is demonstrated in Table 4.4.1 for the 1980/81 cycle data of Sites 1, 2, and 3 and the 1979/80 cycle data of Sites 1, and 3.

Table 4.4.1.   Percentage of total litterfall of total leaf, and bark + twig components.

	1979/80 (2.1.80)			1980/81 (22.10.80)	
	Leaf %	Bark + twig %		Leaf %	Bark + twig%
Site 1	37.3	57.2		28.4	69.5
Site 2	51.7	34.4		20.7	73.7
Site 3	38.7	47.4		24.7	72.0
Site 4	59.7	15.4		47.0	10.1

Multiple regression of the logarithmic transformations of wind-run, mean maximum temperature, and total rainfall with similarly transformed bark + twigs accession values per sampling interval, gave improved correlation with the addition of rainfall to windrun (r = 0.64). Rainfall is generally coincident with periods of high wind in the Hastings area. The lack of correlation between temperature and bark + twig fall was surprising as increases in tree growth during warmer periods of the year would be expected to result in bark slough-ing in particular. An explanation of the lack of correlation is similar to the explanation of the relatively poor overall correlation (r = 0.501) between windrun alone and bark + twig fall, namely, having shed bark and twigs during particular intervals of high wind, the future fall of material is affected for further intervals of high wind i.e. the material has been shed and the available quantity has been reduced. In contrast, the lack of correlation with leaf accession is

due to leaves being physiologically retained even though moribund, and their accession is temperature related.

Annual non-leaf litterfall in these hardwood stands varied between 30.6 and 45.0 percent which is higher than for other hardwood stands, but similar to that of many gymnosperms (Bray and Gorham, 1964), and is in agreement with the findings of Ashton (1975) for *E. regnans* stands in Victoria.

The marked seasonal pattern of litterfall at Hastings was strongly correlated with mean maximum temperature experienced during the accessional intervals, and the precision of the relationship was increased by removal of the non-leafy component of collections. These findings substantiate those of Attiwill *et al.* (1978) in studies of *E. obliqua* litterfall in Victoria, where at least part of the seasonal variation in litterfall was explained in terms of temperature. Their relationship showed hysteresis, with higher rates of litter production during the period of increasing temperatures from winter through spring to summer, and lower rates during the period of decreasing temperature through Autumn. Lee and Correll (1978), working in *E. obliqua* forests in South Australia found that temperature accounted for at least 50 per cent of the variation in litterfall. The bimodal pattern of leaf production found by Specht and Brouwer (1975) was explained in terms of limiting water supply during the mid-summer period, and sensitivity of *Eucalyptus* to low temperature during winter (Cremer, 1975; Scurfield, 1961).

Leaf fall (Rogers and Westman, 1977) and leaf growth have been shown to be roughly synchronous as found by Specht and Brouwer (1975) although leaf initiation preceded leaf fall noticeably. Rogers and Westman (1981) working on a more coastal site only 30 km west of the study area of Specht and Brouwer (1975) found less marked bimodality

of *Eucalyptus* leaf accession that they attributed to the more moderate temperature fluctuations and greater summer moisture availability of their coastal site. They considered that winter growth suppression could be explained by the sensitivity of *Eucalyptus* to low temperature, and the reduction of insolation during winter, which results in a much lower net photosynthetic index (Specht, 1952).

The unimodal pattern of leaf accession at the Hastings sites substantiates the considerations of Rogers and Westman (1981). In these most southern forests of Australia a greater range of temperature change occurs and seasonality is more pronounced. This is evidenced by the summer maxima to winter minima ratios of litterfall that were as high as 23:1, a figure much higher than those cited by Walker (1981) for tall-open, warm temperate eucalypt forests. Furthermore there is appreciable rainfall throughout the year (Fig. 3.2.3) and the effects of water supply upon leaf shedding (Kozlowski, 1976) is not generally of consequence, although severe periods of summer drought have occurred in the South of Tasmania and have been suggested by West (1979) to be causal in the onset of regrowth dieback of *Eucalyptus* species in the Southern Forests. Cremer (1975) also showed that growth of *Eucalyptus* seedlings may be reduced at temperatures in excess of 30°C.

Temperatures in summer rarely exceed 30°C (Fig. 3.2.2) and hence summer growth restrictions were not evident.

Although the lack of high summer temperature and summer water stress in these forests relative to more northern regions of Australia may be expected to yield more readily apparent correlations between leaf fall and climatic factors, it was surprising that the multiple regression of the available factors with leaf fall resulted in the marked correlation of an individual factor (mean maximum temperature

per interval) that was not significantly improved by the addition of any other factor. It might be expected that rainfall would enter the regression negatively but as heavier falls of rain during a sample interval would reduce mean maximum temperatures, this variable may already be masked in its effect on leaf shed. Fritts (1976) discussed multivariate techniques for comparing the tree-growth and climatic relationships, and remarks that "there are so many possibilities for variations in limiting factors that it is surprising that *a priori* modelling by summing one variable during different periods of time has worked at all".

In a review of litter production in forests of the world, Bray and Gorham (1964) demonstrated a relationship for total litterfall and latitude, and stated that the relationship between temperature and litterfall was inverse and linear, with a maximum level of about 11 $t.ha.^{-1}an.^{-1}$ at the Equator, and a little less than 1 $t.ha.^{-1}an.^{-1}$ at latitude 65°N in Europe. Their summary of litter accession data for major climatic zones lists ratios for Arctic/Alpine – cool temperate – warm temperate – equatorial to be 1:3.6:5.1:9.7, ratios that closely followed those of 1:2.7:5.1:7.0 that they list for bole production in the same zones. They remark upon the importance of insolation during the period of photosynthesis, and suggested that the total amount of solar radiation received during the growing season is roughly in the proportion of 1:3:5 for extreme Arctic/Alpine – cool temperate – equatorial.

The annual rate of total litter accession of 4.8–5.6 $t.ha.^{-1}$ in the eucalypt regrowth stands of Sites 1 and 3, and of 4.1–4.9 $t.ha.^{-1}$ in the mixed forest of Site 2, is higher than the mean value (3.61 $t.ha.^{-1}$) for cool – temperate forests listed in Bray and Gorham (1964), but closely fits their plot of total annual litterfall versus

latitude. Ashton (1975) lists 4.1 t.ha.$^{-1}$an^{-1} and 8.1 t.ha.$^{-1}$an.$^{-1}$ for leaf litter accession and total litter accession in a 52 year old *E. regnans* stand of good site quality in the warm – temperate forests of Victoria. Applying the ratio of 3.6:5.1 of Bray and Gorham for cool – temperate : warm – temperate litter production to the leaf litter data of Ashton, a value of 2.9 t.ha.$^{-1}$ results that corresponds to the 2.8–3.4 t.ha.$^{-1}$ for leaf litter accession in the 63 year old, better site quality stand of *E. obliqua* at Site 1. A discrepancy occurs between a similarly calculated value for total litterfall data at Ashton's and this site, values being 5.1:5.7 t.ha.$^{-1}$, but this may be explained by the differing quantities of non-leaf material at each site, particularly where *E. obliqua* with fibrous bark is compared with *E. regnans*.

Litterfall in warm temperate Australian eucalypt forests has been the subject of a number of studies in which attempts have been made to relate the phenomenon to basal area (Van Loon, 1970), tree density (Ashton, 1975), canopy cover (Peet, 1971), and projected cover (Walker, 1981). Van Loon (1970) observed a relationship between stand basal area and total litterfall, and this finding was supported by Fox *et al.* (1979). In contrast, Ashton (1975) found no significant relationship between litterfall and tree density expressed as number of stems. Kittredge (1944) reported relationships between the weight of foliage of trees and stands and their periodic annual growth, or diameter.

The strong correlation between basal area of individual species and their corresponding litterfalls (both parameters logarithmically transformed) over 3 sites studied at Hastings agrees with the general relationship for bole and litter production in different world climatic zones reported by Bray and Gorham (1964), and with the findings of Kittredge (1944), Van Loon (1970), and Fox *et al.* (1979).

An unexpected finding was that the different over- and under-storey species behaved similarly, suggesting an adaptive mechanism which balances photosynthetic production despite varying degrees of insolation. There was no significant difference in the relationship between the 3 stands, which differed in site quality, and contained species of differing age, canopy exposure, leaf size and structure, and phenology. Twenty-three species of 21 genera with 16 families (Curtis, 1963, 1967; Curtis and Morris, 1975) were represented on the 3 sites, with canopy heights ranging from 2-33 m, leaf structures both sclerophyllous and orthophyllous, and leaf sizes ranging from nanophyllous to mesophyllous (Fosberg, 1961).

Considering the data for Sites 1, 2, and 3 at Hastings, there was a linear relationship between the number of live stems per species, and their corresponding leaf accession per site (both parameters logarithmically transformed). However, analysis of variance showed number of stems accounted for 64.3 percent of the variance in litterfall, and there were significant differences in both slope and intercept of the individual regression lines per site.

Thus litterfall should always be expressed relative to basal area per unit area, as this parameter reflects the nett resultant of all effective environmental variables as well as competition within and between species.

The trapping system described in Section 4.2.1 at Sites 2 and 4, that utilised circular, galvanised-iron ground traps at fixed positions spread randomly over the study area, is recommended. Roving of traps was time consuming, and the continual movement about the study area that was necessitated can be of concern when accessional studies are carried out concurrently with decomposition studies that require a minimum of plot disturbance. Analysis of variance between fixed and

roving traps at 3 different sites over 29 sampling occasions demonstrated no significant differences in yield between the modes of positioning. The accuracy of determination cannot be significantly improved without utilising impracticably large numbers of trapping devices, compared with the 10 per 0.1 ha. used in these studies. This number was appreciably greater than the 20-30 per ha. recommended in Phillipson (1971).

There were no significant differences in yields of trapped litter in bins or ground traps, but trapped litter was more speedily harvested from the ground trap.

Comparison of the overstorey litter catches at Site 4 in raised bins with those of ground traps yielded no significant differences in yield. From this finding, it is concluded that litter does not "perch" for a significant length of time in the dense ground cover of this site, but gravitates to the forest floor quite rapidly.

CHAPTER 5

ACCUMULATION

5.1. INTRODUCTION

Accumulated litter, or "standing crop", in these studies is defined as the layer of dead plant material present on the soil surface. No attempt was made to excavate material that may have been buried, or to include material that was standing dead, i.e. dead plant material still attached to living plants.

This definition as stated requires clarification as it was difficult to distinguish between litter and soil organic matter. Satchell (1974) described each of these 2 categories as no more than an analytical convenience. The litter layer and the mineral soil were easily delineated at Sites 1 and 2, whereas at Site 3 they were extremely difficult to distinguish.

Litterbed descriptions follow the revised nomenclature of Heiberg and Chandler (1941).

5.2. LITTERBED CHARACTERISTICS

(i) Depth

The litterbeds of all sites were shallow, and differed between sites (Fig. 5.2.1).

Litter of Sites 1 and 3, the tall-open *E. obliqua* forests, was loosely packed and variable in depth. At Site 1 it was equally stratified into an 'L' layer of fresh leaves, bark and twigs, and a decaying 'F' layer of decomposing leaves admixed with relatively intact bark and twigs. The 'H' layer averaged 2 cm in depth, but varied in pockets to depths of 5 cm. L + F layers together varied between 2 and 5 cm in depth. Localised areas of "perched" litter were scattered over the plot depending upon the position of fallen logs from the original stand.

FIG. 5.2.1. LITTERBED PROFILES

L = layer of fresh leaves, bark and twigs
F = decomposing layer of leaves with relatively intact bark and twigs
H = humus layer
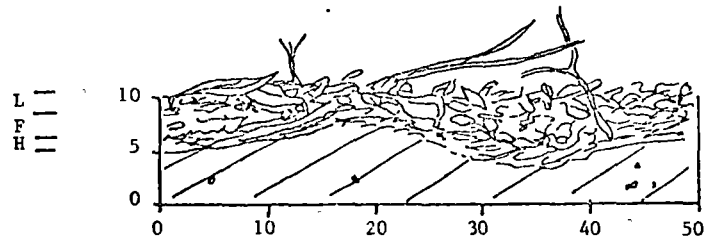
Site 1.   Medium crumb mull litter.
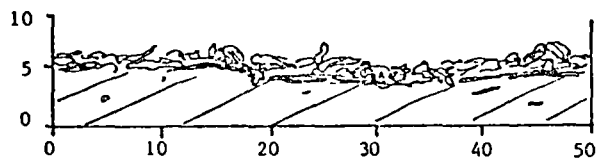
Site 2.   Mor type.
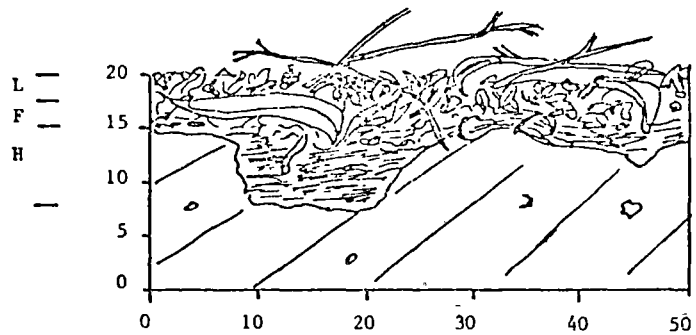
Site 3.   Coarse crumb mull.
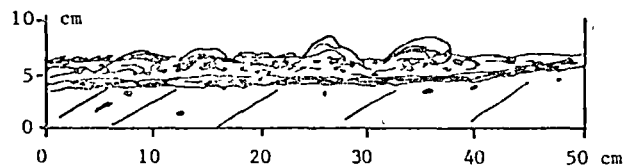
Site 4.   Mor type.

Greater variability in litter depth occurred at Site 3, the L and F layers ranging from 2 to 5 cm as per Site 1, but the 'H' layer varied from 2 to 8 cm. This variation was considered to be the result of the 1940 wildfire that was responsible for the 2 ages of regeneration, and the greater number of stems of understorey species that were present.

There was little tendency for leaf litter to become stratified at Site 2, and it was compact, and the 'F' layer predominated. Average depth was 2 cm with an 'H' layer of about 1 cm, and a clear delineation from the underlying mineral soil.

The litterbed at Site 4 was unstratified and compact, 1-2 cm deep, with indistinguishable 'L' and 'F' layers. The 'H' layer was similarly shallow (about 0.5 cm) and irregular.

(ii) pH

Samples of litter (L + F layers) and humus were taken at random from 25 locations in each of Sites 1, 2, and 3 and bulked to make 5 samples per site. Replicate samples were coarsely macerated, mixed with distilled water in the ratio 1:5 w/v, shaken vigorously, and left to stand for one hour, when pH values were determined electrimetrically. Results are listed below in Table 5.2.1.

Table 5.2.1.   Average pH values of litter per site.

Source of Litter material	Site 1	Site 2	Site 3
L + F layer	4.6	5.1	4.5
Humus	4.0	5.0	4.0
Soil immediately below humus layer	3.6	4.8	3.9

(iii) Moisture content

The moisture-content percentage, on an oven-dry weight basis (Slatyer and McIlroy, 1961) of litter at each site was determined at 6-weekly intervals from data detailed in Section 6.3. Upper trap catches were used to determine the 'L' layer values, and catches from the lower traps that had accumulated for a period greater than 3 months were used to determine values for litter equivalent to the 'F' layer.

Results are presented in Table 5.2.2.

5.3. ESTIMATION OF ACCUMULATED LITTER MATERIALS

5.3.1 Subjective survey of logs and perched litter

Method

The 40 x 25 m plot established at each of Sites 1, 2, and 3 was divided into 40 sub-plots of 5 x 5 m. Each of the 40 sub-plots was surveyed for the percentage ground cover of logs and of perched litter. In some instances logs were supported upon other logs to form a lattice, and where this occurred it was common to find a large proportion of smaller material perched above the ground. The survey estimated the ground cover that perched logs and litter would have occupied had all material been laid side by side. It was possible to obtain values in excess of 100% by this method although this did not occur in this study.

All assessed values were expressed to the nearest 5% ground cover.

Table 5.2.2.   Litter moisture content per site.

Litter material	Site	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81	1.7.81	12.8.81
L	1	204.3	25.0	51.8	20.9	183.0	190.4	315.4									
F		-	30.4	27.8	33.1	173.4	233.6	330.3									
L	2	203.8	33.7	107.8	33.0	189.7	181.5	251.4									
F		-	35.3	55.8	51.4	153.6	244.1	293.4									
L	3	207.3	27.9	33.8	24.3	152.1	147.3	198.2	166.8	30.2	66.5	17.4	104.6	180.3	190.0	260.9	227.9
F		-	31.4	39.2	36.5	166.0	217.2	278.9	246.1	112.9	135.6	36.8	45.5	211.3	250.4	365.2	351.2
L	4	198.0	33.6	25.3	23.4	100.6	136.0	172.5	170.0	17.4	70.8	24.8	63.6	121.7	139.9		
F		-	27.0	23.6	32.0	131.1	220.7	254.3	245.7	78.8	83.8	23.2	60.1	202.5	228.3		

Results

Fig. 5.3.1 illustrates the distribution of logs and perched litter over each of the 3 sites.[1] The mean percentage ground cover of logs and of perched litter are listed in Table 5.3.1.

Table 5.3.1.   Logs and perched litter: % ground cover

| Material | % Ground cover | | |
	Site 1	Site 2	Site 3
Logs	13	17	16
Perched litter	10	7.5	14
(Includes leaves, twigs, bark, and branches)			

5.3.2 Objective estimation of standing crop of woody materials

Method

The survey of percentage ground cover of logs and perched litter was used to selectively sample each site for standing crop of woody materials. A frequency table was compiled and 5 sub-plots (5 x 5 m) selected to cover the occurrence of the range of values obtained. Selected sub-plots are indicated in Fig. 5.3.1.

Each selected sub-plot was delineated with plastic tape by measuring the lengths of the sides and adjusting corner pegs to fit measured diagonals. The lengths and mid-diameters of all woody materials within each sub-plot were recorded and used to calculate the total volume of logs greater than 15 cm in diameter, and of twigs, branches and fallen stems greater than 1.0 cm, but less than 15 cm.

[1]Site 3 was divided into 2 parts to avoid including a large (ca. 3 m diameter) over-mature *E. obliqua* old growth remnant of the original stand, and the excessive bark input that may have resulted from the "halo" effect described by McColl (1966).

FIG. 5.3.1.

◄─────────── 40m ───────────►

15(10)	45(30)	15(10)	10(10)	15(5)	10(5)	5(5)	30(20)
10(5)	10(5)	5(5)	10(5)	10(5)	20(10)	5(5)	5(5)
5(5)	5(5)	5(5)	5(5)	15(5)	10(5)	10(5)	45(50)
10(10)	5(5)	5(5)	20(10)	-5(5)	40(30)	15(20)	10(10)
5(10)	5(5)	5(5)	5(5)	10(5)	30(30)	10(5)	15(10)

25m (vertical)
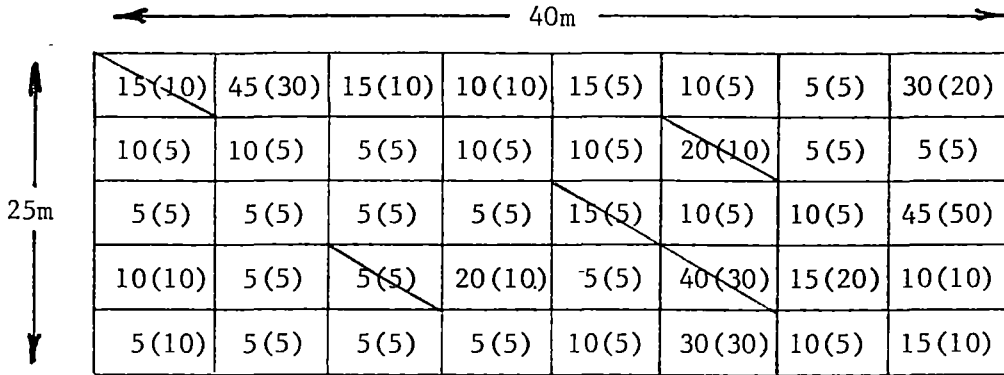
Site 1.   Tall open *E. obliqua* regrowth.

5(5)	10(5)	20(20)	5(5)	5(5)	40(25)	30(10)	10(20)
5(5)	5(5)	60(10)	20(5)	15(5)	25(5)	15(5)	5(5)
5(5)	10(5)	5(5)	20(5)	20(5)	30(10)	15(10)	5(5)
15(5)	5(5)	20(20)	15(5)	5(5)	10(5)	20(5)	10(5)
30(5)	50(5)	25(10)	5(5)	20(5)	20(5)	15(10)	15(10)

Site 2.   Mixed forest of predominantly
          Nothofagus cunninghamii.

◄── 10m ──►

10(5)	10(10)
15(5)	25(15)
20(5)	5(5)
25(10)	30(10)
5(5)	5(5)

◄── 20m ──►

O/G
E. obliqua

◄─────────── 30m ───────────►

20(5)	25(5)	5(10)	5(5)	5(5)	10(5)
20(5)	5(5)	5(5)	5(5)	5(5)	15(5)
35(10)	20(30)	15(20)	35(40)	5(10)	5(5)
20(5)	15(20)	50(40)	40(50)	25(40)	25(10)
20(10)	10(10)	25(40)	15(25)	10(40)	15(5)
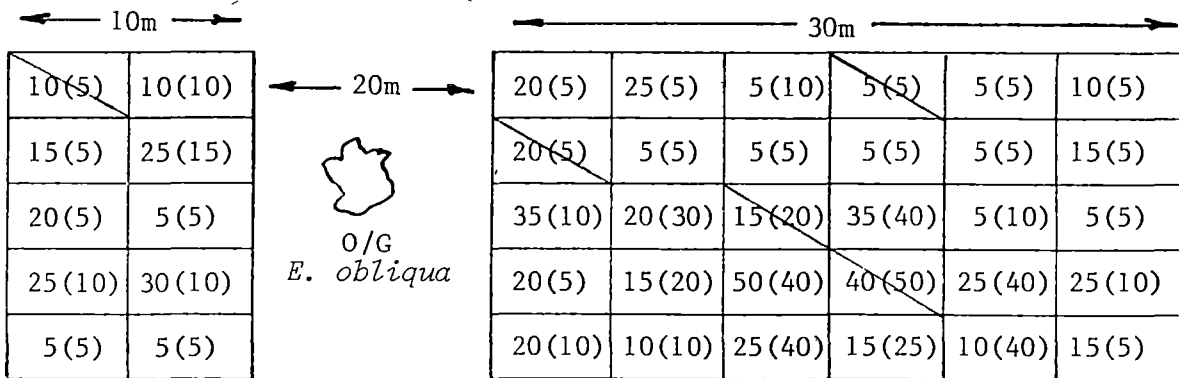
Site 3.   Tall open *O. obliqua* regrowth.

LEGEND

15(25) = 15% cover of logs, 25% cover of perched litter

� = Total area of 5x5m plot assessed for determination of
    woody material >1.0cm diameter

All values were calculated from the sum of the 5 sub-plots on a per ha basis. Materials greater than 15 cm in diameter were considered to have originated from the pre-regeneration stand.

The weight of woody materials per hectare was calculated by applying a factor of 0.785 g.cm^2 to the calculated volume data. This factor is the density of *E. obliqua* at 12% moisture content quoted in Penfold and Willis (1961).

Results

Total accumulation of woody material and litter, the components of that value, and values for litter accession, basal area, site index, and number of standing trees per site are compared in Table 5.3.2.

5.3.3 Estimation of standing crop of litter

Method

Preliminary studies were conducted to assess:

(i)   size of plot, and

(ii) number of samples required to estimate the standing crop of litter (bark, leaves, and twigs less than 1.0 cm in diameter) at each site.

The first study employed a 1 m^2 quadrat to sub-sample the forest floor in 10 locations. This quadrat size was too large for random placement at Sites 1 and 3 due to the number of standing stems. The 'L' and 'F' layers were not separated in this study, and sampling resulted in considerable variation between quadrats, especially at Site 3 where it was difficult to exclude mineral soil from the samples.

A second study employed a circular quadrat of 48 cm diameter that was readily established on the forest floor and could be cast

Table 5.3.2. Comparison of mean values of accession and
accumulation per site with selected site
characteristics.

Parameter	Site 1	Site 2	Site 3	Ratio Site 1 / Site 3
Site Index	30	–	27	1.111
Live basal area ($m^2 ha^{-1}$)	96.91	82.83	69.78	1.389
Total live stems ha^{-1}	6190	8430	9050	0.684
Accession ($t.ha^{-1}$), leaves + bark + twigs <1.0 cm				
1979/80	5.060	4.058	4.769	1.061
1980/81	5.638	4.935	5.502	1.025
1981/82	5.227	5.074	4.412	1.185
Mean (1979/82)	5.308	4.689	4.894	1.085
Accumulation ($t.ha^{-1}$)				
Leaves + bark + twigs <1.0 cm, 1982	22.150	11.932	20.541	1.073
Twigs >1.0 cm <15.0 cm	37.87	11.38	26.67	1.420
Logs >15.0 cm	1051.12	344.15	746.89	1.407
Total excluding logs >15.0 cm	60.02	23.31	47.21	1.271
Total including logs >15.0 cm	1111.14	367.46	794.10	1.399
Total woody material only	1088.99	355.53	773.54	1.408

into randomly selected sampling positions. Ten samples were taken from each site in June, 1982. All material was collected to bare mineral soil, and at Sites 1 and 3 the samples were separated into materials of the 'L' and 'F' layer, where the 'F' layer also contained humus and, unavoidably a proportion of mineral soil. It was not possible to separate litter into 'L' and 'F' layers at Site 2.

Samples from both studies were air-dried in a glasshouse, then separately ground to x 60 mesh (B.S.S.) in a Wiley Mill, and oven-dried for 72 hours at 70°C. Three sub-samples were systematically taken (Anon. 1982) from each sample and the ash content determined on a percentage basis after 3 hours in a muffle furnace at 600°C. Litter standing crop calculations were adjusted relative to individual ash values where 2.5% ash was taken as a mean value for uncontaminated litter.

Results

A comparison of the results of estimates of standing crop of litter obtained by the 2 methods was made for Site 1. The 1 m^2 quadrat gave a mean value of 40.918 t.ha.$^{-1}$, standard deviation of 20.697 t.ha.$^{-1}$, and coefficient of variation percentage of 50.58 between quadrats. In contrast, circular quadrats gave a mean value of 22.15 t.ha.$^{-1}$, standard deviation of 3.289 t.ha.$^{-1}$, and coefficient of variation percentage of 14.8 between quadrats. Ten samples (quadrats) were used in each instance, and in order to obtain values for standing crop of litter within 10% of the true mean and 95% confidence it was calculated that the first study would have required 102 samples and the second study 9 samples. Hence the results of the 1 m^2 quadrat sampling were discarded in favour of data of the circular, smaller, quadrat sampler.

Table 5.3.3 lists the mean value, standard deviation, and percentage coefficient of variation for each site of individual litter layers.

The mean values of standing crop of litter per site are included in Table 5.3.2 as the fraction of the total standing crop less than 1.0 cm in diameter. Sites 1 and 3 were of similar vegetation and a comparison between the sites in relation to various measured parameters is included in Table 5.3.2, derived from the ratios of Site 1/Site 2 values.

5.3.4 *Calculation of litter decay constants*

Preamble

Kittredge (1948), Jenny *et al.* (1949), Greenland and Nye (1959), and Olson (1963) described models and methods for the determination of decay parameters. Olson (1963) described alternative models for litter accumulation and decomposition, and the model for accumulation with continuous litterfall has been selected as best suited to Australian conditions by many workers viz. Lee and Correll (1978), Birk (1979b), Fox *et al.* (1979), Walker (1980), and Pressland (1982), and has been critically examined by Birk and Simpson (1980).

Olson's (1963) continuous input model is based upon the amount of standing crop of litter (X) being dependant upon the balance between litter production (L) and decomposition (k), with the rate of change in X being expressed as:

$$\frac{dx}{dt} = L - kX \qquad \text{(Olson, 1963)}$$

Under steady state conditions, dx/dt = 0, and

$$k = \frac{L}{X}$$

This calculation can be extended to compare the half-life of litter, $t_{1/2}$. If L and k remain constant and the conditions for the

Table 5.3.3. The standing crop of litter and its percentage content of inorganic matter per site (t.ha^{-1}).

	Site 1	Site 2	Site 3
Mean standing crop of litter (t.ha^{-1})	22.150	11.932	20.541
Standard deviation	3.289	3.691	3.933
Coefficient of variation %	14.8	30.94	19.15
Percentage inorganic matter content			
'L' layer: $\bar{x}$	5.30	†	4.17
S	2.32	†	1.19
C.V. %	43.81	†	28.54
'F' layer: $\bar{x}$	20.44	†	14.47
S	14.14	†	6.33
C.V. %	69.18	†	43.75
L+F layers: $\bar{x}$		12.76	
S		9.09	
C.V. %		71.27	

†; not calculated for Site 2.

model remain unchanged, then X may be defined as a function of time, X = 0 when t = 0, and hence:

$$X = \frac{L}{X} (1 - 3^{-kt})$$ (Olson, 1963)

and as dx/dt is proportional to the amount of litter present, then the theoretical half-life of litter may be calculated similarly to calculations of radioactive decay viz.

$$t_{1/2} = \frac{0.693}{k},$$ (Olson, 1963)

and 3/k and 5/k equals the time period required to attain 95 and 99 percent of the final steady state (X_{ss}) level.

Method

The continuous input model of Olson (1963) was applied to the data for litter production and accumulation at Sites 1, 2, and 3, as litter input was continuous and there had been an absence of major perturbations e.g. fire, at Sites 2 and 3 for 42 years, and at Site 1 for 63 years.

Results

Table 5.3.4 lists calculated values for k, $t_{1/2}$, and the time required to attain 95 and 99 percent levels of litter steady state (Xss) at each site, using the litter production value for the year corresponding to the year of standing crop determination, and the mean annual litter production value for the study period, 1979-1982.

5.4.   DISCUSSION

(i) Depth

Litterbed depth was similar between the comparable vegetation types of Sites 1 and 3, and markedly less at Sites 2 and 4. The lack of depth at Site 2 was in keeping with the lower measured value for accumulated litter at this site, and its more rapid decay rate.

Table 5.3.4. Decay constants of total litter[1] at Hastings study sites.

Litter values	Parameter	Site 1	Site 2	Site 3
1982 accession and 1982 accumulation data	k	0.236	0.425	0.215
	$t\frac{1}{2}$	2.936	1.631	3.220
	Xss 95%	12.712	7.059	13,953
	Xss 99%	21.186	11.765	23.256
Mean of 1979/82 accession and 1982 accumulation data	k	0.240	0.393	0.238
	$t\frac{1}{2}$	2.888	1.763	2.912
	Xss 95%	12.500	7.634	12.605
	Xss 99%	20.833	12.723	21.008

1. Total litter = leaves + bark + twigs <1.0 cm in diameter.

(ii) pH

Litter pH values decreased with increasing depth at all sites, but were less acidic than values derived for the underlying soil. These results are in agreement with Ovington and Madgewick (1959).

The acidic litter layer values would seem to favour fungi rather than bacteria as primary decomposer agencies as discussed by Gyllenberg and Eklund (1974) and would be particularly suited to the wood-inhabiting Basidiomycetes that are more tolerant of acidity than those that inhabit litter. Walker (1981) and Pressland (1982) give decomposition rates of wood and bark that are much lower than values for leaf litter. These components predominate, as a consequence of their slower decomposition rate, in the 'F' layer, an environment cited as suitable for wood-inhabiting Basidiomycetes.

Soil arthropod populations may be affected by the acidity of the litter of Sites 1, 2, and 3, as Edwards (1974) refers to the work of several authors that found arthropod populations to be greater in alkaline conditions.

(iii) Moisture content

Litterbed moisture content percentages over an 18 month study period were directly related to mean rainfall and air temperature experienced during the interval of measurement. Moisture content of both the 'L' and 'F' layers increased with increased rainfall, and decreased with increased air temperature. The 'L' layer was drier than the decomposing 'F' layer, with the 'L' layer ranging from 24 to 260% (on the basis of oven-dry weight) and the 'F' layer correspondingly from 36 to 360% at Site 3. Litter at Site 4, the open scrub site, was drier than the other sites with values for the 'L' layer ranging from 23 to 198%, and the 'F' layer from 23 to 254%. These results agree with those of Clary and Ffolliott (1969), who found the

moisture holding capacity of litter varied with depth, with greatest capacities being in the amorphous 'H' layer and lowest in the 'L' layer.

There was a marked seasonal variation in litter moisture content and a marked correspondence in the seasonal pattern between sites.

The influence of moisture on litter breakdown has been discussed by Williams and Gray (1974), low moisture levels reducing litter breakdown rates. Van der Drift (1963) found that decomposition of both mull and mor litter was retarded by drought, and numbers of saprophagous animals in litter were reduced. Lee and Correll (1978) stated that earthworms and macroarthropods fed and moved about in the litter layers only when humid conditions and moderate temperatures prevailed in litter and surface soil. Table 5.2.2 demonstrates that lack of litter moisture seldom occurs in the southern forests.

(iv) Survey of logs and perched litter

Mean values for percentage ground cover of perched litter and logs on the 3 sites (Table 5.3.1) do not agree with the measured values derived from selected sub-plots. The anomalies result from the difficulty of being able to visually convert the spatial distribution of material to one plane, and illustrate the need for an objective method of assessment such as the direct measurement technique of Sneeuwjagt (1973).

Although visual estimation resulted in an incorrect total plot estimation, it did provide a means of selecting sub-plots for detailed examination within sites.

(v) Estimation of standing crop and calculation of decay constants

The data presented in Table 5.3.2, for standing crop of all materials on the 3 study sites, may be considered as 3 basic components.

(i) Leaves + bark +, twigs less than 1.0 cm; represents the standing crop of litter,

(ii) Woody material greater than 1.0 cm but less than 15.0 cm,

(iii) Woody material greater than 15.0 cm (logs).

All woody material at Sites 1 and 3 greater than 15.0 cm in diameter originated from the pre-regeneration stand, and material types (i) and (ii) from the current stand. The rainforest (Site 2) had a mixture of relatively recent windblown material including large stems and limbs of indeterminate age. Only material type (i) was used for the calculation of decay constants and for litter standing crop comparison with other Australian forests as measurement of limb fall were not made in the studies of accession.

A comparison of litter accession, accumulation, and decay constants k, $t_{1/2}$, and 5/k is given in Table 5.4.1 for values derived in this study, and values for other forests of Australia.

Both accession and accumulation amounts of the *E. obliqua* stands of Sites 1 and 3 are greater than those obtained for other *E. obliqua* studies in warm temperate forests of southeastern South Australia cited by Lee and Correll (1978), and northern Victoria cited by Attiwill (1968). Litter production values in this study conformed to the values predicted by Bray and Gorham (1964) for the geographic location and cool, temperate environment of the Southern Forests. Values derived by Attiwill (1968) and Lee and Correll (1978) were below those expected for warm temperate forests of the more northern latitudes.

Proportionality of accession and accumulation was similar in all 3 studies of *E. obliqua*, and hence decay constants were also similar. It is assumed that the cooler temperatures of southern

Table 5.4.1.   Comparison of Hastings forest sites litter data with other Australian forests.

Forest type	Litter fall ($t.ha^{-1}$)	Litter standing crop ($t.ha^{-1}$)	Decay constants			Location	Reference
			k	$k_{\frac{1}{2}}$	$^5/_k$		
Tall open *E. obliqua* Cool temperate, wet sclerophyll	5.31 (5.06-5.64)	22.15	0.24	2.94	21.2	Hastings, Southern Tasmania	This study
Tall, open *E. obliqua* Cool temperate, wet sclerophyll	4.89 (4.41-5.50)	20.54	0.22	3.22	23.3	Hastings, Southern Tasmania	This study
Mixed forest, cool temperate (*N. cunninghamii* predominate)	4.69 (4.06-5.07)	11.93	0.43	1.63	11.8	Hastings, Southern Tasmania	This study
E. obliqua/E. baxteri Warm temperate, dry sclerophyll	2.33 (2.10-2.65)	9.8	0.24	2.91	20.8	South eastern South Australia	Lee and Correll (1978)
E. obliqua Warm temperate, dry sclerophyll	3.56	18.25	0.20	3.55	25.6	Northern Victoria	Attiwill (1968)[c]
E. regnans Temperate, wet sclerophyll	7.76 (7.05-9.95)	21.80	0.36	1.95	14.0	Southern Victoria	Ashton (1975)[c]
F. maculata Spotted Gum forest	4.86 (3.60-6.84)	11.30	0.43	1.61	11.6	South coastal NSW	McColl (1966)[c]
E. marginata Jarrah forest	2.68 (2.30-3.35)	16.30	0.16	4.23	30.5	South western W.A.	Hatch (1955)[c]
E. signata/E. umbra	6.4	27.0	0.24	2.92	21.1	Stradboke Island	Rogers and Westman (1977)[a]

Table 5.4.1.

Comparison of Hastings forest sites litter data with other Australian forests.   Cont'd.

E. pilularis/Angophora costata Open forest	5.2	16.7	0.31	2.23	16.1	Seal Rocks, N.S.W.	Fox *et al.* (1979)
E. pilularis open forest	4.9	12.2	0.40	1.72	12.4	Kendall, Bulls Ground, N.S.W.	Nicholson and Love (1972)[a]
E. sieberi Tall open forest	3.1	14.8	0.21	3.32	23.9	Blue Mountains, N.S.W.	Van Loon (1977)[a]
E. pilularis, open forest	7.1	15.5	0.46	1.51	10.9	Bellangry State Forest, N.S.W.	Van Loon (1970, 1977)[a]
E. pilularis, open forest	4.3	13.9	0.31	2.24	16.2	Manning River National Forest, N.S.W.	Van Loon (1969)[a]
Alpine, open forest	3.56	40.0	0.09	7.79	56.1	Snowy Mountains, N.S.W.	Park (1977)[b]
Open forest	3.70	18.00	0.21	3.38	24.4	Dwellingup, W.A.	Peet (1971)[b]
Open forest	3.80	25.00	0.15	4.56	32.9	N.W. Tasmania	Jackson (1968)[b]
Open forest	5.02	17.48	0.29	2.41	17.4	Canberra area, A.C.T.	Hutchings and Oswald (1975)[b]
Tropical closed forest	5.11	5.62	0.91	0.76	5.5	Innisfail, Queensland	Bailey (1976)[b]
Temperate, closed forest	7.07	12.65	0.56	1.16	8.3	Armidale area, N.S.W.	Watson (1977)[b]

a = Data from Fox *et al.* (1979);   b = Data from Walker (1971);   c = Data from Lee and Correll (1978).

Tasmania were compensated for by improved litter moisture conditions for continued decomposition.

Ashton (1975), working in *E. regnans* forest in Victoria recorded higher accession values that were in agreement with Bray and Gorham (1964), a similar amount of accumulated litter, and hence a faster decomposition rate. This may be expected, given warmer temperatures and adequate litter moisture in those forests. The faster decomposition rate in the closed mixed-forest of Site 2 in this study, was assumed to be attributable to the wetter conditions of the forest floor.

The continuous input model of Olson (1963) includes a number of assumptions that, due to their application to different situations, may result in over-or-under estimation of the litter turnover. The consequent variabilities associated with these assumptions have been detailed by Birk and Simpson (1980). Assumptions included by the model are:

(i) that the system is in steady state, and free from recent major perturbations viz. fire,

(ii) that litter falls continuously throughout the year, and is constant from year to year,

(iii) that a constant proportion (k) of the forest floor turns over annually.

Assumption (i) was satisfied by the conditions of the southern forest sites. Assumption (ii) may have lead to over-or-under estimation as although litter falls continuously throughout the year, there was marked seasonality in the rate of fall, and the amount varied from year to year. This property is not peculiar to these studies, but occurs across a range of forest types as illustrated by the variability of accession measured by several authors in the data of Table

5.4.2. Considering the range of accession values measured in these studies (Table 5.3.2), the related k values ranged from 0.228 to 0.256 with a mean of 0.240, and a value for 1981/82 (the year of standing crop determination) of 0.236. The variation in k due to variation in L was 0.240 ± 0.014, with the percentage change in k $\pm$ 23-25% cited by Birk and Simpson (1980) for jarrah and karri forests due to seasonality, and was less than the variation in k obtained by Lee and Correll (1968) in other *E. obliqua* forests (k = 0.240 ± 0.028, $\pm$ 11.6% change in k), and by Ashton (1975) in *E. regnans* (k = 0.360 ± 0.067, $\pm$ 18.5% change in k).

There was insufficient information to test assumption (iii), but variations in climate from year to year are one way by which the turnover of litter on the forest floor may be affected e.g. the incidence of drought. Climatic conditions for the southern forests were relatively stable during the 3 year period of study.

Variability in k determination was dependent upon the suitability of application of the assumptions of Olson (1963) to the stand under study. Another consideration which may be of at least equal importance and which is not generally mentioned in the literature, is variations that may arise from inadequacy of sampling techniques. Improved sampling technique viz. type and number of traps for measurement of accession, and recognition of the possible inclusion of inorganic matter in standing crop samples, may themselves be responsible for considerable improvement in the estimation of k.

Table 5.3.2 compares accession and standing crop of litter and of woody material between Sites 1 and 3 with their values for Site Index and basal area by calculation of the ratios of Site 1/Site 3 data.

The ratio for live basal area between sites was 1.4, the same value derived for ratios of standing crop of woody material attributable to both the pre-regeneration and current stand. The between sites ratio for Site Index was 1.1, and this ratio was the same for litter accession and litter standing crop of the current stand.

These findings are in agreement with those of Chapter 4 that demonstrated litter production to be significantly correlated with live basal area of individual species, where both are indices of net primary production and of photosynthetic efficiency.

CHAPTER 6

DECOMPOSITION

6.1   DEFINITION

.The Oxford English Dictionary defines decomposition as:

"the action or process of decomposing, separation or resolution (or anything) into its constituent elements; disintegration; putresence."

Decomposition may relate to the physical disintegration of dead plant structures from attachment to living plant, to the stage where its gross cell structure is unrecognisable following detachment. It may also refer to the breakdown of complex organic molecules to carbon dioxide, water, and mineral components.

In all instances of use "decomposition" is generally expressed as the proportion of the initial weight of the substrate lost per unit of time.

6.2   LITTER BAG EXPERIMENT

6.2.1 Introduction

This section describes a series of experiments designed to study specific aspects of the litter decomposition process. Each experiment is treated separately and then discussed with relevance to the overall process. Direct estimation of litter decomposition rate by the use of mesh bags has been discussed in Section 2.1 but a brief review of associated problems and benefits of the technique will assist an understanding of the approach adopted in these investigations.

Problems that arise from the confinement of litter in mesh bags have been considered by many authors e.g. Bocock and Gilbert (1957), Crossley and Hoglund (1962), Suffling and Smith (1974), Kawahara and Sato (1974), Edwards (1977) and Woods and Raison (1982). Nonetheless,

there are many investigations for which the use of litter bags is ideal e.g. the effect of litter fauna upon decomposition rate (Wood 1971, 1974; Weary and Merriam 1978), the relative contribution of various taxonomic groups of litter fauna and their interaction with microorganisms (Edwards and Heath 1963; Macauley 1975) and studies of fungal succession (Macauley 1979). The prime object of litter bags is to confine selected litter material and determine its loss of weight with time, such loss being considered attributable to decomposition. Any influence of confinement within the bag upon loss in weight and its determination will lead to erroneous conclusions regarding litter decomposition under natural conditions. The major sources of error in the estimation of decomposition rate by the use of litter bags arise from:

    (i)   size of mesh

    (ii)   type of leaf material,

    (iii)   time of field placement, and

    (iv)   method of placement.

Confining litter in mesh bags has been shown to create artificial conditions that may result in reduced decay rates (Witkamp and Olson 1963) and the loss of leaf fragments during bag recovery and handling may exaggerate values for weight loss, hence the variability of the estimate of weight loss increases greatly as time progresses (Richards and Charley 1977) The size and type of mesh used in bag construction obviously dictates the degree of effect; fine mesh may exclude soil biota (Bocock and Gilbert 1957, Witkamp and Olson 1963, Edwards 1977), and in moist conditions may modify the microclimate by increasing moisture content of the contents of the bag (Gilbert and Bocock 1962, Witkamp and Olson 1963) although Anderson (1973) could find no consistent effect of widely varying mesh dimensions on the moisture content of leaves in a moist deciduous woodland.

The difficulty in comparing results of various workers has generally been blamed upon the variability of litter material selected for use, and in particular upon the use of green leaves rather than those that are shed naturally. Richards and Charley (1977) and Woods and Raison (1982) consider it imperative that only naturally shed leaves be used so that they are representative of the trophic and nutrient status of leaf fall at the time the bags are set out. Naturally shed leaves, however, may not always be available in sufficient quantities, particularly where studies are undertaken with understorey species.

Time and method of placement of litter bags may have an effect upon measured rates of decay, particularly if green, picked leaves are used. Ideal arrangements would be placement of naturally shed litter *in situ* at the time of maximum litterfall as leaves are then most readily available, and the decay rate measured from this date will relate to the largest possible leaf population. Macauley (1975) found no significant difference in litter decay rate when it was confined in bags placed on the litter surface or on surface soil cleared of litter. Woods and Raison (1982) argue that the less disturbance of the litterbed the more natural the environment, and they recommend placement on the litter surface. Another consideration in favour of placement on the litter surface is the intrusion of silt into litter bags that may result from their placement on bare mineral soil (this problem is discussed in detail in Section 6.3). However, the standard inoculum base that results from bag placement upon bare mineral soil could be an important consideration.

Having considered the problems and criticisms of the use of litter bags, a number of experiments were established to study specific aspects of the decomposition process and the methodology of their

investigation.   Standardised procedures were adhered to for each experiment, and these procedures are detailed under Methods and Materials.

6.2.2 *Methods and Materials.*

(i)   Bag manufacture.

Flat, rectangular bags measuring 250 x 200 mm were manufactured from terylene tulle of 2 mm mesh, sewn together with terylene sail-maker's thread, and identified by stamped aluminium tags that were attached by fine plastic tubing. Each bag was separately weighed and its weight recorded.

The terylene tulle was of fine enough mesh to prevent major loss of leaf fragments, but was not considered a barrier to the entry of litter fauna, as during an allied experiment up to 30 holes had been observed to have been eaten through the mesh material, indicating that larger biota could gain access.

(ii) Leaf drying curves.

These experiments required the use of green, picked leaves as it was not possible to collect sufficient quantities of leaves of understorey species required for replication.   Prior to preparing litter bags the equivalent oven dry weight (70°C) of leaves at some suitable pre-drying condition was determined as it was essential that the same quantities of leaves could be prepared per replication and treatment.   The lowest temperature at which available drying-ovens could operate was 35°C, and this temperature was checked for its suitability.

Collections were made of green picked leaves of all species to be studied.   Only those leaves that were considered likely to be naturally shed from the canopy in the coming summer period of litter-fall were collected.   Collections of individual leaf species were

thoroughly mixed, placed in wire trays and subjected to a drying temp-erature of 35° in air-circulated drying ovens. Table 6.2.1 lists the percentage of original green weight of leaves remaining with time of drying at 35°C, after 48 hr at 70°C, and after 48 hr at 102°C. Drying curves for each species are illustrated in Fig. 6.2.1. The curves demonstrated that it was possible to collect leaves, dry them for 48 hr at 35°C, determine their equivalent oven-dry weight at 70°C, and have adequate time for bag filling and sewing without significant loss in weight.

(iii) Leaf collection and bag preparation.

Accessional data at the most litter-productive site (S1) indic-ated a total annual litterfall of approximately 5.0 t.ha.$^{-1}$ of which about 3.1t were leaves. Litter bag area was 500cm^2 and hence the weight of leaves that may be expected to fall annually upon such an area was 15.5g, and of total litter was 25g. An equivalent oven-dry weight (70°C) of 20g was selected as the standard sample quantity for litter bag packing. The 35°C weight of leaves required to obtain this amount is listed per species in Table 6.2.1.

Leaves of all species were picked green from live, standing trees, from trees felled specifically for collection purposes, or from limbs shot from tree crowns with a .270 calibre rifle. Only those leaves that were considered likely to be naturally shed were plucked (petiole intact), and leaves of the lower crown were avoided.

Twenty grams of equivalent oven-dry weight of leaves per spec-ies were placed into appropriately labelled bags which were then sewn up and stacked in cardboard boxes for transportation to the field.

(iv) Field placement.

Stratified random placement was made of all bags at each site to ensure adequate coverage of the sites, although some subjectivity

Table 6.2.1.   Percentage of original green weight of leaves remaining with drying time at 35°C.

Species \ Time (hr)	% original green weight of leaves with time at 35°C										Weight leaves at 35°C required to yield 20g at 70°C
	15.5	18	22	39	42	112	118	135	After 48 hrs at 70°C	at 105°C	
Eucalyptus obliqua	51.7	50.6	49.3	47.6	47.7	47.3	47.5	57.3	46.3	44.7	20.6
Phebalia marginata	65.8	62.7	57.6	45.3	44.8	43.6	43.7	43.6	42.5	41.7	21.1
Eucryphia lucida	51.6	51.3	50.4	49.9	50.4	49.5	50.5	49.5	48.8	47.9	20.7
Phebalium squameum	54.2	50.5	46.2	40.1	40.4	39.4	40.2	39.4	38.8	38.0	20.8
Atherosperma moschatum	49.1	44.5	37.9	29.9	29.8	29.3	29.6	29.4	28.2	26.6	21.1
Pomaderris apetala	56.3	53.6	49.6	42.0	41.9	41.2	41.5	41.2	40.0	39.2	30.0
Eucalyptus nitida	58.1	56.6	54.1	51.1	51.0	50.5	50.7	50.5	49.5	47.1	20.6
Acacia melanoxylon	49.9	48.4	46.9	44.7	44.9	44.0	44.7	44.1	42.4	42.2	21.2
Nothofagus cunninghamii	44.6	44.2	43.6	43.0	43.3	42.3	43.1	42.3	41.8	40.9	20.7
Phyllocladus aspleniifolius	66.1	62.8	58.6	49.5	49.2	47.7	47.9	47.7	46.5	45.2	21.2

145

FIG. 6.2.1. LEAF DRYING CURVES OF SELECTED SPECIES WITH TIME AT 35°C
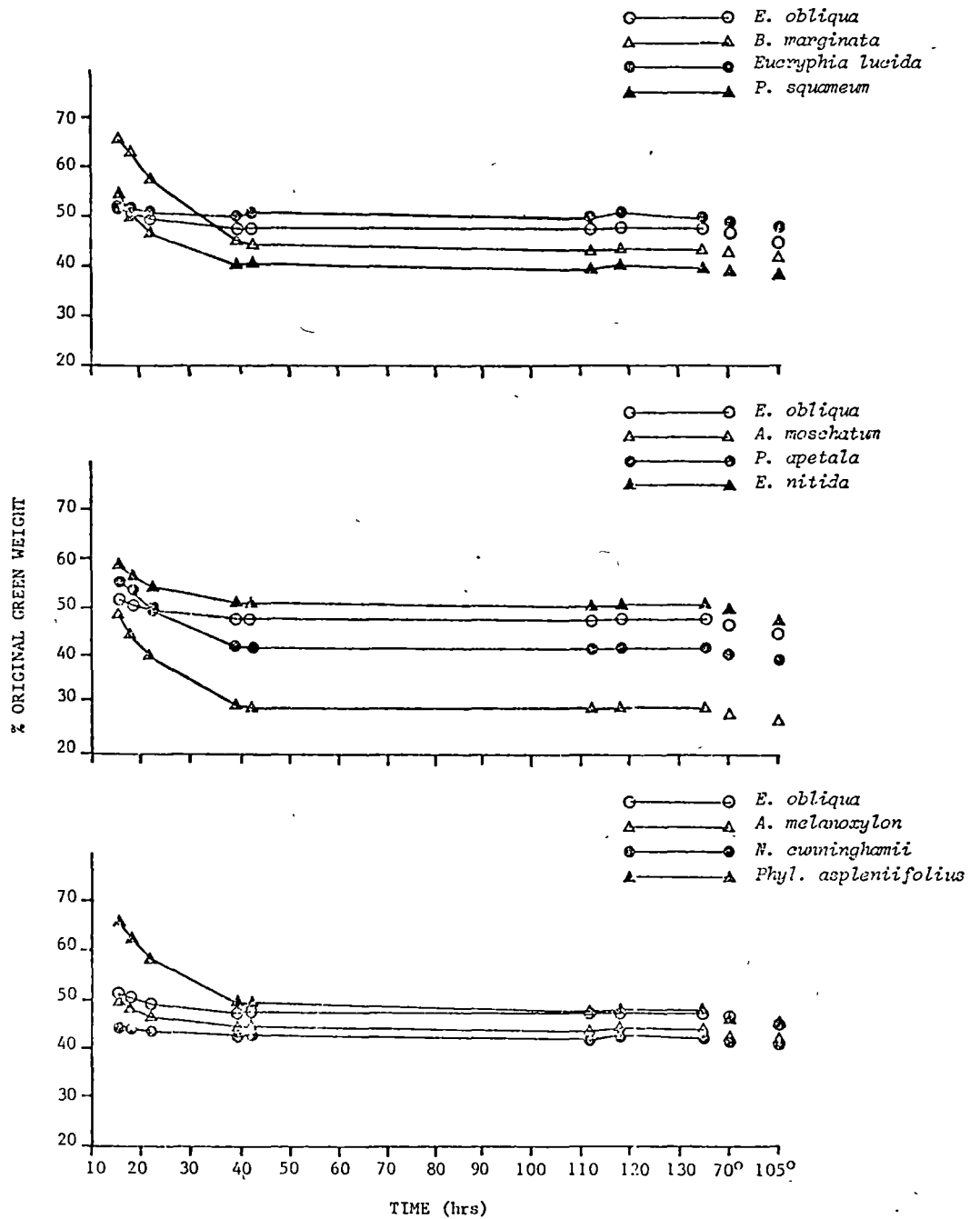
was involved in order to avoid areas of perched litter, logs, and ground depressions that could become waterlogged. Defined animal tracks were also avoided.

Bags were laid flat upon the litterbed surface with as little disturbance as possible, only sticks and twigs being removed to ensure that placement resulted in close contact with the underlying litter layer. Each bag was held in place by 10 gauge, galvanised fencing-wire pegs pinned through two opposite corners. One peg was 20cm long and marked with colour-coded plastic flagging tape to facilitate their re-location at future sampling dates.

(v) Replication.

Except where stated otherwise three replicates of each treatment were used at each study site.

(vi) Field sampling.

One quarter of the total number of bags used in each experiment were sampled after 3, 6, 12 and 18 months in the field.

On each sampling occasion individual bags were carefully lifted to avoid loss of fragmented leaf material. The presence of mycelium within or upon the bag or on the underlying litter surface, the numbers of holes made by biota through the terylene mesh, and macro-arthropods viz. earthworms, millipedes, etc. were recorded. Litter bags were then placed in open polythene bags and stored on edge in cardboard boxes. Woods and Raison (1982) outline a sampling procedure designed to reduce between replicate variation utilising tared paper bags as employed by Suffling and Smith (1974). The wet conditions that often prevail in the stands under study precluded the use of paper bags as they disintegrated.

(vii) Laboratory sampling.

Prior to drying, each litter bag was removed from its plastic bag and placed in 25cm diameter, round plastic dishes together with any fragmented leaf material that had been lost from the litter bag. Dishes were left in strong light in the glasshouse for 60 hours then lifted and any underlying frass and emergent macroarthropods were collected and stored in labelled vials of 70% ethanol. Litter bags and litter debris from the dishes were racked in trays and oven-dried at 70°C for 48 hr, then weighed and individual bag loss in dry weight calculated.

(viii) Species mixes and handling losses.

Where mixtures of leaf species were contained in litter bags, the component species were sorted, redried for 24 hr at 70°C and reweighed to determine the component weight losses. Due to additional handling and sorting, losses were incurred that prevented the balance of calculations required for comparative analyses between individual species effects and effects within species mixes, and it was necessary to adjust the sorted leaf component weights to achieve that balance. It was considered that the degree of fragmentation of individual species within mixtures would be proportional to their respective rates of decomposition, and therefore the apportioning of the weight loss due to the extra handling was made by using the complementary ratio of the weights of the component species in each mix after re-weighing e.g.

Species mix A+B = 12.8g at initial weighing, 70°C,

after time, t, in the field.

After sorting and re-drying, 70°C,   A = 4.7g

                                       B = 6.7g

Sum of sorted components   = 11.4g

Hence handling loss   = 1.4g

Apportionment of loss, A = 1.4/11.4 x 6.7 = 0.82g

B = 1.4/11.4 x 4.7 = 0.58g

Therefore A = 5.5g

B = 7.3g

Sum = 12.8g, the weight of A+B at initial

handling.

(ix) Invertebrate survey.

Taxonomic identification and scoring of numbers of the invert-
ebrates collected from litter bag extractions in the glasshouse were
carried out by Dr. J.L. Madden of this faculty. The aim of the pro-
cedure was to determine whether certain species of invertebrates had a
preference for specific leaf litter species, and to derive information
regarding the role of these decomposer agencies within the litter
layer.

(x) Bacterial colonisation.

Immediately after litter bags were brought in from the field a
representative leaf of each treatment per site was removed and a 12mm
disc aseptically punched from the leaf centre. The remaining leaf
portions were returned to their respective bags. Discs were separ-
ately transferred to 30 ml of Ringer's solution and left to stand with
intermittent hand agitation for 20 minutes. "Orion" urine culture dip
slides coated with a film of MacConkey agar[1] on one side and of
C.L.E.D. medium[1] on the other were dipped in the Ringer's solution and
rotated for 10 seconds, then drained, placed in their containers, and
incubated for 4 days at 23°C. Colony densities were determined from
reference to tables supplied by F.H. Faulding and Co. Ltd., manufact-
urers of Orion dip-slides.

[1]See Appendix D.

This technique was an attempt to devise a means of determining obvious differences that may have existed in bacterial colonisation of the various leaf species. Sampling was possible at the 3 and 6' month collections only, as the majority of leaves thereafter had decomposed and become unsuitable for use.

(xi) Earthworm survey.

During field collections of litter bags the opportunity was taken to determine whether specific leaf species were attractive to earthworms. After lifting, the area beneath each bag was dug to approximately 15cm and the soil and litter sifted for presence of earthworms and macroinvertebrates. This survey was carried out at Site 1 only. Numbers of earthworms collected from bags during laboratory sampling were included in the survey.

6.2.3 Decomposition of leaves

Individual litter bag experiments.

Experiment 1.

Aim

To determine the relative rates of decomposition of leaves of individual overstorey and understorey species, and of selected species mixes.

Methods.

Ten separate species were involved, representing the major vegetation of the four study sites. Eight of these species predominate at S1 and five of them were present at S4. The species selected were:

Eucalyptus obliqua	S1,S4
Eucalyptus nitida	S4
Nothofagus cunninghamii	S1

Atherosperma moschatum	S1
Phyllocladus aspleniifolius	S1
Pomaderris apetala	S1
Eucryphia lucida	S1
Acacia melanoxylon	S1,S4
Phebaleum squameum	S1,S4
Banksia marginata	S4

Observations had shown *Pomaderris* leaves to be rapidly broken down in natural litterbeds, while *Phyllocladus* leaves remained in some instances intact at a depth of at least 0.5m. Mixtures of these species with *E. obliqua* leaves were incorporated into the design to determine whether allelochemical interaction may occur within the litter layer. Where species mixes were packed in litter bags, the total equivalent oven dry weight (E.O.D.W., 70°C) of the mixture was 20gm, the same weight as individual leaf species.

The experiment was established in the tall, open forest at Site 1 and the tall scrubland of Site 4. These sites represented differences in canopy cover, vegetation type, soil drainage and fertility, and litterbed microclimate, and were deliberately selected to determine whether differing rates of decomposition of the confined leaf litter would occur.

All leaves were collected and litter bags placed in the field on August 28th, 1980. A total of 288 bags were involved, representing 12 species/mixes with 3 replications each at 2 sites, and 4 proposed samplings, namely 3, 6, 12, and 18 months.

Results

Mean percentage weight loss per individual species and species mixture are presented for each study site in Table 6.2.2 for each

sampling time, and are compared graphically in Fig. 6.2.2 for Site 1 and Fig. 6.2.3 for Site 4.

All species demonstrated continual decomposition up to the final sampling at 18 months, except for leaves of *Pomaderris apetala* that appeared to stop decomposing between 12 and 18 months. *Phyllocladus aspleniifolias*, decomposed at a very uniform rate up to 18 months. The appearance of the leaves after this period suggested that weight loss could be attributed to weathering or leaching rather than fragmentation and comminution by fungi and arthropods.

Phyllocladus leaves were the slowest to decompose, losing only 21.5% of E.O.D.W. after 18 months, and only 6.0% after the initial 3 months. Excluding *Phyllocladus*, all leaf species demonstrated a rapid weight loss in the initial 3 months, and a relative slowing down of loss rate in the 6 months between the 12 and 18 month sampling (refer Fig. 6.2.2 and 6.2.3).

Phebaleum squameum was the most rapidly decomposed, major weight loss (46.2%) occurring in the initial 3 months in the field.

Decomposition percentages of the individual species and of the species mixes were compared by analysis of variance. Appendix, Statistical Analysis, 11 and 12 lists results of these analyses, and tables the mean decomposition percentages of the inidividual species and of species mixes, ranked according to level and in groups of least significant differences between species/mixture. Due to 50% (18) of the replicates at Site 4 being destroyed by fire between the 12 and 18 month sampling, separate analyses were made of data for 3, 6, and 12 months field exposure (Appendix 11) and 3, 6, 12, and 18 months (Appendix 12).

There were significant differences ($P < 0.001$) in percentage decomposition between species, times, and the species x times inter-

Table 6.2.2. Percent dry weight loss (%) and ranking of relative decomposition rate (R) with time. All figures the mean of 3 replicates.

Species	3 months				6 months				12 months				18 months			
	S1		S4		S1		S4		S1		S4		S1		S4*	
	R	%	R	%	R	%	R	%	R	%	R	%	R	%	R	%
Phyllocladus aspleniifolius	1	6.0	1	5.5	1	8.9	1	9.0	1	14.8	1	13.7	1	21.5	1	18.5
Eucryphia lucida	2	16.0	5	20.0	3	23.7	5	27.9	3	36.2	4	35.8	4	45.0	4	46.5
Banksia marginata	3	17.5	2	14.9	2	23.2	2	20.2	2	36.0	2	33.5	4	45.0	2	41.5
Nothofagus cunninghamii	4	17.7	3	17.4	4	24.4	3	24.4	4	42.3	5	37.3	5	53.5	3	44.0
Acacia melanoxylon	5	18.2	4	19.7	5	29.4	4	24.5	6	46.5	6	38.0	6	56.5	8	56.0
Pomaderris apetala	6	21.9	5	20.0	6	34.5	6	29.0	5	45.2	3	35.3	2	44.0	5	47.0
Eucalyptus nitida	7	27.5	7	27.2	7	37.5	7	31.2	8	53.5	7	47.8	8	61.5	7	54.5
Eucalyptus obliqua	8	33.9	8	32.2	8	45.2	8	38.2	9	55.0	9	60.5	9	63.0	10	79.5
Atherosperma moschatum	9	37.0	9	36.5	9	45.7	9	41.7	7	53.2	8	53.5	7	58.0	7	54.5
Phebalium squameum	10	46.2	10	48.5	10	52.7	10	48.0	10	61.8	10	62.5	10	66.5	9	73.5
E. obliqua + P. apetala		26.9		25.9		36.0		34.0		52.0		52.0		61.0		55.0
E. obliqua component		N.A.		N.A.		43.0		43.3		71.3		62.0		78.3		71.0
P. apetala component		N.A.		N.A.		29.0		24.7		32.7		35.5		43.3		39.0
E. obliqua + Phyl. aspleniifolius		17.0		17.5		24.2		26.3		35.3		36.2		43.0		37.5
E. obliqua component		N.A.		N.A.		40.7		44.7		55.3		57.7		66.3		57.0
Phyl. aspleniifolius component		N.A.		N.A.		7.7		8.0		14.7		14.7		19.7		18.0

*Plot burnt, figure represents one replicate only.

% WEIGHT LOSS OF INDIVIDUAL LEAF LITTER SPECIES WITH TIME IN THE FIELD IN LITTER BAGS

Experiment 1, Site 1.

Experiment 1, Site 4.

% WEIGHT LOSS

MONTHS IN THE FIELD

MONTHS IN THE FIELD

154

○———○ E. obliqua
△———△ E. nitida
□———□ P. apetala
◑———◑ Phyl. aspleniifolius
▲———▲ N. cunninghamii

▣———▣ A. moschatum
◑———◑ Eucryphia lucida
△———▲ A. melanoxylon
▣———▣ Pheb. squameum
◇———◇ B. marginata
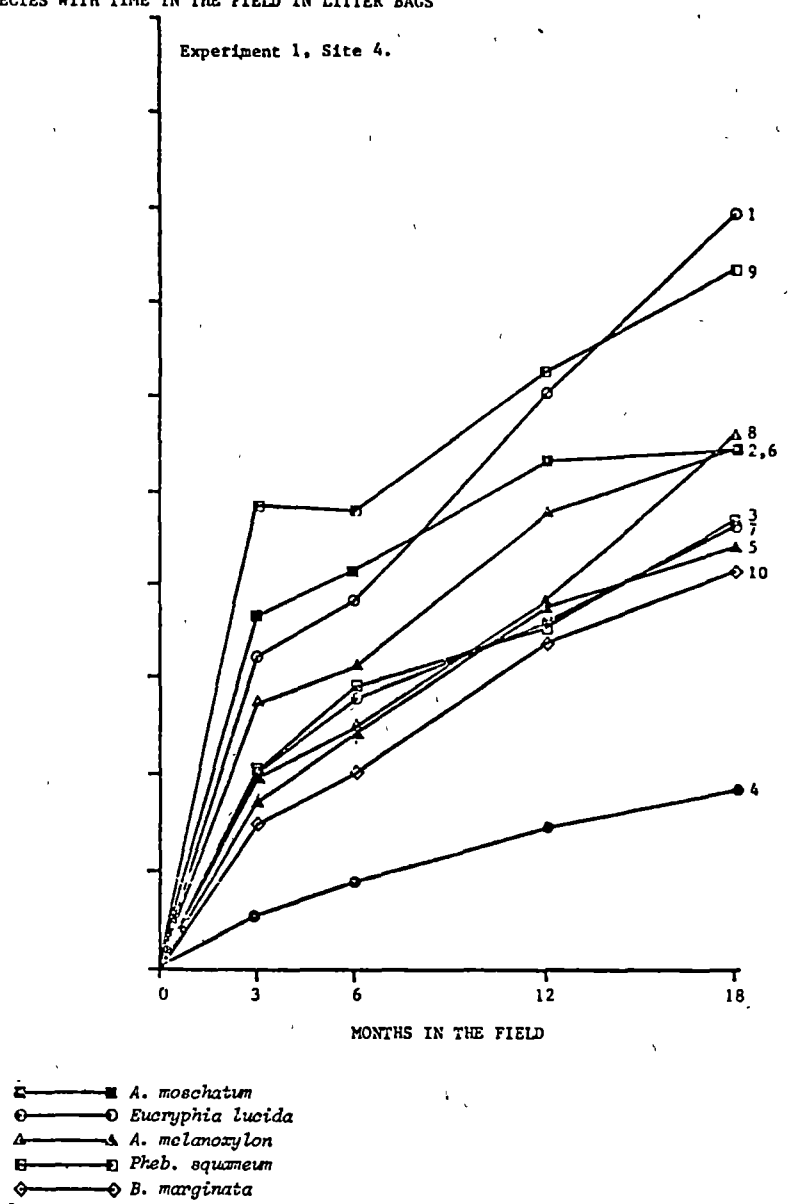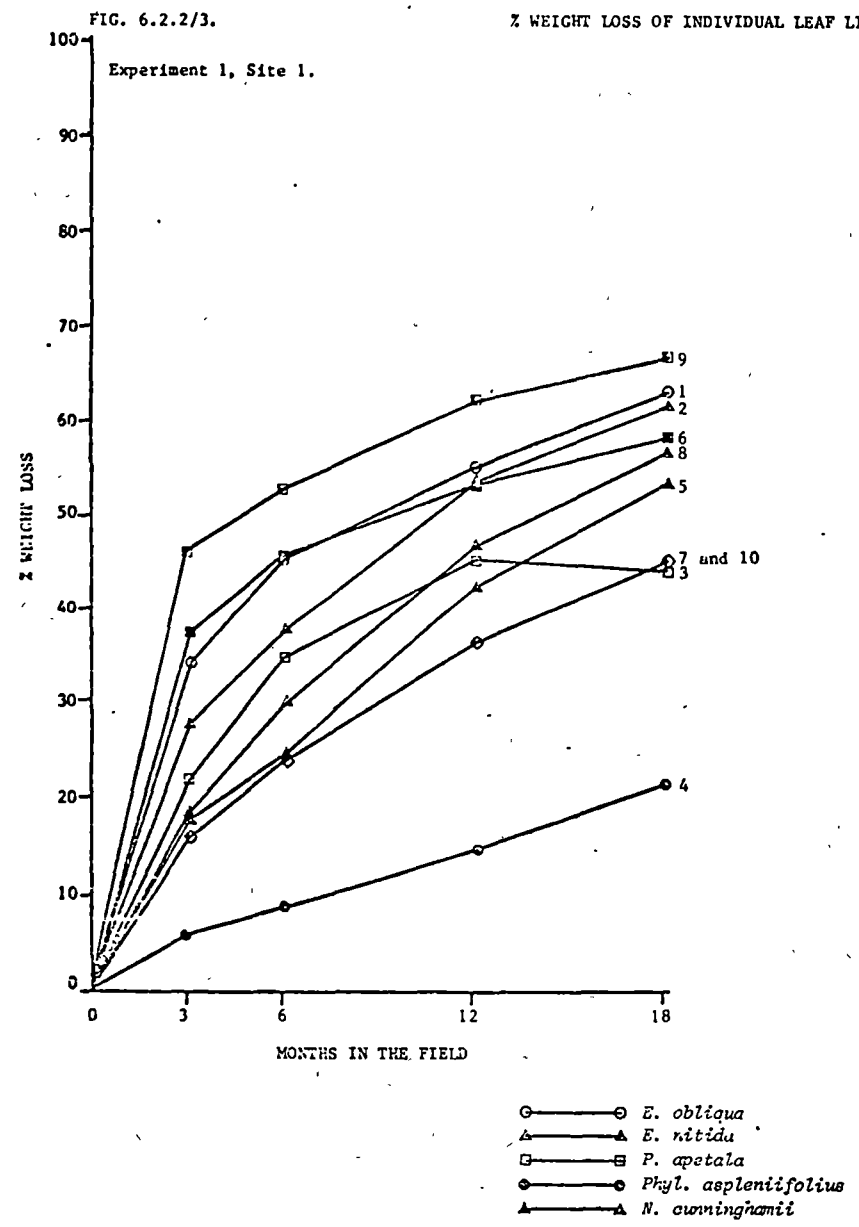
action. Results of the analysis of the 3, 6, and 12 month data separated the 12 species types into 8 groups of significantly differing decomposition rates irrespective of site, viz.

1. *Phyllocladus aspleniifolius* (9.64%).

2. *Banksia marginata* (24.19%) and *E. obliqua* +

    P. aspleniifolius (26.08%).

3. *E. obliqua* + *P. aspleniifolius, Eucryphia lucida*

    (26.58%), and *Nothofagus cunninghamii* (27.22%).

4. *N. cunninghamii* and *Acacia melanoxylon* (29.39%).

5. *A. melanoxylon* and *Pomaderris apetala* (30.97%).

6. *E. nitida* (37.44%) and *E. obliqua* + *P. apetala*

    (37.78%).

7. *E. obliqua* (44.11%) and *Atherosperma moschatum*

    (44.58%).

8. *Phebaleum squameum* (53.19%).

A similar result was obtained from analysis of the 3, 6, 12, and 18 months values. In ranking 5 *A. melanoxylon* and *P. apetala* were reversed in order but did not significantlly differ from each other, and an extra group was involved by *E. obliqua* leaves reversing order with *A. moschatum* and significantly increasing in decomposition between 12 and 18 months.

Experiment 2.

Aim.

To determine,

(i)   the effects of treatment with insecticide (I),

      fungicide (F), alone and together upon the

      decomposition rate of leaf litter, and

(ii) the role of fungi and insects in the decomposition

      process.

Method.

E. *obliqua* and E. *nitida*, and the two species mixes of E. *obliqua* with *Pomaderris apetala* and with *Phyllocladus aspleniifolius* were selected for treatment and bags prepared in August, 1980, as for Expt.1.

The 3 treatments employed as drenches were,

Insecticide (I), 0.5% D.D.T.

Fungicide (F), an equal mixture of 0.5%

Thiram 80, and 0.2% Benlate.

FI, a mixture of F and I in equal volumes.

Litter bags were packed with leaves and then dipped several times into buckets of the prepared treatment formulations, then left to drain before being placed in the field. The corresponding materials of Experiment 1 served as controls.

Sampling techniques conformed with those described in the general methods section, 6.2.2.

Results

Mean values of percentage dry weight losses of each species and mixture of species, per treatment, time of sampling, and site are listed in Table 6.2.3, together with control data of the same materials without treatment (data of Expt.1), and are illustrated in Fig. 6.2.4 to 6.2.7. In these figures the decomposition values of the individual leaf species, of the species mixes, and of individual components of species mixes, have been plotted relative to the value for the same material without treatment, i.e. decomposition values of control data have been deducted from the corresponding treatment data. The effect of treatments are more readily visualised by this technique.

Table 6.2.3. Experiment 2.

Mean percentage dry weight losses of individual species and species mixes, and their components, with time.

Species	Treatment	Percentage Dry Weight Loss							
		3 months		6 months		12 months		18 months	
		Site 1	Site 4	Site 1	Site 4	Site 1	Site 4	Site 1	Site 4
Eucalyptus obliqua	NIL	33.9	32.2	45.2	38.2	55.0	60.5	63.0	79.5
	I	30.2	25.0	40.5	32.4	53.8	49.0	54.0	54.5
	F	22.9	15.5	35.0	16.5	54.5	40.5	62.5	BURNT
	FI	7.4	11.9	28.2	20.7	52.7	44.2	64.0	51.5
Eucalyptus nitida	NIL	27.5	27.2	37.5	31.2	53.5	47.8	61.5	54.5
	I	26.9	27.5	34.7	30.7	46.0	55.3	53.5	56.5
	F	22.4	17.0	33.5	24.9	51.2	40.3	58.5	45.0
	FI	22.0	17.4	31.5	20.9	49.3	37.5	58.5	44.5
Eucalyptus obliqua + *Pomaderris apetala*	NIL	26.9	25.9	36.0	34.0	52.0	52.0	61.0	55.0
	I	27.2	25.0	31.7	32.4	46.5	45.2	49.0	53.5
	F	15.0	12.4	23.4	17.5	41.2	36.8	50.0	55.0
	FI	15.2	11.4	27.0	16.7	41.5	44.2	52.0	46.5
E. obliqua component of *E. obliqua* + *P. apetala*	NIL			43.0	43.3	71.3	62.0	78.3	71.0
	I			37.0	36.7	61.0	58.0	73.0	70.0
	F			29.3	23.3	55.7	45.3	67.7	76.0
	FI			31.7	21.7	54.7	57.0	70.7	60.0
P. apetala component of *E. obliqua* + *P. apetala*	NIL			29.0	24.7	32.7	35.5	43.3	39.0
	I			26.0	24.7	32.3	31.7	(24.7)	37.0
	F			17.3	11.7	26.7	28.3	32.3	34.0
	FI			19.0	11.7	25.0	31.3	33.3	33.0

157

Table 6.2.3.

Experiment 2.　Mean percentage dry weight losses of individual species and species mixes, and their components, with time.　Cont'd.

Species	Treatment	Percentage Dry Weight Loss							
		3 months		6 months		12 months		18 months	
		Site 1	Site 4	Site 1	Site 4	Site 1	Site 4	Site 1	Site 4
Eucalyptus obliqua + Phyllocladus aspleniifolius	NIL	17.0	17.5	24.2	26.3	35.3	36.2	43.0	37.5
	I	20.2	19.0	23.9	23.7	35.0	32.5	43.0	45.0
	F	15.4	11.0	22.9	11.9	34.2	32.0	44.0	BURNT
	FI	14.4	22.4	18.5	14.3	35.5	28.2	42.0	35.0
E. obliqua component of *E. obliqua +*	NIL			40.7	44.7	56.0	57.7	66.3	57.0
P. aspleniifolius	I			38.3	35.0	51.3	48.3	62.0	68.0
	F			32.3	16.0	51.7	47.3	67.7	BURNT
	FI			30.7	22.5	55.7	42.7	62.3	43.0
P. aspleniifolius component of *E. obliqua +*	NIL			7.7	8.0	15.7	14.7	19.7	18.0
P. aspleniifolius	I			9.3	12.3	18.7	16.7	24.3	22.0
	F			13.3	7.7	16.3	16.7	20.7	BURNT
	FI			6.3	6.0	15.3	13.7	21.3	17.0

158

FIG. 6.2.4/5. EFFECTS OF TREATMENTS WITH FUNGICIDE, INSECTICIDE, AND FUNGICIDE PLUS INSECTICIDE
UPON THE DECOMPOSITION OF VARIOUS LEAF MATERIAL TYPES.

Experiment 2. Site 1.   Experiment 2. Site 4.

NO. OF MONTHS IN FIELD

NO. OF MONTHS IN FIELD
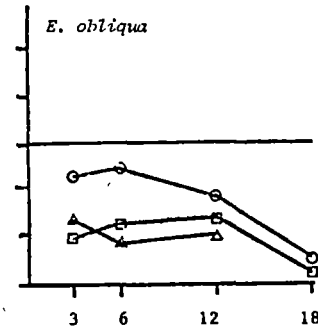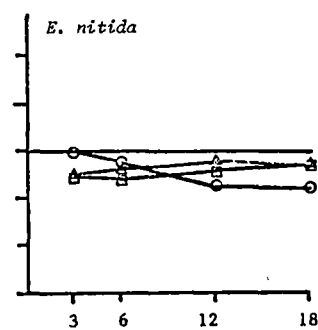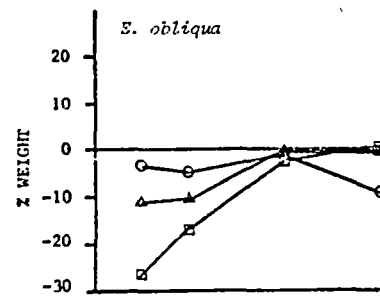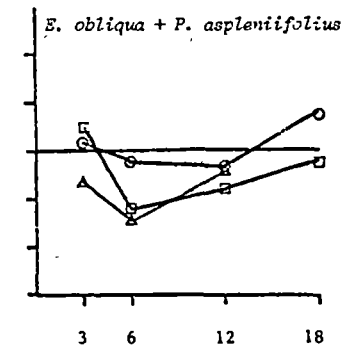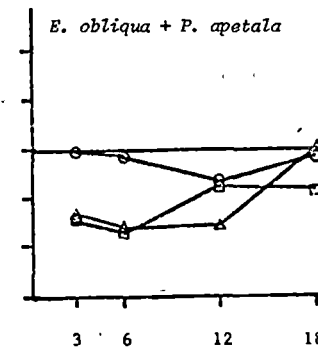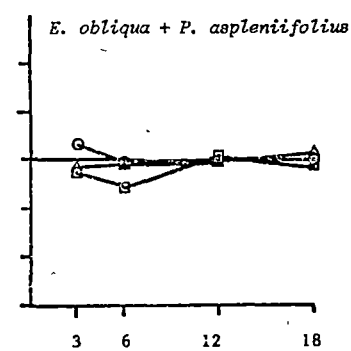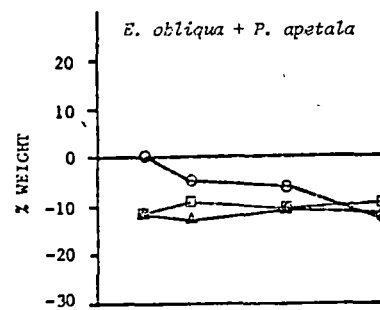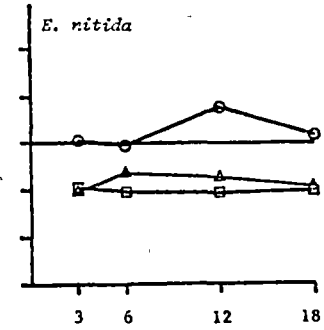
LEGEND

Control
Addition of fungicide, F
   "   " insecticide, I
   "   " F + I

FIG. 6.2.6/7.   EFFECTS OF TREATMENTS WITH FUNGICIDE, INSECTICIDE, AND FUNGICIDE PLUS INSECTICIDE
                 UPON THE DECOMPOSITION OF VARIOUS LEAF MATERIAL TYPES.

Experiment 2. Site 1.   Experiment 2. Site 4.

NO. OF MONTHS IN FIELD

LEGEND   NO. OF MONTHS IN FIELD
──────── Control
△────────△ Addition of fungicide, F
⊘────────⊘   "   " insecticide, I
▫────────▫   "   " F + I
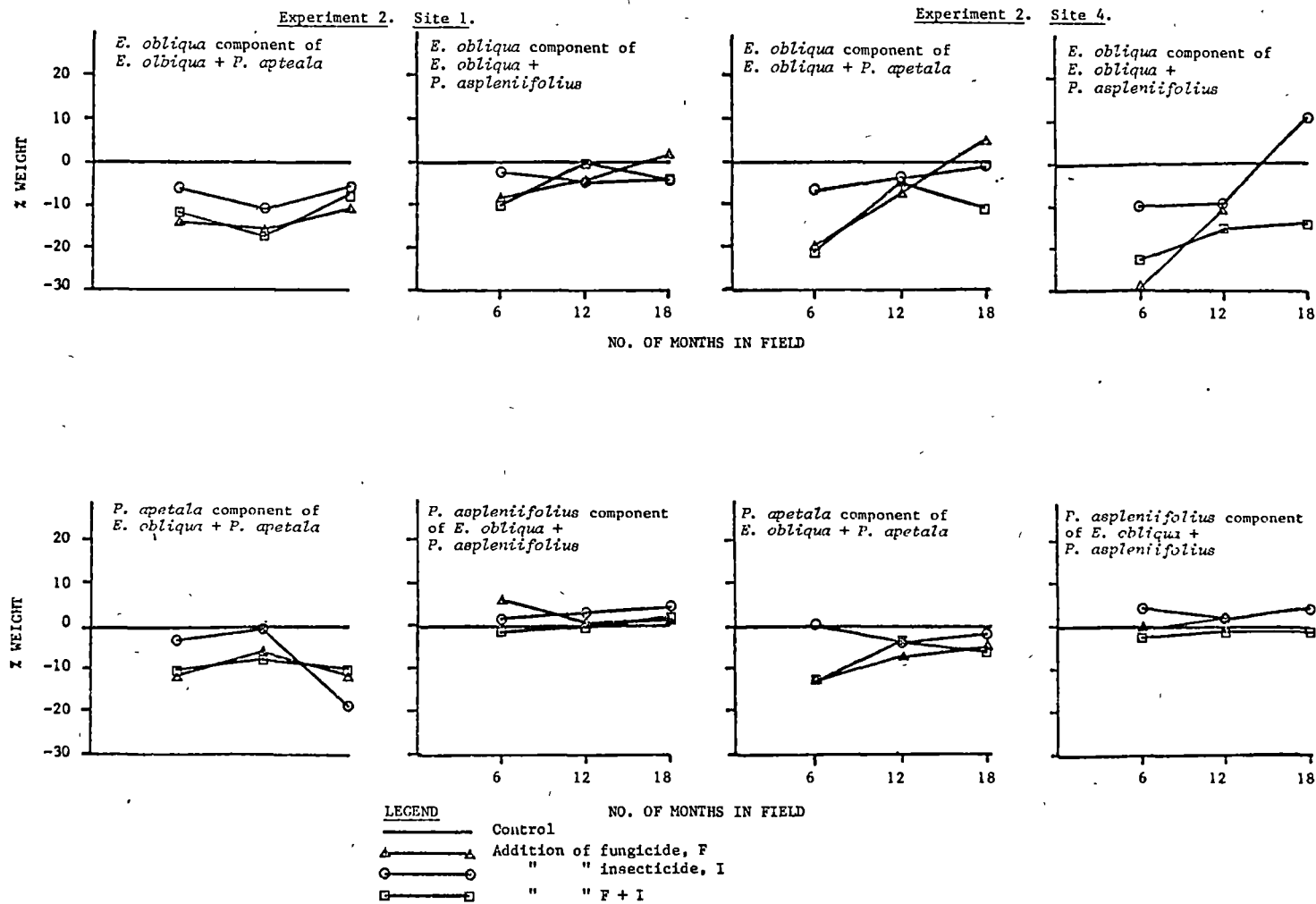
Analysis of variance was used to compare the percentage decomposition values of individual leaf species, and species mixtures, per treatment and sampling time. The analysis of variance table, and tables of means for significantly different parameters are listed in Appendix, Statistical analysis, 13, 14, and 15.

There were highly significant differences in decomposition between species, times of sampling, and with the use of fungicide treatment ($P<0.001$), and a significant difference with the use of insecticide treatment ($P<0.01$). There were highly significant interactions between species decomposition and time of sampling, and between species decomposition and the use of fungicide ($P<0.001$). There was a significant interaction between time of sampling and fungicide treatment ($P<0.01$), and between species and insecticide treatment ($P<0.05$).

There were no significant interactions between the following:

Times x Insecticide

Insecticide x Fungicide

Species x Times x Insecticide

Species x Times x Fungicide

Species x Insecticide x Fungicide.

All leaf types, both individually and in mixture, significantly increased in decomposition with time of field exposure (sampling over 3, 6, and 12 months). The significant differences in decomposition between leaf types at each time of sampling increased with length of field exposure.

At 3 and 6 months there was no significant difference between decomposition rates of *E. obliqua* and *E. nitida*. The 2 mixtures differed significantly between each other, and the eucalypt species

alone. At 12 months there were significant differences between all material types.

Although the analysis indicated that there was no effect of species mixes on *E. obliqua* development reference to the graphical trends (Figs. 6.2.4 to 6.2.7) suggested that *E. obliqua* plus *P. apetala*, and *E. obliqua* plus *P. aspleniifolius* did suppress the decomposition of *E. obliqua* leaves relative to the control, and *P. aspleniifolius* had a more suppressive effect.

The fungicide treatment caused a highly significant ($P < 0.001$) reduction in decomposition at all sampling times. The effect of fungicide treatment decreased with increasing time in the field. Fungicide addition greatly reduced decomposition of *E. obliqua* leaves (by 12.15% of original weight) and leaves of the *E. obliqua* + *P. apetala* mixture (10.92%). There was a marked reduction in *E. nitida* leaf decomposition (6.55% of original weight), and the least effect with *E. obliqua* + *P. aspleniifolius* leaves (4.12%), although this latter reduction remained highly significant ($P < 0.001$).

There was no significant difference in decomposition between fungicide and fungicide + insecticide (FI) treatments, but both were significantly different to the insecticide and control treatments. The inhibitory effect upon decomposition of the fungicide + insecticide treatment was overwhelmingly attributable to the fungicide component.

Addition of insecticide to the leaf material types had no significant effect with the exception that it suppressed decomposition of *E. obliqua* leaves ($P < 0.05$).

Effect of leaf quality upon decomposition rate.

Experiments 3 and 4.

Aims

To determine the effects of leaf development at harvest, and time of field placement upon the decomposition rate of leaf litter.

Preamble

These 2 experiments were designed to determine,

(i) whether seasonal variation in the activities of decomposer agencies limits the time of litter placement, and

(ii) whether leaves selected for use in litter decomposition experiments can be of any type other than naturally shed.

There are many complications involved in deciding what type of litter to use, and when to place it in the field. Collection of naturally shed litter is simple for species that constitute the major component of litterfall, but virtually impossible for many understorey species, particularly when it is necessary to commence studies of a number of species concomittantly, and when periods of major litterfall are not coincident for all species involved.

Although researchers have shown that only a small proportion of litterfall is green (Attiwill *et al.* 1978) it is a natural component, and can arguably be used in studies of the decomposition process. Furthermore, by selecting green leaves of known development and age, and of similar size and condition, it is possible to obtain a more uniform representation of individual leaf species. There are also difficulties in defining a green leaf; they may be up to 3 years of age (*E. obliqua*) and originate from any position in the crown.

It was considered that green leaves of *E. obliqua* selected late in their final year of development would not be considerably higher in nutrient content than senescent leaves.

Methods

The experiments were conducted simultaneously with Experiments 1 and 2, and were a duplication of Experiment 1 in all respects other than their establishment at Site 1 only, and that Experiment 3 used leaves stored at 2°C from August 1980 until their field placement in February 1981, and Experiment 4 used leaves of later development harvested and placed in the field in February 1981.

The comparisons made were:

(i)   August plucked and field established,

(ii)   August plucked, stored, and established in the field

       in February 1981,

(iii) February plucked and field established.

Results

Mean percentage dry weight losses per species and mixture after 3, 6, and 12 months in the field are compared between Experiments 1, 3, and 4 in Table 6.2.4 and are illustrated in Figs. 6.2.8 and 6.2.9.

The percentage decomposition of the 2 species mixtures are separately illustrated in Fig. 6.2.10 to Fig. 6.2.13 by comparing them with the decomposition of their component species, alone and in mixture.

Results of the 3 experiments were compared for each time of sampling by analysis of variance.

The analysis of variance table and tables of means are presented in Appendix, Statistical Analysis, 16 and 17. A comparison of the decomposition percentages of individual species used in species

Table 6.2.4.   Comparison of time of leaf collection and field placement upon the breakdown rate of leaf litter with time.

	Rank (R) and percentage dry weight loss (%) with time																	
	3 months						6 months						12 months					
	Expt. 1		Expt. 3		Expt. 4		Expt. 1		Expt. 3		Expt. 4		Expt. 1		Expt. 3		Expt. 4	
	R	%	R	%	R	%	R	%	R	%	R	%	R	%	R	%	R	%
Phyllocladus aspleniifolius	1	6.0	1	11.0	1	11.5	1	8.9	1	12.5	1	15.2	1	14.8	1	17.0	1	19.0
Eucryphia lucida	2	16.0	3	18.3	2	14.5	3	23.7	4	22.5	3	21.3	3	36.2	3	33.0	2	29.0
Banksia marginata	3	17.5	2	14.5	3	15.2	2	23.2	2	20.3	2	17.3	2	36.0	2	31.5	3	29.5
Nothofagus cunninghamii	4	17.7	4	20.0	4	17.5	4	24.4	3	22.0	4	21.7	4	42.3	4	37.5	4	37.0
Acacia melanoxylon	5	18.2	5	20.8	5	24.0	5	29.4	5	26.5	6	29.5	6	46.5	5	39.5	5	42.5
Pomaderris apetala	6	21.9	6	27.2	7	30.2	6	34.5	7	37.0	8	38.5	5	45.2	6	49.0	7	48.0
Eucalyptus nitida	7	27.5	10	62.0	6	26.2	7	37.5	6	31.0	5	28.0	8	53.5	10	70.5	6	44.5
Eucalyptus obliqua	8	33.9	7	30.0	8	31.0	8	45.2	8	38.3	7	38.2	9	55.0	8	56.5	8	50.5
Atherosperma moschatum	9	37.0	9	43.8	9	34.7	9	45.7	9	51.0	9	42.2	7	53.2	7	55.5	10	57.5
Phebalium squameum	10	46.2	8	43.3	10	42.2	10	52.7	10	51.2	10	49.2	10	61.8	9	61.0	9	56.0
E. obliqua + P. apetala		26.9		28.5		33.3		36.0		39.3		39.5		52.0		53.5		46.5
E. obliqua component		N.A.		32.7		35.3		43.0		45.7		42.7		71.3		66.7		71.5
P. apetala component		N.A.		25.0		32.3		29.0		33.0		36.3		32.7		40.0		29.0
E. obliqua + Phyl. aspleniifolius		17.0		23.2		24.2		24.2		28.2		28.0		35.3		38.0		35.5
E. obliqua component		N.A.		34.7		35.7		40.7		42.0		39.7		55.3		57.7		50.0
Phyl. aspleniifolius component		N.A.		11.7		12.7		7.7		15.3		16.3		14.7		18.3		21.3

Expt. 1: Leaves harvested and placed in the field, August 1980.

Expt. 3: Leaves harvested in August 1980, stored at 2°C, and placed in the field in February, 1981.

Expt. 4: Leaves harvested and placed in the field February, 1981.

All values the mean of 3 replicates.

N.A.:   Data not available.

165

FIG. 6.2.8/9.   EFFECTS OF TIME OF LEAF HARVEST AND FIELD PLACEMENT UPON DECOMPOSITION

MEAN PERCENTAGE ORIGINAL WEIGHT LOSS

E. obliqua

E. obliqua + P. apetala

E. obliqua +
P. aspleniifolius

E. nitida

E. apetala

P. aspleniifolius

P. squameum

B. marginata

Eucryphia lucida

A. selaginoxylon

A. moschatum

N. cunninghamii

MONTHS FIELD EXPOSURE

Experiment 1

Experiment 3

Experiment 4
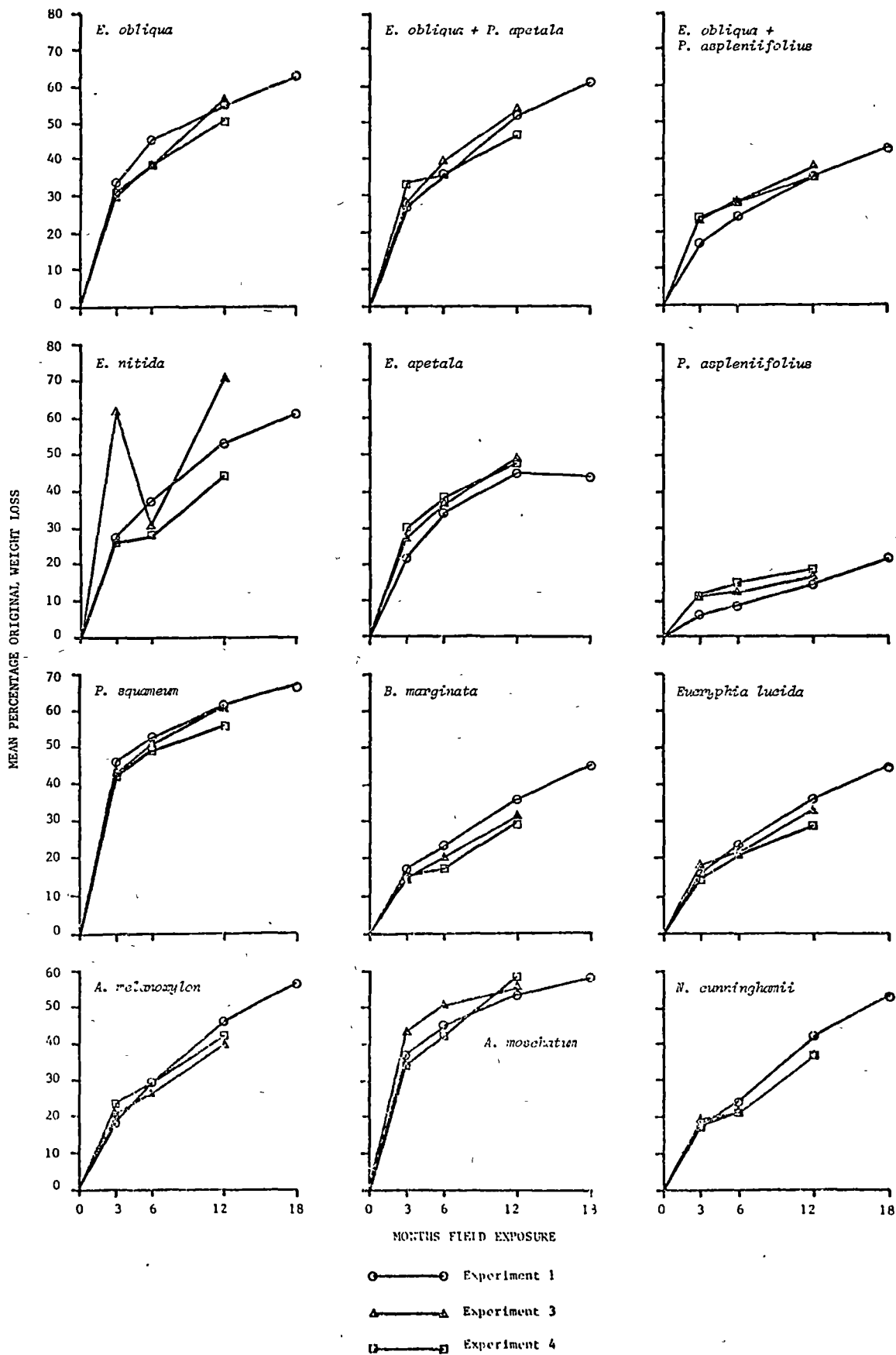
FIG. 6.2.10/11.   EFFECT OF LEAF LITTER SPECIES MIXES UPON THE
DECOMPOSITION OF COMPONENT SPECIES

Experiment 1, Site 1.

Experiment 1, Site 4.

1. E. obliqua alone
2. E. obliqua component of mixture with P. apetala
3. E. obliqua component of mixture with Phyllocladus aspleniifolius
4. E. obliqua + P. apetala mixture
5. E. obliqua + Phyllocladus aspleniifolius mixture
6. P. apetala alone
7. P. apetala component of mixture with E. obliqua
8. Phyllocladus aspleniifolius alone
9. Phyllocladus component of mixture with E. obliqua
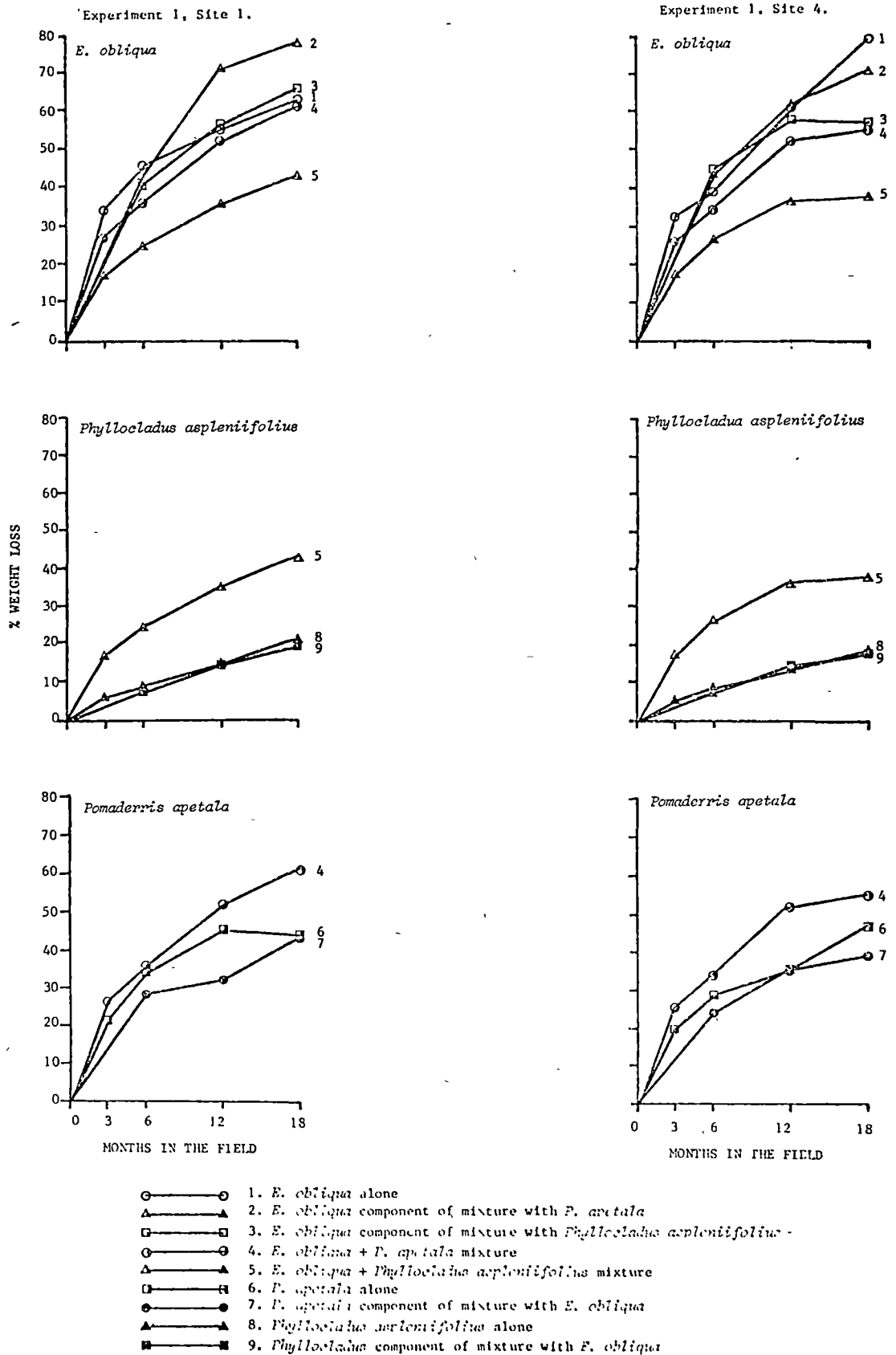
FIG. 6.2.12/13.   EFFECT OF LEAF LITTER SPECIES MIXES UPON THE
                         DECOMPOSITION OF COMPONENT SPECIES

Experiment 3, Site 1.

Experiment 4, Site 1.

MONTHS IN THE FIELD

O————O 1. *E. obliqua* alone
A————A 2. *E. obliqua* component of mixture with *P. apetala*
B————B 3. *E. obliqua* component of mixture with *Phyll. aspleniifolius*
O————O 4. *E. obliqua* + *P. apetala* mixture
A————A 5. *E. obliqua* + *Phyllocladus aspleniifolius* mixture
O————O 6. *P. apetala* alone
●————● 7. *P. apetala* component of mixture with *E. obliqua*
A————A 8. *Phyllocladus aspleniifolius* alone
■————■ 9. *Phyllocladus* component of mixture with *E. obliqua*

mixtures, and the values of their mixtures, was included in the analysis to determine whether mixtures suppressed or enhanced decomposition.

There were significant differences in decomposition between species, experiments, and length of field exposure, and significant interactions with species x experiments, species x times, experiments x times, and species x experiments x times (P<0.001).

There were no significant differences (P>0.05) between comparisons of the decomposition of individual leaf species and the same species in mixtures. Hence, there was no observed allelochemical interaction between the *Pomaderris apetala* and *E. obliqua* leaves in mixture, and the *Phyllocladus aspleniifolius* and *E. obliqua* leaves in mixture when comparing leaves of differing development stage, or differing time of field establishment.

Decomposition percentages of the individual material types are ranked in increasing order in Table 6.2.4 at the 3, 6, and 12 month sampling for each experiment. Changes in rank occurred between experiments, the changes reflecting effect of leaf development upon ensuing decomposition of the different species/mixture. An overall ranking of decomposition is listed in the table of means for between species comparison from the analysis of variance of the 3 experiments in Appendix, Statistical Analysis, 16 and 17. Although there were alterations in ranking of decomposition percentages between times of sampling and between experiments, Figs. 6.2.8 and 9 illustrate the trends within species between experiments to be markedly similar (except for *E. nitida* in Expt.3).

Significant differences (P<0.05) existed between all material types except the 2 eucalypt species, *E. obliqua* and *E. nitida*. *Phyllocladus aspleniifolius* decomposed the least and *Phebaleum*

squameum the most. Anomalous results were obtained in Expt.3 for *E. nitida* decomposition, 62% of original dry weight loss occurring in the first 3 months of field exposure compared with ca. 28% in Expts. 1 and 4. All replicates exhibited similar losses.

Significant differences (P<0.05) were obtained between experiments. Leaves plucked and placed in the field in February, 1981, were the slowest to decompose. Leaves plucked in August, 1980, stored at 2°C prior to field establishment in February, 1981, decomposed more rapidly than the same type of leaf (same harvest) established at the August, 1980, time of harvest.

Progressive decomposition occurred with increasing length of field exposure, and there were highly significant differences between all times of sampling (P<0.001).

Experiment 5.

Aim

To compare the effects of various stages of leaf development at harvest upon their decomposition.

Methods

The same establishment and sampling methods were used as in allied litter bag experiments with the following exceptions.

Ten grammes of leaves (E.O.D.W.) were used in 5 replications per leaf type, and all bags were established in the field at one site (Site 1) in February, 1981. Three *E. obliqua* leaf development stages were used:

(i) Leaves of the original August, 1980, harvest that had been stored at 2°C.

(ii) Green leaves picked from the canopy in February, 1981.

(iii) Naturally shed leaves of normal litterfall trapped on hessian strips supported above the ground over a 3 week period in late January and early February, 1981.

Leaves of both (i) and (ii) were considered to be part of the summer, 1981, accession had they not been picked.

Results

The mean percentage dry weight losses of the 3 different leaf types at 3, 6, and 12 months sampling times are listed in Table 6.2.5, and illustrated in Fig. 6.2.14, and the ANOVA in Appendix, Statistical Analysis, 18.

There were significant differences (P<0.001) between the decomposition percentages of leaves of differing development at harvest. Decomposition of *E. obliqua* leaves harvested in August, 1980, and placed in the field in February, 1981, was greater than leaves harvested and placed in the field in February, 1981. Both harvests by hand picking from tree crowns resulted in more rapid decomposition than leaves that were naturally shed and established in the field at the same time.

There was a significantly increasing degree of decomposition of all *E. obliqua* leaf types with increasing length of time in the field (P<0.001), and the differences in decomposition between leaf types significantly (P<0.05) increased with increasing field exposure.

Results are reported in Chapter 8 covering the enumeration of litter microflora, Section 2.4.

6.2.4 Discussion

A number of conclusions were drawn from the results of the series of litter bag experiments, and these are summarised and discussed.

Table 6.2.5.   Mean percentage dry weight losses of differing
types of *E. obliqua* leaves with time
time in the field.

Leaf type	3 months	6 months	12 months
Green, picked in August 1980, stored 2°C, placed February 1981.	33.0	42.0	57.8
Green, picked and placed in February 1981.	28.0	37.3	46.4
Naturally shed, senescent leaves collected and placed in February 1981.	26.0	30.2	34.8

FIG. 6.2.14.

THE INFLUENCE OF LEAF DEVELOPMENT UPON THE
RATE OF DECOMPOSITION OF *E. OBLIQUA*

Experiment 5, Site 1.

MONTHS IN THE FIELD
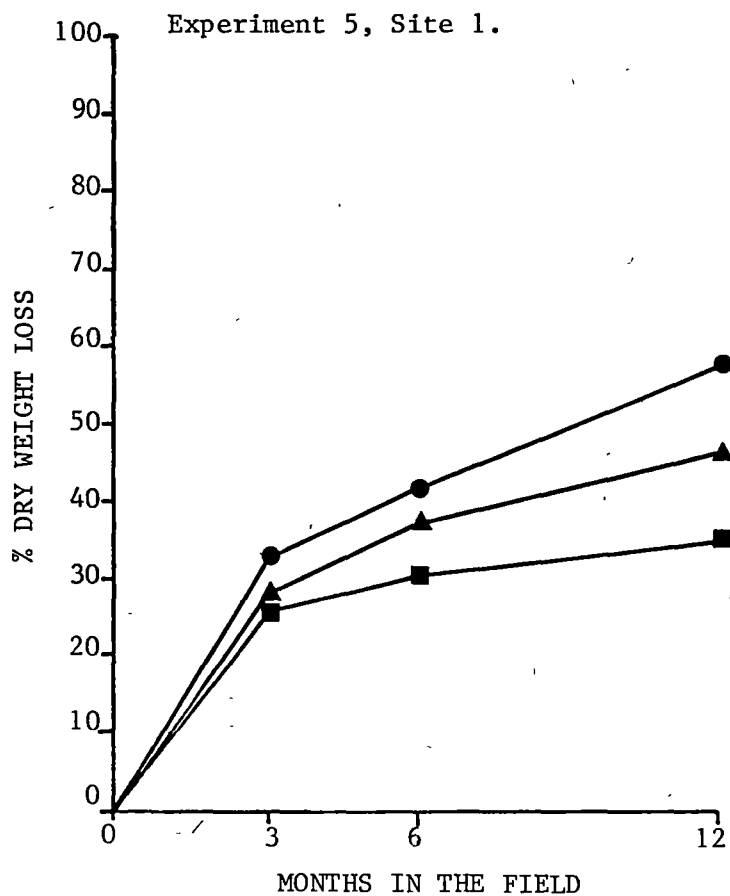
LEGEND

● ━━━━━ ● Plucked in August, stored at $2^{o}C$, placed February 1981
▲ ━━━━━ ▲ Plucked and placed February 1981
■ ━━━━━ ■ Naturally shed, placed February 1981

(a)   Significant differences (P<0.05) in decomposition rate were obtained between leaves of 10 species and leaves of 2 mixtures of 2 species.   Experiments 1, 3, and 4 compared the decomposition of these species with differing leaf development stages and differing times of field establishment (early spring, mid-summer).   The mean decomposition after 12 months of field exposure, expressed as a percentage of original equivalent oven-dry weight, of all material types over the 3 experiments were as listed in Table 6.2.6.   There were significant differences between all material types except *E. obliqua* and *E. nitida*.

(b)   Field observations of many colleagues associated with the Southern Forests had led to the belief that *Pomaderris* leaves were probably most rapidly decomposed in the litter-bed, when in fact this species ranked 7th out of 10, with leaves of *E. obliqua*, *E. nitida*, and *Phebaleum squameum* decomposing appreciably faster, and *Phebaleum* leaves losing more than half their original weight in 12 months.

(c)   Considering the balance that generally exists in biological environments it was hypothesised that in order to maintain balance in the litter-bed, individual leaf species may be expected to decompose at a rate relative to their accession to the forest floor. If not, there would be a preponderance of species with the heaviest fall;   such a preponderance was not observed.   Table 6.2.6 lists the annual leaf fall (t.ha.$^{-1}$ an.$^{-1}$) of the various species at Sites 1, 2, and 3, with data for the fall of *E. nitida* leaves at Site 4 listed in parentheses under Site 1.

All experiments were represented at Site 1 and examination of the data for that site shows a definite overall relationship between the rate of decomposition of individual species and their annual accession, those with the heavier leaf fall having the faster decomp-

Table 6.2.6.   Mean percentage decomposition, annual leaf fall, leaf size and class, and leaf structural classification per species.

Species/mixture	Decomposition %	Leaf fall (t.ha.$^{-1}$an^{-1})			Leaf size[1] (mm) and class[2]	Leaf structure class[2]
		Site 1	Site 2	Site 3		
Phyllocladus aspleniifolius	12.85	0.003	0.10	0.003	15-80 M/Me	S/O
Banksia marginata	22.61	-	-	0.02	30-80,3-10 M/Me	S
Eucryphia lucida	23.83	0.07	0.51	0.03	25-45,10-20 M/Me	O
Nothofagus cunninghamii	26.67	0.05	1.17	0.04	6-18,6-18 M	O
E. obliqua P. aspleniifolius	28.19					
Acacia melanoxylon	30.78	0.18	0.31	0.04	40-100,10-25 Me	S
Pomaderris apetala	36.41	-	0.03	-	40-100,15-30 Me	O
E. obliqua + P. apetala	39.50					
E. obliqua	42.00	2.21	0.27	1.80	60-80,30-40 Me	S
E. nitida	42.31	(1.32)			60-150,10-20 Me	S
Atherosperma moschatum	46.70	0.002	0.09	0.0002	25-80,8-30 Me	O
Phebaleum squameum	51.52	0.37	0.02	0.32	25-80 Me	O

1. Curtis (1963, 1967, 1975).

2. Fosberg (1961);   S = sclerophyllous, O = orthophyllus, N = nanophyllous, M = microphyllous, Me = mesophyllous.

osition rate. *Atherosperma moschatum* leaves did not comply with this relationship, and leaves of *Phebalewm squameum* were not in strict rank, but were in general agreement.

Nothofagus cunninghamii leaves were a minor component of litterfall at Site 1 (0.05 t.ha.$^{-1}$an.$^{-1}$) but the major component at Site 2 (1.17 t.ha.$^{-1}$an.$^{-1}$). At Site 1 this species had a relatively slow rate of decomposition (26.67% in 12 months) yet the litterbed of Site 2 is not deep (ca. 2 cm) nor does it appear to be predominantly composed of *Nothofagus* leaves. It is assumed that different suites of decomposer agencies exist at the two sites, and that the agencies of Site 2 must therefore favour *Nothofagus* leaf decomposition.

(d) Diversity of litter mixes is paralleled by diversity of decomposers.

(e) Table 6.2.6 lists leaf size, class, and structural class-ification. Leaf sizes were obtained from reference to Curtis (1963, 1967; Curtis and Morris, 1975) and size and structural classification were made according to Fosberg (1961). No relationships were apparent between such classification and decomposition rate.

(f) There was a significant interaction between Experiments 1, 3, and 4. Leaves plucked and placed in the field in February, 1981, (Expt. 4) were slowest to decompose. Leaves plucked in August, 1980, and stored at 2°C prior to field establishment in February, 1981, (Expt. 3) decomposed more rapidly than leaves of the same harvest established in the field in August, 1980, (Expt. 1). Leaves of Expt. 4 were harvested late in their development and were expected to be shed before the end of that summer. Leaves of Expt. 1 and 3 were 6 months younger and would be of richer nutrient status and thus decomposed more rapidly than the older, less nutritious leaves of Expt. 4. Field establishment in mid-summer favoured a more rapid initial

decomposition than establishment of leaves of the same development in early Spring, as the inoculum potential and invertebrate populations of the litterbed are relatively greater in the summer than in late winter/early spring. The effect of harvest date, or leaf development, upon subsequent decomposition was greater than the time of field establishment.

(g) These findings are in agreement with recommendations of Richards and Charley (1977), and Woods and Raison (1982) that leaf decomposition studies should ideally use leaves that are naturally shed so that they are representative of the energy and nutrient status of leaf fall at the time the bags are established in the field.

Experiment 5 compared the decomposition of *E. obliqua* leaves harvested in late winter/early spring and mid-summer with naturally shed leaves of mid-summer. All leaf types were established in mid-summer at a time coincident with major leaf fall. Results agreed with those of Expt. 1, 3, and 4, and the naturally shed leaves of low energy and nutrient status decomposed at a significantly slower rate than the harvested leaves. Leaves of August harvest again decomposed more rapidly than leaves of the February harvest.

(h) As explained earlier in this Chapter, it is not practicable to always use naturally shed leaves. Although the differences between leaf decomposition rates were significant between experiments, Table 6.2.7 and examination of Fig. 6.2.8 and 6.2.9 for Expt. 1, 3, and 4, and Fig. 6.2.14 for Expt. 5 illustrate that in reality the differences were trivial, and the trends of results of decomposition with time were markedly similar between experiments. It is concluded that differences were qualitative, not quantitative and it is acceptable to utilise non-naturally shed leaves in studies of leaf decomposition. Improved results will be obtained if leaves are harvested

Table 6.2.7.   Percentage decomposition with time in the field per species.

| Species | Field exposure | 0-3 months | | | 3-6 months | | | 6-12 months | | | 12-18 months |
	Experiment	1	3	4	1	3	4	1	3	4	1
Phyllocladus aspleniifolius		6.0	11.0	11.5	2.9	1.5	3.8	5.9	4.5	3.8	6.7
Eucryphia lucida		16.0	18.3	14.5	7.7	4.2	6.8	12.5	10.5	7.7	8.8
Banksia marginata		17.5	14.5	15.2	5.7	5.8	2.1	12.8	11.2	12.2	9.0
Nothofagus cunninghamii		17.7	20.0	17.5	6.7	2.0	4.2	17.9	15.5	15.3	11.2
Acacia melanoxylon		18.2	20.8	24.0	11.2	5.7	5.5	17.1	13.0	13.0	10.0
Pomaderris apetala		21.9	27.2	30.2	12.6	9.8	8.3	10.7	12.0	9.5	*
Eucalyptus nitida		27.5	62.0	26.2	10.0	*	12.0	17.0	39.5	16.5	8.0
Eucalyptus obliqua		33.9	30.0	31.0	11.3	8.3	7.2	9.8	18.2	12.3	8.0
Atherosperma moschatum		37.0	43.8	34.7	8.7	7.2	7.5	7.5	4.5	15.3	4.8
Phebalium squameum		46.2	43.3	42.2	6.5	7.9	7.0	9.1	9.8	6.8	4.7

* Negative value.

late in their development, and established at the time of heaviest leaf fall, both of which times are coincident.

(i) There were significant increases in decomposition of all material types with increasing length of field exposure in all experiments, except in the case of *Pomaderris apetala* leaves that remained static between the 12 and 18 months sampling.

Leaves of all species except *Phyllocladus aspleniifolius* decomposed most rapidly in the initial 3 months of field exposure, and thereafter at a generally uniform rate between 3 and 6, 6 and 12, and 12 and 18 months (except for *P. apetala* as stated). Leaves of *P. aspleniifolius* decomposed at a uniform rate over the total period of field exposure. Leaf fragmentation at various sampling times is illustrated in Plates 5 and 6. *E. obliqua* and *E. nitida* leaves were the most rapidly fragmented. *Atherosperma* leaves were heavily skeletonised, and leaves of *Phebaleum squameum* had a "blistered" appearance within weeks of being placed on the litterbed. The upper epidermis of this species appeared to separate from the underlying mesophyll tissue, leaving it exposed to decomposer agencies at a very early stage. After 18 months in the field *Phebaleum* leaves had lost 61% of their original equivalent oven dry weight, yet appeared intact and entire, but upon examination were virtually devoid of tissue between the abaxial and adaxial cuticle.

(j) In February, 1981, the litterbed of all sites abounded with mycelia and fruiting bodies of *Mycena* spp., and this fungus was particularly evident on the surface of litter bag leaves of *E. obliqua*, *E. nitida*, and *N. cunninghamii*. Leaves exhibited large areas of bleaching on their surfaces, and bags later became completely interwoven with a mass of brownish-black, threadlike, *Marasmius* spp. mycelia. The fungus was most commonly observed attached to leaf petioles.

Plate 5. *E. obliqua* leaves after 6 months in a litter bag
(Note distinctive areas of bleaching caused by fungal invasion).

Plate 6. *E. obliqua* confined in a litter bag at
12 month sampling.
(Note commencement of leaf fragmentation).

(k) Fig. 6.2.2 and 6.2.3 of Expt. 1, and Fig. 6.2.4 and 6.2.5, and 6.2.6 and 6.2.7 of Expt. 2, illustrate the decomposition of various material types at Site 1 (tall, open forest)and Site 4 (tall scrub). Site 4 experienced extremes of climate compared with Site 1, and it was expected that there would be differences in decomposer agencies at the two sites. The figures demonstrate no apparent effect of site upon the rate of decomposition of individual species or of species mixtures except in the case of the 2 eucalypt species. *E. obliqua* leaves decomposed more rapidly at Site 4 than at Site 1, and *E. nitida* leaves the converse.

(1) There was no allelochemical interaction between leaf species. Analysis of variance demonstrated no significant differences in decomposition of the individual leaf species alone or in mixture.

(m) Experiment 2 investigated the effect of addition of fungicide (F), insecticide (I), and a mixture of both (FI), upon the decomposition of differing leaf material types.

Treatment with F caused a highly significant reduction in the decomposition of all tested material types, with treatment effect decreasing with increasing time in the field between 6 and 12 months. Treatment effect was greatest with *E. obliqua* leaves and leaves of the *E. obliqua* plus *P. apetala* mixture. Treatment with I reduced the decomposition of *E. obliqua* leaves but did not have a significant effect ($P>0.05$) upon the other material types. The mixture of FI caused a significant reduction in decomposition of all material types. The FI effect was not significantly different to the effect of F alone, but was significantly greater than the effect of treatment with I, hence the inhibitory effect of the FI treatment was attributable to the F component of the mixture.

(n) It is concluded that in the litterbeds studied, microflora play the predominant role in leaf decomposition, with invertebrates of *possible* importance to the decomposition of *E. obliqua* leaves.

6.3. THE DEVELOPMENT AND ASSESSMENT OF A SYSTEM TO SIMULTANEOUSLY MONITOR LITTER ACCUMULATION AND DECOMPOSITION IN THE FIELD.

6.3.1 Introduction

The decomposition of litter is both complex and difficult to monitor in the field. Usual methods employ nylon mesh bags or tethered leaves for the determination of (a) loss of weight or leaf area, (b) respiration rate, or (c) the collection of litter leachate (Suffling and Smith 1974, Dickinson and Pugh 1974, Singh and Gupta 1977, Woods and Raison 1982). Each method may have attributes relevant to the particular aspect under study e.g. the use of nylon mesh bags in the comparison of the effects of fungi and insects in *Eucalyptus pauciflora* litter communities (Macauley, 1975). A more general approach is the determination of the decomposition constant, k, from the ratio of annual litterfall to accumulated litter (Olson, 1963).

Ideally a technique designed to study the decomposition of litter in the field should involve a naturally shed mixture of leaves in as natural an environment as possible, with freedom from disturbance by repetitive sampling or handling. An attempt was made to develop a system that fulfilled these requirements and which could simultaneously monitor both the accession and accumulation of litter within the system and thus quantify litter loss with time. Loss in litter weight is considered synonymous with litter decomposition. The aim of this technique was to provide the following information,

(i)   total litter accession at six week intervals

(ii)   annual litter accession

(iii)   accumulation

(iv)   moisture content percent of freshly fallen and

accumulating litter, at each sampling interval

(v)   decomposition at each interval, and

(vi)   relationships between climatic variables and litter

accession and decomposition.

6.3.2 Methods and Materials.

The trap system consisted of a number of identical pairs of traps[1] with the upper trap (A) representing litter accession and the lower trap (B) accumulation. Both traps of each pair were of the same area as the bins and ground traps used in accessional studies[2], i.e. 1810 cm^2. The traps were constructed of 1.5 mm terylene mesh glued with rubber cement to a 100 mm high peripheral wall of 10 x 12 mm nylon mesh (available from hardware stores as "guttergard"). Each trap was tared and established upon the centre of a 1 metre square of 1.5 mm terylene mesh pinned out flat upon the bare mineral soil of the forest floor. It was decided to site the traps on areas cleared of litter to ensure a more uniform inoculum base.

Trap A of each pair fitted tightly within trap B, excluding accessing litter from B. At 6 week intervals the green weights of the contents of both traps were determined using a Mettler P1200 balance adapted for a 6 volt D.C. power supply. The accessed litter for the previous 6 week interval in A was then uniformly distributed over the surface of B to represent accumulating litter. Over a number of collection intervals a measure of the rate of litter loss may be obtained by deducting the accumulated litter weight in B from the sum of the accessional litter weights obtained from trap A.

1. See plate No.7
2. Refer Section 4.2

Plate No.7.   Double trap.

A difficulty inherent to any non-destructive litter study system is that the oven-dry weight of the litter material involved cannot be determined without precluding re-use of the material through destruction of litter biota and alteration of its physical and chemical properties. To avoid this problem, sacrificial traps C and D were established as paired traps corresponding with each A and B trap. Due to the necessary destruction of the D samples, an area of mesh was pinned flat upon the cleared forest floor at the establishment of the experiment that was sufficient to allow replication and to cover the duration of the required sampling period. One square metre of mesh allowed the harvest of 4 D samples, hence 4 m^2 allowed a proposed study period of 96 weeks. One square metre of mesh was the maximum size that could readily be pinned out in spaces available between the boles of overstorey and understorey species.

Figure 6.3.1 illustrates a plan view of a typical layout for one replication of A/B and C/D traps. Five replications were established at random within each of the four 0.10 ha. study plots. A/B traps remained permanently sited throughout the study period, but the C traps were roved about upon the D trap squares. At each sampling date the layer of accumulated litter and mesh below the C traps was cut out with scissors, and the green weight of its contents, and of the litter on C, determined. All sacrificial samples were transported to the laboratory in tared, sealed tins for the determination of their oven-dry weight (70°C) and calculation of moisture content percent (Slatyer and McIlroy, 1961) where,

$$\text{M.C. } \% = \frac{Wg - Wo}{Wo} \cdot 100$$

The known green (Wg) and oven dry (Wo) weights of C and D trapped litter were used to calculate the equivalent oven dry weights of the A and B trapped litter of known green weight, viz.

FIG. 6.3.1.   PLAN VIEW OF ONE REPLICATION OF A/B AND C TRAPS.
              D AT WEEK n CUT OUT FROM BENEATH C AT WEEK n

1 m.sq. pieces of mesh for D sample

C

A/B

overstorey/understorey
boles

Scale:

0   1m
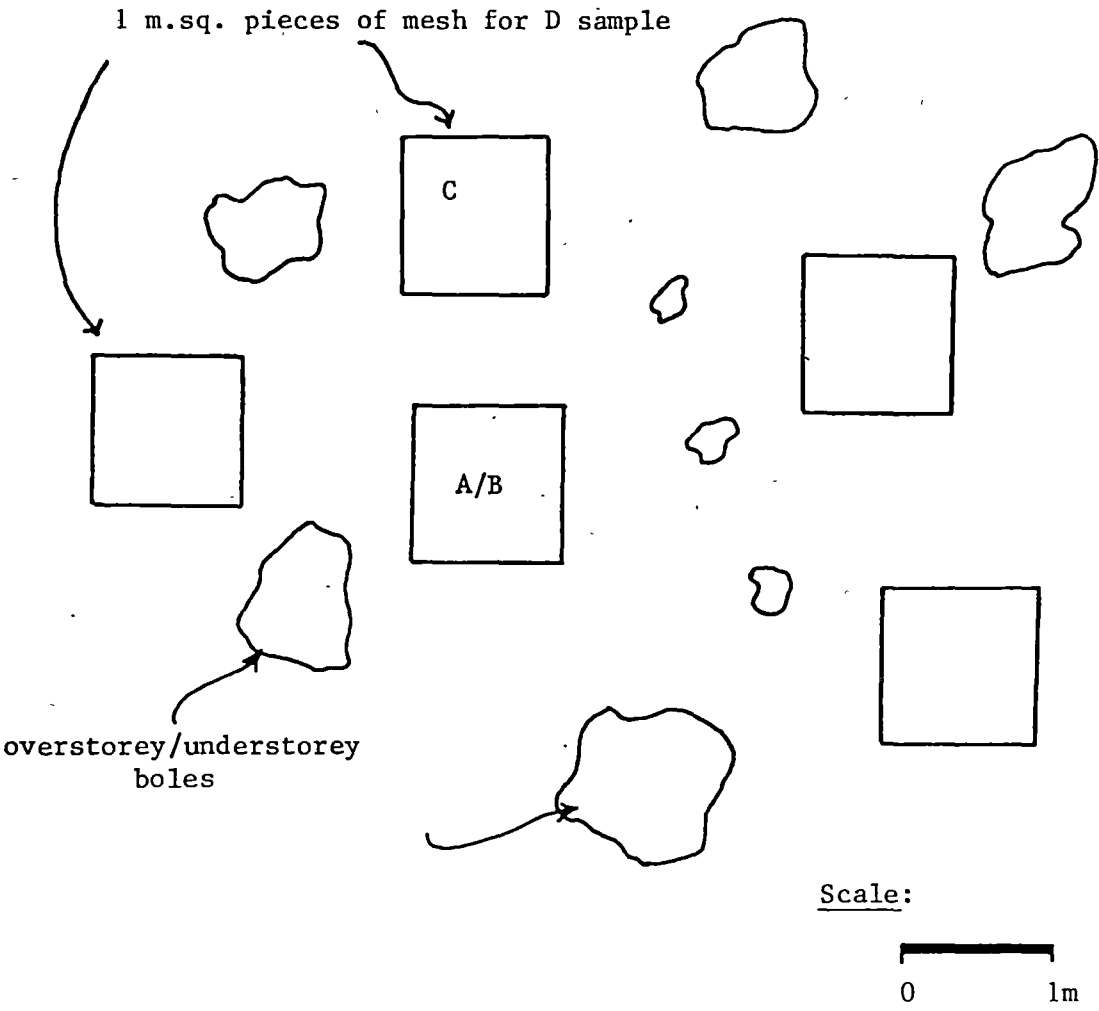
calculated equivalent $\quad WoA = \dfrac{WgA \text{ x } WoC}{WgC}$

All twigs greater than 1.0 cm diameter were removed from all traps at each collection in order to reduce experimental error that may have been introduced through the random fall of larger woody material.

Due to the very wet conditions that often prevail in the Southern Forests the problem of free water held on and between leaf surfaces was one of considerable importance. A standardised procedure was adopted throughout all collections that removed as much free water as possible without excessive physical disturbance of the contained litter. After lifting individual traps from the forest floor free water was removed from the mesh bases and peripheral nylon walls (where applicable) with a sponge. This procedure was not capable of removing the free water held between leaf surfaces within the "matt" of contained litter. If excessive free water could not be accounted for during litter collections, then all determinations would be worthless. A series of preliminary tests were carried out to gain an appreciation of the proposed collection system.

TEST NO.1

Aim

To determine the variability in water-holding capacity of leaf mixtures of known weight.

Method

Entire leaves of 10 overstorey and understorey species were collected both from the crown and the litterbed of the study sites, and were mixed in proportions relating to normal conditions of litter accession.[1] Species selected were,

1. Refer Section 4.3

Eucalyptus obliqua

Nothofagus cunninghamii

Atherosperma moschatum

Phyllocladus aspleniifolius

Pomaderris apetala

Anopterus glandulosus

Eucryphia lucida

Phebaleum squameum

Acacia melanoxylon

Anodopetalum biglandulosum

Leaf mixtures were divided into 3 aliquots representative of very heavy, medium, and light collections, air-dried for 72 hours, weighed and placed in traps constructed for use in the main experiment. Traps plus contents were thoroughly misted with water from a garden hose, lifted, and excess water removed with a sponge in the standardised manner previously described, then weighed.

Results

Variations in wet weight per given weight of air-dried leaves are listed in Table 6.3.1.

Conclusion

There did not appear to be any irregularity in the amount of free water held by the leaf mixes, between repeated samplings.

TEST NO.2

Aim

To check the efficacy of the technique proposed for calculation of the equivalent oven dry weights of litter within paired traps.

Table 6.3.1.   Variability in water-holding capacity of leaf mixtures.

Leaf weight, air-dry (g)	Leaf weight, wetted (g)	Weight free water held (g)
56.5	101.9	45.4
	103.0	46.5
	104.7	48.2
	101.9	45.4
	103.4	46.9
10.0	18.6	8.6
	18.1	8.1
	19.0	9.0
	18.4	8.4
	19.1	9.1
2.0	3.2	1.2
	3.3	1.3
	3.1	1.1

Method

Four aliquots of mixed leaves from the same source as Test 1 were prepared and their air-dried weights determined. Each aliquot was separately placed in a trap, thoroughly wetted, sponged by the standard procedure for removal of excess water, weighed wet, then oven-dried at 70°C for 48 hours and re-weighed. The green weights and oven-dry weights of each aliquot were used to calculate the oven-dry weight of each of the other aliquots given their green weight only. Comparisons were made between the actual and calculated values that were derived.

Results

Free water retention, green weight and oven-dried weights of each aliquot are given in Table 6.3.2 together with the percentage error between the calculated and actual oven-dry weights.

Conclusion

The calculated experimental error range of 0.5 to 5.2% was satisfactory and the procedure was repeated with less homogenous mixtures.

TEST 3

Aim

To check the efficacy of the technique proposed for calculation of the equivalent oven-dry weights of litter within paired traps using litter of various ages.

Method

Pairs of samples were collected from Sites 1 and 2 that represented freshly accessed litter, and perched litter of up to age 23 weeks since accession (trapped on hessian strips held above the ground

Table 6.3.2.   Comparison of actual and calculated oven-dry
weights of litter samples

(a) Calculation of samples 2, 3, and 4 from 1:

Sample No.	Air-dry wt. (g)	Wetted wt. (g)	Free water (g)	Oven-dry wt. (g)	Calculated oven-dry wt. (g)	% error
2	6.8	18.2	11.4	5.9	6.1	2.9
3	6.8	17.6	10.8	6.0	5.9	2.2
4	6.8	17.5	10.7	5.8	5.8	0.5

(b) Calculation of samples 1, 3, and 4 from 2:

Sample No.	Air-dry wt. (g)	Wetted wt. (g)	Free water (g)	Oven-dry wt. (g)	Calculated oven-dry wt. (g)	% error
1	6.3	15.9	9.6	5.3	5.2	2.8
3					5.7	5.2
4					5.7	2.2

(c) Calculation of samples 1, 2, and 4 from 3:

Sample No.	Air-dry wt. (g)	Wetted wt. (g)	Free water (g)	Oven-dry wt. (g)	Calculated oven-dry wt. (g)	% error
1					5.4	1.9
2					6.2	5.1
4					6.0	2.9

(d) Calculation of samples 1, 2, and 3 from 4:

Sample No.	Air-dry wt. (g)	Wetted wt. (g)	Free water (g)	Oven-dry wt. (g)	Calculated oven-dry wt. (g)	% error
1					5.3	0.6
2					6.0	2.2
3					5.8	2.8

that had been used in collections for litter bag experiments). A further 4 collections each were made of litter 0-23 weeks old on the ground, and of litter from the standing crop of Site 1. Green weights and oven dry weights of each sample were determined, and the oven-dry weights of related samples were calculated.

Results

Calculations of actual and calculated oven-dry weights of each sample are listed in Table 6.3.3, together with their respective percentage error.

A larger range of experimental error than that of, Test 2 was obtained in calculating oven-dry weight of perched litter at Site 2 (10.6-11.6%), and with litter from the standing crop or litterbed of Site 1 (4.8-11.4%). Results of calculations with all other litter types from both sites resulted in a percent error range of -0.6-+2.9%.

Discussion

The large range of experimental error with perched litter from Site 2 was attributed to a disproportionate inclusion of Old Growth Eucalypt leaves within the samples. These leaves may have been perched within the crowns of the dense understorey canopy of the mixed-forest for an extended period (normal accessions over 6 week intervals would not contain such an amount). Samples from the litterbed at Site 1 were not comparable with each other, and thus do not relate to the type of material expected in accumulation traps B and D of the proposed experiments.

Conclusion

The method proposed for the calculation of equivalent oven dry weight of non-destructive litter trap contents from the actual green

Table 6.3.3.　　　Check on oven-dry weight estimation.

Litter type	Actual W_g (g)	Actual W_o (g)	Calculated values of W_o (g)				% error
S.1 Perched	19.3	15.1	–	15.3			1.3
	28.7	22.7	22.5	–			0.9
S.2 Perched	45.6	35.7	–	31.9			10.6
	24.6	17.2	19.3	–			11.6
Freshly fallen, S1	24.0	18.3	–	18.7			2.2
	24.1	18.8	18.4	–			2.1
Freshly fallen, S2	39.6	22.6	–	22.9			1.3
	31.8	18.4	18.1	–			1.6
S1. Ground 0-23 weeks on hessian	44.6	30.4	–	31.4	31.4	30.6	0.6-3.3
	35.6	25.1	24.3	–	25.1	24.4	-3.2-0
	29.7	20.9	20.2	20.9	–	20.4	-3.3-0
	51.0	35.0	34.8	36.0	35.9	–	-0.6-2.9
S1. Ground, from litter bed	30.8	22.2	–	21.2	23.6	22.4	0.9- 6.3
	24.3	16.7	17.5	–	18.6	17.7	4.8-11.4
	29.5	22.6	21.3	20.3	–	21.5	-10.2--4.9
	34.5	25.1	24.9	23.7	26.4	–	-0.8-+5.6

and oven dry weights of sacrificial litter trap contents was considered satisfactory.

6.3.3 The Main Experiment

Materials and Methods

Establishment

The trapping systems described in 6.3.2. were established at all study sites on October 10th, 1979. Several traps at Sites 1 and 2 were vandalised or destroyed by animals, and some traps at Site 2 were destroyed by flooding in November, 1980. Traps at these 2 sites were abandoned.

As a guard against animal damage at Sites 3 and 4, a 300 mm high, circular framework of steel mesh was erected around each A/B and C trap. The framework was of sufficient diameter to avoid the $1m^2$ terylene mesh bases of each trapping system and limited in height to allow uninterrupted litter access to the systems.

Termination

Site 4 investigations ended after 84 weeks (14 sampling intervals) and Site 3 after 96 weeks (16 intervals) in the field. The difference in sampling time resulted from a reduction in the available sacrificial trap mesh squares at Site 3 through destruction by fallen woody materials.

Check on trap comparability

At run termination regression analyses were made of green and oven-dry mean yield data of the non-destructive (A/B) and sacrificial (C/D) trapping systems of Sites 3 and 4 per sampling interval. Regression analyses also compared total yields per interval of the A and C traps at each site with the 10 traps of the same area used for the separate accession study described in Chapter 4.

During the final sampling at each site it was possible to determine actual oven-dry weight of all samples, and use the data to determine percentage errors of estimation of oven-dry weights of A and B trap yields from the C and D trap data.

Climatic data

All available meteorological data for the Hastings Chalet station were compiled to relate total or mean values of measured parameters per sampling interval.

The Waite Institute Climatic Index (I) described by Prescott (1946) was calculated for each sampling interval for which rainfall and evaporation data were available using the formula

$$\frac{P}{E^m} = I, \qquad \text{(Prescott, 1946)}$$

where P = rainfall (mm) per interval, E = evaporation (mm), and m is a constant with a mean value of 0.75.

Effective rainfall was calculated for each interval from the formula

$$0.54 = \frac{P}{E^{0.70}}, \qquad \begin{array}{l}\text{(Prescott, 1949; Hounam, 1955;} \\ \text{Vollprecht and Walker, 1957)}\end{array}$$

Mean temperature was listed both as it occurred per interval, and with a lag of one interval (42 days) that closely corresponded with the correction factor lag of 40 days listed for the study region in Prescott's (1942) map showing lag of temperature behind solar radiation.

Climatic values are listed per sampling interval in Table 6.3.4.

Alteration to trapping system

The description of the relative placement of the A/B and C/D

Table 6.3.4.   Litter moisture content percent and climatic data per sampling interval.

Sampling interval	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81	1.7.81	12.8.81
Litter moisture content % S3,B	–	31.7	41.6	32.1	159.4	223.2	279.1	243.8	120.0	133.7	35.2	40.8	206.0	232.5	321.6	353.0
S3,D	–	31.4	39.2	36.5	166.0	217.2	278.9	246.1	112.9	135.6	36.8	45.5	211.3	250.4	365.2	351.2
S4,B	–	27.9	22.0	30.0	130.6	220.6	260.4	249.5	75.5	82.0	22.6	54.9	202.0	185.2		
S4,D	–	27.0	23.6	32.0	131.1	220.7	254.3	245.7	78.8	83.8	23.2	60.1	202.5	228.3		
Maximum temperature, T	27.8	27.1	28.3	33.0	28.2	21.5	16.6	19.4	29.9	29.0	30.0	37.5	28.6	23.2	16.0	16.3
Minimum temperature, T	2.3	3.0	1.8	3.7	1.4	-0.6	-2.0	2.2	-0.6	2.1	3.5	3.2	3.5	1.4	-1.2	-?.6
Mean maximum T	17.8	18.4	18.3	18.8	17.5	14.6	12.5	13.2	16.2	18.0	20.6	22.6	20.5	15.4	12.4	11.4
Mean minimum T	6.8	8.4	9.1	8.6	7.2	6.8	3.8	5.7	6.5	7.2	9.1	10.8	10.0	6.4	5.1	2.1
Mean T	15.1	15.1	15.1	18.4	14.8	10.5	7.3	10.8	14.7	15.6	16.8	20.4	16.1	12.3	7.4	6.9
Mean T with lag, n+i	15.1	15.1	18.4	14.8	10.5	7.3	10.8	14.7	15.6	16.8	20.4	16.1	12.3	7.4	6.9	10.9
Total rainfall (mm)	106.9	165.7	170.2	67.0	150.9	153.6	137.1	331.5	228.2	168.2	46.8	43.0	150.3	296.3	152.3	215.4
Total evaporation (mm)							25.2	42.0	61.5	92.4	120.6	134.4	71.4	52.8	20.5	29.4
Waite Index							12.2	20.1	10.4	5.6	1.3	1.1	6.1	15.1	15.9	17.1
Effective rainfall							5.2	7.4	9.7	12.9	15.4	16.7	10.7	8.7	4.5	5.8

traps as detailed in Section 6.3.2. was applicable from 26.3.1980. Prior to that date, (initial 24 weeks) A traps and C traps were supported above their corresponding B and D traps on 10 cm high stilts which made them susceptible to damage. From 26.3.80 all upper traps A and C were fitted tightly within the lower traps B and D (as detailed in 6.3.2.).

Inorganic matter content

All traps were established upon bare mineral soil to provide a more homogenous base and as a consequence of periods of heavy rainfall it was thought that silt might have been washed into and out of the system, thus leading to erroneous estimates of litter yields.

Upon completing litter yield estimates, the oven-dried trap contents were ground to x60 mesh (B.S.S.) in a Wiley Mill and aliquots were 'ashed' at 600°C for 3 hr in a muffle furnace to determine percent inorganic matter content.

Results

Trap yields

Values of green and oven-dry weight yield of individual traps per interval per Sites 3 and 4 are listed in Appendix C, Table 1 and Table 2. Mean values of green weight yields per trap type are given in Appendix C, Tables 3 and 4 for Site 3 and 4 respectively.

Similarly, mean values of oven-dry weight yields are listed in Appendix, C, Tables 5 and 6 for Sites 3 and 4, where the values of A and B traps are equivalent oven-dry weights calculated from the known values of C and D traps.

Moisture content.

Moisture content percentage of accessing litter (C) and accumulating litter (D) at Sites 3 and 4 are listed in Appendix C, Tables 7

and 8 respectively. Mean values of B and D trap litter for each site are listed in Table 6.3.4.

Inorganic matter content

Results of determinations of inorganic matter content of litter collected in sacrificial traps at each sampling interval were typical of ash contents for normal, unadulterated litter, with values ranging from 2-5%. No allowances were necessary for silt incorporation.

Comparability of trapping systems

Results of regression analyses of green and dry weights of the accessing and accumulating litter of the A/B and C/D systems yielded significant correlations (Appendix, Statistical Analysis, 19) at both sites (r = 0.904 to 0.983).

Regression analyses of accessional data of the decomposition study traps and traps of the accessional study demonstrated a significant correlation between results of the 2 studies at both sites (r = 0.952 at Site 3 and 0.872 at Site 4). Appendix, Statistical Analysis, 20, lists the data.

Comparison of estimated oven-dry weight with known determinations

Table 6.3.5. lists the estimated and actual oven dry weight values of accessional and accumulated litter per trapping system at run termination at each site, and includes a calculated percentage error value.

Results for Site 3 were remarkably similar with percentage error values of zero for accessing litter and 3.3 for accumulated litter. Site 4 results were less error-free due to the greater variability in trap yields on the more open site. Percentage error was 43.0 for accessing and 13.5 for accumulated litter.

Table 6.3.5.   Check comparison of actual and calculated values for
accessed (A) and accumulated (B) litter at run
termination.

	Site 3				Site 4		
Trap No.	96 weeks			Trap No.	84 weeks		
	Actual W_O	Calc. W_O	% error		Actual W_O	Calc. W_O	% error
71 A	2.5	2.3		76 A	N.A.		
B	173.6	167.5		B	109.8	139.7	
72 A	1.3	1.4		77 A	4.5	5.6	
B	93.0	96.9		B	-95.3	131.1	
73 A	1.4	1.5		78 A	2.1	3.4	
B	115.1	137.4		B	49.6	55.1	
74 A	1.3	1.4		79 A	3.7	3.8	
B	134.4	135.0		B	73.9	55.3	
75 A	3.6	3.5		80 A	1.6	3.2	
B	133.9	134.5		B	63.2	63.9	
ΣA	10.1	10.1			11.9	16.0	
$\bar{A}$	2.0	2.0	0		3.0	4.3	43.0
ΣB	650.0	671.3			391.8	445.1	
$\bar{B}$	130.0	134.3	3.3		78.4	89.0	13.5

N.A. = not available.

Calculation of accession, accumulation, and decomposition

Following the regressions, accession to individual trapping systems was taken as the mean value for all A and C traps at each interval per site. The accumulated value of accession at any sampling interval, i, was expressed as the sum of the individual accession intervals for n intervals, i.e.

$$\sum_{i=1}^{n} A_i \quad (or, \quad \sum_{i=1}^{n} C_i)$$

Accumulation, or 'standing crop' of litter at interval n was the weight of litter in the B or D traps after interval n, plus the weight of accessed litter in A and C traps during the nth interval, i.e.

standing crop = $(B_n + A_n)$ or, $(D_n + C_n)$.

Theoretically, $\sum_{i=1}^{n} C_i$ should always be greater than (Dn + Cn) because of decomposition. On 10 sampling occasions however, (Dn + Cn) was greater than $\sum_{i=1}^{n} C_i$, and several hypotheses for this anomaly were considered.

Ho1. Intervals of high rainfall may have washed material into and out of the lower trap.

Conclusion. The anomaly was not consistently related to intervals of high rainfall.

Ho2. Silt may have been incorporated into the lower trap.

Conclusion. Inorganic matter contents were normal for all samples, hence silt was not the cause of error.

Ho3. A massive influx of soil biota.

Conclusion. The "error input" value was too great to be attributable to soil biota, and field observations confirmed this view.

Ho4. "Error input" was attributable to the B and D trap data, and not the A and C trap data.

Conclusion. Regression analyses had shown that accession measured in the trapping systems was highly correlated with data of a separate estimate at each site, and hence "error input" was likely to have been attributable to the lower traps receiving materials unaccounted for by the upper traps.

This final conclusion was strengthened by the realisation that prior to interval 4, all accession traps were raised on 10 cm high stilts above the accumulation traps, and it was possible for litter materials to have blown into the accumulation traps. This material would not have been accounted for by the accession traps, and would lead to an error of the type encountered. The first 4 intervals of measurement were coincident with annual peak litterfall, increasing the chance of significant extraneous input. It was considered that material was more likely to blow into the lower sheltered trap than out of it. Any extraneous input would continue to affect the balance of the system at all other intervals.

At interval 4, all upper traps were lowered to avoid animal damage, and fitted tightly within the lower traps. Hence from this time it was improbable that extraneous material could gain access to the lower traps without some major, visible disturbance. Such disturbances were not observed.

Hypothesis Ho4 was accepted, and data for A and C traps corrected accordingly (Appendix C, Tables 9 to 12).

Rates of accession, a, and of decomposition, d, were calculated from the equations described by Southwood (1966) for population growth rates, i.e.

$$\frac{dn}{dt} = rN, \text{where N is the weight of litter}$$

at time t, and r is the resultant of accession and decomposition rates i.e.

r = a−d, where a = accession rate

d = decomposition rate.

The above equation may be written as:

$$N_{t+1} = N_t e^r$$

or for accession,

$$N_{n+1} = N_n e^a$$

or, $a = \log N_{n+1} - \log N_n$

$= \log \Sigma A_{n+1} - \log \Sigma A_n$

and for decomposition,

$N'{n+1} = N'_n e^{-d}$ (where negative sign signifies rate of loss)

or, $d = \log N'_n - \log N'_{n+1}$

$= \log (An + Bn) - \log B_{n+1}$

The difference, r, or (a−d) represents net accumulation in the trapping systems i.e. net gain when r values are positive and net loss (decomposition) when r values are negative.

Under steady state conditions, annual rates of a and d should yield a−d = 0.

Individual A and B trap data per sampling interval (with A and C trap values corrected for "error input") at Sites 3 and 4 are listed in Appendix C, Tables 9-12 respectively.

Table 6.3.6. lists calculated values for mean log (An + Bn), mean log B_{n+1}, mean log ΣAn and the standard errors of the means. Included in the table are calculated values of the accumulation rate (a, in g per g of standing crop), and net accumulation/decomposition (a−d, g per g of standing crop) at Site 3. Data for traps at Site 4 are similarly listed in Table 6.3.7.

Table 6.3.6.   Double trap.   Site 3.   Mean net accumulation/decomposition per trap system.

Trap system	Sampling interval	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81	1.7.81	12.8.81
B	Mean log (An + Bn)	0.743	1.400	1.722	1.936	1.900	1.907	1.842	1.923	2.119	2.098	2.184	2.230	2.202	2.231	2.175	2.128
	S.E.M.	0.091	0.085	0.067	0.017	0.038	0.038	0.036	0.046	0.043	0.042	0.042	0.041	0.052	0.038	0.040	0.038
	Mean log Bn + 1	0.743	1.376	1.663	1.852	1.868	0.819	1.850	2.022	2.079	2.148	2.173	2.171	2.207	2.164	2.121	-
	S.E.M.	0.091	0.087	0.057	0.044	0.037	0.037	0.048	0.041	0.040	0.044	0.042	0.051	0.039	0.042	0.038	-
	Mean log ΣA	0.767	1.400	1.733	1.978	2.013	2.042	2.056	2.103	2.186	2.201	2.234	2.284	2.309	2.328	2.335	2.339
	S.E.M.	0.088	0.085	0.067	0.018	0.017	0.017	0.018	0.017	0.025	0.025	0.023	0.023	0.025	0.025	0.025	0.025
	Mean calculated a	0.633	0.333	0.245	0.036	0.029	0.014	0.047	0.083	0.015	0.033	0.050	0.025	0.019	0.007	0.004	-
	Mean calculated d	-	0.024	0.059	0.084	0.032	0.088	-0.008	-0.099	0.040	-0.050	0.011	0.059	-0.050	0.067	0.054	-
	a-d	0.633	0.309	0.186	-0.048	-0.003	-0.074	0.055	0.182	-0.025	0.083	0.039	-0.034	0.024	-0.060	-0.050	-
D	Mean log (Cn _ Dn)	1.446	1.731	1.872	1.987	1.877	1.723	1.826	1.939	2.051	1.970	2.175	2.249	2.191	2.226	2.168	2.174
	S.E.M.	0.058	0.062	0.063	0.055	0.066	0.057	0.062	0.048	0.084	0.039	0.040	0.064	0.075	0.074	0.047	0.035
	Mean log Dn + 1	1.446	1.462	1.780	1.823	1.677	1.796	1.890	1.926	1.944	2.144	2.188	2.156	2.203	2.213	2.167	-
	S.E.M.	0.038	0.102	0.043	0.075	0.066	0.066	0.045	0.090	0.041	0.044	0.074	0.080	0.080	0.039	0.036	-
	Mean log ΣC	1.433	1.731	2.018	2.148	2.174	2.189	2.201	2.227	2.294	2.306	2.326	2.369	2.390	2.404	2.409	2.414
	S.E.M.	0.034	0.062	0.047	0.057	0.053	0.052	0.051	0.050	0.050	0.048	0.048	0.046	0.044	0.044	0.044	0.044
	Mean calculated a	0.298	0.287	0.130	0.026	0.015	0.012	0.026	0.067	0.012	0.020	0.043	0.021	0.014	0.005	0.005	-
	Mean calculated d	-	0.269	0.092	0.164	0.200	-0.073	0.064	0.013	0.107	-0.174	-0.013	0.093	-0.012	0.013	0.001	-
	a-d	0.298	0.018	0.038	-0.138	-0.185	0.085	0.090	0.054	-0.095	0.194	0.056	-0.072	0.026	0.018	0.006	-

Table 6.3.7.   Double trap.   Site 4.   Mean net accumulation/decomposition per trap system.

Trap system	Sampling interval	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81
	Mean log (An + Bn)	0.759	1.254	1.426	1.590	1.615	1.600	1.640	1.607	1.753	1.745	1.821	1.894	1.966	1.934
	S.E.M.	0.076	0.114	0.117	0.088	0.089	0.087	0.089	0.079	0.117	0.134	0.118	0.080	0.072	0.094
	Mean log Bn + 1	0.759	1.184	1.353	1.546	1.553	1.618	1.574	1.661	1.713	1.766	1.782	1.907	1.910	-
B	S.E.M.	0.076	0.143	0.092	0.095	0.095	0.086	0.080	0.125	0.130	0.123	0.093	0.076	0.091	-
	Mean log ΣA	0.759	1.254	1.464	1.660	1.715	1.748	1.764	1.784	1.849	1.875	1.919	2.004	2.050	2.067
	S.E.M.	0.076	0.114	0.104	0.093	0.088	0.083	0.081	0.083	0.086	0.091	0.089	0.078	0.078	0.078
	Mean calculated a	0.495	0.210	0.196	0.055	0.033	0.016	0.020	0.065	0.026	0.044	0.085	0.046	0.017	-
	Mean calculated d	-	0.070	0.073	0.044	0.062	-0.018	0.066	-0.054	0.040	0.021	0.039	-0.013	0.056	-
	a-d	0.495	0.140	0.123	0.011	-0.029	0.034	-0.046	0.119	-0.014	0.023	0.046	0.059	-0.039	-
	Mean log (Cn + Dn)	1.332	1.560	1.511	1.666	1.687	1.576	1.684	1.746	1.770	1.720	1.861	1.905	1.949	1.969
	S.E.M.	0.038	0.053	0.043	0.044	0.074	0.040	0.047	0.061	0.082	0.036	0.075	0.142	0.095	0.102
	Mean log Dn + 1	1.332	1.295	1.355	1.626	1.531	1.661	1.702	1.694	1.680	1.819	1.822	1.904	1.946	-
D	S.E.M.	0.038	0.070	0.026	0.086	0.038	0.045	0.061	0.086	0.037	0.078	0.154	0.096	0.106	-
	Mean log ΣC	1.332	1.560	1.691	1.863	1.898	1.918	1.931	1.958	2.000	2.018	2.045	2.096	.2.128	2.143
	S.E.M.	0.038	0.053	0.035	0.039	0.037	0.038	0.038	0.037	0.045	0.047	0.046	0.049	0.046	0.043
	Mean calculated a	0.228	0.131	0.172	0.035	0.020	0.013	0.027	0.042	0.018	0.027	0.051	0.032	0.015	-
	Mean calculated d	-	0.265	0.156	0.040	0.156	-0.085	-0.018	0.052	0.090	-0.099	0.039	0.001	0.003	-
	a-d	0.228	-0.134	0.016	-0.005	-0.136	0.098	0.045	-0.010	-0.072	0.126	0.012	0.031	0.012	-

Net accumulation/decomposition at Site 3 and 4 per sampling interval is illustrated in Fig. 6.3.2. and 6.3.3. respectively. In both figures the logarithmic values of litter moisture content and mean maximum temperature are illustrated per sampling interval.

Figure 6.3.4. illustrates the mean log ΣA_n (sum of accessed litter at each interval) and the mean log (An + Bn) (accumulated litter, or standing crop of litter, at each interval) for Sites 3 and 4.

Sampling intervals during which decomposition occurred are listed in Table 6.3.8. for both A and B accumulating litter traps at Sites 3 and 4, together with corresponding ranges of litter moisture content, and litter mean maximum temperature per sampling interval. Litter temperatures were interpolated from the data of Chapter 3, Section 2.3, that related Y (litter temperature on site) to X (Hastings Chalet air temperature) as follows:

Site 1 (relates to Site 3),

$$Y = 5.7139 + 0.3055X$$

Site 4,

$$Y = 4.3267 + 0.5236X$$

Discussion

The double trap system demonstrated intervals of decomposition within the standing crop of litter at both sites.

Major periods of decomposition occurred in the Spring and Autumn and Site 4 was the most responsive and reactive, decomposition beginning earlier than at Site 3. This greater sensitivity was attributable to the more open structure of the vegetation at Site 4.

Fig. 6.3.4. demonstrates a tendency towards steady state in trap systems of both sites with increasing time. Initially there was zero standing crop in the trap systems and net decomposition was not

FIG. 6.3.2   SITF 3.   NET ACCUMULATION IN B AND D TRAPS VERSUS
              LOG MEAN MAXIMUM TEMPERATURE AND LOG LITTER MC%

LEGEND

Net accumulation/decomposition   Trap B   □————□
                                 D   ⊙————⊙
Log litter moisture content %   Trap B   ————————
Log mean maximum temperature   ————————
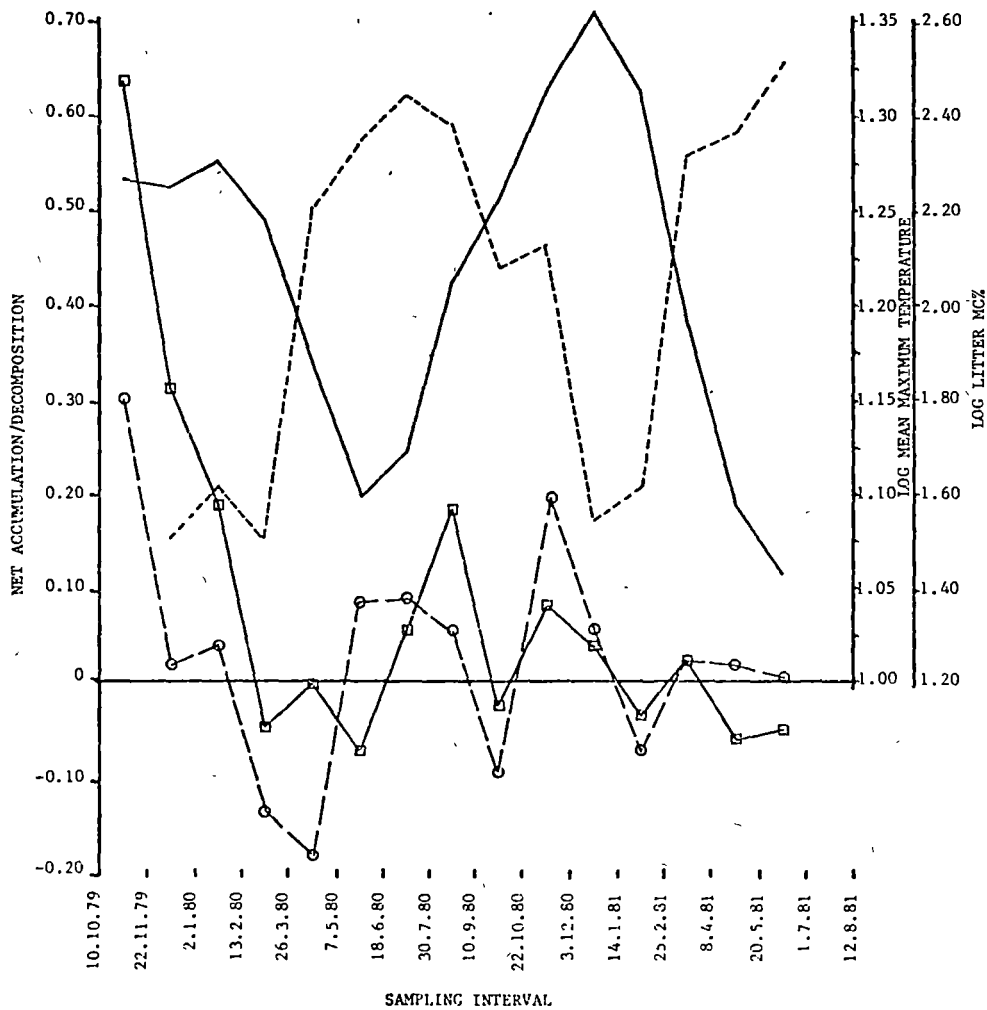
SAMPLING INTERVAL

FIG. 6.3.3.   SITE 4.   NET ACCUMULATION IN B AND D TRAPS VERSUS
               LOG MEAN MAXIMUM TEMPERATURE AND LOG LITTER MC%.

LEGEND

Net accumulation/decomposition Trap B   □————□
                                  " D   ⊖————⊖
Log mean litter MC %   Trap B   ————————
Log mean maximum temperature   _____
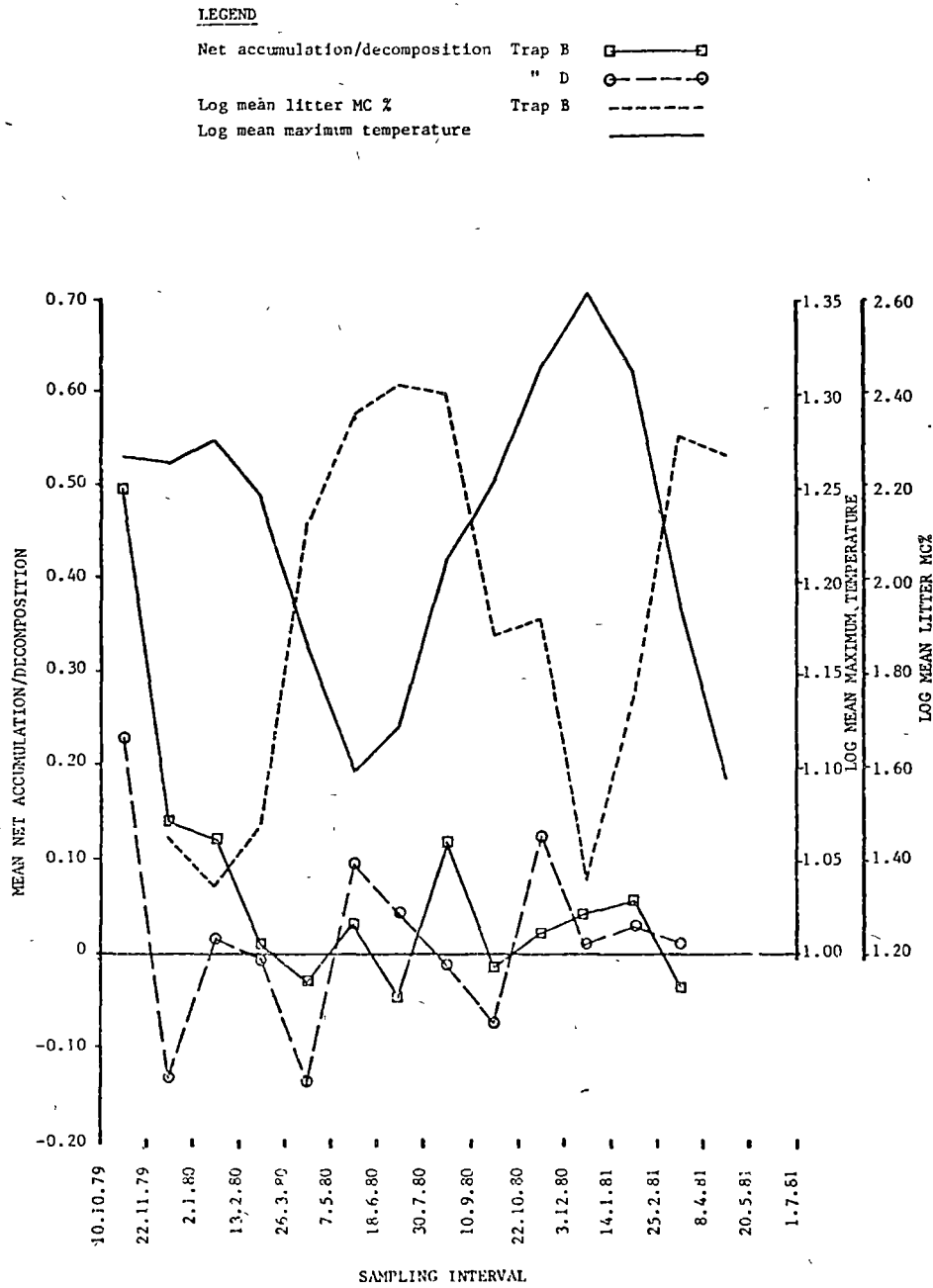
SAMPLING INTERVAL

FIG. 6.3.4.   SITES 3 AND 4.   A AND B TRAP SYSTEMS.
SUM OF ACCESSED LITTER AND TOTAL ACCUMULATED LITTER
PER SAMPLING INTERVAL.
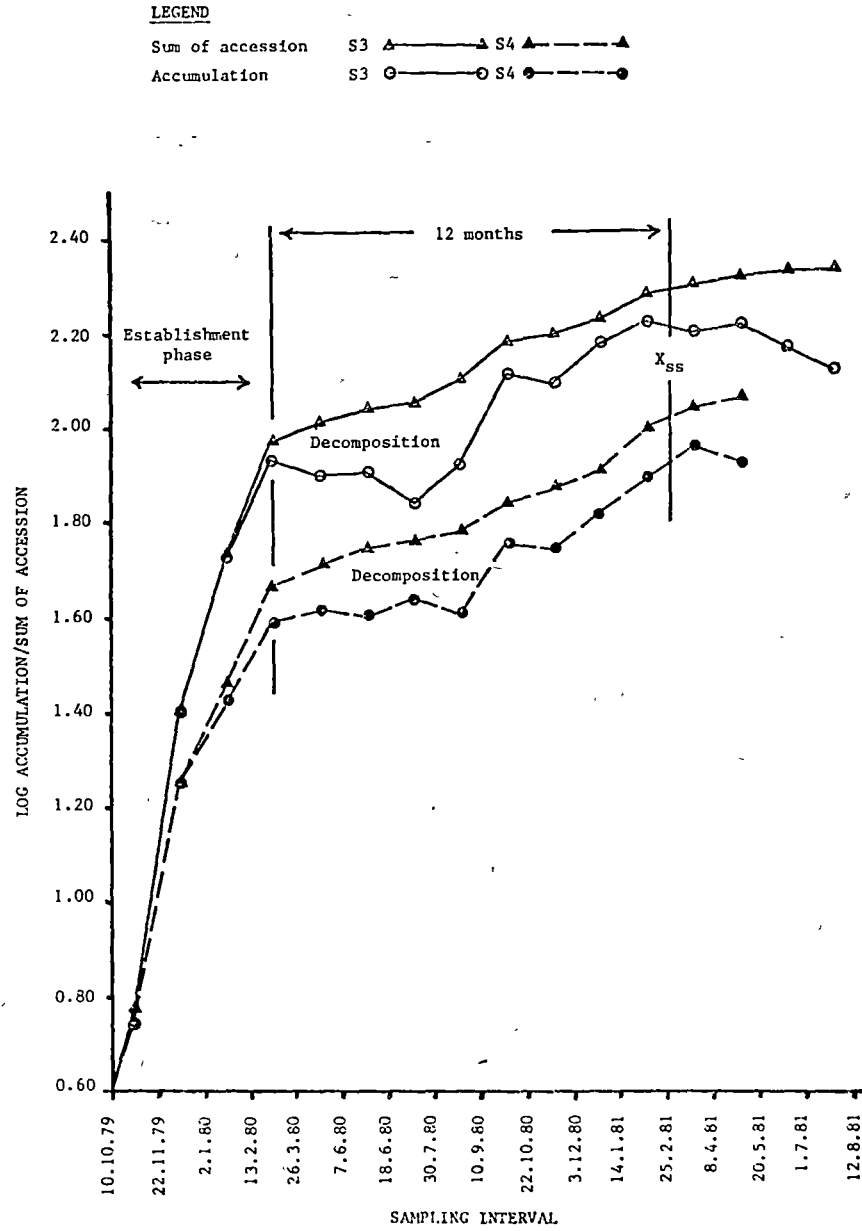
Table 6.3.8.   Litter moisture content (%) and Mean maximum air and litter temperatures (°C) per sampling intervals during which decomposition occurred.

Site	Sampling interval		Litter moisture content (%)	Mean maximum temperature range (°C)	
	B trap	D trap		Air	Litter
3	26.3.80	26.3.80	32.1 – 41.6	18.3 – 18.8	11.3 – 11.5
		7.5.80	36.5 – 166.0	18.8 ‑ 17.5	11.5 – 11.06
	18.6.80		159.4 – 223.2	17.5 – 14.6	11.06 – 10.2
	22.10.80	22.10.80	112.9 – 246.1	13.2 – 16.2	9.7 – 10.7
	25.2.81	25.2.81	35.2 – 45.5	20.6 – 22.6	12.0 – 12.6
	20.5.81		206.0 – 232.5	20.5 – 15.4	12.0 – 10.4
	1.7.81		232.5 – 321.6	15.4 – 12.4	10.4 – 9.5
4		2.1.80	27.0	17.8 – 18.4	13.6 – 14.0
	7.5.80	7.5.80	30.0 – 131.1	18.8 – 17.5	14.2 – 13.5
	30.7.80		220.6 – 260.4	14.6 – 12.5	12.0 – 10.9
	22.10.80	22.10.80	249.5 – 75.5	13.2 – 16.2	11.2 – 12.8
	8.4.81		54.9 – 202.0	10.8 – 10.0	10.0 – 9.6

apparent until after 24 weeks of data collection on 26.3.80. There was then an apparent net loss which attained minimal levels at both sites after approximately 12 months. The sampling at which loss was minimal (25.2.81) corresponded to the peak period of litterfall.

Litter moisture content at both sites was inversely related to temperature. Nagy and Macauley (1982) have demonstrated that biological decomposition is significant when substrate moisture content is greater than 13%. In these studies the moisture content of the standing crop was always in excess of that value, and hence moisture was at no stage considered to be limiting. Thus any implied relationship between litter moisture content and decomposition must be attributable to the moisture content/temperature relationship. Decomposition occurred at litter moisture contents of 320% (dry weight basis) and therefore excessive moisture was not a limiting factor.

The interdependancy of litter temperature, moisture content, and climatic variables presented in Table 6.3.4, confounded application of multicomponent analyses. Such analyses may assume greater importance in climates where rainfall and moisture content may limit the decomposition process e.g. *E. obliqua* forests of South Australia (Lee and Correll, 1978). Examination of Fig. 6.3.2 and 6.3.3 demonstrated that litter decomposition was associated with periods of increasing or high temperatures.

Data of this experiment lead to the view that there was an ever-present inoculum base that was activated by increasing litter temperatures, and which was not affected by litter moisture under conditions at Hastings. Adequate temperature for microfloral activity was therefore considered to be the major factor affecting litter decomposition in these forests.

The double trap system had a number of desirable attributes. These were:

(i)   Natural accession and accumulation could be monitored simultaneously with decomposition.

(ii)   Decomposition was monitored *in situ*, utilising naturally shed leaves in a naturally occurring species mixture, eliminating the problems associated with the use of green leaves, and the more artificial environment of litter bags, and

(iii)   The sampling technique permitted determination of both accessing and accumulating litter rates.

The system could be employed to monitor changes in litter pH, microfloral and faunal succession, and energetics of the litter system.

An improvement to the system may be achieved by commencing with a pre-determined quantity of litter in the lower traps (B and D) that equalled the standing crop of litter in the stand under study. This would enable litter steady-state conditions to exist from commencement of the study, and would allow a further merit, the determination of decay constants, k, from derived values.

CHAPTER 7

INVERTEBRATE FAUNA OF THE HASTINGS STUDY SITES AND THE EFFECTS OF VARIOUS TREATMENTS.

7.1   INTRODUCTION

Invertebrates in forest litter systems have a functional role that has been considered as –

(a)   the comminution of large items (leaves, bark, twigs etc.) into a size more accessible and available to microbiota,

(b)   the transport and incorporation of organic matter into soil, with subsequent improvement of aeration and water holding capacity.

(c)   the acceleration of litter turnover and movement of nutrients, and

(d)   the dispersal of microbiota (Ghilarov, 1971; Reichle, 1971).

These functions have been stressed in *Eucalyptus* systems by Wood (1974), Ashton (1975), Springett (1976), Richards and Charley (1977), Macauley (1975), but studies in Tasmanian cool temperate forests are few e.g. Howard (1975), Friend (1981). A recent review of techniques for the study of decomposition in eucalypt forests (Woods and Raison, 1982) indirectly refers to the involvement of invertebrates in comminution, and preference of groups for leaves of different ages and species.

The invertebrates associated with litter bag experiments at Sites 1 and 4 of these studies were examined, and results are expressed in general terms only. A more complete analysis will be published later.

A definitive appraisal of the invertebrates was not a major aim of this study, and estimates were limited by the low number of repl-

icates (3) for each treatment. The numbers of invertebrates within bags was generally related to the numbers occurring in the litter beneath the relevant bag. In general, numbers beneath the bags were 5-10 times greater than within the bags. This tended to reduce the variability in replicate bags and no transformations were applied to the data.

7.2   METHODS

Harvested litter bags of Experiments 1-5 (Chapter 6) were placed separately in plastic dishes in a glasshouse and allowed to air dry for 48 hours prior to sorting, oven drying, and weighing. Invertebrates leaving the bags during the period were collected and stored in 70% ethanol. Initial checks of bags indicated that the majority of readily observed animals vacated the bags during the 48 hour drying period.

Collections were examined beneath a binocular microscope and total counts made of all taxa. Counts of the 3 replicate samples were pooled and compared.

Previous analyses (Madden, unpublished, pers.comm.) had indicated that there were in excess of 100 ordinal groups in litter, and in this exercise these were condensed into 46 groups which were divided into 4 major categories, viz.

(1) *Cryptozoa* (excluding hexapods).

Oligochaetes, crustacea (ostracoda, copepoda, isopoda, amphipoda), diplopoda, araneida, mollusca, etc.

(2) *Acarina*. Cryptostigmata (oribatids, phthiracarids), mesostigmata (uropodina, gamasids, macrochelids) and prostigmata (cunaxids, trombids).

(3) *Hexapoda*. Collembolla, symphylans, hemipterans, dipterans, coleopterans, lepidopterans, etc., and

(4) *Nematodes*.

The hexapods and some of the acarina were further sub-divided into families.

At harvest at Site 1, the volumes of soil beneath each litter bag (25 x 20 cm) was removed to a depth of 20 cm (0.1 m^3) and hand sorted for macroinvertebrates on a white plastic sheet. Earthworms were collected and weighed upon return to the laboratory.

Measures of the diversity of the 3 major groups (Cryptozoa, acarina, and hexopoda) were calculated for both treatments and times of sampling, and were compared using the Shannon-Weaver diversity and relative diversity measures, H and J respectively:

$$H = \sum_{i=1}^{k} p_i \log p_i = \frac{n \log n - \sum_{i=1}^{k} f_i \log f_i}{n}$$

(where p_i = proportion found in category n_i; n = sample size, and f_i = frequency of observations in category i).

$$H_{max} = \log k, \text{ and}$$

$$J = \frac{H}{H_{max}} \qquad \text{(Southwood, 1978)}$$

The preference of different taxa for differing leaf species was measured at 12 months after field placement of litter bags. Individual leaf species were ranked in order of extent of decomposition and compared to the ranked abundances of the taxa per species bag(s) using the Spearman Rank Correlation Coefficient (Zar, 1974).

7.3   RESULTS

The litter bags were progressively colonised by all taxa and maximum diversities occurred in Spring, 12 months after bag establishment (Table 7.1). Population densities of most groups were higher at

Table 7.1.   Temporal trends in selected taxa within litter bags at Sites 1 and 4, Hastings, Tasmania. (Nos. m^{-2})

Site	Time after placement (months)	Oligochaeta	Ostracoda	Copepoda	Pseudo-scorpiones	Oribatida	Phthiracarid	Uropodina	Mesostigmata (other)	Poduridae	Entomobryidae	Chironomidae	Tipilidae	Lepidoptera	Staphylinidae	Nematoda
1	6	0.1	11.7	0	0.5	2.2	0.6	0.3	1.2	29.2	0.2	0.9	0.2	0.3	0.3	0
	12	12.1	114.6	39.6	0	10.6	6.9	2.8	5.3	24.0	2.8	14.6	3.2	1.3	1.4	3.4
	18	0.4	23.2	1.2	0.7	2.1	0.9	1.9	5.2	6.7	0.1	6.6	4.3	0.5	0.1	0.9
4	6	0.1	0.4	0	5.0	3.7	1.2	0.3	1.5	0.3	0	0.2	0.1	0.5	0.3	0
	12	0.4	0.8	71.0	1.2	17.0	0.2	8.9	5.6	0.5	5.0	11.0	3.0	0.2	0.5	2.5
	18	0	0.5	0	0	0.2	0	0.3	1.3	1.8	0.3	0.2	0.1	0.2	0	0.1

Site 1 than at Site 4 (Table 7.2). Ostracods, phthiracarids, rhaga-
diid and trombid mites, podurine collembolla, the chiranomid complex
(chironomids, ceratopogonids, mycetophilids, sciarids) and coleoptera
were all suppressed by conditions of Site 4, whereas copepods, entomo-
bryid collembolla, and uropodine acarina were favoured.

There was an apparent coincidence between seasonal trends in
decomposition and invertebrate numbers from 6-18 months after place-
ment, although maximum decomposition preceded this period during which
invertebrate numbers and diversity were low, and confined leaves were
intact.

Relative diversities of invertebrates infesting *E. obliqua* at
Sites 1 and 4 indicated that cryptozoa tended to colonise the bags
initially, but generally only one or two taxa gained dominance (Table
7.2). This observation was emphasized at Site 4 in the Spring when
all taxa except the copepoda were severely reduced. The acarina were
well established at both sites at 6 months while the hexapods did not
achieve maximum diversity until the spring. Hexapod diversity had
declined at 18 months as had the acarina at Site 1. Leaves which
decomposed fastest had higher diversities for each major group than
leaves which decomposed slowly (Table 7.3).

The numbers of earthworms found in the litter bags were related
to the number occurring in the soil beneath. Contents of individual
litter bags significantly influenced the numbers of earthworms within
and beneath the bags. Earthworm numbers within bags, and bags plus
soil, were significantly correlated with the order of decomposition
($P<0.5$). Numbers and biomass per unit area declined throughout the
experimental period, and the average weight of worms increased to the
spring sample and then declined (Table 7.4). These relationships
prevailed in the absence of any observable fragmentation of leaves
(except for *E. obliqua*).

Table 7.2.   Relative diversities (J) of invertebrate groups at
              3, 6, 12 and 18 months after placement of litter
              bags at Sites 1 and 4, Hastings, Tasmania.
              (Bags placed August, 1980).

Group	Time after bag placement (months)			
	3	6	12	18
A. Cryptozoa				
Site 1	0.724	0.265	0.471	0.440
Site 4	*	0.621	0.094	0.538
B. Acarina				
Site 1	*	0.896	0.911	0.504
Site 4	*	0.813	0.757	0.875
C. Hexapoda				
Site 1	*	0.232	0.775	0.665
Site 4	*	0.479	0.747	0.486

* = too few.

Table 7.3.   The relative diversities (J) of (a) cryptozoa,
              (b) acarina and (c) hexapoda associated with fast
              and slow decomposing leaves, Site 1, Hastings.
              (Placed August 1980 - harvested August 1981).

Tree species	Fast decomposers			Slow decomposers		
Invertebrate group	*E. obliqua*	*P. squameum*	*A. moschatum*	*E. lucida*	*N. cunninghamii*	*P. aspleniifolius*
(a) Cryptozoa	0.537	0.568	0.506	0.429	0.321	0.315
(b) Acarina	0.871	0.825	0.562	0.872	0.945	0.739
(c) Lexapoda	0.868	0.746	0.868	0.808	0.710	0.741

Table 7.4.   Density, biomass and average weight of earthworms in soil beneath litter
bags at 3, 6, 12 and 18 months after placement in August, 1980,
at Hastings, Tasmania.
(mean, standard error for n = 12).

| | Time (months) after placement | | | |
	3	6	12	18
Density (m^{-2})	31.83 ± 7.00	22.33 ± 6.45	9.50 ± 2.67	13.40 ± 3.88
Biomass ($g.m^{-2}$)	16.58 ± 4.27	11.84 ± 2.52	8.65 ± 2.29	5.36 ± 1.96
Ave. weight (g) live	0.47 ± 0.09	0.61 ± 0.15	0.75 ± 0.19	0.49 ± 0.16
Decomposition (%) of *E. obliqua*	34.0	17.0	16.8	17.8

Numbers of nematodes, cecidomyid larvae, and chironomids were also positively correlated with the order of leaf species decomposition nematodes (R_s = 0.756 P<0.05), cecidomyid larvae (R_s = 0.51, P<0.10), while phthiracarid mites were negatively correlated (R_s = 0.713 P<0.02). No other groups exhibited such relationships with the order of decomposition.

In contrast to the cryptozoa and the hexapods, acarine preference and numbers suggested that they exploited situations in which decomposition was low, or proceeding in the absence of the other two groups. Their higher diversity at both sites indicated the different roles played by representatives of the group.

Cryptozoa and hexapods were positively correlated (P<0.10) but acarine numbers were not related to either group. Nematodes were predominantly rhabditids.

Litter bags confining *E. obliqua* leaves plucked in August, stored at 2°C, and placed in the field in February were colonised by invertebrates more rapidly than either February plucked, or naturally shed leaves, placed in the field in February. Both cryptozoa and the chironomid complex were favoured on August plucked leaves, while naturally shed leaves favoured greater acarine numbers (Table 7.5).

Lepidopterous larvae were more abundant at Site 1 than Site 4, and consisted of 17 species belonging to 5 families. The Oecophoridae and Gelichiidae were the major families, followed by an unknown family, Geometridae and Tortricidae.

Addition of pesticides to litter bags prior to their placement affected significant changes which, in most taxa, declined in time (Table 7.6). Insecticide alone or in combination with fungicide drastically reduced the dipteran complex but favoured an increase in earthworm numbers. Treatment with fungicide also increased earthworm

Table 7.5.   Average numbers of major invertebrates in leaf litter
bags (0.05 m^2) originally containing 20g. *E. obliqua*
leaves harvested (1) August, 1980 and stored at 2°C
(CA), (2) February, 1981 (CB), and (3) naturally shed
in February, 1981 (CC).   Bags placed in February,
1981;   n = 5 per treatment, T = 3 months and R = 6
months after placement.

	CAT	CAR	CBT	CBR	CCT	CCR
Cryptozoa						
Oligochaeta	0.2	0.6	0	0.8	0	0.2
Ostracoda	10.8	42.8	22.0	25.6	15.0	22.0
Copepoda	19.4	76.2	8.6	61.4	7.2	69.6
Mollusca	0.2	1.0	0	0.2	0	0.2
Isopoda	0.2	0.4	0	0	0	0.2
Acarina						
Oribatidae A	0.2	1.6	0.8	2.2	0.2	10.8
B	10.2	2.4	5.2	5.8	2.4	10.8
Rhagidiidae	1.0	0	2.0	0	1.0	0.2
Trachytina	0.6	1.2	0.4	0.4	0.8	0.2
Phthiracaridae	0	1.0	1.0	2.2	1.0	2.2
Uropodinidae	0.4	1.2	0	0	0.6	0.4
Hexapoda						
Poduridae	58.4	29.2	11.2	32.6	9.6	22.0
Entomobryidae	0.2	0.8	0.2	0.6	0.6	0.4
Ceratocombus	0.2	1.2	0.2	0.6	0.2	0.8
Cyclorrapha	0	0.4	0	0	0	0
Chironomidae	7.4	15.4	3.6	5.0	4.4	2.4
Tipulidae	0.4	2.8	0	1.6	0	0.8
Psychodidae	0.8	1.4	0.8	0.6	0.8	0.4
Ceccidomyidae	0	1.4	0	1.0	0	0

Table 7.6   Average numbers of invertebrates per litter bag at 6, 12 and 18 months after placement (August 1980) of pesticide treated *E. obliqua* leaves. Site 1, Hastings, Tasmania.

Time	6 Months				12 Months				18 Months			
Taxa	Control	Insecticide	Fungicide	Insecticide + Fungicide	Control	Insecticide	Fungicide	Insecticide + Fungicide	Control	Insecticide	Fungicide	Insecticide + Fungicide
Ostracoda	11.5	0	0	0	142.0	98.0	81.0	85.0	20.0	24.0	31.5	15.8
Copepoda	0	0	0	0	50.0	57.0	35.2	76.0	1.3	0.3	0	1.3
Mollusca	0	0	0	0	2.0	1.3	1.0	0.6	0.3	0.7	0.3	0.3
Isopoda	0.5	0	0	0.3	3.3	3.0	2.7	2.2	1.3	1.4	1.0	1.4
Diplopoda	0.5	0.3	0	0.3	0.3	0	0.1	0.3	1.2	0.2	0.2	0.7
Oribatid A	1.0	0	0.3	0	1.5	13	1.0	0.3	0.6	1.0	0.2	0.2
Rhagidiidae	1.8	1	0	0	2.7	0	0	0	0	0.5	0	0
Oribatid B	1.3	1.5	0.8	1.5	10.5	15.4	9.8	9.9	0.4	0.3	1.6	0.8
Trachytina	0.3	0.5	0	0	2.5	2.3	1.6	3.9	0.2	0.3	0.2	0.2
Phthiracarid	0.3	1.0	0.3	0.5	7.8	3.2	5.4	3.6	0.9	0.1	1.4	0
Uropodina	0.3	0	0	0	4.9	1.9	2.5	2.5	2.3	0.6	0	0.3
Mesostigmata (other)	1.3	0.3	0.5	1.3	8.1	4.5	5.8	2.5	12.7	2.3	3.7	2.5
Poduridae	27.0	14.3	9.8	24.9	27.4	18.5	23.8	20.3	1.5	2.5	5.8	3.9
Entomobryidae	0.3	0	0	0	1.7	3.9	1.8	1.5	0	0	0.2	0.1
Aphidae	0.3	0.3	0.3	0.3	5.7	2.8	3.9	2.4	1.5	0.6	0.6	0.3
Ceratocombus	0.3	0	0	0	2.8	0.3	1.8	0.9	0	0	0	0
Rhyparochrominae	0.5	0.3	0.3	0.5	0	0	0	0	0	0	0	0
Cyclorrapha	0.3	0	0.3	0	1.3	0.2	0.8	0.1	0.5	0	0.3	0.3
Chironomid*	1.3	0	0	0	23.8	1.8	17.0	5.4	8.7	0.2	1.3	1.5
Tipulid	0.3	0.3	0.3	0	4.4	0.3	3.2	0.9	5.7	0.1	0.1	0
Psychodid	0.3	0	0	0	11.5	0	4.9	0	0.4	0	0.1	0
Cecidomyid	0.3	0	0	0	6.6	17.3	4.4	17.4	1.2	0.2	0.5	0.4
Stratiomyid+	0	0	0	0	4.0	0.2	1.3	0.1	0.1	0	0.3	0

* Chironomid + Mycetophilidae.   + Stratyiomyidae + Ceratopogonidae.

221

numbers (Table 7.7). Cecidomyid larvae greatly increased in number in the 6-12 months post establishment period in insecticide treated bags.

The litter bag environment favoured the abundance of some groups, notably the ostracods, copepods, and collembolla, but other groups e.g. amphipods were under-represented. Conditions at Hastings during the study period favoured an increase of ostracods and copepods which were 20-50 fold higher in numbers than in the preceding season (Madden, unpublished).

7.4   DISCUSSION

The tentative results of this aspect of the study have indicated that the invertebrates were not primarily involved in the decomposition process at Hastings. No direct attack occurred on leaves until they had been conditioned by microbiota, despite differences in numbers associated with leaves of different species and mixtures, differing leaf ages, and treatment with pesticides. Early invasion of litter bags by cryptozoa appeared to be due to suitability as a refuge, although the ostracods and copepods were observed to actively filter the surface film of water on intact leaves. Earthworms were attracted to, and accumulated within the bags and in the soil beneath in order of the extent of decomposition of the confined leaves, irrespective of whether the leaves were intact or not. The earthworms at Hastings were megascolecid worms, and Wood (1974) observed that surface inhabiting species of this family did not transport material from the litter to the soil. The significant preference exhibited by earthworms in the absence of fragmentation suggests that leachates, or microbiota exploiting leachates from the bags were responsible for the results obtained. The increase in earthworm numbers together with the resurgence of cecidomyid numbers following pesticide treatment suggests that the growth of microbiota in the absence of grazing contrib-

Table 7.7.   Total numbers of earthworms beneath bags associated
with pesticide treatments of *E. obliqua* leaves.

A = numerical
B = log (X+1)

	Control	Insecticide	Fungicide	Insecticide + Fungicide
A	32.00 ± 6.32	90.25 ± 7.47	58.63 ± 13.30	51.75 ± 4.00
B	1.42 ± 0.19	1.95 ± 0.06	1.07 ± 0.34	1.71 ± 0.16

uted significantly to the preferences observed. Furthermore, the weight of individual earthworms increased while both numbers and total biomass declined. This occurred at a time when invertebrate activity and decomposition were restricted by low temperature.

E. obliqua leaves were the first of the tested leaf species to fragment, following initial colonisation by fungi and bacteria, which in turn were exploited mainly by diptera (surface and mesophyll) and lepidoptera, diplopoda, and isopoda (gross feeding).

There were generally lower numbers of most taxa under the more extreme and variable climatic conditions at Site 4, yet decomposition proceeded at approximately the same rate and in the same order at both sites. It was apparent from the results that the climate of the Southern Forests limits the incidence of active populations of invertebrates to the period, spring – summer, and this "habitat favourability" (Southwood, 1977), which is limited by winter temperatures and summer dryness, must also affect the microbiota, and collectively determine decomposition rates.

The coincidence of peak invertebrate numbers at a time when leaf fragmentation commenced indicates the importance of the group in the retention of otherwise labile nutrients within their biomass as emphasized by Reichle (1971), Dickinson and Pugh (1974), and Swift, Heal and Anderson (1980).

In contrast to the macroinvertebrates and hexapods, acarine preference and numbers suggested that they exploit situations in which decomposition is slow, or proceeding in the relative absence of the other 2 groups. Their higher diversity at both sites indicates the different roles played by representatives of the group.

The majority of nematodes sampled were rhabditid or bacteriovore which outnumbered the tylenchid or fungivore forms. Together

with earthworm preference, this finding emphasises the importance of bacteria in primary decomposition, as stated in Chapter 8.

It is concluded that the role of invertebrates within these cool temperate forests is to facilitate the breakdown of litter pre-conditioned by microbiota, and to sequester otherwise labile nutrients within their biomass.

CHAPTER 8

LEAF LITTER MICROFLORA

8.1. INTRODUCTION

Jensen (1974) demonstrated that the number of bacteria on freshly fallen litter is correlated with the susceptibility of different types of litter to decomposition, fewer being found on the more resistant types. Goodfellow and Dawson (1978) found the phylloplane bacteria of *Picea sitchensis* Carriere to form only a small fraction of the total bacterial flora of forest ecosystems, and stated that they have at best only a minor role in the decomposition process. Bacteria and fungi were at least ten times more numerous in the litter layer than the mineral horizon. Austin *et al.* (1978) describe gram-negative bacteria to be characteristic of the phylloplane, although they may also be present in freshly fallen litter. The presence of gram-negative bacteria and carotenoid-producing yeasts may be expected in the phylloplane, and is of ecological significance as they are representative of fitness traits that should result in selective advantage through providing protection against dessication and insolation. Various authors (Hissett and Gray 1973, Goodfellow *et al.* 1976) have shown that despite the spatial proximity of living trees, litter, and mineral soil, these habitats appear to contain independent bacterial communities, characterised by populations of only a few taxa at any one time.

Macauley (1979) found the pattern of succession on the untreated leaf litter of *E. pauciflora* to be similar to that on *E. regnans* (Macauley and Thrower 1966), and apart from the similarity of successional patterns of the major groups of fungi, individual species of fungi were common to both eucalypt species.

Decomposition studies discussed in Chapter 6 demonstrated differences in breakdown rates of various leaf species of the overstorey and understorey with up to 18 months exposure to breakdown agencies of the litterbed. It was hypothesised that the varying rates of decomposition were most likely attributable to inherent resistance or susceptibility of individual leaf species to the various decomposer agencies, resulting from their physical and/or chemical properties e.g. high carbohydrate status could be expected to increase susceptibility to both microfloral and invertebrate attack, and high phenolic content to increase resistance to microflora (and the converse in both instances).

This Chapter describes a series of investigations designed to determine the role of bacteria and fungi both in the phylloplane and within the litterbed (Section 8.2), and to examine the hypothesis that the role of these agencies may be controlled by their phenolic or carbohydrate status (Section 8.3), or the presence or absence of mycotoxins (Section 8.4).

Investigations were concentrated upon the major component of leaf litterfall, and of those species of leaves that had demonstrated extremes of the range of decomposition rates determined in litterbag experiments. *E. obliqua* forms overstorey at all four study sites, and is the major component of litterfall on three of the sites. Observations of the litterbeds did not indicate an undue preponderance of *E. obliqua* leaves, and hence it was assumed that decomposer agencies are active in their colonisation of this species. *Phebaleum squameum* leaves were the most rapidly decomposed (53.2 % of initial oven-dry weight after 12 months in the field) of ten leaf species confined in litter bag experiments and therefore could be expected to be free of substances inhibitory to decomposers, and likely to contain substances

e.g. carbohydrates, that promote colonisation. *Phyllocladus asplen-iifolius* leaves were the least decomposed (9.6% of initial oven-dry weight after 12 months) and could be expected to exhibit the converse to leaves of *P. squameum*.

8.2. ENUMERATION OF BACTERIA AND FUNGI COLONISING OVERSTOREY AND UNDERSTOREY LEAVES IN THE PHYLLOPLANE AND THE LITTERBED

8.2.1 Methods and Materials

Sampling

Field. Leaves of the three selected species were collected from trees adjacent to both Site 1 (tall, open, *E. obliqua* regrowth forest) and Site 2 (mixed-forest) and were of four types viz.

G, green, fully developed canopy leaves

S, senescent, fully developed canopy leaves

L, fully developed, recently shed leaves on the surface

    of the litterbed

D, decomposing leaves from within the litterbed.

Canopy leaves of *E. obliqua* were picked from limbs of the upper crown of three co-dominant trees at each site. Limbs were shot down with a .270 calibre rifle. Leaves of *Phebaleum squameum* were picked from the upper crowns of three trees felled adjacent to each site, and *Phyllocladus aspleniifolius* leaves were picked from a similar number of trees that were climbed at each site.

Fifty leaves of each type per species were collected with sterile gloves and bulked in sealable plastic bags.

Laboratory. Leaf sampling and plating methods basically conformed with those outlined by Pennycook (1974). One leaf disc was punched with a sterile 10 mm cork borer from the centre of each leaf (mid-ribs were avoidable with *E. obliqua* leaves only). The 50 discs of each sample were then placed in 100 ml of sterile tap water in

sealable plastic bags and washed with thorough agitation for 3 minutes in a laboratory "stomacher".

Plating

Serial dilutions of the leaf washings of a tenfold to a thousandfold were made with sterile tap water[1], and 1 ml of each dilution then pour-plated with 10 ml each of a fungal and a bacterial selective agar medium in 85 mm diameter plastic petri dishes. Plates were incubated, inverted, in the dark at 23°C. Three replicates of each medium were pour-plated per dilution of each species and each leaf type.

Martin's (1950) glucose-peptone-rose bengal-streptomycin agar[2] with the addition of 40 g.ml^{-1} of chlortetracycline (Pennycook, 1974) was used for fungal culture, and Jensen's (1930) glucose-casein agar[2] for bacterial culture.

Colony counts

All plates were counted, with ideal counts per plate being the dilution with 22-220 colonies. Counts were expressed as population densities per unit area of leaf per species per litter type (each leaf disc had two surfaces), viz.

Number of discs = 50

Area of discs = 50 (3.142 x 0.5^2) x 2 = 78.55 cm^2

Volume washings = 100 ml

Hence, number of colonies = colony count x 1.27307 per cm^2 leaf surface x dilution.

---

1. Pennycook (1974) found no significant differences in population densities of bacteria, yeasts and fungi when macerated in sterile tap water as compared with peptone water or Ringers solution.
2. Refer Appendix D.

Enumeration of microflora colonising E. obliqua leaves, Fern Gully, Mt. Wellington

An evaluation of techniques was made in early September, 1981, with *E. obliqua* leaves collected from Fern Gully, Mt. Wellington. Leaf types were the same (G, S, L and D) as those intended for use from Hastings, but only 5 leaves per type were sampled. All methods were used as described, but plate counts were adjusted to account for the smaller sample number.

Enumeration of leaf litter microflora at Hastings

Sampling and plating were carried out as described under Section 8.2.2 in late Spetember 1981 (Spring).

8.2.2 Results

Evaluation of techniques

Results of counts per dilution of the four leaf types of *E. obliqua* from Mt. Wellington are listed in Table 8.2.1 and illustrated in Fig. 8.2.1. The techniques seemed suitable for the purpose and no changes were made. Although results indicated dilutions of $10^{-2}, 10^{-3}$, and 10^{-4} to be superfluous, they were retained to ensure an adequate range of dilution when enumerating the microflora of the different species sampled at Hastings.

Enumeration of leaf microflora at Hastings

Results of colony counts of bacteria and fungi of G, S, L, and D samples of *E. obliqua, Phebaleum squameum*, and *Phyllocladus aspleniifolius* at study Sites 1 and 2 at Hastings are listed in Table 8.2.2 per dilution for each leaf type per species, and are illustrated in Fig. 8.2.2.

Use of dip slides for comparison of the degree of bacterial colonisation

Mean value per leaf species and treatment are recorded in Table 8.2.3 for Sites 1 and 4.

Table 8.2.1.   Enumeration of leaf microflora, *E. obliqua* leaves, Fern Gully, Mt. Wellington.

LEAF TYPE		FUNGI (Martin's Agar)					BACTERIA (Jensen's Agar)				
		1	10^{-1}	10^{-2}	10^{-3}	10^{-4}	1	10^{-1}	10^{-2}	10^{-3}	10^{-4}
G (Canopy)	Total	197	49	24	NIL	NIL	480	12	NIL	NIL	NIL
	Mean	39.4	9.8	4.8	NIL	NIL	160	4	NIL	NIL	NIL
S (Canopy)	Total	6227	662	61	NIL	1	553	36.9	NIL	NIL	NIL
	Mean	1255	132	12.2	NIL	0.2	184	12.3	NIL	NIL	NIL
L (Litterbed)	Total	209	49	NIL	NIL	NIL	12467	135	NIL	NIL	NIL
	Mean	41.8	9.8	NIL	NIL	NIL	4156	45	NIL	NIL	NIL
D (Litterbed)	Total	14904	1661	161	25	NIL		1132	N.A.	N.A.	N.A.
	Mean	2981	332	32.2	5	NIL	>1000	226.4			

Fungal counts made of 5 replicates.

Bacterial counts made of 3 replicates.

N.A. not available.

FIG. 8.2.1.   ENUMERATION OF LEAF SURFACE MICROFLORA OF
E. OBLIQUA, FERN GULLY, MT. WELLINGTON

LEGEND

G = Green, canopy

S = Senescent, canopy

L = Litterbed surface

D = Decomposing within litterbed
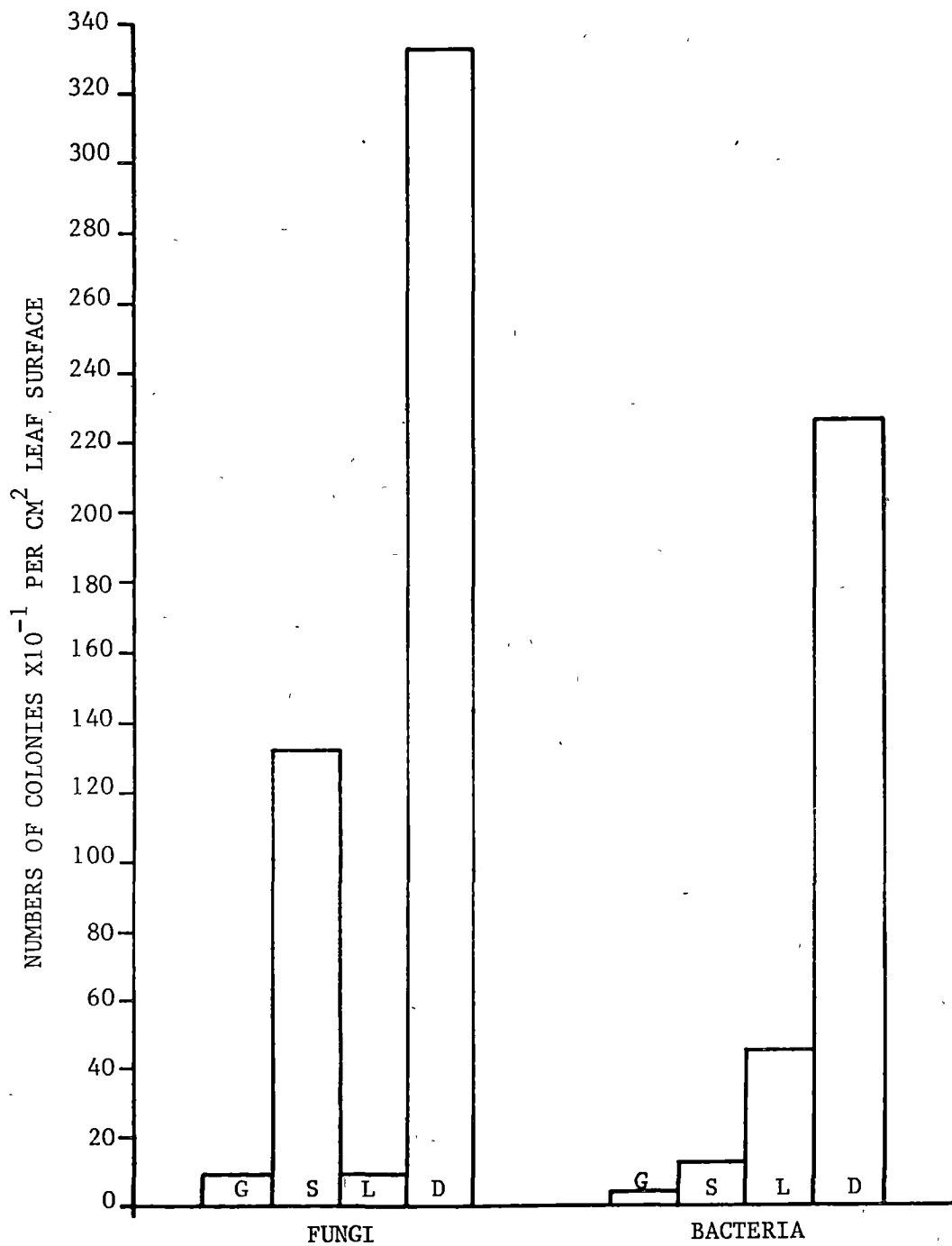
Table 8.2.2.   Enumeration of leaf microflora of selected species at Hastings in Spring, 1981.

All figures the mean of 3 replicate counts.

SPECIES	LEAF TYPE	FUNGI			BACTERIA		
		10^{-1}	10^{-2}	10^{-3}	10^{-1}	10^{-2}	10^{-3}
E. obliqua	G	3.0	1.3	NIL	>200	118.0	25.9
	S	148.6	34.0	NIL	161.3	12.7	25.5
	L	42.0	6.0	NIL	97.2	14.0	1.3
	D	142.6	50.1	3.4	>200	>200	345.9
Phebaleum squameum	G	39.1	3.4	NIL	65.4	9.8	3.4
	S	373.4	42.4	NIL	>200	225.5	21.3
	L	42.0	4.7	NIL	>200	190.5	12.7
	D	57.7	19.1	NIL	>200	>200	1683.0
Phyllocladus aspleniifolius	G	17.4	3.4	NIL	35.2	3.4	0.9
	S	93.3	12.7	NIL	>200	343.7	N.A. (34.4)
	L	75.5	34.0	NIL	>200	>200	72.6
	D	67.1	7.6	NIL	>200	>200	258.0

N.A., not available, data interpolated from data for 10^{-2} dilution, i.e. 34.4

233

FIG. 8.2.2.   ENUMERATION OF LEAF SURFACE MICROFLORA OF SELECTED
SPECIES AT HASTINGS, SPRING, 1981

LEGEND

G = Green, canopy

S = Senescent, canopy

L = Litter surface

D = Decomposing within litterbed
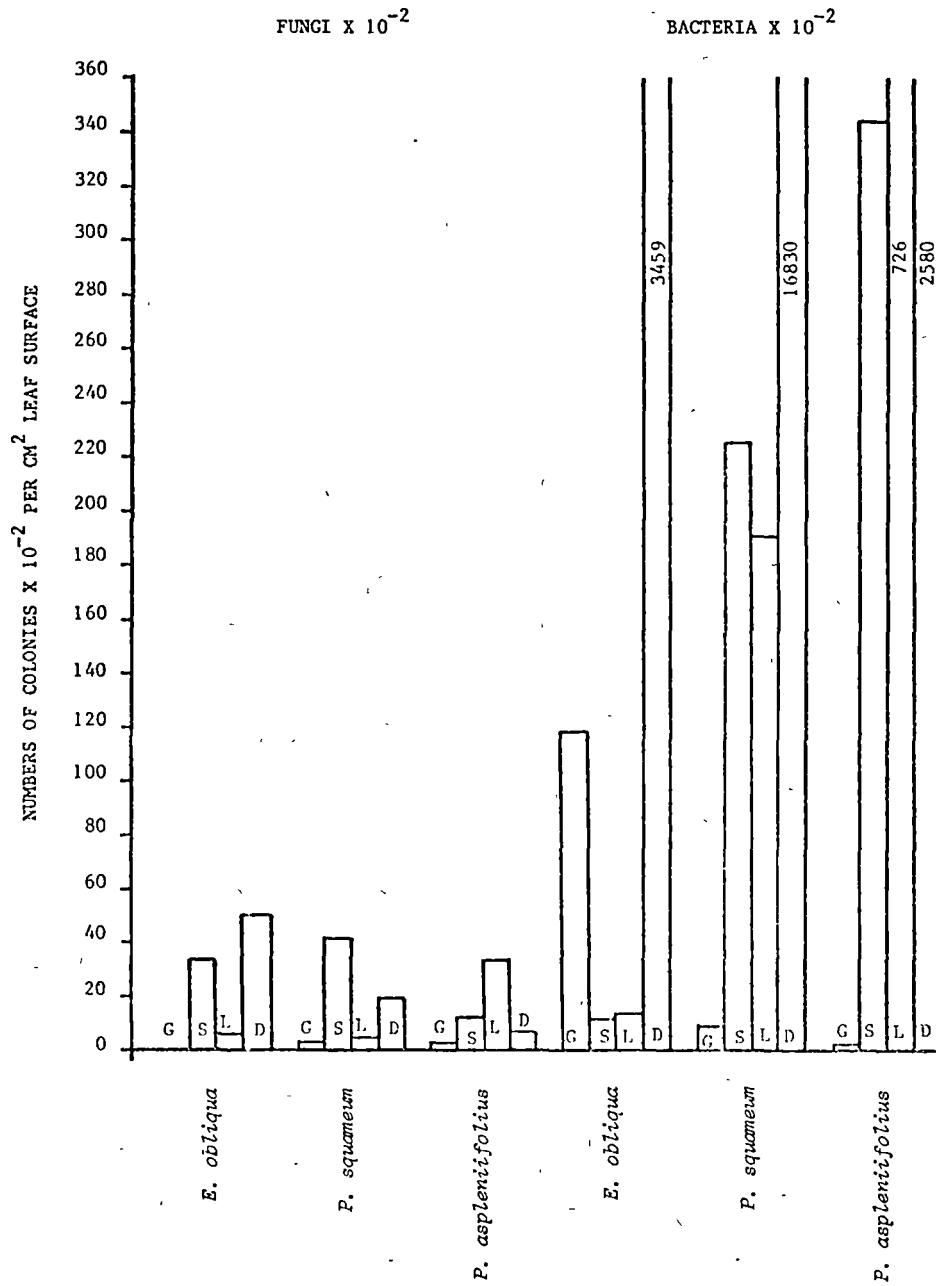
Fig. 8.2.3 and 8.2.4 illustrate the bacterial colony numbers of untreated litter bag leaves cultured on both media at both sites at 3 and 6 months sampling times.

8.2.3 Discussion

Enumeration of leaf microflora on E. obliqua leaves, Mt. Wellington

Evaluation of techniques

Populations of fungi and bacteria were similar and low on the surface of green leaves in the canopy, ca. 100 colonies/cm^2. Senescent leaves in the canopy had higher population densities of fungi (1320 colonies/cm^2), but the bacterial population did not differ significantly (123 colonies/cm^2).

Green leaves on the litter surface had the same population density of fungi as green leaves in the canopy, but bacterial population density increased to 450 colonies/cm^2. The greatest numbers of propagules were enumerated on the surfaces of decomposing *E. obliqua* leaves within the litterbed, with fungal colony numbers of 33320/cm^2 and bacteria 2264/cm^2.

Enumeration of leaf microflora of selected species at Hastings

There was little difference between the population density of fungi colonising the surface of green *E. obliqua* canopy leaves at Hastings and Mt. Wellington. Population densities were low at both localities. Bacterial numbers were similar between recently shed *E. obliqua* leaves on the litterbed surface at both localities, but the other three leaf types (green in the canopy, senescent in the canopy, and decomposing in the litterbed) had greater bacterial populations at Hastings (x10 to x30).

The differences in population densities of both fungi and bacteria on the four leaf types of the three species sampled at Hastings

FIG. 8.2.3/4   BACTERIAL COLONISATION OF LITTER BAG LEAVES.

NO. BACTERIAL COLONIES
(McCONKEY AGAR)

NO. BACTERIAL COLONIES
(CLED MEDIUM)

10^5 Site 1   22 Site 1

10^4

92

12,62,92,122 10^3 42,102,112   22,42,62,102,112 12,32,82

10^2 42

SOME   SOME 52,72,102,112,122

42,102,112 5 12,22,62   52,122 62
22,32,52,72,82 0 32,52,72,82,92,122   12,32,72,82 92

112 10^5 Site 4   112 Site 4

10^4 42 12

62,82,102,122 10^3 12,32   12,22,62,82,122 32,112

92   92,102 22

SOME 82   SOME 42,62,72,92

5   32 82
   22,42,62   52,72 52,102,122
12,22,32,42,52,72 0 52,72,92,102,112,122

3 MONTHS   6 MONTHS   3 MONTHS   6 MONTHS
MONTHS IN THE FIELD   MONTHS IN THE FIELD

LEGEND
12. E. obliqua
22. E. nitida
32. N. cunninghamii
42. A. moschatum
52. P. aspleniifolius
62. P. apetala
72. E. lucida
82. A. melanoxylon
92. P. aquaticum
102. E. marginata
112. E. obliqua with P. apetala
122. E. obliqua with P. aspleniifolius

Table 8.2.3.   Bacterial colonisation of litter bag leaves.

Species and treatment		Site 1				Site 4			
		McConkey		CLED		McConkey		CLED	
		3 months	6 months	3 months	6 months	3 months	6 months	3 months	6 months
E. obliqua	NIL	$<10^3$P/M	C(2)	NIL	10^3Y/G	NIL	$<10^3$P	10^3Y/G	10^4G
	I	NIL	10^3P	NIL	Y(1)	P/M(2)	NIL	10^4G	10^3G
	F	NIL	NIL	Y(1),G(2)	NIL	NIL	NIL	10^3Y	10^3G
	FI	(MISSING)	10^3P	(MISSING)	NIL	NIL	NIL	G(1)	NIL
E. obliqua from mixture with P. apetala	NIL	P/M(1)	10^3C	10^3Y/G	G(some)	10^5P/M	NIL	10^5(G)	10^3G
	I	NIL	$<10^3$C	NIL	10^3G	NIL	NIL	NIL	NIL
	F	NIL	NIL	G(2)	10^3G	NIL	NIL	G(1),Y(1)	10^3G
	FI	NIL	NIL	10^3G/Y	NIL	P/M(3)	NIL	10^3G+Y	NIL
E. obliqua from mixture with P. aspleniifolius	NIL	10^3P/M	NIL	Y(3)	Y(some)	10^3P/M	NIL	10^3G	NIL
	I	P/M(1)	NIL	G(1)	$<10^3$G	NIL	10^3P	NIL	$<10^3$G
	F	NIL	NIL	NIL	NIL	P/M(3)	NIL	G(4),Y(1)	NIL
	FI	NIL	NIL	Y(1)	10^4G	P/M(1)	$<10^3$P	10^3G	NIL
E. nitida	NIL	NIL	C(1)	10^3Y	10^5C,10^3Y	NIL	P(1)	10^3G	$<10^3$G
	I	P/M(1)	$<10^3$P	NIL	G(some)	NIL	NIL	W(1)	NIL
	F	NIL	10^3P	NIL	10^3G	NIL	NIL	NIL	NIL
	FI	NIL	NIL	NIL	NIL	NIL	NIL	NIL	NIL
N. cunninghamii	NIL	NIL	NIL	NIL	10^3G	NIL	10^3P	Y(1)	10^3G
A. moschatum	NIL	P/M(2)	10^3P	10^3Y	$<10^3$Y	NIL	P(1)	10^4Y/G	G(some)
P. aspleniifolius	NIL	NIL	NIL	G(1)	O/Y(some)	NIL	NIL	NIL	NIL
P. apetala	NIL	10^3P/M	C(3)	10^3G	Y(1),C(2)	10^3P/M	C(1)	10^3Y	G(some)
E. lucida	NIL	NIL	NIL	NIL	G(s),Y(s)	NIL	NIL	NIL	G(some)
A. relamorylon	NIL	NIL	NIL	NIL	10^3G	10^3P/M	P(some)	10^3G	Y(1)
P. couunrun	NIL	10^3P	NIL	10^4Y	NIL	$<10^3$P/M	NIL	$<10^3$G	G,C(come)
B. marginata	NIL	P/M(1)	10^3C	10^3Y/G	G(some)	10^3P/M	NIL	$<10^3$Y/G	NIL

LEGEND: P/M = Pink/mauve bacterial colony   C = Colourless bacterial colony   F = Fungicide treatment

Y/G = Yellow/green bacterial colony   O = Orange bacterial colony 10^5 = Colonies/ml

G   = Green bacterial colony   W = White bacterial colony   (2) = 2 individual colonies

Y   = Yellow bacterial colony   I = Insecticide treatment   G(s) = Green, some

237

are illustrated in Fig. 8.2.2. Fungi were most numerous on senescent canopy leaves and decomposing litterbed leaves of *E. obliqua* and *P. squameum*, and on recently shed leaves of *P. aspleniifolius*. There was not however, a remarkable difference in colony numbers between any of the leaf development stages of the three species, which was surprising considering the between-species differences in decomposition rates evident in litter bag experiments that had occurred during their initial 3 months of field exposure between August and December, 1980.

Bacterial numbers were greatest on decomposing litterbed leaves of all three species, with five times the number present on *P. squameum* as on *E. obliqua* or *P. aspleniifolius*. Low population densities were present on senescent, canopy and freshly shed *E. obliqua* leaves on the litter surface, whilst high population densities were present on these leaf types of *P. squameum* and *P. aspleniifolius*, with the greatest number counted present on the latter species. Low numbers of bacteria were present on green canopy leaves of *P. squameum* and *P. aspleniifolius* (65.4×10^{-1} and 35.2×10^{-1} respectively) but relatively high numbers were counted on *E. obliqua* (11.8×10^{-2}).

There was a general trend for the numbers of bacteria on leaf surfaces to increase with increasing leaf age through green, canopy-senescent, canopy-recently shed, litter surface-decomposing, litterbed.

Use of dip slides for comparison of the degree of bacterial colonisation

In general, the bacterial colonisation of leaves was greater at 3 months than at 6 months on both media at both sites. Treatment with insecticide and fungicide separately and in combination caused a reduction of bacterial colony numbers at 3 months at both sites on McConkey agar, but not on CLED medium.

The number of dip slides were not sufficient to allow sound conclusions to be drawn. However, their use in greater number would seem to be a worthwhile and convenient technique for monitoring bacterial colonisation and succession on litter in the field.

8.3. PHENOLIC AND CARBOHYDRATE STATUS OF SELECTED LEAVES OF OVERSTOREY AND UNDERSTOREY SPECIES

Aim

To determine whether differences existed between leaf species in their relative levels of contained carbohydrates and phenolics, and if differences occurred, whether they could be related to the rate of leaf decomposition derived from results of litter bag experiments.

Methods

Leaves of *E. obliqua*, *P. squameum*, and *P. aspleniifolius* were collected green from the canopy, senesced upon the fresh litterfall layer, and decomposing from within the litterbed. The species selected respectively represented leaves that were rapidly, very rapidly, and slowly decomposed.

After 14 days storage at $-5°C$, ten 1.0 cm diameter discs were punched from separate leaf centres, and phenolics and carbohydrates were extracted by immersion in 70% methanol for 10 days.

0.2 l of each extract were spotted onto cellulose TLC plates and separation affected by a 4 hour run with a solvent of n-butanol:benzene:pyridine:water (5:1:3:3). Phenolics were detected under ultra-violet light, spots marked directly onto the thin-layer plates and their colours and relative intensities described. Sugars were detected by spraying with aniline hydrogen phthalate and then heating for 10 minutes at $100°C$. Solvent and spray reagent were prepared according to Harborne (1973).

Reference materials were glucose and phenol (0.1 mg.ml^{-1} pyridine).

Results

Rf (x100) values, colour and intensity of detected phenolics are listed in Table 8.3.1. Seven phenolics were present in *E. obliqua* leaves of the canopy and the litter layer surface with five common to both leaf types, and intensity of four decreasing from canopy to litter layer. Five phenolics were common to the canopy leaves and leaves of the litter layer in *P. squameum* but intensity of four of these increased in the litter surface layer. Six phenolics were common to the canopy and litter surface layer leaves of *P. aspleniifolius*, and like *P. squameum*, intensity increased in leaves of the litter surface layer. There were no phenolics detected in extracts from decomposing leaves of all species.

Rf (x100) value of the phenol control was .97.

Rf (x100) value of the glucose control was .28, and this value was coincident with the only carbohydrate detected in all leaf species in both the canopy and from the surface of the litter layer. No carbohydrate was detectable in extracts of all leaf species from the decomposing litterbed, and intensity of the detected carbohydrate from *P. squameum* was appreciably less than the other two species.

Discussion

In general, leaves of *P. aspleniifolius* contained greater concentrations of extracted phenolics. Less phenolics were extracted from leaves of *P. squameum* than from *E. obliqua* or *P. aspleniifolius*.

Neither carbohydrates nor phenolics were extracted from leaves of all three species in the decomposing litter layer. This finding is contrary to the hypothesis that phenolics were responsible for the

Table 8.3.1.   Description of extracted leaf phenolics.

Species:	E. obliqua			P. squameum			P. aspleniifolius		
Leaf type	Rf (x100)	Colour	Intensity	Rf (x100)	Colour	Intensity	Rf (x100)	Colour	Intensity
Canopy, green	6	Violet	+	45	Blue – fluorescent	+	45	Blue – fluorescent	+
	36	Blue – fluorescent	+	51	Blue – fluorescent	+	64	Pink	+
	51	Blue – fluorescent	+	59	Violet	+ +	72	Pale – blue	+
	57	Violet	+ +	78	Violet	+ +	90	Violet	+
	65	Violet	+ + +	92	Blue – fluorescent	+ +	104	Mauve	+ +
	81	Violet	+ +				122*	Deep red	+ + +
	93	Brown	+ + +						
Litter surface, senesced	28	Violet	+	45	Blue – fluorescent	+ +	45	Blue – fluorescent	+
	36	Blue – fluorescent	+	51	Blue – fluorescent	+	64	Pink	+ +
	47	Blue – fluorescent	+	59	Violet	+ + +	72	Pale blue	+
	51	Violet	+	78	Violet	+ + +	90	Violet	+
	64	Violet	+	92	Blue – fluorescent	+ + +	104	Mauve	+ +
	81	Violet	+ +				133*	Deep red	+ + +
Litterbed	-	-	-	-	-	-	-	-	-

* = considered the same, difference caused by interference.

241

longevity of leaves of *P. aspleniifolius* in the litterbed, unless a phenolic complex that is not extractable in 70% methanol is involved.

The faster decomposition rate of *P. squameum* leaves may be a reflection of the lesser amount of phenolics present compared with *E. obliqua* and *P. aspleniifolius* (Davies, 1971).

Lack of extractable carbohydrates or phenolics from leaves of all 3 species of the decomposing litter layers was in agreement with the rapid leaching of these substances reported by Wood (1971, 1974).

8.4.   MYCOTOXIC EFFECT OF LEAF LITTER LEACHATES

Preamble

It was postulated that the marked differences in breakdown rate of leaf litter of various species may be attributable to mycotoxic effects of the leachate of some species, or to nutritional responses to the leachate of others. These investigations were designed to determine whether such responses existed, and to compare the relative effects of leachates of selected leaf litter species.

Differences in leaf breakdown rates were measurable during the August to December, 1980, period of the litter bag studies, and although seasonal effects upon leaf leachates may exist, it was considered that sampling during this period should adequately test the hypothesis.

Phebaleum squameum, Phyllocladus aspleniifolius, and *E. obliqua* leaves were selected for the same reasons given in studies of Section 8.2, i.e. should differences exist between species they should be apparent between those leaf species situated at the extremes of the scale of decomposition rate determined in litter bag experiments (Section 6.2). Leaf leachates of these species were incorporated into pour-plates and their effects upon a common inoculum were determined

from comparisons of microfloral enumeration between leachates (treatments) and a control of sterile tap water.

The aims of these investigations were to determine,

(a)   whether mycotoxic effects were attributable to leaf leachates,

(b)   whether leaf leachates promoted microfloral activity,

(c)   whether an *in vitro* technique of leaf disc plating could be used to visualise the inhibition or promotion of growth of litterbed microflora,

(d)   pH of various leaf leachates.

Due to problems that arose from techniques a number of preliminary tests were carried out before successful assays were obtained. Initial tests are briefly discussed in order to outline the problems encountered (results available) and detailed results are given only for the first successful run and the final, larger, confirmatory investigation. Hence this topic is presented under the following headings:

8.4.2 General methods and materials.

8.4.3 Problems encountered in initial assays.

8.4.4 Experiment 1. Details and results.

8.4.5 Experiment 2. Details and results.

8.4.6 Discussion of results.

8.4.2 Methods and materials. Leaf collection

Leaves of *E. obliqua*, *Phebaleum squameum* and *Phyllocladus aspleniifolius* were picked with sterile gloves at random from the litter surface of Sites 1 and 2, and bulked per species in sealable plastic bags. All were relatively green, fully developed leaves that were considered to have only recently been shed. These leaves were used in the preparation of treatment leachates.

Decomposing leaves were similarly picked from several random locations within the lower litterbed layers of each site and bulked in a sealable plastic bag. These leaves were used for the preparation of a standard inoculum after sub-sampling the bulked collection to provide 50 leaves in the ratio of normal accessional quantities per species viz.

40	*E. obliqua*
2	*Acacia melanoxylon*
2	*Phebaleum squameum*
1	*Pittosporum bicolor*
1	*Eucryphia lucida*
1	*Nothofagus cunninghamii*
1	*Atherosperma moschatum*
1	*Anopterus glandulosus*
1	*Phyllocladus aspleniifolius*

Leachate preparation

Fifty leaves were randomly selected from each bulked collection and a 10 mm disc was aseptically punched from the centre of each leaf with a cork-borer. The 50 disc samples of each species were washed in 100 ml of sterile tap water for 5 minutes in a laboratory "stomacher", and the washings filtered through a 0.45 micron millipore filter to exclude leaf microflora. The filtrates of the washings of each species comprised the treatment leachates, and 50 discs per 100 ml of sterile tap water was a standard 'dose'.

Inoculum preparation

The 50 decomposed leaves were similarly punched and washed, but not filtered, and served as a standard inoculum.

Plating

The standard inoculum washings were serially diluted from x1 to 10^{-4}, and pour-plated on 5 replicate plates per dilution of either Martin's (1950) agar with inclusion of streptomycin and chlortetracycline (Pennycock 1974), potato-dextrose agar, Jensen's (1930) agar, or nutrient agar, and 1.0 ml of sterile tap water was added as a control.

Filtered washings of *E. obliqua*, *P. squameum*, and *P. aspleniifolius* were substituted for the 1.0 ml of sterile tap water in preparation of treatment plates. There were 5 replicate plates per medium per inoculum dilution of each treatment. All plates were inverted and incubated in the dark at 23°C.

Counts

Numbers of fungi and bacteria present on control and treatment plates were counted after 5 to 7 days. Martin's agar or potato-dextrose agar was used for the enumeration of fungi and Jensen's medium or nutrient agar for bacteria.

Comparison of the numbers of colonies of fungi and bacteria per treatment against control numbers enabled direct measurement of the relative effects of the leaf leachates upon the growth of the litter-bed microflora.

In some instances, colony numbers were too numerous to count on plates, and hence counts were made by *camera lucida* of sections of the plate surface.

Check on millipore filtration

Washings were plated without inoculum to compare the microfloral population densities of the tested species, and filtrates were similarly plated to ensure that all microflora had been excluded by millipore filtration.

pH

The pH of each leaf leachate was measured with a Radiometer pH
meter.

Leaf disc plating

In an attempt to visualise the inhibitory or promotive charact-
eristics of leaves upon litterbed microfloral culture, discs of the 3
species were aseptically punched with a 10 mm cork borer, surface
sterilised by immersion in a 1:9 chlorize-deionized water solution for
3 minutes, and then placed flat upon the surface of 10 ml of prev-
iously poured plates of either Martin's or nutrient agar. Two discs
were placed upon the agar surface of each plate as the medium was
setting. A second layer of 10 ml of the appropriate medium was poured
over the discs and allowed to cool. When set, 0.1 ml of the standard-
ised inoculum at x1 and 10^{-1} dilution with sterile tap water, were
uniformly spread over the plates with a sterilised bent glass rod.
Plates were incubated in the dark at 23°C for up to 10 days, and exam-
ined daily from day 4 to determine whether zones of cultural growth
inhibition or promotion were associated with areas of the plates adj-
acent to leaf discs.

8.4.3 Problems encountered with initial assays

In October, 1981, two initial attempts were made to enumerate
the microflora of the leaf leachates, the control inoculum, and the
inoculum plus leachates. Both runs gave ambiguous results due to
problems associated with millipore filtration. Leaf washings result-
ing from the vigorous agitation of the laboratory "stomacher" contain-
ed the leaf discs and some particulate matter removed from leaf surf-
aces and from the exposed leaf margins resulting from their punch-
ing. *E. obliqua* washings were pale yellow, *Phebaleum squameum* wash-

No colonies of fungi or bacteria were evident in the pour-plates of filtered *P. squameum* and *P. aspleniifolius* leachates, hence filtration was complete and colony counts of the microflora could be attributed solely to the effects of the leachates.

There was no inhibition or promotion of fungal growth in the inoculum by leachates of either leaf species.

Bacterial numbers were so great at the inoculum dilutions employed (x1, 10^{-1}, 10^{-2}) on both Jensen's and nutrient agars that plate counts could not be made accurately by normal means. *Camera lucida* counts were made of the nutrient agar cultures of the inoculum control, and of the filtered leachates of both species plus the inoculum at the dilution level of 10^{-2}. Counts were made over 10 fields of view (0.23 cm^2) spread randomly over the plate surface for each of 3 replicate plates. Results of the counts are given below, expressed as the mean number of bacterial colonies per field of view:

Control, inoculum + 1 ml sterile tap water = 7.4

P. squameum filtrate + inoculum = 59.4

P. aspleniifolius filtrate + inoculum = 2.8

Given that the mean number of colonies cultured on nutrient agar from the control was a relative number of 1.0, then *P. aspleniifolius* inhibited bacterial growth to a relative level of 0.38 and *P. squameum* promoted growth to a relative level of 8.02. These results are illustrated in Fig. 8.4.2.

The result for *P. aspleniifolius* was confirmed by bacterial colony counts of unfiltered leaf washing listed in Table 8.4.1. Whereas both the inoculum and the *P. squameum* unfiltered leaf washings gave colony counts in excess of 1.0 x 10^5 per cm^2 of leaf surface, those of *P. aspleniifolius* reduced the counts to 2.33 x 10^3.

ings light green, and those of *P. aspleniifolius* pale brown. Their filtration under vacuum took up to 15 minutes to complete, and a series of filters had to be employed due to their continued blockage with leaf material. Filtrates of *P. squameum* in Run 1 and of *P. aspleniifolius* in Run 2 were contaminated, i.e. the filtration had not been successful and some bacteria had not been excluded. A very small, rod-shaped, flagellate, gram-negative bacterium persisted in filtrates of *P. squameum*. However, this organism was eliminated from filtrates of later runs by repeated filtration and greater care during filter changes.

Results of both runs indicated differences in the effects of leachates upon the enumeration of inoculum microflora, and hence investigations were continued.

8.4.4 Experiment 1. Details and results

Methods conformed with those described in Section 8.4.2. Four media were employed to ensure that results were not affected by the antibiotics included in Martin's agar, and as a means of increasing replication. This was the first of two main investigations and *E. obliqua* leaves were excluded at this stage in order to concentrate upon detection of differences in effects of the leachates of *P. squameum* and of *P. aspleniifolius*

Effects of leaf leachates upon inoculum culture

The numbers of colonies of fungi (including yeasts) and of bacteria were enumerated on the 4 media and expressed per cm^2 of leaf surface area of the inoculum. Results for the unfiltered leachates, the control inoculum, and for the inoculum plus leachates are listed in Table 8.4.1 and illustrated in Fig. 8.4.1.

Table 8.4.1. Numbers of fungal and bacterial colonies per treatment and control on Martin's (M) Potato-dextrose (PDA), Jensen's (J) and nutrient agars (NA) at 23°C.

MEDIUM	FUNGI				BACTERIA					
	M		PDA		J			NA ϕ		
	DILUTION		DILUTION		DILUTION			DILUTION		
TREATMENT	0	10^{-1}	0	10^{-1}	0	10^{-1}	10^{-2}	0	10^{-1}	10^{-2}
Control. Inoculum + 1 ml. st. tap water	98.0	41.3	Colonies merged		>1000	>1000	>1000	>1000	>1000	>1000
P. squameum, unfiltered, alone	22.0	19.7	Colonies merged		>1000	>1000	>1000	>1000	>1000	>1000
P. squameum, filtered + 1 ml. inoculum	97.0	15.3	Colonies merged		>1000	>1000	>1000	>1000	>1000	>1000
P. aspleniifolius unfiltered, alone	23.7	1.3	12.3	3.3	>1000	>500	34.7	>1000	71.3	23.3
P. aspleniifolius, filtered + 1 ml. inoculum	97.7	27.0	Colonies merged		>1000	>1000	>1000	>1000	>1000	ca.1000

ϕ, *Camera lucida* counts made.

All data the mean of three replicates (data available) expressed as numbers of colonies per cm^2 of inoculum leaf surface area.

FIG. 8.4.1.   NUMBERS OF FUNGAL AND BACTERIAL COLONIES CULTURED PER TREATMENT ON
MARTIN'S AGAR (FUNGI) AND JENSEN'S AND NUTRIENT AGAR
(BACTERIA) AT 23°C

FUNGI (X10)

Martin's agar counts

BACTERIA (X10^2)

Jensen's agar   Nutrient agar

NUMBERS OF COLONIES PER SQ.CM. LEAF SURFACE AREA
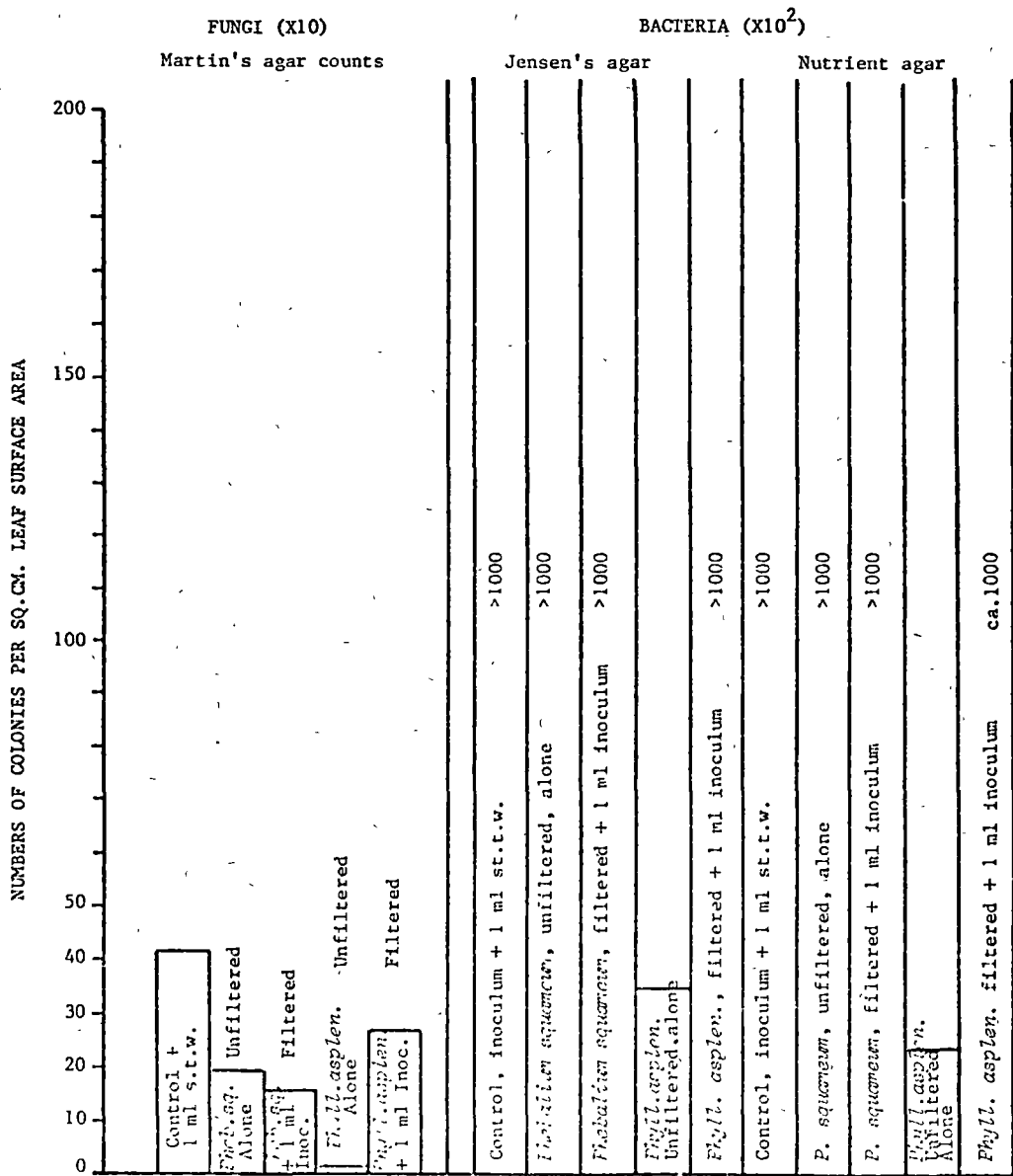
Leaf disc plating

Surface sterilised discs of *P. squameum* and *P. aspleniifolius* were incorporated into plates of all four media, inoculated with 0.1 ml of the standard inoculum, and the growth of the inoculum compared.

There was no evident promotion nor inhibition of inoculum growth on all plates with doses of either species. A brown zone (halo) up to 8 mm wide encircled the leaf discs of *P. aspleniifolius* (see Fig. 8.4.3) on all media, but this zone had no apparent effect upon the inoculum.

8.4.5 Experiment 2. Details and results

Previous investigations demonstrated that there were significant effects upon the culture of litterbed microflora by aqueous filtrates of leaf washings of different species. This investigation was designed to determine,

(a) the effects of leaf leachates of *E. obliqua, P. squameum*, and *P. aspleniifolius* of increasing concentration upon litterbed microflora,

(b) the pH of the leachates.

Methods conformed with those of previous investigations except that a range of leachate concentrations were assayed. Increasing leachate concentration was obtained by increasing the numbers of leaf discs of the 3 species washed in the laboratory stomacher.

Leachate preparation

250 leaves of *P. squameum*, 300 leaves of *E. obliqua*, and 475 leaves of *P. aspleniifolius* were collected from the litterbed surface of Sites 1 and 2 on 17th November, 1981. *P. aspleniifolius* leaves were difficult to find in adequate numbers and approximately 275 were

FIG. 8.4.2. *CAMERA LUCIDA* COUNTS OF BACTERIAL COLONIES PER
TREATMENT CULTURED ON NA PLATES AT 23°C
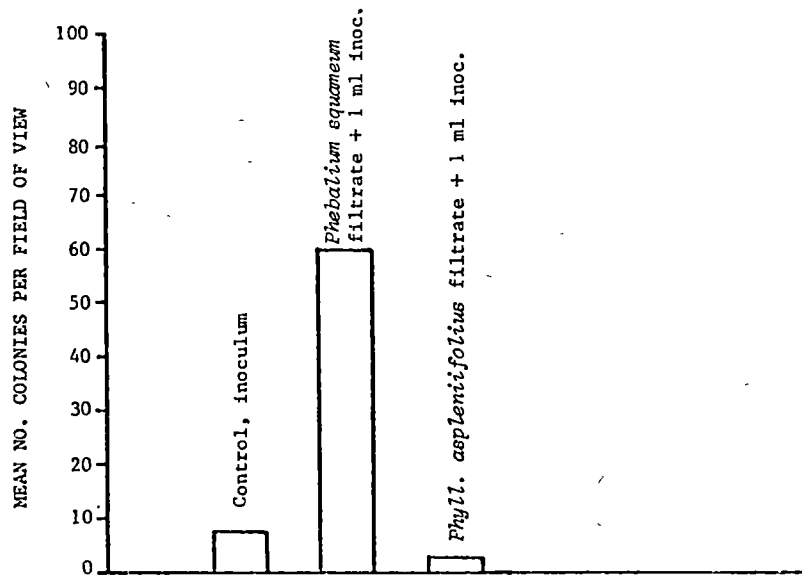
FIG. 8.4.3.   LEAF DISC PLATING

P. squameun disc, 10 mm

P. aspleniifolius
disc, 10 mm

Petri dish plate of
culture medium

Brown zone around disc

85 mm
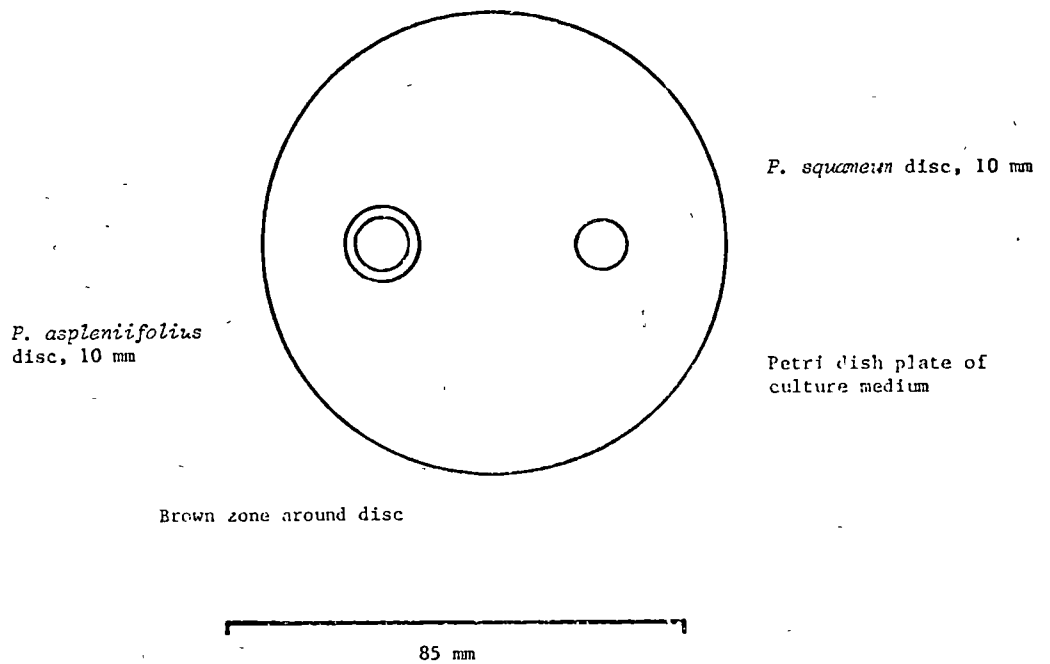
collected from a larger mixed-forest similar to Site 2, at North Lune, 2 km south-east of the main study area.

Four concentrations of leaf leachate were prepared per species. *P. squameum* and *P. aspleniifolius* had demonstrated marked effects upon bacterial culture from the litterbed and hence their concentrations were selected as:

25 discs/100 ml sterile tap water, 'stomached' 5 minutes

50 "   "   "

100 "   "   "

200 "   "   "

E. obliqua had demonstrated little effect upon the litterbed microflora in preliminary investigations and hence the leachate concentrations were increased viz. 50, 100, 200, and 400 discs/100 ml sterile tap water. It was necessary to take more than one disc from some leaves to obtain the numbers required.

Effects of leachates upon inoculum culture

Martin's agar was used for the enumeration of yeasts and fungi, and nutrient agar for the enumeration of bacteria.

The control, and the inoculum were prepared in the standard manner, i.e. 50 discs of selected, decomposing leaves "stomached" in 100 ml sterile tap water, but the number of dilutions were reduced to 10^{-1} and 10^{-2} for fungal enumeration, and 10^{-2} and 10^{-4} for bacteria. Hence there were 2 media, 2 dilution levels per medium, 3 species of four differing leachate concentrations, the inoculum control, and 5 replications per sample.

Table 8.4.2 lists the results of counts of the numbers of fungal and bacterial colonies per leachate concentration plus inoculum, and of the inoculum plus sterile water control. Counts were expressed as the mean number of colonies per cm^2 of inoculum leaf surface, and

Table 8.4.2. Numbers of fungal (M) and bacterial (NA) colonies per treatment and control cultured in Martin's (M) agar and nutrient agar (NA) at 23°C.

NO. DISCS/100 ml. MEDIUM TREATMENT DILUTION	25/100		50/100		100/100		200/100		400/100	
	M 10^{-2}	NA 10^{-4}	M 10^{-2}	NA 10^{-4}	M 10^{-2}	NA 10^{-4}	M 10^{-2}	NA 10^{-4}	M 10^{-2}	NA 10^{-4}
Inoculum (I) + 1 ml. sterile tapwater, Control			22.9	117.1						
Phebaleum squameum filtrate + 1 ml. (I)	21.4	40.5	21.9	2780.9$^\phi$	21.4	7535.5$^\phi$	20.4	21248.5$^\phi$		
E. obliqua filtrate + 1 ml. (I)			21.4	84.3	19.6	55.8	20.1	28.8	23.4	3.1
Phyllocladus aspleniifolius filtrate + 1 ml. (I)	23.2	19.9	19.9	26.2	22.9	9.2	21.9	N.A.		

N.A., filtrate contaminated.

ϕ, counts made by *camera lucida*.

All data the means of 5 replicates.

254

are illustrated in Fig. 8.4.4. The number of bacterial colonies on the nutrient agar plates of the *P. squameum* treatments were so great at the 50, 100, and 200 disc concentrations that counts had to be made by *camera lucida*. Five counts per replicate plate were made of each of these concentrations, and the means were included in Table 8.4.2 to allow comparison of treatment effects.

Filtered washings of all species were plated on both media with negative results at all concentrations except one, indicating that filtration had removed all treatment leaf microflora. The exception was the 200 disc concentration of *P. aspleniifolius*.

There were no apparent effects upon fungal culture of the litterbed inoculum by any of the filtered leachates of the 3 species at all concentrations.

Effects upon bacterial culture were marked and differed between species, in agreement with the trends of Experiment 1. Table 8.4.3 summarises the data of Table 8.4.2 by comparing the mean numbers of bacterial colonies of the inoculum control as a relative number of 1.0 against the mean relative numbers of the treatment leachates of vary- ing concentration. These results are illustrated in Fig. 8.4.5.

There was a progressively increasing promotional effect upon bacterial growth by *P. squameum* leachates with their increasing con- centration, and a similarly increasing inhibitional effect by leach- ates of both *E. obliqua* and *P. aspleniifolius*. Inhibition by *P. aspleniifolius* leachates was most pronounced.

pH of inoculum and filtered leachates of treatment species

Acidity of the filtrates of aqueous washings of the 3 treatment species increased with increasing leachate concentration. *P. squameum* exhibited an almost linear relationship between pH and leachate con-

FIG. 8.4.4.   MEAN NUMBERS OF BACTERIAL AND FUNGAL COLONIES
PER CONTROL AND TREATMENT

LEGEND

PS,   *Phebaleum squameum*

EO,   *Eucalyptus obliqua*

PA,   *Phyllocladus aspleniifolius*

25/100, concentration of 25 leaf discs in 100 ml washings
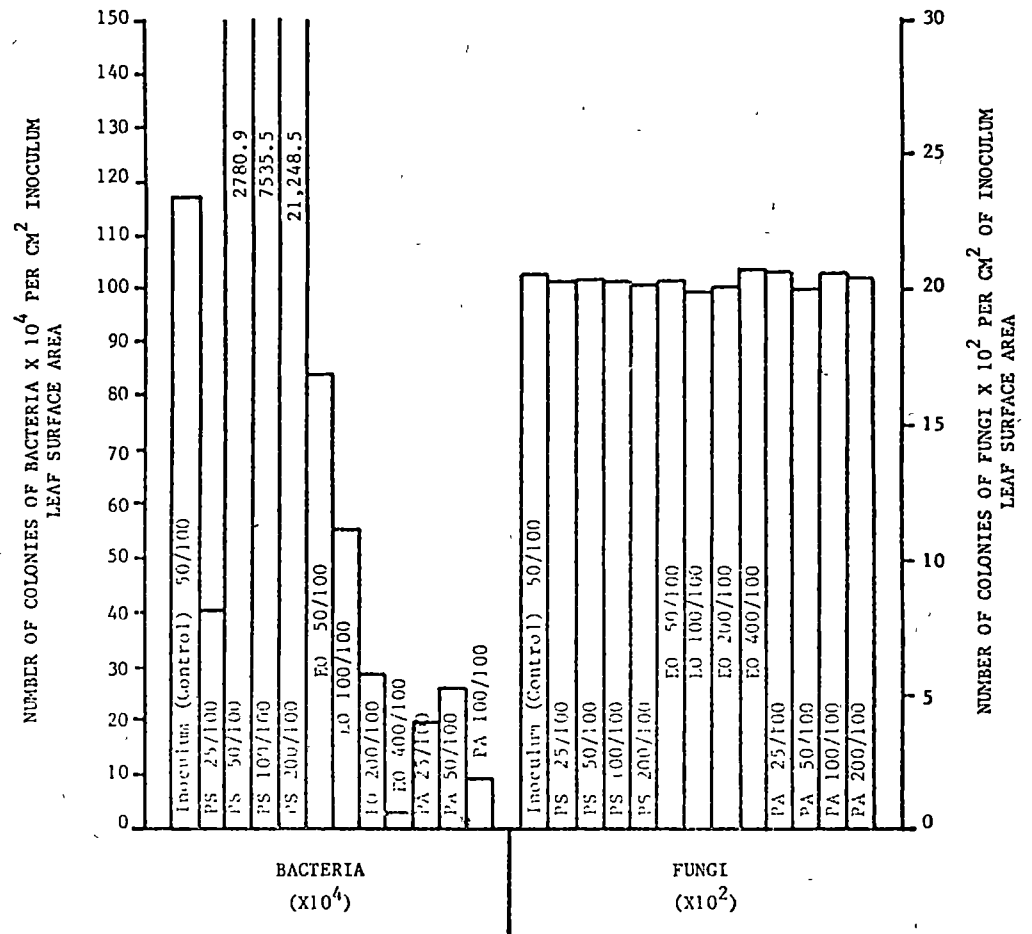
Table 8.4.3. Relative effects of leachate concentrations per species compared to inoculum control upon bacterial culture in nutrient agar.

CONCENTRATION / TREATMENT	25 discs/100 ml	50 discs/100 ml	100 discs/100 ml	200 discs/100 ml	400 discs/100 ml
Inoculum, control	–	1.00	–	–	–
Phebaleum squameum	0.35	23.74	64.34	181.43	–
Eucalyptus obliqua	–	0.72	0.48	0.25	0.03
Phyllocladus aspleniifolius	0.17	0.22	0.08	N.A.	–

N.A., filtrate contaminated.

258

FIG. 8.4.5. RELATIVE EFFECTS OF LEAF LEACHATES UPON BACTERIAL GROWTH OF INOCULUM COMPARED WITH INOCULUM CONTROL
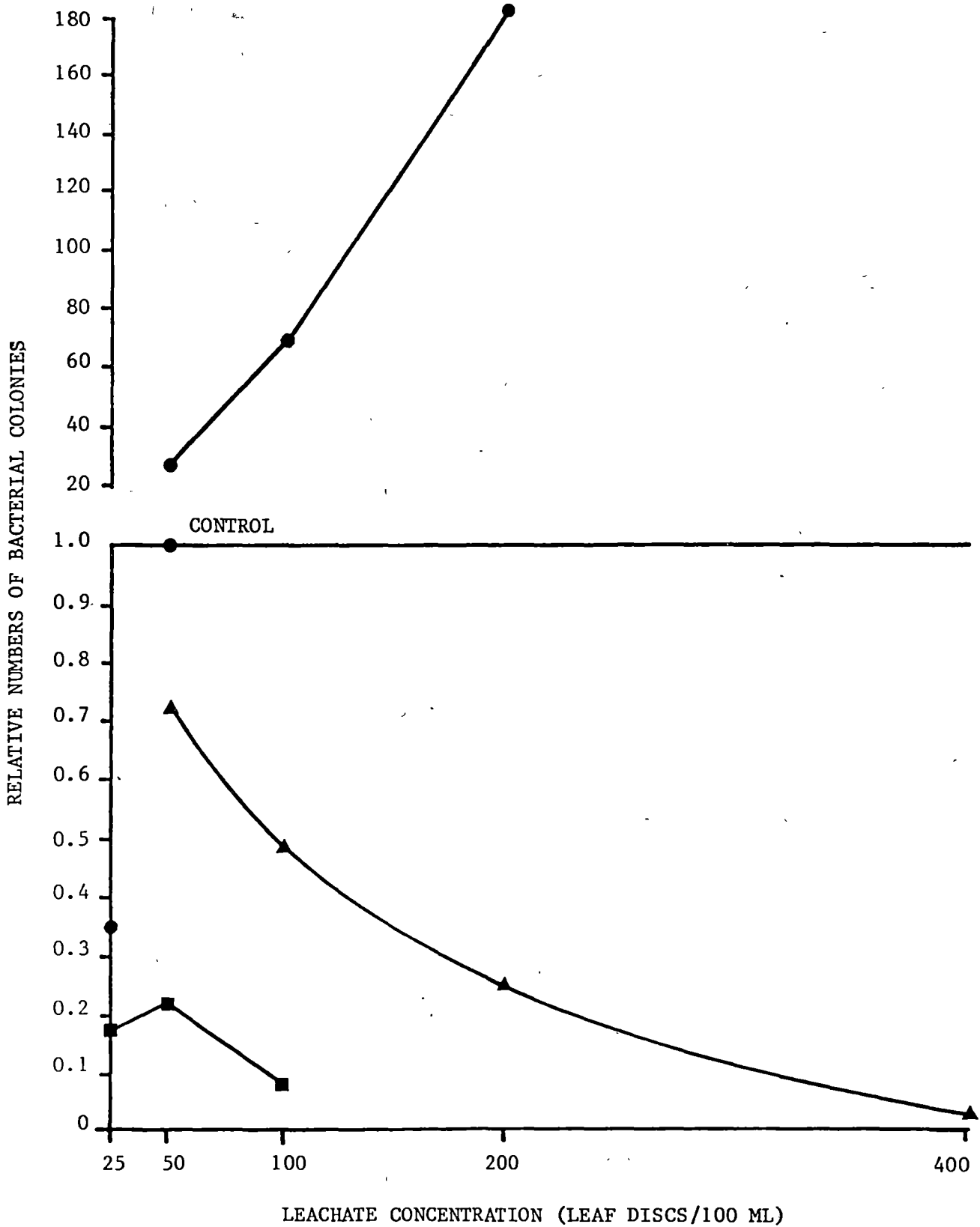
centration, and *E. obliqua* a similar relationship for leachate concentrations between 50 and 200 discs/100 ml sterile tap water.

Results of pH measurements are given in Table 8.4.4 and illustrated in Fig. 8.4.6.

8.4.6 Discussion

A seasonal enumeration of the microflora of leaves of the phylloplane and litterbed was beyond the means of these studies, but a Spring sampling in September, 1981, was expected to yield results pertinent to the relative activity of fungi and bacteria in the phylloplane and litterbed, particularly as rapid decomposition occurred of some leaf species confined upon the litter surface during the same period in 1980 (litter bag studies). Enumeration of microflora of the fastest (*P. squameum*) and slowest (*P. aspleniifolius*) decomposing species, and of the major litter component (*E. obliqua*) was expected to demonstrate the relative activity of fungi and bacteria in the two environments. Additional information regarding leaves of the litter surface and the decomposed leaves of the litterbed was available from leaf leachate studies in October and November, 1981.

There was little difference between September and November in the population densities of fungi on leaves of the litterbed, and little difference between the population densities of the various development stages of the leaves of the 3 species, or of the decomposing leaves used in the preparation of basic inoculum for leaf leachate studies. The lack of difference in fungal population was surprising considering the between-species differences in breakdown rates that occurred in litter bags during the same season of 1980. The lack of fungal activity suggests that the initial rapid breakdown of the litter bag leaves was attributable to bacteria as litter bag experi-

Table 8.4.4.   pH of inoculum and leaf leachates.

Species	No. discs per 100 ml	Leaf surface area (cm^2)	pH
E. obliqua, filtered leachate	50	78.55	6.1
	100	157.10	5.7
	200	314.20	5.1
	400	628.40	4.7
P. squameum, filtered leachate	25	39.28	6.1
	50	78.55	5.9
	100	157.10	5.6
	200	314.20	4.7
P. aspleniifolius, filtered leachate	25	39.28	6.2
	50	78.55	6.2
	100	157.10	5.4
	200	314.20	4.9
Inoculum, unfiltered, mixed species	50	78.55	5.6

FIG. 8.4.6. pH OF INOCULUM AND LEAF LEACHATES
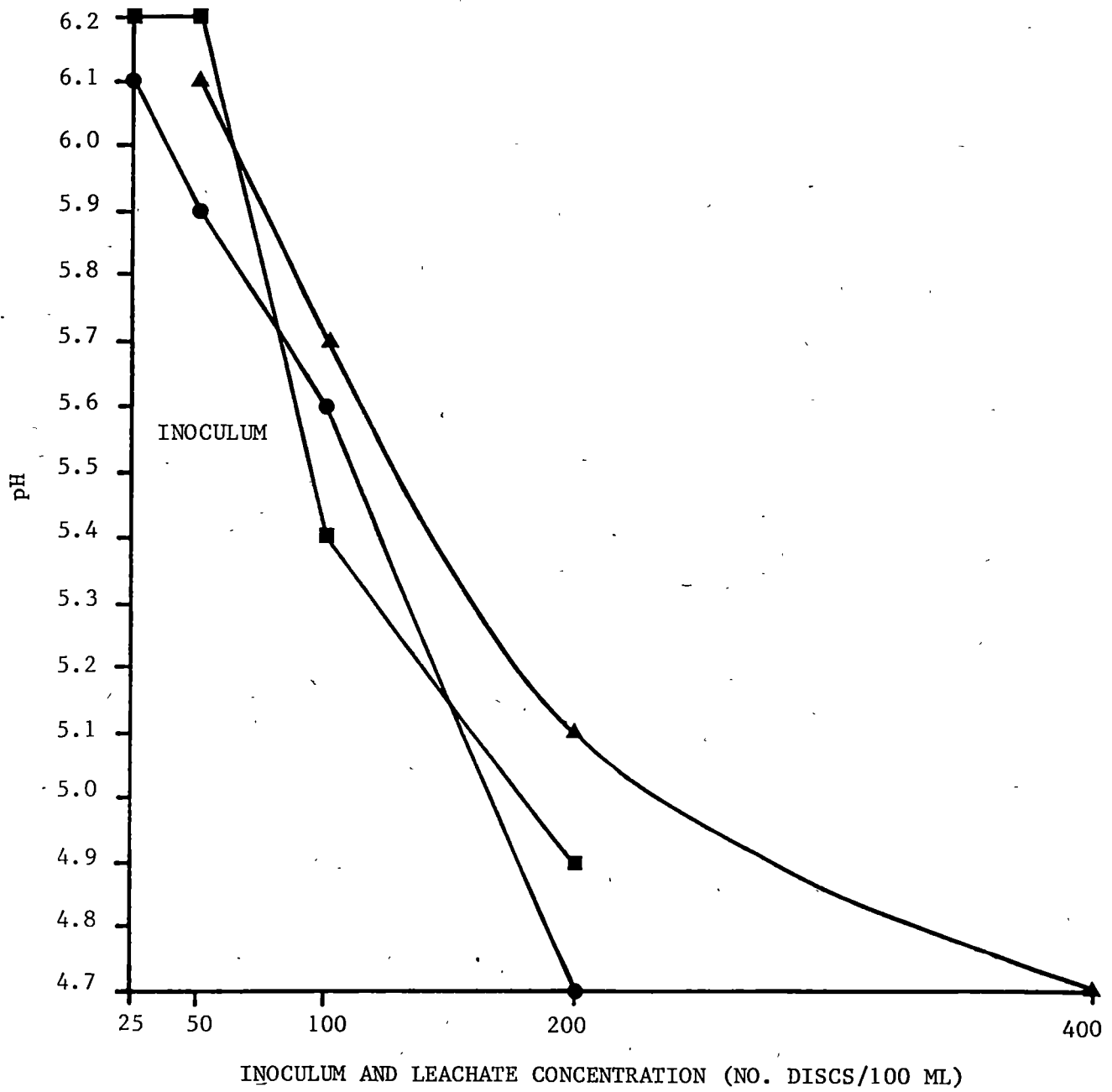
LEGEND

P. *squameum* leachate

E. *obliqua* leachate

P. *aspleniifolius* leachate

ments had already demonstrated microflora to predominate over invert-
ebrates as decomposers.

There was a general trend for bacterial numbers to increase
with increasing leaf age through green, canopy, to sensecent canopy,
to the litter surface, to the decomposing litter layers. Populations
increased between early and late Spring on leaves of the litter surf-
ace (sampled for leachate preparation) and the lower litterbed (inoc-
ulum preparation for the leachate studies).

Two methods of observing the effects of leaf leachates of sel-
ected species upon the culture of litterbed microflora were attempt-
ed. One method directly incorporated leaf discs into an uninoculated
culture medium, and the other studied the effects of aqueous leachates
upon the same inoculum microflora. In both instances the leaf mater-
ial employed had their natural microflora removed either by surface
sterilisation or by millipore filtration.

No differences were apparent between effects of incorporating
whole leaf discs of *P. squameum*, *E. obliqua*, or *P. aspleniifolius* into
the selective media on the culture of either the bacterial or fungal
populations of an inoculum prepared from decomposing leaves of the
litterbed. In contrast leaf leachates of the 3 species had no effect
upon the culture of the fungal fraction of the decomposing leaf inoc-
ulum, but marked differences were obtained between the 3 species in
their effect upon the culture of the bacterial fraction.

Leaves of *P. squameum* promoted the growth of bacteria in the
inoculum, growth promotion increasing directly with increasing leach-
ate concentration to a factor of 180 when compared with a sterile tap
water plus inoculum control.

Leachates of both *E. obliqua* and *P. aspleniifolius* leaves
inhibited bacterial culture from the inoculum, inhibition increasing

as the concentration of the leachates increased. At equal concentrations of leachate (50 leaf discs of 10 mm diameter washed in 100 ml of sterile tap water) their relative effects upon bacterial culture of the inoculum, compared with a sterile tap water control with bacterial numbers of 1.0 were:

P. squameum leachate	23.74
E. obliqua leachate	0.72
P. aspleniifolius leachate	0.22

These results reflect the rapid rate of *P. squameum* leaf breakdown during the initial 3 months of the confinement in litter bags, and the slow rate of breakdown of leaves of *P. aspleniifolius*.

The pH of all leachates increased in acidity with increasing leachate concentration. The range of values was from 6.2 to 4.7, with the *P. squameum* leachates the most acid of the 3 species, indicating that increasing acidity with concentration of the leachates of *E. obliqua* and *P. aspleniifolius* was not the cause of their inhibition to bacterial culture, as remarkable growth promotion was caused by the 200 discs/100 ml concentration of the *P. squameum* leachate with pH 4.7.

CHAPTER IX

## SYNTHESIS AND DISCUSSION

INTRODUCTION

This chapter brings together the significant findings of the study and incorporates them into a working schema (Fig. 9.1) of the cool temperate forest system of Tasmania. It also relates certain findings of decomposition to other Australian studies.

The study area

The litter systems of a range of forest types characteristic of the Southern Forests of Tasmania were studied for 3-1/2 years near Hastings Chalet (Lat. 43°24'S; Long. 146°20'E). Study sites encompassed commercially productive *Eucalyptus obliqua* regrowth forests — mixed *Nothofagus/Atherosperma* forests — tall scrub, with eucalypt overstorey basal area 85-43 m^2 ha^{-1}. Stem numbers ranged from 8940-13,440 per ha. and Site Index from 30-18, with stand ages from 38-400 years. Altitude and topography of all sites were similar (60-80 m.a.s.l.; 2-8% slope) and soils were duplex, yellow podzolics. Mean monthly maximum temperature was 21°C for January and 11°C for July, with mean annual rainfall 1400 mm.

Accession

There was a marked correspondence in the temporal patterns of litter accession between sites that were maintained regardless of differences in accessional patterns between individual annual cycles (Fig. 4.3.1). Annual cycles of overstorey and understorey leaf accession (Figs. 4.3.2 to 4.3.9) were unimodal and strongly seasonal, with peak litterfall occurring during summer (January-March) and minimum falls in winter (June-August), similar to results of Hatch (1955), Stoate (1958), McColl (1966), Webb *et al.* (1969), Van Loon

FIG. 9.1.   LITTER SYSTEM SCHEMA.

EFFECTIVE VARIABLES

Climate
Light intensity
Site index
Diversity
Competition
Basal area

Temperature
Rainfall
Wind

Index 'I'
- Temperature
- Rainfall
- Evaporation
  Moisture content
  pH
  Microflora
  Fauna

OBSERVED EVENTS

PRODUCER

LITTER FALL

LITTER

SOIL

KEY PROCESSES

Photosynthesis ——— Production

Senescence

Accumulation
Decomposition
Constant, 'k'

Nutrient cycling

265
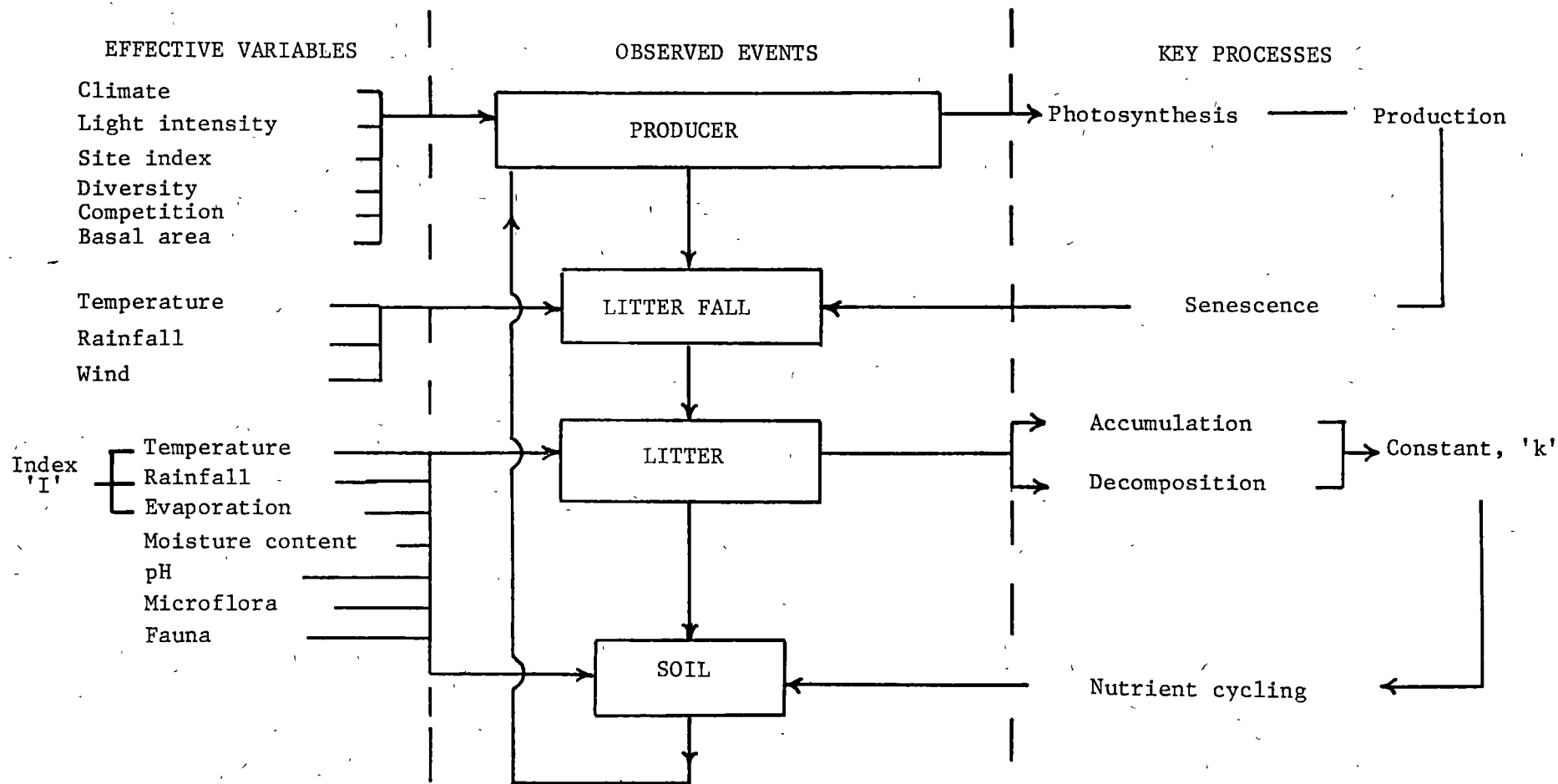
(1970), Ashton (1975), Rogers and Westman (1977, 1981), and Walker (1981). Total litterfall exhibited biomodality, with secondary peaks of fall evident for sampling intervals ending in October 1980, and September 1981. The bimodality of total litterfall of the 1979/80 and 1980/81 cycles was attributable to the bark and twig component that were correlated with windrun and rainfall (r = 0.64) during those intervals(coincident with equinoxial gales).

The marked seasonal pattern of litterfall was significantly correlated with mean maximum temperature experienced during accessional intervals, and the precision of the relationship was improved by removal of the non-leaf component of collections (Table 4.3.10). These findings substantiated those of Attiwill *et al.* (1978) in studies of *E. obliqua* litterfall in Victoria, where part of the seasonal variation was explained in terms of temperature, and of Lee and Correll (1978) who, working in *E. obliqua* stands in S.A., found temperature accounted for 50% of the variation in litterfall.

Annual leaf accession rates (t.ha.$^{-1}$) and the numbers of live stems per ha. per species at the two eucalypt regrowth and the mixed forest sites were compared by regression analysis, using logarithmic transformation of both parameters, and analysis of variance. A relationship existed that accounted for 64.3 percent of the variance, but there were significant differences in both slope and intercept of the individual regression lines per site. In contrast, logarithmic transformation of annual leaf accession rate and basal area (m^{2}ha^{-1}) of individual species per site resulted in a highly significant correlation (P<0.001) and no significant difference (P>0.05) in slope or intercept of the regressions for individual sites. The relationship existed regardless of taxonomic group, canopy class, leaf size or structure, suggesting an adaptative mechanism which balances photosynthetic production despite varying degrees of insolation.

Annual rates of total litter accession in the *E. obliqua*
regrowth stands over 3 years of measurement ranged from 4.8 to 5.6
t.ha.$^{-1}$, and from 4.1 to 4.9 t.ha.$^{-1}$ in the mixed forest. Non-leaf
litterfall varied between 30.6 and 45.0 percent. The maximum to
minimum ratio of total litterfall in the eucalypt study sites varied
from 1:7.4 to 1:22.3, and in the mixed forest from 1:7.8 to 1:12.1.
Ratios for leaf fall were 1:5.0 to 1:22.6, and 1:7.8 to 1:16.7,
respectively.

Analysis of variance between fixed and roving collection de-
vices, and between standard bins and ground traps yielded no signif-
icant differences in litter estimates. Use of the ground traps at
fixed positions is recommended.

Accumulation

The standing crop of litter was measured as 22.150, and
20.541 t.ha.$^{-1}$ in the 2 eucalypt stands, and 11.932 t.ha.$^{-1}$ in the
mixed forest. Decay constants, 'k' (Olsen, 1963), were 0.236 and
0.215, and 0.425 respectively. Values of 'k' for these *E. obliqua*
forests were similar to the value obtained by Lee and Correll (1978)
for *E. obliqua* forests in S.A.

Comparison of the standing crop of woody material attributable
to both the pre-regeneration and the current stand of the 2 eucalypt
sites demonstrated a ratio of 1.4, the same value derived for their
ratio of basal areas. Between sites ratio for Site Index was 1.1, and
this value was the same for litter accession and litter standing crop
of the 2 stands. Litter production was shown to be significantly
correlated with live basal area of individual species where both par-
ametes are indices of net primary production, and of photosynthetic
efficiency.

Decomposition

Relative rates of decomposition of individual species of leaves of both overstorey and understorey components were measured, in litter bag experiments, and the decomposition of naturally accumulating litter was monitored *in situ* by a new, double-trap technique.

Significant differences ($P<0.05$) in decomposition rate were obtained between leaves of 10 species and leaves of 2 mixtures of 2 species. There were significant differences between all material types except *E. obliqua* and *E. nitida*. The fastest decomposition occurred with leaves of the understorey species, *Phebaleum squameum*, and the slowest with *Phyllocladus aspleniifolius*. Percent dry weight losses in the first 12 months of field exposure were 51.5 and 12.9 respectively. Leaves of *E. obliqua* lost 42.0, and *E. nitida* 42.3 percent of their initial dry weight in 12 months. During this period there was an absence of leaf fragmentation except in the case of the eucalypt leaf species.

There was a general agreement between the rate of decomposition of individual species and their annual accession, those with the heavier fall having the faster decomposition rates.

No relationships were apparent between the leaves of taxonomic groups (Curtis, 1963, 1967; Curtis and Morris, 1975), their size, class, or structure (Fosberg, 1961), and their decomposition rate.

Significant increases in decomposition occurred with increasing length of field exposure for all species except *Pomaderris apetala* leaves, that remained static between the 12 and 18 months sampling. Leaves of all species except *Phyllocladus aspleniifolius* decomposed most rapidly in the initial 3 months of field exposure, and thereafter at a generally uniform rate between 3 and 6, 6 and 12, and 12 and 18 months (except as stated for *P. apetala*). *Phyllocladus aspleniifolius*

leaves decomposed at a low and uniform rate over the 18 months study period.

Leaves decomposed at similar rates in both the tall, open eucalypt stand (Site 1), and the tall scrub (Site 4), regardless of the more extreme microclimate at the latter site. Exceptions were leaves of *E. obliqua* that decomposed more rapidly at Site 4, and *E. nitida* that decomposed more rapidly at Site 1.

Analysis of variance demonstrated no significant differences in decomposition of leaves of species mixes alone, or in mixture.

The treatment of leaves with fungicide caused a significant reduction in decomposition compared with control leaves without treatments. The reduction was apparent at all sampling times (3, 6, and 12 months) but the treatment effect decreased after 6 months field exposure. Treatment effect was greatest with *E. obliqua* leaves and leaves of the *E. obliqua/P. apetala* mixture. Treatment with insecticide reduced the decomposition rate of *E. obliqua* leaves but did not have a significant effect ($P>0.05$) upon the other material types. Treatment with a mixture of fungicide and insecticide had a similar effect to treatment with fungicide alone, and was significantly more effective in reducing decomposition rates than the use of insecticide. The inhibitory effect of the mixture was thus attributed to the fungicide component.

It was concluded that in the litterbeds studied, microflora were the predominant decomposer agencies of leaf litter decomposition, with litter fauna of possible importance to the decomposition of *E. obliqua* leaves.

A series of experiments were conducted to examine the effects of leaf development, and times of placement and of leaf harvest upon subsequent leaf decomposition rates. Improved results were obtained

with senesced leaves established in the field coincident with the period of heaviest leaf fall (January-February). The trends of decomposition were similar between green leaves and senesced leaves, and it was considered that given situations where naturally shed leaves cannot be harvested in adequate quantities, then the use of green leaves will result in faster decomposition rates, but the general trend will be the same as for naturally shed material. The use of green leaves may even be advantageous as they emphasize the decomposition process.

Investigations of the relative effects of incorporation of leaf material of species with differing decomposition rate upon the culture of bacterial and fungal populations of an inoculum prepared from decomposing leaves of the litterbed resulted in:

(i) Incorporation of leaf discs: no differences between species in the subsequent culture of bacterial or fungal populations.

(ii) Incorporation of leaf leachates: no differences per species in the culture of populations of fungi, but marked differences in the culture of bacteria. Leaf leachates of *Phebaleum squameum* enhanced the growth of bacteria, growth increasing directly with increasing leachate concentration to a factor of 180 compared with a sterile tap water control. This result emphasises the point that plate counts may not be real counts, and suggests that bacterial growth enhancement may be the result of additional nutrient provided by the leaf leachate, and not available in the standard media. *E. obliqua* and *Phyllocladus aspleniifolius* leaf leachates inhibited bacterial culture from the inoculum, inhibition increasing with increasing leachate concentration. The relative effects of the 3 leaf spieces upon bacterial culture as compared to a value of 1.0 for sterile tap water control were *P. squameum* 23.74, *E. obliqua* 0.72, *P. asplen-*

iifolius 0.22. This result reflected the rapid decomposition rate of *P. squameum* during the initial 3 months of litter bag experiments, and the slow decomposition rate of *P. aspleniifolius*.

Leachate acidity was not responsible for the differences in bacterial culture.

The relative phenolic and carbohydrate status of leachates of leaves of the 3 species collected from the green canopy, litter surface, and decomposing litter layer were compared by thin-layer chromatography. In general leaves of *P. aspleniifolius* contained greater concentrations of extractable phenolics. Less phenolics were extracted from *P. squameum* leaves than from leaves of *E. obliqua* or *P. aspleniifolius*. However, an absence of either carbohydrates or simple phenolics in decomposing leaf extracts suggests that they are rapidly decomposed, and hence their relative phenolic status cannot be responsible for their intrinsic differences in decomposition rate.

A trapping system was devised that enabled accumulation and decomposition rates to be monitored in the field under conditions more natural than those created by litter bags. Results led to the view that there was an ever present inoculum base that was activated by increasing litter temperatures, and which was not affected by litter moisture under the conditions at Hastings. Hence adequate temperature for microfloral activity was the major factor affecting litter decomposition in these studies.

Litter moisture and temperature were considered of prime importance to litterbed decomposition processes. In *E. obliqua* forests in Southern Tasmania cooler temperatures but year round adequacy of moisture resulted in a similar decay constant, 'k', value to *E. obliqua* forests in South Australia, where temperatures are higher but moisture is limiting for 6 months of the year (Lee and Correll, 1978).

The importance of moisture and temperature upon litter decomposition has been discussed by many authors (Waksman and Gerretsen, 1931; Jenny *et al.*, 1949; Handley, 1954; Olson and Crossley, 1961; Witkamp and Van der Drift, 1961; Witkamp, 1963, 1969; Franz, 1962; Wood, 1974; Williams and Gray, 1974; Ashton, 1975; Richards and Charley, 1977; Singh and Gupta, 1977; Meentemeyer, 1978). Waksman and Gerretsen (1931) studied the decomposition of fresh plant material (oat straw) and its chemical constituents and found that the higher the temperature, the more rapid was decomposition of the plant material. Temperature increase had a marked effect in increasing decomposition of the lignin content of the straw. Meentemeyer (1978) formulated a general model of the interaction control of actual evapotranspiration (AET) and lignin concentration of litter on decomposition rates, with the aim of predicting regional decay rates, and to determine the relative control of litter decomposition rates by macroclimate and litter quality. For climates ranging from sub-polar to warm temperate, AET (macroclimate index), was several orders of magnitude of greater importance for the prediction of decay rates than lignin concentration (index of litter quality).

Davidson (1933, 1934a, 1934b) investigated the distribution of the lucerne flea, *Smynthurus viridis*, in South Australia, and developed a monthly hydric index, $\frac{r}{e}$ (where r = rainfall and e = evaporation) that enabled maps for Australia to be compiled that indicated areas and periods in which *S. viridis* could exist in the active stage. Davidson's studies found that, given favourable temperature, $\frac{r}{e}$ most usefully indicated when *S. viridis* activity and population increase could occur. Davidson (1935) defined the monthly value of $\frac{r}{e} = 0.5$ - - -

"as the lower limit at which adequate moisture will be available for plant growth", and Davidson (1936) developed a series of defined monthly wetness or dryness values for regions of Australia, as he considered moisture to be the major influence affecting seasonal activity and distribution of insects. Gentilli (1971, 1977) discusses the development of a range of climatic indices, notably the Waite Institute Climatic Index (Prescott, 1946, 1949; Prescott *et al.*, 1952), and the development of a monthly index of hydric biopotential (Gentilli, 1971).

In these studies the monthly Waite Index and monthly mean temperature were combined to derive a climatic index for localities ranging from tropical closed forest in Queensland to cool temperate, tall, open forest in Southern Tasmania, including alpine forests of the Snowy Mountains and warm temperate forests of NSW, WA, SA, and Victoria. The Waite index was calculated from $\frac{r}{e^m}$, where r and e were monthly rainfall and actual evaporation (mm), and m was a constant, 0.75 (Prescott *et al.*, 1952). The mean temperature of all months in the year with a Waite Index value greater than 2.0 but less than 4.0 were summed to give an annual hydric and thermic grade. The range 2.0 to 4.0 was selected as the range of values indicative of optimum conditions for biological activity, i.e. not too wet and not too dry.

The importance of relative humidity and substrate moisture content to eucalypt leaf litter decomposition has been discussed by Nagy and Macauley (1982).

Table 9.1 lists the calculated climatic index and the decay constant 'k' (Olson, 1963) for each of 23 Australian litter studies.

Fig. 9.2 illustrates a curvilinear relationship between calculated 'I' (the climatic index) and the decay constant, 'k'. There were two obvious anomalies (Sites 4 and 23) both of which were represent-

Table 9.1.   Relationship between calculated decay constants, k, and a climatic index, I, for a range of Australian forests.

Reference no.	Location	Latitude	Forest type	L, Annual litterfall (t.ha.$^{-1}$)	X, Standing crop (t.ha.$^{-1}$)	k	I	Authority
1	Innisfail, Q.	17°32'S	Tropical, closed forest	5.11	5.62	0.91	89.1	Bailey (1976) in Walker (1981). (A)
2	Rockhampton, Q.	24°08'S	Grassy, open forest	6.5	2.93	0.45	70.0	Nicholls (unpubl.) in Walker (1981). (A)
3			Closed grass-land	10.0	6.0	0.60	70.0	Walker (1981). (A)
4	Brisbane, Q.	27°33'S	E. umbra/ E. baileyana	3.25	10.2	0.32	165.6	Birk (1979a,b). (A)
5	Alice Springs, N.T.	23°28'S	Woodland	0.3	2.2	0.14	0	Winkworth (1973) in Walker (1981). (A)
6	Canberra, A.C.T.	35°17'S	Open forest	5.02	17.48	0.30	29.7	Hutchings and Oswald (1975). (A)
7	Armidale, N.S.W.	30°39'S	E. saligna/	10.01	12.37	0.81	86.9	Richards and Charley (1977). (A)
8			E. viminalis	3.85	4.52	0.85	86.9	
9			Temperate closed forest	7.07	12.65	0.56	86.9	Watson (1977) in Walker (1981). (A)
10	Dwellingup, W.A.	32°47'S	E. marginata	2.68	16.3	0.16	29.5	Hatch (1955). (B)
11			E. marginata	2.37	18.78	0.12	29.5	Peet (1971).
12	Kendal	31°58'S	E. pilularis	4.9	12.2	0.40	59.5	Nicholson and Love (1972).
13	Bellangry	(Taree, N.S.W. data)	E. pilularis	7.1	15.5	0.46	59.5	Van Loon (1970, 1977).
14	Manning River		E. pilularis	4.3	13.9	0.33	59.5	Van Loon (1969). (B)
15	Snowy Mountains, N.S.W.	36°40'S	Alpine, open forest	3.56	40.0	0.09	27.9	Park (1977) in Walker (1981). (B)
16	Bridgewater, S.A.	35°S (Adelaide)	E. obliqua/ E. baxteri	2.33	9.8	0.24	26.6	Lee and Correll (1978). (A)
17	N.E. TAS.	41°S	Open forest	3.8	25.0	0.15	38.3	Jackson (1968). (A)

Table 9.1.

Relationship between calculated decay constants, k, and a climatic index, I, for a range of Australian forests.   Cont'd

Reference no.	Location	Latitude	Forest type	L, Annual litterfall (t.ha.$^{-1}$)	X, Standing crop (t.ha.$^{-1}$)	k	I	Authority	
18	Hastings, TAS.	43°30'S	E. obliqua	5.31	22.5	0.24	16.9	This study.	(B)
19			E. obliqua	4.89	20.54	0.22	16.9	" "	
20			Mixed forest	4.69	11.93	0.43	16.9	" "	
21	Mt. Disappointment (VIC.)	37°20'S	E. obliqua	3.56	18.25	0.20	37.0	Attiwill (1968).	(C)
22	Wallaby Creek, VIC.	37°20'S	E. regnans	7.76	21.8	0.36	37.0	Ashton (1975).	(C)
23	Stradbroke Is., Q.	27°50'S	E. signata E. umbra	6.43	27.0	0.24	90.2	Rogers and Westman (1977).	(B)

(A) = Climatic data in Gentilli (1971).

(B) = Climatic data ex. Meteorological Bureau.

(C) = Temperature data ex. Melbourne and Metropolitan Board of Works,
        Evaporation and rainfall data ex. (B).

FIG. 9.2.   RELATIONSHIP BETWEEN k AND I FOR AUSTRALIAN FORESTS.

276

FIG. 9.3.　　　RELATIONSHIP BETWEEN $\sqrt{k}$ AND I FOR AUSTRALIAN FORESTS

$$Y_e = 0.31534 + 0.0059.X$$
$$r = 0.8396$$
$$n = 21$$
$$P < 0.001 \quad (4,23 \text{ excluded} - \text{refer text})$$

Σ T°C for months with $\dfrac{P}{E^{0.75}} \geqslant 2 \leqslant 4$
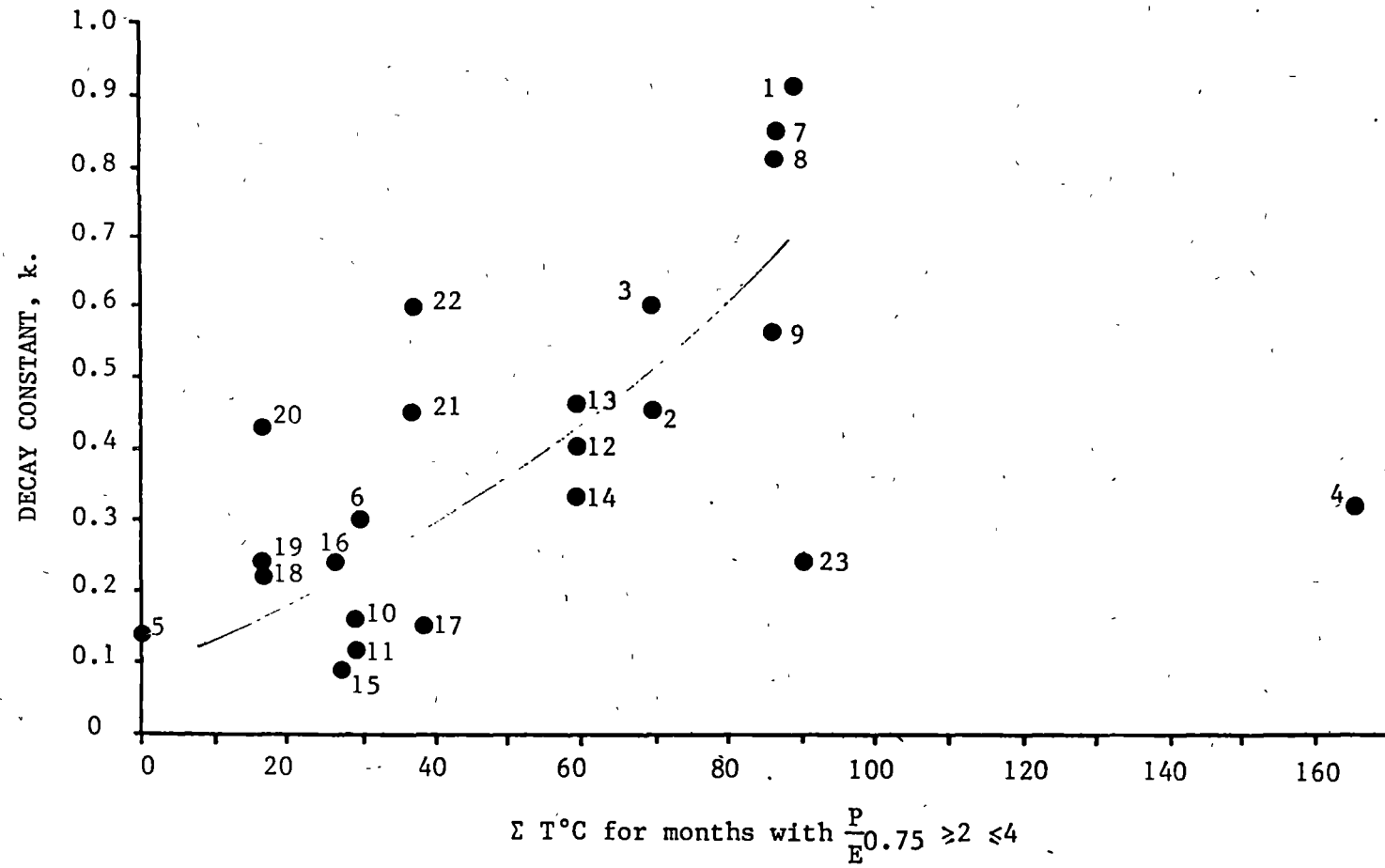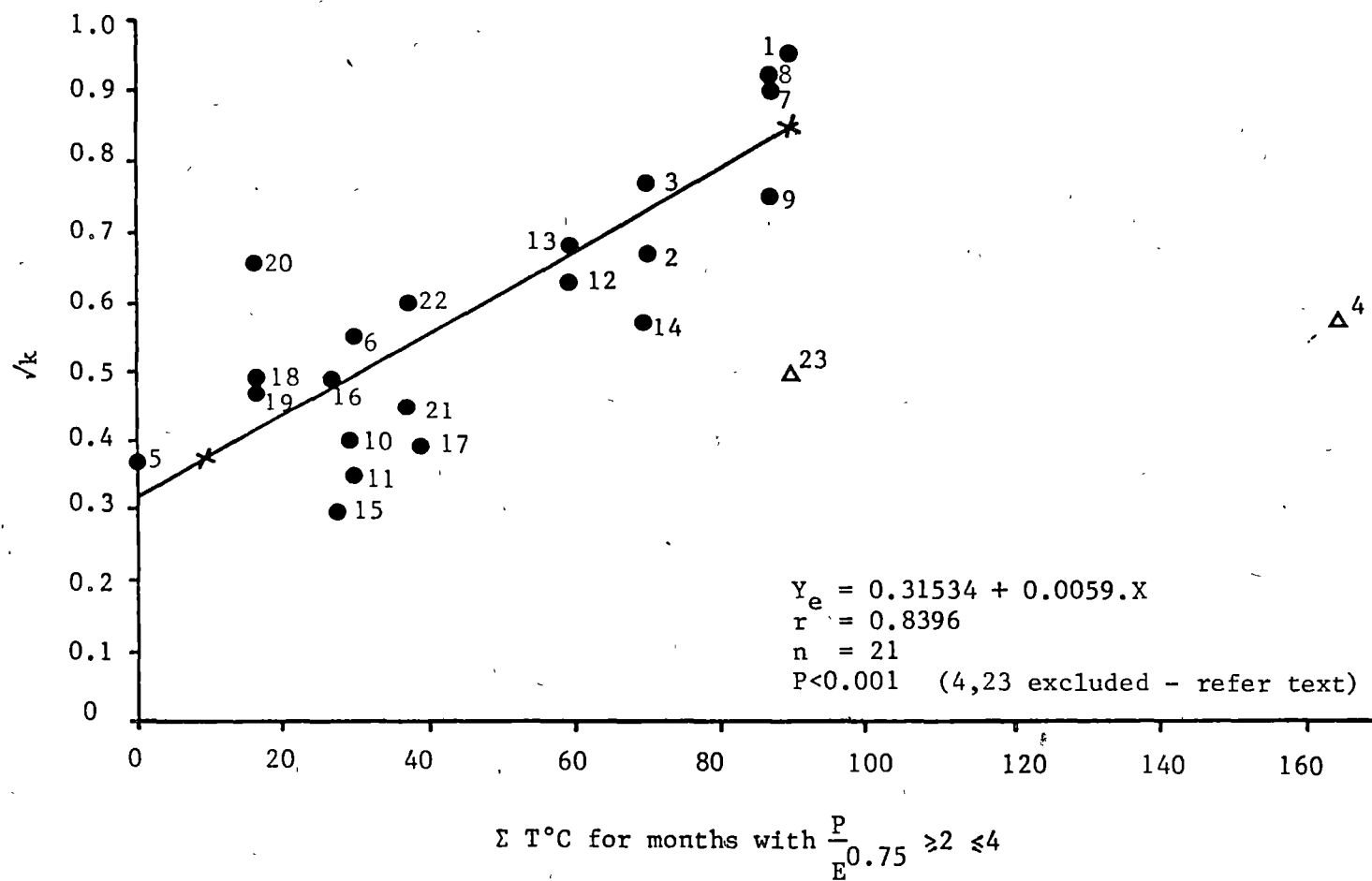
ative of mixed *Eucalyptus* and *Angophora* communities near Brisbane. Study No.4 (Birk, 1979a,b) was carried out in layered open-forest on shallow, stony soils derived from sandstone grit conglomerate material, and study No.23 (Rogers and Westman, 1977) on deep, nutrient poor sands. It was considered that the low value for 'k' derived for both study areas was attributable to the rapid drainage and subsequent drying of the litter layer that would affect the decomposition rate. For these reasons, the k values for studies No.4 and 23 were considered aberrant and were excluded from the data set.

Fig. 9.3 illustrates a linear relationship betwen the square root of 'k' and the climatic index, 'I'. Linear regression analysis resulted in a highly significant (P<0.0001) correlation between $\sqrt{k}$ and I, with r = 0.84, n = 21, and S.E. = 0.1069. The significance of the correlation between a climatic index and decay rates for a range of forest communities supported the finding of Meentemeyer (1978) that macroclimate is of greater importance to litter decomposition than litter quality.

As discussed, total litterfall at Hastings was found to be significantly correlated with mean maximum temperature (both parameters logarithmically transformed) experienced during the period of accession (r = 0.73-0.87, n = 17, p<0.0005), and this relationship was not improved by the addition of other climatic variables. Rainfall at Hastings was at no stage limiting to tree growth, but lack of moisture may be a limiting factor in other Australian forests. Fig. 9.4 illustrates the relationship between log litterfall, L (t.ha^{-1} x 10) and log 'I' for the same studies of Table 9.1. Linear regression analysis of the logarithmically transformed parameters resulted in a singificant correlation (P<0.0001) with r = 0.69, n = 21, and S.E. = 0.1823.

FIG. 9.4.   RELATIONSHIP BETWEEN LOG LITTERFALL AND LOG INDEX, I.

Log Litterfall = 0.67782 + 0.61304 Log Index, I.

$r = 0.687$, (P<0.0001)

$n = 21$, S.E. = 0.1823
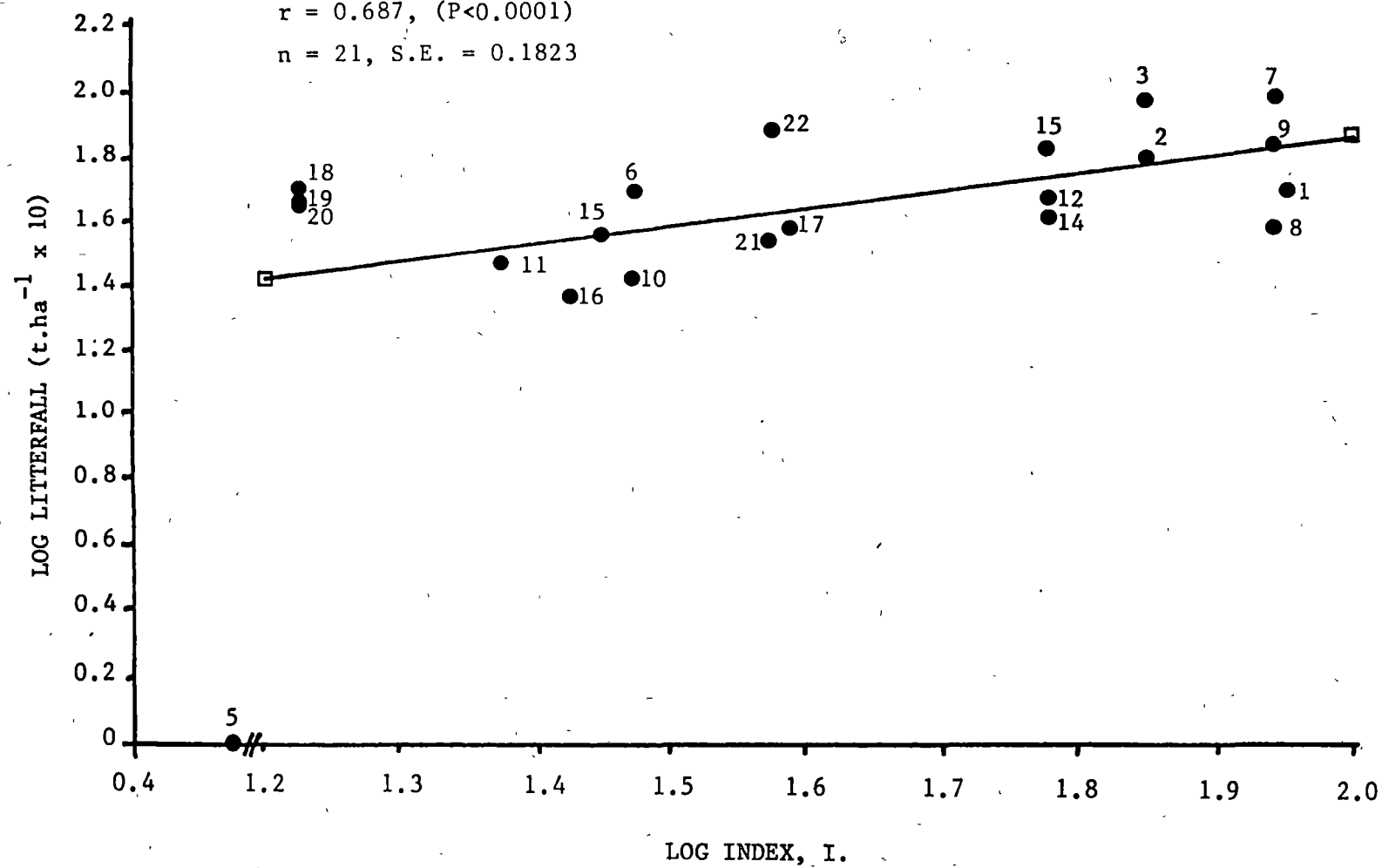
Thus temperature and moisture are the major factors affecting the litter processes of accession, decomposition, and hence accumulation. The macroclimate will influence the relative importance of litter microflora and fauna in litter decomposition. In the cool, temperate forests of Tasmania the microflora are the dominant decomposer agency, whereas in warmer climates the litter fauna may predominate.

The importance of the macroclimate to the various litter processes, and in particular litter accumulation, lends itself to application in fuel dynamics studies for prescribed burning in forest management.

REFERENCES

ALEXANDER, M. (1971). Microbial Ecology, John Wiley, New York and London.

ALLISON, F.E. and MURPHY, R.M. (1963). Comparative rates of decomposition in soil of wood and bark particles of several hardwood species. Soil Sci. Soc. Am. Proc. 26, pp463-66.

ANDERSON, J.M. (1973). The breakdown and decomposition of Sweet Chestnut and Beech leaf litter in two deciduous woodland soils. I. Breakdown, leaching, and decomposition. Oecologia 12, pp251-274.

ANDERSON, J.M. and MACFADYEN, A. (1977) (Eds.). The role of terrestrial and aquatic organisms in decomposition processes. 17th. Symposium of Brit. Ecol. Soc., Blackwell Sci. Pub., Oxford. 474p.

ANON. (1978). D.E. McLeod, CSIRO, Division of Forest Research, Dover. pers.comm.

ANON. (1982). J.L. Honeysett and A.M. Graley, CSIRO, Division of Soils, Hobart. pers.comm.

ASHTON, D.H. (1975). Studies of litter in *E. regnans* forests. Aust. J. Bot. 23, pp413-33.

ASHTON, D.H. and MACAULEY, B.J. (1972). Winter leaf spot disease of seedlings of *E. regnans* and its relation to forest litter. Trans. Brit. Mycol. Soc. 58(3) pp377-86.

ATTIWILL, P.M. (1966a). Chemical composition of rainwater in relation to the cycling of nutrients in mature eucalypt forests. Plant Soil 24, pp390-406.

ATTIWILL, P.M. (1966b). A method for estimating crown weight in Eucalyptus, and some implications of relationships between crown weight and stem diameter. Ecology 47, 795-804.

ATTIWILL, P.M. (1968). The loss of elements from decomposing litter. Ecology 49, pp142-5.

ATTIWILL, P.M. (1979). Nutrient cycling in a *Eucalyptus obliqua* (L'Herit.) Forest. III. Growth, biomass, and net primary production. Aust. J. Bot. 27, pp439-58.

ATTIWILL, P.M., GUTHRIE, H.B. and LEUNIG, R. (1978). Nutrient cycling in *E. obliqua* Forest. I. Litter production and nutrient return. Aust. J. Bot. 26, pp79-91.

AUSTIN, B., GOODFELLOW, M. and DICKINSON, C.H. (1978). Numerical taxanomy of phylloplane bacteria isolated from *Lolium perenne*. J. gen. Microbiol. 104, pp139-155.

BAILEY, S.W. (1976). Seasonal variation of litterfall in three North Queensland rainforests. CSIRO Aust. Div. Soils Tech. Memo. 28/1976.

BAMBER, R.K. (1975). Why heartwood forms. 17th. Forest Products Research Conference. CSIRO Division of Building Research and Chemical Technology, pp3.

BAZILEVIC, N.I., DROSDOV, A.V. and RODIN, L.E. (1971). World forest productivity, its basic regularities and relationship with climatic factors. *In*: Productivity of forest ecosystems (Ed. P. Duvigneaud) Unesco, Paris. pp135-53.

BEVEGE, D.I. (1978). Biomass and nutrient distribution in indigenous forest ecosystems. Qld. Dept. For. Tech. Paper No.6, pp20.

BIRK, E.M. (1979a). Overstorey and understorey litterfall in a eucalypt forest : spatial and temporal variability. Aust. J. Bot. 27, 145-56.

BIRK, E.M. (1979b). Disappearance of overstorey and understorey litter in an open eucalypt forest. Aust. J. Ecol. 4, pp207-22.

BIRK, E.M. and SIMPSON, R.W. (1980). Steady state and the continuous input model of litter accumulation and decomposition in Australian eucalypt forests. Ecology 61(3) pp481-85.

BLACK, J.N. (1956). The distribution of solar radiation over the earth's surface. Arch. Met. Wien. Ser. B, 7, pp165-89.

BOCOCK, K.L. (1963). Changes in the amount of nitrogen in decomposing leaf litter of sessile oak. J. Ecol. 51, pp555-66.

BOCOCK, K.L. (1964). Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J. Ecol. 52, pp273-84.

BOCOCK, K.L. and GILBERT, O.J.W. (1957). The disapearance of leaf litter under different woodland conditions. Pl. Soil. 9, pp179-85.

BONNEVIE-SVENDSEN, C. and GJEMS, O. (1957). Amount and chemical composition of the litter from larch, beech, Norway spruce and Scots pine stands and its effect on the soil. Medd. Norske Skogsforsoksv. 48, pp111-174.

BOWLING, P.J. and McLEOD, D.E. (1968). A note on the presence of *Armillaria* in second growth eucalypt stands in southern Tasmania. Aust. For. Res. 3, pp38-40.

BRASELL, H., UNWIN, G.L. and STOCKER, G.C. (1977). The pattern and chemical composition of litterfall in two forest types of tropical Australia. Unpubl. mimeographed. 20pp.

BRAY, J.R. and GORHAM, E. (1964). Litter production in Forest of the World. Adv. Ecol. Res., 2, pp101-54.

BUNNELL, F.L., TAIT, D.E.N. and FLANAGAN, P.W. (1977). Microbial respiration and substrate weight loss. II. A model of the influences of chemical composition Soil Biol. Biochem. 9, pp41-7.

BURGES, N.A. (1965). *In*: Experimental Pedology (Eds. E.G. Hallsworth and D.V. Crawford). Butterworths, London, pp189-198.

CABLE, D.R. (1958) Estimating surface area of Ponderosa Pine foliage in central Arizona. For. Sci. 4, pp45-9.

CARNAHAN, J.A. (1976). Natural vegetation. *In*: Atlas of Australian Resources. Second series. Aust. Dept. Nat. Resources, Div. of Natl. Mapping, Canberra.

CHARLEY, J.L. and RICHARDS, B.N. (1974). Energy and nutrient dynamics of forest floors. IFA. 7th. Terrest. Conf. Proc. Vol.1, pp25-34.

CLARY, W.P. and FFOLLIOTT, P.F. (1969) Water holding capacity of Ponderosa Pine forest floor layers. Journal of Soil and Water Conservation 24, pp22-23.

CREMER, K.W. (1975). Temperature and other climatic influences on shoot development and growth of *Eucalyptus regnans*. Aust. J. Bot. 23, pp27-44.

CROMER, R.N., RAUPACH, M., CLARKE, A.R.P. and CAMERON, J.N. (1975). Eucalyptus plantations in Australia - the potential for intensive production and utilisation. Appita 29, pp165-73.

CROSBY, J.S. (1961). Litter and duff fuel in short leaf pine stands in Southeast Missouri. Tech. Pap. cent. St. For. Exp. Sta. 178, 10pp.

CROSSLEY, D.A. and HOGLUND, M.P. (1962). A litter bag method for the study of microarthropods inhabiting leaf litter. Ecology 43, pp571-73.

CURTIS, W.M. (1963). The Students Flora of Tasmania. Part 2. L.G. Shea, Government Printer, Tasmania.

CURTIS, W.M. (1967) The Students Flora of Tasmania. Part 3. D.E. Wilkinson, Government Printer, Tasmania.

CURTIS, W.M. and MORRIS, D.I. (1975). The Students Flora of Tasmania. Part 1. (2nd Ed.). T.J. Hughes, Government Printer, Tasmania.

DAVIDSON, J. (1934a). The Lucerne Flea, *Sminthurus viridis* L. (Collemibola) in Australia. Comm. of Aust., CSIR, Bull.79, 66pp.

DAVIDSON, J. (1934b). The monthly precipitation-evaporation ratio in Australia, as determined by saturation deficit. Trans. Roy. Soc. S.Aust. 58, pp33-36.

DAVIDSON, J. (1934c). Climate in relation to insect ecology in Australia, 1. Mean monthly precipitation and atmospheric saturation deficit in Australia. Trans. Roy. Soc. S.Aust. 85, pp197-210.

DAVIDSON, J. (1935). Climate in relation to insect ecology in Australia, 2. Mean monthly precipitation-evaporation ratio. Trans. Roy. Soc. S.Australia 59, pp107-214.

DAVIDSON, J. (1936). Climate in relation to insect ecology in Australia, 3. Bioclimatic zones in Australia. Trans. Roy. Soc. S.Aust. 60, pp88-92.

DAVIES, R.I. (1971). Relation of polyphenols to decomposition of organic matter and to pedogenetic processes. Soil Science 111, No.1, pp80-85.

DICK, R.S. (1975). A map of the climates of Australia: according to Koppens principles of definition. Queens. Geogr. J. (3rd series) 3, 33-69.

DICKINSON, C.H. and PUGH, G.J.F. (1974) Biology of Plant Litter Decomposition Vols. I and II Academic Press.

DUVIGNEAUD, P. (1971). Productivity of Forest Ecosystems. Unesco, Paris.

EDWARDS, P.J. (1974). Macroarthropods. *In*: Biology of plant litter decomposition, Vol.2 (Eds. G.H. Dickinson and G.J.F. Pugh). Academic Press, London and New York pp533-554.

EDWARDS, P.J. (1977). II. The production and disappearance of litter. J. Ecol. 65, pp971-92.

EDWARDS, C.A. and HEATH, G.W. (1973). Role of soil organisms in the breakdown of leaf material. *In*: Soil organisms (Eds. J. Doekson and J Van der Drift). North Holland, Amsterdam.

EICKER, A. (1973). The mycoflora of *E. maculata*. Soil Biol. and Biochem. 5, pp441-48.

FELLER, M.C. (1978). Nutrient movement into soils beneath eucalypt and exotic conifer forests in southern central Victoria. Aust. J. Ecol. 3, pp357-72.

FELLER, M.C. (1980). Biomass and nutrient distribution in two eucalypt forest ecosystems. Aust. J. Ecol. 5, pp309-33.

FELTON, K.C. (1972). Eucalypt diebacks in Tasmania. Appita 26, pp207-8.

FISHER, R.A. and YATES, F. (1963). Statistical tables for biological, agricultural and medical research. Oliver and Boyd, London.

FLORENCE, R.G. (1961). Studies in the ecology of Blackbutt (*Eucalyptus pilularis* Sn.) Ph.D. Thesis, Univ. Sydney.

FOSBERG, F.R. (1961). A classification of vegetation for general purposes. Trop. Ecol. 2, PP1-28 (Republished in modified form in G.F. Peterken. 1967). Guide to the check sheet for IBP areas. IBP Handbook No.4 Blackwell Scientific Publications, Oxford and Edinburgh, pp73-120).

FOX, B.J., FOX, M.D. and McKAY, G.M. (1979). Litter accumulation after fire in a eucalypt forest. Aust. J. Bot. 27, pp157-65.

FRANZ, H. (1962). Habitat characteristics with particular reference to the soil. *In*: Progress in soil zoology (Ed. P.W. Murphy) Butterworths, London. pp311-318.

FRIEND, J.A. (1980). The taxonomy, zoogeography and aspects of the ecology of the terrestrial amphipods (Amphipoda:Talitridae) of Tasmania. Ph.D. Thesis, University of Tasmania.

FRITTS, H.C. (1976). Tree Rings and Climate. Academic Press, N.Y.

GALBRAITH, J. (1977) Collins field guide to the wild flowers of S.E. Australia. W. Collins Sons and Co. Ltd., London and Glasgow.

GENTILLI, J. (1971). Climates of Australia and New Zealand (*In*: World Survey of Climatology, Vol.13. Ed-in-Chief, H.E. Landsberg) Elsevier Publ. Co., Amsterdam, London, N.Y. pp119-88.

GENTILLI, J. (1977). Australian Climate Patterns. Thomas Nelson, Melbourne.

GILBERT, J.M. (1959). Forest succession in the Florentine Valley, Tasmania. Pap Proc. R. Soc. Tasm. 93, pp129-52.

GHILAROV, M.S. (1971). Invertebrates which destroy the forest litter and ways to increase their activity. *In*: Productivity of forest ecosystems. (Ed. P. Duvigneaud) Unesco, Paris, pp433-442.

GILBERT, O. and BOCOCK, K.L. (1960). Changes in leaf litter when placed on the surface of soils with contrasting humus types. II. Changes in the nitrogen content of oak and ash leaf litter. J. Soil Sci. 11(1), pp10-19.

GILBERT, O. and BOCOCK, K.L. (1962). Some methods of studying the disappearance and decomposition of leaf litter. *In*: Progress in Soil Zoology (Ed. P.W. Murphy) Butterworths, London. pp348-52.

GOODFELLOW, M., AUSTIN, B. and DAWSON, D. (1976). Classification of and identification of phylloplane bacteria using numerical taxonomy. (*In*: Microbiology of aerial plant surfaces. Ed. C.H. Dickinson and T.F. Preece). Academic Press, Liverpool. pp275-92.

GOODFELLOW, M. and DAWSON, D. (1978). Qualitative and quantitative studies of bacteria colonising *Picea sitchensis* litter. Soil Biol. Biochem. 10, pp303-7.

GOSZ, J.R., LIKENS, G.E. and BORMANN, F.H. (1973). Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecological Monographs 43, pp173-91.

GREEN, J.W. (1968). Tables of random permutations. Bull. 44, Comm. of Aust., Dept. National Development, Forestry and Timber Bureau, Canberra.

GREENLAND, D.J. and NYE, P.H. (1959). Increases in the carbon and nitrogen contents of tropical soil under natural fallows. J. Soil Sci. 10, pp284-99.

GYLLENBERG, H.G. and EKLUND, E. (1974). Bacteria. *In*: Biology of plant litter decomposition (Eds. C.H. Dickinson and G.J.F. Pugh). Academic Press, London and New York.

HARBORNE, J.B. (1973). Phytochemical methods. Chapman and Hall, London. p217.

HARLEY, J.L. (1971). Fungi in ecosystems. J. Appl. Ecol. 8(3), pp627-42.

HANNON, N.J. (1958). The status of nitrogen in the Hawkesbury sandstone soils and their plant communities in the Sydney district. II The distribution and circulation of nitrogen. Proc Linn. Soc. NSW 83, pp65-85.

HATCH, A.B. (1955). The influence of plant litter in the Jarrah forest soils of the Dwellingup Region of W.A. F.T.B. Leaflet 70. Canberra, 18pp.

HEATH, G.W., ARNOLD, M.K. and EDWARDS, C.A. (1966). Studies in leaf litter breakdown. I. Breakdown rates of leaves of different species. Pedobiologia Bd., 6, pp1-12.

HEIBERG, S.O. and CHANDLER, R.F.Jr. (1941). A revised nomenclature of forest humus layers for the NE United States. Soil Science 52, pp87-99.

HINGSTON, F.J., TURTON, A.G. and DIMMOCK, G.M. (1979). Nutrient distribution in karri (*Eucalyptus diversicolor* F.Muell.) ecosystems in southwest Western Australia. For. Ecol. Manag. 2, pp133-58.

HISSETT, R. and GRAY, T.R.G. (1973). Bacterial populations of litter and soil in a deciduous woodland. I. Qualitative studies. Rev. Ecol. Biol. Sol. 10, pp495-508.

HOUNAM, C.E. (1955). Determination of the end of the growing season. Australia, Bur. Meteorol., Meteorol. Studies 4, 16pp.

HOWARD, T.M. (1973). Studies in the ecology of *N. cunninghamii* Oerst. II. Phenology. Aust. J. Bot. 21, pp79-92.

HOWARD, T.M. (1975). Litter fauna in *Nothofagus cunninghamii* forests. Proc. Roy. Soc. Vic. 87(1-2), pp207-14.

HUDSON, H.J. (1968). The ecology of fungi on plant remains above the soil. New Phytol. 67, pp837-74.

HUTCHINGS, P.T. and OSWALD, K.M. (1975). Litterfall and litter accumulation in eucalypt forests of the Australian Capital Territory. Proc 3rd. Aust. Specialist Conf. Soil Biol., Adelaide.

JACKSON, W.D. (1965). Vegetation. *In*: Atlas of Tasmania, (Ed. J.L. Davies). Mercury Press Pty. Ltd., Hobart, Tasmania.

JACKSON, W.D. (1968). Fire and the Tasmanian Flora. *In*: Tasmanian Year Book, Government Printer Hobart, pp50-5.

JACKSON, W.D. (1968). Fire, air, water and earth - an elemental ecology of Tasmania. Proc Ecol. Soc. Aust. 3, pp9-16.

JACOBS, M.R. (1955). Growth Habits of the Eucalypts. Govt. Printer, Canberra.

JENNY, H., GESSEL, S.P. and BINGHAM, F.T. (1949). Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68, pp419-32.

JENSEN, H.L. (1930). Actinomycetes in Danish Soils. Soil Science 30, pp59-77.

JENSEN, V. (1974). Decomposition of Angiosperm tree leaf litter. *In*: Biology of plant litter decomposition (Eds. C.H. Dickinson and G.S.F. Pugh) Vol.1 Academic Press, London. pp69-104.

JONES, D.L. and CLEMENSHA, S.C. (1981). Australian Ferns and Fern Allies. A.H. and A.W. Reed P/L., Sydney, Aust.

KAWAHARA, T. and SATO, A. (1974). Decomposition of litter in forest floor. (1) Study on the decomposition rate by litter bag method. Jap. For. Soc. J. 56, pp258-261.

KENDRICK, W.B. (1959). The time factor in the decomposition of coniferous leaf litter. Can. J. Bot. 37, pp907-12.

KEVAN, D.K. (1962). Soil animals. Witherby, London.

KING, H.G.C. and HEATH, G.W. (1967). The chemical analysis of small samples of leaf material and the relationship between the disappearance and composition of leaves. Pedobiologia, Bd.7, pp192-97.

KIRITA, H. and HOZUMI, K. (1969). Loss of weight of leaf litter caught in litter trays during the period between successive collections - a proposed correction to account for the loss. Jap. Jour. Ecol. 19, pp243-46.

KITTREDGE, J. (1944). Estimation of the amount of foliage of trees and stands. J. For. 42, pp905-12.

KITTREDGE, J. (1948). Forest Influences. McGraw-Hill, New York.

KOZLOWSKI, T.T. (1976). Water supply and leaf shedding. *In*: Water deficits and plant growth Vol.IV. (Ed. T.J. Kozlowski) Academic Press, New York. pp191-205.

LANG, G.E. (1974). Litter dynamics in a mixed oak forest on the New Jersey Piedmont. Bull. Torrey Bot. Club. 101, pp277-86.

LAST, F.T. and DEIGHTON, F.C. (1965). The non-parasitic microflora on the surfaces of living leaves. Trans. Brit. Mycol. Soc. 48, pp83-99.

LAWRENCE, P.R. (1978). Provisional Site Index and Yield Tables for Eucalypts in Southern Tasmania. Forestry Commission, Hobart.

LEE, K.E. and BUTLER, J.H.A. (1977). Termites, soil, organic matter decomposition and nutrient cycling. Ecol. Bull. (Stockholm) 25, pp544-48.

LEE, K.E. and CORRELL, R.L. (1978). Litterfall and its relationship to nutrient cycling in a S.A. dry sclerophyll forest. Aust. J. Ecol. 3, pp243-52.

LEIGH, J.H., WILSON, A.D. and MULHAM, W.E. (1978). Seasonal variations in leaf fall and quality of the leaves of four Australian fodder trees. Aust. Rangelands J. 1, pp137-41.

LEITH, H. and WHITTAKER, R.L. (1975). *In*: Primary productivity of the Biosphere (Preface). Springer-Verlay: New York.

LOUB, W. (1962). Some European soil groups and their characteristic microflora. *In*: Progress in soil zoology (Ed. P.W. Murphy) Butterworths, London. pp311-18.

LUTZ, H.J. and CHANDLER, R.F.Jr. (1946). Forest Soils. John Wiley, New York.

MACAULEY, B.J. (1975) Biodegradation of litter in *Eucalyptus pauci-flora* communities. I. Techniques for comparing the effects of fungi and insects. Soil Biol. Biochem. 7, pp341-44.

MACAULEY, B.J. (1979). Biodegradation of litter in *E. pauciflora* communities. II. Fungal succession in fungicide and insecticide treated leaves. Soil Biol. Biochem. 11, pp175-79.

MACAULEY, B.J. and THROWER, L.B. (1966). Succession of fungi in leaf litter of *E. regnans*. Trans. Br. Mycol. Soc. 49(3), pp509-20.

MADDEN, J.L. (Unpub.). Senior Lecturer in Entomology, Department of Agricultural Science, University of Tasmania, Hobart. Pers.comm.

MAGGS, J. and PEARSON, C.J. (1977). Litter fall and litter layer decay in coastal scrub at Sydney, Australia. Oecologia 31, pp239-50.

MARTIN, J.P. (1950). Use of acid, rose bengal, and streptomycin in the plate method for estimating soil fungi. Soil Science, 69, pp215-32.

McARTHUR, A.G. (1962). Control burning in eucalypt forests. Leaflet 80, Forestry and Timber Bureau Australia, Commonwealth Govt. Printer, Canberra.

McARTHUR, A.G. (1967). Fire behaviour in eucalypt forests. Leaflet 107, Commonwealth of Australia, Forestry and Timber Bureau, Commmonwealth Govt. Printer, Canberra.

McCOLL, J.G. (1966). Accession and decomposition of litter in spotted gum forests. Aust. For. 30, pp191-98.

McCOLL, J.G. and HUMPHREYS, F.R. (1967). Relationships between some nutritional factors and the distribution of *Eucalyptus gummifera* and *E. maculata*. Ecology 48, pp766-71.

MEDWECKA-KORNAS, A. (1967)   Ecosystem studies in the beech forest and

    meadow in the Ojcow National Park. *In*: Studia Natururae, Ser. A.

    (Ed. A. Medwecka-Korna), Krakow, Wydawnictwo Nankowe, Zaklad

    Ochrony Przyrody. 213.

MEDWECKA-KORNAS, A. (1971). Plant   litter. *In*: Quantitative   Soil

    Ecology. IBP Handbook No.18 (Ed. J. Phillipson). Blackwell Sci.

    Public., Oxford.

MEENTEMEYER, V. (1978). Macroclimate and lignin control of litter

    decomposition rates. Ecology 59(3), pp465-72.

MUNSELL COLOR CO. (1954). Soil Color Charts. Baltimore.

NAGY, L.A. and MACAULEY, B.J. (1982). Eucalyptus leaf litter decomp-

    osition: effects of relative humidity and substrate moisture

    content. Soil Biol. Biochem 14, pp233-36.

NEF, L. (1957). État actuel des connaissances sur le role des animaux

    dans la décomposition des litières de foréts.   Agricultura,

    Louvain (Sér.2) 5(3), pp245-316.

NEILSEN, W.A. and PALZER, C. (1977). Analysis of foliar samples of

    healthy and dieback *Eucalyptus obliqua*. Aust. For. 40, pp219-22.

NETER, J.   and   WASSERMAN, W. (1974). Applied   linear   statistical

    models. Irwin Inc., Illinois.

NEWBOULD, P.J. (1967). Methods for estimating the primary production

    of forests. Blackwell Sci. Publ. Oxford and Edinburgh.

NICHOLSON, C.A. and LOVE, L.A. (1972). Fuel equilibrium studies; dry

    blackbutt type. For. Comm. NSW. Internal Report.

NICOLLS, K.D. and DIMMOCK, G.M. (1965). Soils. *In*: Atlas of Tasmania

    (Ed. J.L. Davies) Mercury Press, Hobart.

NORTHCOTE, K.H. (1971). *In*: A factual key for the recognition of

    Australian soils. 3rd. Ed. (Rellim. Glenside: South Australia).

REICHLE, D.E. (1971). Energy and nutrient metabolism of soil and litter invertebrates. *In*: Productivity of forest ecosystems (Ed. P. Duvigneaud) Unesco, Paris. pp465-77.

RICHARDS, B.N. and CHARLEY, J.L. (1977). Carbon and nitrogen flux through native forest floors. *In*: Nutrient cycling in indigenous forest ecosystems. CSIRO Division of Land Res. Management. pp65-81.

RODIN, L.E. and BASILEVIC, N.I. (1968). World distribution of plant biomass. Functioning of Terrestrial Ecosystems at the Primary Production Level. (Ed. F.E. Eckardt) Unesco, Paris. pp516.

ROGERS, R.W. and WESTMAN, W.E. (1977). Seasonal nutrient dynamics of litter in a subtropical eucalypt forest, North Stradbroke Island. Aust. J. Bot. 25, pp47-58.

ROGERS, R.W. and WESTMAN, W.E. (1981). Growth rhythms and productivity of a coastal subtropical eucalypt forest. Aust. J. Ecol. 6, pp85-98.

RUSCOE, Q.W. (1971a). Mycroflora of living and dead tree leaves of *Nothofagus truncata*. Trans. Br. Mycol. Soc. 56(3), pp463-74.

RUSCOE, Q.W. (1971b). The soil mycroflora of a hard Beech forest. N.Z. J. Sci. 14, pp554-67.

SATCHELL, J.E. (1967). Lumbricidae. *In*: Soil Biology (Eds. A. Burgess and F. Raw) Academic Press, London. pp259-322.

SATCHELL, J.E. (1974). Litter - interface of animate/inaminate matter. (In: Biology of plant litter decomposition, Vol.1. (Eds. C.H. Dickinson and G.J.F. Pugh) Academic Press, London and New York.

SATTOO, T. (1962). Notes on Kittredge's method of estimation of amount of leaves of forest stand. J. Jap. For. Soc. 44, pp267-72.

PENNYCOOK, S.R. (1974). Studies on the phylloplane microflora of unsprayed Dougherty apple tres. Ph.D. Thesis, University of Auckland, N.Z.

PHILLIPSON, J. (1961). Quantitative Soil Ecology. IBP. Handbook No.18, Blackwell Sci. Publ., Oxford.

PLOWMAN, K.P. (1979). Litter and soil fauna of two Australian subtropical forests. Aust. J. Ecol. 4, pp87-104.

PODGER, F.D., KILE, G.A., BIRD, T., TURNBULL, C.R.A. and McLEOD, D.E. (1980). An unexplained decline in some forests of *Eucalyptus obliqua* and *E. regnans* in Southern Tasmania. Aust. For. Res. 10, pp53-70.

PREECE, T.F. and DICKINSON, C.H. (1971). (Eds.). Ecology of leaf surface microorganisms. Academic Press, London and New York. 640pp.

PRESCOTT, J.A. (1942). The phase and amplitude of Australian mean monthly temperatures. Trans. Roy. Soc. S.Australia 66, pp46-9.

PRESCOTT, J.A. (1946). A climatic index. Nature 157, p555.

PRESCOTT, J.A. (1949). A climatic index for the leaching factor in soil formation. J. Soil Sci., 1, pp9-10.

PRESCOTT, J.A., COLLINS, J.A. and SHIRPURKAR, G.R. (1952). The comparative climatology of Australia and Argentina. Geograph. Rev. 42, pp118-33.

PRESSLAND, A.J. (1982). Litter production and decomposition from an overstorey of *Eucalyptus* spp. on two catchments in the New England region of New South Wales. Aust. J. Ecol. 7, pp171-80.

RAISON, R,J, (1980). A review of the role of fire in nutrient cycling in Australian native forests, and of methodology for studying the fire-nutrient interaction. Aust. J. Ecol. 5, pp15-21.

O'CONNELL, A.M., GROVE, T.S. and DIMMOCK, G.M. (1978). Nutrients in the litter of Jarrah forest soils. Aust. J. Ecol. 3, pp253-60.

OLSON, J.S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, pp322-31.

OLSON, J.S. and CROSSLEY, D.A. (1963). Tracer studies of the breakdown of forest litter. *In*: Radioecology. Proceedings of the first national symposium on radioecology, Colorado State University, Fort Collins, New York. Reinhold Publ. Corp. pp411-416.

OVINGTON, J.D. (1961). Some aspects of energy flow in plantations of *Pinus sylvestris*L. Ann. Bot. 25(97), pp12-20.

OVINGTON, J.D. and MADGEWICK, H.A.I. (1959). The growth and composition of natural stands of birch. 1. Dry matter production. Plant and Soil, 10, pp271-83.

OVINGTON, J.D. and MURRAY, G. (1964). Determination of acorn fall. Quant. J. For. 58(2), pp152-9.

OVINGTON, J.D. and NEWBOULD, P.J. General procedures for determining the organic production of woodlands. IBP Methodology Leaflet, Mimeograph by IBP Central Office.

PARK, G.N. (1977). Nutrient cycling and secondary succession in sub-alpine forests and woodlands. Ph.D. Thesis, Aust. Nat. Univ.

PEET, G.B. (1965). A fire danger rating and controlled burning guide for the northern jarrah forest of Western Australia. Bull. For. Dept. W.A. No.74.

PEET, G.B. (1971). Litter accumulation in Jarrah and Karri forests. Aust. For. 35, pp258-62.

PENFOLD, A.R. and WILLIS, J.L. (1961). The Eucalypts: Botany, Cultivation, and Utilisation. World Crops Books, Interscience Publ., London. p200.

SPECHT, R.L. and BROUWER, Y.M. (1975). Seasonal shoot growth of *Eucalyptus* spp. in the Brisbane area of Queensland (with notes on shoot growth and litterfall in other areas of Australia). Aust. J. Bot. 23, pp459-74.

SPECHT, R.L. and GROVES, R.H. (1966). A comparison of the phosphorous nutrition of Australian heath plants and introduced economic plants. Aust. J. Bot. 14, pp201-21.

STEPHENS, C.G. (1962). A manual of Australian soil. CSIRO Australia, Melbourne.

STOATE, T.N. (1958). Silvicultural and soils research. A. Karri silviculture. Rep. For. Dep. W.A. 25, pp25.

SPRINGETT, J.A. (1976a). Effect of prescribed burning on the soil fauna and on litter decomposition in W.A. forests. Aust. J. Ecol. 1, pp77-82.

SPRINGETT, J.A. (1976b). Effect of planting *P. pinaster* on populations of soil microarthropods and on litter decomposition at Gnangara, W.A. AUST. J. Ecol. 1, pp83-87.

SUFFLING, R. and SMITH, D.W. (1974). Litter decomposition studies using mesh bags: spillage inaccuracies and the effects of repeated artificial drying. Can. J. Bot. 52, pp2157-63.

TUKEY, H.B. (1971). Leaching of substances from plants. *In*: Ecology of leaf surface micro-organisms (Eds. T.F. Preece and C.H. Dickinson) Academic Press, London and New York. pp67-80.

VAN DER DRIFT, J. (1958). The soil fauna in an Oakwood forest with different types of humus formation. Paper Colloquium on Research Methods in Soil Zoology, Int. Soc. Soil Sci., Rothamstead, No.6.

VAN DER DRIFT, J. (1963). The disappearance of litter in mull and mor in connection with weather conditions and the activity of the macrofauna. *In*: Soil organisms (Ed. J. Doeksen and J. van der Drift) North Holland Pub. Co., Amsterdam. pp125-133.

SCOTT, D.R.M. (1955). Amount of chemical composition of the organic matter contributed by overstorey and understorey vegetation to forest soil. Yale School For. Bull. 62, 73pp.

SCURFIELD, G. (1961). The effects of temperature and day length on species of *Eucalyptus*. Aust. J. Bot. 9, pp36-56.

SHANKS, R.E. and OLSON, J.S. (1961). First-year breakdown of leaf litter in Southern Appalachian forests. Science, 134, pp194-5.

SINGH, J.S. and GUPTA, S.R. (1977). Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. 43, pp449-528.

SLATYER, R.O. (1974). Effects of water stress on plant morphogenesis. *In*: Plant morphogenesis as the basis for the scientific management of Rangelands. USDA. Misc. Publ. 1271, pp3-13.

SLATYER, R.O. and McILROY, I.C. (1961). Practical Microclimatology. Unesco, Paris.

SNEEUWJAGT, R.J. (1973). Measuring forest fuels. Res. Paper 9, Forests Dept. W.A.

SOUTHWOOD, T.R.E. (1977). Habitat, the template for ecological strategies. Br. Ecol. Soc. Presidential Address. J. Anim. Ecol. 46, pp337-65.

SOUTHWOOD, T.R.E. (1978). Ecological methods: with particular reference to the study of insect populations. The English Language Book Society and Chapman and Hall, Cambridge.

SPECHT, R.L. (1970). Vegetation. *In*: The Australian environment (G.W. Leeper, Ed.) 4th.ed. (rev.). CSIRO Aust. and Melbourne University Press, pp44-67.

SPECHT, R.L. (1981). Nutrient release from decomposing leaf litter of *Banksia ornata*, Dark Island Heathland, South Australia. Aust. J. Ecol. 6, pp59-63.

VAN LOON, A.P. (1969). Investigations into the effects of prescribed burns on young even-aged blackbutt. For. Comm. NSW Res. Note 23.

VAN LOON, A.P. (1970). All that litter is not old. A look at fuel accumulation in Blackbutt forests on the mid-north coast of NSW. A preliminary summary. Unpub. Report NSW Forestry Comm. Sydney.

VAN LOON, A.P. (1977). Bushland fuel quantities in the Blue Mountains, litter and understorey. For. Comm. NSW Res. Note No.33.

VOLLPRECHT, R. and WALKER, D.R. (1975). Determination of the length of the growing season. Aust. Meteor. Mag. 17, pp37–46.

WAKEFIELD, N.A. (1975). Ferns of Victoria and Tasmania (Rev. ed. by J.A. Willis). Field Naturalist's Club of Victoria.

WAKSMAN, S.A. and GERRETSEN, F.C. (1931). Influence of temperature and moisture upon the nature and extent of decomposition of plant residues by micro-organisms. Ecology 12(1), pp33–60.

WALKER, J. (1981). Fuel dynamics in Australian vegetation. *In*: Fire and the Australian Biota. (Ed. A.M. Gill, R.H. Groves, and I.R. Noble). Pub. Aust. Ac. Soc., pp101–27.

WANG, T.S.C., YANG, T. and CHUANG, T. (1967). Soil phenolic acids as plant growth inhibitors. Soil Sci. 103, pp239–46.

WATSON, G.W. (1977). Metabolism of forest floors. M.Sc. Thesis, University of New England.

WEARY, G.C. and MERRIAM, H.G. (1978). Litter composition in a red maple woodlot under natural conditions and under insecticide treatment. Ecology 59, pp180–184.

WEBB, L.J., TRACEY, J.G., WILLIAMS, W.T. and LANCE, G.N. (1968). The pattern of mineral return in leaf litter of three subtropical Australian forests. Aust. For. 33, pp99–110.

WEST, P.W. (1979). Date of onset of regrowth dieback and its relation to summer drought in eucalypt forest of Southern Tasmania. Annals Appl. Biol. 93, pp337–350.

WESTMAN, W.E. and ROGERS, R.W. (1977). Biomass and structure of a subtropical eucalypt forest, North Stradbroke Island. Aust. J. Bot. 25, pp171-91.

WHITTAKER, R.H. (1970). Communities and ecosystems, Macmillan, New York. pp162.

WILLIAMS, S.T. and GRAY, T.R.G. (1974). Decomposition of litter on the soil surface. *In*: Biology of plant litter decomposition (Ed. C.H. Dickinson and G.J.F. Pugh) Academic Press, London and New York. pp611-632.

WILM, H.G. (1946). The design and analysis of methods for sampling microclimatic factors. Amer. Stat. Assoc. J. 41, pp221-32.

WINKWORTH, R.E. (1973). Ecophysiology of mulga (*Acacia aneura*). Trop. Grassl. 7, pp43-8.

WITKAMP, M. (1963). Microbial populations of leaf litter in relation to environmental conditions and decomposition. Ecology 44(2), pp370-77.

WITKAMP, M. (1966). Decomposition of leaf litter in relation to environment, microflora, and microbial respiration. Ecology 47, pp194-201.

WITKAMP, M. (1971). Soils as components of ecosystems. Ann. Rev. Ecol. Syst. 2, pp85-110.

WITKAMP, M. and AUSMUS, B.S. (1975). Processes in decomposition and nutrient transfer in forest systems. *In*: The role of terrestrial and aquatic organisms in decomposition processes. (Eds. J.M. Anderson and A. Macfadyen) Blackwell, Oxford. pp375-96.

WITKAMP, M. and OLSON, J.S. (1963). Breakdown of confined and non-confined oak litter. Oikos 14(2), pp139-47.

WITKAMP, M. and VAN DER DRIFT, J. (1961). Breakdown of forest litter in relation to environmental factors. Pl. and Soil 15(4), pp295-311.

WOOD, T.G. (1970). The decomposition of litter in montane and alpine soils on Mt. Kosciusko, Australia. Nature 226, pp561-2.

WOOD, T.G. (1971). Effects of soil fauna on the decomposition of Eucalypt leaf litter in the Snowy Mountains. *In*: Organisms du sol et production primaire, C.R. 4 ème Coll. Int. Zool. Soc. (I.N.R.A., Ed.) Paris. pp349-58.

WOOD, T.G. (1974). Field investigations on the decomposition of leaves of *E. delegatensis* in relation to environmental factors. Pedobiologia Bd. 14, pp343-371.

WOOD, T.G. (1974). The distribution of earthworms (Megascolecidae) in relation to soils vegetation and altitude on the slopes of Mt. Kosciusko, Australia. J. Anim. Ecol. 43, pp87-106.

WOOD, T.G. (1976). The role of termites (Isoptera) in decomposition processes. *In*: The role of terrestrial and aguatic organisms in decomposition processes (Eds. J.M. Anderson and A. Macfadyen) Blackwell Sci. Publ. Oxford. pp145-68.

WOODS, P.V. and RAISON, R.J. (1982). An appraisal of techniques for the study of litter decomposition in eucalypt forests. Aust. J. Ecol. 7, pp215-25.

ZAR, J.H. (1974). Biostatistical analysis. Prentice Hall. Inc. New Jersey.

APPENDIX A.   SUPPLEMENTARY SITE DESCRIPTIVE DATA

APPENDIX B.   SUPPLEMENTARY ACCESSIONAL DATA

APPENDIX C.   SUPPLEMENTARY DATA RELATED TO DECOMPOSITION STUDIES

APPENDIX D.   MEDIA AND REAGENTS

APPENDIX E.   STATISTICAL ANALYSES

APPENDIX A.

Table 1.   Basal area (B.A.) m^2ha^{-1} and stem numbers per ha, per species, Site 1.

Species	Live B.A.	Dead B.A.	Live stems	Dead stems	Total B.A.	Total stems
E. *obliqua*	57.72	6.25	950	530	63.97	1480
P. *squameum*	14.007	2.29	2160	1090	16.30	3250
A. *melanoxylon*	5.99	2.91	390	430	8.90	820
M. *squarrosa*	12.44	1.05	1110	430	13.49	1540
P. *bicolor*	0.503	–	90	–	0.50	90
N. *cunninghamii*	3.19	0.036	180	20	3.23	200
A. *moschatum*	0.21	0.07	110	20	0.28	130
P. *aspleniifolius*	0.006	–	20	–	0.006	20
L. *scoparium*	0.043	0.02	10	10	0.063	20
A. *verticillata*	0.12	–	30	–	0.12	30
A. *glandulosus*	0.079	0.002	130	10	0.08	140
A. *biglandulosum*	1.14	0.13	430	50	1.27	480
C. *glauca*	0.12	0.071	40	30	0.19	70
C. *nitida*	0.014	–	20	–	0.014	20
T. *disticha*	0.003	–	20	–	0.003	20
E. *lucida*	1.29	0.76	450	130	2.04	580
D. *lanceolata*	0.033	–	50	–	0.033	50
Total	96.91	13.58	6190	2750	110.49	8940

Data are for all species present on the plot with DBHob greater than 1.0 cm.

APPENDIX A.

Table 2.   Basal area (B.A.) m^2ha^{-1} and stem numbers per ha, per species, Site 2.

Species	Live B.A.	Dead B.A.	Live stems	Dead stems	Total B.A.	Total stems
E. obliqua	3.22	0.017	60	10	3.24	70
P. squameum	0.47	0.013	80	10	0.49	90
A. melanoxylon	8.02	0.041	170	10	8.06	180
M. squarrosa	2.52	–	100	–	2.52	100
P. bicolor	0.12	0.0038	90	10	0.12	100
N. cunninghamii	39.49	0.55	810	90	4.0032	900
A. moschatum	6.43	0.33	1770	150	6.76	1920
P. aspleniifolius	3.97	0.23	210	20	4.19	230
A. glandulosus	1.81	0.23	1380	300	2.05	1680
C. glauca	0.43	0.052	160	40	0.48	200
C. nitida	0.059	0.036	30	10	0.095	40
T. distidia	0.044	0.0025	180	10	0.046	190
E. lucida	14.06	4.10	2510	390	18.17	2900
D. lanceolata	0.203	–	80	–	0.203	80
P. apetala	0.97	0.062	70	30	1.04	100
C. quadrifida	0.68	0.077	630	50	0.76	680
O. diversifolia	0.101	0.0025	90	10	0.104	100
O. argophylla	0.23	–	10	–	0.23	10
Total	82.83	5.74	8430	1140	88.57	9570

APPENDIX A.

Table 3.   Basal area (B.A.) m^2ha^{-1} and stem numbers per ha, per species, Site 3.

	Live B.A.	Dead B.A.	Live stems	Dead stems	Total B.A.	Total stems
E. obliqua	32.38	0.84	650	210	33.22	860
P. squameum	12.22	2.16	3480	1860	14.38	5340
A. melanoxylon	2.03	0.39	130	120	2.42	250
M. squarrosa	8.99	0.56	1520	500	9.56	2020
P. bicolor	0.0011	–	10	–	0.0011	10
N. cunninghamii	0.88	0.013	200	30	0.89	230
A. moschatum	0.033	0.0038	60	20	0.036	80
P. aspleniifolius	0.0026	–	20	–	0.0026	20
Leptospermum spp.	8.06	1.33	1000	470	9.38	1470
A. verticillata	0.73	0.305	160	140	1.0301	300
A. glandulosus	0.15	0.034	220	50	0.18	270
A. biglandulosum	0.28	0.0086	340	10	0.29	350
C. glauca	2.36	0.907	700	750	3.27	1450
C. nitida	0.07	0.029	120	50	0.101	170
T. distidia	0.0031	–	20	–	0.0031	20
E. lucida	0.62	0.094	360	160	0.72	520
D. lanceolata	0.0068	–	30	–	0.0068	30
B. marginata	0.96	0.0079	30	20	0.97	50
Total	69.78	6.68	9050	4390	76.46	13440

APPENDIX A.

Table 4.   Mean height and D.B.H.o.b. of selected dominants
per site.

Site No.	Species	DBHob (cm)	At (m)
1 (1915)	*Eucalyptus obliqua* " " " " " " " "	58.2 47.6 50.0 59.5 64.7	33.3 33.8 32.6 34.2 36.9
	MEAN	56.0	34.2
2	*Nothofagus cunninghamii* *Acacia melanoxylon* *Phyllocladus aspleniifolius*	49.7 42.8 48.2	23.9 21.4 24.1
	MEAN	46.9	23.1
3 (1915)	*Eucalyptus obliqua* " " " " " " " "	50.5 61.5 57.4 81.0 68.5	27.1 29.4 26.5 35.6 35.1
	MEAN	63.8	30.7
3 (1940)	*Eucalyptus obliqua* " " " " " " " "	29.5 39.0 26.6 22.5 32.1	24.8 28.9 22.9 22.5 22.1
	MEAN	29.9	24.2
4 (1940)	*Eucalyptus obliqua* *Eucalyptus nitida* " " " " " "	7.6 21.3 – 20.6 11.1	12.7 12.4 15.9 11.6 10.4
	MEAN	15.2	12.6

APPENDIX A.

Table 5.   Height layering of understorey species.

Species	Site 1	Site 2	Site 3	Site 4
Acacia melanoxylon	18.0	17.6	13.8	
Melaleuca squarrosa	16.4	14.3	15.0	3.5
Phebalium squameum	14.4	11.0	15.0	3.5
Eucryphia lucida	13.1	12.8	13.8	
Atherosperma moschatum	11.0	11.5	5.0	
Anodopetalum biglandulosum	6.5		5.0	
Pittosporum bicolor	5.5	3.5		
Nothofagus cunninghamii	3.5	16.7	13.8	
Cenarrhenes nitida	2.5		6.0	4.0
Anopterus glandulosus	2.0	5.0	3.0	
Phyllocladus aspleniifolius	3.0	16.6	4.0	
Drymis lanceolata	2.5	3.5	1.5	
Tropocarpa distida	2.0	4.0	1.5	
Cyathodes glauca		6.0	8.3	
Olearia argophylla		7.0		
Orites diversifolia		7.0		
Pomaderris apetala		12.8		
Coprosma quadrifida		5.0		
Leptospermum			16.2	6.5
Acacia verticillata			11.7	
Banksia marginata			11.7	5.0
Bauera rubioides				2.5
Oxylobium ellipticum				3.0
Agastachys odorata				3.0
Acacia riceana				3.0
Acacia mucronata				4.0

APPENDIX A.

Table 6.   Vegetation present on study sites.

Species	Common name	% Frequency Site no.			
		1	2	3	4
GYMNOSPERMAE					
PODACARPACEAE					
Phyllocladus aspleniifolius (Labill.) Hook.f.	Celery-Top Pine	20	48	35	–
ANGIOSPERMAE					
MONOCOTYLEDONEAE					
LILIACEAE					
Drymophila cyanocarpa R.Br.	Turquoise Berry	15	–	32	P
CYPERACEAE					
Gahnia grandis (Labill. ut *Scleria* sp., 1800) S.T. Blake	Cutting Grass	50	58	15	P
DICOTYLEDONEAE					
RANUNCULACEAE					
Clematis aristata R.Br. ex DC.	Tasmanian Clematis	–	2	–	–
WINTERACEAE					
Drimys lanceolata (Ooir.) Baill.	Mountain Pepper	20	15	2	–
PITTOSPORACEAE					
Pittosporum bicolor Hook.	Cheesewood, Tallow-wood	35	10	2	–
Billardiera longiflora Labill.	Climbing Blueberry	–	–	10	–
ELAEOCARPACEAE					
Aristotelia peduncularis (Labill.) Hook.f.	Heartberry	45	52	52	–
RUTACEAE					
Phebalium squameum (Labill.) Engler.	Lancewood, Satinwood	90	8	100	P
RHAMNACEAE					
Pomaderris apetala Labill.	Native Pear, Dogwood	–	12	–	–
MIMOSACEAE					
Acacia verticillata (L'Herit).Welld.	Prickly Moses	10	–	40	–
" *melanoxylon* R.Br.	Blackwood	80	32	28	–

APPENDIX A.

Table 6.   Vegetation present on study sites.   Cont'd /2.

Species	Common name	% Frequency Site no.			
		1	2	3	4
MIMOSACEAE Cont'd					
Acacia mucronata Willd. ex. H.Wendl.	Narrow-leafed Wattle	-	-	-	P
" riceana Henslow	Tasmanian Prickly Moses	-	-	-.	P
FABACEAE					
Oxylobium ellipticum (Labill.) R.Br.	Golden Rosemary	-	-	-	P
CUNONIACEAE					
Anodopetalum biglandulosum A. Cunn. ex. Endl.	Horizontal	65	-	28	-
Bauera rubioides Andr.	River Rose	-	-	-	P
ESCALLONIACEAE					
Anopterus glandulosus Labill.	Native Laurel	55	90	35	-
DROSERACEAE					
Drosera binata Labill.	Forked Sundew	-	-	-	P
EUCRYPHIACEAE					
Eucryphia lucida (Labill.) Baill.	Featherwood	90	98	45	-
HALORAGACEAE					
Gonocarpus tuicroides DC.	Germander Raspwort	-	-	-	P
MYRTACEAE					
Leptospermum scoparium J.R. & G Forst	Manuka	10	2	82	P
" nitidum Hook.f.	Giant Tea-tree	-	-	-	P
Melaleuca squarrosa Donn. ex. Sm.	Scented Paper-bark	88	12	92	P
" squamea Labill.	Mealy Honey-Myrtle	-	-	-	P
Eucalyptus obliqua L'Herit.	Stringybark, Messmate	88	8	80	P
" nitida Hook.f.	Smithton Peppermint	-	-	-	P
ARALIACEAE					
Pseudopanax gunnii Philipson	Native Ivy-Bush	-	-	8	-
RUBIACEAE					
Coprosma quadrifida (Labill.) Robinson	Native Currant	25	55	2	-

APPENDIX A.

Table 6.   Vegetation present on study sites.   Cont'd /3.

Species	Common name	% Frequency Site no.			
		1	2	3	4
ASTERACEAE					
Olearia argophylla F. Muell.	Musk	–	2	–	–
EPACRIDACEAE					
Cyathodes glauca Labill.	Cheeseberry	30	30	75	–
Trochocarpa disticha (R.Br.) Spreng	Spreading Trochocarpa	25	45	22	–
Prionotes cerenthoides (Labill.) R.Br.	Climbing Heath	–	–	8	–
Monotoca glauca (Labill.) Druce	Currant Wood	–	–	–	P
Sprengelia incarnata Sm	Pink Swamp Heath	–	–	–	P
APOCYNACEAE					
Parsonsia straminea (R.Br.) F. Muell.	Twining Silk-Pod	–	35	2	–
MONIMACEAE					
Atherosperma moschatum Labill.	Sassafrass	35	80	10	–
PROTEACEAE					
Cenarrhenes nitida Labill.	Native Plum	15	5	15	P
Banksia marginata Cav.	Honeysuckle	–	–	10	P
Orites diversifolia R.Br.	Varied Orites	–	18	–	–
Agastachys odorata R.Br.	White Waratah	–	–	–	P
THYMELACEAE					
Pimelea drupaceae Labill.	Bushman's Bootlace	10	–	–	–
FAGACEAE					
Nothofagus cunninghamii (Hook.) Oerst.	Myrtle	60	78	30	–
PTERIDOPHYTA					
HYMENOPHYLLACEAE					
Hymenophyllum flabellatum	Filmy Fern	15	8	–	–
DICKSONIACEAE					
Dicksonia antarctica Labill.	Soft Tree Fern	–	15	–	–

APPENDIX A.

Table 6.   Vegetation present on study sites.   Cont'd /4.

Species	Common name	% Frequency Site no.			
		1	2	3	4
GRAMMITIDACEAE					
Grammitis billardieri Willd.	Finger Fern	45	20	30	–
BLECHNACEAE					
Blechnum nudum (Labill.) Mett. ex.	Fishbone Water-Fern	–	22	–	–
" *wattsii* Tindale	Hard Water-Fern	100	98	90	–
DENNSTAEDTIACEAE					
Histiopteris incisa (Thunb.) J. Sm.	Bats-Wing Fern	15	–	–	–
Hypolepis rugosula (Labill.) J. Sm.	Ruddy Ground Fern	20	2	8	–
Pteridium esculentum (Forst.) Nakai	Austral Bracken	–	–	28	P
GLEICHENIACEAE					
Sticherus tener (R.Br.) Ching.	Silky Fan Fern	10	28	2	–
Gleichenia dicarpa R.Br.	Pouched Coral Fern	–	2	–	P
PSILOTACEAE					
Tmesipteris billardieri Endl.	Long Fork-Fern	–	2	–	–
LYCOPSIDA					
LYCOPODIACEAE					
Lycopodium deuterodensum Herter.	Bushy Club-moss	–	–	–	P

311

Table 7. Hastings Chalet meteorological data.

Accession period	No. days in accession	Collection no.	Max. T°C	Min. T°C	Mean max. T°C	Mean min. T°C	No. days temperature recorded	No. days per period with temperature				Total rainfall (mm)	Total evaporation (mm)	Hastings Mean windrun (km.24hr^{-1})
								≥10	≥15	≥20	≥25			
20.12.78														
31. 1.79	42	1	32.0	1.0	21.2	6.8	40	100	100	68	12	87.7		
14. 3.79	42	2	30.5	1.0	20.6	5.9	42	100	98	55	10	81.3		
25. 4.79	42	3	25.4	-2.8	17.8	3.5	37	100	78	27	3	152.1		
6. 6.79	42	4	17.5	-1.2	13.5	2.6	24	92	29	-	-	90.2		
18. 7.79	42	5	17.7	-1.7	13.1	3.3	41	93	20	-	-	77.2		
29. 8.79	42	6	17.2	-2.2	12.1	3.0	42	74	17	-	-	186.5		
10.10.79	42	7	20.4	-2.0	14.7	4.6	41	93	44	2	-	201.4		
21.11.79	42	8	27.8	2.3	17.8	6.8	41	100	78	22	5	106.9		
2. 1.80	42	9	27.1	3.0	18.4	8.4	41	100	80	32	7	165.7		
13. 2.80	42	10	28.3	1.8	18.3	9.1	42	100	88	29	5	170.2		
26. 3.80	42	11	33.0	3.7	18.8	8.6	42	100	90	29	2	67.0		
7. 5.80	40	12	28.2	1.4	17.5	7.2	37	100	62	30	8	150.9		
18. 6.80	43	13	21.5	-0.6	14.6	6.8	41	93	37	5	-	153.6		
30. 7.80	42	14	16.6	-2.0	12.5	3.8	42	93	12	-	-	137.1	25.2	25.2
10. 9.80	42	15	19.4	2.2	13.2	5.7	42	88	24	-	-	331.5	42.0	56.1
22.10.80	41	16	29.9	-0.6	16.2	6.5	39	95	54	18	3	228.2	61.5	78.5
3.12.80	42	17	29.0	2.1	18.0	7.2	42	100	74	29	10	168.2	92.4	55.5
14. 1.81	42	18	30.0	3.5	20.6	9.1	40	100	88	58	12	46.8	120.6	51.5
25. 2.81	42	19	37.5	3.2	22.6	10.8	41	100	100	66	24	43.0	134.4	53.4
7. 4.81	42	20	28.6	3.5	20.5	10.0	42	100	98	43	17	150.3	71.4	29.9

APPENDIX A.

Table 7.

Hastings Chalet meteorological data.   Cont'd.

Accession period	No. days in accession	Collection no.	Max. T°C	Min. T°C	Mean max. T°C	Mean min. T°C	No. days temperature recorded	No. days per period with temperature				Total rainfall (mm)	Total evapor- (mm)	Hastings Mean windrun (km.24hr^{-1})
								≥10	≥15	≥20	≥25			
21. 5.81	44	21	23.2	1.4	15.4	6.4	41	95	54	7	–	296.3	52.8	49.0
1. 7.81	41	22	16.0	–1.2	12.4	5.1	41	95	5	–	–	152.3	20.5	15.6
12. 8.81	42	23	16.3	–2.6	11.4	2.1	41	68	7	–	–	215.4	29.4	24.4
23. 9.81	42	24	21.1	0.6	14.1	5.2	41	93	37	2	–	218.1	58.8	62.1
4.11.81	42	25	30.7	1.4	17.0	6.4	41	100	66	20	5	182.3	109.2	70.3
16.12.81	42	26	28.2	2.0	17.5	7.8	42	100	69	24	5	142.3	113.4	55.5
27. 1.82	42	27	32.8	3.0	20.8	9.5	40	100	100	58	12	78.8	147.0	82.6
10. 3.82	42	28	38.9	4.8	20.7	9.4	42	100	98	45	10	116.3	138.6	70.0
21. 4.82	42	29	29.7	1.4	18.0	8.1	42	100	79	19	2	63.6	75.6	39.0

313

Table 1.

Litter accession, Site 1.   Bins.

All data represent the total weight (g) in 10 traps of total area 1.8098 m^2

Material type	Interval No. / Date	1 / 31.1.79	2 / 14.3.79	3 / 26.4.79	4 / 7.6.79	5 / 19.7.79	6 / 29.8.79	7 / 10.10.79	8 / 21.11.79	9 / 2.1.80	10 / 13.2.80	11 / 26.3.80	12 / 7.5.80	13 / 17.6.80	14 / 30.7.80
Leaves of:															
E. obliqua		160.600	126.500	38.640	8.320	8.958	2.804	6.336	17.826	44.380	97.274	99.204	39.327	31.372	12.214
E. nitida															
N. cunninghamii		1.582	3.987	1.511	0.630	0.741	0.169	0.223	0.354	0.508	1.960	2.652	1.442	0.216	0.311
A. moschatum			0.041	0.099	0.044					0.244	0.219		0.438		0.010
P. aspleniifolius		0.058									0.027				
A. melanoxylon		8.319	7.459	2.864	1.681	2.268	1.572	4.045	2.092	3.048	4.245	4.578	5.445	5.331	1.016
E. lucida		3.657	3.301	1.851	0.373	0.152	0.064	0.263	2.411	2.174	3.066	17.902	1.650	0.337	0.070
P. aoureum		14.185	18.761	9.515	3.927	6.073	3.078	3.781	2.992	5.909	8.594	12.003	9.691	8.159	7.278
B. marginata															
P. bicolor		0.253		0.173		0.132				0.044					
P. metala												0.011			
A. biglandulosum		1.164	1.820	3.204	0.206	0.152	0.052	0.110	0.172	0.017	0.591	0.259	0.794	0.430	0.012
A. glandulosus													0.099		
D. lanceolata															
O. argophylla												0.539			
C. nitida		0.032	0.065												
O. ellipticum															
Miscellaneous spp.		18.392	26.328	9.604	1.076	1.241	0.608	0.509	1.512	5.275	11.300	23.979	14.652	6.305	1.784
Dust-frass-floral parts		5.919	7.387	2.673	2.646	0.737	0.383	3.772	4.906	10.127	11.552	13.961	1.593	0.680	0.624
Bark and twigs		47.674	32.423	63.902	24.958	33.425	3.013	10.385	8.887	94.557	33.347	115.885	6.970	6.259	4.257
Ferns and mosses					0.002		0.001	0.002	0.003					0.006	0.002
Grasses			0.003	0.001								0.144			
TOTAL		261.847	228.040	134.043	43.867	53.879	11.744	29.765	41.344	167.099	173.880	291.799	82.378	59.594	27.573

N.B. Individual trap data available.

314

APPENDIX B.   Table 1.

Litter accession, Site. 1.   Cont'd.

| Material type | Interval No. | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 |
	Date	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	7.4.81	20.5.81	1.7.81	12.8.81	23.9.81	4.11.81	15.12.81	27.1.82	10.3.82	21.4.82
Leaves of:																
E. obliqua		10.150	27.495	26.449	56.795	170.983	74.634	N.A.	9.485	8.793	22.232	25.470	55.467	106.711	13.589	35.550
E. nitida																
N. cunninghamii		1.154	1.121	0.617	0.698											
A. moschatum		0.080	0.066		0.159											
P. asplenifolius			0.462													
A. melanoxylon		3.459	6.191	4.745	5.584											
E. lucida		0.443	1.052	3.469	3.104											
P. aquarium		6.611	9.307	9.025	6.847											
B. marginata																
P. bicolor		0.048	0.096	0.145	0.018											
P. apetala			0.039													
A. biglandulosum		0.259	0.161	0.205	0.832											
A. glandulosus			0.200		0.326											
D. lanceolata																
O. argophylla																
C. nitida																
O. ellipticum																
Miscellaneous spp.		2.977	4.731	5.936	10.401	19.224	14.689									
Dust-frass-floral parts		2.792	3.576	1.416	3.103											
Bark and twigs		24.713	124.369	9.390	18.607											
Ferns and mosses		0.001	0.040	1.302	0.001											
Grasses																
TOTAL		52.687	178.906	62.699	106.475	274.833	152.447	66.461	25.601	24.012	158.267	86.263	87.505	176.930	25.337	77.864
ALL OTHER MATERIAL						84.626	63.124	N.A.	16.116	15.219	136.035	60.793	32.038	70.219	11.748	42.314

N.B.   Sorting restricted from 14.1.81;   N.A. not available.

Litter accession, Site 2.   Bins.

All data represent the total weight (gm) in 10 devices (1.8098 m^2)

Material type	Interval No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Date	31.1.79	14.3.79	26.4.79	7.6.79	19.7.79	29.8.79	10.10.79	21.11.79	2.1.80	13.2.80	26.3.80	7.5.80	17.6.80	30.7.80	10.9.80
Leaves of:																
E. obliqua		19.790	3.750	6.010	2.950	1.495	0.840	2.323	3.043	11.654	28.565	9.756	3.150	1.891	2.192	2.275
E. nitida																
N. cunninghamii		25.861	73.718	62.950	16.943	4.128	1.551	5.207	11.546	15.583	21.389	68.522	40.791	9.163	3.536	4.915
A. moschatum		4.042	4.015	4.430	0.903	0.769	0.212	0.674	0.428	2.387	2.780	4.837	1.569	1.484	0.758	1.389
P. aspleniifolius		4.077	6.342	5.770	0.929	0.307	0.232		0.044	0.890	2.965	2.295	2.275	1.348	0.459	0.582
A. melanoxylon		9.328	10.634	6.213	2.034	4.138	2.402	8.639	5.274	10.190	7.591	13.211	3.969	8.846	1.821	4.021
E. lucida		25.118	9.224	16.318	4.635	1.438	0.440	1.536	34.267	15.777	24.898	20.061	9.118	2.983	1.223	1.004
P. squameum		0.505	0.094	0.073	0.667	0.722	0.335	0.741	0.356	0.273	0.510	0.090	1.985		0.221	1.192
B. marginata																
P. bicolor		1.484	0.057	0.083				0.112	0.039		0.106					
P. oxelata		1.230	1.579	0.632	0.132	0.351		0.995	1.182	3.108	3.602	1.023	0.281	2.071	0.194	0.147
A. biglandulosum			0.059					0.046			0.501		0.028	0.023		
A. glandulosus		1.496	4.068	2.278	1.503			0.491	0.132	0.160	2.454	3.115	1.299	0.990	0.443	1.086	0.441
D. lanceolata		1.417														
O. argophylla				0.266					0.756	1.045	0.333	0.132		0.692		
C. nitida		0.154	0.257	0.501							0.397					
O. ellipticum																
Miscellaneous spp.		8.140	4.139	2.739	1.170	1.096	0.582	0.860	2.516	6.810	8.603	3.815	1.737	0.625	1.147	1.651
Dust-frass-floral parts		8.225	3.755	7.976	3.734	4.325	1.307	10.320	16.220	16.787	28.667	19.908	2.303	1.457	1.609	5.999
Bark and twigs		21.747	4.325	7.759	13.701	17.709	5.614	31.729	19.264	46.698	22.831	43.222	7.002	8.632	1.404	21.659
Ferns and mosses		0.509	0.011	0.464	0.022	0.017	0.094	1.674	0.110	0.220	0.004	0.174	0.306	0.006	0.004	0.118
Grasses					0.004	0.044	0.021							0.069		
TOTAL		133.121	126.026	124.457	49.322	36.539	14.121	64.988	95.205	135.876	156.857	188.345	75.404	39.733	15.654	45.423

N.B. Individual trap data available.

316

APPENDIX B.   Table 2.

Litter accession, Site 2. Bins.   Cont'd.

Material type	Interval No. Date	16 22.10.80	17 3.12.80	18 14.1.81	19 25.2.81	20 7.4.81	21 20.5.81	22 1.7.81	23 12.8.81	24 23.9.81	25 4.11.81	26 15.12.81	27 27.1.82	28 10.3.82	29 21.4.82
Leaves of:															
E. obliqua		15.238	3.888	12.772	38.603	5.384	N.A.	1.115	1.303	5.050	3.593	13.429	23.509	2.058	0.640
E. nitida															
N. cunninghamii		10.200	6.144	17.140											
A. moschatum		1.930	0.872	1.989											
P. asplenifolius		0.830	0.408	3.490											
A. melanoxylon		5.326	9.332	34.212											
E. lucida		9.944	17.747	20.503											
P. aqueum		0.689	0.031	0.858											
B. marginata															
P. bicolor															
P. apetala		0.274	2.902	2.844											
A. biglandulosum															
A. glandulosus			0.606	1.985											
D. lanceolata			0.345	0.317											
O. argophylla		0.219	0.252												
C. nitida		0.112		0.373											
O. ellipticum															
Miscellaneous spp.		2.394	2.067	8.215	5.439	15.215	N.A.								
Dust-frass-floral parts		12.008	3.533	7.432											
Bark and twigs		167.455	11.082	7.333											
Ferns and mosses		0.596	0.027	0.025											
Grasses		-	0.040												
TOTAL		227.215	59.276	119.486	175.674	155.137	117.247	40.334	22.572	133.553	99.580	94.411	133.061	11.278	9.602
UNSORTED MATERIAL					131.632	134.538	N.A.	39.219	21.269	128.503	95.987	80.982	109.552	9.219	8.961

317

APPENDIX B.

Table 3.   Litter accession, Site 2.   Ground Traps.

All data represent total weight (gm) in 10 traps (1.8098 m^2)

Material type	Interval No. / Date	1 / 31.1.79	2 / 14.3.79	3 / 26.4.79	4 / 7.6.79	5 / 19.7.79	6 / 29.8.79	7 / 10.10.79	8 / 21.11.79	9 / 2.1.80	10 / 13.2.80	11 / 26.3.80	12 / 7.5.80	13 / 17.6.80	14 / 30.7.80	15 / 20.9.80
Leaves of:																
E. obliqua		21.450	15.590	5.690	0.478	0.703	0.620	1.105	0.791	11.946	17.854	25.230	3.508	4.826	2.444	3.040
E. nitida																
N. cunninghamii		21.169	58.880	83.600	22.604	6.504	2.384	5.077	15.518	13.810	29.348	51.215	41.833	9.723	4.573	4.739
A. moschatum		2.686	2.783	3.141	2.533	0.841	0.398	0.241	0.489	1.075	1.428	3.914	1.193	1.412	0.418	0.905
P. aspleniifolium		2.480	5.336	4.411	0.717	0.820	0.333	0.334	0.026	1.274	1.877	7.071	2.254	2.158	0.269	0.783
A. melanoxylon		12.776	7.438	5.532	3.443	2.128	2.206	5.323	2.185	6.213	12.732	9.261	4.001	4.222	2.276	2.443
E. lucida		24.066	18.503	16.378	5.074	2.014	0.789	0.595	59.900	18.859	28.428	17.001	10.342	3.283	1.181	1.134
P. acuminem		1.991	1.675	1.080	0.385	0.670	0.253	0.135	0.147	0.530	0.942	1.428	0.773	0.696	0.359	0.626
B. marginata																
P. bicolor		0.266					0.161				2.046	0.090				
P. axetala		6.800	2.989	2.215	1.368	1.149	1.319	0.696	4.404	3.103	5.111	2.089	1.557	0.816	0.171	0.376
A. biglandulosum			0.044								0.010					
A. glandulosus		2.150	1.901	0.960		0.799		0.609		0.309	2.507	1.555	0.844	0.629	0.484	0.783
D. lanceolata		0.048	0.039													
O. argophylla		0.105														
C. nitida		0.218	0.575				0.140									
O. elliptica																
Miscellaneous spp.		6.097	6.690	2.148	0.756	1.030	0.311	0.360	1.582	4.560	4.549	6.881	1.956	1.159	0.500	0.831
Dust-frass-floral parts		8.054	8.074	7.276	1.891	3.101	0.788	7.492	18.059	15.720	27.820	17.841	3.152	1.636	1.605	3.845
Bark and twigs		26.297	7.944	9.550	16.555	21.859	4.154	12.229	41.280	41.274	26.771	69.184	8.940	2.893	15.570	9.541
Fern and mosses		0.075	0.030	0.499	0.064	2.660	0.007	0.189	0.088	0.308	0.163	0.139	0.205	0.048	0.006	0.029
Grasses			0.435		0.272	0.014	0.291	0.369			0.194	0.226	0.128	0.173	0.001		-
TOTAL		136.731	138.929	142.482	56.140	44.528	14.154	34.754	144.469	119.294	161.812	214.096	80.731	33.502	29.856	29.075

N.B. Individual trap data available.

318

APPENDIX B.   Table 3.

Litter accession, Site 2.   Ground Traps.   Cont'd.

Material type	Interval No. Date	16 22.10.80	17 3.12.80	18 14.1.81	19 25.2.81	20 7.4.81	21 20.5.81	22 1.7.81	23 12.8.81	24 23.9.81	25 4.11.81	26 15.12.81	27 27.1.82	28 10.3.82	29 21.4.82
Leaves of:															
E. obliqua		11.282	17.605	35.919	'25.923	11.122	N.A.	1.872	1.447	12.462	5.766	4.824	21.830	25.249	6.793
E. nitida															
N. cunninghamii		8.617	5.839	15.949											
A. moschatum		1.336	1.221	1.788											
P. aspleniifolius		2.785	0.567	2.097											
A. melanoxylon		5.087	5.899	16.134											
E. lucida		7.913	22.598	24.309											
P. aquareum		0.928	0.951	0.499											
B. marginata															
P. bicolor															
P. tasmania		1.871	2.465	5.245											
A. biglandulosum															
A. glandulosum		0.079	0.714	3.367											
D. lanceolata															
O. argophylla				0.325											
C. nitida			0.122												
O. ellipticum															
Miscellaneous spp.		2.115	2.865	6.307	15.866	13.678	N.A.								
Dust-grass-floral parts		11.601	4.868	10.257											
Bark and twigs		118.974	24.671	18.528											
Ferns and mosses		0.297	0.221	0.249											
Grasses		0.600	0.050												
TOTAL		173.685	90.706	140.973	169.004	186.197	109.943	41.004	19.880	145.963	117.579	87.408	130.901	153.358	114.164
UNSORTED MATERIAL					127.215	161.397		39.132	18.433	133.501	111.813	82.584	109.071	128.109	107.371

APPENDIX B.

Table 4.   Litter accession, Site 3.   Bins.

All data represent total weight (gm) in 10 traps (1.8098 m^2)

Material type	Interval No. Date	1 31.1.79	2 14.3.79	3 26.4.79	4 7.6.79	5 19.7.79	6 29.8.79	7 10.10.79	8 32.11.79	9 2.1.80	10 13.2.80	11 26.3.80	12 7.5.80	13 17.6.80	14 30.7.80	15 10.9.80
Leaves of:																
E. obliqua		126.195	97.446	28.148	12.342	7.095	3.889	4.115	16.565	45.084	78.049	80.546	36.477	25.174	14.025	12.790
E. nitida																
N. cunninghamii		3.325	2.298	0.766	0.474	0.098	0.031	0.008	0.204	0.121	0.374	0.733	0.846	0.282	0.104	0.182
A. moschatum		0.010			0.009					0.029	0.001	0.066				
P. aspleniifolius								0.051								0.054
A. melanoxylon		2.580	0.532	1.331	0.247	0.329	0.882	0.091	0.447	0.243	1.014	3.752	1.069	3.570	0.672	1.652
E. lucida		1.209	1.368	0.496	0.283	0.087	0.035	0.064	0.501	0.999	2.536	0.762	0.254	0.093	0.061	0.034
P. aquaticum		11.640	13.585	11.207	3.695	4.830	3.030	3.508	2.921	7.837	7.584	15.030	9.302	7.615	5.870	11.302
B. marginata		0.333	1.746	0.632	0.028	0.285	0.064	0.080	0.006	0.475	1.535	1.232	0.171	0.158	0.270	0.223
P. bicolor																
P. apetala																
A. biglandulosum		0.073	0.250	2.664	0.074	0.069	0.004			0.023	0.012		0.052		0.086	0.047
A. glandulosus		0.265									0.207					
D. lanceolata														0.081		
O. argophylla																
C. nitida										0.606	0.071					
O. ellipticum																
Miscellaneous spp.		35.676	25.627	12.347	2.077	2.169	2.357	1.866	6.838	15.543	28.824	20.585	14.009	7.795	2.690	3.927
Dust-frass-floral parts		14.774	6.205	2.766	0.510	0.942	1.901	4.238	3.732	25.220	12.730	13.348	2.511	2.033	1.218	8.921
Bark and twigs		118.612	10.619	16.311	52.402	15.954	5.863	9.949	12.532	86.984	39.116	86.050	6.691	7.437	4.708	33.071
Ferns and mosses				0.005			0.002		0.041			0.001	0.002			
Grasses				0.002						0.002	0.019			0.001		0.004
TOTAL		314.692	159.676	76.684	72.132	31.858	18.058	23.970	43.789	183.183	172.054	222.106	71.383	54.238	29.971	72.207

N.B. Individual trap data available.

APPENDIX B.   Table 4.

Litter accession, Site 3.   Bins.   Cont'd.

Material type	Interval No. Date	16 22.10.80	17 3.12.80	18 14.1.81	19 25.2.81	20 7.4.81	21 20.5.81	22 1.7.81	23 12.8.81	24 23.9.81	25 4.11.81	26 15.12.81	27 27.1.82	28 10.3.82	29 21.4.82
Leaves of:															
E. obliqua		33.702	16.914	57.023	103.875	42.279	N.A.	11.470	5.938	22.008	17.555	40.189	89.602	90.946	26.493
E. nitida															
N. cunninghamii		0.378	0.147	0.314											
A. moschatum															
P. aspleniifolius															
A. melanoxylon		0.436	0.128	2.560											
E. lucida		0.624	1.168	0.700											
P. squameum		8.031	8.231	8.583											
B. marginata		0.073	0.138	1.111											
P. bicolor															
P. coetala															
A. biglandulosum			0.011												
A. glandulosus															
D. lanceolata															
O. argophylla															
C. nitida				0.148											
O. ellipticum															
Miscellaneous spp.		13.085	12.355	23.243	17.276	8.248	N.A.								
Dust-frass-floral parts		7.562	2.049	6.668											
Bark and twigs		164.422	5.644	12.117											
Ferns and mosses		0.002	0.002	0.001											
Grasses															
TOTAL		228.315	46.787	112.868	207.007	111.392	69.087	25.704	20.002	131.017	78.770	80.106	165.139	188.320	67.413
UNSORTED MATERIAL					85.856	55.865	N.A.	14.234	14.064	109.009	61.215	39.917	75.537	97.374	40.920

APPENDIX B.

Table 5.   Litter accession, Site 4.   Bins – raised.

All data represent total weight (g) in 10 bins (1.8098 m^2)

Material type / Interval No. Date	1 31.1.79	2 14.3.79	3 26.4.79	4 7.6.79	5 19.7.79	6 29.8.79	7 10.10.79	8 21.11.79	9 2.1.80	10 13.2.80	11 26.3.80	12 7.5.80	13 17.6.80	14 30.7.80	15 10.9.80	16 22.10.80
Leaves of:																
E. obliqua		1.618		1.044	1.007				0.461		1.469	0.443	1.610	0.239		
E. nitida	31.978	25.026	5.445	2.617	4.095	1.754	1.159	6.348	6.402	17.441	11.969	10.894	8.688	4.662	5.482	3.180
K. cunninghamii																
A. moschatum																
P. aspleniifolius																
A. melanoxylon																
E. lucida																
P. squameus	0.015		0.122					0.009	0.172	0.027	0.089	0.050	0.140			0.412
B. marginata	0.379	0.315	0.294	0.072	0.063	0.033	0.049	0.050	0.227	1.241	1.336	0.332	0.149	0.012	0.041	0.403
P. bicolor																
P. apetala																
A. biglandulosum																
A. glandulosus																
D. lanceolata																
O. argophylla																
C. nitida																
u. ellipticum					0.001								0.015			0.049
Miscellaneous spp.	3.981	4.266	2.103	0.604	0.558	0.260	0.590	1.520	2.082	4.590	8.874	4.619	1.002	0.310	0.637	1.565
Dust-frass-floral parts	3.349	0.392	0.289	0.366	0.192	0.004	0.103	1.192	0.775	1.938	3.597	0.187	0.268	0.191	0.809	2.218
Bark and twigs	6.162	2.489	1.828	1.126	1.303	0.253	0.514	0.983	2.646	5.426	19.632	0.989	1.037	0.801	1.149	9.830
Ferns and mosses														0.001		
Grasses		0.006	0.001	0.001	0.003			0.004			0.006		0.002		0.019	
TOTAL	46.132	34.173	10.082	5.830	7.222	2.304	2.436	10.106	12.765	30.686	46.972	17.514	12.911	6.216	8.137	17.657

N.B. Individual trap data available.

Bins discontinued from 22.10.80.

APPENDIX B.

Table 6.   Litter accession, Site 4.   Ground traps.

All data represent total weight (g) in 10 traps (1.8098 m^2)

Material type	Interval No. Date	1 31.1.79	2 14.3.79	3 26.4.79	4 7.6.79	5 19.7.79	6 29.8.79	7 10.10.79	8 21.11.79	9 2.1.80	10 13.2.80	11 26.3.80	12 7.5.80	13 17.6.80	14 30.7.80	15 10.9.80
Leaves of:																
E. obliqua			1.088	0.520	1.193	0.427			0.219			1.118			0.551	0.882
E. nitida		31.335	25.436	8.674	3.254	4.739	2.080	3.119	4.703	11.982	16.371	14.099	11.685	8.161	5.619	8.781
N. cunninghamii																
A. rosolarum																
P. aspleniifolius																
A. melanoxylon		0.104								0.013						
E. lucida																
P. aquaneum		0.393	0.248	0.027			0.078		0.013	0.131	0.574	0.981	0.260	0.105	0.109	
B. marginata		6.124	9.157	6.872	1.331	1.282	0.630	0.437	0.483	2.001	7.737	10.403	3.967	2.940	1.024	1.246
P. bicolor																
P. apetala																
A. biglandulosum																
A. glandulosus																
D. lanceolata																
O. argophylla																
C. nitida					0.008											
O. ellipticum			0.555	0.635	0.244	0.303	0.200	0.178	0.586	1.765	2.319	1.260	0.370	0.232	0.077	0.233
Miscellaneous spp.		42.282	19.312	15.180	3.996	4.274	3.364	2.543	6.384	17.661	24.203	22.634	13.618	5.052	1.734	3.364
Dust-frass-floral parts		13.813	2.061	10.180	0.438	0.476	0.535	0.765	5.460	8.785	11.593	8.248	1.549	2.145	0.524	0.850
Bark and twigs		58.194	16.172	10.680	2.613	6.274	3.178	2.716	2.946	11.882	9.194	12.685	3.021	2.142	1.714	5.465
Ferns and mosses		1.883	0.415	0.641	0.203	0.056	0.178	0.123	0.255	0.651	0.278	0.510	0.107	0.043	0.020	0.382
Grasses			0.319	0.355	0.197	0.082	0.526	0.203	0.195	1.307	0.382	0.555	0.064		0.003	0.152
TOTAL		154.128	74.763	53.764	13.477	17.913	10.769	10.084	21.154	56.178	72.651	72.493	34.641	20.824	11.381	21.375

N.B. Individual trap data available.

323

APPENDIX B.   Table 6.

Litter accession, Site 4.   Ground Traps.   Cont'd.

| Material type | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 |
Date	22.10.80	3.12.80	14.1.81	25.2.81	7.4.81	20.5.81	1.7.81	12.8.81	23.9.81	4.11.81	15.12.81	27.1.82	10.3.82	21.4.82
Leaves of:														
E. obliqua	2.091			0.647	0.263	N.A.			0.483	0.513		DESTROYED BY FIRE		
E. nitida	8.496	6.650	15.297	25.060	11.363	N.A.	2.924	2.397	4.314	6.816				
N. cunninghamii														
A. moschatum														
P. aspleniifolius														
A. melanoxylon														
E. lucida														
P. squameum	0.259	0.443	0.293											
B. marginata	2.469	1.503	4.468											
P. bicolor														
P. aoetala														
A. biglandulosum														
A. glandulosus														
D. lanceolata														
O. argophylla														
C. nitida		0.302												
O. ellipticum	1.002	0.868	1.790											
Miscellaneous spp.	11.086	11.018	19.882	3.578	4.314	N.A.								
Dust-frass-floral parts	5.691	3.702	4.964											
Bark and twigs	20.659	4.271	7.179											
Ferns and mosses	1.543	0.129	0.339											
Grasses	0.893	0.170	0.222											
TOTAL	53.989	29.056	54.665	76.148	55.017	30.618	11.468	6.579	36.151	28.031	36.151	DESTROYED BY FIRE		
UNSORTED MATERIAL				46.863	39.077	N.A.	8.544	4.182	28.822	23.234	28.822			

Table 1. Site 3. Double traps. Litter input and accumulation per trap.
Actual and calculated values 6-48 weeks.

Trap no.	22.11.79 - 6 wks			2.1.80 - 12 wks			13.2.80 - 18 wks			26.3.80 - 24 wks			7.5.80 - 30 wks			18.6.80 - 36 wks			30.7.80 - 42 wks			10.9.80 - 48 wks		
	Actual		Calc.	Actual		Calc.	Actual		Calc.	Actual		Calc.	Actual		Calc.	Actual		Calc.	Actual		Calc.	Actual		Calc.
	Wg	Wo	Wo	Wg	Wo	Wo	Wg	Wo	Wo	Wg	Wo	Wo	Wg	Wo	Wo	Wg	Wo	Wo	Wg	Wo	Wo	Wg	Wo	Wo
71 A	23.7		8.5	22.9		17.9	29.7		22.8	42.2		34.0	19.7		7.7	24.1		10.1	12.7		4.1	36.5		15.8
B	*			14.2		11.1	44.9		32.4	66.0		51.7	228.8		94.3	273.9		88.4	342.4		88.5	333.4		89.4
C	22.6	8.1		14.3	11.2		35.6	27.3		43.7	35.2		22.2	8.7		13.4	5.6		13.4	5.0		26.3	11.4	
D	*			29.1	22.8		71.0	51.2		70.8	55.5		247.1	101.8		95.7	30.9		357.9	92.5		271.6	72.8	
72 A	7.5		2.2	8.5		6.6	16.9		12.1	24.3		19.7	16.7		6.7	18.7		8.2	10.2		3.4	20.9		7.9
B				4.4		3.1	15.0		10.8	35.2		27.3	222.0		80.7	251.0		81.6	184.6		53.0	183.5		49.7
C	9.1	2.7		22.8	17.7		22.0	15.7		27.6	22.4		25.0	10.0		16.1	7.1		9.5	3.2		11.7	4.4	
D				49.1	34.9		31.2	22.4		55.1	42.7		146.0	53.1		138.8	45.1		159.2	45.7		198.8	53.8	
73 A	11.9		5.8	22.5		18.3	25.5		19.1	31.0		25.2	21.8		8.5	13.8		5.6	6.9		2.2	40.3		14.8
B				5.5		4.4	37.2		28.6	66.9		49.0	180.0		74.1	220.9		66.3	251.2		69.7	243.4		81.4
C	8.4	4.1		9.6	7.8		19.6	14.7		24.7	20.1		17.6	6.9		14.7	6.0		12.5	3.9		21.2	7.8	
D				35.9	28.6		27.8	21.4		92.8	68.0		238.8	98.3		143.5	43.1		242.1	67.2		263.0	88.0	
74 A	13.6		4.0	14.5		11.3	30.3		22.6	28.2		22.7	22.4		8.7	16.3		5.5	13.4		4.1	46.5		18.3
B				7.8		5.9	45.1		29.3	74.6		55.9	149.7		52.9	203.6		55.6	230.8		60.0	238.2		60.6
C	13.2	3.9		19.2	14.9		19.0	14.2		31.1	24.6		21.0	8.2		14.0	4.7		13.7	4.2		36.5	14.4	
D				42.6	32.4		77.2	50.2		100.3	75.1		162.3	57.3		287.1	78.4		303.3	78.9		361.6	97.1	
75 A	15.8		4.2	14.2		10.8	28.6		21.8	39.0		31.7	21.4		8.8	15.0		6.6	11.4		4.1	26.9		8.6
B				7.7		5.8	34.6		25.8	70.3		53.4	174.2		60.8	220.6		81.9	262.0		63.2	257.0		81.2
C	18.1	4.8		8.9	6.8		21.5	16.4		25.1	20.4		18.8	7.7		2.5	1.1		15.1	5.4		33.4	10.7	
D				30.2	22.9		22.4	16.7		86.7	65.8		123.1	43.0		139.2	51.7		175.8	42.4		266.7	84.3	

Wg = green weight (g)

Wo = oven-dried weight (70°C,g)

Calc. = calculated viz.

$$\text{Calc. Wo A} = \frac{Wg\ A \times Wo\ C}{Wg\ C}$$

* = no accumulation for this period

APPENDIX C.

Table 1.

Site 3.   Double traps.   Litter input and accumulation per trap.   Cont'd.
Actual and calculated values 54-96 weeks.

Trap No.	22.10.80 - 54 wks Actual Wg	Wo	Calc. Wo	3.12.80 - 60 wks Actual Wg	Wo	Calc. Wo	14.1.81 - 66 wks Actual Wg	Wo	Calc. Wo	25.2.81 - 72 wks Actual Wg	Wo	Calc. Wo	8.4.81 - 78 wks Actual Wg	Wo	Calc. Wo	20.5.81 - 84 wks Actual Wg	Wo	Calc. Wo	1.7.81 - 90 wks Actual Wg	Wo	Calc. Wo	12.8.81 - 96 wks Actual Wg	Wo	Calc. Wo
71 A	36.7		29.8	9.7		6.5	17.6		15.0	57.7		25.7	51.1		18.9	22.7		8.0	16.7		4.8	7.0	2.5	2.3
B	297.1		142.0	365.3		155.9	246.6		160.2	272.3		202.6	605.0		188.5	705.6		331.7	795.3		186.6	759.4	173.6	167.5
C	42.3	34.3		8.1	5.4		17.5	14.9		56.1	25.0		33.5	12.4		28.5	10.1		6.3	1.8		5.4	1.6	
D	290.2	138.7		195.6	83.5		196.9	127.9		278.5	207.2		571.1	177.9		586.1	275.5		619.4	145.3		732.1	161.5	
72 A	20.7		15.3	7.7		4.8	11.3		9.3	42.7		19.6	20.4		7.5	21.6		7.5	14.9		4.7	3.7	1.3	1.4
B	146.5		84.2	193.1		90.8	121.4		98.7	148.1		119.5	338.0		98.9	379.0		131.1	440.6		104.6	438.3	93.0	96.9
C	17.3	12.8		8.3	5.2		8.0	6.6		36.6	16.8		30.2	11.1		17.1	5.9		6.4	2.1		6.8	2.5	
D	77.8	44.7		261.9	123.2		249.7	203.1		310.2	250.2		278.5	81.5		509.7	176.3		526.3	124.9		550.7	121.7	
73 A	27.3		22.0	7.6		4.8	18.4		15.5	27.3		16.9	24.2		10.4	18.9		7.1	9.4		1.7	4.8	1.4	1.5
B	226.7		112.9	270.9		117.6	186.7		133.9	189.2		128.2	449.6		143.7	513.6		157.6	591.6		147.4	562.7	115.1	137.4
C	42.3	34.1		6.6	4.2		11.9	10.0		37.1	23.0		21.1	9.1		20.3	7.6		7.6	1.4		10.4	3.2	
D	197.6	98.4		158.7	68.9		161.2	115.6		146.5	99.3		328.9	105.1		425.5	130.6		685.6	170.8		538.9	131.6	
74 A	34.1		25.0	15.3		7.8	13.6		12.2	50.8		24.7	44.4		12.7	23.9		8.2	10.0		3.1	5.3	1.3	1.4
B	241.4		87.2	303.2		110.5	239.4		108.0	252.6		170.0	497.7		186.0	598.3		136.6	660.7		142.1	636.7	134.4	135.0
C	39.8	29.2		11.7	6.0		11.4	10.2		41.1	20.0		59.2	16.9		30.2	10.3		24.5	7.6		11.4	3.0	
D	312.2	112.8		230.7	84.1		191.8	144.2		209.9	141.3		536.9	200.7		403.0	92.0		818.6	176.1		909.6	197.9	
75 A	57.0		43.1	8.0		4.7	10.8		9.7	40.4		18.9	23.9		8.6	47.6		15.0	12.0		4.2	11.4	3.6	3.5
B	223.3		109.5	307.1		135.4	194.8		144.6	240.0		138.8	447.4		142.9	526.6		182.4	644.5		161.7	630.8	133.9	134.5
C	45.2	34.2		9.9	5.8		9.3	7.9		51.3	24.0		24.1	8.7		19.7	6.2		9.1	3.2		7.8	2.4	
D	126.4	62.0		200.2	88.3		164.0	121.7		207.9	120.2		615.1	196.4		510.3	176.8		845.0	212.0		640.8	136.6	

Wg = green weight (g)

Wo = oven dried weight (70°C,g)

Calc. = calculated viz.

$$\text{Calc. Wo A} = \frac{Wg\,A \times Wo\,C}{Wg\,C}$$

Table 2.

Site 4. Double traps. Litter input and accumulation per trap.
Actual and calculated values 6-48 weeks.

Trap No.	22.11.79 - 6 wks Actual Wg	Wo	Calc. Wo	2.1.80 - 12 wks Actual Wg	Wo	Calc. Wo	13.2.80 - 18 wks Actual Wg	Wo	Calc. Wo	26.3.80 - 24 wks Actual Wg	Wo	Calc. Wo	7.5.80 - 30 wks Actual Wg	Wo	Calc. Wo	18.6.80 - 36 wks Actual Wg	Wo	Calc. Wo	30.7.80 - 42 wks Actual Wg	Wo	Calc. Wo	10.9.80 - 48 wks Actual Wg	Wo	Calc. Wo
76 A	19.5		6.0	15.8		9.9	16.7		14.5	19.1		15.6	15.1		7.9	11.3		4.9	6.8		3.0	8.4		2.5
B	*			10.2		8.1	34.8		27.8	46.1		37.7	140.8		58.1	192.5		62.6	218.7		64.1	218.3		60.9
C	25.7	7.9		15.7	9.8		13.7	11.9		14.6	11.9		14.3	7.5		13.4	5.8		12.6	5.6		7.3	2.2	
D	*			28.9	22.9		43.3	34.6		26.5	21.7		135.7	56.0		126.1	41.0		213.7	62.6		185.0	51.6	
77 A	21.1		6.8	18.1		13.9	16.7		13.5	16.8		13.4	14.9		6.7	9.8		3.6	7.1		2.1	14.1		6.9
B				9.7		7.5	39.2		34.0	47.9		37.0	135.5		57.9	191.2		57.9	206.7		52.4	201.5		56.0
C	23.1	7.4		12.2	9.4		19.2	15.5		12.7	10.1		14.2	6.4		10.5	3.9		5.3	1.6		33.2	16.2	
D				25.8	19.9		21.0	18.2		35.1	27.1		122.4	52.3		138.3	41.9		192.2	48.7		160.1	44.5	
78 A	16.2		5.7	9.4		7.5	7.7		6.6	6.3		5.2	8.5		3.6	9.8		3.6	5.5		1.8	2.2		0.4
B				9.2		7.1	20.8		16.4	25.7		18.7	51.2		19.7	99.1		29.5	212.5		55.5	109.6		29.7
C	12.3	4.3		6.0	4.8		7.1	6.1		6.5	5.4		9.8	4.2		9.2	3.4		5.1	1.7		10.2	1.7	
D				21.4	16.6		18.8	14.8		28.8	20.9		146.3	56.4		102.4	30.5		129.5	33.8		127.7	34.6	
79 A	6.5		2.1	5.2		3.9	6.3		4.3	7.9		6.4	10.2		4.5	8.9		3.7	4.7		1.6	4.8		1.8
B				4.1		3.3	11.2		9.1	17.8		13.7	65.5		25.5	71.6		22.0	84.0		26.3	88.4		29.0
C	10.6	3.5		9.6	7.2		5.9	4.0		9.4	7.6		14.7	6.5		8.2	3.4		7.2	2.5		13.3	4.9	
D				35.4	28.5		27.3	22.2		25.2	19.4		106.7	41.6		106.9	32.9		156.9	49.1		250.0	82.0	
80 A	7.8		3.0	6.5		5.4	8.8		7.1	5.7		4.6	10.3		7.9	6.2		3.7	4.0		1.8	7.3		4.1
B				5.6		4.4	7.5		5.9	22.9		16.3	52.0		31.8	75.4		24.7	83.7		25.2	84.8		25.2
C	8.7	3.3		9.8	8.2		8.9	7.2		9.7	7.8		7.2	5.5		4.2	2.5		4.8	2.2		3.9	2.2	
D				26.7	21.2		18.5	14.5		35.2	25.0		32.2	19.7		80.3	26.3		132.4	39.8		167.7	49.9	

Wg = green weight (g)

Wo = oven-dried weight (70°C, g)

Calc. = calculated viz.

$$\text{Calc. Wo A} = \frac{\text{Wg A} \times \text{Wo C}}{\text{Wg C}}$$

* = no accumulation for this period

APPENDIX C.

Table 2.

Site 4. Double traps.   Litter input and accumulation per trap.
Actual and calculated values 54-84 weeks.   Cont'd.

Trap No.	22.10.80 - 54 wks Actual Wg	Wo	Calc. Wo	3.12.80 - 60 wks Actual Wg	Wo	Calc. Wo	14.1.81 - 66 wks Actual Wg	Wo	Calc. Wo	25.2.81 - 72 wks Actual Wg	Wo	Calc. Wo	8.4.81 - 78 wks Actual Wg	Wo	Calc. Wo	20.5.81 - 84 wks Actual Wg	Wo	Calc. Wo	
76 A	11.7		9.8	20.7		-13.9	16.0		13.9	30.3		24.0	35.5		20.7	17.7	N.A.	7.8	
B	172.3		116.8	207.0		123.8	161.5		133.7	160.5		130.0	405.1		138.0	492.0	109.8	139.7	
C	21.1	17.7		4.9	3.3		14.3	12.4		32.0	25.3		29.8	17.4		13.2	5.8		N.A. = not available
D	126.1	85.5		32.4	49.3		145.0	120.0		235.3	190.6		451.0	153.6		588.0	167.0		
77 A	22.2		18.3	10.1		6.1	11.3		9.7	34.2		16.4	30.5		12.0	14.5	4.5	5.6	
B	136.5		68.4	184.9		78.0	117.7		94.1	144.2		71.2	328.5		103.6	393.3	95.3	131.1	
C	16.9	13.9		24.8	14.9		5.5	4.7		21.9	10.5		20.9	8.2		11.1	4.3		
D	103.2	51.7		107.4	45.3		70.2	56.1		64.2	31.7		331.3	104.4		452.9	151.0		
78 A	3.7		2.9	3.2		1.2	8.8		7.1	16.5		10.9	13.4		5.4	8.3	2.1	3.4	
B	77.0		26.6	51.9		21.8	42.1		32.3	69.2		47.2	226.7		75.4	197.4	49.6	55.1	
C	13.5	10.6		6.4	2.4		9.1	7.3		22.1	14.6		12.1	4.9		6.4	2.6		
D	82.0	28.3		85.8	36.0		70.8	54.4		126.3	86.1		123.8	41.2		251.7	70.3		
79 A	5.3		4.6	3.2		2.4	5.6		3.8	35.4		25.9	38.7		14.4	11.0	3.7	3.8	
B	46.5		33.3	53.8		37.4	41.0		33.7	51.3		38.4	170.3		53.6	240.2	73.9	55.3	
C	5.6	4.9		0.8	0.6		5.3	3.6		19.8	14.5		12.9	4.8		7.0	2.4		
D	95.1	65.3		86.7	60.3		96.6	79.3		117.0	87.6		215.8	67.9		241.4	55.6		
80 A	18.7		18.7	4.7		3.4	8.3		6.9	19.8		10.2	12.7		7.6	5.6	1.6	3.2	
B	45.5		28.5	61.7		46.5	58.6		49.6	93.9		48.4	167.8		59.2	217.1	63.2	63.9	
C	2.3	2.2		2.5	1.8		7.2	6.0		14.6	7.5		21.0	12.6		12.3	7.0		
D	57.8	36.2		68.8	51.9		50.8	43.0		55.1	28.4		208.2	73.5		185.8	54.7		

Wg = green weight (g)

Wo = oven-dried weight (70°C, g)

Calc. = calculated viz.

$$\text{Calc. Wo A} = \frac{\text{Wg A} \times \text{Wo C}}{\text{Wg C}}$$

Table 3.   Site 3.   Mean values of green weight (Wg), yields.
6-96 weeks.

Date	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81	1.7.81	12.8.81
No. weeks	6	12	18	24	30	36	42	48	54	60	66	72	78	84	90	96
ΣA	72.5	82.6	131.0	164.7	102.0	87.9	54.6	171.1	175.8	48.3	71.7	218.9	164.0	134.7	63.0	33.1
ΣB		39.6	176.8	313.0	954.7	1170.0	1271.0	1255.5	1135.0	1439.6	988.9	1102.2	2097.7	2723.1	3132.7	3027.9
ΣC	71.4	74.8	117.7	151.6	104.6	60.7	64.2	129.1	186.9	44.6	58.1	222.2	168.1	115.8	53.9	41.8
ΣD		186.9	229.6	405.7	917.3	804.3	1238.3	1361.7	1004.2	1047.1	963.6	1153.0	2330.5	2434.6	3494.9	3372.1
$\bar{A}$	14.5	16.5	26.2	32.9	20.4	17.6	10.9	34.2	35.2	9.7	14.3	43.8	32.8	26.9	12.6	6.6
$\bar{B}$		7.9	35.4	62.6	190.9	234.0	254.2	255.1	227.0	287.9	197.8	220.4	419.5	544.6	626.5	605.6
$\bar{C}$	14.3	15.0	23.5	30.3	20.9	12.1	12.8	25.8	37.4	8.9	11.6	44.4	33.6	23.2	10.8	8.4
$\bar{D}$		37.4	45.9	81.1	183.5	160.9	247.7	272.3	200.8	209.4	192.7	230.6	466.1	486.9	699.0	674.4

329

Table 4.   Site 4.   Mean values of green weight (Wg), yields.
6-84 weeks.

Date	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81
No. weeks	6	12	18	24	30	36	42	48	54	60	66	72	78	84
ΣA	71.1	55.0	56.2	55.8	59.0	46.0	28.1	36.8	61.6	41.8	50.0	136.2	130.8	57.1
ΣB		38.8	113.5	160.4	445.0	629.8	805.6	702.6	479.8	559.3	420.9	519.1	1298.4	1540.0
ΣC	80.4	53.3	54.8	53.3	60.2	45.5	35.0	67.9	59.4	39.4	41.4	110.4	96.7	50.0
ΣD		138.2	128.9	150.8	543.3	554.0	824.7	890.5	464.2	431.1	433.4	597.9	1330.1	1719.8
$\bar{A}$	14.2	11.0	11.2	11.2	11.8	9.2	5.6	7.4	12.3	8.4	10.0	27.2	26.2	11.4
$\bar{B}$		7.8	22.7	32.1	89.0	126.0	161.1	140.5	96.0	111.9	84.2	103.8	259.7	308.0
$\bar{C}$	16.1	10.7	11.0	10.7	12.0	9.1	7.0	13.6	11.9	7.9	8.3	22.1	19.3	10.0
$\bar{D}$		27.6	25.8	30.2	108.7	110.8	164.9	178.1	92.8	86.2	86.7	119.6	266.0	344.0

Table 5.   Site 3.   Mean values of oven dry weight (Wo, 70°C) yields, actual and calculated per trap, 6-96 weeks.

Date No. weeks	22.11.79 6	2.1.80 12	13.2.80 18	26.3.80 24	7.5.80 30	18.6.80 36	30.7.80 42	10.9.80 48	22.10.80 54	3.12.80 60	14.1.81 66	25.2.81 72	8.4.81 78	20.5.81 84	1.7.81 90	12.8.81 96
ΣA	24.7	64.9	98.4	133.3	40.4	36.0	17.9	65.4	135.2	28.6	61.2	105.8	58.1	45.8	18.5	10.1
ΣB		30.3	126.9	237.3	362.8	373.8	334.4	362.3	535.8	610.2	717.4	759.1	760.0	939.4	742.4	671.3
ΣC	23.6	58.4	88.3	122.7	41.5	24.5	21.7	48.7	144.6	26.6	49.6	108.8	58.2	40.1	16.1	12.7
ΣD		141.6	161.9	307.1	353.5	249.2	326.7	396.0	456.6	448.0	712.5	818.2	761.6	851.2	829.1	744.3
$\bar{A}$	4.9	13.0	19.7	26.7	8.1	7.2	3.6	13.1	27.0	5.7	12.2	21.2	11.6	9.2	3.7	2.0
$\bar{B}$		6.1	25.4	47.5	72.6	74.8	66.9	72.5	107.2	122.0	143.5	151.8	152.0	163.8	148.5	134.3
$\bar{C}$	4.7	11.7	17.7	24.5	8.3	4.9	4.3	9.7	28.9	5.3	9.9	21.8	11.6	8.0	3.2	2.5
$\bar{D}$		28.3	32.4	61.4	70.7	49.8	65.3	79.2	91.3	89.6	142.5	163.7	152.3	170.2	165.8	148.9

A and B values represent equivalent oven dry weight by calculation.

C and D are actual values.

Table 6.   Site 4.   Mean values of oven dry weight (Wo, $70^{\circ}C$) yields, actual and calculated, per trap, 6-84 weeks.

Date	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81
No. weeks	6	12	18	24	30	36	42	48	54	60	66	72	78	84
ΣA	23.6	40.6	46.0	45.2	30.6	19.5	10.3	15.7	54.3	27.0	41.4	87.4	60.1	23.8
ΣB		30.4	93.2	123.4	193.0	196.7	223.5	200.8	273.6	307.5	343.4	335.2	429.8	539.9
ΣC	26.4	39.4	44.7	42.8	30.1	19.0	13.6	27.2	49.3	23.0	34.0	72.4	47.9	22.1
ΣD		109.1	104.3	114.1	226.0	172.6	234.0	262.6	267.0	242.8	352.8	424.4	440.6	498.6
$\bar{A}$	4.7	8.1	9.2	9.0	6.1	3.9	2.1	3.1	10.9	5.4	8.3	17.5	12.0	4.8
$\bar{B}$		6.1	18.6	24.7	38.6	39.3	44.7	40.2	54.7	61.5	68.7	67.0	86.0	108.0
$\bar{C}$	5.3	7.9	8.9	8.6	6.0	3.8	2.7	5.4	9.9	4.6	6.8	14.5	9.6	4.4
$\bar{D}$		21.8	20.9	22.8	45.2	34.5	46.8	52.5	53.4	48.6	70.6	84.9	88.1	99.7

A and B values represent equivalent oven dry weight by calculation.

C and D are actual values.

332

Table 7.   Site 3.   Moisture content percent of accessing and accumulating litter in sacrificial traps C and D, 6-96 weeks.

Sampling date	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81	1.7.81	12.8.81
No. weeks	6	12	18	24	30	36	42	48	54	60	66	72	78	84	90	96
71 C	179.0	27.7	30.4	24.2	155.2	139.3	168.0	130.7	23.3	50.0	17.4	124.4	170.2	182.2	250.0	237.5
71 D	*	27.6	38.7	27.6	142.7	209.7	286.9	273.1	109.2	134.3	53.9	34.4	221.0	310.6	326.3	353.3
72 C	237.0	28.8	40.1	24.6	150.0	126.8	196.9	165.9	35.2	59.6	21.2	117.9	172.1	189.8	204.8	172.0
72 D		40.7	39.3	29.0	174.9	207.8	248.4	269.5	74.0	112.6	22.9	24.0	241.7	189.1	321.4	352.5
73 C	104.9	23.1	33.3	25.9	155.1	145.0	220.5	171.8	24.0	57.1	19.0	61.3	131.9	167.1	442.9	275.0
73 D		25.5	29.9	36.5	142.9	232.9	260.3	198.9	100.8	130.3	39.4	47.5	212.9	225.8	514.8	309.5
74 C	238.5	28.9	33.8	24.0	156.1	197.9	226.2	153.5	36.3	95.0	11.8	105.5	250.3	193.2	222.4	280.0
74 D		31.5	53.8	33.6	183.2	266.2	284.4	272.4	176.8	174.3	33.0	48.5	167.5	338.0	364.8	371.5
75 C	277.1	30.9	31.1	23.0	144.2	127.3	179.6	212.1	32.2	70.7	17.7	113.8	177.0	217.7	184.4	225.0
75 D		31.9	34.1	31.8	186.3	169.2	314.6	216.4	103.9	126.7	34.8	73.0	213.2	188.6	298.6	369.1
ΣC	1036.5	139.3	168.8	121.6	760.6	736.3	991.2	834.0	151.0	332.4	87.1	522.9	901.5	950.0	1304.5	1139.5
$\bar{C}$	207.3	27.9	33.8	24.3	152.1	147.3	198.2	166.8	30.2	66.5	17.4	104.6	180.3	190.0	260.9	227.9
ΣD	*	157.2	195.8	182.7	830.0	1085.8	1394.6	1230.3	564.7	678.2	184.0	227.4	1056.3	1252.1	1825.9	1755.9
$\bar{D}$		31.4	39.2	36.5	166.0	217.2	278.9	246.1	112.9	135.6	36.8	45.5	211.3	250.4	365.2	351.2

* No accumulated litter

APPENDIX C.

Table 8.　　　　Site 4.　Moisture content percent of accessing and accumulating litter in sacrificial traps C and D, 6-84 weeks.

Sampling date	22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81
No. weeks	6	12	18	24	30	36	42	48	54	60	66	72	78	84
76 C	225.3	60.2	15.1	22.7	90.7	131.0	125.0	231.8	19.2	48.5	15.3	26.5	71.3	127.6
76 D	*	26.2	25.1	22.1	142.3	207.6	241.4	258.5	47.5	67.1	20.8	23.5	193.6	109.9
77 C	212.2	29.8	23.9	25.7	121.9	169.2	231.3	104.9	21.6	66.4	17.0	108.6	154.9	158.1
77 D		29.6	15.4	29.5	134.0	230.1	294.7	259.8	51.5	137.1	25.1	102.5	217.3	199.9
78 C	186.0	25.0	16.4	20.4	133.3	170.6	200.0	264.7	27.4	166.7	24.7	51.4	146.9	146.2
78 D		28.9	27.0	37.8	159.4	235.7	283.2	269.1	189.8	138.3	30.1	46.7	200.5	258.0
79 C	202.9	33.3	47.5	23.7	126.2	141.2	188.0	171.4	14.3	33.3	47.2	36.6	168.8	191.7
79 D		24.2	23.0	29.9	156.5	224.9	219.6	204.9	45.6	43.8	21.8	33.6	217.8	334.2
80 C	163.6	19.5	23.6	24.4	30.9	68.0	118.2	77.3	4.5	38.9	20.0	94.7	66.7	75.7
80 D		25.9	27.6	40.8	63.5	205.3	232.7	236.1	59.7	32.6	18.1	94.0	185.3	239.7
ΣC	990.0	167.8	126.5	116.9	503.0	680.0	862.5	850.1	87.0	353.8	124.2	317.8	608.6	699.3
$\bar{C}$	198.0	33.6	25.3	23.4	100.6	136.0	172.5	170.0	17.4	70.8	24.8	63.6	121.7	139.9
ΣD	*	134.8	118.1	160.1	655.7	1103.7	1271.6	1228.4	394.1	418.9	115.9	300.3	1012.5	1141.7
$\bar{D}$		27.0	23.6	32.0	131.1	220.7	254.3	245.7	78.8	83.8	23.2	60.1	202.5	228.3

* No accumulated litter

Table 9. Double trap. Individual A (corrected) and B values, Site 3.

Sampling interval		22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81	1.7.81	12.8.81
71	A	11.1	23.9	25.3	45.1	7.7	10.1	4.1	15.8	29.8	6.5	15 0	25.7	18.9	8.0	4.8	2.3
	Accumulated A	11.1	35.0	60.3	105.4	113.1	123.2	127.3	143.1	172.9	179.4	194.4	220.1	239.0	247.0	251.8	254.1
	B	-	11.1	32.4	51.7	94.3	88.4	88.5	89.4	142.0	155.9	160.2	202.6	188.5	211.3	186.6	167.5
72	A	3.1	8.6	18.5	59.8	6.7	8.2	3.4	7.9	15.3	4.8	9.3	19.6	7.5	7.5	4.7	1.4
	Accumulated A	3.1	11.7	30.2	90.0	96.7	104.9	108.3	116.2	131.5	136.3	145.6	165.2	172.7	180.2	184.9	186.3
	B	-	3.1	10.8	27.3	80.7	81.6	53.0	49.7	84.2	90.8	98.7	119.5	98.9	131.1	104.6	96.9
73	A	5.8	22.8	24.9	30.9	8.5	5.6	2.2	14.8	22.0	4.8	15.5	16.9	10.4	7.1	1.7	1.5
	Accumulated A	5.8	28.6	53.5	84.4	92.9	98.5	100.7	115.5	137.5	142.3	157.8	174.7	185.1	192.2	193.9	195.4
	B	-	4.4	28.6	49.0	74.1	66.3	69.7	81.4	112.9	117.6	133.9	128.2	143.7	157.6	147.4	137.4
74	A	5.9	25.3	40.6	22.7	8.7	5.5	4.1	18.3	25.0	7.8	12.2	24.7	12.7	8.2	3.1	1.4
	Accumulated A	5.9	31.2	71.8	94.5	103.2	108.7	112.8	131.1	156.1	163.9	176.1	200.8	213.5	221.7	224.8	226.2
	B	-	5.9	29.3	55.9	52.9	55.6	60.0	60.6	87.2	110.5	180.0	170.0	186.0	136.6	142.1	135.0
75	A	5.8	21.6	38.4	36.5	8.8	6.6	4.1	8.6	43.1	4.7	9.2	18.9	8.6	15.0	4.2	3.5
	Accumulated A	5.8	27.4	65.8	102.3	111.1	117.7	121.8	130.4	173.5	178.2	187.4	206.3	214.9	229.9	234.1	237.6
	B	-	5.8	25.8	53.4	60.8	81.9	63.2	81.2	109.5	135.4	144.6	138.8	142.9	182.4	161.7	134.5

APPENDIX C.

Table 10.   Double trap.   Individual C (corrected) and D values, Site 3.

Sampling interval		22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81	1.7.81	12.8.81
71	C	22.8	43.1	36.2	55.2	8.7	5.6	5.0	11.4	34.3	5.4	14.9	25.0	12.4	10.1	1.8	1.6
	Accumulated C	22.8	65.9	102.1	157.3	166.0	171.6	176.6	188.0	222.3	227.7	242.6	267.6	280.0	290.1	291.9	293.5
	D	-	22.8	51.2	55.5	101.8	30.9	92.5	72.8	138.7	83.7	127.9	207.2	177.9	275.5	145.3	161.5
72	C	34.9	19.7	22.3	22.4	10.0	7.1	3.2	4.4	12.8	5.2	6.6	16.8	11.1	5.9	2.1	2.5
	Accumulated C	34.9	54.6	76.9	99.3	109.3	116.4	119.6	124.0	136.8	142.0	148.6	165.4	176.5	182.4	184.5	187.0
	D	-	34.9	22.4	42.7	53.1	45.1	45.7	53.8	44.7	123.2	203.1	250.2	81.5	176.3	124.9	121.7
73	C	28.6	17.3	56.1	71.6	6.9	6.0	3.9	7.8	34.1	4.2	10.0	23.0	9.1	7.6	1.4	3.2
	Accumulated C	28.6	45.9	130.6	202.2	209.1	215.1	219.0	226.8	260.9	265.1	275.1	298.1	307.2	314.8	316.2	319.4
	D	-	28.6	21.4	68.0	98.3	43.1	67.2	88.0	98.4	68.9	115.6	99.3	105.1	130.6	170.8	131.6
74	C	32.4	46.3	56.3	24.6	8.2	4.7	4.2	14.4	29.2	6.0	10.2	20.0	16.9	10.3	7.6	3.0
	Accumulated C	32.4	78.7	135.0	159.6	167.8	172.5	176.7	191.1	220.3	226.3	236.5	256.5	273.4	283.7	291.3	294.3
	D	-	32.4	50.2	75.1	57.3	78.4	78.9	97.1	112.8	84.1	144.2	141.3	200.7	92.0	176.1	192.9
75	C	22.9	11.9	54.2	20.4	7.7	1.1	5.4	10.7	34.2	5.8	7.9	24.0	8.7	6.2	3.2	2.4
	Accumulated C	22.9	34.8	89.0	109.4	117.1	118.2	123.6	134.3	168.5	174.3	182.2	206.2	214.9	221.1	224.3	226.7
	D	-	22.9	16.7	65.8	43.0	51.7	42.4	84.3	62.0	88.3	121.7	120.2	196.4	176.8	212.0	136.6

Table 11.   Double trap.   Individual A (corrected) and B values, Site 4.

Sampling interval		22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81
76	A	8.1	21.8	21.8	27.7	7.9	4.9	3.0	2.5	9.8	13.9	13.9	24.0	20.7	7.8
	Accumulated A	8.1	29.9	51.7	79.4	87.3	92.2	95.2	97.7	107.5	121.4	135.3	159.3	180.0	187.8
	B	-	8.1	27.8	37.7	58.1	62.6	64.1	60.9	116.8	123.8	133.7	130.0	138.0	139.7
77	A	7.5	27.2	16.3	23.7	6.7	3.6	2.1	6.9	18.3	6.1	9.7	16.4	12.0	5.6
	Accumulated A	7.5	34.7	51.0	74.7	81.4	85.0	87.1	94.0	112.3	118.4	128.1	144.5	156.5	162.1
	B	-	7.5	34.0	37.0	57.9	57.9	52.4	56.0	68.4	78.0	94.1	71.2	103.6	131.1
78	A	7.1	10.7	6.6	5.2	3.6	3.6	1.8	0.4	2.9	1.2	7.1	10.9	5.4	3.4
	Accumulated A	7.1	17.8	24.4	29.6	33.2	36.8	38.6	39.0	41.9	43.1	50.2	61.1	66.5	69.9
	B	-	7.1	16.4	18.7	19.7	29.5	55.5	29.7	26.6	21.8	32.3	47.2	75.4	55.1
79	A	3.3	7.0	8.0	15.2	4.5	3.7	1.6	1.8	4.6	2.4	3.8	25.9	14.4	3.8
	Accumulated A	3.3	10.3	18.3	33.5	38.0	41.7	43.3	45.1	49.7	52.1	55.9	81.8	96.2	100.0
	B	-	3.3	9.1	13.7	25.5	22.0	26.3	29.0	33.3	37.4	33.7	38.4	53.6	55.3
80	A	4.4	5.4	7.9	16.3	7.9	3.7	1.8	4.1	18.7	3.4	6.9	10.2	7.6	3.2
	Accumulated A	4.4	9.8	17.7	34.0	41.9	45.6	47.4	51.5	70.2	73.6	80.5	90.7	98.3	101.5
	B	-	4.4	5.9	6.3	31.8	24.7	25.2	25.2	28.5	46.5	49.6	48.4	59.2	63.9

APPENDIX C.

Table 12.   Double trap.   Individual C (corrected) and D values, Site 4.

Sampling interval		22.11.79	2.1.80	13.2.80	26.3.80	7.5.80	18.6.80	30.7.80	10.9.80	22.10.80	3.12.80	14.1.81	25.2.81	8.4.81	20.5.81
76	C	22.9	26.7	11.9	26.4	7.5	5.8	5.6	2.2	17.7	3.3	12.4	25.3	17.4	5.8
	Accumulated C	22.9	49.6	61.5	87.9	95.4	101.2	106.8	109.0	126.7	130.0	142.4	167.7	185.1	190.9
	D	-	22.9	34.6	21.7	56.0	41.0	62.6	51.6	85.5	49.3	120.0	190.6	153.6	167.0
77	C	19.9	10.8	15.5	20.0	6.4	3.9	1.6	16.2	13.9	14.9	4.7	10.5	8.2	4.3
	Accumulated C	19.9	30.7	46.2	66.2	72.6	76.5	78.1	94.3	108.2	123.1	127.8	138.3	146.5	150.8
	D	-	19.9	18.2	27.1	52.3	41.9	48.7	44.5	51.7	45.3	56.1	31.7	104.4	151.0
78	C	16.6	10.5	11.8	41.2	4.2	3.4	1.7	1.7	10.6	2.4	7.3	14.6	4.9	2.6
	Accumulated C	16.6	27.1	38.9	80.1	84.3	87.7	89.4	91.1	101.7	104.1	111.4	126.0	130.9	133.5
	D	-	16.6	14.8	20.9	56.4	30.5	33.8	34.6	28.3	36.0	54.4	86.1	41.2	70.3
79	C	28.5	18.7	8.7	26.9	6.5	3.4	2.5	4.9	4.9	0.6	3.6	14.5	4.8	2.4
	Accumulated C	28.5	47.2	55.9	82.8	89.3	92.7	95.2	100.1	105.0	105.6	109.2	123.7	128.5	130.9
	D	-	28.5	22.2	19.4	41.6	32.9	49.1	82.0	65.3	60.3	79.3	87.6	67.9	55.6
80	C	21.2	11.2	13.5	7.8	5.5	2.5	2.2	2.2	2.2	1.8	6.0	7.5	12.6	7.0
	Accumulated C	21.2	32.4	45.9	53.7	59.2	61.7	63.9	66.1	68.3	70.1	76.1	83.6	96.2	103.2
	D	-	21.2	14.5	25.0	19.7	26.3	39.8	49.9	36.2	51.9	43.0	28.4	73.5	54.7

338

APPENDIX D.

MEDIA AND REAGENTS.

Martin's (1950) glucose-peptone-rose bengal-streptomycin agar, with chlortetracycline (Pennycook 1974).

tap water	1000 ml
dxtrose	10 g
peptone	5 g
$K\ H_2PO_4$	1 g
$MgSO_4.7H_2O$	0.5 g
agar	20 g
rose bengal	1:15,000 (0.07 g)

autoclave then add

streptomycin	40 $g.ml^{-1}$
chlortetracycline	40 $g.ml^{-1}$

Jensen's (1930) glucose-casein agar.

glucose	2.0 g

0.2g casein dissolved in 10cc 0.1 N.NaOH

K_2HPO_4	0.5 g
$MgSO_4$	0.2 g
FeCl3	0.1 g
agar	15 g
$d.H_2O$	1000 ml
pH 5.5-6.6	

Nutrient agar

Nutrient broth:

beef extract	3.0 g
peptone	5.0 g
$d.H_2O$	1000 ml
add agar	15.0 g

Ringer's solution (1/4 strength)

NaCl	2.25 g
KCl	0.11 g
CaCl2	0.12 g
$NaHCO_3$	0.05 g
$d.H_2O$	1000 ml

Potato-dextrose agar

Potatoes	200 g
Dextrose	20 g
Agar	15 g
d.H_2O	1000 ml

C.L.E.D. medium

Peptone	4 g
'Lab-Lemco' powder	3 g
Tryptone	4 g
Lactose	10 g
L-Cystine	0.128 g
Bromothymol blue	0.02 g
Agar	15 g

pH ca. 7.3

MacConkey agar

Peptone	20 g
Lactose	10 g
Bile Salts	5 g
NaCl	5 g
Neutral Red	0.075 g
Agar	12 g

pH ca. 7.4

APPENDIX. STATISTICAL ANALYSIS, 1.

Comparison of fixed and roving bins at Sites 1, 2, and 3

Analysis of variance.   LOG Y. Litter yield transformed to logs.

Source of variation	DF (MV)	SS	MS	VR
Between traps				
Treatment	1	0.0321	0.0321	0.076
Residual	14	5.8955	0.4211	2.352
Within traps				
Time	14	208.4905	14.8922	83.173
Treatment.Time	14	1.1635	0.0831	0.464
Residual	224	40.1073	0.1791	
Grand total	269	256.5940		

Table of back transformed log mean data per interaction.

Time	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Fixed bins	21.031	16.412	11.023	3.200	3.529	1.204	3.831	5.165	16.411	15.256	21.999	6.379	4.464	1.819	4.821
Roving bins	21.052	18.672	10.186	3.865	3.800	1.025	3.161	5.191	13.763	17.184	24.730	6.903	4.918	2.316	4.341

APPENDIX, STATISTICAL ANALYSIS, 2.

Comparison of litter catches in 3 fixed and 7 roving devices at Sites 1, 2, and 3 over 29 sampling intervals.

<u>Analysis of variance</u>

Source	df	SS	MS	F
Site	2	1.5	0.7651	4.07
Treatments (adjusted for times)	1	0.4	0.3537	1.88 n.s.
Times (adjusted for treatments)	~28	450.0	16.0698	85.57
Treatments x Times	26(2)	8.6	0.3289	1.75 n.s.
Residual	808(2)	151.7	0.1878	
Total	865			

Note: n.s.; not significant.

Standard deviation for a single device = 0.433g.

Standard deviation for the mean of any 10 devices = 0.137g.

APPENDIX. STATISTICAL ANALYSIS. 3.

Comparison of bins and ground traps at Site 2

Analysis of variance.   LOG Y. Litter yield transformed to logs.

Source of variation	DF (MV)	SS	MS	VR
Between traps				
Treatment	1	0.0006	0.0006	0.001
Residual	18	8.1985	0.4555	2.562
Within traps				
Time	14	200.4412	14.3172	80.522
Treatment.Time	14	3.8747	0.2768	1.557
Residual	251 (1)	44.6290	0.1778	
Grand total	298	257.1440		

Table of back transformed log mean data per interaction.

Time	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Bins	13.001	12.466	12.037	4.768	3.013	1.105	4.953	9.070	12.730	15.029	18.486	2.625	3.717	1.507	4.393
Ground traps	13.330	13.477	13.695	5.312	3.846	1.259	3.111	9.650	10.924	15.348	20.863	1.045	3.174	2.100	2.627

APPENDIX.   STATISTICAL ANALYSIS, 4.

Comparison of overstorey catch of *Eucalyptus obliqua* and *E. nitida* in bins-on-stilts and ground traps at Site 4

Analysis of variance.   LOG Y.   Litter yield transformed to logs.

Source of variation	DF (MV)	SS	MS	VR
Between traps				
Treatment	1	1.1368	1.1368	0.242
Residual	18	84.4074	4.6893	9.137
Within traps				
Time	14	217.9408	15.5672	30.333
Treatment.Time	14	8.2991	0.5928	1.155
Residual	238 (14)	122.1450	0.5132	
Grand total	285	433.9291		

Table of back transformed log mean data per interaction.

Time	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Bins, raised	2.912	2.326	0.392	0.323	0.445	0.151	0.097	0.544	0.634	1.394	1.098	0.941	0.718	0.410	0.418
Ground traps	2.912	2.284	0.723	0.386	0.427	0.167	0.170	0.299	1.075	1.471	1.318	1.022	0.676	0.293	0.761

APPENDIX, STATISTICAL ANALYSIS, 5.

Relationship between log basal area of individual species at Sites 1, 2, and 3, and their respective log leaf accession per annum.

To test for common slope and intercept:

Test for coincidence : analysis of variance.

	df	SS	MS	F	
(B-A); †	4	0.417	0.10425	1.22	
					n.s.
Residual; ††	31	2.650	0.08548		

Percentage variance accounted for: 92.7.

Note: †; (common line residual - full model residual).

†; full model residual.

n.s.; no significant difference in slope or intercept of the regressions for individual sites.

Table of regression coefficients : standard errors, t-values

		ESTIMATE	S.E.	t
INTERCEPT	Site 1	-1.54098	0.31362	-4.91
	Site 2	-0.81301	0.40949	-1.99
	Site 3	-1.50710	0.28960	-5.20
	Common	-1.37627	0.19026	-7.23
SLOPE	Log B.A. Site 1	0.98723	0.07453	13.25
	Log B.A. Site 2	0.86182	0.09609	8.97
	Log B.A. Site 3	0.99264	0.07333	13.54
	Common	0.96973	0.04588	21.13

APPENDIX, STATISTICAL ANALYSIS, 6.

Relationship between live numbers of stems and their corresponding annual leaf accession per site.

Analysis of variance.

Test for coincidence: common slope and intercept.

	df	SS	MS	F	
(B-A) †	4	5.96	1.49	3.55	*
Residual ††	31	13.01	0.4197		

Percentage variance accounted for 64.3.

Note: †;   (common line residual - full model residual).

   ††;   full model residual.

   *;   significant difference, P<0.05.

Test for common slope:

	df	SS	MS	F	
(C-A) †	2	3.2	1.6	3.812	*
Residual ††	31	13.01	0.4197		

Test for common intercept:

	df	SS	MS	F	
(D-A) †	2	4.51	2.255	5.37	**
Residual ††	31	13.01	0.4197		

Note: **   P<0.01

APPENDIX, STATISTICAL ANALYSIS, 6   Cont'd.

Regression coefficients: Live number of stems per site versus
corresponding annual leaf accession.

	ESTIMATE	S.E.	t
Site 1	-1.67729	0.74316	-2.26
Site 2	1.18808	0.58665	2.03
Site 3	-0.95262	0.68317	-1.39
Log stem. Site 1	1.73479	0.30170	5.75
Log stem. Site 2	0.70025	0.24390	2.87
Log stem. Site 3	1.35170	0.27793	4.86

APPENDIX, STATISTICAL ANALYSIS, 7.

Relationship between log leaf accession and log mean maximum temperature per sampling interval at Sites 1, 2, 3, and 4.

Analysis of variance.

Test for coincidence: common slope and intercept.

	df	SS	MS	F	
(B-A) †	6	1.459	0.243	6.95	***
Residual ††	60	2.127	0.035		

Note: †; (common line residual – full model residual).

  ††; full model residual.

  ***; P<0.001.

Test for common slope.

	df	SS	MS	F	
(C-A) †	3	0.051	0.017	0.48	n.s.
Residual ††	60	2.127	0.03545		

APPENDIX, STATISTICAL ANALYSIS, 7   Cont'd.

Table of regression coefficients, standard errors, t-values.

		ESTIMATE	S.E.	t
INTERCEPT	Site 1	−3.4444	0.7568	−4.55
	Site 2	−3.4547	0.7568	−4.56
	Site 3	−2.8619	0.7568	−3.78
	Site 4	−2.6979	0.7568	−3.56
	Common	−3.1147	0.4685	−6.65
SLOPE	Site 1	4.8631	0.6269	7.76
	Site 2	4.8335	0.6269	7.71
	Site 3	4.3461	0.6269	6.93
	Site 4	3.9460	0.6269	6.29
	Common	4.4972	0.3881	11.59

APPENDIX, STATISTICAL ANALYSIS, 8.

Relationship between log bark and twig accession and log mean maximum temperature per sampling interval at Sites 1, 2, 3, and 4.

Analysis of variance: test for coincidence.

	df	SS	MS	F
(B–A) †	6	4.22	0.7033	3.973
Residual ††	64	11.33	0.1770	

Note: †; (common line residual – full model residual).

†††; full model residual.

Regression coefficients, standard errors, t-values.

		ESTIMATE	S.E.	t
	Site 1	-1.55679	1.60206	-0.97
	Site 2	1.09927	1.60206	0.69
	Site 3	-0.34536	1.60206	-0.22
	Site 4	-3.11366	1.60206	-1.94
Log temp.	Site 1	2.99721	1.32039	2.27
Log temp.	Site 2	0.68434	1.32039	0.52
Log temp.	Site 3	1.97571	1.32039	1.50
Log temp.	Site 4	3.81809	1.32039	2.89

APPENDIX, STATISTICAL ANALYSIS, 9.

Relationship between log bark and twig accession and log mean windrun per sampling interval, at Sites 1, 2, 3, and 4.

Analysis of variance: test for coincidence.

	df	SS	MS	F
(B-A) †	6	4.009	0.6681	3.498
Residual ††	64	9.361	0.1910	

Note: †; (common line residual - full model residual).

†; full model residual.

Regression coefficients, standard errors, t-values.

		ESTIMATE	S.E.	t
	Site 1	-2.53938	1.65906	-1.53
	Site 2	-3.77166	1.65906	-2.27
	Site 3	-3.43627	1.65906	-2.07
	Site 4	-0.99025	1.65906	-0.60
Logwind.	Site 1	2.17814	0.78234	2.78
Logwind.	Site 2	2.69169	0.78234	3.44
Logwind.	Site 3	2.58961	0.78234	3.31
Logwind.	Site 4	1.18078	0.78234	1.51

APPENDIX, STATISTICAL ANALYSIS, 10.

Multiple regression of log mean windrun, log mean maximum temperature, and log total rainfall with log bark + twig accession per sampling interval.

Regression coefficients

Y - variate : Log bark + twigs.

	ESTIMATE	S.E.	t
Constant	-2.7778	0.9979	-2.78
Windrun	2.2116	0.4699	4.71

Correlation matrix

DF = 66

		1	2	3	4
Mean maximum temperature	1	1.000			
Total rain	2	-0.3266	1.000		
Mean windrun	3	0.3389	0.4259	1.000	
Log bark + twigs	4	0.4388	-0.1493	0.5013	1.000

DECOMPOSITION STUDIES. Litter bag Experiment 1.   (b) Sites 1 and 4 at 3, 6, 12 and 18 months.   Note that 18 values missing
at 18 months sampling at Site 4.   Missing values estimated.

Analysis of variance.

Source of variation	DF	SS	MS	VR	
Between sites	1	191.99	191.99	11.552	
Within sites					
Species	11	36134.45	3284.95	197.653	***
Times	3	31617.18	10539.06	634.127	***
Species.Times	33	2346.45	71.10	4.278	***
Residual	221(18)	3672.97	16.62		
Grand total	269	73963.04			

N.B.:   *** P<0.001

Table of means: between species.

Species	Ulex europaeus dalmatica follius	Banksia marginata	E. obliqua + P. asplenifolius	Eucryphia lucida	Nothofagus cunninghamii	Pomaderris apetala	Acacia melanoxylon	Eucalyptus nitida	E. obliqua + P. apetala	Athero sperma moschatum	Eucalyptus obliqua	Phebalium squameum
Rank	1	2	3	4	5	6	7	8	9	10	11	12
Mean % wt.loss	12.26	29.11$_a$	29.87$_{ab}$	31.30$_b$	33.09$_{bc}$	34.41$_{cd}$	36.10$_d$	42.72$_e$	42.92$_e$	46.99	49.79	56.85

APPENDIX. STATISTICAL ANALYSIS, 12.

DECOMPOSITION STUDIES. Litter bag Experiment 1. (a) Sites 1 and 4 at 3, 6, and 12 months, with data for 18 months sampling excluded due to 18 missing values caused by fire.

Analysis of variance.

Source of variation	DF	SS	MS	VR	
Between sites	1	137.76	137.76	11.542	
Within sites					
Species	11	26440.73	2403.70	201.384	***
Times	2	13980.84	6990.42	585.662	***
Species.Times	22	933.24	42.42	3.554	***
Residual	179	2136.53	11.94		
Grand total	215	43629.11			

N.B.: *** P<0.001

Between species: L.S.D. (2.275)

Species	*Phyllocladus aspleniifolius*	*Banksia marginata*	*E. obliqua + P. aspleniifolius*	*Eucryphia lucida*	*Nothofagus cunninghamii*	*Acacia melanoxylon*	*Pomaderris apetala*	*Eucalyptus nitida*	*E. obliqua + E. apetala*	*Eucalyptus obliqua*	*Atherosperma moschatum*	*Phebalium squameum*
Rank	1	2	3	4	5	6	7	8	9	10	11	12
Mean % wt.loss	9.64	24.19$_a$	26.08$_{ab}$	26.58$_b$	27.22$_{bc}$	29.39$_{cd}$	30.97$_d$	37.44$_e$	37.78$_e$	44.11$_f$	44.58$_f$	53.19

APPENDIX, STATISTICAL ANALYSIS, 13.

Comparison of the effects of treatments with insecticide, fungicide, and a mixture of insecticide and fungicide upon the decomposition of individual leaf species and mixtures of leaf species.

Analysis of variance.

Source of variation	DF	SS	MS	VR	
Species	3	5584.99	1861.66	81.575	***
Times	2	28444.77	14222.38	623.201	***
Insecticide	1	173.49	173.49	7.602	**
Fungicide	1	5128.85	5128.85	224.738	***
Species.Times	6	976.06	162.68	7.128	***
Species.Insecticide	3	232.06	77.35	3.390	*
Times.Insecticide	2	10.11	5.05	0.221	NS
Species.Fungicide	3	758.88	252.96	11.084	***
Times. Fungicide	2	256.50	128.25	5.620	**
Insecticide.Fungicide	1	63.88	63.88	2.799	NS
Species.Times. Insecticide	6	193.57	32.26	1.414	NS
Species.Times. Fungicide	6	220.42	36.74	1.610	NS
Species.Insecticide. Fungicide	3	89.39	29.80	1.306	NS
Times.Insecticide. Fungicide	2	54.53	27.27	1.195	NS
Residual	244(2)	5568.44	22.82		
Grand total	285	47755.94			

Note: *** $P<0.001$
      ** $P<0.01$
      * $P<0.05$

APPENDIX, STATISTICAL ANALYSIS, 14.

Tables of means: percentage decomposition.

Species.Times interaction

Times (months) Species	3	6	12	MEAN	L.S.D.$_{0.05}$ values	
E. obliqua	22.33	32.06	51.25	35.22	Times	1.380
E. nitida	23.42	30.58	47.63	33.88	Species	1.592
E.o. + P. apetala	19.85	27.10	44.94	30.63	Times. species	2.758
E.o. + P. aspleniifolius	17.08	20.79	33.60	23.83		
MEAN	20.67	27.64	44.35			

Times.Fungicide interaction

Fungicide Times (months)	With	Without	MEAN	L.S.D.$_{0.05}$ values	
3	15.79	25.55	20.67	Fungicide	1.126
6	22.74	32.53	27.64	Times	1.380
12	41.47	47.24	44.35	Times.Fungicide	1.950
MEAN	26.67	35.11			

Species.Fungicide interaction

Fungicide Species	With	Without	MEAN	L.S.D.$_{0.05}$ values	
E. obliqua	29.14	41.29	35.22	Fungicide	1.126
E. nitida	30.60	37.15	33.88	Species	1.592
E.o. + P. apetala	25.17	36.09	30.63	Species. Fungicide	2.252
E.o. + P. aspleniifolius	21.77	25.89	23.83		
MEAN	26.67	35.11			

APPENDIX, STATISTICAL ANALYSIS, 15.

Species.Insecticide interaction

Insecticide Species	With	Without	MEAN	L.S.D.$_{0.05}$ values	
E. obliqua	32.97	37.46	35.22	Insecticide	1.126
E. nitida	33.26	34.49	33.88	Species	1.592
E.o. + *P. apetala*	30.19	31.07	30.63	Species. Insecticide	2.252
E.o. + *P. aspleniifolius*	24.02	23.64	23.83		
MEAN	30.11	31.66			

Insecticide.Fungicide interaction

Fungicide Insecticide	With	Without	MEAN	L.S.D.$_{0.05}$ values	
With	26.97	36.35	30.11	Fungicide	1.126
Without	26.36	33.86	31.66	Insecticide	1.126
MEAN	26.67	35.11		Fungicide. Insecticide	1.592

Comparison of leaf development stage at harvest, time of field establishment, and between species effects in species mixes, upon decomposition.

Analysis of variance.

Source of variation					
Species	11	38176.997	3470.636	699.634	***
E. obliqua + P. aspleniifolius/2 vs. combined E. obliqua, P. aspleniifolius	1	1.580	1.580	0.319	n.s.
E. obliqua + P. aspleniifolius/2 vs. combined E. obliqua, P. aspleniifolius	1	9.330	9.330	1.881	n.s.
Deviations	9	38166.087	4240.676	854.863	
Experiments	2	380.969	190.485	38.399	***
Times	2	17633.076	8816.538	1777.296	***
Species.Experiments	22	2828.698	128.577	25.919	***
Species.Times	22	1927.424	87.610	17.661	***
Experiments.Times	4	402.480	100.745	20.309	***
Species.Experiments.Times	44	1729.131	39.298	7.922	***
Residual	216	1071.500	4.961		
Grand total	323	64150.775			

Note: n.s., not significant $P > 0.05$
$***$ $P < 0.001$

Table of means

Between species (L.S.D. 1.212)

Species	Wittsteinia vacciniacea	Banksia marginata	Eucryphia lucida	Nothofagus cunninghamii	E. obliqua + P. aspleniifolius	Acacia melanoxylon	Pomaderris apetala	E. obliqua + P. apetala	Eucalyptus obliqua	Eucalyptus nitida	Anthcnosperma moschatum	Phcbalium aquaticum
Rank	1	2	3	4	5	6	7	8	9	10	11	12
Mean % wt.loss	12.85	22.61	23.83	26.67	28.19	30.78	36.41	39.50	42.00a	42.31a	46.70	51.52

Between Experiments.Times.Species Interaction.

Experiments	1			3			4			MEAN Species		L.S.D. 0.05
Times	3	6	12	3	6	12	3	6	12			
Species												
E. obliqua	33.83	45.17	54.83	30.00	38.33	56.33	31.00	38.17	50.33	42.00	Between species means	1.212
E. nitida	27.50	37.50	53.50	62.00	31.00	70.67	26.17	28.00	44.50	42.31	Between experiments means	0.606
N. cunninghamii	17.67	24.33	42.33	20.00	22.00	37.67	17.50	21.67	36.83	26.67	Between times means	0.606
A. moschatum	37.00	45.67	53.17	43.83	50.83	55.33	34.67	42.17	57.67	46.70	Between	
P. aspleniifolius	6.00	8.83	14.83	11.00	12.50	16.83	11.50	15.17	19.00	12.85	species.experiments means	2.100
P. apetala	21.83	34.50	45.17	27.17	33.67	48.83	30.17	38.50	47.83	36.41	Between	
Eucryphia lucida	16.00	23.67	36.17	18.33	22.50	33.00	14.50	21.33	29.00	23.83	species.times means	2.100
A. melanoxylon	18.17	29.33	46.67	20.83	26.50	39.67	24.00	29.50	42.33	30.78	Between	
P. aparnun	46.17	52.67	61.83	43.33	51.17	61.00	42.17	49.17	56.17	51.52	experiments.times means	1.050
B. marginata	17.50	23.17	36.00	14.50	20.33	31.67	15.17	17.33	27.83	22.61	Between	
E. obliqua + P. apetala	26.83	36.00	52.00	28.50	39.33	53.33	33.33	39.50	46.67	39.50	experiments.times.species means	3.938
E. obliqua + P. aspleniifolius	17.00	24.17	35.33	23.17	28.17	38.00	24.17	28.00	35.67	28.19		
MEAN Times	23.79	32.08	44.32	28.56	31.36	45.19	25.36	30.71	41.15			
MEAN Experiments		33.40			35.04			32.41				

359

APPENDIX.   STATISTICAL ANALYSIS. 18.

Comparison of the decomposition of *E. obliqua* leaves of differing development.

Analysis of variance.

Source of variation	DF	SS	MS	VR	
Species	2	1498.47	749.23	71.424	***
Times	2	2267.34	1133.67	108.071	***
Species.Times	4	331.77	82.94	7.907	***
Residual	35(1)	367.15	10.49		
Grand total	43	4464.73			

Note: *** P<0.001

Tables of means: Species.times interaction.

Times Species	3	6	12	Mean		L.S.D$_{0.05}$
E. obliqua August 80	33.40	42.00	57.80	44.40	Between Times means	2.366
E. obliqua February 81	27.80	37.25	46.40	37.15	Between Species means	2.366
E. obliqua February 81 fall	25.80	30.20	34.80	30.27	Between Species.Times means	4.096
MEAN	29.00	36.48	46.33			

Note: *E. obliqua* August 80 = leaves plucked in August.

   E. obliqua February 81 = leaves plucked in February 81.

   E. obliqua February 81 fall = leaves naturally shed in February 81.

APPENDIX.   S .\TISTICAL ANALYSIS, TABLE *19*

Sampling date	Accession, Site 3					Accession, Site 4				
	A (g)	C (g)	A+C (g)	A+C t.ha^{-1}	Bins t.ha^{-1}	A (g)	C (g)	A+C (g)	A+C t.ha^{-1}	Traps t.ha^{-1}
22.11.79	24.7	23.6	48.3	0.266	0.242	23.6	26.4	50.0	0.276	0.117
2.1.80	64.9	58.4	123.3	0.681	1.012	40.6	39.4	80.0	0.442	0.310
13.2.80	98.4	88.3	186.7	1.032	0.951	46.0	44.7	90.7	0.501	0.401
26.3.80	133.3	122.7	256.0	1.414	1.227	45.2	42.8	88.0	0.486	0.401
7.5.80	40.4	41.5	81.9	0.452	0.394	30.6	30.1	60.7	0.335	0.191
18.6.80	36.0	24.5	60.5	0.334	0.300	19.5	19.0	38.5	0.213	0.115
30.7.80	17.9	21.7	39.6	0.219	0.166	10.3	13.6	23.9	0.132	0.063
10.9.80	65.4	48.7	114.1	0.630	0.399	15.7	25.2	42.9	0.237	0.118
22.10.80	135.2	144.6	279.8	1.546	1.261	54.3	49.3	103.6	0.572	0.298
3.12.80	28.6	26.6	55.2	0.305	.0.259	27.0	23.0	50.0	0.276	0.161
14.1.81	61.2	49.6	110.8	0.612	0.624	41.4	34.0	75.4	0.417	0.302
25.2.81	105.8	108.8	214.6	1.186	1.144	87.4	72.4	159.8	0.883	0.421
8.4.81	58.1	58.2	116.3	0.643	0.615	60.1	47.9	108.0	0.597	0.304
20.5.81	45.8	40.0	85.9	0.475	0.382	23.8	22.1	45.9	0.253	0.169
1.7.81	18.5	26.1	44.6	0.246	0.142					
12.8.81	10.1	12.7	22.8	0.126	0.111					

Regression of A+C versus Bins.

Site 3:

$Ye = 0.012 + 0.89. X$

$r = 0.952$

Site 4:

$Ye = 0.027 + 0.534. X$

$r = 0.872$

APPENDIX.   STATISTICAL ANALYSIS, TABLE 20.

Site	Regression	Data	Regression equation $Y_e = a + b.x$	Correlation coefficient, r	Standard error of estimate $\hat{s}_e$
3	A vs. C	Wg	$A_e = 2.56 + (0.944)C$	0.970	
		Wo	$A_e = 0.70 + (0.991)C$	0.979	1.3
	B vs. D	Wg	$B_e = 25.6 + (0.904)D$	0.977	
		Wo	$B_e = -1.31 + (0.988)D$	0.952	14.9
4	A vs. C	Wg	$A_e = -3.15 + (1.31)C$	0.904	
		Wo	$A_e = -1.53 + (1.29)C$	0.973	0.91
	B vs. D	Wg	$B_e = 3.89 + (0.909)D$	0.983	
		Wo	$B_e = 1.52 + (0.915)D$	0.964	7.9